

VEGETATION STRUCTURE CONSTRAINS PRIMARY PRODUCTION RESPONSE TO WATER AVAILABILITY IN THE PATAGONIAN STEPPE

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Abstract. Grassland aboveground net primary production (ANPP) increases linearly with precipitation in space and time, but temporal models relating time series of ANPP and annual precipitation for single sites show lower slopes and regression coefficients than are shown by spatial models. The analysis of several ANPP time series showed lags in the ecosystem response to increased water availability, which may explain the difference between spatial and temporal models. The lags may result from constraints that ecosystems experience after drought. Our objective was to explore the structural constraints of the ANPP response to rainfall variability in a semiarid ecosystem, the Patagonian steppe, in southern Argentina.

We designed a 3-yr rainfall manipulation experiment where we decreased water input with rainout shelters during two consecutive years, which included three levels of rainfall interception (30%, 55%, and 80%) and a control. In the third year, we irrigated one-half of the plots of each rainfall-interception treatment. We evaluated the immediate effects of drought on current-year ANPP and the effects of previous-year drought on vegetation recovery after water supplementation.

ANPP ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) was linearly related to annual precipitation input (APPT; mm/yr) along the experimental precipitation gradient ($\text{ANPP} = 0.13 \times \text{APPT} + 58.3$; $r^2 = 0.34$, $P < 0.01$), and this relationship was mostly accounted for by changes in the ANPP of grasses. Plant density (D ; no. individuals/ mm^2) was related to the precipitation received during the drought period ($D = 0.11 \times \text{APPT} + 18$; $r^2 = 0.39$, $P < 0.05$). The recovery of plants after irrigation was lower for those plots that had experienced experimental drought the previous years relative to controls, and the lags were proportional to the intensity of drought. Therefore, our results suggest that the density of plants may constrain the recovery of vegetation after drought, and these constraints may determine lags that limit the capacity of the ecosystem to take advantage of wet years after dry years.

Key words: Argentina; lags; Patagonia; rainfall manipulations; semiarid ecosystems; temporal models.

INTRODUCTION

Net primary production represents the main energy input to terrestrial ecosystems, and the amount and seasonality of aboveground net primary productivity (ANPP) determines forage availability and constrains herbivore carrying capacity. ANPP increases linearly along spatial precipitation gradients from deserts to steppes and grasslands in North America, South America, and Africa (Webb et al. 1978, Lauenroth 1979, Sala et al. 1988, McNaughton et al. 1993, Paruelo et al. 1998). Accordingly, a site receiving higher mean annual precipitation shows higher mean annual primary production than a site receiving lower mean annual precipitation. Similarly, annual precipitation is the variable that accounts for most of the interannual variability in ANPP for individual sites in arid/semiarid regions (Smoliak 1986, Le Houérou et al. 1988,

Lauenroth and Sala 1992, Briggs and Knapp 1995, Jobbágy et al. 2002) and thereby, during a year with a higher amount of annual precipitation, we would expect higher ANPP than during a drought year. However, temporal models relating time series of ANPP and annual precipitation for single sites show much lower slopes and regression coefficients than spatial models (Lauenroth and Sala 1992). The difference between temporal and spatial models appears to be a general phenomenon of arid and semiarid ecosystems, which has been reported for many ecosystems (Lauenroth and Sala 1992, Paruelo et al. 1999, Jobbágy and Sala 2000, Huxman et al. 2004). Controls of primary production of grasslands at a regional scale appear to be different from controls at a single location through time.

Examination of time series of ANPP and annual precipitation in both North and South American grasslands (Lauenroth and Sala 1992) reveal some interesting time lags in the recovery of ANPP from dry conditions, even when the subsequent year had above-average precipitation. These time lags may contribute to the

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departure of the temporal model from the spatial model at high annual precipitation and suggest the presence of biotic constraints on ANPP (Lauenroth and Sala 1992). The structure of the vegetation, ranging from canopy cover and plant density to species composition determines the density of meristems where plant growth occurs, and so may provide a constraint within which fluctuations in precipitation cause reduced fluctuations in production. Drought conditions can result in plant, root, branch, and tiller mortality and thereby can reduce meristems, thus decreasing the capacity of vegetation to respond to high resource availability (Benson et al. 2004). As a result of meristem limitation, we would expect production to be lower in wet years preceded by dry years than in wet years preceded by wet or by normal years.

Because arid and semiarid ecosystems comprise 40% of the terrestrial land cover (Ajtay et al. 1979), their response to interannual rainfall variability may have important consequences for global patterns of productivity under future climate scenarios. Two functional groups, grasses and shrubs, comprise the bulk of ANPP of arid and semiarid steppes. In the steppes of the Occidental District of Patagonia, Argentina, those two functional types account for 96% of ANPP (Soriano 1956, Golluscio et al. 1982), and have contrasting rooting systems, phenologies, and water utilization patterns. Grasses have a shallow root system and absorb water predominantly from the upper layers of the soil. In contrast, shrubs have deep roots and absorb most water from deeper soil layers (Sala et al. 1997). Patterns in resource acquisition are associated with phenological patterns. Most shrub species are deciduous, with sharp transitions between phases, whereas grasses maintain green leaves during the entire year (Golluscio and Sala 1993). As a consequence, changes in the amount and distribution of annual precipitation may change the balance between grasses and shrubs, producing changes in the structure and functioning of arid ecosystems (Schlesinger et al. 1990, Brown et al. 1997, Jackson et al. 2002).

