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Effect of interannual precipitation variability on dryland productivity: A global synthesis

Laureano A. Gherardi[1,2] | Osvaldo E. Sala[1,2,3]

[2]School of Life Sciences, Arizona State University, Tempe, Arizona

[3]School of Sustainability, Arizona State University, Tempe, Arizona

[1]Global Drylands Center,Arizona State University,Tempe,Arizona

Correspondence
Laureano A. Gherardi, Global Drylands Center, Arizona State University, Tempe, AZ.
Email: Lau@asu.edu

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Abstract

Climate-change assessments project increasing precipitation variability through increased frequency of extreme events. However, the effects of interannual precipitation variance per se on ecosystem functioning have been largely understudied. Here, we report on the effects of interannual precipitation variability on the primary production of global drylands, which include deserts, steppes, shrublands, grasslands, and prairies and cover about 40% of the terrestrial earth surface. We used a global database that has 43 datasets, which are uniformly distributed in parameter space and each has at least 10 years of data. We found (a) that at the global scale, precipitation variability has a negative effect on aboveground net primary production. (b) Expected increases in interannual precipitation variability for the year 2,100 may result in a decrease of up to 12% of the global terrestrial carbon sink. (c) The effect of precipitation interannual variability on dryland productivity changes from positive to negative along a precipitation gradient. Arid sites with mean precipitation under 300 mm/year responded positively to increases in precipitation variability, whereas sites with mean precipitation over 300 mm/year responded negatively. We propose three complementary mechanisms to explain this result: (a) concave-up and concave-down precipitation–production relationships in arid vs. humid systems, (b) shift in the distribution of water in the soil profile, and (c) altered frequency of positive and negative legacies. Our results demonstrated that enhanced precipitation variability will have direct impacts on global drylands that can potentially affect the future terrestrial carbon sink.

KEYWORDS

aboveground net primary production, climate change, interannual variability, legacy effect, nonlinear response, precipitation, soil water

1 | INTRODUCTION

In addition to changes in precipitation amount, the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2013) projects increasing precipitation variability through high frequency of extreme events at various temporal scales. However, the effects of interannual precipitation variance per se on ecosystem functioning have been largely understudied. Here, we report on the effects of interannual precipitation variability on the primary production of global drylands, which include deserts, steppes, shrublands, grasslands, and prairies and cover about 45% of the terrestrial earth surface (Prăvălie, 2016).

Mechanisms explaining changes in precipitation variability vary among temporal scales. At short scales, increasing precipitation variation is related to enhanced water-holding capacity of a warmer atmosphere at 7% per degree Kelvin of warming as predicted by Clausius–Clapeyron relationship (Kharin, Zwiers, Zhang, & Hegerl, 2007; Trenberth, Dai, Rasmussen, & Parsons, 2003). Such estimation could be constrained to 2.5% per degree of warming by available energy in the troposphere (Liu, Wang, Cane, Yim, & Lee, 2013). Recent studies have shown that extreme rainfall can be enhanced up to 15% per degree K but only for large precipitation events (Pendergrass, 2018). At interannual to multiyear scales, changes in precipitation patterns are related to intensification of atmospheric circulations such as El Niño Southern Oscillation (Easterling et al., 2000; Lewis, Brando, Phillips, Heijden, & Nepstad, 2011) and large-scale rearrangements of atmospheric modes (Seneviratne, Luthi, Litschi, & Schar, 2006).

The effects of precipitation variance on ecosystem functioning have been especially understudied at interannual and global scales due to usual short-term and local funding limitations. Empirical studies exploring within year (intraannual) precipitation variability effects on aboveground net primary production (ANPP) are very insightful but also scarce and inconclusive. Previous works have reported negative responses due to leaf-level water stress of the dominant species (Knapp et al., 2002), null ANPP responses with positive trends supported by changes in soil-water regimes (Thomey et al., 2011) and mixed responses across sites due to differential sensitivity to precipitation (Heisler-White, Blair, Kelly, Harmoney, & Knapp, 2009). At the interannual scale, a long-term manipulative experiment located in an arid grassland in New Mexico, USA, showed that precipitation variability had a negative effect on ecosystem productivity (Gherardi & Sala, 2015a, 2015b). Here, we aimed at exploring the effects of interannual precipitation variability on ANPP across dryland ecosystems globally.

