

Nitrogen rather than water availability limits aboveground primary productivity in an arid ecosystem: substantial differences between grasses and shrubs

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Abstract

Changes in water and nitrogen availability can affect the structure and function of arid ecosystems. How these resources affect aboveground primary productivity (ANPP) remains far from clear. We examined the N and water limitation of ANPP from the species to the community level and the response of ANPP to annual precipitation in a Patagonian steppe. We conducted a 7-year field experiment with water addition (+W), nitrogen addition (+N), and +NW. Destructive methods for grasses and allometric relationships for shrubs were used to assess ANPP and vegetation indices (NDVI and MSAVI2) to estimate community ANPP. An increase in ANPP of one grass species (*Pappostipa humilis*) and a decrease of the grass *Poa ligularis* under +N were observed. Some shrubs species exhibited mortality under nitrogen addition. Nitrogen exerted a positive effect on grass ANPP and amplified the sensitivity of grass ANPP to annual precipitation. However, +N had not effects on the shrub ANPP and shrub ANPP-precipitation relationship. Water addition by itself had no effect on ANPP for either shrubs or grasses. However, shrubs responded positively to an unusually wet year regardless of treatment and were also more sensitive to changes in annual precipitation than grasses. Total ANPP increased significantly in +N relative to the C and +W, but without changes in the sensitivity to annual precipitation. The results suggest that the responses of grasses and shrubs to water inputs is driven by soil moisture redistribution and rooting depth and that grass and community ANPP is more limited by N than by water.

Nitrogen rather than water availability limits aboveground primary productivity in an arid ecosystem: substantial differences between grasses and shrubs

Short title: Aboveground primary productivity in response to nitrogen and water addition

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Author Contributions: FGS, SJB and GG conceived and designed the experiments. LCS, FGS, SJB, AB, AC and JOA conducted fieldwork. VDV performed imaging analysis. LCS performed statistical analyses. LCS, SJB and GG wrote the manuscript. GYH and NSA contributed to the discussion of the results.

Abstract

Changes in water and nitrogen availability can affect the structure and function of arid ecosystems. How these resources affect aboveground primary productivity (ANPP) remains far from clear. We examined the N and water limitation of ANPP from the species to the community level and the response of ANPP to annual precipitation in a Patagonian steppe. We conducted a 7-year field experiment with water addition (+W), nitrogen addition (+N), and +NW. Destructive methods for grasses and allometric relationships for shrubs were used to assess ANPP and vegetation indices (NDVI and MSAVI2) to estimate community ANPP. An increase in ANPP of one grass species (*Pappostipa humilis*) and a decrease of the grass *Poa ligularis* under +N were observed. Some shrubs species exhibited mortality under nitrogen addition. Nitrogen exerted a positive effect on grass ANPP and amplified the sensitivity of grass ANPP to annual precipitation. However, +N had not effects on the shrub ANPP and shrub ANPP-precipitation relationship. Water addition by itself had no effect on ANPP for either shrubs or grasses. However, shrubs responded positively to an unusually wet year regardless of treatment and were also more sensitive to changes in annual precipitation than grasses. Total ANPP increased significantly in +N relative to the C and +W, but without changes in the sensitivity to annual precipitation. The results suggest that the responses of grasses and shrubs to water inputs is driven by soil moisture redistribution and rooting depth and that grass and community ANPP is more limited by N than by water.

Keywords: anomalous precipitation, water addition, nitrogen addition, Patagonian steppes, rooting depth, soil water distribution

Introduction

Aboveground net primary productivity (ANPP) is an attribute that integrates key aspects of ecosystem functioning. The ANPP is related to carbon and water cycling and energy fluxes. In arid and semiarid ecosystems, it has been generally observed that ANPP is strongly limited by water and nutrient availability (Guo et al., 2022; Lü et al., 2014; Ma et al., 2020; X. Zhang et al., 2021). Several studies have indicated a positive linear relationship between ANPP and annual precipitation across multiples sites (Bai et al., 2008; A. K. Knapp & Smith, 2001; Sala et al., 2012). At a specific site, the response of ANPP to precipitation can be linear (Sala et al., 2012; Wang et al., 2014; Wilcox et al., 2017; Yahdjian & Sala, 2006) or non-linear, with positive (Ahlström et al., 2015; Felton et al., 2019; L. Zhang et al., 2022; T. Zhang et al., 2020) or negative effects (Hou et al., 2021; Wu et al., 2018). These inconsistent relationships between ANPP and precipitation may be due to differences in species composition, the range of precipitation considered, or biogeochemical factors affecting the sensitivity of species to changes in precipitation (Deng et al., 2021; Felton et al., 2019; Knapp et al., 2017). For example, in some cases nutrient limitations restrict the effect of water on ANPP (Austin & Sala, 2002; Harpole et al., 2007; X. Zhang et al., 2021). On the other hand, increased soil N content alone usually stimulates primary productivity (Austin & Sala, 2002; Harpole et al., 2007; LeBauer & Treseder, 2008; Tang et al., 2017; Xia & Wan, 2008; Yue et al., 2020). Furthermore, many studies indicate that the ANPP of arid ecosystems is co-limited by water and nutrients (Guo et al., 2022; Harpole et al., 2007; Lü et al., 2014),

In addition to the typical water and nutrient restrictions to which arid ecosystems are exposed, it should be considered that these ecosystems are sensitive to climate change and other global changes (Li et al., 2021; Niu & Wan, 2008; Rudgers et al., 2018). Changes in the amount and temporal pattern of precipitation are predicted for arid regions, with increases or decreases depending on the region, but with a significant increase in extreme events (Drumond et al., 2019; Giorgi et al., 2019; Saurral et al., 2017). Moreover, global N deposition is increasing as a consequence of intensive anthropic activities (agriculture, oil, gas production, among others) even in arid and semiarid regions (Bobbink et al., 2010; Dentener et al., 2006; Gruber & Galloway, 2008). Increased N deposition and altered precipitation regimes can have significant impacts on carbon, water and nutrient cycling (Gruber & Galloway, 2008; Harpole et al., 2007; Nielsen & Ball, 2015), through changes in vegetation structure and ANPP (Song et al., 2019; Stevens et al., 2015). Some studies (Ahlström et al., 2015; c et al., 2020; Poulter et al., 2014) have shown that semiarid regions play a key role, more than other ecosystems, in regulating intra- and interannual variability of the global carbon cycle. These changes in N and water inputs to which ecosystems are exposed may occur at the same time, and their interaction may not be directly predicted by the additive effects of individual resources. Some studies have shown that the effects of water and N amendment on primary productivity are additive (Gong et al., 2011; X. Zhang et al., 2021), while others show non-additive effects (Gao et al., 2011; Niu et al., 2009).