Our ability to forecast ecosystem responses to climate change is constrained by the scarcity of field studies and proxy data sets, and also by our understanding of the mechanisms underlying terrestrial ecosystem responses to precipitation variability. Several studies have examined net primary productivity in relation to regional rainfall gradients (Sala et al. 1988, Austin and Sala 2002), interannual variability in rainfall (Lauenroth and Sala 1992, Silvertown et al. 1994, Briggs and Knapp 1995, Jobbágy and Sala 2000), seasonal rainfall distributions (Reynolds et al. 1999, Svejcar et al. 1999), and within-growing-season rainfall distribution (Knapp et al. 2002, Fay et al. 2003). However, fewer studies have addressed the mechanisms that govern the temporal dynamics of the response of ANPP to annual precipitation, and the capacity of ecosystems to recover after droughts of different intensity (e.g., see Wiegand et al. 2004).

In the present paper, we explored ANPP responses to rainfall variability in a semiarid ecosystem by means of a rainfall-manipulation experiment. Our main objectives were to evaluate whether previous-year conditions accounted for part of the variation in the relationship between current-year production and current-year precipitation, and to identify mechanisms responsible for the effects of previous-year conditions. We hypothesized that (1) droughts result in lags in the response of ecosystems to increases in water availability, (2) the magnitude of the lags is proportional to the intensity of the drought, and (3) the lags are explained by vegetation structural constraints (number of leaves, canopy cover, density, or species composition) caused by the drought, that then control the recovery of primary production after precipitation returns.

To test these hypotheses, we designed a rainfall manipulation experiment in the Patagonian steppe, in southern Argentina, where we decreased during two years water input with rainout shelters, which included three levels of rainfall interception (30%, 55%, and 80%) and a control (Yahdjian and Sala 2002). During the third year, we supplemented one-half of the plots of each drought treatment with water to simulate a wet year. We monitored the effect of previous drought on ANPP and the role of several components of vegetation structure (vegetation cover, plant density, number of tillers per tussock, and leaf elongation in grasses and number and elongation of twigs in shrubs) as a constraint of the recovery phenomenon.

MATERIALS AND METHODS

Study site

We conducted this study in the Río Mayo Experimental station managed by the Instituto Nacional de Tecnología Agropecuaria (INTA), Chubut, in the Patagonian region of Argentina (45°41' S, 70°16' W; elevation 500 m above sea level) from May 1999 to May 2002. Long-term mean annual temperature of the site was 8.4°C, with mean monthly temperature ranging from 1°C in July to 15°C in January. Mean annual rainfall, recorded over 20 years, was 168 mm, with a range between 90 and 275 mm, and was concentrated during fall and winter (March–September). The asynchrony of precipitation and temperature results in high potential evapotranspiration and low water availability from the middle of the spring to the end of the summer (Paruelo and Sala 1995), while there is a recharge of the soil profile almost every year during the cold season (June–August) (Sala et al. 1989). The topography is flat; soils are coarse textured with pebbles, which account for 47% of soil weight in the upper layer, and have a cemented calcareous layer at a depth of about 45 cm (Paruelo et al. 1988). The combination of flat topography and coarse-textured soils determines minimum runoff and runon and relatively high infiltration rates (Paruelo and Sala 1995). Volumetric water content at field capacity (soil water potential, SWP, -0.01 MPa) in



PLATE 1. Rainout shelters in the Patagonian steppe employed to intercept different amounts of incoming rainfall, simulating droughts of differing intensity. Photo Credit: L. Yahdjian.

the upper layer is 8% and the available water ($-0.01 \text{ MPa} < \text{SWP} < -5.9 \text{ MPa}$) for the first 45 cm of the profile is 23 mm (Paruelo et al. 1988). Organic matter in the upper soil layer in bare soil patches is 0.4% and pH is neutral (Paruelo et al. 1988). Soil ammonium concentration at 0–5 cm depth varied during the year between 0.02 and 0.10 g/m^2 , and soil nitrate concentration between 0.002 and 0.02 g/m^2 and accumulates during drought (Yahdjian et al. 2006). The vegetation is a mixture of tussock grasses and shrubs that have a basal cover of 32% and 15%, respectively, the rest being bare soil (Sala et al. 1989). Tussock grasses are represented principally by *Stipa speciosa* Trin et Ruprecht, *S. humilis* Cav., and *Poa ligularis* Nees ap. Steud. The dominant shrubs are *Mulinum spinosum* (Cav.) Pers., *Adesmia campestris* (Rendle) Rowlee, and *Senecio filaginoides* DC (Golluscio et al. 1982). We recorded rainfall and other standard meteorological variables during the course of this experiment using an automatic weather station equipped with a data logger (Campbell SCI 21X, Campbell Scientific, Logan, Utah, USA), located near the experimental area.

Experimental design

We performed a two-way factorial experiment with four rainfall regimes the first two years (0%, 30%, 55%, and 80% rainfall interception) by two rainfall regimes the third year (control vs. irrigated with two events of 21 mm). We selected 40 individuals of the dominant shrub *Mulinum spinosum*, and established a 3.76- m^2 ($2 \times 1.88 \text{ m}$) plot around each shrub in a 2-ha sampling area from

which large herbivores had been excluded since 1998. We randomly assigned the plots to our rainfall-interception treatments and control (see Plate 1). We used 10 replicates for the drought treatments, which lasted two consecutive years. During the third year, we removed the rainout shelters and irrigated half of the ten replicate plots of each interception-level treatment. Plots receiving the irrigation treatment were chosen at random.

Rainfall manipulations

We imposed three levels of rainfall interception with three rainout-shelter types, which had a roof made of bands of transparent acrylic without UV filter (acrilico-paolini; Paolini, San Martín, Buenos Aires, Argentina). Each shelter type blocked different amounts of incoming rainfall, depending on the number of bands. We tested the performance of the three kinds of shelters by measuring the amount of water intercepted by each rainout-shelter type, and we found 29%, 47%, and 71% rainfall interception for the three interception treatments, which were very close to the expected values (Yahdjian and Sala 2002). We used a 20-yr precipitation record and estimated that the probability of occurrence of a year with precipitation 29% lower than average was 0.24; for a year with precipitation 47% lower than average, the probability was 0.14; and for a year with precipitation 71% lower than average, the probability was 0.05. The average size of precipitation events under the rainout shelters was reduced, as we did not manipulate the number of rainfall events, but rather the amount of each event (Yahdjian and Sala 2002). Soil

water content under rainout shelters, at 0–15 and 0–30 cm depth, was significantly lower than soil water content in control plots, with a small edge effect (<20 cm; Yahdjian and Sala 2002). Shelter effects on radiation, air temperature, and soil temperature were minimal; the maximum effect was observed under the shelter designed to intercept the largest fraction of precipitation (80%), with daily average radiation reduction <15%, and mean temperature changes of 2°C cooler under shelters than outside (Yahdjian and Sala 2002).

