











RESEARCH ARTICLE

Forage provision is more affected by droughts in arid and semi-arid than in mesic rangelands

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Handling Editor: Nathalie Butt**Abstract**

1. Droughts are projected to increase in magnitude, frequency and duration in the near future. In rangelands, the provision of valuable ecosystem services such as forage supply for livestock productivity is intimately linked to rainfall patterns, which makes it particularly vulnerable to droughts. Nonetheless, rangelands can differ in their sensitivity to droughts as shown by strong differences in the impacts of inter-annual precipitation changes on vegetation productivity in different sites. The aim of this study was to assess the sensitivity to droughts of nine rangelands located across a broad aridity gradient in Argentina, South America.
2. We experimentally imposed comparable droughts under field conditions by reducing a fixed proportion of each incoming precipitation event within-year during three consecutive years and tracked changes in total aboveground and forage productivity.
3. We found that arid and semi-arid rangelands were more severely impaired in their forage provision by drought than mesic rangelands, that is that sensitivity to drought declined as aridity decreased. Forage productivity decreased on average by c. 50%, in arid and semi-arid rangelands, whereas mesic sites did not exhibit significant changes between drought and control treatments. The negative impact in forage productivity of arid and semi-arid rangelands was mainly driven by the productivity reduction of few key plant species at each site. In seven of the nine rangelands, we found detrimental effects of drought on forage productivity during the first experimental-drought year, and in five of them the impact was further accentuated until the end of the experiment, which indicates how serious can these events be.

4. *Synthesis and applications.* Our main findings indicate that the drought-induced impacts on forage provision are higher as aridity increases. This pattern highlights the urgent need to implement strategies to mitigate the detrimental consequences of drought, particularly in arid and semiarid rangelands, where forage provision is strongly associated with human well-being. Management approaches focused on key forage species, such as reducing the grazing pressure during drought periods according to these species' productivity dynamics can attenuate impacts on vulnerable ecosystems, preserving the rangelands' integrity while maintaining high long-term productivity levels.

KEYWORDS

Argentina rangelands, aridity, climate change, drought, ecosystem services, experimental rainfall manipulation, sensitivity to drought

1 | INTRODUCTION

Climate change forecasts project alterations in precipitation regimes, which will have an impact on most terrestrial ecosystems (IPCC, 2019). Droughts are increasing in magnitude, frequency and duration mainly in arid and semi-arid ecosystems (Griffin-Nolan et al., 2019), which may exacerbate their aridity (Dai, 2011). These events alter natural ecosystems by affecting community composition and the functioning of terrestrial ecosystems, therefore producing ecological effects that exceed their normal range of temporal variation (Du et al., 2018). Drought effects differ among contrasting ecosystems (Knapp et al., 2015), but meaningful comparisons have been difficult because of site baseline differences in the intensity and duration of drought events. Few field studies assessed the response of ecosystem function and plant species composition to droughts covering broad spatial and temporal scales across diverse ecosystems, and even fewer comparative field studies including sites with contrasting forage productivity (FP) and plant composition (Griffin-Nolan et al., 2019). Particularly, there is a lack of a full understanding of how droughts are impacting and will further impact rangelands and their forage provision across environmental gradients.

Rangeland ecosystems encompass 40% of the land surface, represent a third of the net global primary productivity and host a third of the human population (Estell et al., 2012). Also, rangelands sustain 50% of global livestock productivity, an essential activity in many countries (Sala et al., 2017). Rangelands span biomes from semi-deserts to open forests, including grass-shrub steppes and grasslands (Matos et al., 2020), comprising systems vulnerable to global change drivers such as climate and land-use change (Díaz et al., 2019). The FP supplied by rangelands that is needed to feed livestock is strongly controlled by annual precipitation (Weltzin et al., 2003), and thus, is frequently affected by extended drought periods (Derner et al., 2018). Rangelands may be substantially impaired under predicted droughts (Gaitán et al., 2018), which thus represent a high risk to the sustainability of livestock rearing worldwide (Yahdjian & Sala, 2008). Since human well-being in rangelands strongly depends

on forage supply for domestic herbivores (Oñatibia et al., 2020), it is crucial to estimate the impact of droughts on FP.

Sensitivity is defined as the impact in certain functional attributes of a system, such as primary productivity, in the face of changes in a driver, for example drought (Smith et al., 2017). Rangelands differ in their sensitivity to drought, which is related to the aridity level and the identity and traits of dominant species (Knapp et al., 2015; Munson et al., 2018). Across rainfall gradients, plant species differ in traits involved in the trade-off between resistance to water stress and competitive ability by fast growth (Graff & Aguiar, 2017). The plant species avoided by grazers show more conservative strategies towards the scarcity of water. Specifically, arid rangelands mostly possess stress-tolerant plant life-forms usually not suitable as livestock fodder (non-palatable; Coughenour, 1985); in contrast, preferred forage species are generally less tolerant to drought (Milchunas et al., 1995; Volaire, 2018). Likewise, arid regions tend to have low FP (Blanco et al., 2019) and in some cases may be more sensitive to decreased precipitation than mesic ecosystems (Stuart-Haëntjens et al., 2018). Besides, the duration of a drought can condition the later response of the plant community (Hoover et al., 2021), including the forage plant species (Staniak & Kocoń, 2015). Long droughts, surpassing a growing season, might induce a noticeable reduction in arid rangelands' productivity (Reynolds et al., 2004; Winkler et al., 2019). Thus, forage species chronically face water deficit and, after long drought periods, leaf and tiller mortality (even whole-plant mortality) would prevent species to recover and overcome droughts (Voltaire, 2018). Conversely, less variability is expected in FP in the face of drought for mesic regions since other factors such as nutrients or light availability are the main constraints for plant growth (Seabloom et al., 2020).

In sum, it is still unclear to what degree droughts affect forage provision in mesic rangelands. On the one hand, stress-intolerant species dominate those plant communities (Jung et al., 2020). On the other hand, mesic rangelands have a large forage biomass stock and high plant cover, which can buffer and compensate drought effects (Finch et al., 2016). Therefore, they might exhibit low sensitivity to drought

events. Then, a comparative assessment of how droughts impact FP among arid, semi-arid and mesic ecosystems is sorely needed.

Rangelands located in the Southern extreme of South America account for over two thirds of Argentina's continental area (Anderson et al., 2011), and span environmental gradients from arid to mesic climates, with a precipitation range from 150 to 1500 mm year⁻¹ (Yahdjian & Sala, 2008). They sustain one of the most important economic activities of the region, the rearing of cattle and sheep (Kröpfl et al., 2013; Modernel et al., 2019), and will likely be unevenly affected by forecasted droughts (Minetti et al., 2010). Forage provision in the arid and semi-arid rangeland regions of Argentina is determined by a few native palatable species that result from a long evolutionary history of grazing, with grass steppes in Patagonia likely having been grazed by wild herbivores for a longer period than highly productive grasslands in mesic regions (Lauenroth, 1998). However, few studies have focused on regional responses (Petrie et al., 2018), and relatively few have assessed drought effects on forage supply across wide spatial gradients (Golodets et al., 2015). Indeed, the sensitivity to water stress of forage species, determined by their forage aptitude using local knowledge, has not been assessed through the approach of field coordinated distributed manipulative experiments (Fraser et al., 2013).