In addition to changes in ANPP due to changes in water and nutrient availability, species composition, species interaction, and stability of dominant species may be modified with the addition of limiting resources (Guo et al., 2022; Lannes et al., 2016; Yue et al., 2020; X. Zhang et al., 2021). The addition of water usually increases species composition and ecosystem functioning (Hu et al., 2022; Weltzin et al., 2003; Yue et al., 2020). Plant diversity can be affected by N addition through competition exclusion, species invasion, or soil nutrient imbalances (Liu et al., 2019; Tian et al., 2016). However, plant community responses to N addition vary between ecosystems and, although the most common response is the reduction of species diversity by competitive exclusion, the opposite effect has been found in resource-poor ecosystems (Bai et al., 2010; Chalcraft et al., 2008; Ladwig et al., 2012). Long-term N addition can decrease soil pH and affect the growth and survival of species sensitive to soil acidification caused by excessive N input, thus reducing plant diversity (Fang et al., 2012; Ke et al., 2023; Wallace et al., 2007).

The Patagonia region of southern Argentina is mainly represented by arid/semiarid ecosystems with pronounced interannual precipitation variability (Jobbágy & Sala, 2000; Paruelo et al., 1998) and a low pool of available soil N (Carbonell Silletta et al., 2019; Yahdjian et al., 2014). Climate change predictions indicate a reduction in precipitation in Patagonia, except in some areas such as the northwest of Chubut, where there is

a tendency to increase rainfall (Barros et al., 2015; Saurral et al., 2017). Also, although N deposition in arid areas is lower than in other ecosystems, it is expected to increase, depositing mostly on natural vegetation (Dentener et al. 2006; Gruber & Galloway 2008). Several studies have evaluated the patterns and controls of aboveground production in relation to climatic variables and vegetation structure in the Patagonian steppe at both spatial and temporal scales (Austin & Sala, 2002; Fernández et al., 1991; Gaitán et al., 2014; Jobbágy & Sala, 2000; Sala et al., 2012; Yahdjian & Sala, 2010). Other studies have evaluated the ecosystem response to reduced water inputs (Yahdjian & Sala, 2006), increased water inputs following previous years of water restriction (Yahdjian & Sala, 2006), or a single relatively large experimental rainfall event applied during the summer (Golluscio et al., 1998). These studies have been short-term (1 to 2 years) and have evaluated the immediate plant response to changes in water inputs. However, there are no studies that have evaluated the longer-term effects of both water and nitrogen additions, as well as the interaction of the addition of both resources.

In this research, we explore how soil N additions and water inputs and their interaction affect the structure of vegetation and aboveground primary productivity in a Patagonian steppe. We hypothesized that N and water addition increases ANPP and that this effect is higher with the co-addition of both resources, and higher in species with shallow root systems (grasses) than in higher in species with deeper root systems (shrubs). Furthermore, we hypothesized that at the temporal scale ANPP is positively correlated with precipitation, a relationship that is strengthened with increased nutrient availability. The last hypothesis proposes that nitrogen addition, alone or together with water addition, induces an increase in the abundance of nitrophilous grasses. We carried out a field experiment with water and nitrogen addition during 2013-2019. We also took advantage of the large interannual variability in precipitation observed between 2015 and 2019 to test the second hypothesis. In March 2017, a large part of the Patagonian steppe experienced an extreme rain event that added about 80% more water than the mean annual precipitation of the last four decades in the study area. This was a unique opportunity to assess the ecosystem response to an extreme precipitation event.

Materials and Methods

Study site and plant species

The study site is located at the Río Mayo Experimental Field Station of INTA (Instituto Nacional de Tecnología Agropecuaria) in South Central Patagonia (45°24'11"S 70°17'37"W, 500 m a.s.l.). The historical mean annual temperature (1982-2018) is 9.4degC, with a mean monthly temperature in January of 15degC and in July of 2degC. The historical mean annual precipitation (1982-2018) is 130 mm, with an annual range between 50 and 250 mm. Most precipitation occurs in the autumn and winter, while summer precipitation events are isolated and unpredictable. Most of the precipitation events are less than 5 mm (88% of the total), and 55% of them are less than 1 mm (Cavallaro et al., 2020). Soils are coarse textured (sandy), have a high gravel content and a calcareous layer at a depth of 45-150 cm. Soil nitrogen content is low, around 0.05% (Carbonell Silletta et al., 2022). Soil water content varies seasonally in the shallowest layers down to 1 m depth, increasing from about 5 to 20% between May and September, while remaining relatively constant and close to 10% throughout the year at higher depths (Pereyra et al., 2017).

The study site corresponds to a grass-shrub steppe in the southern end of the Western District of the Patagonian Province. The major land use in the region is sheep grazing (Golluscio et al., 1998). The Patagonian steppes are arid to semiarid ecosystems characterized by a low plant species diversity and a low plant density, with a vegetation cover of 30 to 40% (Pereyra et al., 2017). The vegetation is distributed in patches composed of shrubs and grasses on a bare soil matrix (Soriano et al., 1994). The dominant shrub species in the study area are *Azorella prolifera* (Cav.) G.M. Plunkett & A.N. Nicolas (ex *Mulinum spinosum*), *Adesmia volckmannii* Phil. and *Senecio filaginoides* DC. Dominant grass species, which are C3, include *Pappostipa speciosa* (Trin. & Rupr.) Romasch., *Pappostipa humilis* (Cav.) Romasch. and *Poa ligularis* Nees ex Steud (Table 1). The dominant life forms of the Patagonian steppe have root systems that collectively explore the entire soil profile down to at least 2 m depth (Bucci et al., 2011) (Table 1).

Experiment design

The experiment consists of 20 plots of 625 m² each in a 4 ha. enclosure, 5 plots per treatment: control (C), N addition (+N), water addition (+W) and addition of both nitrogen and water (+NW). The experiment started in 2013 and continues to the present. The delimitation of the plots was established semi-randomly, taking into account that those were homogeneous in terms of plant cover. Between each plot, at least 10 m buffer area was set to avoid interference among plots. The plots with water addition treatment are equipped with a semi-automatic system of sprinkler irrigation in which the amount of historical annual precipitation for the site is increased by approximately 25%, distributed in events of 5 mm each during the growing season. Freshwater extracted from a well located next to the closure was used to water addition treatment (see Fig. S1 for more details of experimental design). Water addition is canceled during the winter, which is the wettest period and to avoid also damage to the irrigation system by freezing water. Nitrogen is added twice a year by applying 100 kg/ha/yr in the form of urea and diammonium phosphate (160 kg and 154 kg, respectively). One of the additions is performed at the beginning of winter and the other at the end of winter, to favor the dissolution of the fertilizer in the soil during the wet season. The amount of N added per year was similar to that applied in manipulative experiments in other arid ecosystems (Bai et al., 2010; Ladwig et al., 2012; Reichmann et al., 2013). The addition of diammonium phosphate was performed to also add phosphorus in order to avoid any possible limitation of this nutrient that interferes with the effect of the addition of N (Luo et al., 2022).

