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Plant production along a grazing gradient in a semiarid Patagonian rangeland, Argentina

M. Victoria Campanella · Alejandro J. Bisigato · C. Mario Rostagno

Abstract Patagonian rangelands have been grazed by sheep since early twentieth century. However, there is still a degree of uncertainty regarding how production of grass and shrub species changes along a grazing gradient. The study was undertaken in Northeastern Patagonia, Argentina. The characteristic vegetation in the area is a mosaic of herbaceous steppe with shrubs (HSS) and shrub steppe (SS). Grazing intensity was estimated through sheep paths density. Individual plant production and plant density were used to determine grass and shrub production per unit area, in both plant communities over three years. Community production was obtained as the sum of grass and shrub components. Differences were explored in shrub and grass production among communities and years, and linear regressions between sheep paths density and the proportion of each plant community along the transect were performed. Mean community production was lower in SS than HSS; shrubs did not compensate for the decline in grass production in spite of the increase in shrub density. SS presented the highest community production in the most humid year, while HSS production peaks in the year of average precipitation. We found that as the number of sheep paths increases (i.e., higher grazing intensities), the SS community replaces HSS, resulting in a reduction of forage for sheep. The results showed that changes in vegetation structure as a result of grazing strongly influenced above-ground production. Results also indicate that the response of vegetation to changes in annual precipitation is community specific.

Keywords Shrub encroachment · Grass production · Shrub production · Inter-annual precipitation

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Introduction

Desertification is a consequence of both climatic change and human activities (Mouat et al. 1997; Reynolds et al. 2005). The conversion of grasslands into shrublands is one form of desertification (Huenneke et al. 2002; Parizek et al. 2002). Shrub invasion has environmental and economic concerns because shrublands present lower carrying capacity, and the soil between shrubs is exposed to erosion processes by wind and/or water (Schlesinger et al. 1990; Huenneke et al. 2002; Chartier and Rostagno 2006). Soil losses (e.g., organic matter and nitrogen) can limit vegetative

growth and production generating an erosion–vegetation feedback that aggravates desertification (Fisher et al. 1987; Schlesinger et al. 1990; Breshears and Barnes 1999; Cheng et al. 2004). Regardless of the decrease in herbaceous production which reduces the economic capacity of rangelands (Zarovalli et al. 2007), shrub encroachment, sometimes, is important for enhancing carbon accumulation (Castro and Freitas 2009). Woody plants contain more carbon, are long-lived, and decompose more slowly than herbaceous plants (Castro and Freitas 2009). Moreover, Aguiar et al. (1996) pointed out that above-ground primary production (ANPP) was directly affected by the relative abundance of grasses and shrubs. They found that changes in composition of plant functional groups affected the land–atmosphere exchange of energy and materials.

Although soil properties vary drastically (e.g., soil nutrient content and spatial variability of soil resources) with desertification (Schlesinger et al. 1990; Bisigato et al. 2008; Ravi et al. 2010), ANPP is not always affected. Huenneke et al. (2002) found that the invasion of grasslands by desert shrubs resulted in a minor but detectable decrease in above-ground production, whereas Schlesinger et al. (1990) and Asner and Heidebrecht (2005) found that the conversion of grasslands into shrublands in southern New Mexico was not accompanied by a reduction in ANPP. However, Schlesinger et al. (1990) also highlighted that despite the fact that ANPP did not change there was a reduction in forage production due to the increment in non-palatable shrub production.

