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Review

Legacies of precipitation fluctuations on primary production: theory and data synthesis

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Variability of above-ground net primary production (ANPP) of arid to sub-humid ecosystems displays a closer association with precipitation when considered across space (based on multiyear averages for different locations) than through time (based on year-to-year change at single locations). Here, we propose a theory of controls of ANPP based on four hypotheses about legacies of wet and dry years that explains space versus time differences in ANPP–precipitation relationships. We tested the hypotheses using 16 long-term series of ANPP. We found that legacies revealed by the association of current- versus previous-year conditions through the temporal series occur across all ecosystem types from deserts to mesic grasslands. Therefore, previous-year precipitation and ANPP control a significant fraction of current-year production. We developed unified models for the controls of ANPP through space and time. The relative importance of current-versus previous-year precipitation changes along a gradient of mean annual precipitation with the importance of current-year PPT decreasing, whereas the importance of previous-year PPT remains constant as mean annual precipitation increases. Finally, our results suggest that ANPP will respond to climate-change-driven alterations in water availability and, more importantly, that the magnitude of the response will increase with time.

Keywords: primary production; legacies; spatial and temporal models; precipitation effects

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1. INTRODUCTION

Because arid and semiarid lands occupy over 40 per cent of the Earth's land surface [1,2], determining their patterns and controls of above-ground net primary production (ANPP) is critical to understanding the global carbon (C) cycle, and in predicting changes in this cycle with directional changes in climate. A better understanding of the mechanisms controlling the C cycle will improve predictions about ecosystem responses to increased temperature, precipitation variability and other changes expected in arid and semiarid systems. Current models predict, for most arid regions, a transition throughout the century to a more arid and more variable climate [3]. In November 2011, the Intergovernmental Panel on Climate Change (IPCC) released the 'Summary for Policymakers', stressing expected global increases in drought and extremely wet years [4–6]. For example, in southwestern North America, an ensemble of global circulation models predict a change in climate that could match Dust Bowl conditions of the 1930s [7]. The IPCC A1B scenario suggests a decrease in precipitation amount of 5–10% for the southwestern US as well as an increase in inter-annual variability [8], with changes in seasonality (less summer and more winter precipitation) [3]. Expected increases in temperature with global warming would negatively affect ANPP via changes in the water balance [9]. It is also likely that sequences of wet years (e.g. 1940s) will continue to be followed by a sequence of dry years (drought of the 1950s) and vice versa.

Ecologists typically agree that water availability is the most frequently limiting factor to the functioning of arid and semiarid ecosystems [10,11], and they have studied patterns of ANPP in many regions around the world, from the Great Plains of North America to the Mongolian Plateau (figure 1 and table 1). A very strong spatial relationship between mean annual precipitation (MAP) and ANPP across sites within a region clearly emerges from these studies (figure 2). It is remarkable that simple models using only MAP can account for such a large fraction of the spatial variability in ANPP from desert grasslands to mesic prairies. For example, in the Great Plains of North America, the model encompassed ecosystems

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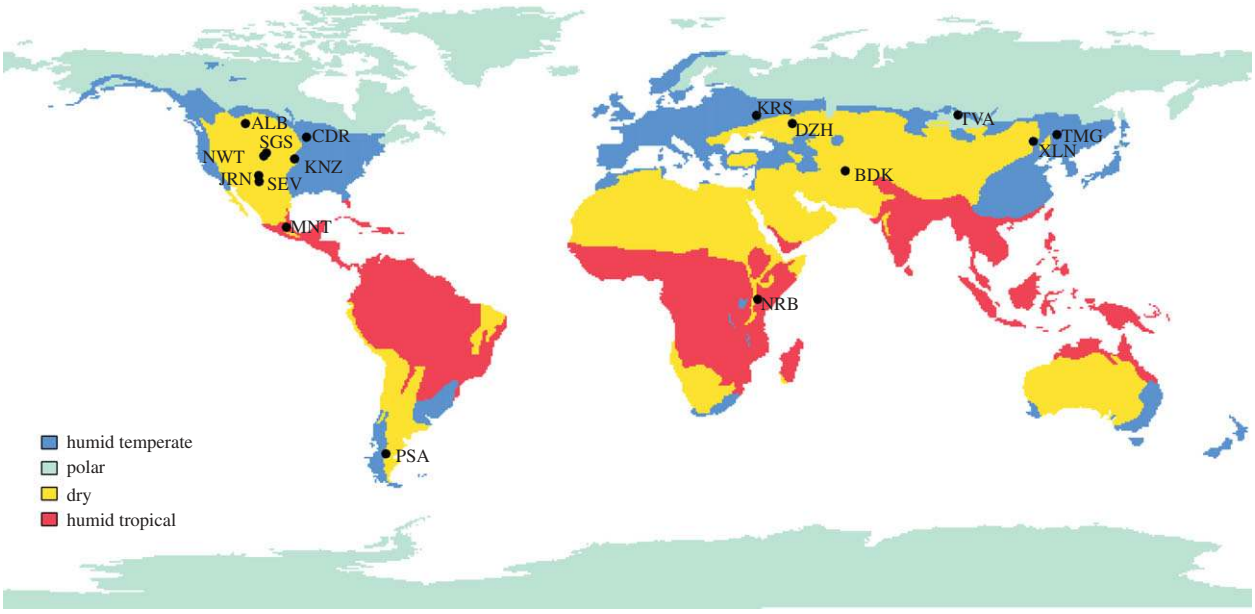