Environmental variables

Temperature and precipitation data were obtained from a meteorological station located 2 km from the study site (<http://sipas.inta.gob.ar/>). The volumetric soil water content was continuously determined by sensors using the dielectric constant of the surrounding soil medium (ECH2O, Dielectric aquameter, Decagon Devices, Inc). In each plot, sensors were installed at 10, 40, 100 and 200 cm depth. The sensors were connected to CR1000 automatic data acquisition systems (Campbell Scientific Inc.) powered by batteries charged by a solar panel. Data were recorded every 30 min. Soil psychrometers (PST-55, Wescor, Logan, UT) were used to continuously monitor soil water potential at 40 cm depth, which was measured every 30 min and data were recorded with a datalogger (CR-7, Campbell Scientific Inc.).

Data for pH, total nitrogen, inorganic nitrogen, available phosphorus, and carbon content in the upper soil layer were obtained in November 2018. Three soil cores (5 cm diameter, 5 cm depth) were randomly taken from each plot and mixed well to obtain a composite sample (n = 5). The pH was determined in a 1:2.5 solution of distilled and deionized H₂O. Soil organic matter, total nitrogen and available phosphorus were analyzed by the Soil Laboratory (INTA Chubut, Argentina). Total nitrogen was determined by the Kjeldahl method (Bremner, 1996), inorganic nitrogen by the distillation method (Bremner & Keeney, 1965), phosphorus by the Olsen method (Olsen et al., 1954), and organic matter by the wet oxidation method (Walkley & Black, 1934). The C content of the organic matter was then determined using the factor proposed by Van Bemmelen, of 1,724, which assumes that 58% of the organic matter is composed of C (Tabatabai, 1996). The C/N ratio was also calculated by dividing the carbon content by the nitrogen content (Bremner, 1996).

Vegetation cover and leaf nitrogen content

Changes in vegetation cover between 2012 (before the start of the experiment) and 2019 (i.e., 6 years after the start of the experiment) were determined using the intercept point method (Mueller-Dombois & Ellenberg, 1974). For this, the plant interception was determined every one meter along the two diagonals of each plot. Subsequently, the percent cover of each species and bare soil in each plot was calculated annually by dividing the number of positive touches for each species or bare soil by the total number of touches. It should be noted that ephemeral herbaceous species, mainly present during October and November, were not taken into account in the vegetation cover analysis.

Leaves were collected in December 2017 for analyses of nitrogen concentrations. Fully expanded and healthy

leaves from different individuals of each species and in each plot were collected to obtain a composite sample per plot and species. Total leaf N content was measured using the Kjeldahl technique.

Tussock size and annual grass productivity

To determine tussock size of *P. ligularis* and *P. speciosa*, aboveground volume of the tussocks was calculated using the equation of Derner et al. (2012):

$$V = 1/3 \Pi h (r^2 + rR + R^2)$$

where V is the volume, h is the distance from the soil surface to the top of tussock (height), r is the radius of the basal area occupied by tussock, and R is the radius of the area at top of tussock. We used this equation because the circumference of tussocks increases from the base to the top. Since a high number of *P. humilis* tussocks was observed in the +N and +NW plots four years after the start of the experiment, this species was also included in this study. However, in C and +W plots we did not find an adequate number of *P. humilis* tussocks to consider sampling and further statistical analysis. Determinations were made on randomly selected tussocks in December 2019.

To determine the annual grass productivity, a 50 x 50 cm quadrat was randomly selected in each plot, taking into account that if the quadrat fell on a shrub individual, it was selected again to avoid shrubs in the samples. This is due to the difficulty of estimating annual shrub growth using this method, as there are few shrub individuals per unit area, which would overestimate the calculated ANPP. All aboveground plant biomass was cut at the soil level and transferred to the laboratory, where green biomass, dry biomass, and litter were separated. The plant biomass was then oven-dried at 70 °C for 72 h. Cacti and herbaceous dicotyledons were excluded from the analysis due to their low representativeness in the samples (<1%). Subsequently, biomass was weighted and ANPP was determined as the biomass of each type divided by the quadrat area in each year and expressed as g m⁻² yr⁻¹. Productivity was measured once a year during peak green grass biomass (December) from 2013 to 2019. We chose to harvest in this month because both temperature and soil moisture are favorable for growth, while later (summer) the temperature is higher, but soil water availability decreases and atmospheric water demand increases. Moreover, a study applying eddy covariance techniques in the same Patagonian steppe shows the peak of gross primary productivity and ecosystem net carbon exchange in December (Burek et al. 2023, under revision). Sala & Austin (2000) determined that the method for ANPP estimation that introduces the least error in grasslands with marked seasonality is that consisting of a single annual harvest.

Shrub size and annual shrub productivity

Three individuals of each of the most abundant shrub species at the site (*A. prolifera*, *A. volckmannii*, and *S. filaginoides*) were selected and targeted per plot in 2015. In December of each year from 2015 to 2019, the height and major and perpendicular diameter of each selected individual were measured. To determine the major and perpendicular diameter of each, photographs were taken of the top of the canopy including a scale, and the images were analyzed with the ImageJ program (Ferreira & Rasband, 2012). The biomass of each individual was estimated by applying allometric relationships estimated by Oñatibia et al. (2010) for the same species and in an area close to that of the present study. The equations used were the following:

$$b = 0.000003 \times dh^{3.9321} \text{ for } A. \text{ prolifera}$$

$$b = 0.0002 \times dh^{3.1402} \text{ for } A. \text{ volckmannii}$$

$$b = 0.0002 \times dh^{3.1876} \text{ for } S. \text{ filaginoides}$$

where b is the estimated aboveground biomass (g) and dh is the average diameter between the major and perpendicular plus plant height (cm). Annual growth was determined as the change in estimated biomass between consecutive years and expressed per area. ANPP was estimated as annual growth per area multiplied

by the percent cover of each species at the site. When dead individuals were observed among those marked, this was recorded and the number of dead plants per year was determined. In that case, new individuals were marked and measured. If plants considered dead sprouted in subsequent years, they were removed from the dead plant category.

