Precipitation legacies in desert grassland primary production occur through previous-year tiller density

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Abstract. In arid ecosystems, current-year precipitation often explains only a small proportion of annual aboveground net primary production (ANPP). We hypothesized that lags in the response of ecosystems to changes in water availability explain this low explanatory power, and that lags result from legacies from transitions from dry to wet years or the reverse. We explored five hypotheses regarding the magnitude of legacies, two possible mechanisms, and the differential effect of previous dry or wet years on the legacy magnitude. We used a three-year manipulative experiment with five levels of rainfall in the first two years (−80% and −50% reduced annual precipitation (PPT), ambient, +50% and +80% increased PPT), and reversed treatments in year 3. Legacies of previous two years, which were dry or wet, accounted for a large fraction (20%) of interannual variability in production on year 3. Legacies in ANPP were similar in absolute value for both types of precipitation transitions, and their magnitude was a function of the difference between previous and current-year precipitation. Tiller density accounted for 40% of legacy variability, while nitrogen and carryover water availability showed no effect. Understanding responses to changes in interannual precipitation will assist in assessing ecosystem responses to climate change-induced increases in precipitation variability.

Key words: aboveground net primary production; Chihuahuan Desert; desert grasslands; precipitation legacies; rainfall manipulation; tiller dynamics.

INTRODUCTION

Water availability is the most frequent limiting factor of the functioning of arid and semi-arid ecosystems (Noy-Meir 1973, Lauenroth 1979). For example, there is a strong relationship between mean annual precipitation and mean aboveground net primary production (ANPP) across sites in grasslands of central North America (r² = 0.94 [Sala et al. 1988]; r² = 0.55 [Knapp and Smith 2001]), the Patagonian Steppe (r² = 0.79 [Jobbágy et al. 2002]), the African savannas (McNaughton et al. 1993), and in steppes of Inner Mongolia Plateau (r² = 0.76 [Bai et al. 2008]). Although it is tempting to use this tight relationship to predict changes in productivity through time under a changing climate at a particular site, the temporal relationship between ANPP and annual precipitation (PPT) for individual sites is weak. Annual PPT accounts for only 20–40% of the interannual variability of ANPP (Lauenroth and Sala 1992, Briggs and Knapp 1995, Jobbágy and Sala 2000, Huxman et al. 2004, Sala et al. 2012). We hypothesized that lags in ecosystem response to changes in water availability can explain both the low predictive power of annual precipitation, and the difference between spatial and temporal models relating ANPP and PPT. Lags were expected to result from legacies of wet or dry years such that ANPP would be lower than predicted by current-year precipitation if previous-year precipitation was lower than current-year precipitation. Similarly, ANPP would be higher than expected if the previous year was wetter than the current year.

We defined legacies (in units of grams per square meter per year) as the difference between observed ANPP and expected ANPP deduced from a long-term precipitation–production relationship for this site (Peters et al. 2012):

\[ \text{Legacy} = (\text{ANPP}_\text{observed} - \text{ANPP}_\text{predicted}) \]  

We explored five hypotheses regarding the magnitude of the legacies, the mechanisms leading to legacies, and the differential effect of previous drier or wetter years relative to current year on the magnitude of legacies.

Hypothesis 1 states that the magnitude of legacies is a function of the difference between previous-year precipitation and current-year precipitation (ΔPPT), and there is a first-order linear relationship between the change in PPT (ΔPPT) and the magnitude of the legacy. This is the most parsimonious prediction based on the linear
relationships between PPT and ANPP at both spatial and temporal scales. Mechanisms behind this hypothesis are presented in hypotheses 2–4.