The relationship between primary productivity and precipitation has been a long-standing topic in ecology (Bai et al., 2008; Sala, Gherardi, Reichmann, Jobbagy, & Peters, 2012; Sala, Parton, Joyce, & Lauenroth, 1988) because ANPP is an indicator of ecosystem functioning closely related to energy flux and carbon cycling. Most studies looking at "precipitation variability" effects on aboveground net primary production (ANPP) have looked at time series of precipitation and ANPP (Smoliak, 1986) assessing the effect of amount of precipitation over time, not that of variability per se, on ANPP. Other studies evaluated the relationship between production to rainfall variability ratios (Lauenroth & Sala, 1992; Wiegand, Snyman, Kellner, & Paruelo, 2004; Yang, Fang, Ma, & Wang, 2008). Although important contributions, these studies did not test for the effects of precipitation variation per se as a determinant of productivity and independent of the effects of precipitation amount. Recent studies have highlighted the importance of the effects of precipitation variability on ecosystem functioning and structure (Knapp et al., 2008; Rudgers et al., 2018). Proposed mechanisms explaining the effects of enhanced precipitation variability include nonlinear ANPP responses to precipitation (Hsu, Powell, & Adler, 2012), increased physiological stress on dominant species (Knapp et al., 2002), and shifts in the depth of soil-water distribution (Sala, Gherardi, & Peters, 2015).

Our work attempted to answer two questions. **First question:** Is there an overall effect of interannual precipitation variability on dryland ANPP at a global scale? Enhanced interannual precipitation variability results from increased frequency of extreme events, both dry and wet. Dry years have a negative effect on ANPP, while wet years have a positive effect on ANPP (Jobbágy, Sala, & Paruelo, 2002; Lauenroth & Sala, 1992; Sala et al., 1988). The overall effect of precipitation variability on ANPP will depend on the relative magnitude of positive and negative ecosystem responses to precipitation. If positive and negative ANPP deviations are of the same magnitude, the effects of dry and wet years would be similar canceling each other and resulting in null effect of precipitation variability. On the contrary, if positive ANPP responses caused by wet years are larger than negative deviations caused by dry years, the effect of enhanced precipitation variability would be positive. Finally, if ANPP decreases due to dry conditions are larger than the ANPP increase during wet years, the effect of increased precipitation variability would be negative. These relative ANPP responses to wet and dry years may be affected by the shape of the ANPP response to precipitation (Hsu et al., 2012) or by legacy effects (Sala et al., 2015). The overall effect of precipitation variability will hinge on linear to nonlinear ANPP responses to precipitation or on the relative importance of negative and positive legacy effects. **Second question:** Does the effect of precipitation variability change along a precipitation gradient from arid to mesic ecosystems, from desert grasslands to prairies? There is evidence showing that the slope of the ANPP–precipitation relationship decreases along gradients of mean-annual precipitation (Huxman et al., 2004; Sala et al., 2012). Moreover, the mechanism behind this general pattern is associated with the limited response of mesic grasslands to extreme wet events resulting from colimitation of water availability with other resources such as nitrogen (Yahdjian, Gherardi, & Sala, 2011). On the contrary, water limitation in arid ecosystems is relatively strong and colimitation by other resources is less frequent.

In order to answer these questions, we present a global synthesis of long-term datasets that cover a wide range of geographical and environmental spaces (Figure 1 and Supporting Information Figure S1) characteristic of drylands representing the functioning of most treeless ecosystems (Knapp et al., 2015; Reynolds et al., 2007). This collection of sites includes ecosystems dominated by grasses, shrubs, and codominated by grasses and shrubs.