MSAVI2 and NDVI

The MSAVI2 and NDVI were used as a proxy for ANPP at a larger spatial scale than the ANPP estimated at the plant or quadrat scale. Five field NDVI spectral reflectance sensors (SRS sensors, Decagon Inc, Pullman, WA, USA) were used to estimate NDVI. An upward-looking hemispherical sensor provided reference values of sky irradiance against which the canopy radiance values of the four downward-looking sensors (one sensor per treatment) were normalized. The SRS sensors were positioned above the plots at a height of approximately 9 m above the ground, covering an area of about 80.6 m². The downward-looking hemispherical sensors were installed facing the canopy at a 45° angle. A data logger (Em50, Decagon Inc, Pullman, WA, USA) recorded data from each sensor every 1 min and expressed as 30-min averages. We calculated NDVI as:

$$\text{NDVI} = (\rho_{\text{NIR}} - \rho_{\text{red}}) / (\rho_{\text{NIR}} + \rho_{\text{red}}) = (R_{\text{n}}/I_{\text{n}} - R_{\text{r}}/I_{\text{r}}) / (R_{\text{n}}/I_{\text{n}} + R_{\text{r}}/I_{\text{r}})$$

where ρ_{NIR} and ρ_{red} are the percent reflectance in the near infrared (NIR) and red respectively, R_{n} and R_{r} are the radiation reflected by the canopy in the NIR and red, and I_{n} and I_{r} are the incident radiation in the NIR and red, respectively. We assumed that the percent reflectance is the ratio of reflected radiation to incident radiation in the specified waveband.

We calculated daily averages, using values acquired only during the noon hour, to reduce data variability due to changes in sun-sensor-surface illumination geometry throughout the day. The data were recorded from July 2019 to July 2020. A technical problem with the downward-looking hemispherical sensor placed in the +N plot prevented obtaining the data for this treatment.

The Copernicus Sentinel-2 mission consists of two polar-orbiting satellites providing multi-spectral imagery with high resolution (10 m to 60 m) and revisiting time (5 days). Twenty-three Level 1C from July 2019 to June 2020 (image dates are given in Fig. S2) corresponding to tile T19GCK were obtained from the Copernicus Open Access Hub. Images were visually inspected to avoid cloud coverage over the study area. Level 1C products consists of atmospherically corrected TOA (top-of-atmosphere) reflectance images, projected in the UTM WGS84 system and Images converted to BOA (bottom-of-atmosphere).

For each image, the MSAVI version 2 index (MSAVI2) was estimated (Qi et al., 1994). This index is a better alternative to widely used NDVI for arid and semiarid environments as it reduces the effect of soil signal when vegetation cover is sparse.

$$\text{MSAVI2} = \frac{[2 \times \rho_{\text{b8}} + 1 - \sqrt{(2 \times \rho_{\text{b8}} + 1)^2 - 8 \times (\rho_{\text{b8}} - \rho_{\text{b4}})}]}{2}$$

where ρ_{b8} and ρ_{b4} are the at-the-ground reflectance of bands 8 and 4, respectively. Then, for each date, data for all pixels corresponding to field plots were extracted, including between 5 and 7 pixels for each plot (the central coordinates of each plot are shown in Table S1). All the image processing and data extraction for Sentinel-2 imagery was done in the SNAP software (ESA, European Union). The Sen2Cor plugin was used for the TOA to BOA correction, and the MSAVI2 processor for index estimation.

Statistical analysis

To evaluate the effect of the treatments on each soil variable (total nitrogen, inorganic nitrogen, available phosphorus, carbon content, C/N ratio and pH), ANOVAs using linear models (LM) were used. ANOVAs were also tested to assess the effect of the treatments on the percent cover of each species and leaf nitrogen content. To evaluate the effect of the interaction between treatments and years on the number of dead plants, a generalized linear model (GLM) with binomial distribution and test- χ^2 was tested. Differences in tussock size between treatments were evaluated with an ANOVA for each species. *P. humilis* was excluded from this analysis due to the lack of data in the C and +W. Generalized least squares models (GLSs) were

used to evaluate the effect of the interaction between treatments and years on the ANPP of each shrub species. In this model, a temporal correlation structure between years was used for each sample (corAR1). Then, the shrub ANPP, integrating the ANPP of the three species of shrubs, the grass ANPP and the total ANPP (shrubs + grasses) were evaluated with ANOVAs, using LMs, to test the effect of the treatments in the different years. Multiple regression analysis, using LMs, were performed to evaluate the effect of the treatments on the relationship between annual precipitation, or precipitation plus irrigation in the case of +W and +NW treatments, and ANPP (shrub ANPP, grass ANPP and total ANPP). Generalized additive models (GAMs) were used to adjust the vegetation indices (NDVI and MSAVI2) through year for each treatment. In addition, an ANOVA with LM test was used to test the effect of the treatments on daily NDVI.

All statistical analyses were performed with R software version 4.1.2 (R Development Core Team, 2023). The GLSs were carried out using the “gls” function of the R package “nlme” version 3.1-162 (Pinheiro et al., 2023; Pinheiro & Bates, 2000). GLMs were performed using the “glm” function of the R package “lme4” version 1.1-15 (Bates et al., 2015). GAMs were carried out using the “gam” function of the R package “mgcv” version 1.8-31 (Wood, 2004). When necessary, all models were adjusted using variance models. Model selection was based on the Akaike’s information criterion (corrected for small sample size, AICc) (Burnham & Anderson, 2002). Tukey’s post-hoc analysis were used for multiple comparisons of LMs and GLSs models when the F-test or χ^2 tests were significant, using the “glht” function of the R package “multcomp” version 1.4-8 (Hothorn et al., 2008). The multiple comparisons of GAMs models were performed with the “emmeans” function of the R package “emmeans” version 1.8.6 (Lenth, 2023). The “visreg” function of the R package “visreg” version 2.7.0 (Breheny & Burchett, 2017) and the “ggplot” function of the R package “ggplot2” version 3.3.5 (Wickham, 2016) were used to graphically represent the results.

Results

Environmental variables

Precipitation, air temperature, and soil water content data for 2015-2019, years for which we have data of both grass and shrub ANPP, are shown in Fig. 1. The mean daily air temperature for 2015-2019 was 9°C, and the maximum and minimum temperatures were about 25°C (December 2018) and -9°C (June 2017), respectively (Fig.1A). Annual precipitation for the period of 2015-2019 ranged from 92 to 233 mm, with 2019 being the driest and 2017 the wettest year. Between March 29 and April 02, 2017, an extreme precipitation event of 100 mm was recorded (Fig. 1A). Precipitation in 2013 and 2014, years for which information of grass productivity is available, was 152.5 and 99.5 mm, respectively. Soil volumetric water content showed a marked seasonal pattern in the top soil layer (10 cm), ranging from 5% in summer to 15-20% in winter and early spring (Fig. 1B). Water addition events were identifiable at that depth, with transient increases in soil water content. At 40 cm depth, soil water content had a similar pattern to that of the upper layer, but water addition events were not visible at that depth (Fig. 1C). The extreme precipitation event in autumn 2017 resulted in a higher increase in water content throughout the soil profile compared to other years, but there was a delay in such increase in deeper soil layers. At 100 and 200 cm soil depth, water content was relatively constant, between 6 and 9% in all treatments except in 2017 (Fig. 1D, 1E). A soil water retention curve indicated that soil water potential at 40 cm depth was near 0 MPa when moisture was higher than 12% and was higher than -1 MPa when moisture was between 9 and 12% (Fig. S3).