Hypothesis 2 states that legacies result from changes in tiller density. This hypothesis is based on the rare frequency of sexual reproduction of dominant perennial grasses in most grassland ecosystems (Neilson 1986, Lauenroth et al. 1994, Hartnett and Fay 1998), where population persistence of perennial grasses relies upon tiller recruitment from axillary buds located at the base of tillers (Langer 1972). Evidence suggests that the number of axillary buds produced in each tiller is an inflexible trait (Hendrickson and Briske 1997, Flemmer et al. 2002); thus tiller density would be a sensitive response variable to current and past changes in water availability. When dry years precede wet years, tiller density can constrain ANPP by limiting recruitment of new tillers and maximum leaf area despite higher than previous resource availability. On the contrary, when wet years precede dry years, existing high tiller density may enhance productivity because the maintenance cost of leaves and buds is lower than the extra carbon/energy that plants can acquire by having such structures (Sala et al. 2012). Shrub ANPP in the Chihuahuan Desert showed small interannual variation and weak response to annual precipitation in a 14-year observational study (regressions not significant; Peters et al. 2012). Thus, changes in grass productivity may account for the majority of total ANPP legacies in this ecosystem, and tiller density is the appropriate response variable to assess the strength of vegetation structure controls on ANPP.

Hypothesis 3 states that legacies result from biogeochemical phenomena, with mineral nitrogen (N) availability limiting ANPP when the preceding year was drier than the current year, and enhancing ANPP when the previous year was wetter than the current year. This hypothesis is based on the assumption that the amount of N at the beginning of the growing season is a function of previous year ANPP. In other words, previous year ANPP determines the input of labile organic matter that controls N availability and modulates ecosystem response to water availability.

Hypothesis 4 states that legacies result from soil moisture carry-over between years. Soil moisture may have a delayed response to changes in precipitation (Sherry et al. 2008), and we may detect differences in soil moisture at the beginning of the growing season in years following dry years compared with years following wet years.

Hypothesis 5 states that there is an asymmetric response of legacies to PPT transitions such that the absolute magnitude of a legacy is different if the ecosystem transitions from a wet year to a dry year than if it transitions from a dry to a wet year. We expect that drought legacies would be linear with the magnitude of drought, but wet-year legacies would be more than proportional to change in precipitation based on a cost-benefit analysis of plant responses. Deploying new roots and leaves has a cost for plants incurred at the time of production, whereas the benefits result from the resources that those structures acquire over their lifetime (Lauenroth et al. 1987). Because plants have already invested resources required to grow new structures, the threshold for abscising them may be higher than the threshold for deploying them (Bloom et al. 1985). An increase in precipitation from one year to the next would increase the number of tillers, but a decrease in precipitation of similar magnitude would not result in tiller death. High sensitivity to increased resources may benefit plants because they can acquire resources that otherwise would be lost. This sensitivity would be particularly important for transient resources, such as soil water in arid systems, which are lost via evaporation if not used rapidly by plants (Schwinning and Sala 2004). 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 results from a study of long-term ANPP trends for 11 sites where the absolute values of extreme positive ANPP deviations were larger than the extreme negative deviations (Knapp and Smith 2001).

We tested our hypotheses with a PPT and N manipulative experiment in the Chihuahuan Desert where we reproduced wet-to-dry and dry-to-wet transitions in annual PPT to test hypotheses 1, 2, 4, and 5, and fertilized with N to test hypothesis 3. We examined the relationship between the response variable of legacy and change in PPT, tiller density, and N availability.

**Methods**

**Site description**

The study was conducted in the Jornada Basin Long Term Ecological Research site (32.5°N, 106.8°W, 1188 m above sea level) located in the northern Chihuahuan Desert, New Mexico, USA. Mean annual precipitation is 264 mm and average temperature is 14.4°C. We conducted our three-year experiment (2007–2009) in a desert grassland dominated by Bouteloua eriopoda (Torr.) Torr. (black grama) followed by Prosopis glandulosa Torr. (honey mesquite), which jointly account for 65% of plant cover. Soils are coarse-textured, well-drained, sandy loam soils (Typic Paleothids) (Soil Survey Staff 1999) with a layer of calcium carbonate that is often found at depths from 64 to 76 cm (Herbel et al. 1972, Gibbens et al. 1986).