Figure 1. Location of study sites (table 1) and their corresponding ecosystem provinces ([12], digital vector data on a 0.3° resolution Cartesian Orthonormal Geodetic (latitude/longitude) global polygon network and derived raster data on a 10-min Cartesian Orthonormal Geodetic (latitude/longitude) 1080 × 2160 grid. One independent spatial layer with three attributes. 10 235 790 bytes in 15 files). Circles indicate all the study sites used in this paper: PSA, Rio Mayo, Chubut, Argentina; SEV, Sevilleta, NM, USA; JRN, Jornada, NM, USA; DZH, Dzhanybek, Volgograd, Kazakhstan; BDK, Badkhyz, Kushka, Turkmenistan; TVA, Tuva, Kyzyl ,Russia; XLN, Xilingol, China; ALB, Manyberries, Alberta, Canada; SGS, Shortgrass Steppe, Colorado, USA; TMG, Tumugi, Ulan Hot, China; MNT, Montecillo, Texcoco, Mexico; KRS, Kursk, Russia; NWT, Niwot Ridge, CO, USA; KNZ, Konza Prairie, KS, USA; NRB, Nairobi, Kenya; CDR, Cedar Creek, MN, USA.

Table 1. Above-ground net primary production (ANPP) data series used in this study. Site acronym (ID) and name/location, together with geographical coordinates and mean annual precipitation (MAP), are indicated. The year of start and end of data series and the number of years with data (in brackets) are shown. The slope and its standard deviation (in brackets) and fit (R^2) for linear regressions models linking annual ANPP and annual precipitation through time at each site are presented.

ID	site name	latitude	longitude	MAP (mm)	start-end of record (years)	slope (s.d.)	R^2
PSA [13,14]	Rio Mayo, Argentina	−45.68	−70.28	156	1983–1997 (10)	0.141 (0.069)	0.35*
SEV [15]	Sevilleta, USA	34.35	−106.88	205	1999–2008 (10)	0.087 (0.594)	0[a]
JRN [15]	Jornada, USA	32.60	−106.85	271	1990–2008 (19)	0.456 (0.180)	0.27**
DZH [16]	Dzhanybek, Kazakhstan	49.33	46.78	286	1955–1989 (34)	0.284 (0.067)	0.36***
BDK [17]	Badkhyz, Turkmenistan	35.68	62.00	300	1948–1982 (31)	0.129 (0.079)	0.08[a]
TVA [18]	Tuva, Russia	51.83	94.42	304	1978–1985 (7)	0.165 (0.096)	0.37[a]
XLN [19]	Xilingol, China	43.72	116.63	317	1980–1989 (10)	0.493 (0.210)	0.41**
ALB [20]	Manyberries, Canada	49.40	−110.69	326	1930–1983 (50)	0.140 (0.019)	0.54***
SGS [21]	Shortgrass Steppe, USA	40.83	−104.72	327	1939–2007 (66)	0.155 (0.030)	0.29***
TMG [22]	Tumugi, China	46.10	123.00	410	1981–1990 (10)	0.472 (0.095)	0.76**
MNT [23]	Montecillo, Mexico	19.46	−98.91	541	1984–1989 (6)	0.360 (0.178)	0.50[a]
KRS [24]	Kursk, Russia	51.67	36.50	585	1954–1983 (30)	0.146 (0.245)	0.01[a]
NWT [15]	Niwot Ridge, USA	39.99	−105.38	700	1982–1997 (14)	0.000 (0.062)	0[a]
KNZ [15]	Konza Prairie, USA	39.10	−96.61	788	1984–2005 (22)	0.134 (0.092)	0.10[a]
NRB [25]	Nairobi, Kenya	−1.33	36.83	835	1984–1994 (10)	0.016 (0.135)	0[a]
CDR [15]	Cedar Creek, USA	45.40	−93.20	841	1982–1998 (17)	0.023 (0.136)	0[a]
					weighted average[b]	0.179	

[a]n.s., non-significant.
[b]Slope average weighted by number of years.
*$p < 0.10$, **$p < 0.05$, ***$p < 0.001$.

ranging from 200 to 1200 mm of MAP, and explained 94 per cent of the variability of ANPP among sites [26]. Moreover, all these models, which were developed for different grassland regions around the world from North America to Africa and Asia and with different species composition with different evolutionary history,