Patagonian rangelands have been grazed by sheep since the early twentieth century (Ares et al. 1990). As in other arid ecosystems, this disturbance has triggered changes in vegetation (Beeskow et al. 1995; Bisigato and Bertiller 1997; Bertiller et al. 2002; Bisigato et al. 2005) and soils (Rostagno 1989; Chartier and Rostagno 2006; Carrera et al. 2007; Bisigato et al. 2008). There was a major effort, particularly in semiarid Patagonian rangelands, to investigate soil erosion processes in different communities (Rostagno 1989; Parizek et al. 2002; Chartier and Rostagno 2006; Chartier et al. 2011; Palacio et al. 2014). Those studies found that eroded soils, dominated by shrub steppes, present lower infiltration rates than un-eroded ones (Parizek et al. 2002; Chartier et al. 2011). Moreover, shrub steppes present higher rates of fine particles, litter, and nutrients lost through overland-flow than

herbaceous steppes with shrubs (Chartier et al. 2013). On the other hand, there is still a degree of uncertainty regarding how the production of grass and woody components interacts in these communities and the effect in above-ground production on response to grazing. The objectives of this study were (1) to compare plant production in two dominant plant communities, an herbaceous steppe with shrubs (HSS) and a shrub steppe (SS) in a semiarid Patagonian rangeland, and (2) to evaluate how changes in grazing intensity affect the proportion of these two communities and the consequent effect on above-ground production.

Methods

Study site

The study was undertaken in the Punta Ninfas area (42°57′S, 64°33′W, 78 m a.s.l., Fig. 1), in Northeastern Patagonia where sheep grazing for wool and meat production has been practiced since the beginning of the last century. Continuous grazing is carried out in paddocks of about 2500 ha, and the means stocking rate is 0.3 sheep ha^{-1} (Chartier et al. 2013). Sheep range free within paddocks. Over a 13-year period, mean air temperature was 12.7 °C and mean annual precipitation was 259.3 mm (Chartier and Rostagno 2006; Campanella et al. 2016), which was approximately evenly distributed throughout the year. The characteristic vegetation is a mosaic of herbaceous steppes with shrubs and shrub steppes (Beeskow et al. 1995). Stands of both communities alternate over short distances (Chartier and Rostagno 2006). In both communities, *Chuquiraga avellanedae* Lorentz is the main shrub and *Nassella tenuis* (Phil.) Barkworth is the dominant perennial grass, but their relative abundance differs between communities. *Chuquiraga avellanedae* is the most common species at the shrub steppe and *N. tenuis* dominates the herbaceous steppe with shrubs. These two species constitute 71.44 % of the total plant cover (Beeskow et al. 1995). *Chuquiraga avellanedae* is considered an unpalatable species and is rarely consumed by sheep, while *Nassella tenuis* is the main forage source in the region (Siffredi 2012). Other shrub species are *Nassauvia ulicina* (Hook. f.) Macloskie (unpalatable) and *Mulinum spinosum* (Cav.) Pers (intermediately palatable). Less abundant

Fig. 1 Study site in the northeast of Patagonia, Argentina

perennial grasses are *Piptochaetium napostaense* [Speg.] Hackel ap Stuckert, *Pappostipa speciosa* (Trin. and Rupr.) Romasch., and *Poa ligularis* Nees ex Steud. All grass species are palatable (Siffredi 2012). Dwarf shrubs and herbs are minor components. Total aerial cover ranged from 35 to 65 %, while shrub height ranged from 50 to 150 cm (Beeskow et al. 1995). These communities also differ in superficial (0–5 cm depth) and sub-superficial (5–15 cm depth) soil characteristics, which were used to identify both communities in the field. Shrub steppe soil has finer texture, a shallow A horizon and a Bt

horizon locally exposed. Moreover, shrub steppe presents lower litter cover, and higher bare soil and gravel cover compared to herbaceous steppe with shrubs (Chartier and Rostagno 2006; Chartier et al. 2011). Xeric Calciargid is the prevailing soil in the study area with Xeric Haplocalcid as the subdominant soil (Chartier and Rostagno 2006). The analyses were concentrated on the two most important life forms in these steppes, perennial grasses and shrubs, and within these groups, on *N. tenuis* and *C. avellanedae* to characterize the responses of grasses and shrubs, respectively.