2 | MATERIALS AND METHODS

2.1 | Data collection

We collected 43 long-term (≥10 years) datasets from locations around the world where mean precipitation coefficient of variation spanned from 8% to 38%, mean-annual precipitation ranged from 165 to 901 mm, and mean-annual temperature ranged from −1.9 to 19.6°C (Figure 1 and Supporting Information Table S1). We collected data from three sources: (A) Existing databases from the Long Term Ecological Research (LTER) network, available through the EcoTrends project, the Oak Ridge National Laboratory (ORNL). (B) Data from publications, which were extracted from tables or figures whenever it was not available through a data repository, and (C) directly from researchers. In order to have enough temporal representation of each dataset in our analyses, we limited our searches to datasets

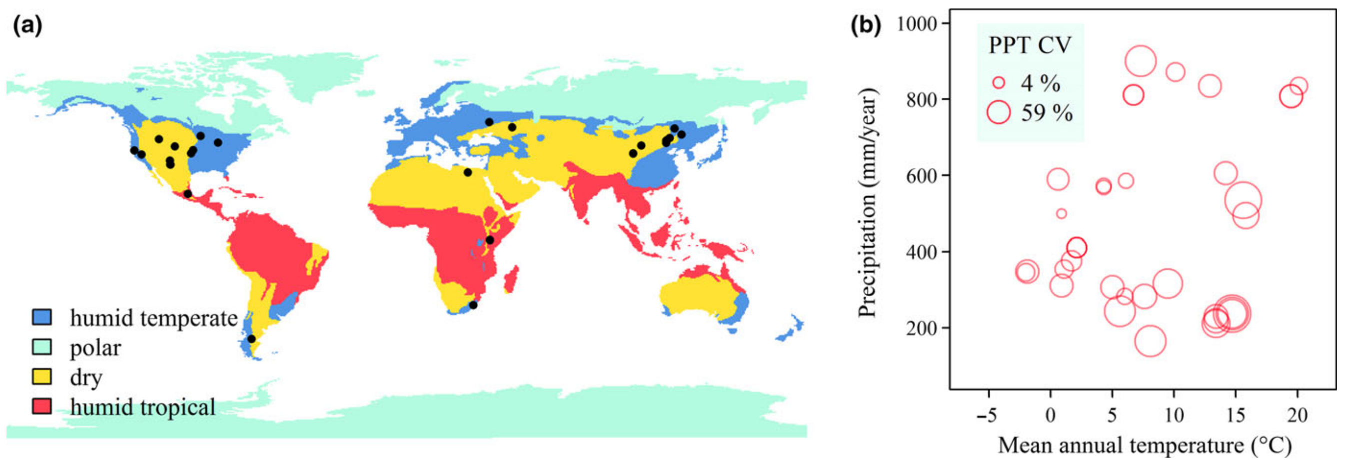

FIGURE 1 Geographical and climatological distribution of sites from where long-term aboveground net primary production data were obtained for this study. (a) Geographical location of study sites and their correspondent ecosystem province (Bailey, 1989/1993). (b) Climatological distribution of sites along temperature and precipitation gradients. Circle size indicates precipitation coefficient of variation for 5-year periods

that consisted, at least, of 10 consecutive years (Table S1). We also excluded floodplain and playa sites (McKenna & Sala, 2018) where water input through run-on may overshadow precipitation input and mask its effects.

2.2 | Data analysis

We aggregated our data in 5-year moving windows and calculated precipitation coefficient of variation (CV), mean precipitation, and mean ANPP for each time window. This approach allowed us to test directly the effect of precipitation variability as an explanatory variable for each site. For the overall ANPP response to precipitation CV, we fitted a mixed-effect model where we tested for precipitation CV fixed effect and for precipitation CV and site random effects allowing for random intercepts and slopes for each site (Figure 2, Supporting Information Data S1). We used overlapping window analyses because nonoverlapping windows reduce significantly the sample size and are very inefficient (Harri & Brorsen, 2009). However, in order to account for the overlapping nature of our data, we ran a bootstrapped analysis that provides conservative estimates (Adams, Gurevitch, & Rosenberg, 1997) for effect size and confidence intervals. We ran ten thousand iterations of the same mixed-model analysis presented in Figure 2 but using a random subset of replicates that may overlap or not. We obtained similar results than those obtained using overlapping windows (Supporting Information Data S1 and Figure S1). Therefore, we kept the overlapping window analysis because it increases the number of events included in within site tests. Otherwise, a site with only 10 years of data would have only two nonoverlapping events limiting the scope of within site inference.