Inorganic N and available P content were higher in the +N and +NW treatments than in the control (Table 2). The addition of nitrogen alone increased the inorganic N content about three times more than the co-addition of nutrients and water ($p < 0.001$). Available P content increased about three times in +N and +NW treatments compared with the control ($p < 0.05$). Total N and C and N/C ratio were not significantly different between treatments (Table 2). Soil pH was lower in the +N and +NW treatments than in the control, decreasing from 7.15 in the control to 6.40 and 6.48 in those treatments, respectively (Table 2).

Vegetation cover, plant mortality and leaf nitrogen content

The vegetation cover before the start of the experiment was similar among plots ($p > 0.05$ for all species,

Table S2). After 6 years of starting the experiment, shrub cover did not change (Table 3), but it tended to be lower in the treatments with nitrogen addition compared to the control (Fig. 2A). The +N and +NW treatments increased the percentage of dead shrub ($p = 0.02$ and $p = 0.007$ with respect to the control, respectively), being higher in the year prior to the extreme rain event of 2017 compared to the following years ($p < 0.01$) (Table 3, Fig. 2B).

The grass cover after 6 years under resources addition (water and nitrogen) was similar among treatments, however, nitrogen addition modified grass species composition (Table 3, Fig. 3). The +N and +NW treatments resulted in a decrease in *P. ligularis* grass cover ($p < 0.0001$) and an increase in *P. humilis* grass cover ($p < 0.0001$), with no change in *P. speciosa* cover ($p > 0.05$), although this species also tended to decrease in the +N and +NW plots (Fig. S4). *P. ligularis* tussock size in the treatments with nitrogen addition was also significantly reduced compared to the control ($p = 0.03$) (Fig. S5, Table S3). The +W treatment had no effect on tussock size ($p > 0.05$) or grass cover ($p > 0.05$). The +NW treatment had no differential effect with respect to the effect of adding nitrogen alone ($p > 0.05$).

All studied species (shrubs and grasses) significantly increased the leaf nitrogen content in the nitrogen addition treatments (Table S4). *Adesmia volckmannii* and *P. ligularis* were the species with the highest and the lowest leaf nitrogen content, respectively, in the control plots. The higher change in leaf nitrogen content was observed in *P. ligularis* (1.08% in C and 2.41% in +N) and the lower change was found in *A. volckmannii* (2.36% in C and 2.81% in +N).

Shrub and grass ANPP

The ANPP of each shrub species varied differently among treatments and years. In the wet year (2017), ANPP of *A. proliфера* in the nitrogen addition plots doubled ANPP in the control plots ($p = 0.04$) (Fig. S6). Moreover, the ANPP of *A. proliфера* was higher in 2017 than in 2016 in the +N treatment ($p < 0.001$) and was higher in 2017 than in the others studied years in the +NW treatment ($p < 0.05$). The water addition treatment only affected *A. volckmannii* such that its ANPP increased in the +W plots ($p = 0.005$) and, in addition, this species increased ANPP during the wet year, being more than double in 2017 than in the rest of the years ($p < 0.01$) (Fig. S6). The ANPP of *S. filaginoides* decreased in +NW compared to C ($p = 0.001$) and was higher in 2017 than in 2019 in all treatments, with intermediate values in 2016 and 2018 ($p < 0.05$) (Fig. S6).

Total shrub ANPP in the +N, +W and +NW treatments were not significantly different compared to the control (Table 3, Fig. 4A). Shrub ANPP was about two folds higher in 2017 as a consequence of the anomalous precipitation in late March of that year than in the other study years, regardless of treatments ($p < 0.01$) (Table 3, Fig. 4A). Grass ANPP was not affected by the treatments until two years after the start of the experiment (Fig. 4B). From 2015 to 2019, grass ANPP was higher in +N and +NW than in C ($p < 0.02$) (Table 3, Fig. 4B). There was no difference between grass ANPP in +W and C ($p > 0.5$). When comparing within-treatment grass ANPP across years, we found no interannual differences in the control (Fig 4B). However, grass ANPP in nitrogen addition plots was higher in 2017 and 2018 than in 2014 ($p < 0.02$) and ANPP in +NW treatment was higher in 2017 than in 2014 ($p = 0.03$) (Fig. 4B). Community-level ANPP (shrubs + grasses) increased significantly in the treatments with nitrogen addition ($p < 0.001$) compared to the control (Table 3, Fig. 4C). The total ANPP was higher in the wet year (2017) than in 2016 ($p = 0.001$) and 2019 ($p < 0.001$) (Fig. 4C).

MSAVI2 and NDVI

The MSAVI2 vegetation index obtained from Sentinel 2 images showed values between 0.023 and 0.096 (Fig. 5). The maximum values were found in November and the minimum in May. The GAM fitted to the data had a significant treatment effect (Table 4). During the analyzed period, MSAVI2 in +W was not different from C except during summer when it was higher than in C (Fig. 5A). MSAVI2 in +N and +NW was higher than in C throughout the year (Fig. 5A).

The ground based daily NDVI values recorded from July 2019 to July 2020 ranged from 0.05 to 0.32, showing

the maximum value in November and the minimum value in June (Fig. 6A). The results of the GAM fitting throughout the period (Table 4, Fig. 6A), as well as the results of the ANOVA tested with all daily values (Table 3, Fig. 6B), indicated significant effects of the treatments on NDVI. The treatments significantly increased NDVI compared to the control ($p < 0.0001$), the effect being higher in +NW ($p < 0.0001$). It should be noted that the maximum difference in NDVI between +W and C occurred in spring while it was much lower in autumn and winter (Fig. 6A).

Relationships between ANPP and precipitation (ambient + experimental)

The interannual variability in water inputs ranged from 92 to 233 mm in the plots without experimental water addition and from 122 to 263 in plots with water addition. A positive relationship with the same adjusted slope (0.21) was found between annual water input and shrub ANPP in all treatments (Fig. 7A). The intercept of the ANPP-water input relationship was lower in +NW than in C ($p = 0.004$), while in +N and +W there was no difference compared to C ($p > 0.05$) (Fig. 7A). Grass ANPP also was positively and linearly correlated to water input (Fig. 7B), although the nitrogen addition (i.e., +N and +NW treatments) had a higher positive effect ($p < 0.004$) (Fig. 7B). The +W treatment did not affect the response of grass ANPP to water input compared to C ($p > 0.5$) (Fig. 7B). The relationship between total ANPP and water input was significantly modified by the treatments. The +N and +NW treatments enhanced the intercept of the function fitted to the ANPP-water input relationship ($p < 0.001$), while the +W treatment decreased it ($p = 0.03$) (Fig. 7C).