Plant production estimation

Individual production and density of plants were used to determine production per unit area (Fernández et al. 1991) for the herbaceous steppe with shrubs (HSS) and the shrub steppe (SS). These measurements were performed in three consecutive years (2012–2014).

Shrub production

Shrub above-ground production (vegetative growth) was determined nondestructively using a double sampling approach described by Fernández et al. (1991). We developed allometric relationships between field growth measurements (length of new shoots and canopy area) and new biomass (see Eq. 1 supplemental material in Campanella et al. 2016). In mid-December, new shoot lengths were measured in a 15×15 cm quadrat in 15 individuals of *C. avellanedae* in HSS and SS. Within a 2500 ha paddock, five sites were randomly selected each year. The minimum distance between the sites sampled each year was 370 m. As most of the stands have a size in the order of tens of meters, this distance between stands excludes the possibility of sampling neighbor stands and reduces the risk of spatial dependence. Each site included one stand of each community, where three individuals were sampled employing a stratified random procedure to encompass a wide range of plant sizes. The canopy area was also measured, estimated by the crown diameter method (Mueller-Dombois and Ellenberg 1974). With this information, we estimated shrub production using the equation developed for this species at this site (see Eq. 1 supplemental material in Campanella et al. 2016). Additionally, within the same paddock, a second set of ten sites were randomly selected. Each site included one stand of each community, where *C. avellanedae* density (shrub density, SD) was measured by recording all the individuals present in 40 to 200 m^2 quadrats. Quadrat size varied among stands because they differed in area.

For each community (c) and year (y), production per shrub (PPs$_{cy}$) was calculated following Campanella et al. (2016) as

$$\mathrm{PPs_{cy}}\left(\mathrm{g\ ind^{-1}\ year^{-1}}\right) = \mathrm{SPUA_{cy}}\left(\mathrm{g\ m^{-2}\ year^{-1}}\right) \times \mathrm{mAREA_c}\left(\mathrm{m^2\ ind^{-1}}\right),$$

where SPUA$_{cy}$ is the average production per shrub unit area, and mAREA$_c$ is the average shrub area in each plant community. Sixty plants per community, six in each quadrat where SD was measured, were randomly chosen and canopy area estimated by the crown diameter method. Mean production per shrub (mPPs$_c$) was calculated as the average of PPs$_{cy}$ values of all years.

Shrub production per area (SP$_{cy}$) was calculated as

$$\mathrm{SP_{cy}}\left(\mathrm{g\ m^{-2}\ year^{-1}}\right) = \mathrm{PPs_{cy}}\left(\mathrm{g\ ind^{-1}\ year^{-1}}\right) \times \mathrm{SD_c}\left(\mathrm{ind\ m^{-2}}\right),$$

where SD$_c$ is shrub density at each plant community. Since recruitment and mortality rates of shrubs are very low, SD$_c$ was assumed constant during the 3 years.

Grass production

We used the method of summing positive changes in live plus recent dead biomass to calculate grass production (Fernández et al. 1991). For the three years, harvest months were December, March, June, and October. Individuals were randomly chosen in ten stands of each community, randomly located throughout the same 2500 ha paddock where shrub production was evaluated. Different stands were sampled each season and year. Plant allometric relationships were developed relating above-ground biomass and basal diameters of *N. tenuis* plants (Guevara et al. 2002). For each plant community and season, we performed regression models using 30 individuals (see supplemental material Table S2 in Campanella et al. 2016). Finally, *N. tenuis* density (grass density, GD) was measured in ten different stands (1.5 m^2 quadrat, 5 per stand) per plant community and year.

For each community (c) and year (y), production per grass (PPg$_{cy}$) was calculated as

$$\mathrm{PPg_{cy}}\left(\mathrm{g\ ind^{-1}\ year^{-1}}\right) = \mathrm{GPUA_{cy}}\left(\mathrm{g\ m^{-2}\ year^{-1}}\right) \times \mathrm{mAREA_c}\left(\mathrm{m^2\ ind^{-1}}\right),$$

where GPUA$_{cy}$ is the average production per grass unit area and mAREA$_c$ is the average grass area in each plant community. Mean production per grass (mPPg$_c$) was calculated as the average of PPg$_{cy}$ values of all years.

