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Grazing-induced morphological and growth rate changes in *Anarthrophyllum rigidum*, a Patagonian leguminous shrub

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ABSTRACT

Grazing influences the morphology and growth rate of shrubs, and consequently, their population dynamics. It has been shown that grazing directly affects the growth of shrubs. On the other hand, the reduction of grass biomass by herbivores reduces soil–water competition between grasses and shrubs, and indirectly, could enhance the growth of shrubs. However, the assessment of the long-term effects of grazing on the growth of shrubs in the arid Patagonia has been hampered by the lack of long and homogeneous records of plant population dynamics and primary production. In this study, we combined growth-ring and allometric analyses to assess the long-term effect of grazing on individuals of *Anarthrophyllum rigidum*, a leguminous shrub widely distributed across the Patagonian steppe. *A. rigidum* has evergreen leaves rich in proteins that constitute an important complement to the diet of sheep, particularly in winter when the abundance of grasses is reduced. Our observations indicate that individuals of *A. rigidum* nearby the water source used by livestock were smaller in size (35.5 cm *vs.* 67.39 cm), presented a larger number of basal branches (23 *vs.* 12), and showed slower rates of growth (8.2 mm $year^{-1}$ *vs.* 14.3 mm $year^{-1}$) than individuals located far from the water source. This first quantification of the long-term effects of grazing on *A. rigidum* in the dry Patagonian steppe suggests that beneficial effects of grazing through the reduction of grasses that compete with shrubs for soil–water should be more obvious for livestock non-preferred than preferred shrubs

Introduction

Studies on grazing in xeric steppes have shown either negative or positive effects of herbivory on shrubs. The positive effect of browsing is given by a less intensive competition for soil–water due to the preferential reduction of grass cover by grazing, whereas the negative effect is given by overgrazing on shrub biomass. Most of the Patagonian grasses have a shallow root system that captures most of the water from small precipitation pulses and inhibits the water penetration into the soil profile (Soriano et al., 1987; Sala et al., 1989). This rooting-niche separation is the hypothesis that explains the coexistence of woody and grassy plants (Weigand et al., 2006; Cipriotti and Aguiar, 2011). As overgrazing reduces grass cover (Agnew, 1997), it increases the amount of water available for shrubs which in turn produces an increase of 22–28% in the productivity of the Patagonian shrubs (Sala et al., 1989). This separation of the niche, between root systems in grass and shrubs, was proposed as the motive for the shrub encroachment, other indirect effect the grazing (Cipriotti and Aguiar, 2011). Similar interactions explain, for example, the higher competitive abilities of the shrub *Prosopis glandulosa* in grazed than in non-grazed fields in Texas (Van Auken and Bush, 1989).

On the other hand, grazing directly affects the rate of growth of shrubs by reducing their photosynthetic biomass and causing morphological changes with important consequences for the structure and dynamics of shrub populations. Frequently, grazing produces significant changes in the size of dominant shrubs going from tall to medium or small-size shrubs (Bisigato and Bertiller, 1997). Another important effect of grazing on shrubs is the removal of apical buds, which cause an increase in the number of shafts due to the activation of lateral buds (Vallentine, 2000; Morales, 2007). In the Patagonian steppes, sheep consume large amounts of shrubs in autumn and winter when grass biomass is scarce and poor in nutrients (Posse et al., 1996). In this season, sheep incorporate in their diet between 10 and 20% of shrubby species (Aguiar and Sala, 1998). Quantifying the direct effects of grazing on shrubs requires both direct measurements and records of temporal changes in shrub growth; the lack of this information makes

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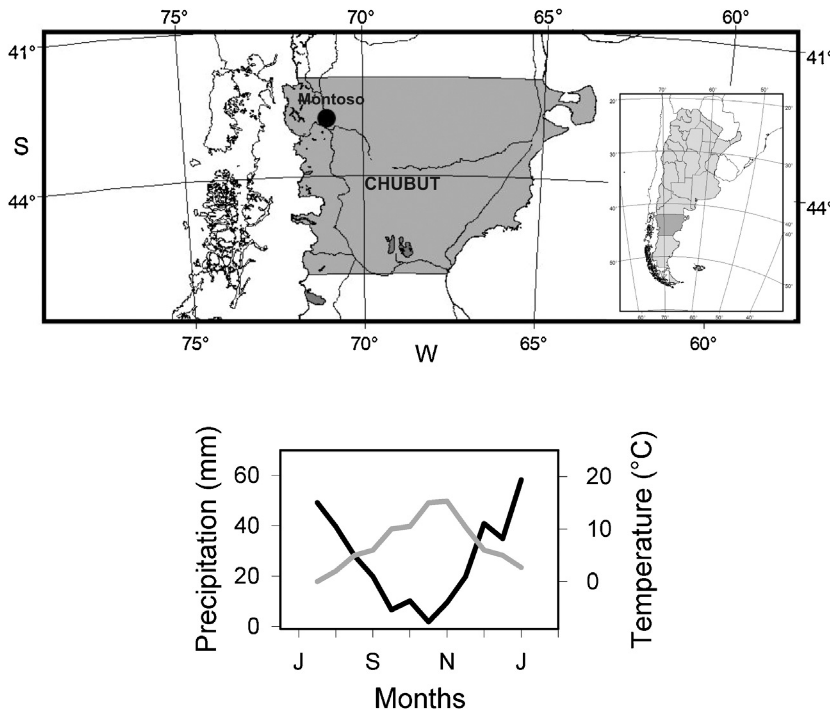