The aim of this study was to compare the effects of manipulatively induced drought on FP to evaluate the drought sensitivity of rangelands located along a wide aridity gradient, from arid to mesic regions. We predict that (a) water availability, the main limiting factor of aboveground net primary productivity (ANPP), also controls FP;

(b) the proportion of total ANPP that corresponds to FP increases from arid to mesic rangelands, since forage species are less tolerant to water limitation; thus, arid rangelands will have a lower proportion of forage biomass and based on a fewer species than mesic rangelands, (c) arid rangelands will exhibit greater FP sensitivity to droughts than mesic ones and (d) we expect to find a persistent negative trend of decrease in FP along successive drought years, particularly in arid and semi-arid rangelands. Specifically, we (a) described the spatial variation of the FP and the proportion of FP to ANPP across a natural aridity gradient in Argentina, (b) assessed the drought sensitivity of FP across the gradient and (c) evaluated the temporal dynamics of drought effects on the FP along three consecutive drought experimental years.

2 | MATERIALS AND METHODS

2.1 | Aridity gradient

In order to evaluate the effect of drought on FP, we conducted a coordinated drought experiment (with the appropriate permits and licences for fieldwork) in nine rangelands scattered across a natural aridity gradient (Figure 1), with mean annual precipitation (MAP) ranging from 170 to 950 mm year⁻¹ and from 5 to 21°C mean annual temperature (Table 1). Our study did not require for ethical approval. We studied natural rangelands, typically subjected to extensive livestock grazing, including grass steppes, grass-shrub steppes,

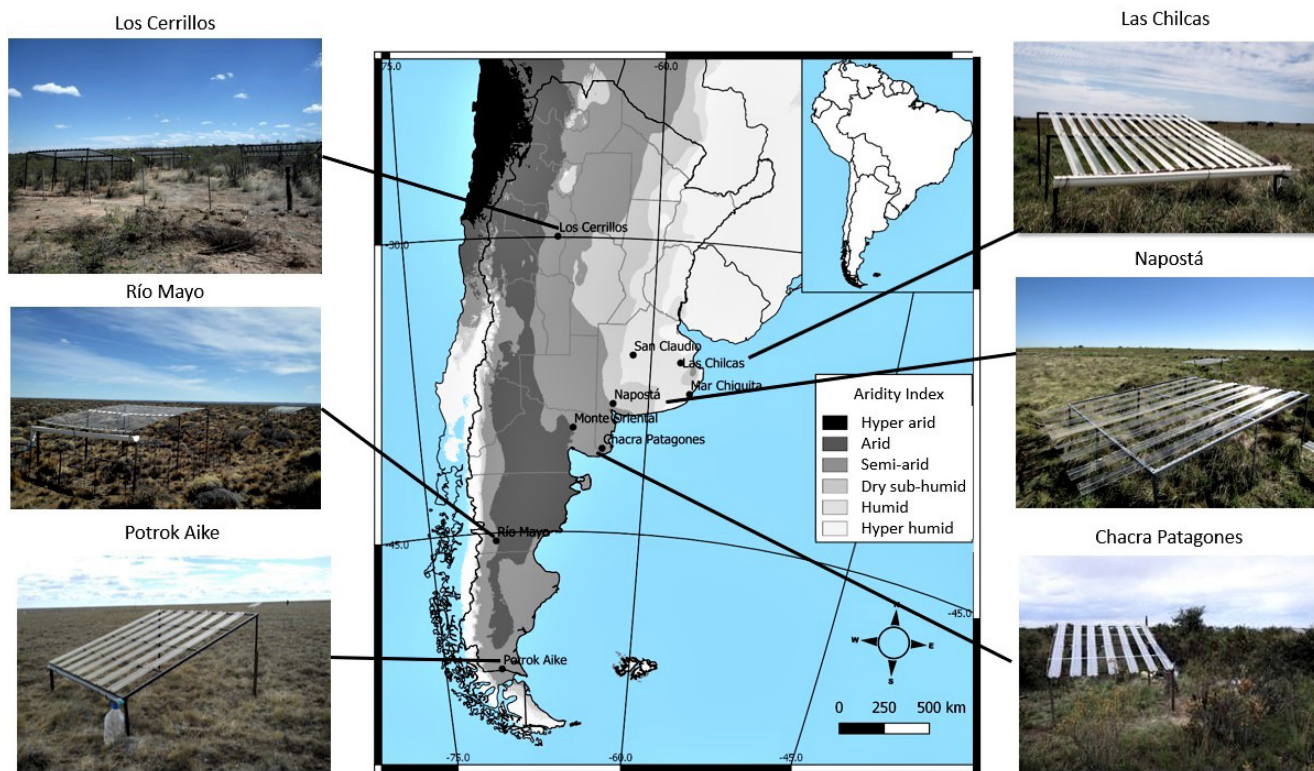


FIGURE 1 Rangeland sites spanning across the natural aridity gradient in Argentina, South America. The photos show the experimental drought simulations with the rain-out shelters in six representative rangeland sites (for further description, see Section 2).

TABLE 1 Climatic characterization of the nine sites located along an aridity gradient in Argentina. Mean annual precipitation (MAP; mm year^{-1}), mean annual temperature (MAT; $^{\circ}\text{C}$), potential evapotranspiration (PET; mm year^{-1}), the aridity index (AI; MAP/PET) and the aridity category sensu Le Houérou (1996). The long-term series for MAP and MAT considered time ranges from 1980 to the present; PET data were provided by WorldClim database from 1970 to the present

Site ID	Latitude; longitude	MAP (mm)	MAT ($^{\circ}\text{C}$)	PET (mm year^{-1})	AI (MAP/PET)	Aridity category
Río Mayo	-45.3977; -70.3059	170	9.5	1,544	0.11	Arid
Los Cerrillos	-29.9503; -65.8735	390	21	2,103	0.18	Semi-arid
Potrok Aike	-51.9160; -70.4074	202.5	5	969	0.20	Arid/semi-arid
Monte Oriental	-39.6829; -64.8543	383	14.1	1,935	0.20	Arid/semi-arid
Chacra Patagones	-40.7231; -62.8989	400	14.4	1,849	0.21	Semi-arid
Campo Experimental Napostá, convenio UNS y MDA-PBA	-38.4239; -62.2879	553	15	1,707	0.32	Semi-arid
Mar Chiquita	-37.7151; -57.4245	927	15.5	1,399	0.66	Mesic
Las Chilcas	-36.1632; -58.1556	950.5	15	1,319	0.72	Mesic
San Claudio	-35.9154; -61.1484	950	14.5	1,268	0.75	Mesic

and highly productive grasslands that encompass a large range in plant species diversity, ANPP, FP, soil type and texture, land-use history, and livestock type (Table 2; Table S4; Figure S1; Oyarzabal et al., 2018; Peri et al., 2021). Considering the aridity index (MAP/potential evapotranspiration; the lower, the drier) the nine rangelands were equally distributed into arid, semi-arid, and mesic ecosystems with two of them, which possessed an aridity index value edge of the category classified as "arid, semi-arid" (Le Houérou, 1996; Table 1).