We applied the experimental rainfall additions during the growing season of the third experimental year, in November and January, to simulate a wet year. Each event consisted of 80 L of water uniformly scattered in each plot with a sprinkler, to simulate a natural rainfall event of 21 mm. The rate of water application was similar to the rate of absorption by the soil, to prevent water from pooling on the soil surface. We extracted the irrigation water from a local well, and we analyzed water for nitrates and ammonium concentration, using an Alpkem autoanalyzer (O-I Corporation, College Station, Texas, USA), which uses a colorimetric analysis of inorganic nitrogen in liquid extracts.

Response variables

We measured the effect of precipitation manipulation treatments on soil moisture to evaluate the magnitude of our treatments, and the impact of precipitation manipulations on plant water availability. We evaluated plant and vegetation responses to water manipulations by monitoring plant cover, ANPP, plant density, species diversity, leaf growth, and the number of tillers in grasses, and growth and twig elongation in shrubs. We monitored response variables at different points in time during the three water manipulation years. We reported results from most variables only at the end of the drought period (year 2) and at the end of the water supplementation phase (year 3).

We monitored volumetric soil-water content (SWC) during water manipulations in the 40 plots at 0–15 and 0–30 cm depth with the time domain reflectometry (TDR) technique (Reeves and Smith 1992), employing a Tektronix 1502C (Beaverton, Oregon, USA). We chose these depths because grasses concentrate most of their roots above 30 cm (Soriano et al. 1987) and because soil moisture dynamics in the upper soil profile are crucial for plant performance and for other important aspects of ecosystem functioning like decomposition, nutrient cycling, and carbon storage. At the initiation of the study in May 1999, we inserted two pairs of TDR probes, one to 15 cm and one to 30 cm depth, in bare soil in each plot and determined the initial SWC. We left the probes in place to monitor this variable during the course of the study at various intervals, more frequently around the moments when we irrigated. We always measured SWC at the same time of the day (mid-morning), and only made comparisons among treatments within each date.

We monitored responses of plant cover to our precipitation manipulation treatments using the line-intercept method (Canfield 1941). A meter tape was laid out on the ground and the crowns that overlap or intercept the line were recorded by species to the nearest 1 cm. At the initiation of the study, we installed two perpendicular 2.74-m lines in each plot, which coincided with the diagonals of the plots, and we determined the percentage of cover of the plant community in each of the 40 plots, averaging the percentage of cover on the two perpendicular lines. We did not find significant differences in the initial vegetation cover, plant density, and species composition among plots assigned to the different treatments. We employed the same lines to measure the canopy cover of each plot at the peak of the growing season of the three rainfall-manipulation years.

We evaluated the responses of ANPP to precipitation manipulation treatments using estimates of plant cover per species that were then transformed into biomass employing specific cover-biomass regressions constructed for this site (P. Flombaum and O. E. Sala, *unpublished manuscript*). We equated ANPP with peak biomass, which in our study site occurs in January (Jobbágy and Sala 2000). Sala and Austin (2000) reviewed the errors associated with different methods used to estimate ANPP in the field and concluded that a single harvest at peak biomass is the best method to obtain an estimate of ANPP in grasslands with strong seasonal variability like the Patagonian steppe.

We estimated plant density and diversity of the plant community at the end of the rainfall-interception period (May 2001). To estimate plant density (D), we used the information of the line intercepts, and we calculated a value of density for each plot, with the method described by McIntyre (1953):

$$D = \frac{2/\pi \sum (1/Ch)}{n \times L}$$

where D is the plant density expressed as the number of plants per square meter, Ch is the chord intercepted by each individual (in meters), n is number of transects, and L is the length of the transects (in meters). This is a good method to estimate density for established perennials in open shrub or grassland communities with plants of fairly regular geometry, as is the case in our study site (Fernández et al. 1991). As grasses in the steppe form tussocks with clear edges, grass plant individuals can be easily determined and counted.

We estimated diversity by calculating diversity indices using the information of the percent cover of grass and shrub species from the line intercepts. We calculated the Shannon's diversity index, H' (Shannon and Weaver 1949), which estimates diversity by taking into account the richness and evenness components of diversity:

$$H' = -\sum [f_i \times \ln(f_i)]$$

where f_i is the proportional cover of the i th species. We

calculated evenness with Simpson's index, E (Simpson 1949):

$$E = 1 - \sum (f_i)^2.$$

To estimate richness, we added all the grass and shrub species present in each plot.

We measured leaf elongation and we counted the number of tillers of individuals of the dominant grass, *Stipa speciosa*, which we selected as representative of the grass functional type. We estimated leaf elongation on expanding leaves following the technique described by Soriano et al. (1976). We first placed a 3 mm wide rod vertically near the tiller containing the leaf to be measured, and then attached the tiller and the leaf to the rod with two plastic rings and marked the location of the leaf tip on the rod. We periodically recorded the difference between current and previous position of the leaf tip on the rod, and replaced the selected leaf by another expanding leaf of the same tussock when the ligule was visible. We measured leaf elongation selecting one expanding leaf from one tussock of *S. speciosa* in each of the 40 plots. To estimate the number of tillers per plant under the different rainfall manipulations, we selected another tussock of *S. speciosa* in three plots per treatment, and recorded periodically the basal diameter and the number of tillers per tussock.