Fig. 1. Location of the sampling site in north-western Chubut, Argentina. Monthly variations in total precipitation and mean temperature at the Montoso weather station are also shown.

it very difficult to estimate the impact of grazing on vegetation. One possibility to overcome this limitation is to search for alternative records to estimate the effect of grazing in shrubby steppes. The analysis of allometric relationships between different plant variables has been a useful tool to identify the impacts on plants caused by different types of disturbances including grazing (Escós et al., 1997; Grace and Fownes, 1998; Breceda et al., 2005). Additionally, tree-ring analysis has been successfully used to determine changes in the rate of growth of trees affected by disturbances (Fritts and Swetnam, 1989). In recent studies, dendrochronological methods have been successfully used to establish the rate of growth of shrubs in the Patagonia steppe (Srur and Villalba, 2009). In this study, we combine both approaches to compare dendrochronological-derived growth rates with parameters such shrub height, number of stems, and diameter of the main branches to assess the impact of hervibory on individuals of *Anarthrophyllum rigidum* under different grazing intensity in Western Patagonia, Argentina.

Materials and methods

Site description

Sampling was conducted in Estancia Montoso (42.82° S, 70.97° W; Fig. 1) located at 730 m of elevation, Chubut, Argentina. The study area was used as wintering place (from May to December) by sheep since early 20th century. Total annual precipitation of 315 ± 87 mm (mean ± SD; 45-year) is concentrated in autumn–winter. Mean annual temperature is 9.3 °C ranging from 2.9 °C in July to 16 °C in January. The vegetation of the Patagonian Occidental District is a very open shrub steppe of *ca.* 50% cover (32% grasses *vs.* 18% shrubs), with shrubs between 60 and 180 cm in height. The dominant grasses are *Pappostipa speciosa*, *P. humilis*, *Hordeum comosum*, *Poa lanuginosa*, and *P. ligularis*, while the dominant shrubs are *Adesmia volckmanni*, *Berberis heterophylla*, *Senecio filaginoides*, and *Mulinum spinosum* (Golluscio et al., 1982; Paruelo et al., 1992; León et al., 1998). The steppe is enriched in certain sites with dense populations of the shrub *A. rigidum* (León et al., 1998).

Several authors have documented that the grazing pressure decreases with increasing distance from the livestock water sources. Generally, a concentric ring, named piosphere, is observed around the water points. In this zone density and biomass of palatable vegetation decrease and those of species resistant to grazing increase along a centripetal radius (Barker and Lange, 1969). In our study area, we recorded a decrease in the cover of preferred species (palatable, 2A), an increase of non-preferred (unpalatable, Fig. 2A) and a larger density of sheep feces (Fig. 2B) toward the water source.

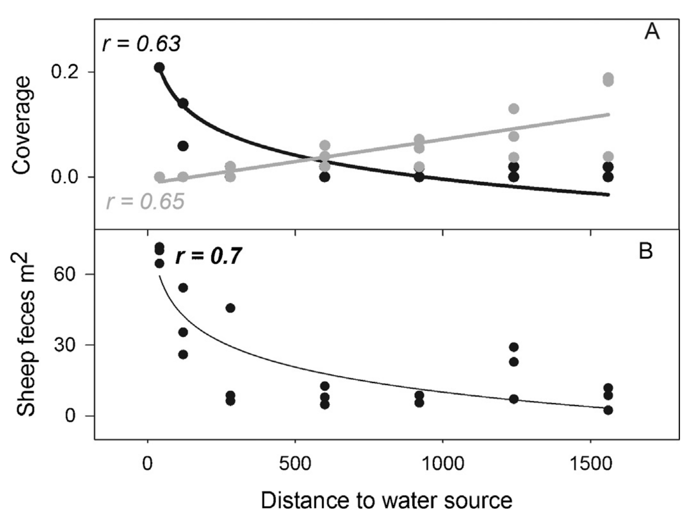

Fig. 2. Change of preferred to non-preferred species by sheep as increasing distance from the water source and their correspondence with grazing intensities. In (A) coverage of the palatable (black) and unpalatable (gray) species *versus* the distances from the water source. In (B) number of sheep droppings for m^2 *versus* distances to the water source.