**Experimental design**

During the first two years, manipulations consisted of five levels of precipitation: −80% and −50% reduced, ambient control, and +50% and +80% increased; half of the plots were fertilized with ammonium nitrate (n = 12, 2.5 × 2.5 m plots per treatment). The first two years preconditioned the experimental plots for year three, in which we created wet-to-dry and dry-to-wet transitions in annual PPT by switching half of the replicate plots of
each precipitation level to either a reduced PPT or an increased PPT treatment. PPT transitions imposed during the third year resulted in a broad range of ΔPPT that included 10 different scenarios of wetter to drier and drier to wetter transitions (ΔPPT = average water year PPT of years 1 and 2 minus water year PPT of year 3; \( n = 6 \) plots per ΔPPT level). In addition, we kept ambient PPT plots throughout the duration of the study (\( n = 6 \)), resulting in an experiment with 132 plots. An equivalent observational study would have needed at least 12 years to obtain comparable ΔPPTs. Ambient water year precipitation was 344 mm, 312 mm, and 117 mm in 2007, 2008, and 2009, respectively. Growing season precipitation accounted for 40%, 84%, and 63% of water year PPT each year. Due to a drier than average growing season during 2009, wet treatments received five additional irrigations of 20 mm each during September.

Since the objective of this study was to assess the effect of previous-year precipitation on current-year ANPP, the design did not alter the seasonal PPT pattern, the onset of the growing season, or the proportion of growing season PPT to total PPT each year. Consequently, all treatments had simultaneous rains, a similar number of PPT events, and the same amount of days between each PPT event. Given our full factorial design, both wet–dry and dry–wet PPT transitions shared the same seasonal distribution of PPT across years, and the only variable that changed among treatments was annual PPT amount. Thus, the experimental design excludes the possibility that any of the results reported here were due to differences in the timing or seasonality of precipitation between years.

Plots were established in three blocks on a level upland with flat slopes (1–5%) that were fenced from cattle grazing since 1996. We used a randomized complete block design and randomly assigned one treatment combination to each plot within each block. We chose plots of similar vegetation cover, so that initial cover of the dominant shrub and grass species was not statistically different (\( P > 0.05 \)) among the three blocks. We preselected 170 plots and measured black grama and mesquite cover, then selected 132 plots in which plant cover fell within a 95% confidence interval of the mean cover of the dominant shrub and grass species. ANPP was calculated differently in the southwestern rangelands of the United States study site where ANPP was calculated differently from other studies. Shelters have a metal structure that supports transparent acrylic “shingles” per shelter. Rainout shelters were installed in November 2006. Similar rainout shelters are being used in many studies from the Patagonian steppe, the Arctic tundra, the shortgrass steppe, the Mediterranean and Californian grasslands to the southwestern rangelands of the United States (Heisser-White et al. 2008, Adler et al. 2009, Fiala et al. 2009, Levine et al. 2010, Rao and Allen 2010, Matias et al. 2011). Shelters have a metal structure that supports V-shaped clear acrylic bands or shingles molded from acrylic ACRYLITE FF (CYRO Industries, Parsippany, New Jersey, USA.) This material has high light transmission (>92% PAR transmitted) and <3% change in light transmission over a 10-yr period. Shelters intercept a fraction of incoming precipitation, which is then routed outside the plot by a gutter. Yahdjian and Sala (2002) tested the shelters’ effect on the microenvironment, and found only a small edge effect of ~20 cm on soil water content; hence we excluded the edge area from our sampling.

For the water addition treatments, an irrigation system was used to water plots with sprinklers the day after a PPT event (defined as >2 mm) using rainfall collected off site and transported to treatment plots. Water addition treatments were installed at the beginning of the summer monsoon season in June of 2007. A wireless datalogger located <300 m from our experiment recorded daily precipitation data that we used to apply the water treatment.