Next, we extracted precipitation coefficient of variation effect size (fixed plus random effects) estimated from the output and fitted a linear model with long-term mean-annual precipitation as explanatory variable (Figure 3).

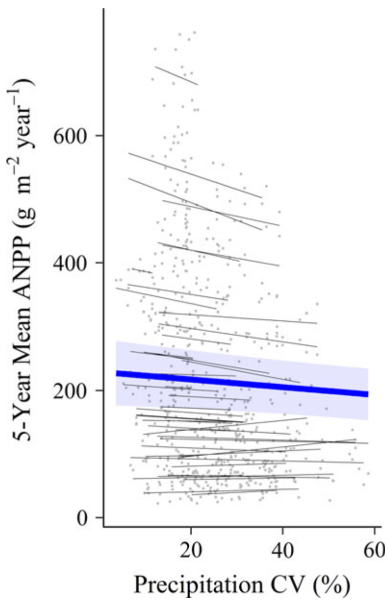

FIGURE 2 Overall negative effect of increasing interannual precipitation variability on aboveground net primary production (ANPP). Precipitation variability was depicted by the coefficient of variation of annual precipitation (CV) assessed in 5-year windows. Thin lines are mixed-effect model fits for each site. Thick line indicates overall response across sites, and the shaded band indicates 95% confidence interval (5-year mean ANPP = 229 – 0.6 × Precipitation CV). Each point corresponds to a 5-year moving window mean for ANPP and coefficient of variation of precipitation (p = 0.02, fixed effect size = –0.6, SE = 0.27)

In order to explore nonlinear responses, we fitted linear and nonlinear models to subsets of ANPP–precipitation data for sites with long-term mean-annual precipitation below 300 mm/year and above 300 mm/year. Nonlinear models consisted of exponential and logarithmic models covering both concave-up and concave-down responses (Figure 4), while the linear model represented the null

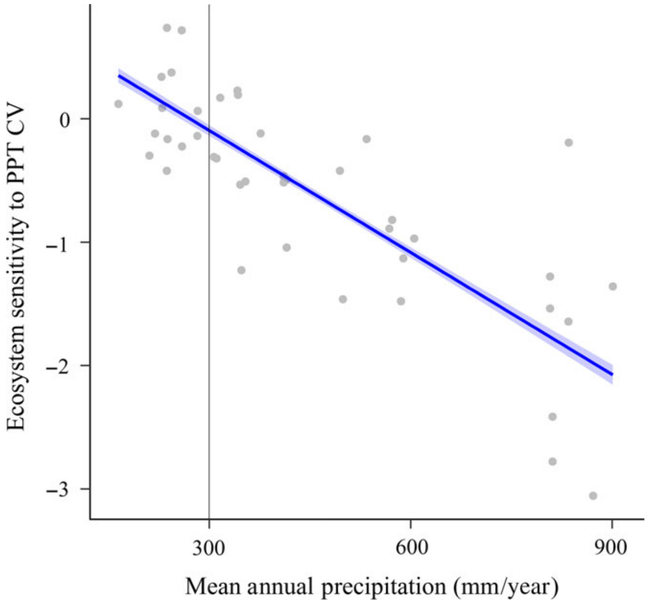

FIGURE 3 Ecosystem sensitivity to precipitation variability, which is here defined as the change in 5-year mean aboveground net primary productivity per unit change in 5-year precipitation coefficient of variation, as a function of mean-annual precipitation of different dryland sites. Ecosystem sensitivity was positive in drylands with <300 mm annual precipitation indicating that productivity increased with precipitation variability. Ecosystem sensitivity to precipitation variability was negative in sites with long-term precipitation above 300 mm. Ecosystem sensitivity corresponds to estimates of mixed-model effect size (fixed plus random effects) of precipitation coefficient of variation on primary productivity for each site as a function of long-term mean-annual precipitation. Line indicates linear model fit (Ecosystem sensitivity = 0.89 – 0.003 × Long-term mean-annual precipitation; $p < 0.001$, $R^2 = 0.68$), and the shaded band shows 95% confidence interval