Grass production (GP$_{cy}$) was calculated as

$$GP_{cy}\left(g\ m^{-2}\ year^{-1}\right) = PPg_{cy}\left(g\ ind^{-1}\ year^{-1}\right) \\ \times GD_{cy}\left(ind\ m^{-2}\right),$$

where GD_{cy} is grass density at each plant community and year.

Community production

For each plant community (c) and year (y), community production (CP_{cy}) was calculated as the sum of grass and shrub components:

$$CP_{cy}\left(g\ m^{-2}\ year^{-1}\right) = SP_{cy}\left(g\ m^{-2}\ year^{-1}\right) \\ + GP_{cy}\left(g\ m^{-2}\ year^{-1}\right).$$

Grazing intensity gradient

A 100 m transect was randomly located in 15 sites placed in two paddocks with the usual stocking rate in the area (0.3 sheep ha^{-1} throughout the year). The length of the transect intercepted by each plant community was measured and the number of well-defined sheep paths was counted, avoiding small runoff paths (Pazos et al. 2007). These sites were different from those employed to estimate shrub and grass production.

Climatic measurements

During the study period (2012–2014), the daily precipitation was registered with a Davis Vantage Pro weather station (Davis Instruments Corp., US).

Statistical analyses

ANOVA was used to evaluate the significance of the differences between communities in SD, GD, mAREA, mPPs, and mPPg. GD and mAREA were log-transformed to meet ANOVA assumptions. The differences in SP, GP, and CP among communities and years by two-way ANOVA were explored as well; linear regressions between sheep paths density and the proportion of each plant community along the transect were performed. Statistical analyses were performed using package 'stats' of the R-Project (http://www.r-project.org).

Results

Climatic measurements

Annual precipitation for the years 2012, 2013, and 2014 was 221.8, 354.6, and 252.8 mm, respectively. Annual precipitation during the first and the second years (2012 and 2013) was $\sim 15\ \%$ below and $\sim 37\ \%$ above the long-term average, respectively. Annual precipitation during the last year (2014) was near the long-term average (259.3 mm).

Species characteristics in the two communities

Tussock grasses were larger and presented a higher density in HSS than in SS (Table 1). Conversely, shrubs were less numerous per unit area and larger in HSS than in SS. mPPs and mPPg were lower in SS than in HSS (Table 1).

Shrub, grass, and community production

There was a significant community by year interaction (Fig. 2) not only both in grass ($F_{2,54} = 56.69$; $P < 0.0001$) and shrub production ($F_{2,54} = 48.57$; $P < 0.0001$), but also in community production ($F_{2,54} = 62.79$; $P < 0.0001$). For HSS, differences in community production (CP) were ($F_{2,29} = 11.97$; $P < 0.0001$) attributable to the variation of grass production (GP, $F_{2,29} = 56.49$; $P < 0.0001$), which was higher in 2014 (Fig. 2a). Instead, shrub production (SP) did not change among years ($F_{2,29} = 0.34$; $P = 0.715$) in the HSS community. However, community (CP, $F_{2,29} = 313.08$; $P < 0.0001$), grass (GP, $F_{2,29} = 14.79$; $P < 0.0001$), and shrub (SP, $F_{2,29} = 295.62$; $P < 0.0001$) production differed among years in SS. In the second year (2013), the most humid year, SS presented the highest production in all components (CP, GP, and SP) (Fig. 2b, c). When considering mean production, HSS presented higher plant community production than SS (53.2 vs. 29.6 g m^{-2} $year^{-1}$). This was attributable to the fact that there was more grass production in HSS than SS (24.8 vs. 0.5 g m^{-2} $year^{-1}$) since mean shrub production did not differ between communities (28.4 g m^{-2} $year^{-1}$ in HSS vs. 29.1 g m^{-2} $year^{-1}$ in SS).