\textbf{Fertilization.—Ammonium nitrate fertilizer was applied twice each growing season in mid- and late July from 2007 to 2009, and consisted of 10 g N-NH4N03-m~2-yr~1. We are confident that this level of fertilizer is similar to the levels of fertilizer used in this ecosystem (Sala and Austin 2000). Shelters were only removed to perform nondestructive annual measurements of vegetation production of grasses was equated to green biomass at peak growing season. Grass biomass (grams per square meter) = 264.56 X percentage cover of grass, \( N = 20 \), \( r^2 = 0.88, P < 0.01 \); grass cover was between 0.09% and 0.80%. Shrub biomass (grams per square meter) = 184.61 X shrub percentage cover, \( N = 20 \), \( r^2 = 0.88, P < 0.01 \); cover ranged between 0.08% and 0.75%. Regressions were forced through zero (Flombaum and Sala 2007). We recorded green interception per species for all plants present in the plot with three parallel lines, each of 250 cm length and evenly spaced from the east border, and used the regressions to obtain an estimate of biomass by species. Annual aboveground primary production of grasses was equated to green biomass at peak biomass (Sala and Austin 2000). We are confident of our biomass–cover regressions as they give comparable estimates of ANPP to those from the LTER-IBP exclosure, a grassland with similar characteristics to our study site where ANPP was calculated differently from other studies. This approach allows us to compare relative differences in ANPP to those from the LTER-IBP.
and EC-20 soil moisture sensors (Decagon Devices, Pullman, Washington, USA) were installed vertically at 20 cm and 30–50 cm depth, respectively, always above soil carbonate layers. We used an ECELO check to measure volumetric water content (VWC) measurements the first, third, and fifth days following a precipitation event >2 mm, and every 2–3 weeks during the period in between rainfall events. Here, we report soil moisture values for 11 May 2009, the last sampling date in the spring of 2009, just before treatments were switched in June of 2009. Probes were calibrated for soils at the site following the protocol developed by the manufacturer ($r^2$ of 0.98 and 0.96 for EC-5 and EC-20 probes).

Precipitation legacy.—Legacies were estimated from Eq. 1, where ANPP$_{observed}$ was the actual ANPP of grasses and shrubs measured for each individual plot during the last year of manipulations, and ANPP$_{predicted}$ for each experimental PPT level was estimated from the equation:

$$\text{ANPP} = 15.1 + 0.39 \times \text{PPT} \quad \text{(in millimeters per year)} \quad \text{(Peters et al. 2012).}$$

Tiller density.—We counted the number of physiologically active tillers (grass leaf-bearing units) of $B.\$ eriopoda$ at peak biomass in the second year of rainfall manipulations. Tillers were counted within a 40 cm diameter ring located in each plot, and expressed as number of tillers per square meter. Given the spatial heterogeneity of the vegetation, rings were located in a black grama patch with the highest proportion of grass cover within the plot. Physiologically active tillers were those with at least one green leaf present at the time of sampling.

Soil reactive nitrogen and leaf N.—We sampled soils at the beginning of the growing season in year 3 after switching PPT treatments. Soil cores of 5 cm diameter by 10 cm depth were subjected to standard KCl extraction of $NO_3^-$ and $NH_4^+$ within five hours of collection. KCl extraction of $NO_3^-$ and $NH_4^+$ consisted in sieving soils through a 2-mm mesh, and extracting a 10-g subsample in 50 mL of 2 mol/L KCl solution. Nitrate and ammonium concentration in the KCl extracts was estimated using colorimetric methods with a two-channel QuikChem 8500 flow injection analyzer (Lachat Instruments, Hach Company, Loveland, Colorado, USA). Soil N concentration was corrected for soil water content (Jarrell et al. 1999) after drying a subsample in an oven at 105°C for 48 h. We analyzed the N content in leaves (percentage of mass) of mesquite and black grama to assess the effectiveness of the fertilization treatment. Leaves were collected during 2008 and 2009 growing seasons (21 July 2008 and 8 October 2009) and were dried at 60°C, ground, and analyzed for N content in an elemental analyzer (Costech Analytical, ECS 4010; Valencia, California, USA).

Soil moisture.—Volumetric water content was measured in six plots per treatment before switching precipitation treatments in the spring of year 3. EC-5 and EC-20 soil moisture sensors (Decagon Devices, Pullman, Washington, USA) were installed vertically at 5–10 cm and 30–50 cm depth, respectively, always above soil carbonate layers. We used an ECH2O check handheld (Decagon Devices) to take volumetric water content (VWC) measurements the first, third, and fifth days following a precipitation event >2 mm, and every 2–3 weeks during the period in between rainfall events.