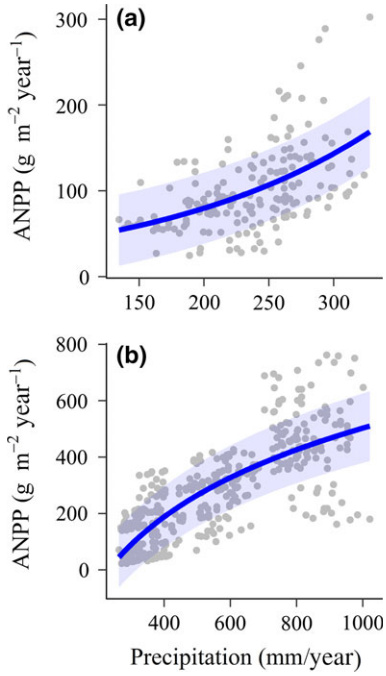

FIGURE 4 Nonlinear aboveground net primary productivity (ANPP) response to annual precipitation amount for sites below and above 300 mm of mean-annual precipitation. Mean 5-year aboveground net primary production as a function of mean 5-year precipitation for sites where long-term mean precipitation was below 300 mm/year (a, ANPP = 24.6 × exp[0.006 × Precipitation]) and for sites above 300 mm/year of mean-annual precipitation (b, ANPP = −1872 + 343 × log[Precipitation]). Model fits show the best model among linear and nonlinear models compared through AIC (Supporting Information Data S1). Bands indicate 95% confidence interval

hypothesis. Then, we selected the best model using the AICc (Sakamoto, Ishiguro, & Kitagawa, 1986) information criterion (Supporting Information Data S1).

We performed all analyses and created all figures using R version 3.0.2 (R Core Team, 2016). Data were square-root-transformed to meet model assumptions when necessary but presented in original format for simplicity. The map presented on figure one was drawn using packages: ade4 (Dray & Dufour, 2007), RSEIS (Lees, 2012), and adehabitat (Calenge, 2006). Linear and nonlinear mixed-effect models were fitted using the nlme package (Pinheiro, Bates, DebRoy, & Sarkar, 2018), and data aggregation and calculations were done using package reshape (Wickham, 2007).

2.3 | Legacy effect calculation

Legacies are the fraction of current ANPP accounted for ANPP or precipitation conditions that occurred in the previous year (Sala et al, 2012). Legacies are calculated as the difference between observed and expected ANPP, which then was estimated using annual precipitation for each year and in each site (Reichmann, Sala, & Peters, 2013; Sala et al., 2012). We considered positive and negative legacies when their magnitude was larger than or smaller than one-half standard deviation from the mean legacy effect at each site. In order to estimate legacy effects, the expected and observed ANPP must be from independent sources otherwise the legacies are incorporated in the ANPP-PPT model and tend to zero. For example, if we estimated expected ANPP from least squares models for each site and then subtracted observed ANPP, the mean legacy effect will always tend to zero because the legacy estimations would be represented by deviations of each observation to the fitted model that, by definition, minimizes deviations. Here, we used observed ANPP from our database and two independent estimates of expected ANPP using previously published models (Sala et al., 1988, 2012). The Sala et al. (1988) is a continental-scale spatial model fitted for the Great Plains of North America but almost identical models were found in Africa (McNaughton, 1985) and Asia (Bai et al., 2008). The advantage of using a spatial model is its generality. The problem is that it has a common *Y*-intercept and slope for all sites that in reality are different from that of temporal models of specific sites. To overcome this limitation, we used the slope of a generalized temporal model (Sala et al., 2012) derived from temporal models fit to several sites across drylands and specific *Y*-intercepts for each site from our database. This solution provides a generalized slope similar to that of temporal models and realistic *Y*-intercepts for each site. The answer to our question of the magnitude of the legacy effect in sites with less or more than 300 mm of annual precipitation was the same with the two approaches. Similar answers obtained using different approaches provide an indication of the robustness of the conclusions (Table 1).