2.2 | Experiment set-up and plot design

All the experimental sites are part of an international collaborative research network consisting of coordinated distributed drought experiments, The Drought Network (IDE; <http://droughtnet>). The sites followed a common experimental protocol which allows reliable comparisons among contrasting ecosystems (Knapp et al., 2017) and included experimental rainfall manipulations to understand the ecological drought impacts (Hoover & Rogers, 2016). The simulation of droughts was induced through a passive well-tested design based on rainout shelters that intercept a fraction of the incoming precipitation (Yahdjian & Sala, 2002), a fraction which differ among sites to emulate a drought that occurred only once in the last 100 years (Knapp et al., 2017). To determine the percentage of precipitation to intercept, we applied the standardized protocol disposed by The Drought Network and ran the Precipitation Manipulation Tool. This is a software that allows to upload the longest precipitation time series of each site (<https://drought-net.colostate.edu/>

[terrestrial-precipitation-analysis-package](#); Lemoine et al., 2016). Antecedent conditions did vary as sites differed in their previous pre-treatment precipitation (Table S1). Thus, we reduced annual precipitation from 60% in arid sites to 50% in mesic ones (Table S1). Intercepted precipitation was collected in gutters and directed away by pipes in order to avoid water infiltrating into the experimental drought plots. The rainout shelters were constructed with transparent plastic tiles, placed above the plant canopy (1.20 to 1.60m height) in order to minimize impacts on micrometeorological conditions (Figure 1 see photos). Except for a decrease of 11% to 20% of incident radiation (compared to the measurement outside the shelter), which are relatively low compared to other materials and did not imply significant reductions for plant canopy light interception (Yahdjian & Sala, 2002), no other side effects were detected. The rainout-shelter design employed in this study has proven to accomplish the desired reduction in water input and the expected effects on soil moisture (Gherardi & Sala, 2013; Yahdjian & Sala, 2002), and a considerable number of studies have set up drought experiments that imposed passive reductions in precipitation using this rainfall shelters design with similar results (see for example Byrne et al., 2017; Knapp et al., 2002; Siebert et al., 2019). The experimental plots (of at least 3×3 m) were installed in autumn on different years (2015 to 2017) following a completely randomized block design that included control plots of the same size. At each experimental site, the experiments were generally replicated three times ($n = 3$), although some sites had four replicates ($n = 4$). All experimental sites were fenced to prevent grazing on experimental plots.

TABLE 2 Vegetational and grazing use characterization of the nine sites located along an aridity gradient in Argentina. The grazing history (long: More than 50 years of grazing use in the site; short: Less than 50 years of grazing use in the site); the enclosure years and the grazing system (type of use = low <40%, moderate 40%–60% and high >60%; moment of grazing = continuous year-round; rotational during specific season) prior study mean aboveground productivity (ANPP_M), mean forage productivity (FP_M), and precipitation use efficiency (PUE_M; ANPP_M/MAP) are informed. Also, the vegetal community characteristics are included with the main dominant functional groups and forage dominant species

Site ID	Grazing history	Enclosure years prior study	Grazing system prior study	Main forage functional groups	ANPP _M (g m ⁻² year ⁻¹)	FP _M (g m ⁻² year ⁻¹)	PUE _M (g m ⁻² year ⁻¹ mm ⁻¹)	Vegetation characteristics	Dominant forage plant species
Río Mayo	Long	1	Low; Continuous (year-round)	C ₃ bunchgrass	29.01	18.05	0.17	Grass-shrub steppe	<i>Pappostipa speciosa</i> <i>Poa ligularis</i>
Los Cerrillos	Short	18	Moderate; Rotational (dormant season)	C ₄ bunchgrass	268.99	148.31	0.69	Grass-shrub steppe	<i>Aristida mendocina</i> ; <i>Setaria pameana</i> ; <i>Cordobea argenta</i> ; <i>Larrea divaricata</i>
Potrok Aike	Long	20	Moderate; Rotational (summer)	C ₃ bunchgrass	45.56	19.22	0.22	Grass steppe	<i>Poa spiciformis</i> ; <i>Pappostipa speciosa</i>
Monte Oriental	Long	1	Moderate; Rotational (spring-summer)	C ₃ bunchgrass	229.38	95.50	0.60	Grass-shrub steppe	<i>Nassella tenuis</i>
Chacra Patagones	Long	4	Moderate to high; Continuous (year-round)	C ₃ bunchgrass	103.80	47.72	0.25	Grassland	<i>Nassella longiglumis</i>
Campo Experimental Napostá, convenio UNS y MDA-PBA	Long	10	Moderate; Continuous (year-round)	C ₃ bunchgrasses	347.72	246.13	0.63	Grassland	<i>Nassella messiana</i> <i>Avena barbata</i>
Mar Chiquita	Short	55	NA	C ₃ bunchgrasses	919.34	644.56	0.99	Grassland	<i>Schedonorus arundinaceus</i> <i>Agrostis montevidiensis</i>
Las Chilcas	Short	7	Moderate; Continuous (year-round)	C ₃ bunchgrass	583.45	473.50	0.61	Grassland	<i>Schedonorus arundinaceus</i>
San Claudio	Short	25	NA	C ₃ bunchgrass	932.80	923.36	0.99	Grassland	<i>Schedonorus arundinaceus</i>