Results

We were able to experimentally reproduce hypothesized legacies. We found lower ANPP than expected during the last year of manipulations in treatments where water year precipitation in the previous year was lower than current year, and higher ANPP than expected in those treatments that had higher precipitation in the previous year compared to the current year (Fig. 1A). Legacies in ANPP increased linearly with the
Legacies in ANPP produced by wet-to-dry or dry-to-wet PPT transitions did not differ in slope between fertilized and unfertilized treatments (Fig. 1A), and PPT legacies were not related to soil inorganic N (Fig. 1C). The increase in soil-available N (Fig. 2B) and leaf N concentration (Fig. 3) with fertilization showed the effectiveness of the treatment. Soil-available N increased 20 times in fertilized compared to control treatments (N effect $F_{1,127} = 698.5, P < 0.0001$), and N concentration was significantly higher in fertilized than in unfertilized leaves of the grass B. eriopoda in both 2008 and 2009 ($F_{1,18} = 7.11; P = 0.016$, and $F_{1,113} = 14.84; P = 0.0002$, respectively; Fig. 3A). Similarly, N concentration was higher in the grass than in the shrub during the first two years of manipulations. Grasses that experienced drought had lower tiller density than those that experienced ambient or increased PPT in years 1 and 2 (tiller density$_{t-1} = 1292.19 + 1.2$ PPT$_{t-1}; F_{1,127} = 19.22, P < 0.0001, R^2 = 0.13$; Fig. 2A).

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higher in fertilized than unfertilized leaves of *P. glandulosa* in 2009 but not in 2008 ($F_{1,17} = 1.72, P = 0.2$, and $F_{1,123} = 10.10, P = 0.002$ for 2008 and 2009, respectively; Fig. 3B).

Soil moisture measured prior to wet-to-dry and dry-to-wet transitions on 11 May 2009 was not different among precipitation treatments either at 30–50 cm or at 5–10 cm depths (ANOVA $F_{1,26} = 1.969, P = 0.172$ and $F_{1,28} = 0.606; P = 0.443$ respectively; Fig. 4). Thus, differences in precipitation among treatments have no water availability carryover effect from one year to the next.

**DISCUSSION**

Our results support the hypothesis that changes in annual precipitation result in legacies in ANPP and that legacies are proportional to the difference between current and previous precipitation. The magnitude of the legacies is quite relevant: 15 g m$^{-2}$ yr$^{-1}$ (Fig. 1), which represents ~20% of the three-year average total productivity of ambient PPT treatments. We experiment-
tally reproduced wetter to drier and drier to wetter transitions in annual PPT that resulted in legacies in ANPP, as suggested by long-term data for many grassland sites (Laufenroth and Sala 1992, Sala et al. 2012). The use of relatively inexpensive rainout shelters allowed us to conduct a well-replicated experiment, including switching treatments in year 3, across a broader range of ΔPPT than most irrigation or drought-only experiments (Fay et al. 2003, Yahdjian and Sala 2006, Shinoda et al. 2010). In the Patagonian Steppe, Yahdjian and Sala (2006) reproduced drought PPT legacies, and showed that they were a consequence of previous dry years. Here, we found drought and wet legacies in ANPP, and unraveled the potential mechanisms explaining them.

Our results also support the hypothesis that legacies result from changes in tiller density. The number of tillers at the end of the previous growing season explained ~40% of legacy variability. In a manner similar to other semiarid ecosystems, perennialing structures are key to population persistence in the Chihuahuan Desert. In grasslands, perennialing structures such as tillers become important because recruitment from seed is an episodic and rare phenomenon, and annuals account for a small fraction of total ANPP (<5%) (Laufenroth et al. 1994). Tillers bear meristematic tissue located at or beneath the soil surface in the form of axillary buds that are responsible for vegetative reproduction. Because it is assumed that the number of dormant buds per tiller is fixed (Hendrickson and Briske 1997, Fießmer et al. 2002), changes in tiller density may impact ANPP. In our study, tiller density accounted for an extra 13% of ANPP variability. Our data suggest that PPT affects the capacity of plants to replace tiller populations, and that ANPP is constrained by tiller density following dry years and enhanced following wet years. Our results support the hypothesis posed by Laufenroth and Sala (1992) that temporal controls of ANPP respond to slow changes in vegetation structure.