2.4 | Carbon fixation calculation

We used the response surface from the mixed-model analysis to estimate the dryland sensitivity to precipitation variability expressed as the change in primary productivity per percent unit change in precipitation coefficient of variation. We used predictions of the Clausius–Clapeyron relationship (Trenberth et al., 2003) constrained to 2.5% per degree by available energy in the troposphere (Liu et al., 2013) and a projected temperature increase between 2 and 6°C to estimate potential precipitation variability changes for the year 2,100. In order to be conservative, we did not consider recent estimates of a 15% precipitation variability increase per degree K (Pendergrass, 2018). We estimated potential carbon sequestered on ANPP (C-ANPP) as one half of aboveground net primary production because plant tissue usually contains about 50% carbon (Schlesinger & Bernhardt, 1997). We calculated change in C-ANPP as the product of ecosystem sensitivity to precipitation variability times the expected precipitation variability change by total grassland area (Equation 1) of 52,500,000 km^2 (World Resources Institute 2000, based on IGBP data).

$$\begin{aligned} \text{C} - \text{ANPP change} = \text{Ecosystem Sensitivity}* \\ \text{PPT CV change} * \text{Dryland Area} \end{aligned} \tag{1}$$

This estimate provided context and highlighted the potential impact of projected precipitation variability on the carbon cycle, which indeed depends on the future of numerous climatic and land-use variables. We argue that this is a conservative estimate because it only considers aboveground carbon overlooking all carbon fixed belowground and because we did not take into account recent variability increase estimates of 15% per degree K. Including any of these two considerations would double the estimates presented here.

TABLE 1 Number, relative size of positive and negative legacies for sites below and above 300 mm/year of long-term mean-annual precipitation. We calculated legacy effects as the difference between independent estimates of expected and observed aboveground net primary production (ANPP). We calculated relative legacy size as the ratio between each year's legacy and mean legacy. We used yearly ANPP values in our dataset as observed ANPP and estimated expected ANPP using two models of the ANPP–precipitation relationship

	Legacy effects			
	Positive		Negative	
	Number	Relative size	Number	Relative size
Sala et al (1988) Model				
Below 300 mm	29	4.6	28	3.5
Above 300 mm	163	4.9	175	6.4
Unified temporal model				
Below 300 mm	31	8.3	32	3.1
Above 300 mm	141	7.6	134	9.7

3 | RESULTS AND DISCUSSION

Interannual precipitation variability had a negative overall effect on ANPP at the global scale (Figure 2). Across drylands from arid steppes to mesic prairies, primary productivity decreased by ~60 kg km^{-2} $year^{-1}$ per unit percent increase in precipitation coefficient of variation. Our results are robust because they did not change when we used different time windows (4, 5, or 6 years) and because they were insensitive to using overlapping windows or randomly selected 5-year intervals (Supporting Information Data S1 and Figure S1). The "Coupled Model Intercomparison Project phase 5" projected, depending on the emission path, increases in temperature for the year 2,100 between 2 and 6°C (Wuebbles et al., 2014) that are expected to increase precipitation variability between 5% and 17% (Kharin et al., 2007; Trenberth et al., 2003). Our results indicated that this increase in precipitation variability may result in an ANPP decrease for global drylands ranging between 307 and 1,043 kg km^{-2} $year^{-1}$. Given the extension of ecosystems included in this assessment, increased precipitation variability per se may result in a decline in global C-ANPP from about 0.1–0.3 Pg C $year^{-1}$, where C-ANPP is the amount of carbon in aboveground net primary production. This decline in C-ANPP represents 4%–12% of the mean C sink reported by the global carbon project for the last decade (Le Quéré et al., 2017; Poulter et al., 2014).

Our analysis further showed that ANPP responses to precipitation variability were modulated by long-term precipitation resulting in opposite responses along a mean-annual precipitation gradient from arid to mesic sites (Figure 3). Ecosystems with long-term precipitation below 300 mm/year showed a positive ANPP response to precipitation coefficient of variation, while sites above 300 mm/year showed a negative response (Figure 3). We proposed three explanations for the contrasting effect of precipitation variability on ANPP from arid to mesic drylands. Such explanations are not exclusive and may represent parts of the same phenomenon.