Discussion

Seven-years monitoring of a large-scale field nitrogen and water addition experiment in a Patagonian steppe showed that plant productivity, cover and mortality responded differentially to soil nitrogen addition and water addition. This response also differed between and within functional groups (grasses and shrubs). Although water availability is considered the most important environmental factor limiting productivity in drought-prone ecosystems, our results indicate that addition of 25% more water than historical annual precipitation resulted in a total ANPP similar to the ANPP in the control plots, while the nitrogen addition had a positive effect on ANPP.

The total ANPP in control plots reported in our study was similar to that estimated for other semiarid steppes (e.g., Bai et al., 2010; Gao et al., 2011). The range of ANPP values obtained in our study in the control plots (41-98 g m⁻² yr⁻¹) is consistent with that reported by Jobbagy & Sala (2000) for a similar Patagonian steppe (21-75 g m⁻²yr⁻¹). We determined the ANPP in early December, while that in previous studies developed in the Patagonian steppes (e.g., Gherardi & Sala, 2015; Jobbagy & Sala, 2000; Yahdjian & Sala, 2006), ANPP has been estimated in January. Despite the similar range of ANPP between our study and the others, we consider late November or early December as the most accurate measurement period to estimate ANPP since the maximum NDVI and MSAVI2 were observed in this period. Therefore, measurements done in January instead at the end of November or early December could result in relatively low ANPP estimates in the Patagonian steppe.

Response of plant species to water and nitrogen addition: plant cover and mortality

The large increase in the abundance of *P. humilis* observed after 7 years of soil nitrogen addition supported our hypothesis that N enrichment favors the growth of nitrophilous species. On the other hand, nitrogen addition had a significant negative effect on *P. ligularis* by almost completely reducing its presence in those plots, while persistent tussocks were smaller. A plausible explanation for these results may be that *P. humilis* is a better competitor on nitrogen-rich soils than *P. ligularis* and *P. speciosa* which perform better in poor soils. *Pappostipa humilis* has been positively associated with the shrub *A. volckmannii*, a N-fixing species (Armas et al., 2008). The leaves of this shrub species had a higher leaf N content than the other shrub

species in our study, and therefore a higher amount of N in the soil next to plants of this species is consistent with the hypothesis that high soil N levels favor the establishment of *P. humilis*.

On the other hand, the response of *P. ligularis* and *P. speciosa* could be a consequence of the combination of acidification and ammonium toxicity. In a previous study at the same site, Carbonell Silletta et al. (2022) found a lower soil pH and a large increase in the $\text{NH}_4\text{-N}/\text{NO}_3\text{-N}$ ratio in the +N plots compared to the C and +W plots. Several studies have shown that these soil changes are detrimental to plant germination, growth and survival and have been proposed as some of the potential mechanisms explaining biodiversity loss in response to N enrichment (Bai et al., 2010; Liu et al., 2019; Y. Zhang et al., 2014). Some responses of grasses found in our study contradict those found by Campana et al. (2022). These authors observed that *P. ligularis* responded positively to nitrogen addition increasing its biomass, while *P. humilis* was not affected and showed a tendency to decrease aboveground biomass. The discrepancy between these two studies could be due to the different amount and frequency of N addition.

We hypothesized that grasses are more sensitive to water addition than shrubs due to differences in root distribution (Bucci et al., 2011). However, the +W treatment did not affect any of the grass species studied here. *Poa ligularis* has been previously mentioned as a more plastic species than *P. speciosa*, increasing its biomass under optimal water conditions (Couso & Fernandez, 2012). On the other hand, Golluscio et al. (1998) observed short-term physiological responses to summer water addition in *P. speciosa*. In our study, the only species that responded to water treatment was the shrub *A. volckmannii* which substantially increased its productivity. Our results indicate a low plasticity of Patagonian steppe species to water addition. Although in a recent study in the same area Cavallaro et al. (2023) observed that these species are relatively plastic to water addition, the magnitude of plasticity was higher in functional traits than in morphological traits. Increased leaf carbon assimilation under the +W treatment observed by Cavallaro et al. (2023) was not reflected in higher productivity in the present study. Photoassimilates were probably allocated to roots or other functions (e.g., anti-herbivory defenses) rather than to increase ANPP.

Soil nitrogen addition also caused mortality of some shrub individuals, mainly *S. filaginoides*, which resulted in a lower ANPP for this species. Soil N addition in excess of plant nutritional N demand could trigger a nitrogen saturation response (Wallace et al., 2007). Therefore, the advantage of N addition on plant productivity may decrease with continuous N enrichment (Tian et al., 2016). This response is species-specific and, therefore, species differences to N saturation could explain the similar total shrub ANPP found in this study, despite increased mortality in some species. Across global grasslands, the mean ANPP saturation threshold has been estimated at $150 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Peng et al., 2020), higher than that applied in the present study.

Plant functional groups and plant community ANPP responses to experimental water and nitrogen addition

Several studies indicate that arid ecosystems are more restricted by water than nutrients or are co-limited by both (Guo et al., 2022; Hall et al., 2011; Lu et al., 2014; Robertson et al., 2009). However, our results contradict this idea, at least for grasses, due to the lack of response of ANPP to water addition. This response was also found by Swindon et al. (2019) in another semiarid steppe. However, in that study, ANPP increased when water addition was combined with nitrogen addition. We observed non co-limitation between these resources, as grass ANPP increased in similar magnitude under +N and +NW. A similar water content in the shallow soil layers over the years, regardless of water inputs (natural or experimental), could explain the lack of response of grasses in our study. According to soil water release curves, the shallow soil layers, where grasses have most of their roots (Bucci et al., 2011), had water potentials close to 0 MP during a large part of the growing season of all study years. We suggest that grasses in this steppe are not limited by water until December, which is the peak of the growing season.

The increase in grass ANPP in response to nitrogen addition has also been observed in other studies (Gherardi & Sala, 2015; Henry & Aherne, 2014; Kowaljow et al., 2010; Tang et al., 2017; Yahdjian et al., 2014). Decreases in abundance and tussock size of *P. ligularis* and *P. speciosa* were offset by changes in *P. humilis* abundance, such that grass ANPP was higher in the +N and +NW plots relative to the other treat-

ments. Although grass ANPP increased significantly with nitrogen addition, this response can be interpreted as a negative effect for this grassland where livestock grazing is the main land use (Adler et al., 2004) and a highly palatable species as *Poa ligularis* is replaced by a species of low forage value (*P. humilis*) (Cenzano et al., 2013; Onatibia & Aguiar, 2016).