Table 1 Mean individual area (mAREA), shrub density (SD), and mean production per shrub (mPPs) of *C. avellanedae*, and mean individual area (mAREA), grass density (GD), and mean production per grass (mPPg) of *N. tenuis* in the herbaceous shrub steppe (HSS) and the shrub steppe (SS)

	C. avellanedae		*N. tenuis*	
	HSS	SS	HSS	SS
mAREA (cm^2)	7509 ± 495 (60)[a]	5574 ± 314 (60)[b]	6.8 ± 0.5 (360)[a]	3.6 ± 0.2 (360)[b]
SD or GD[†] (# ind. m^{-2})	0.31 ± 0.06 (10)[b]	0.99 ± 0.10 (10)[a]	122.4 ± 8.9 (30)[a]	11.0 ± 1.7 (30)[b]
mPPs or mPPg (g ind.$^{-1}$ year^{-1})	91.8 ± 5.9 (3)[a]	29.2 ± 23.2 (3)[b]	0.18 ± 0.07 (3)[a]	0.06 ± 0.02 (3)[b]

Values are mean ± 1 standard error. Numbers between brackets indicate the number of individuals (mAREA), stands (SD and GD), or years (mPP). In the case of mPPs and mPPg, each year is the average of 15 shrubs and 30 grasses, respectively. Different lowercase letters for a given variable indicate significant differences between communities in each species
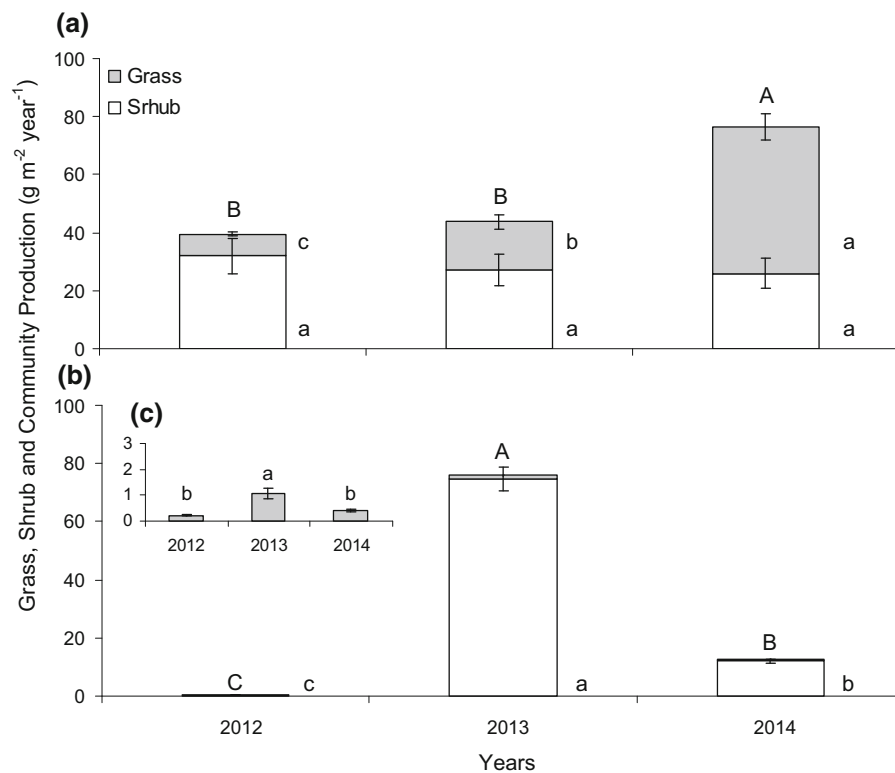
[†] Note: average of 3 years

Fig. 2 Shrub and grass production of the **a** herbaceous steppe with shrubs (HSS) and **b** shrub steppe (SS) for the 3 years. Community production is the sum of the grass and shrub components. In each plant community, different *capital letters* indicate significant differences in community production among years while different *lower case letters* indicate significant differences in production among years for each component (shrub or grass). *Inset* **c** represents grass production in SS. Values are mean ± 1 standard error

Grazing intensity gradient

The proportion of SS in the mosaic increased as sheep paths density increased (Fig. 3). At high intensity grazing, the SS community replaced HSS, while at the lowest path density, HSS comprised about 70 % of the area (intercept in ∼ 30 for SS).