The first explanation is based on ANPP responses to precipitation amount that determine the overall response to precipitation variability over multiyear periods (Gherardi & Sala, 2015b; Rudgers et al., 2018). In order to test this rationale, we fitted linear and nonlinear mixed models for sites with long-term precipitation below and above 300 mm/year. In arid sites (<300 mm/year mean-annual precipitation), ANPP responded to increasing precipitation in a concave-up fashion. Sites with long-term precipitation above 300 mm/year showed a concave-down response, all tested through Akaike's information criterion (AICc) (Figure 4a,b and Supporting Information Data S1). The Jensen's inequality indicates that the effect of precipitation variability on ANPP depends on the curvature of the relationship between precipitation amount and ANPP (Gherardi & Sala, 2015b; Hsu et al., 2012). Increase precipitation variance results in higher frequency of positive and negative precipitation extremes or anomalies. In the case when the ANPP–precipitation relationship is concave up, the absolute effect of enhanced frequency of extreme positive precipitation is larger than the absolute effect of enhanced negative anomalies. Therefore, positive ANPP responses resulting from wet years overcompensate ANPP reductions caused by dry years resulting in a positive mean ANPP response to increased precipitation variability (Figure 4a). Conversely, in the case of a concave-down or saturating ANPP–precipitation relationship, the effect of negative anomalies or dry years is larger in absolute value than the effect of extreme wet years (Figure 4b). Therefore, ANPP responses to positive precipitation extremes do not compensate productivity decrease caused by dry years resulting in a negative mean ANPP response to precipitation variability of mesic sites. Pioneer efforts did not find significant nonlinearities when analyzing within site responses (Hsu et al., 2012) probably because of lack of statistical power. Our mixed-model approach allowed us to find significant relationships at regional to global scales.

The concave-up, linear or concave-down shape of the ANPP–precipitation relationship represents a continuum of responses accounted for by the shifting frequency of multiple resource limitation along gradients of long-term mean-annual precipitation (Huxman et al., 2004; Yahdjian et al., 2011). In arid sites, ANPP is most frequently limited by soil-water availability with nutrient and light limitation occurring only during or after rainy periods. On the contrary, more mesic drylands are less frequently limited by soil-water availability and more commonly limited by nutrient availability. Therefore, an extremely wet year in humid locations has a smaller effect than in arid ecosystems. A meta-analysis of N fertilization studies showing increases in the fertilization response ratio with mean-annual precipitation confirms the shifting frequency in resource limitation (Yahdjian et al., 2011). Similarly, global analyses of the ANPP–annual precipitation show a decline in the slope of the relationship between annual ANPP and annual precipitation with mean-annual precipitation ranging from deserts to prairies (Huxman et al., 2004; Sala et al., 2012).

The second explanation for why mean-annual precipitation modulated the effect of precipitation variance on ANPP is related to legacy effects. Legacies are defined as the negative effect of a dry year or positive effect of a wet year on ANPP after it has occurred (Sala et al., 2012). For example, negative legacies caused by a dry year affect plant-community structure and reduce grass-tiller density that in a subsequent wet year constrains the ability of ecosystems to exploit available resources (Reichmann & Sala, 2014). Positive and negative legacies are proportional to the difference in precipitation between current and previous year (Reichmann et al., 2013). Therefore, increased interannual precipitation variability would increase the magnitude of legacies by increasing the difference in precipitation between current and previous years. If positive and negative legacies were of the same magnitude, they would cancel each other; and increased precipitation variance would have no effect on mean multiyear ANPP. If negative legacies were larger than positive legacies, increased interannual precipitation variability would have a negative impact and if positive legacies were larger than negative legacies, ANPP response to increased precipitation variation would be positive. We estimated legacy magnitude as the difference between observed ANPP and two independent estimations of expected ANPP (Sala et al., 2012). We assessed the number and the relative size of positive and negative legacies on annual productivity for sites below 300 mm/year and above 300 mm/year of long-term precipitation (Table 1). The size of legacy effects relative to the mean legacy effect was larger for positive than for negative legacies at sites that received <300 mm/year. On the contrary, sites above 300 mm/year showed that the relative size of negative legacies was larger than positive legacies (Table 1). Both estimations of legacies showed qualitatively similar results providing support for our conclusion.