2.3 | Data collection

We took pre-treatment measurements (Time 0) describing the plant community, soil and long-term plant species composition and abundance. Also, ANPP and soil properties of each site were collected to be considered as predictors of drought sensitivity (Table 2; Tables S2–S4). During the experiment, we annually estimated plant cover of each species in permanent plots of 1 m² in the center area of each treatment plot, and aboveground biomass at the peak of the growing season, inside a core-sampling area in each drought or control plot, excluding a buffer area to minimize edge effects. For the Río Mayo and Chacra Patagones sites, the estimation of ANPP was made non-destructively (Table 2), through allometric equations that related the relative cover of each plant species present with their aboveground biomass (e.g. Flombaum & Sala, 2007). For the rest of the sites, ANPP was estimated by clipping to the soil surface all aboveground biomass within two frames of 0.2×0.5 m during the peak of biomass productivity (Sala & Austin, 2000), preventing to repeat clipping the same area each year. The harvested material was sorted into green, senescent (yellowish) and dead components for the main plant functional groups: grasses, forbs, legumes and shrubs; then dried to constant weight in a stove for 48h to obtain dry matter. We repeated plant measurements during three consecutive years in drought and control plots, except in San Claudio, where we failed to harvest during the third experimental year because of a national COVID-19 quarantine and in Chacra Patagones during the first year because of logistic complications. For all sites, we calculated FP following Easdale and Aguiar (2012): we multiplied the plant cover of each species by the ANPP of the corresponding plant functional group (grasses, forbs, legumes, shrubs) to obtain species ANPP (ANPP_{spp}), and then we multiplied ANPP_{spp} by a forage aptitude factor (unitless, detailed for each species in each site in Table S2) based on Easdale and Aguiar (2012) guidelines and considering the literature (Ambrosino et al., 2021; Guevara et al., 2002; Ojeda et al., 2018; Oñatibia et al., 2015). We then asked for the approval of local experts of each site for the classification of the forage aptitude factors. The forage aptitude factor classified plant species according to three categories of consumption of grazers: highly consumed (forage aptitude factor = 1), moderately consumed (forage aptitude factor = 0.5) and avoided by grazers (forage aptitude factor = 0). Then, FP values for each site and year were used to assess drought sensitivity using an absolute metric, which has been used in previous studies (Koerner et al., 2015; Raynor et al., 2020; Smith et al., 2017; Susan Moran et al., 2014; Wilcox et al., 2015, 2017) and a relative index (Bondaruk, Oñatibia, Wilcox, & Yahdjian, *in press*), following equations, respectively.

$$\text{Absolute sensitivity} = \frac{(FP_C - FP_D)}{(PPT_C - PPT_D)}, \quad (1)$$

where, FP_C and FP_D refer to FP in control and drought plots respectively, and PPT_C and PPT_D is annual precipitation for the same experimental plots. Absolute sensitivity indicates FP reduction in gm⁻² per each mm reduced,

$$\text{Relative sensitivity} = \frac{[(FP_C - FP_D) / FP_M]}{[(PPT_C - PPT_D) / MAP]}, \quad (2)$$

where FP_C and PPT_C refer to FP and annual precipitation respectively in control plots, whereas FP_D and PPT_D to those drought experimental plots; FP_M is the average of FP in control plots for each site during four experimental years and MAP is the long-term mean precipitation of each site (estimated through series of annual precipitation from 1980 to the present). Relative sensitivity values above zero indicate decreases in FP with drought, above 1 a huge negative impairment whereas, values below zero imply more FP in drought than in control plots.

Finally, to determine drought effects along time for forage species, we calculated the change of total FP between treatments for each site and year. Estimations followed the difference of FP_C and FP_D relative to FP_C along the 3 years and for the comparison between pre-treatment (FP_{T0}) and the third drought year (FP_{D0T3}; see further details in Table S2).

2.4 | Data analysis

We analysed the data from all sites in R software (R Core Team, 2020). We used linear regressions models (*lm* function) to describe changes of FP and ANPP along the aridity gradient and to fit the data of the proportion of FP to ANPP for each site of the gradient. We used linear mixed-effects models with separate repeated measures analysis of variance to evaluate differences between treatments (drought and control) for FP for each site, with year, treatment, and their interaction as fixed effects, while sampling block was considered as a random effect (random intercept). Pre-treatment values were incorporated and considered in the analysis using the *offset* function which corrects for initial differences. To analyse FP sensitivity to drought along the aridity gradient, we tested linear and non-linear regressions for relative and absolute sensitivity and then selected the best-fitted models for each response variable based on the Akaike Criterion. In particular, for the absolute sensitivity index, we concluded that the non-linear model was the best model based on the AIC (AIC linear model: 21.2 vs. AIC non-linear model -50.86), which takes into account the trade-off between fit (residual error) and parsimony (i.e., model complexity in terms of number of parameters), and the determination coefficient (*R*² linear model: 0.32 vs. *R*² non-linear model: 0.51). We used the *lme* function and *nmls* packages (Bates et al., 2015). Models followed the assumptions of homocedasticity of variances

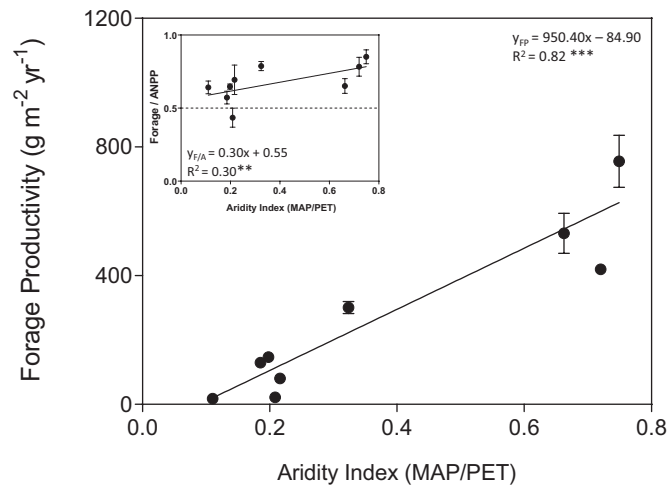


FIGURE 2 Mean forage productivity (\pm SE) for control plots averaged for 4 years in $\text{g m}^{-2} \text{yr}^{-1}$ at nine rangelands spread across an aridity gradient (mean annual precipitation/potential evapotranspiration) in Argentina, South America. Inset: Linear relationship of the proportion of mean forage productivity and the mean aboveground productivity across the aridity gradient. Statistical significances are indicated with standard statistical nomenclature (** $p < 0.01$; *** $p < 0.001$).

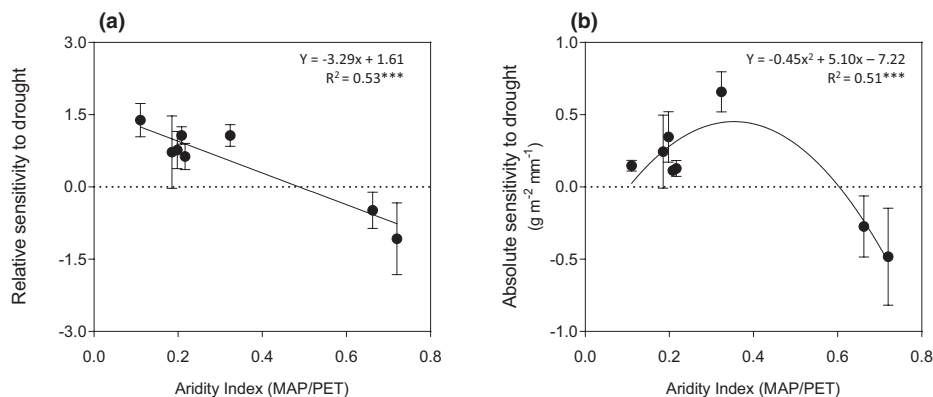


FIGURE 3 Relative (a) and Absolute (b) sensitivity to drought of forage productivity of rangelands located across an aridity gradient in Argentina, South America after 3 years of extreme drought. Sensitivity calculations considered are Equations 1 and 2 corresponding to the third experimental year. In each panel, the lineal (a) and quadratic equations (b) are indicated along with R^2 and statistical significance of the model (** $p < 0.01$; *** $p < 0.001$).

and normal distribution of residuals, assessed through *Levene* and *Shapiro-Wilks* tests, respectively.