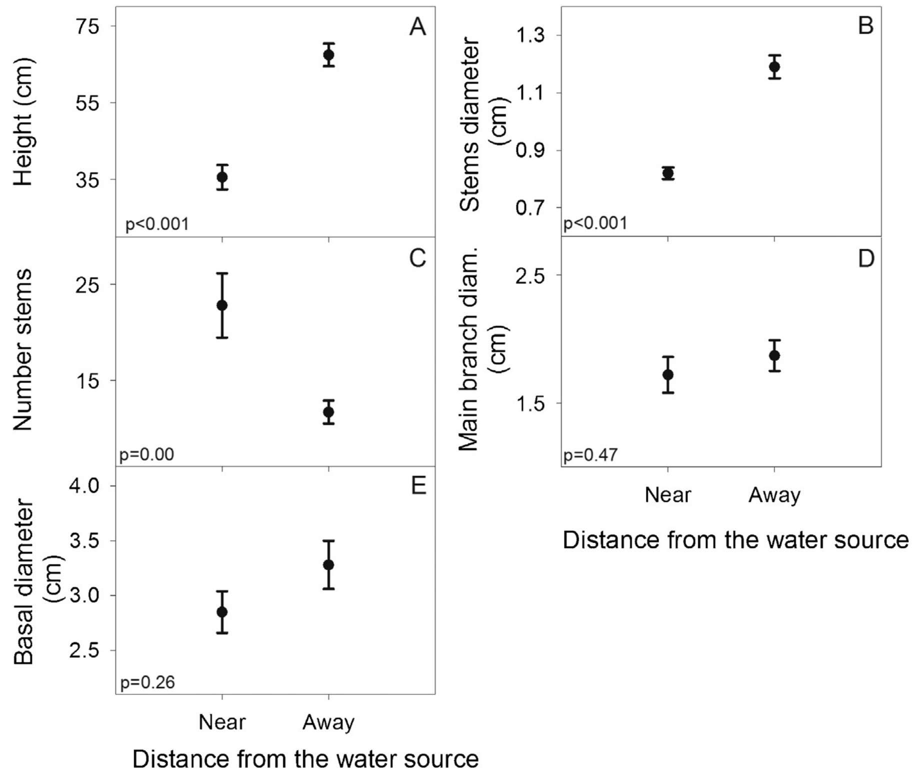

Fig. 3. Effect of grazing on allometric parameters. Individuals near the water source are lower in height with a larger number of thinner stems than shrubs far from the water source. No statistical differences in relation to basal diameter and the main branch were recorded between sites. *p* values at the bottom left corner shown the statistical significance for the comparisons.

To estimate the coverage of preferred and non-preferred species, we sampled three transects starting at the water source. Each transect consisted of 50 observation points separated from each other by 80 cm At each point we registered the number of interceptions of each species to a vertical pole. The coverage of each species in percentage was estimated by dividing the number of interceptions of each species in relation to total number of interceptions per transect.

Species description

A. rigidum (Fabaceae) is a 0.80–1.60 m height shrub. The crown size ranges from 0.09 to 1.4 m^2. Its bark is ashen or yellow ochre (Correa, 1984). *A. rigidum* keeps green leaves during winter. With more than 10% of protein in its leaves, *A. rigidum* represents a very desirable component in the diet of sheep (Somlo et al., 1985, 1997; Garbulsky and Deregibus, 1997). It also provides shelter during winter months, increasing sheep survival rates.

Sampling and measurements

We sampled individuals of *A. rigidum* under two different grazing conditions in a large paddock of Estancia Montoso. We randomly chose 10 individuals in the intensely grazed site (near to a water source), and 11 individuals moderately grazed (located more than 2 km far from the water source). For each individual we recorded the height, number of stems, diameter of each stem, diameter of the main branch and basal diameter, and collected transversal cross-sections and increment borer samples. Cross-sections and increment borer samples were polished and dated following standard dendrochronological procedures (Stokes and Smiley, 1968). Once the samples were dated correctly, we measured the ring widths with a Velmex measuring system with a precision of 0.001 mm. We used the program COFECHA (Holmes, 1983) to control the quality of the dating process. Since our samples do not exceed 75 years in length, ring width series were compared between them using 30-year segments displaced from each other by 15 years. Using a 30-year segment for comparison, the critical level for correlation between series is $r = 0.42$. The mean series inter-correlations were $r = 0.48$ and $r = 0.47$ for the samples from the sites close and far from the water source, respectively. We calculated the average annual growth rate and accumulated growth in each site with the program AGE from the Dendrochronology Program Library (Holmes, 1999). For this, and irrespective of the calendar date, the central ring (in contact with the pith) in each sample was assigned the year $t = 1$. Thus, mean cumulative diameter growth results from averaging all cumulative growths on basis of the biological age of each shrub.