We measured the growth of *M. spinosum* shrubs, which dominate the shrub group in abundance and biomass (Fernández et al. 1991), on individuals placed in the center of our plots, by counting and measuring the length of all branches in 10 × 25 cm quadrants located at the top of the individuals. At the end of the growing season, we measured the length of twig growth for the year, which is easy to identify in *M. spinosum*. During early spring and winter, we could not count or measure twigs of *M. spinosum* because it had no green twigs.

Statistics

Statistical analyses were performed using PROC GLM in the SAS version 6.12 packages (SAS Institute 1997). Unless otherwise stated, significance was assumed at $P < 0.05$. We analyzed data for soil water content (SWC) for the rainfall-interception period with repeated measures ANOVA, with rainfall treatments as the main effect. SWCs before and after irrigation were compared with a t test. We fitted data of total ANPP, and for grasses and shrubs, vs. annual precipitation using a linear model. We performed regressions with all the data and tested for the goodness of fit to the linear model with the class module of the PROC GLM of the same SAS version. For the sake of clarity we plotted the mean values with their standard errors. For the last date, January 2002, we performed a multiple regression analysis with the R -square selection method in the REG procedure of SAS. Appropriate transformations of the primary data were used when needed to meet the assumptions of the statistical analysis.

RESULTS

Precipitation and soil water content

Annual precipitation in Río Mayo was very similar during the two years of the rainfall-interception experiment, with 140 mm the first year and 155 mm the second, and also was similar to the 20-yr mean of 168 mm. For the third year of the experiment, annual rainfall was 176 mm. The seasonal distribution of rainfall during the 3-yr experimental period was typical of the Patagonian steppe, with maximum precipitation occurring in fall and winter periods (March–September; Fig. 1a). We calculated monthly amounts of water input in each precipitation interception treatment, subtracting the observed interception percentages (29%, 47%, and 71% of incoming precipitation) from the incoming monthly rainfall in our study site (Fig. 1a). On an annual basis, during the second year of the rainfall-interception experiment, the amounts of precipitation received were 45 mm, 80 mm, 100 mm, and 155 mm in the 71%, 47%, 29%, and 0% interception treatments, respectively. During the third year of rainfall manipulations, the simulated rainfall events added a total of 42 mm/yr (Fig. 1a), which represented 24% more rainfall in irrigated plots than in controls (218 mm/yr vs. 176 mm/yr). The probability of the occurrence of such a wet year was 0.24, based on the 20-yr rainfall records. The water employed for irrigation had low concentrations of ammonium and nitrate (0.02 ± 0.004 ppm, and 0.3 ± 0.02 ppm, respectively [mean \pm se] for $n = 3$).

Rainfall manipulation caused consistent changes in soil water content during the entire experiment (Fig. 1b). Volumetric soil water contents at 0–15 cm depth were affected similarly to those at 0–30 cm depth (Yahdjian and Sala 2002), therefore we only report 0–30 cm values from Yahdjian and Sala (2002). Soil water content was significantly lower ($P < 0.05$) in the sheltered plots than in the control, except in January, which is one of the months with highest potential evapotranspiration and lowest precipitation (Fig. 1b). Soil water content at 0–30 cm depth was significantly augmented after rainfall supplementation in both applications ($n = 20$, $t = 4.74$; $P < 0.0001$ in November and $n = 20$, $t = 3.99$; $P < 0.01$ in January) (Fig. 1b).

Drought effects

Total ANPP ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) during the second rainfall-interception year was significantly and linearly related to annual precipitation input (APPT; mm/yr) along the experimental precipitation gradient (total ANPP = $0.13 \times \text{APPT} + 58.3$; $r^2 = 0.34$, $P < 0.01$; Fig. 2). Reductions in total ANPP were not accompanied by an increase in standing dead biomass ($P > 0.05$), but by an increase in bare ground (bare = $-0.07 \times \text{APPT} + 58.4$; $r^2 = 0.25$, $P < 0.05$). At the end of the drought period, the mean cover of bare soil (\pm SE) was $48\% \pm 2.1\%$ in control plots, $51\% \pm 1.9\%$ in the 30% interception treatment, $52\% \pm 2.2\%$ in the 55% interception treatment, and $56\% \pm 2.1\%$ in the 80% interception treatment.