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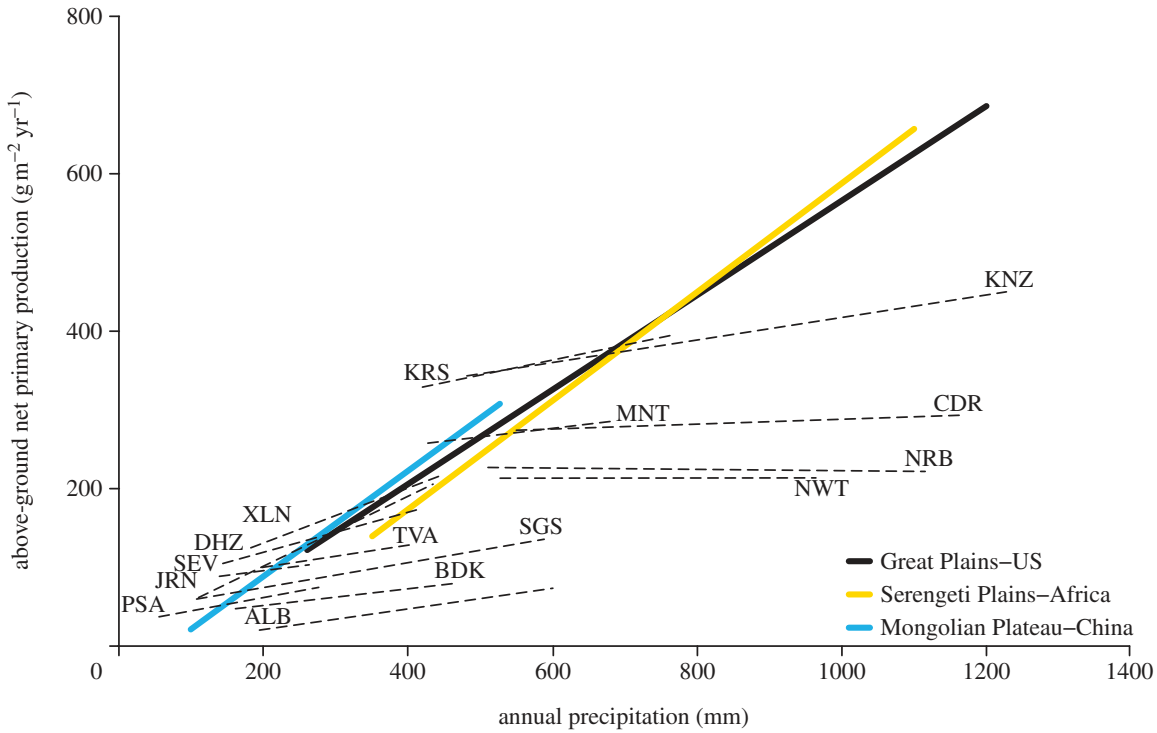

Figure 2. Relationships between ANPP (g m^{-2} yr^{-1}) and mean annual precipitation (mm) for regional spatial models (filled lines) developed in the Great Plains of the US (black, ANPP $= -34 + 0.60 \times$ MAP $R^2 = 0.94$) [26], the Serengeti Plains of East Africa (red, ANPP $= -102 + 0.69 \times$ MAP $R^2 = 0.48$) [27, p. 843], and the Mongolian Plateau of China (blue, ANPP $= -45.13 + 0.67 \times$ MAP $R^2 = 0.76$) [28]; and for long-term temporal models (dashed lines) fitted to the 16 sites (figure 1 and table 1) included in this paper. Spatial models were constructed using average mean annual precipitation and ANPP for 9498, 20 and 21 sites, respectively, along regional precipitation gradients. Temporal models were constructed based on annual precipitation/production time series (more than 6 years) for each individual site.

are remarkably similar with MAP/ANPP slopes converging at values of 0.60–0.69 g m^{-2} mm^{-1} (figure 2). We developed a new, unified spatial model for the relationship of ANPP and MAP by weighting the three models by their sample size.

$$\text{ANPP} = -34.17 + 0.6 \times \text{MAP}. \tag{1.1}$$

It is tempting to apply these tight spatial relationships to predict changes in ecosystem productivity through time at a site, given the urge to predict ANPP under a changing climate [29]. However, the temporal relationship between ANPP and PPT at a given site is far weaker than the spatial relationships built across many sites, and the site-specific slope is different from the across-sites model (figure 2). Our synthesis of 16 studies of the relationship between annual precipitation and ANPP along several years accounted for a much smaller fraction of the interannual variability in ANPP than the spatial model using MAP accounted for the variability among sites (table 1). On average, temporal models explained only 13 per cent of the interannual variability in ANPP (0–77% depending on the site), and were non-significant in more than half of the studies. In addition, temporal models had a much lower slope for the relationship between ANPP and annual PPT, which ranged from 0 to 0.56 g m^{-2} mm^{-1}, compared with 0.60–0.69 g m^{-2} mm^{-1} in the spatial ones (table 1 and figure 2). In synthesis, these results suggest an inadequate understanding of the relationship between interannual variability in precipitation and production, and the mechanisms that drive it.

In this work, we first develop a theory of the controls of ANPP through space and time, and its mechanisms. Second, we synthesize published studies of the relationship between ANPP and PPT, and assess them against theory. While the correlation approach that we follow does not unravel mechanisms, it is capable of rejecting hypotheses deduced from the general theory of the controls of ANPP from arid to sub-humid ecosystems. Finally, we put our findings in a climate change context and suggest some future lines of research.

2. GENERAL THEORY OF CONTROLS OF ABOVE-GROUND NET PRIMARY PRODUCTION IN WATER-LIMITED ECOSYSTEMS

Here, we present novel hypotheses about potential mechanisms accounting for the precipitation–ANPP relationship through space and time in arid to sub-humid ecosystems. Our hypotheses introduce a point of view that is different from the traditional biogeochemical explanation [30] where nutrients and water interact to limit growth with little attention to plant and community structure. We focus instead on interactions between plant community structure and resource loss.

We suggest that the differences between spatial and temporal controls in ANPP, as shown in the previous section (figure 2), result from lags in the response of ecosystems to changes in water availability. Long-term data suggest the existence of time lags in the response of

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ANPP to changes in annual PPT. In the North American Shortgrass Steppe, for example, the year 1954 was the driest in the 1939–1993 period and had the lowest ANPP [21]. The following year had average precipitation, but ANPP was still below the mean, and 1956 again showed below-average precipitation while ANPP continued to rise. Similar patterns suggesting the existence of lags exist in other long-term ANPP records [13,31].