The lack of response of shrubs to the +W treatment is probably due to the amount of water applied in each irrigation pulse. Apparently, it was not enough to increase soil moisture below the 10 cm layer where the shrubs explore most of the soil profile. Shrub ANPP only increased significantly during the wet year, regardless of the treatments. These findings suggest that shrubs, more than grasses, may be restricted by soil water availability and only respond to higher precipitation when it causes an increase in water content in deeper soil layers. Although in this study site less than 10% of the roots are below 1 m depth, they contribute about 35% of the total water use (Pereyra et al., 2017). Therefore, the higher shrub ANPP during the wet year could be correlated with soil water recharge, root distribution, and hydraulic efficiency of deeper shrub roots. Consistent with our findings, Burek et al. (2023, under revision) found at the same study site, using the eddy covariance method, a higher net carbon exchange in 2017 ($283.9 \text{ g C m}^{-2} \text{ yr}^{-1}$) than in 2015 ($218.6 \text{ g C m}^{-2} \text{ yr}^{-1}$), which was related to higher soil water content throughout the soil profile (0-2 m depth).

Unlike grasses, shrub ANPP was insensitive to nitrogen addition. These results are in agreement with studies in similar steppes (Fernandez et al., 2018; Reichmann et al., 2013; Yahdjian et al., 2014). Although ANPP did not change under the +N treatment, shrubs increased N uptake under nitrogen addition resulting in a large increase in leaf N content. These leaf changes did not scale up to alter the biomass production of woody species because nitrogen use efficiency substantially decreased in all nitrogen addition treatments. Similar results were reported by Lu et al. (2014) in temperate semiarid steppes of China. The results of community-level ANPP determinations using destructive methods and allometric relationships were consistent with the findings obtained using field spectral reflectance sensors placed at 9 m height and satellite imagery. Both approaches indicated that soil nitrogen enrichment had a positive effect on aboveground plant productivity. The higher NDVI in the +W plots relative to the C plots could be explained by the presence of forbs and some minor species which were not sampled for ANPP determination using destructive methods and allometric relationships.

Relationship between aboveground productivity and annual water inputs (ambient precipitation and experimental water addition)

Arid and semiarid ecosystems are considered highly sensitive to precipitation changes (Haverd et al., 2016; Huxman et al., 2004; Maestre et al., 2012). Several studies show a linear relationship between interannual ANPP and precipitation (Sala et al., 2012; Wang et al., 2014). Recently, however, Knapp et al. (2017) proposed that with the inclusion of precipitation extremes, the common linear relationship may change to a nonlinear one, reflected in “concave up” or “concave down” ANPP-precipitation relationships. Consistent with the linear model, we found symmetric relationships with ANPP of each functional group and total ANPP under all treatments, even when our data set included an anomalous year. In previous studies in a similar Patagonian steppe (Fernandez et al., 1991; Jobbagy & Sala, 2000), at least grass ANPP was not associated with precipitation.

The sensitivity of grass ANPP to annual water inputs was higher in the +N and +NW treatments than in the C and the +W treatment. Therefore, our results suggest that increasing N availability can enhance ANPP response to increased precipitation, as shown by other studies (Ma et al., 2020; Meng et al., 2022; Zhang et al., 2021). When water availability is not a limiting factor for plant growth, as was observed for grasses in our study, plants often exhibit increased biomass production in response to improved soil N availability. Differences in the slopes of the ANPP-water input relationships suggest that grasses in the control plots were generally less sensitive to annual precipitation than shrubs. It provides evidence that soil water redistribution during wet years benefits deep-rooted species more than grasses, as grasses are less water-limited because shallow soil layers are recharged during the fall and winter seasons.

At the community level, although N enrichment increased productivity, it did not improve the sensitivity of

ANPP to precipitation, probably due to the combined effects of precipitation and nitrogen addition on shrubs and grasses, highlighting the importance of community structure. The lower intercept value of the function fitted to the +W treatment compared to the control suggests higher nutrient limitation by increasing plant N demand or N losses (Mudge et al., 2017; Ren et al., 2017). However, in previous works in the Patagonian steppe, Carbonell Silletta et al. (2022) found no change in soil nutrient availability with water addition and Cavallaro et al. (2023) found increased rates of transpiration and photosynthesis in +W plots. This suggests that by increasing water input without nitrogen addition, more photosynthates are allocated to other functions rather than aboveground growth.

Conclusions

Our results show that nitrogen addition rather than water addition improves community ANPP, mainly due to the effects on the grasses and to the shift in the dominance of *P. ligularis* to *P. humilis*. Our study revealed that the relationship between ANPP and annual precipitation can be described by linear models across dry and wet years. Grasses and shrubs responded differently to increased precipitation, with shrubs being more sensitive than grasses to wet years. However, under increased nutrient availability, the response of grass ANPP to annual water input was amplified (i.e., steeper slope of the ANPP-water input relationship), whereas shrubs showed no change in ANPP with nitrogen addition. Therefore, the higher sensitivity of shrub ANPP to increased precipitation compared to that of grasses suggests that under climate change scenarios with increased precipitation, shrubs could dominate the community, whereas if this change occurs with high N deposition, an encroachment of grasses by a single species may take place in the long term.

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Table 1. Family, life form, leaf phenology, plant height and maximum rooting depth for species of Patagonian steppe included in this study

Species	Family	Life form	Leaf phenology	Plant height (cm)	Maximum rooting depth (cm)
<i>Azorella proliferata</i>	Apiaceae	Shrub	Deciduous	40.8 ±1.8	<100
<i>Adesmia volckmannii</i>	Fabaceae	Shrub	Deciduous	76.2 ±4.5	<200

<i>Pappostipa humilis</i>	Poaceae	Grass	Evergreen	33.2 ±1.6	<50
<i>Pappostipa speciosa</i>	Poaceae	Grass	Evergreen	33.2 ±1.6	<50
<i>Poa ligularis</i>	Poaceae	Grass	Evergreen	29.7 ±1.5	<50
<i>Senecio filaginoides</i>	Asteraceae	Shrub	Evergreen	36.1 ±1.4	<100

+ Values of plant height are means ± standard error (n = 15).