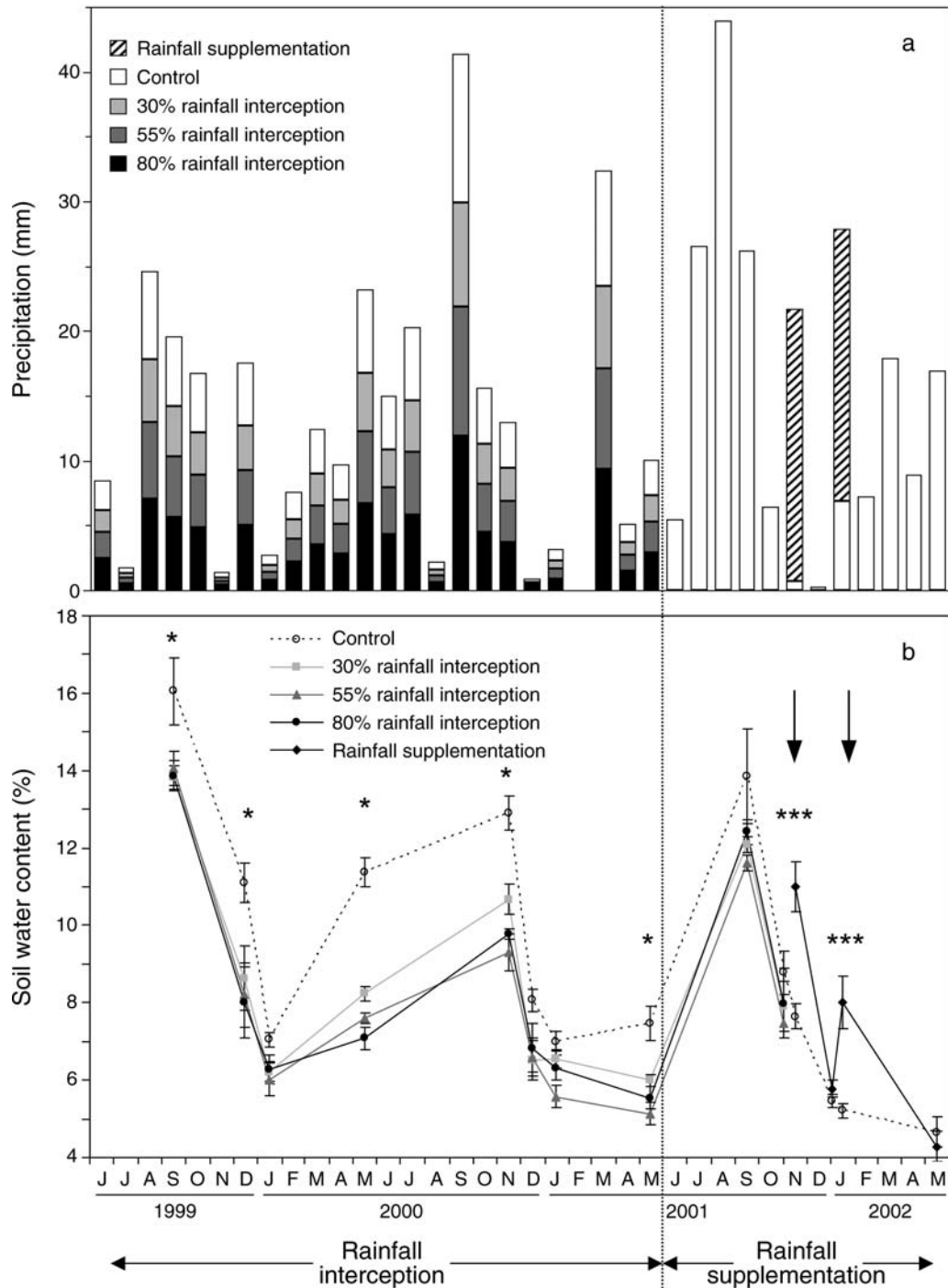


FIG. 1. Effects of water manipulation treatments on rainfall inputs (top panel) and volumetric soil water content at 0–30 cm depth (bottom panel) for June 1999–May 2002. For the first two years, treatments included four levels of water interception (0%, 30%, 55%, and 80%), and for the third year, treatments were rainfall supplementation and control. (a) Monthly rainfall inputs. Open bars correspond to treatments receiving ambient rainfall quantities; solid bars (black and gray shades) correspond to rainfall inputs in plots from the different rainfall interception treatments during years 1 and 2; hatched bars indicate rainfall supplementation on irrigation plots during year 3. (b) Volumetric soil water content. Open symbols correspond to treatments receiving ambient rainfall quantities, and solid symbols correspond to treatments with rainfall interception or rainfall supplementation. Points represent mean values \pm SE with $n = 10$ plots for years 1 and 2 (redrawn from Yahdjian and Sala [2002]), and $n = 20$ for year 3. Significant differences among treatments within each date are indicated with asterisks. Arrows represent water supplementation events.

* $P < 0.05$; *** $P < 0.001$.

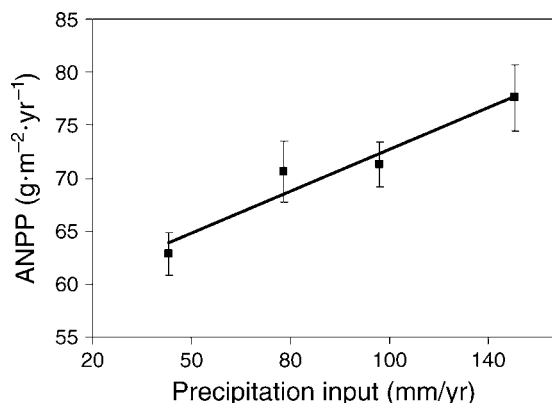


FIG. 2. Effects of experimental rainfall interception on aboveground net primary production at the end of the rainfall interception period. The experimental precipitation gradient was created using four levels of water interception: 0% (control), 30%, 55%, and 80% of incoming rainfall; which resulted in 155 mm, 100 mm, 80 mm, and 45 mm of annual precipitation, respectively. A regression model relating total ANPP along the experimental precipitation gradient is $ANPP = 0.13 \times APPT + 58.3$; $r^2 = 0.34$, $P < 0.01$. Points represent mean values ($\pm SE$) for $n = 10$ plots, with ANPP in $g \cdot m^{-2} \cdot yr^{-1}$ and APPT in mm/yr.

The density of individuals of tussock grasses and shrubs (D ; individuals/ m^2) was related to the precipitation received during the precipitation interception period and, at the end of the rainfall-interception period, plant density significantly decreased with decreasing annual precipitation input (APPT; mm/yr) along the experimental precipitation gradient ($D = 0.11 \times APPT + 18$; $r^2 = 0.39$, $P < 0.05$; Fig. 3). Thus, reduced recruitment of seedlings or increased mortality of already established individuals may provide a mechanistic link between alterations in precipitation and ANPP response.

Aboveground net primary productivity of grasses during the second rainfall-interception year was significantly related to annual precipitation input (grass ANPP = $0.09 \times APPT + 13.16$; $r^2 = 0.24$, $P < 0.05$), and this relationship was mostly accounted for by the sensitivity to drought of the grass *Stipa humilis* (Table 1). The second grass species most sensitive to drought was *S. speciosa*, while *Poa ligularis* showed no response to decreases in water input (Table 1). Shrub ANPP was unrelated to annual precipitation (Table 1; $P > 0.05$). Among shrubs, the only species that showed some sensitivity to drought was *Senecio filaginoides* (Table 1).