ANPP lags also have been reported to occur at time scales shorter than the year. For example, Li & Guo [32] reported 50-day lags in the response of NDVI to changes in precipitation in a Canadian grassland. Different functional groups of plants exhibit different lags, while grass primary production showed maximum correlation with precipitation occurring in the previous two months; shrub primary production showed maximum correlation with the precipitation accumulated during the previous 24 months [13]. Sherry *et al.* [33] also found lags of two to nine months in the ANPP response to changes in soil water availability resulting from experimental warming. Finally, lags in other variables such as community composition can be even longer. In the Tallgrass Prairie, the irrigation effect on the shift in the dominant grass species was not observable until after 10 years of treatment [34]; in the Shortgrass Steppe, the effects of severe drought on the relative cover of ruderals and dominant grass species were not detectable until after 4–7 years of treatment [35].

Here, we focus on lags that result from legacies of wet and dry years that, in turn, lead to hysteresis in the ANPP response to annual precipitation. Legacies in changes in water availability are the effects on plants and ecosystems that remain after the extreme precipitation event is over. Legacies, as defined here, are the effect of a drought after the drought has subsided, or the effect of an extremely wet period after it has occurred. Legacy is quantified as the difference between the observed ANPP and the expected ANPP, which is estimated using actual precipitation and the temporal precipitation–ANPP relationship for the site.

$$\text{Legacy} = \text{ANPP}_{\text{observed}} - \text{ANPP}_{\text{expected}}. \qquad (2.1)$$

We hypothesize that the magnitude of the legacy depends on the direction of change (from low to high versus from high to low). We suggest four alternative hypotheses for the effects of precipitation on ANPP legacies (figure 3).

Hypothesis 1 (*Linear-Positive Legacy*) is that the legacy is linear and directly proportional to the magnitude of the difference between current and previous-year precipitation (figure 3, H1). Drought (negative) and wet (positive) legacies are similar in absolute value but opposite in sign. Ecosystems that experience less water-availability in the previous year relative to the current year will have a lower productivity than expected based on current-year precipitation (figure 4*a*). Rationale for this hypothesis is the carryover effect from the previous year, which could be structural or biogeochemical. Negative legacies from a drought could result from the death of individual plants or plant parts that constrain resource capture and growth, once wet conditions arrive. A positive legacy would occur following a wet period when ecosystems have more leaves and roots than typical or average, thus allowing for a more

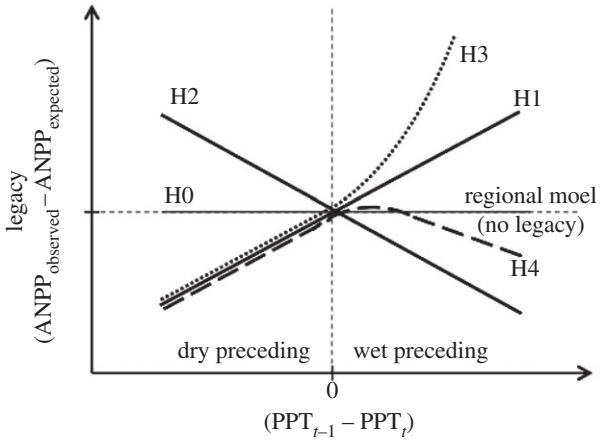

Figure 3. Alternative hypotheses regarding legacy effects on ANPP. Legacies, which are the deviation of ANPP from the value expected based solely on current year (*t*) precipitation (temporal ANPP–PPT models in figure 2), are shown as a function of the difference between previous year precipitation (PPT_{t-1}) and current year precipitation (PPT_t). Legacies are equal to zero when previous year precipitation equals current year PPT or if there are no legacies, and there were no effects of previous conditions, which is the H0 of the legacies. For H1, H3 and H4, named Linear-Positive Legacies, Growing Positive Legacies and Always-Negative Legacies, production in years following a dry year should be lower than production during years with the same precipitation but following an average year. Production in years following a wet year can be lower, equal or higher than expected. For H2, Linear-Negative Legacies, production is higher if previous year is drier than current year and lower than expected if previous year was wetter than current year.

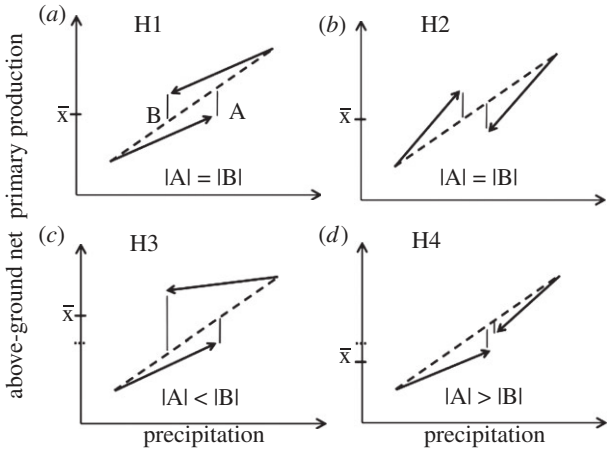

Figure 4. Effect of alternative hypotheses vis à vis legacy effects on the transition from a dry year to a wet year and from a wet year to a dry year, and the effects of transitions on ANPP. Dashed lines represent a no-legacy situation, while arrows depict dry–wet and wet–dry transitions and their effect on ANPP. Letters A and B represent the magnitude of the legacy; (*a*,*b*) H1 and H2, Previous dry or wet-year condition results in lags of the same magnitude but opposite sign; (*c*) H3, wet legacies larger than dry legacies; (*d*) H4, dry and wet legacies have negative effects.