Table 2. Total nitrogen (%), inorganic nitrogen (ppm), C content (%), C/N ratio, available phosphorus (ppm) and pH in soil upper layer (up 5 cm depth) for control (C), nutrient addition (+N), water addition (+W) and co-addition of nutrient and water (+NW) treatments. Each value represents the mean and CI (n =3). Different letters following the values indicate significant differences between treatments

	Treatment	Treatment	Treatment	Treatment	Results of ANOVA
	C	+N	+W	+NW	
Total N	0.041 (0.008)	0.044 (0.013)	0.041 (0.014)	0.050 (0.014)	df=3, F = 0.56, p=0.65
Inorganic N	0.64 (0.33) a	11.28 (3.43) c	0.48 (0.26) a	3.91 (1.44) b	df=3, F =19.4, p=0.0005
C	0.392 (0.08)	0.477 (0.137)	0.427 (0.137)	0.489 (0.137)	df=3, F=0.80, p=0.52
C/N ratio	10.62 (3.33)	10.06 (5.42)	13.13 (5.43)	9.62 (5.42)	df=3, F=0.39, p=0.76
Available P	14.78 (4.21) a	54.74 (15.25) b	15.63 (4.44) a	59.37 (16.52) b	df=3, F=16.6, p<0.0001
pH	7.15 (0.20) a	6.40 (0.20) b	7.10 (0.20) a	6.48 (0.20) b	df=3, F=20.2, p=0.0004

Table 3. Results of ANOVAs (df, F-value and p -value) on the effects of Treatment and/or Year on shrub and grass cover, ANPP of shrubs, grasses and total (shrubs + grasses), and NDVI (daily values). Results of a GLM (df, χ^2 and p) on the effects of Treatment and Year on dead shrub individuals.

	d.f.	F-value or χ^2	p-value		d.f.	F-value	p-value
Shrub cover				Shrub ANPP			
Treatment	3	2.6	0.09	Treatment	3	3.96	0.01
Dead shrub individuals				Year	3	6.75	0.0004
Treatment	3	22.5	<0.0001	Treatment * Year	9	0.8	0.62
Year	3	32.74	<0.0001	Grass ANPP			
Treatment * Year	9	14.27	0.11	Treatment	3	22.44	<0.0001
Grass cover				Year	6	3.40	0.004
Treatment	3	2.43	0.10	Treatment * Year	18	3.44	<0.0001
<i>P. humilis</i> cover				Total ANPP			
Treatment	3	42.71	<0.0001	Treatment	3	20.81	<0.0001
<i>P. speciosa</i> cover				Year	3	8.15	0.0001
Treatment	3	3.29	0.048	Treatment * Year	9	0.62	0.78
<i>P. ligularis</i> cover				NDVI			
Treatment	3	24.58	<0.0001	Treatment	2	549.05	<0.0001

Table 4. Results of GAMs on the effects of Treatment and time on MSAVI2 and NDVI for the period July 2019 to July 2020

	MSAVI2	MSAVI2	NDVI	NDVI
Parameter				
Family	Gaussian	Gaussian	Gaussian	Gaussian
Link function	Identity	Identity	Identity	Identity

	MSAVI2	MSAVI2	NDVI	NDVI
Adjusted R ²	0.52	0.52	0.973	0.973
Deviance explained (%)	53.1	53.1	97.4	97.4
	d.f.	p-value	d.f.	p-value
Covariates				
Treatment	-2.7	<0.0001	-8.07	<0.0001
s(time) * Treatment	-27.6	0.001	-17.82	<0.0001

Table 5. Results of multiple linear regressions (df, F-value and p -value) on the effects of Treatment and Precipitation (or Precipitation + Irrigation in +W and +NW treatments) on ANPP of shrubs, grasses and total (shrubs + grasses)

	d.f.	F-value	p -value
Shrub ANPP			
Treatment	3	17.86	0.0001
Precipitation	1	266.88	<0.0001
Treatment * Precipitation	3	0.006	0.99
Grass ANPP			
Treatment	3	68.97	<0.0001
Precipitation	1	27.02	0.0001
Treatment * Precipitation	3	4.24	0.025
Total ANPP			
Treatment	3	234.75	<0.0001
Precipitation	1	106.07	<0.0001
Treatment * Precipitation	3	0	1

Legends of figures

Figure 1. (A) Daily precipitation (mm) and air temperature (°C) from 2015 to 2020. Soil volumetric water content at (B) 10 cm depth, (C) 40 cm depth, (D) 100 cm depth and (E) 200 cm depth for control (C), nutrient addition (+N), water addition (+W) and co-addition of nutrient and water (+NW) treatments, from 2015 to 2019. Values within panel A indicate the annual precipitation.

Figure 2. (A) Percentage of shrub coverage in 2019 and (B) Percentage of dead shrub individuals from 2016 to 2019, for control (C), nutrient addition (+N), water addition (+W) and co-addition of nutrient and water (+NW) treatments. Bars represent mean \pm CI (n=5). Different lowercase letters indicate significant differences between treatments for each year. Different uppercase letters indicate significant differences between years. ns = not significant

Figure 3. (A) Percentage of total grass coverage and by species: (B) *P. humilis*, (C) *P. speciosa* and (D) *P. ligularis*, for control (C), nutrient addition (+N), water addition (+W) and co-addition of nutrient and water (+NW) treatments. Bars represent mean \pm CI (n=5). Different letters indicate significant differences between treatments. ns = not significant

Figure 4. ANPP ($\text{g m}^{-2} \text{y}^{-1}$) of (A) shrubs, (B) grasses and (C) shrubs + grasses, for control (C), nutrient addition (+N), water addition (+W) and co-addition of nutrient and water (+NW) treatments. Bars represent mean \pm CI (n= 5). Different lowercase letters indicate significant differences between treatments for each year. Different uppercase letters indicate significant differences between years

Figure 5. (A) MSAVI2 vegetation index obtained from Sentinel-2 images for control (C), nutrient addition (+N), water addition (+W) and co-addition of nutrient and water (+NW) treatments from July 2019 to

July 2020. Each point corresponds to the index of a pixel within each plot. The lines correspond to the GAM fitting and the ribbons to the 95% confidence limits. Different letters indicate significant differences between treatments. (B) MSAVI2 indices for four dates, each representative of a season (in order: winter, spring, summer, and fall). Squares represent plots, and each 10x10m pixel is colored according to MSAVI2 value

Figure 6. (A) Daily NDVI for control (C), water addition (+W) and co-addition of nutrient and water (+NW) treatments from July 2019 to July 2020. The lines correspond to the GAM fitting and the ribbons to the 95% confidence limits. (B) Boxplots of NDVI for each treatment. Different letters indicate significant differences between treatments. Note: data corresponding to +N treatment are missing due to technical problems with the downward-looking hemispherical sensor

Figure 7. ANPP ($\text{g m}^{-2} \text{ y}^{-1}$) in relation to water input (ambient + experimental precipitation, mm) for (A) shrubs, (B) grasses and (C) shrubs + grasses, for control (C), nutrient addition (+N), water addition (+W) and co-addition of nutrient and water (+NW) treatments. The points and error bars are the mean and CI of the statistical analysis shown in figure 5. Different lowercase letters indicate significant differences between treatments