Fig. 3 Percentage of plant communities in the mosaic along the grazing gradient estimated by sheep paths. *HSS* herbaceous steppe with shrubs and *SS* shrub steppe

$y = 0.83x + 29.22$
$r^2 = 0.84$
$P < 0.0001$
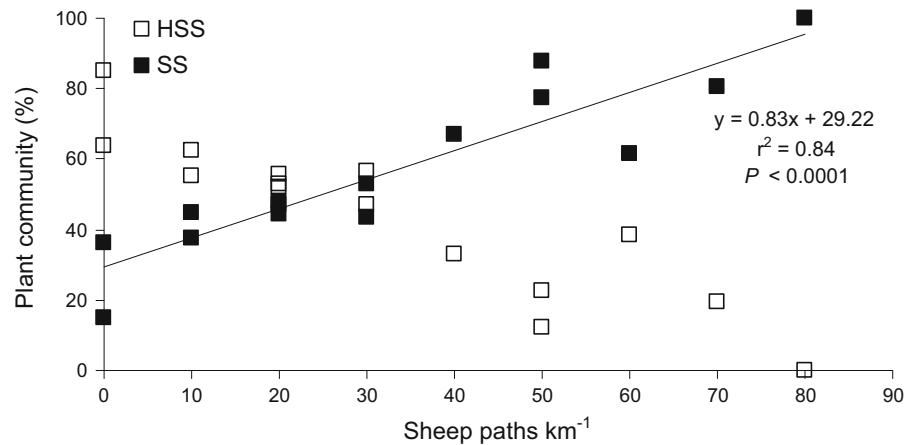
Discussion

As the number of sheep paths increases (i.e., an increase in grazing intensity), the SS community replaces HSS. Taking into account the results of lower community production in SS as compared with HSS, the conversion of the HSS into a SS by continuous sheep grazing in this study area could result in a decrease in ANPP. A similar study, using a modeling approach carried out at another Patagonian site, exhibited a decrease in total plant production as grazing intensity increased. This is because shrubs did not compensate entirely for the decline in grass production (Aguiar et al. 1996). These results are explained by the fact that grass cover and standing biomass were negatively correlated, whereas shrub cover was positively correlated with grazing intensity at both sites (Aguiar et al. 1996; Beeskow et al. 1995). However, increases in above-ground carbon storage with shifts to woody vegetation have been documented by some authors in other arid ecosystems around the world (Asner et al. 2003; Hughes et al. 2006). The differences among studies are probably due to the differences in traits of the encroaching shrubs (e.g., canopy structure, timing of growth, root systems, among others) (Eldridge et al. 2011; Peters et al. 2013; Quero et al. 2013; Eldridge and Soliveres 2014). In accordance with this study's results at a local scale, Gaitán et al. (2014) suggested that shrub encroachment could cause a decline in ANPP at a regional scale because of the stronger effect of grass cover on ANPP compared to shrub cover.