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exhaustive exploitation of resources in the next year. Biogeochemical phenomena can also result in legacies. Ecosystems transitioning from wet to dry conditions may have higher nitrogen (N) availability than ecosystems shifting from dry to wet conditions if N availability depends on litter input of the previous year, which in turn depends on water availability.

Hypothesis 2 (*Linear-Negative Legacy*) suggests an opposite effect of legacies (linear but inversely proportional) with dry- and wet-preceding conditions, respectively, enhancing or decreasing current-year production relative to expected ANPP, which is estimated using current-year precipitation (figure 3, H2). Consequently, in a transition from dry to wet, productivity is higher than expected based on current-year precipitation, and, in a wet to dry transition, productivity is lower than expected (figure 4*b*). In this hypothesis, productivity legacies result from a trophic cascade mechanism [36]. For example, following an extraordinary productive year, above- or below-ground herbivore density may be higher than what can be supported by current-year ANPP, reducing leaf and root area and their capacity to capture resources such as nutrients and water. Similarly, following an unproductive year, herbivore pressure may be lower than expected based on current-year ANPP. An alternative explanation is based on the differential response of N mineralization and immobilization to changes in water availability. Mineralization is insensitive to changes in precipitation, but immobilization is more sensitive resulting in increased soil NO_3^- concentration after drought [37]. Consequently, following an unproductive year, ecosystems have a higher availability of mineral N than following a productive year.

Hypothesis 3 (*Growing-Positive Legacy*) suggests that the magnitude of drought legacies are linear with the magnitude of drought, but wet-year legacies are more than proportional to the magnitude of the difference between current and previous (wet) year (figure 3, H3). The rationale for the asymmetric response results from the analysis of costs and benefits of alternative plant responses. Deploying new roots and leaves has a cost for plants (which is incurred at the time of production), whereas the benefits result from the resources that those structures acquire (over the life of the structures) [38]. Because plants have already invested most of the resources required to grow new structures, the threshold for abscising them may be higher than the threshold for deploying them. In other words, the absolute change in water necessary to trigger deployment of new structures is smaller than the absolute change in water required for abscising organs. For example, *Bouteloua gracilis*, the dominant grass species of the Shortgrass Steppe, was able to deploy new roots 40 h after interruption of a prolonged drought [38]. High sensitivity to increased resources may benefit plants, if they are able to acquire resources that otherwise would disappear, such as transient soil water, which is lost via evaporation when not used rapidly [39]. Shedding roots or leaves may only have a benefit for plants when the probability of capturing new resources is very low. This hypothesis may explain the results of Knapp & Smith [40] who found in a study of long-term ANPP trends for 11 LTER sites that the absolute values of extreme positive ANPP deviations were larger than the extreme negative deviations.

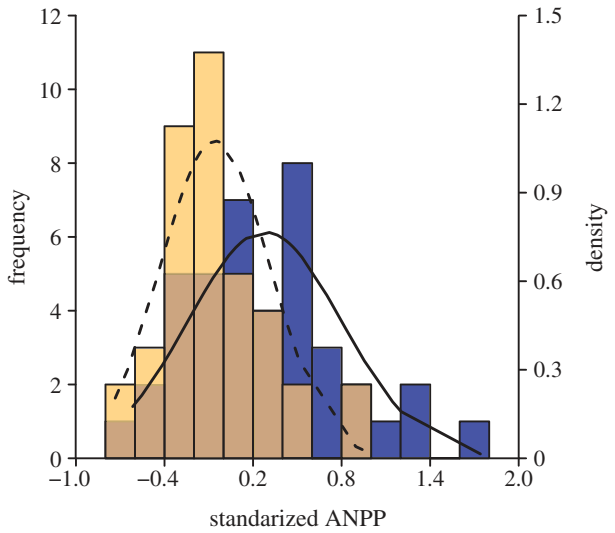

Figure 5. Frequency distribution of standardized (relative to each series average) ANPP values following exceptionally productive (greater than mean + 1 s.d.) or unproductive (less than mean − 1 s.d.) conditions during the previous years. Frequency distributions and density functions show a significant departure from the mean for years that were preceded by previously unproductive (brown bars, dotted line) or highly productive (blue bars, filled line).

Hypothesis 4 (*Always-Negative Legacies*) suggests negative dry and wet legacies (figure 3, H4). In this case, wet years cause plants to have too many leaves and roots with a high respiratory maintenance cost that negatively affects ANPP if the wet year is followed by a dry year. This cost/benefit ratio can be envisioned in carbon or energy units used in deploying new leaves and roots, and the extra carbon/energy that plants acquire as a result of these new structures [38]. In a highly variable environment, too many roots and leaves may be a liability for the carbon/energy balance of plants because of the high maintenance cost of roots and leaves relative to gross primary production.