3 | RESULTS

3.1 | FP across the aridity gradient

Forage productivity increased across the aridity gradient ($R^2 = 0.82$, $p < 0.001$) from $18.03 \pm 2.25 \text{ g DM m}^{-2} \text{ year}^{-1}$ in the most arid rangeland to $923.40 \pm 75.08 \text{ g m}^{-2} \text{ year}^{-1}$ (Mean \pm SE) in the humid extreme (Figure 2). Across the aridity gradient, the proportion of forage relative to total ANPP varied between 0.40 and 0.85 (Figure 2 inset). Arid and semi-arid rangelands showed a mean FP/ANPP ratio of 0.54 and 0.67, respectively, whereas mesic ecosystems had a ratio of 0.72. Eight out of the nine sites supported more than a half of their ANPP as forage biomass (Figure 2 inset, dashed line).

3.2 | Sensitivity to drought of FP after three drought years

After 3 years of experimentally imposed drought, mean FP of arid and semi-arid sites decreased by 48.5% and 50% respectively, whereas in mesic sites drought plots showed an increase of 50% compared to control plots. The sensitivity of FP to drought assessed through our two standardized sensitivity indices exhibited a decrease towards mesic sites (Methods Equations 1 and 2; Figure 3). The relative sensitivity linearly decreased along the aridity index gradient (Figure 3a; $R^2 = 0.53$; $p < 0.001$), while the absolute sensitivity showed a nonlinear relationship (Figure 3b; $R^2 = 0.51$; $p < 0.001$) mainly driven by the high sensitivity of a semi-arid site (Napostá). Thus, using the relative sensitivity index, the most impaired sites (i.e. those with standardized sensitivity index >1) are those in arid regions, but according to the absolute drought index, the most impaired ones are in semi-arid regions (Figure 3). Sites in mesic regions did not show any sensitivity

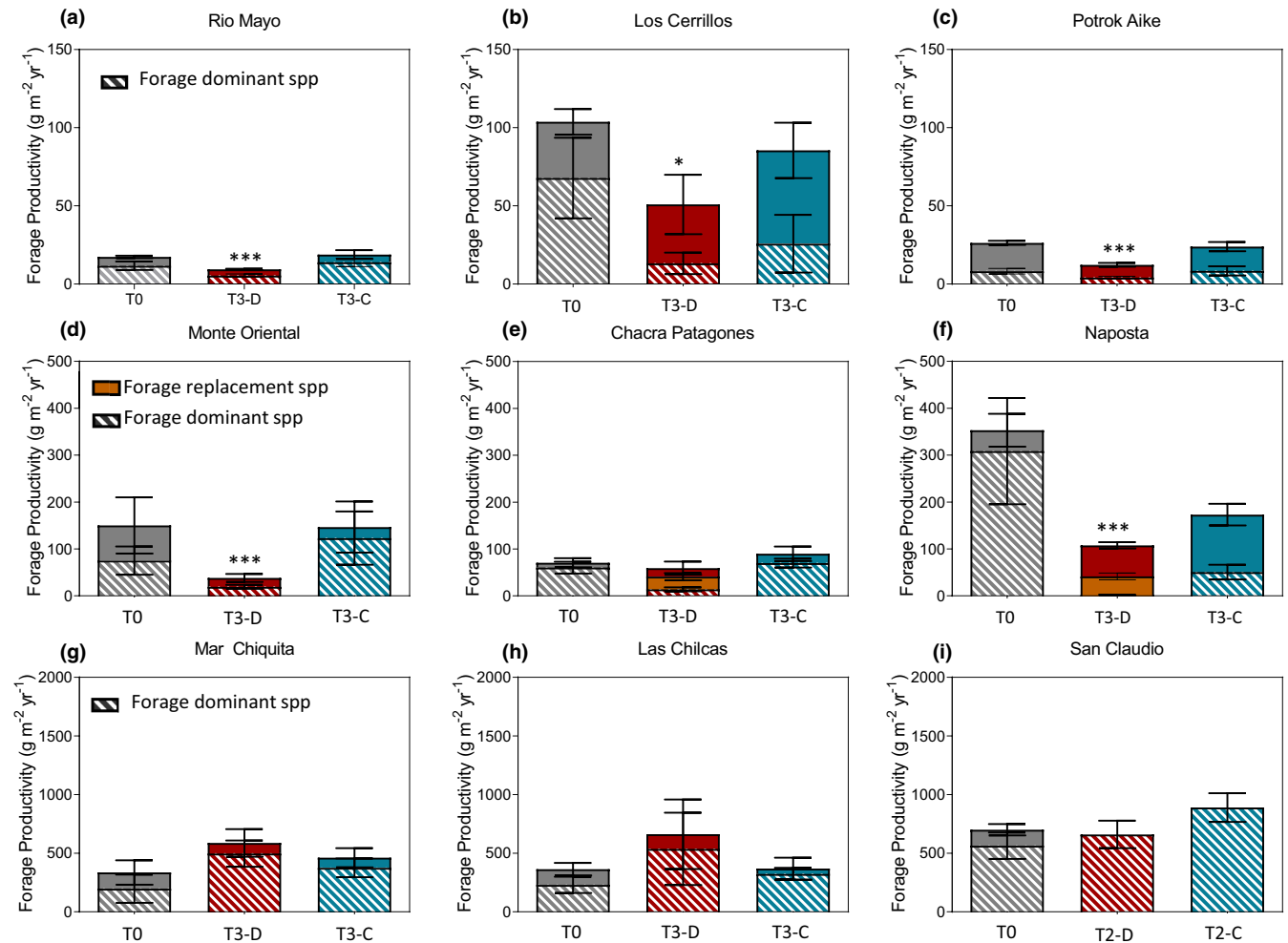


FIGURE 4 Forage productivity in $\text{g m}^{-2} \text{ year}^{-1}$ (mean \pm SE for $n = 3$ and $n = 4$, respectively) of the nine rangelands (from arid (a) to mesic (i)) for pre-treatment year (T0) and after three experimental years for both treatments (T3-D for drought plots and T3-C for control plots)-in exception for the Mesic site San Claudio which we only had data till the second year (see Section 2). Drought treatment is graphed in red bars and control in blue bars. T0 values are averaged between treatments as there were no significant differences and plotted in grey left columns. The striped bars refer to the forage productivity of the dominant forage species (forage dominant spp) and the orange bars stand for the productivity of the forage species that replace the main dominant forage species (forage replacement spp). Significant differences are indicated with standard statistical nomenclature (** $p < 0.001$; * $p < 0.05$).

to drought for the 3 years (Figure 3 -dots below zero-), with positive FP changes in some years (Figure 3). Overall, in arid rangelands, FP decreased relatively more than the percentage of reduction in precipitation (Table S1; Figure 3a). The absolute sensitivity index (FP reduction in g m^{-2} per each mm reduced) of some arid and semi-arid sites showed low values even when FP reductions were in some cases remarkable (e.g. Río Mayo-Potrok Aike-Chacra Patagones; Figure 3b).