Statistics

We evaluated the effect of grazing intensity (based on the distance from the water source) on height, number of stems, main branch and basal diameters by means of *t*-tests for independent samples. These variables met the required assumptions of normality and homogeneity of variance. Normality assumption was tested by Shapiro–Wilks test, while homogeneity of variances between groups using the Levene's test. The Mann–Whitney *U*-tests was used to compare median stem diameters between sites near and far from the water source, since these data do not meet the normality assumption. We related the cumulative growth (response variable) against time (explanatory variable) for each site using a simple lineal regression. Then, we performed a multiple linear regression using a dummy variable coding two categories: individuals nearby the water source as 1 whereas those far from the water source as 0, including the interaction terms between sites and times in the model. The coefficient for the dummy variable measures the differential effect in mean cumulative growth between categories 1 and 0 (Di Rienzo et al., 2011). Statistical analyses were carried out using Infostat Version 2011 (Di Rienzo et al., 2011). Values of $p < 0.05$ were considered statistically significant in all analyses.

Results

The allometric variables showed significant reductions in height and stems diameter, heavily grazed Individuals of *A. rigidum* nearby the water source are smaller in size (35.5 cm *vs.* 67.39 cm) and present a larger number of basal branches (23 *vs.* 12, Fig. 3A and B). A significant increase in the number of stems for the individuals located nearby in relation to those located away from the water source (Fig. 3C). Main stem and basal diameters presented no significant differences between sites (Fig. 3D and E).

For the site far from the water source, we recorded significant positive correlations between allometric variables ($r = 0.57$ for height against basal diameter, $r = 0.67$ for height against main stem diameter and $r = 0.76$, for basal against main stem diameters; $p < 0.01$ in all cases). However, the number of stems was no significant correlated to other allometric variables. No significant relationships were recorded between allometric variables in the site near to water source (heavy grazing).

Although the mean annual radial increments during the first 28 years of growth increase from 8.2 mm year^{-1} to 14.3 mm year^{-1} for sites located close and far from the water source, respectively, given the large variability between individuals, these differences are not statistical significant at a 95% confidence level. However, important differences in the rates of growth between sites are recorded when the cumulative growth increments are compared over the common period of 28 years (Fig. 4A). Individuals nearby the water source show slower growth rates than those far from the water source. The mean cumulative radial growth showed significant differences between sites since the seventh year of growth. After this period, the curves presented different slopes, showing that the cumulative radial growth was lower at the intensely grazed (near to the water source) than the moderately grazed site (far away from the water source, Fig. 4B). Consequently, the growth curve of the intensely grazed site showed a lower general slope than the estimated for the moderately grazed site over the 28 years of comparison. Linear regression estimates for the cumulative radial growth between sites were significantly different ($r^2 = 0.98$, $p < 0.0001$). We find, not only, site effect on growth but also with age–site interaction Therefore the site also had a significant effect on the relationship between the expected cumulative radial growth and the age, being less the growth in individuals located in intensely grazed site related to moderately grazed one (Fig. 4C).