3. LONG-TERM DATA ANALYSIS AND SYNTHESIS

To test our hypotheses, we used 16 studies that had estimates of ANPP for more than 6 years (table 1). All studies focused on arid to subhumid grass- or shrub-dominated systems (i.e. rangelands). Humid and tree-dominated systems were excluded because their ANPP is primarily limited by different resources than grasslands. First, we standardized ANPP and PPT values for individual years at each site relative to the site ANPP and PPT long-term average ((value − mean)/mean). Consequently, we were able to pool all sites and years by removing spatial ANPP and PPT differences (all sites have standardized ANPP and PPT mean equal to zero). Analysis of the frequency distribution of the pooled ANPP data shows that those years preceded by exceptionally unproductive ones had a significantly lower ANPP than years preceded by highly productive years ($F_{1,77} = 10.76$ $p = 0.001$; figure 5). Here, exceptionally productive or

unproductive years were defined as those having ANPP values above or below one standard deviation in the frequency distribution of all standardized ANPP data.

Our results (figure 5) show that legacies play an important role in explaining current-year production such that the null hypothesis (H0), of no legacies, is rejected (figure 3). Moreover, the geographical and ecosystem-type breadth of the dataset indicates that the legacy phenomenon is generalized across all rangeland ecosystem types. In addition, these results reject H2, Linear-Negative Legacies, which indicated that dry legacies have a positive value and wet legacies a negative value. Indeed, years preceded by an extraordinarily unproductive year had a significantly lower ANPP than years that were preceded by an extraordinarily productive year. This analysis also rejected H4, Always-Negative Legacies, which stated that both dry and wet legacies are negative. A deduction from the Always-Negative Legacies hypothesis is that the frequency distribution of ANPP in years preceded by extraordinarily productive conditions should not be different from the frequency distribution of ANPP preceded by years extraordinarily unproductive. In other words, the mean of ANPP in years preceded by unproductive conditions should not be different from the mean in years preceded by productive conditions. But indeed, both frequency distributions are different (figure 5). Finally, this analysis cannot distinguish between Linear-Positive Legacies and Growing-Positive Legacies hypotheses (H1 and H3).

Field manipulative experiments support our analysis of long-term ANPP observations. For example in the Patagonian Steppe, a study that reduced incoming precipitation by 30, 55 and 80 per cent showed that plots with drought in previous year had lower productivity than plots with control precipitation in previous year [41]. Moreover, this study showed that the magnitude of decline in productivity the year after drought was related to the difference in precipitation between control and drought treatments. A study in a Chihuahuan Desert Grassland also showed a significant effect of previous-year precipitation on current-year productivity [42].

These two research approaches, field experimentation and long-term data analysis, complement each other. The long-term data analysis provides access to longer temporal and broader spatial scales than can be approached experimentally [43–45]. Experimentation provides a unique insight into mechanisms behind observed patterns and provides clear causality tests. Manipulative studies showing the existence of legacies also demonstrated that the principal mechanism was associated with ecosystem and community structure [41,42]. In one case, the density of individuals, which was reduced under drought, constrained production in the following year [41]. Legacies of wet and dry years also showed a structural mechanism through tiller density that either constrained production in years preceded by drought or enhanced production in years preceded by wet conditions [42].

Standardization of ANPP and PPT data from 16 sites relative to the mean of each site ((value − mean)/mean) allowed us to explore the controls of ANPP across time (figure 6*a*). This new relationship combines all the

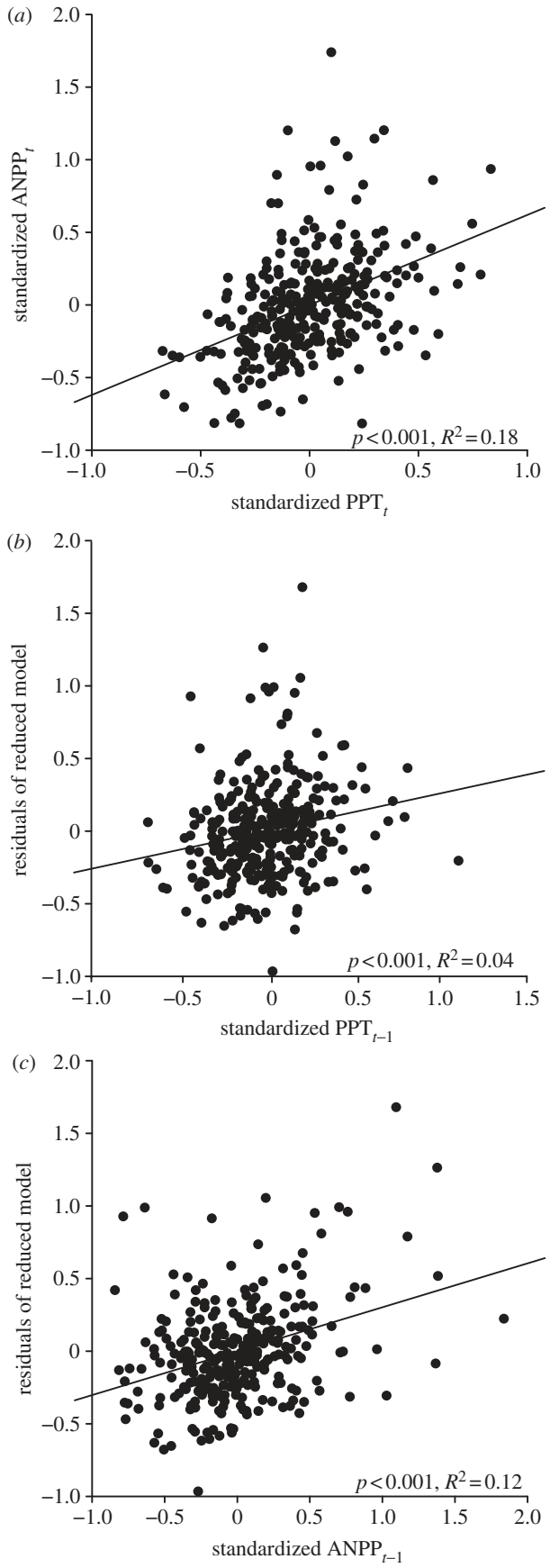

Figure 6. (*a*) Analysis of the pooled 16 study sites for the relationship between standardized ANPP and standardized precipitation (PPT) of the current year (*t*), (*b*) linear residuals of the previous association with the precipitation and (*c*) ANPP of the previous year ($t-1$). ANPP and PPT values for each site were standardized according to their site-specific mean (standardized value = (absolute value − mean)/mean).