These results indicate that the reduction in SS production was due to a decrease in grass production

in spite of the increase in shrub density. The lower grass production in SS was not only a consequence of a lower production per grass individual but also because of a large decrease in grass density (Table 1). Chartier and Rostagno (2006) proposed that the replacement of HSS by SS is a consequence of the exposure of a clay-rich horizon which does not support grass germination and survival. Since grasses are more palatable than shrubs, the reduction in grass production results in a strong decline in forage availability. In contrast, HSS presented lower shrub density but the production per shrub was higher resulting in similar production between communities. Similarly, in a modeling study, the reduction of ANPP in grasslands dominated by *Festuca pallescens* due to overgrazing was related to the decrease in tussock density (Paruelo et al. 2008). The results are also in concordance with a recent meta-analysis that elucidates the relative importance of different environmental variables on ANPP (Ruppert et al. 2012). These authors found that total precipitation and land-use intensity were the main explanatory variables. Precipitation had a positive, whereas land-use intensity a negative effect on ANPP (Ruppert et al. 2012).

A significant interaction between plant community and year was found, indicating that plant communities differ in their response to changes in annual precipitation. In the case of SS, it showed a conspicuously greater shrub production in the wetter year. A possible mechanistic explanation would be related to differences in soil characteristics between communities. Shrub steppe soils present areas of exposed clay-rich argillic horizon (Bt horizon) and a shallower A horizon in comparison to herbaceous steppes with shrubs (Súnico et al. 1996; Chartier and Rostagno

2006). The loss of the A horizon and the exposure of enriched-clay layers are associated with a reduction in infiltration rates and a rise in runoff (Chartier et al. 2011; Rostagno and Degorgue 2011). In relation to this, Fensham et al. (2015) found that greater clay content in soils improve woody growth during periods of above average precipitation because clay-rich soils hold more moisture than sandy soils (Fravolini et al. 2005). In contrast, a different mechanism could be acting in the case of HSS, where higher production was found in the year with average precipitation. It can be argued that N. tenuis production could be nitrogen limited in years of high precipitation. A long-term study conducted in the Chihuahuan Desert showed that the shrub *Dasylirion leiophyllum* (Engelm.) exhibited its highest production during the wettest years, while the grass species *Bouteloua curtipendula* (Michx.) Torr. was N-limited in those years (Robertson et al. 2009). Also, it is important to mention the effect of the previous year's precipitation on ANPP (Oestherheld et al. 2001; Ruppert et al. 2012). High tiller and/or plant density can enhance ANPP in normal or dry years preceded by wet years and also can constrain ANPP in a wet year following a dry year (Yahdjian and Sala 2006; Reichmann et al. 2013; Peters et al. 2014). Despite our study only encompassing 3 years, it nevertheless revealed that precipitation has a community-specific influence on plant production. However, long-term studies are required to elucidate the complex interactions among species composition, precipitation, and soil characteristics. Also, it can be concluded that grazing management actions should take into account the precipitation amount and the proportion of communities in each site.

Global climate change models predict more extreme precipitation events in most arid regions (Easterling et al. 2000). Changes towards fewer, larger precipitation events could drive water below the shallow soil layers, used by grasses, into deeper soil layers that are better exploited by woody plants (Kulmatiski and Beard 2013; Campanella et al. 2016). The study's findings showed that shrubs had greater production than perennial grasses in wetter years. These findings plus the fact that heavy sheep grazing replaces HSS by SS (Fig. 3), reduces tussock density (Table 1) and herbaceous production (Fig. 2), suggests a poor recovery of herbaceous stratum in the future context of global change. This trend in more extreme rainfall events can also accelerate the erosion

process (Chartier and Rostagno 2006) generating an erosion-vegetation feedback that may prevent the recovery of herbaceous stratum.

In conclusion, mean community production was lower in SS than HSS. Shrubs did not compensate entirely for the decline in grass production, in spite of the increase in shrub density. SS presented the highest community production in the most humid year, while HSS production was higher in the year of average precipitation. Regarding the grazing effect on plant community structure, it can be concluded that as grazing intensity increases (i.e., the number of sheep paths increases), the SS community replaces HSS. The study results showed that changes in vegetation structure as a result of grazing strongly influenced above-ground production in this semiarid Patagonian rangeland. As well, the results also indicate that the response of vegetation to changes in annual precipitation is community specific.

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