Diversity, estimated with the Shannon diversity index, was significantly lower ($P = 0.053$) in plots of the 80% rainfall-interception treatment, while there were no differences among the intermediate rainfall-interception and control plots (Table 1). Evenness was marginally lower ($P = 0.089$) in plots with 80% rainfall interception (Table 1), while drought treatments did not affect the richness, as the mean number of species of grasses and shrubs was not significantly different among treatments

(Table 1). The dominant grass, *S. speciosa*, showed no leaf elongation response to rainfall interception, except once during the spring of the second year (Table 2). The number of tillers per plant was slightly lower in treatments with low water input, but differences were not statistically significant (Table 2). The growth of twigs of *Mulinum spinosum* did not respond to rainfall-interception treatments (Table 2).

Recovery after drought

Aboveground net primary production was significantly related to annual precipitation ($ANPP = 0.3 \times APPT + 47.1$; $r^2 = 0.48$, $P < 0.01$) in a model constructed with the three lower-than-average precipitation inputs, two near-average precipitation inputs (corresponding to the control treatment in two consecutive years), and one higher-than-average precipitation level (corresponding to irrigated plots that had been control plots during the precipitation interception period) (Fig. 4). However, ANPP during the third year of the rainfall manipulation experiment in plots that had experienced 30%, 55%, or 80% rainfall interception during the previous two years (plots with drought legacy) was significantly lower ($P < 0.05$) than ANPP in controls (Fig. 4). These differences were observed in irrigated and in nonirrigated plots, and represented an estimate of the lags in the response of ANPP when a wet or an average year follows a dry year.

The magnitude of the lags increased with the intensity of the drought experienced by vegetation during previous years. The relative magnitude of the lags or relative drought legacy (RDL) was estimated as

$$RDL = \frac{ANPP \text{ control} - ANPP \text{ drought legacy}}{ANPP \text{ control}}$$

where ANPP control was the ANPP during the third experimental year in plots that had not experienced drought and ANPP drought legacy was the ANPP measured during the third year in plots that had experienced

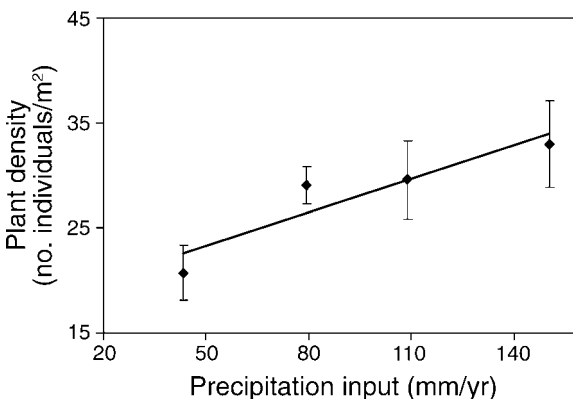


FIG. 3. Density of grass and shrub individuals (D) along the experimental rainfall gradient at the end of the rainfall interception period. The rainfall gradient is described in Fig. 2. The regression model is $D = 0.11 \times APPT + 18$; $r^2 = 0.39$, $P < 0.05$. Points represent mean values ($\pm SE$) for $n = 10$.

TABLE 1. Aboveground net primary production (ANPP; g·m⁻²·yr⁻¹), diversity, evenness, and richness of grass and shrub species for the rainfall interception treatments during the second year of manipulations.

	Rainfall interception treatments (%)			
	0	30	55	80
Rainfall input (mm)	155	100	80	45
Grass ANPP	26.5 ^a ± 2.4	22.8 ^{ab} ± 2.2	21.2 ^{ab} ± 2.8	16.3 ^b ± 3.2
<i>Stipa humilis</i>	4.1 ^a ± 0.6	2.6 ^b ± 0.1	2.1 ^b ± 0.3	1.2 ^c ± 0.4
<i>Stipa speciosa</i>	11.2 ^a ± 1.7	8.5 ^b ± 1.3	8.0 ^b ± 1.1	6.5 ^b ± 1.2
<i>Poa ligularis</i>	9.6 ± 1.3	10.6 ± 1.8	10.9 ± 0.8	7.7 ± 1.7
Shrub ANPP	51.1 ± 4.5	48.5 ± 5.0	49.4 ± 4.3	46.6 ± 4
<i>Senecio filaginoides</i>	4.9 ^a ± 2.6	7.0 ^a ± 2.9	2.2 ^b ± 2.2	3.0 ^b ± 2.0
<i>Mulinum spinosum</i>	44.7 ± 12.3	39.3 ± 11.3	46.1 ± 15.6	42.8 ± 16.2
<i>Adesmia campestris</i>	1.5 ± 0.9	2.2 ± 1.6	1.1 ± 0.5	0.8 ± 0.08
Diversity (<i>H'</i>)	1.100 ^a ± 0.074	1.164 ^a ± 0.068	1.144 ^a ± 0.05	0.917 ^b ± 0.074
Evenness	0.585 ^a ± 0.027	0.604 ^a ± 0.033	0.615 ^a ± 0.028	0.502 ^b ± 0.044
Richness	4.5 ± 0.23	4.9 ± 0.23	4.1 ± 0.18	4.8 ± 0.36

Notes: Values are means ± SE for *n* = 10 plots. Statistical comparisons were performed across treatments, and different superscript letters indicate statistical differences at *P* = 0.001 for ANPP, *P* = 0.053 for diversity values, and *P* = 0.089 for evenness values.

different levels of drought (by 30%, 55%, and 80% rainfall interception) during previous years. Therefore, the relative drought legacy quantifies the relative decrease in ANPP due to the legacy left behind by previous drought. When plotted against the relative precipitation decrease (RPPT) experienced during previous years (RPPT in our case is 0.30, 0.55, and 0.80), the relative drought legacy showed a linear relationship (RDL = 0.45 × RPPT + 0.024; *r*² = 0.65, *P* < 0.01; Fig. 5). The magnitude of the legacy, or the decrease in production due to previous drought, was less

than proportional to the decrease in precipitation because the slope of the RDL-RPPT relationship was < 1.