The response patterns to the three-consecutive experimental-drought years were mostly idiosyncratic across rangeland sites and related to the response pattern of the dominant forage species. In general, forage species were more affected than species avoided by grazers, which in arid ecosystems represented a 42% versus 33% reduction for forage and non-forage species respectively, whereas in semi-arid sites it was 57% the reduction in forage species productivity

versus an 84% increase in the productivity of species avoided by grazers. (Table S3). Río Mayo, the driest site of the gradient, halved its FP, mainly driven by the negative impact of drought on the most abundant grass-species, *Poa ligularis*, which reduced its productivity more than 60% relative to control (Table S2; Figure 4,5). Potrok Aike also showed important forage reductions (48%; Figure 4), in this case mostly explained by biomass reduction (>50%) of the main forage species (*Poa spiciformis* and *Festuca pyrogea*; Table S2; Figure 4). Two of the semi-arid sites exhibited reductions of 74% and 62% of their FP (Naposta and Monte Oriental; Figure S3), again through the decline of the two main dominant forage species, *Nassella neesiana* and *Nassella tenuis*, which were reduced 96% and 62%, respectively (Table S2). In other arid and semi-arid sites (Los Cerrillos and Chacra Patagones), FP was reduced in a lesser degree (-28% and -30%, respectively; Figure 4), although in Chacra Patagones the

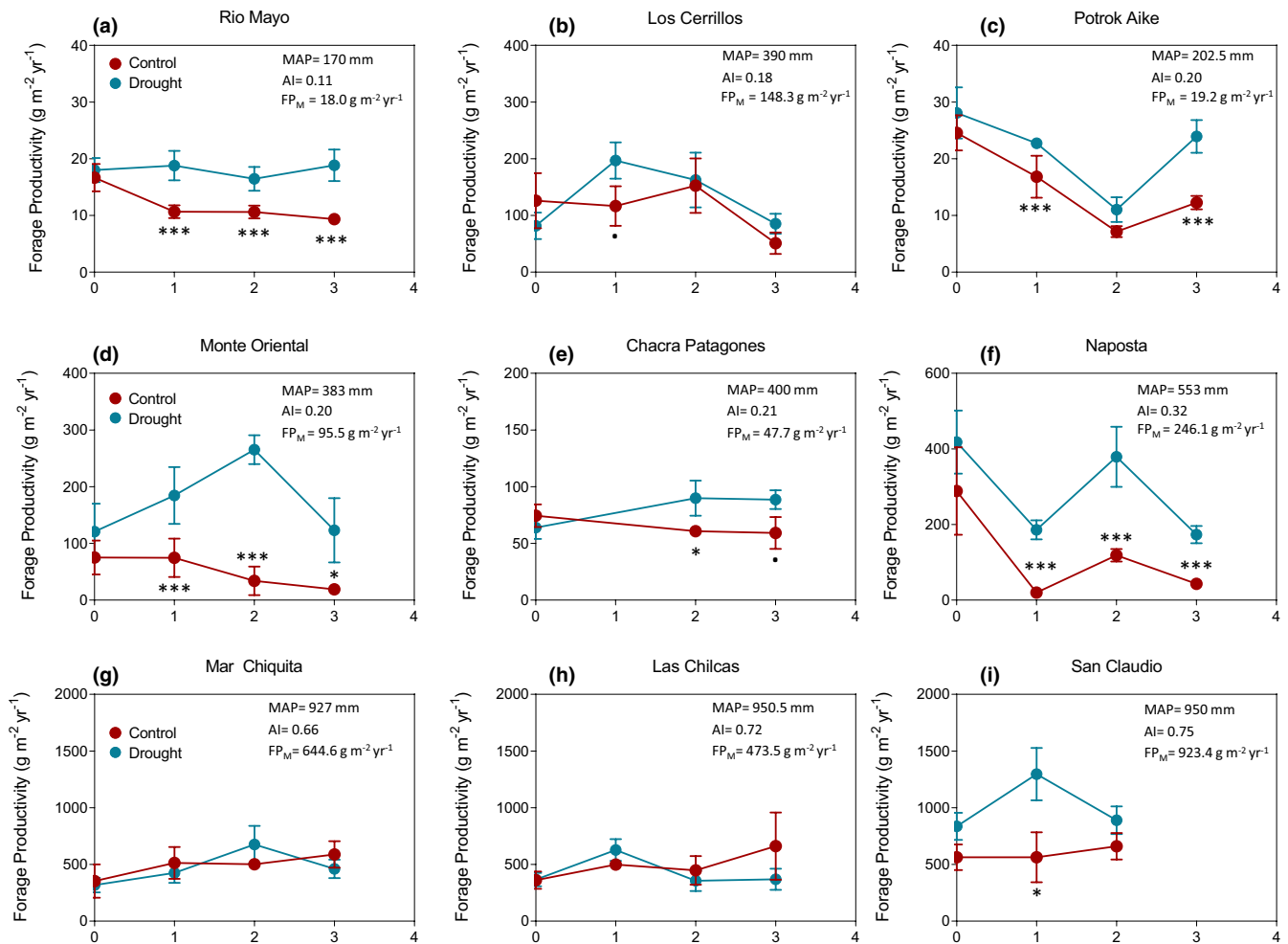


FIGURE 5 Change of forage productivity ($\text{g m}^{-2} \text{ year}^{-1}$) for each rangeland (from arid (a) to mesic (i)), from the beginning of the experiment (time 0) to the last year of analysis (time 3). Drought treatment is depicted in red and control in blue. Points indicate mean values ($\pm \text{SE}$). Specific information from sites is detailed on each panel: The mean annual precipitation (MAP, mm year^{-1}), the aridity index (AI, unitless) and the mean forage productivity (FP_M , $\text{g m}^{-2} \text{ year}^{-1}$). Significant differences between treatments are indicated as *** $p < 0.001$; * $p < 0.05$; dot means marginal significance with $p = 0.08$.

dominant forage species (*Nassella longiglumis*) dropped 78%, while non-dominant forage species (*P. ligularis*) showed a positive change (+127%) after 3 years of drought (Table S2; Figure 4). In Los Cerrillos, one of the three main dominant forage species reduced its productivity by 56%, while other species, the grass *Aristida mendocina* and the shrub *Cordobia argenta* (a dwarf shrub of intermediate palatability), increased in 52% and 138%, respectively (Table S2). Finally, mesic sites exhibited no negative effects of drought on FP, which is mostly explained by the higher productivity of their dominant forage species (mainly *Schedonorus arundinaceus*, ex *Festuca arundinacea*), despite the important reduction (–86%) in a native perennial forage species (*Poa lanigera*) in one of the sites (Table S2).