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Table 2. Correlation between ANPP and precipitation (PPT) for the current (t) and previous ($t-1$) year and autocorrelations (t versus $t-1$) for ANPP and PPT at the 16 study sites. ANPP, but not PPT, shows a significant and positive autocorrelation in 37% of the sites. Significant correlations at $\alpha = 0.1$ are in bold.

	Pearson correlation			
site	$ANPP_t$, PPT_t	$ANPP_t$, $ANPP_{t-1}$	$ANPP_t$, PPT_{t-1}	PPT_t, PPT_{t-1}
PSA	**0.66**	−0.54	**−0.71**	**−0.78**
SEV	0.07	**0.80**	0.19	−0.16
JRN	**0.53**	**0.58**	0.31	0.17
DZH	**0.55**	−0.20	0.14	**−0.30**
BDK	0.24	0.12	0.03	−0.05
TVA	0.49	−0.09	0.46	**0.90**
XLN	0.42	−0.03	0.23	−0.58
ALB	**0.76**	**0.34**	**0.41**	0.11
SGS	**0.55**	**0.31**	**0.24**	−0.03
TMG	**0.88**	0.43	0.24	−0.07
MNT	0.25	0.58	0.40	0.28
KRS	0.14	**0.35**	0.08	−0.19
NWT	0.01	**0.57**	**0.63**	0.12
KNZ	0.33	0.11	0.25	0.15
NRB	−0.20	0.22	**−0.79**	0.36
CDR	0.06	0.27	0.27	0.20
average	0.36	0.24	0.15	0.01

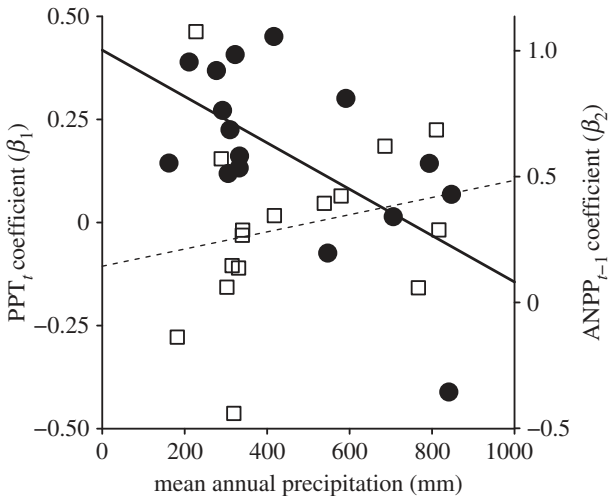

Figure 7. Effects of current-year precipitation 'β_1' (dots) and previous-year ANPP 'β_2' (open squares) on ANPP across the mean annual precipitation (MAP) gradient of 16 study sites reported in table 1. The effects of current year (t) PPT and previous year ($t-1$) ANPP is captured by the slope coefficients β_0 and β_1 of a multiple regression at each of the 16 study sites. The adjusted model is $ANPP = \beta_0 + \beta_1 PPT_t + \beta_2 ANPP_{t-1}$. The effect of PPT_t on ANPP decreases significantly with MAP ($\beta_1 = 0.42 - 0.0006 \times MAP$, $p = 0.013$, $R^2 = 0.37$, $n = 16$). While being predominantly positive, the effect of $ANPP_{t-1}$ shows no significant trends with MAP ($\beta_2 = 0.15 \pm 0.088$ s.e., $p = 0.44$, $R^2 = 0.04$).

temporal models depicted in figure 2 to yield a common model describing the relationship between annual precipitation and ANPP through time. The generalized model for ANPP–PPT through time is

$$stdANPP_t = 0.62 \times stdPPT_t, \tag{3.1}$$

where $stdANPP_t$ is the standardized ANPP (($ANPP_t$− mean)/mean), and $stdPPT_t$ is the standardized PPT of year t ((PPT_t− MAP)/MAP). This model explains 18 per cent of stdANPP variability ($t_{320} = 8.4$, $R^2 = 0.18$, $p < 0.001$) (figure 6*a*).

A significant fraction of the residuals of the temporal-ANPP generalized model (3.1), which related stdANPP and current-year stdPPT, is accounted for by previous-year PPT and ANPP (figure 6*b*,*c*; residuals $= 0.26 \times PPT_{t-1}$, R^2 0.04, $t_{320} = 3.66$, $p < 0.001$; residuals $= 0.30 \times ANPP_{t-1}$, $R^2 = 0.12$, $t_{320} = 6.33$, $p < 0.001$). These analyses represent other tests that rejected the H0 and H2 and H4, Linear-Negative Legacies and Always-Negative Legacies. Previous-year stdANPP explained a larger fraction of the residuals of the temporal stdANPP–stdPPT model than previous-year stdPPT, suggesting that ecosystems amplify the legacy effects of previous-year precipitation. The amplification provides support for H3, Growing-Positive Legacies, which suggested a non-linear response to previous-year precipitation. However, these data do not allow testing for the asymmetrical response proposed in Growing-Positive Legacies hypothesis. Additionally, previous year ANPP captures the effects of other possible controls of productivity that are not related to previous-year PPT.