The third explanation relates to changes in water distribution in the soil profile that ultimately determines water availability for plants. Increased precipitation variability deepens soil-water distribution (Sala et al., 2015) because of the disproportionate effects of wet and dry years on the depth of water penetration in the soil. Precipitation during dry years only fills the topsoil, while in wet years, it reaches deep soil layers (Sala, Lauenroth, & Parton, 1992). Evaporation losses occur only from the uppermost soil layer and represent a larger fraction of the total water loss during a dry year than during a wet year. For example, a modeling experiment indicated that for a site with mean-annual precipitation of 300 mm/year, soil evaporation accounted for 50% of losses, while for a site with precipitation of 600 mm/year, evaporation explained only 20% of water losses (Sala et al., 2015). The depth of penetration per unit of precipitation increases with the amount of rainfall because water lost through evaporation decreases in relative importance. Increased interannual precipitation variability results from enhanced frequency of extremely dry and wet years. Since the effect of extreme wet and dry years on soil-water depth is not symmetrical, increased precipitation variability leads to a deeper soil moisture profile. In arid sites, deep water infiltration reduces surface evaporation increasing plant-available water and ANPP. In mesic sites, high precipitation variability enhances deep-percolation losses decreasing plant-available water and ANPP. This mechanism contributes to the explanation of the contrasting responses of ecosystems to increased interannual precipitation variability along the long-term precipitation gradient. We found that precipitation coefficient of variation and mean at each site for all 5-year windows were not associated with each other (Supporting Information Data S1). Therefore, high variability periods were not wetter or drier than low variability periods, excluding this as an explanation of the patterns reported here.

Addressing the effects of precipitation variability on ANPP across space, under current, and future climate conditions requires a series of complementary studies (Cottingham, Fey, Fritschie, & Trout-Haney, 2017; Munafò & Davey Smith, 2018). Data synthesis provides a long-term perspective and broad breadth of the global distribution of the precipitation response in geographical and parameter space but the correlative nature of these studies limits elucidation of cause–effect relationships. Manipulative experiments, on the contrary, provide the cause–effect assessment but lack the long-term and spatially broad perspective. Finally, simulation models complement the previous two approaches by allowing the exploration of situations that have not yet existed and mechanisms that are difficult to measure. Our synthesis of 43 datasets of ANPP from sites around the world yielded a pattern of positive effects of enhanced precipitation variability on ANPP for sites <300 mm/year of long-term precipitation and an opposite pattern for sites >300 mm/year. These results agreed with continental modeling and previous data synthesis efforts (Sala et al., 1988, 2015). The model assessed the impacts of enhanced precipitation variability and suggested a similar breaking point at around 380 mm/year of long-term precipitation below which enhanced precipitation variability increased plant-available water, and above this point ecosystems showed the opposite pattern (Sala et al., 2015). The data synthesis of ANPP from >900 sites in the US Great Plains, which were independent from those used here, also showed a break point at approximately the same long-term mean-annual precipitation (Sala et al., 1988). In drier sites, coarse-textured soils had higher production than fine-textured soils; and the opposite was true in more mesic environments. Finally, manipulative experiments (Gherardi & Sala, 2015a, 2015b) located in a dry grassland in the southwestern United States showed positive effects of interannual precipitation variability for shrubs and negative for grasses driven by changes in the soil-water distribution and species interactions. Further regional-scale experimentation is needed to explore causation and biotic mechanisms, which are essential to make meaningful predictions of the future effects of climate change on drylands, which account for most of the interannual variability of the terrestrial carbon sink (Poulter et al., 2014).

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ORCID

Laureano A. Gherardi http://orcid.org/0000-0001-5743-1096
Osvaldo E. Sala https://orcid.org/0000-0003-0142-9450

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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