3.3 | Drought impact on FP along time

The pattern of the initial and cumulative FP response to drought along the three experimental-drought years was variable among

rangelands (Figure 5). Sites exposed to comparable persistent experimental droughts showed different patterns: (a) large average differences between treatments in favour of controls during the 3 years (Figure 5a,d,f); (b) an initial shock of the drought with large reductions in FP the first year (Figure 5a,c,d,f,i); (c) cumulative effects with larger drought effects during the second and third years, leading to reductions ranging from 50% to 64% of FP (Figure 5a,d,e,f); and (d) no clear drought effects in any year (Figure 5g,h). Also, from the pre-treatment condition up to the third experimental year, in all arid and semi-arid sites the FP decreased on average in drought-induced plots from 46% to 49.5% emphasizing a cumulative drought effect (Figures 5a–f and 6).

4 | DISCUSSION

We addressed the question of how rangeland FP is expected to respond to extended periods of drought across an aridity gradient. We

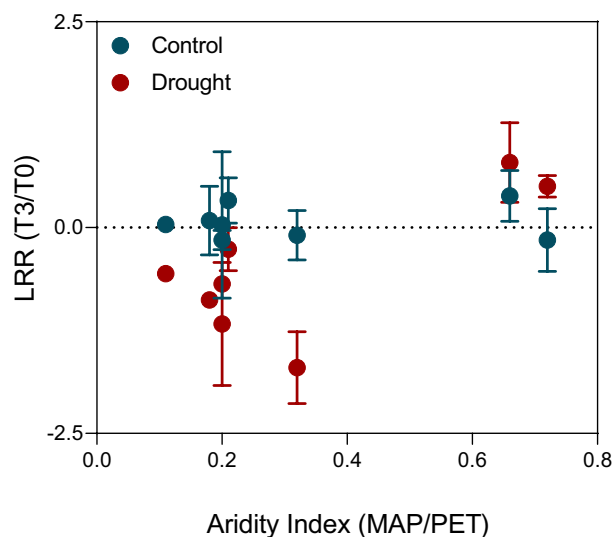


FIGURE 6 Effect size (natural log response ratio) of treatments on forage productivity in control (blue) and drought (red) plots between time 3 and time 0 (pre-treatment) across an aridity gradient in Argentina, South America. Points indicate mean values (\pm SE).

found that both FP and ANPP (Petrie et al., 2018), increased linearly across the aridity and the MAP gradient (Figure S1). These results are in line with those reported for the ANPP of North American temperate grasslands (Sala et al., 1988). However, slopes of linear regressions are different (0.6 in Sala et al., 1988 vs. 1.10 for ANPP in this study). Since we found a significant trend of increasing proportion of FP to ANPP from arid to mesic sites, such difference between slopes may be explained by forage species in mesic sites producing more than other plant species of natural grasslands. Our results confirmed water availability as the main control for both ANPP and FP and are also consistent with the prediction that drought impacts on FP are larger in arid and semi-arid rangelands, which present inherent water limitations for plant growth and few forage species with low biomass in their plant communities (Blanco et al., 2019). Overall, arid and semi-arid sites were more affected than mesic ecosystems, with five sites exhibiting an initial shock in the first experimental drought year and four of these undergoing a cumulative effect after three multi-year drought. Therefore, FP of arid sites showed the most relative sensitivity to drought values; however, these sites showed moderate absolute sensitivity values because they have low precipitation use-efficiency (Table 2). In contrast, mesic sites in general did not show the expected negative effects in their FP, exhibiting insensitivity to drought events instead. Moreover, they surprisingly showed 36%–70% more FP during the third year of experimental drought than under control conditions.

Multiple studies have been carried out analysing drought impacts on aboveground primary productivity (e.g. Breshears et al., 2016; Petrie et al., 2018) but very few focused on changes in forage supply (Lauenroth & Sala, 1992). Also, previous studies focused on Northern Hemisphere grassland regions (Lei et al., 2016; Petrie et al., 2018), with less consideration of Southern Hemisphere

grasslands. Here, we evaluated South American rangelands, a region traditionally dedicated to extensive livestock production (Modernel et al., 2019). We found that, even in arid sites, more than 50% of total ANPP corresponded to forage for livestock. This was possible by tapping on local knowledge (Ambrosino et al., 2021; Easdale & Aguiar, 2012; Guevara et al., 2002; Ojeda et al., 2018; Oñatibia et al., 2015), a key aspect to understand the relationship between the provision of ecosystem services and their appropriation by people (Díaz et al., 2018; Linstädter et al., 2013).

4.1 | Drought impacts on forage supply: Differences in sensitivity

We found differences in drought sensitivity among rangelands with contrasting plant species composition and productivity. Dominant species identity plays a key role as a determinant of drought sensitivity or resistance, especially because these species differ in their sensitivities to droughts (Hoover et al., 2014a, 2014b) and they do so in a predictable way along the aridity gradient. After a drought of similar magnitude, arid and semi-arid rangelands showed more severe FP decreases than mesic ones, since arid rangelands have few grazer-consumed species that supply forage, which are highly sensitive to drought events (Coughenour, 1985; Milchunas et al., 1995) and therefore under stress exhibited a severe reduction in their productivity compared to species avoided by grazers (Table S3; e.g. Napostá). Harsh environments have selected plant resistance traits, which confer the capacity to withstand disturbances such as grazing and water-limitation for a while (Blumenthal et al., 2020). Nonetheless, forage species in those areas can tolerate moderate short-term water limitations (Volaire, 2018) but end up severely impacted when they extend for longer periods (Oñatibia et al., 2020; Quiroga et al., 2010); this is particularly so for perennial C_3 grasses (Hoover et al., 2019). Our simulated droughts may have exacerbated the water limitation that these forage species naturally endure (Herrmann et al., 2016), probably surpassing, after a three-year drought, the resistance threshold of forage species (Qian et al., 2022; Stuart-Haëntjens et al., 2018).