Analysis of the pooled data reinforces conclusions derived from table 2 and figure 2: (i) temporal models account for much less of the ANPP variability (36%) than spatial models (94, 76 and 48%); (ii) the average slope of temporal models (0.18) is much shallower than the slope of the unified spatial model (0.6) (equation (1.1)).

The relative importance of current-year precipitation decreases with increasing mean annual precipitation (MAP) within the 100–900 mm MAP range expressed by the magnitude of β_1, the coefficient associated with current-year precipitation in a multiple regression model that includes current-year PPT and previous-year ANPP (figure 7 and equation (3.2)).

$$ANPP = \beta_0 + \beta_1\ PPT_t + \beta_2\ ANPP_{t-1}. \tag{3.2}$$

As MAP increases, the frequency of years in which ecosystems are not limited by water also increases. Huxman *et al.* [46] reported a similar trend from deserts to forests. As water becomes less frequently the limiting factor of ANPP, other factors such as N availability become the dominant limiting factor. A recent meta-analysis of N fertilization studies in arid to subhumid ecosystems demonstrated how the frequency of N limitation increases with MAP [47]. The ratio of ANPP in fertilized versus control plots increased with MAP at a rate of 0.3 per cent per millimetre of MAP.

The effect of previous-year ANPP on current-year ANPP is expressed by the magnitude of β_2, the coefficient associated with previous-year ANPP in a multiple regression model (equation (3.2)) that includes current-year PPT (β_1) and previous-year ANPP (β_2). The magnitude of β_2 did not change with MAP (figure 7). Results from this multiple regression analysis

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support the findings associated with figure 5, and stress the importance of previous-year conditions as a control of current-year ANPP along a MAP gradient ranging from 150 to 900 mm.

4. CONCLUSIONS, RESULT IMPLICATIONS AND FUTURE DIRECTIONS

Theory explains, and long-term data analysis and experimentation support, the notion that there are legacies from dry and wet years, and that dry legacies reduce ANPP in current year, and wet legacies increase ANPP relative to the ANPP expected on current-year PPT. Legacies result in lags in ecosystem response and represent an explanation for the differential behaviour of spatial and temporal models of ANPP and PPT as was originally suggested [21]. The phenomenon of legacies to changes in water availability is ubiquitous in arid to subhumid ecosystems, because all sites from North and South America to China and central Europe show a similar behaviour.

Mechanisms driving legacies are similar to those behind differences between spatial and temporal models of ANPP. These mechanisms fit within the framework of pulse–press ecosystem responses [48]. There is a hierarchy of responses to changes in resource availability, in general [49], and in water availability, in particular. Depending on the duration of the resource alteration, pulses can become presses and different response mechanisms are involved. For example, short-term changes in water availability result in changes in leaf water potential and stomatal conductance that are reversed in a matter of hours [50]. Longer changes in water availability, such as those that occur at the annual scale, can result in structural changes in the ecosystem that result in death of individuals or portions of individuals [41,42]. Structural changes require a longer time to occur and to be reversed, and are responsible for legacies reported at the annual scale. Changes resulting from multi-year alterations in water availability [31] may result in other types of structural changes that take even longer to revert. Finally, directional changes in water availability will result in changes in species composition through migration that would mimic the structure and functioning of ecosystems in equilibrium with novel conditions.

Global climate change will result in alterations in the ecosystem water balance as a result of either direct change in precipitation and/or increase in temperature, which indirectly will affect water availability through evaporative demand. Our results suggest that ANPP will respond to changes in water availability and, more importantly, that the magnitude of the response will increase with time. Independently of the rate of change of climate, the ANPP response to a constant modification in water availability will increase through time. At first, the transient response of ANPP to changes in water availability will be that depicted by the temporal model, which is shallower than the spatial model (figure 2). This response will be mediated by physiological changes and constrained by a constant ecosystem structure. Afterwards as slower ecosystem variables such as the relative species abundance start changing, the magnitude of the ANPP response will increase. Finally, when the ecosystem structure reaches equilibrium, the ANPP will resemble predictions of the spatial model. In other words, the temporal models describe the transient ANPP response to climate change and the spatial model describes the equilibrium condition.

Envisioning climate change as a directional change in water availability, the ANPP response will depend on the magnitude of the alteration and time since it occurred. In reality, changes in water availability and the ecosystem response both will be gradual. An important area of research would be to explore how long the transient response will last or the time until the ecosystem will reach equilibrium with the new water availability conditions. In other words, it would be important to assess the rate at which the transient response turns into the equilibrium response. We hypothesize that the rate of change of ecosystems in response to a change in water availability will vary among ecosystem types and will depend on the life-history of organisms, the proximity of alternative flora and the size of nutrient stocks. We expect that ecosystems dominated by long-lived species will have a slower response rate and take longer to reach a new equilibrium than systems with short-lived species. Ecosystems close to ecotones will be able to change their species composition faster than those located close to the centre of that vegetation type. In addition, ecosystems with large nutrient stocks will respond slower than those with ephemeral stocks.

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