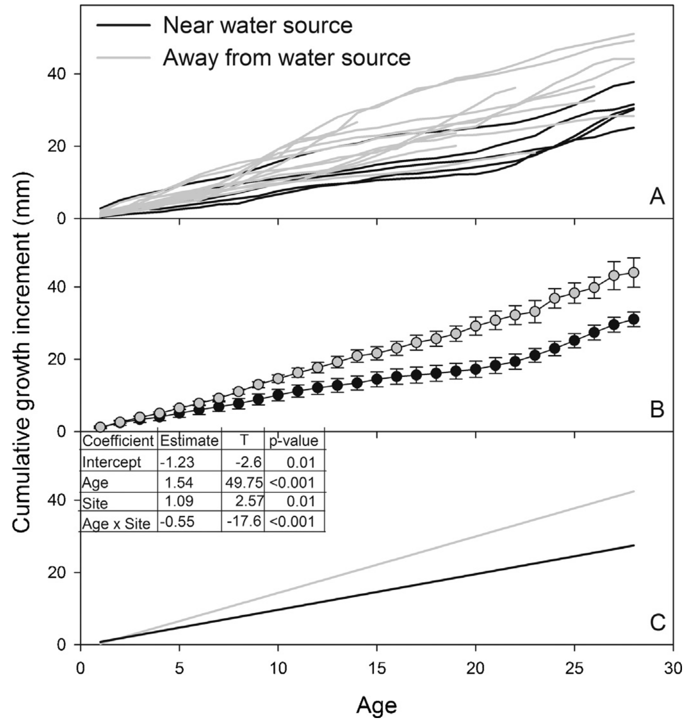

Fig. 4. Cumulative radial growth (CRG) of *Anarthrophyllum rigidum* as a function of time in intensely and moderately grazed sites. The comparison of the CRG shows that the shrubs close to the water source grow slower than those located farther away from the water source. (A) Cumulative radial growth for all shrubs in both sites (CRG). (B) Mean CRG and their standard errors (gray and black lines and symbols for moderately and intensely grazed sites, respectively). (C) Linear regression CRG *versus* time for each site separately. The *t* and *p* values for the different terms of the multiple regressions applied to the whole dataset are also indicated.

Discussion

Since the 1950s, several ecologists have noted a degradation of the landscape in the Patagonia steppe (Soriano, 1956; Boelcke, 1957). The effects of grazing on different functional vegetation types play a key role to establish the grazing management practices to reverse the current deterioration of the Patagonian plant communities. Landscape degradation is related to changes in coverage and physiognomy of grasses (Aguiar and Sala, 1998; Bertiller and Bisigato, 1998) and shrub encroachment (León and Aguiar, 1985; Bertiller et al., 1995; Paruelo et al., 2008; Cipriotti and Aguiar, 2011).

The proximity to water sources and the quantity/quality of the available forage to sheep are the major factors influencing grazing patterns in the Patagonian steppe (Adler et al., 2001). Our results show that the grazing modifies the architecture and the rate of radial growth of the leguminous shrub *A. rigidum*. The stem diameter, height, and cumulative radial increment were lower in shrubs located near than far from the water source, an indication that heavy grazing directly reduced the size and growth of *A. rigidum*. Our results are consistent with observations by Bisigato and Bertiller (1997) indicating that grazing by sheep causes a reduction in the size of the shrubs in the Monte phytogeographic province in Patagonia. Significant correlations between allometric traits were recorded in the moderate-grazed but not in the severely grazed site. According to these observations we concluded that overgrazing strongly affects not only the size and rate of growth, but also the morphology of shrubs. The larger number of stems recorded in the intensely-grazed area, suggests that the removal of apical buds by grazing causes an activation of lateral buds and the consequent increase in the number of stems per individual. This processes have extensively been documented elsewhere (Vallentine, 2000; Torrano and Valderrábano, 2004; Morales, 2007).

The use of the annual rings in the wood of *A. rigidum* allowed us comparing 28 years of growth between severely and moderately grazed sites, achieving a long-term perspective of the relationships between herbivory and shrub productivity. Small differences in radial growth between areas with different grazing regime during the first years of growth may be related to a compensation process or tolerance of shrubs to grazing. However, after 3–6 years of persistent browsing, a decrease in radial growth is recorded in intensively grazed sites. Our results are consistent with those presented by Teague (1992), who noted that defoliation for short periods may induced an increase in productivity, but a decrease when grazing persists overtime. We showed that compensation period is for 7 years.

To our knowledge, this study represents the first quantification of the long-term effect of grazing on Patagonian shrubs. When the supply of winter pastures is reduced, the shrub *A. rigidum* constitutes an important component of the protein intake in the sheep diet. Our results indicate that the detrimental effect of grazing by sheep is more important than the indirect beneficial effect of a reduction in competition due to grass removal by sheep. In sites severely grazed, the loss of shrub biomass appears to be not compensated by the larger amount of water in the soil due to the removal of grasses. Previous studies indicate an increase in the productivity of the shrubs in response to the removal of grasses both in Patagonia (Sala et al., 1989) and Texas (Van Auken and Bush, 1989). However, in both cases the removal of grasses was conducted with an evaluation of the indirect effect of grazing on shrubs. Our results suggest that, when the removal of grasses is accompanied by a substantial loss of photosynthetic biomass in the shrubs, the direct effect of grazing on shrubs may counteract the benefits of grass removal. The balance between indirect positive and direct negative effects of grazing on shrubs may lead to more favorable net effects on non-preferred than on preferred shrubs by sheep.

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