Rangelands are mostly subjected to domestic grazing disturbances, therefore some insights related to grazing under drought scenarios emerge from our findings, mainly for arid and semi-arid rangelands. The high reduction in forage provision that we found in these rangelands under severe droughts suggests that grazing pressure must be substantially reduced during and after drought periods, since the combination of aridity and grazing disturbance generates a synergistic effect that may collapse plant populations of key forage species (Oñatibia et al., 2020). We did not include grazing disturbance in our experimental design, but frequently the functional traits that enable grazing tolerance are positively associated with drought tolerance (Coughenour, 1985; Oñatibia et al., 2020; Quiroga et al., 2010). Thus, the few forage species (those with high palatability) are least resistant to drought compared to those avoided by grazers (Tables S2 and S3), which

supports the trade-off between grazing-preference and drought-resistance. Further, in certain arid and semi-arid rangelands, future drought scenarios may increase the abundance and presence of woody species with low palatability (Hoover et al., 2017), jeopardizing the future provision of forage for livestock of these plant communities (Anadón et al., 2014). For instance, in an arid rangeland, we observed a substantial dwarf-shrub increase whereas perennial grasses biomass was reduced by more than a half (see Los Cerrillos; Table S2). Therefore, drought may drive arid and semi-arid rangelands to compositional changes, shifting to increased dominance of non-forage species or exotic annual grass species (e.g. see Napostá; Table S2), crossing degradation thresholds which may boost future non-forage shrub encroachments (Estell et al., 2012), or transform annual-dominated to perennial-dominated grasslands (Nie et al., 2008).

The lack of drought sensitivity we found in mesic rangelands may be partially attributed to the high dominance of tall fescue (*Schedonorus arundinaceus*), a naturalized C₃ forage species, which exhibit drought-tolerance under some conditions (Cernoch & Kopecky, 2020). This biological invasion contributes to the resistance to drought-simulation and may even drive and explain the unexpected positive effect to the imposed water shortage. Tall fescue roots and aboveground traits allow persistence and growth that enhance water uptake in deeper soil layers ensuring the survival of the aerial plant portion under drought stress (Huang & Gao, 2000). Also, tallgrass C₃ species may exhibit a lack of response to drought by a stable belowground bud bank, which generally showed insensitivity to drought at mesic compared to arid and semiarid grasslands, with vegetation constraints due to meristem limitation (Qian et al., 2022; Vanderweide et al., 2014). Then, this mechanism favouring more tiller recruitment (Fernández et al., 2002; Hendrickson & Briske, 1997) adds to other tall-grass characteristics such as activity during the cool season and summer dormancy mechanisms, which may mediate responses to climate, allowing the development of water stress avoidance (Carroll et al., 2021; Ott et al., 2019). Moreover, our results are consistent with findings in other mesic grasslands with different plant community composition (European example: Kreyling et al., 2008). In mesic regions dominated by highly productive forage species (as tall-grasses) with high plant cover, plant leaves commonly overlap (Table S2) and tend to allocate more resources belowground during droughts (e.g. in bud banks, see Dalglish & Hartnett, 2006; Qian et al., 2022, 2017), which may compensate drought impacts (Finch et al., 2016). Also, since mesic grasslands are generally more constrained by nutrients or light availability than by water availability (Huxman et al., 2004; Seabloom et al., 2020), this may explain the absence of a negative response to drought. Finally, despite we imposed a reduction in precipitation, a lack of treatment effects in our mesic rangelands may not be attributable to their high drought resistance (Hoover et al., 2018), but to the successive three wet years in the region during the experiment (Table S1), which likely contributed to avoid a severe water shortages and consequently eluded the expected negative effects on FP and ANPP. The

present study was focused on precipitation inputs, although we recognize that knowing the connection between precipitation, soil moisture and the physiological thresholds of dominant species in each ecosystem will improve our understanding of the sensitivity to drought along environmental gradients (Hoover et al., 2018).

4.2 | Drought impact on forage along time

During drought periods, most arid and semi-arid rangelands assessed in the present study showed a continuous decline in FP over time that was already evident in the first drought year. The pattern is consistent with previous studies suggesting that arid and semi-arid grasslands are the most susceptible ecosystems to drought (Lei et al., 2016), and others that exhibited a cumulative effect of reduced forage yields under experimental drought conditions (Hofer et al., 2017). Also, previous studies showed that forage species fail to cope with droughts (Volaire et al., 2014). This may be explained as stress-related decreases in plant biomass may negatively affect canopy photosynthesis (Staniak & Kocor, 2015), which then fails to provide the energy needed for more belowground exploration of deeper soil layers for available water, developing negative feedback.

Moreover, another aspect that would further limit the ability to respond and compensate the reduction in FP with drought in arid sites is related to their high proportion of sand in their soils (Table S4). Sandy soils show low soil-storage capacity, which combined with typically high evaporation demand in arid regions exacerbated soil water depletion (An et al., 2018). Besides, mesic sites did not show a negative impact in plant productivity across years and exhibited a relative stable response, which may be associated with low inter-annual variability in precipitation and frequent wet years (Bailing et al., 2018). Also, their large forage stocks may buffer against droughts through impeding light to reach the soils and may end up with low soil evaporation (Finch et al., 2016). The observed results highlight some concerns faced over short-term and ongoing drought events along years in arid and semi-arid rangelands, which require attention and demand the implementation of mitigation actions during droughts.

5 | CONCLUSION

Worldwide, rangelands would expect more frequent and severe droughts, particularly in arid and semi-arid regions (Dai, 2011). Our study spanned rangelands in the Southern extreme of South America, using a gradient approach and concerned with the possible loss of essential ecosystem services that sustain human activities in these regions (Sala et al., 2017). Our findings highlight that drought-induced productivity declines are exacerbated in arid and semi-arid rangelands, because they exhibit high sensitivity to drought of the forage provision. The negative effects of water shortage together with intensive grazing threaten the preservation

of the few key forage species present in them, jeopardizing the future of extensive livestock productivity, currently based almost exclusively on natural forage supply (Oñatibia et al., 2020). The development of adaptive-management strategies for livestock rearing, such as adjusting the grazing pressure according to the forage dynamics of key species, together with supplementation strategies, subdivision of paddocks and periodic herding, will allow decoupling the deleterious effects of plant water stress from those of grazing consumption (Peri et al., 2021). Additionally, another effective tool to make decisions in advance would be the early warning systems developed by agrometeorology institutions, to anticipate the occurrence of droughts, and contribute to reducing environmental and productive risks. Our main results highlight the urgent need to increase such land management efforts to mitigate drought detrimental consequences on most rangelands and therefore adapt to climate variability (Hoover et al., 2020). Approaches such as the one in this work generate critical knowledge and contribute to the application for strategic practices in vulnerable ecosystems to attenuate the degradation of the most key grass forage species, which can improve the rangelands' health (Bailey & Brown, 2011) while maintaining high productivity levels (Dermer et al., 2018).

AUTHOR CONTRIBUTIONS

V.F.B., G.R.O., R.J.F. & L.Y. contribute with the conceptualization. V.F.B., G.R.O., W.A., L.B., M.B., A.K., A.L., J.P., G.P., P.P., R.E.Q. & L.Y. collected the data. V.F.B. conducted the analyses. V.F.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository: <https://doi.org/10.5061/dryad.x0k6djh6> (Bondaruk, Oñatibia, Fernández, et al., 2022).

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