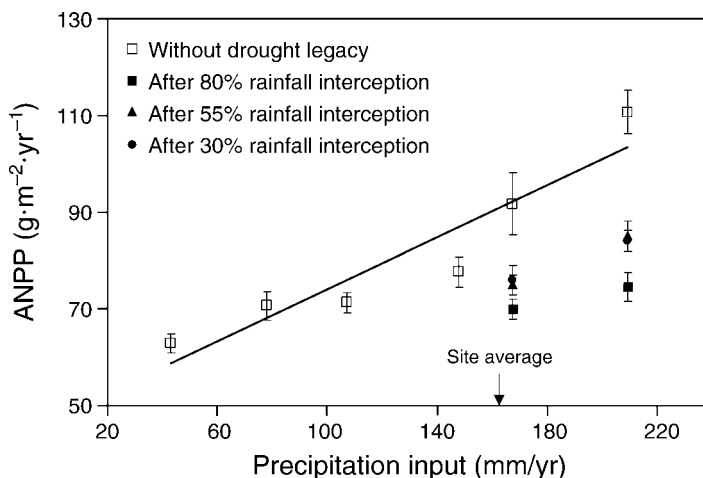
Not all the species of the Patagonian steppe showed the same response to increases in water availability, as neither of the two main functional types, grasses and shrubs, had the same sensitivity to changes in water input. Grasses increased their ANPP with water addition and the increase was different for plots that had experienced different magnitudes of drought during the previous two years (ANOVA; drought, *F*_{3,10} = 3.78,

TABLE 2. Plant growth responses in the grass *Stipa speciosa* and in the shrub *Mulinum spinosum* during two years of water-interception treatments.

Parameter	Winter				Spring				Summer			
	0	30	55	80	0	30	55	80	0	30	55	80
Year 1												
<i>Stipa speciosa</i>												
Leaf elongation (mm/d)	0.30 (0.07)	0.26 (0.07)	0.29 (0.09)	0.21 (0.07)	1.30 (0.17)	1.62 (0.18)	1.47 (0.20)	1.12 (0.24)	0.19 (0.03)	0.14 (0.02)	0.14 (0.02)	0.13 (0.03)
No. tillers/plant									96.0 (29.7)	96.3 (39.8)	111.0 (22.3)	96.7 (38.2)
<i>Mulinum spinosum</i>												
Branch length (cm)									3.79 (0.48)	4.02 (0.17)	4.50 (0.70)	4.07 (0.27)
No. twigs/dm ² plant canopy									20.0 (1.15)	17.8 (1.95)	20.3 (1.07)	19.2 (1.42)
Year 2												
<i>Stipa speciosa</i>												
Leaf elongation (mm/d)	0.30 (0.04)	0.26 (0.08)	0.26 (0.06)	0.29 (0.08)	1.39 ^{ab} (0.22)	1.57 ^a (0.14)	1.55 ^a (0.12)	1.00 ^b (0.12)	0.72 (0.13)	0.78 (0.15)	0.71 (0.17)	0.83 (0.17)
No. tillers/plant	104.7 (31.0)	97.7 (31.3)	123.7 (34.9)	97.3 (44.7)	87.0 (31.0)	101.3 (42.3)	85.0 (24.3)	99.0 (43.8)	80.3 (26.2)	65.7 (28.9)	61.0 (34.0)	52.0 (16.7)
<i>Mulinum spinosum</i>												
Branch length (cm)									3.21 (0.10)	3.43 (0.28)	3.27 (0.40)	3.61 (0.49)
No. twigs/dm ² plant canopy									16.3 (0.56)	17.9 (1.17)	16.9 (1.42)	16.9 (1.27)

Notes: Values are means (SE) for *n* = 10 plots, except for the number of tillers/plant of *S. speciosa*, where *n* = 3. Groups with different superscript letters are significantly different (*P* < 0.05).

FIG. 4. Aboveground net primary production (ANPP) response to precipitation input measured along the experimental precipitation gradient. The regression model is $ANPP = 0.30 \times APPT + 47.1$; $r^2 = 0.48$, $P < 0.01$. Empty squares are ANPP values for the second year of rainfall interception and ANPP for irrigated and nonirrigated plots that were control plots during previous years. Solid points are ANPP values estimated in plots with a drought legacy, i.e., ANPP during year 3 in irrigated and nonirrigated plots that experienced 30% (circle), 55% (triangle), and 80% (square) rainfall interception during the previous two years.



$P = 0.020$; irrigation, $F_{1,20} = 2.63$, $P = 0.091$). On the contrary, shrubs did not respond to irrigation. The species of grasses that responded most to water addition were *S. humilis* and *S. speciosa*. However, only *S. humilis* showed an effect for the drought experienced during the previous two years, as its biomass increased more in irrigated plots that were control plots for the drought treatment than in irrigated plots that had experienced an 80% interception of rainfall.