Our results do not support the hypothesis that legacies result from N limitation. With the fertilization experiment, we aimed at removing hypothetical N limitation that could result in biogeochemical PPT legacies. Even though fertilization increased N concentration in soil and in leaves, it did not modify legacies. Our explanation for the lack of biogeochemical legacies is that soil N concentration may respond primarily to recent soil water conditions. Since soil microorganisms can respond faster than plants (Schwinning and Sala 2004), PPT transitions may result only in short-term changes in N availability (Yahdjian and Sala 2010; Reichmann et al. 2013).

We rejected the hypothesis that legacies were the result of soil moisture carryover that could have occurred because water in the 30–50 cm layer was not used in the previous growing season or was brought there by mesquite hydraulic lift (Richards and Caldwell 1987). Thus, the significant and positive relationship between legacy and ΔPPT cannot be attributed to differences in soil moisture between dry preceding or wet preceding years, but rather to biotic mechanisms mediating the ecosystem response to antecedent environmental conditions. The lack of soil moisture carryover from one year to the next provides additional support to our biotic hypothesis that vegetation structure mediates the ANPP response to PPT transitions. Long-term analysis of soil water data from another summer precipitation treatment supports the idea that in arid and semiarid ecosystems, characterized by a large difference between PPT and PET, all the incoming precipitation is lost by the end of the growing season (Sala et al. 1992).

We rejected the hypothesis that legacies are asymmetric for positive or negative changes in PPT. Instead, the relationship between legacy magnitude and ΔPPT from wet-to-dry transitions had the same slope as legacies from dry-to-wet. This result has implications for the functioning of ecosystems under future climates. Some global change models predict a transition to a more arid climate in southwestern North America (Seager et al. 2007). More importantly, an increase in interannual variability of precipitation, including increased frequency of extreme events, is likely to occur (Solomon et al. 2007). Our results imply that, in the absence of long-term changes in PPT amount, changes in interannual

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**Fig. 4.** The effect of precipitation treatments on soil moisture at 5–10 cm and 30–50 cm depth prior to PPT transitions. There were no significant differences in soil moisture among precipitation treatments either at shallow (open circles) or deep (solid circles) soil depth. Soil moisture was recorded during the dry, hot spring of 2009 on 11 May, reflecting soil water status prior to the treatment switch in June of 2009. Data points represent volumetric soil water content (%), mean ± SE, n = 6 (ANOVA, F₁,26 = 1.969, P = 0.172, for soil moisture at 5–10 cm; F₁,26 = 0.606, P = 0.443, for soil moisture at 30–50 cm).
variability of PPT would not affect average ANPP because wet legacies would offset dry legacies.

Precipitation seasonality exerts an important control on ecosystem processes, from productivity (Gao and Reynolds 2003, Xiao and Moody 2004), to heterotrophic respiration (Potts et al. 2006), to species interactions (Suttle et al. 2007). Seasonality changes in the Southwest are associated with frequency of El Niño events that increase winter precipitation but have small effects on summer monsoons (Sheppard et al. 2002). Chihuahuan Desert grasslands have a high potential to respond to changes in seasonality as a result of their mixture of C3 and C4 species with differential rooting depth (Throop et al. 2012). Given the complexity of the interactions between seasonality and legacies, this paper focused exclusively on the latter. Independent studies of the effects of seasonality on this ecosystem type are needed to fully understand the consequences of climate change on ecosystem functioning.

Few studies have addressed the effect of changes in interannual PPT variability on ANPP in grasslands. Most studies focused on the response of productivity to changes in intra-annual precipitation and showed opposite responses ranging from 18% ANPP reduction to 70% ANPP increase, depending on the site (Fay et al. 2002, 2003, Knapp et al. 2002, Heisler-White et al. 2009). Mechanisms that control productivity response to intra-annual PPT patterns may be different from those operating at interannual scales, highlighting the value of studying PPT variability at different temporal scales.