Current-year ANPP responded to annual precipitation of the current year, and also to the production experienced during previous years. A multiple regression model in which we added the ANPP of the previous year to the model relating APPT and ANPP was $ANPP_t = -1.47 + 0.1 APPT_t + 0.9 ANPP_{t-1}$ ($r^2 = 0.41$, $P < 0.001$)

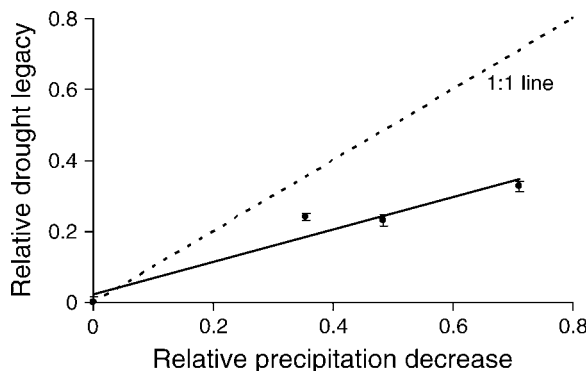


FIG. 5. Relative drought legacy (RDL), or lag response of aboveground net primary production (ANPP) to four levels (0%, 30%, 55%, and 80%) of relative precipitation decrease during two previous years. The relative drought legacy was estimated with ANPP during year 3 in irrigated plots with different histories of drought as $([ANPP \text{ in control plots}] - [ANPP \text{ in plots with drought legacy}] / [ANPP \text{ in control plots}])$. Similarly, the relative precipitation decrease (RPPT) was calculated with precipitation of year 2 as $([PPT \text{ in control plots}] - [PPT \text{ in rainfall-interception plots}] / [PPT \text{ in control plots}])$. The regression model is $RDL = 0.45 \times RPPT + 0.024$; $r^2 = 0.65$, $P < 0.01$. Data points are means \pm SE for $n = 5$.

where $ANPP_t$ is annual production ($g \cdot m^{-2} \cdot yr^{-1}$) during the third year of our experimental rainfall manipulations, and $APPT_t$ is annual precipitation (mm) in year 3. The addition of ANPP of the previous year ($ANPP_{t-1}$, that is, ANPP during the second year of the rainfall-interception period) in the model increased the percent of the variance accounted for by the model relating current ANPP and current year PPT from 24% to 41%.

DISCUSSION

Our results support the hypothesis that, after a period of drought, ANPP recovery in a steppe grassland shows lags in its response to increased water availability. We successfully reproduced experimentally the lags in the ANPP recovery after a drought, which were observed in the long-term data sets. We found higher total ANPP values in plots that had not experienced drought than in plots with a history of rainfall deficit. This result was observed both in irrigated plots, where we simulated a wet year, and in plots that received the precipitation amount of the site during the third experimental year.

Our results also support the hypothesis that lags in ANPP recovery after periods of drought are proportional to the intensity of previous drought. ANPP during year 3 from plots that experienced 80% rainfall interception during years 1 and 2 was lower, both in irrigated and in nonirrigated plots, than ANPP for year 3 from plots of either 30% or 55% rainfall interception treatments. As a consequence, the relative drought legacy increased with increasing drought intensity. The magnitude of the reduction in production resulting from previous drought was less than proportional to the relative magnitude of the drought. For example, an 80% decrease in precipitation in previous years resulted in a 38% reduction in production relative to the plots that had not experienced a drought.

The lags in ANPP recovery that we found in the Patagonian steppe apparently were a consequence of structural constraints that vegetation imposed on primary production recovery. During drought not only

production but the density of individuals of grasses and shrubs was reduced. When water became available after drought, the density of plants appeared as the main factor constraining the capacity of the vegetation to respond to increased water input. We suggest that reduction in plant density could be one of the mechanisms of the ANPP lags in the Patagonian steppe.

Previous studies in grasslands have reported a correlation between current and previous-year precipitation with ANPP and implied causality (Lauenroth and Sala 1992, Knapp et al. 1998, Jobbágy and Sala 2000, Oesterheld et al. 2001). We suggest that this work represents a step forward in our understanding because it experimentally tested the hypothesis of the lags and it proposes a mechanism. We found that ANPP increased with precipitation along our experimental gradient, and this pattern was similar to the relationships between ANPP and annual precipitation through time, which were developed using long time-series from different sites. However, the model constructed in the present study accounted for a higher proportion of the variance than models constructed with temporal series (Lauenroth and Sala 1992, Knapp et al. 1998, Jobbágy and Sala 2000). We hypothesize that the difference between our model and temporal models reported in the literature may be the result of our experimental conditions, where only precipitation input differed among treatments while all other environmental conditions (e.g., temperature, wind speed, radiation) were kept constant.

Grass productivity responded to our drought treatments but shrub productivity did not. We speculate that this differential behavior results from shrubs integrating water resources over broader temporal and spatial scales than grasses. Shrubs in the Patagonian steppe have deep roots and absorb water predominantly from deep soil layers that are recharged less frequently, whereas grasses have shallow rooting systems and absorb most of the water from the upper soil layers that recharge frequently (Sala et al. 1989). Consequently, shrubs explored a larger volume of soil than grasses that, in turn, buffers the water status of shrubs from year-to-year variability in precipitation. Analysis of time series of precipitation and productivity for the Patagonian steppe showed that grass production had maximum correlation with precipitation during the three months previous to the estimate of production, but shrub production had the highest correlation with precipitation received in the previous 14 months (Jobbágy and Sala 2000). We speculate that shrubs would have responded to rainfall interception if the manipulation experiment had lasted longer. Similarly, Golluscio et al. (1998) conducted a manipulative experiment in the Patagonian steppe that found grasses to always respond to experimental large summer rainfall events, while shrubs only exploited large rainfall events when soil water potential in deep soil layers was low.

Diversity was reduced in plots where 80% of precipitation was excluded, which was accounted for by a reduction in species evenness. Experimental drought

reduced evenness presumably because of the differential responses of grass species, with *S. humilis* being the most sensitive. Knapp et al. (2002), working with a rainfall manipulation experiment that reduced 30% of incoming rainfall in the Konza Prairie in North America, found that the effect of drought on the diversity of the plant community was not statistically significant, even after four years of water exclusion, while they did find an effect on biodiversity due to altered rainfall timing, which increased the variability of soil water content.

In conclusion, there exist lags in the response of ANPP to incoming annual precipitation that are proportional to the intensity of drought experienced before, and these lags could be the result of vegetation structure constraints. Our results suggest that the main characteristic of vegetation structure that constrains primary productivity in the Patagonian steppe when a wet year follows a dry year may be plant density.

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