

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 carry-over 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 semiarid 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 ($r^2 = 0.94$ [Sala et al. 1988]; $r^2 = 0.55$ [Knapp and Smith 2001]), the Patagonian Steppe ($r^2 = 0.79$ [Jobbágy et al. 2002]), the African savannas (McNaughton et al. 1993), and in steppes of Inner Mongolia Plateau ($r^2 = 0.76$ [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):

$$\text{Legacy} = (\text{ANPP}_{\text{observed}} - \text{ANPP}_{\text{predicted}}). \quad (1)$$

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

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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 Δ PPT that included 10 different scenarios of wetter to drier and drier to wetter transitions (Δ PPT = average water year PPT of years 1 and 2 minus water year PPT of year 3; $n = 6$ plots per Δ PPT 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 Δ PPTs. 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 for mesquite and black grama. In the remaining 132 plots, mean black grama cover was $0.19\% \pm 0.08\%$ (mean \pm standard error). Mean mesquite cover was $0.11\% \pm 0.03\%$.

Water manipulation.—We installed individual rainout shelters in reduced-PPT plots (methods from Yahdjian and Sala 2002). Shelters were only removed to perform measurements underneath them. Reduction of 50% or 80% of rainfall was achieved using different numbers of 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

(Heisler-White et al. 2008, Adler et al. 2009, Fiala et al. 2009, Levine et al. 2010, Rao and Allen 2010, Matías 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.

Fertilization.—Ammonium nitrate fertilizer was applied twice each growing season in mid- and late July from 2007 to 2009, and consisted of $10 \text{ g N-NH}_4\text{NO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ dissolved in water. The same amount of water, equivalent to a 2-mm rain, was applied to the control N plots.

Response variables

Aboveground net primary production.—We estimated ANPP in the third year of manipulations from nondestructive annual measurements of vegetation cover data and site-specific cover-to-biomass regressions following standard procedures (Flombaum and Sala 2007). We double-sampled cover and biomass in an area adjacent to our experiment and obtained regression coefficients for grasses and shrubs. The data set consisted of forty 20×100 cm plots where we measured plant cover and harvested perennial grasses and shrubs at peak growing season. Grass biomass (grams per square meter) = $264.56 \times$ percentage cover of grass, $N = 20$, $r^2 = 0.68$, $P < 0.001$; grass cover was between 0.09% and 0.80%. Shrub biomass (grams per square meter) = $184.61 \times$ shrub percentage cover, $N = 20$, $r^2 = 0.88$, $P < 0.001$; 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 enclosure, a grassland with similar characteristics to our study site where ANPP was calculated differently

(Huenneke et al. 2001) (i.e., 173 ± 24.23 g dry biomass·m⁻²·yr⁻¹ estimated in our control plots vs. 191.8 g dry biomass·m⁻²·yr⁻¹ at the IBP site in 2008; data available online).⁵

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 a long-term linear regression of precipitation and production (grass + shrub) obtained in similar grasslands of the Jornada Basin, where ANPP (g dry biomass·m⁻²·yr⁻¹) = $15.1 + 0.39 \times \text{PPT}$ (in millimeters per year) (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 NO₃⁻ and NH₄⁺ within five hours of collection. KCl extraction of NO₃⁻ and NH₄⁺ 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 by 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. 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).

Statistical analyses

We used general linear models to test the relationship between PPT legacies and changes in PPT, tiller density, and N availability, and used the *F* test of extra sum of squares and partial R^2 for determining how the proposed mechanisms contribute to the prediction of ANPP. We tested for asymmetries with an ANCOVA model with legacy as the dependent variable, and type of legacy (dry or wet, qualitative) and ΔPPT (quantitative) as predictor variables. Legacies were tested for normal distribution with a Shapiro-Wilk test on the probability distribution to discard asymmetries. We used the lowest Akaike Information Criterion (AIC) for selecting among linear, exponential, logarithmic, and power models of PPT legacies as a function of ΔPPT . Soil moisture carry-over was tested with an ANOVA on soil moisture differences among treatments in the dry spring before the onset of the last growing season and treatment switch. We examined the effectiveness of the fertilization treatment with an ANOVA test on leaf nitrogen content in grasses and shrubs. For all analyses, statistical significance was determined at $\alpha = 0.05$. Block was included in the analyses as a random effect. The JMP v.9.0.2 from SAS Institute (SAS Institute 2009) was used for all analyses. For the purpose of this study, we defined annual precipitation as the water year precipitation received between 1 October and the following 30 September. We calculated water year precipitation input per precipitation treatment by either adding the irrigated amount, or by subtracting the percentage intercepted by rainout shelters to the ambient PPT. ΔPPT was calculated as the difference between previous and current year PPT ($\Delta\text{PPT} = \text{PPT}_{t-1} - \text{PPT}_t$), where previous-year PPT was the average water year PPT received in each treatment during the first two years, and current PPT was the water year PPT received in each treatment in the last year of manipulations.

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

⁵ <http://jornada-www.nmsu.edu/datacat.php>

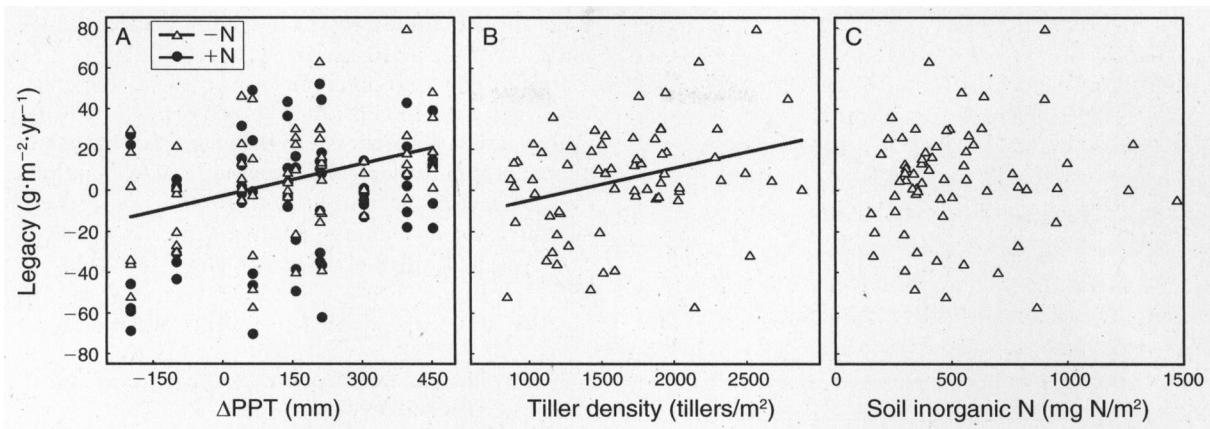


FIG. 1. Precipitation legacies in total aboveground net primary production as a function of (A) the difference between current and previous-year precipitation (Δ PPT), (B) previous-year tiller density, and (C) soil inorganic nitrogen ($\text{NO}_3^- + \text{NH}_4^+$) at the beginning of the current-year growing season. Legacies are the differences between observed and expected annual aboveground net primary production (ANPP) calculated from year-3 ANPP. Legacies were proportional to the difference between previous and current-year PPT, and previous-year tiller density; Δ PPT $>$ 0 for treatments with wet-to-dry PPT transitions; Δ PPT $<$ 0 for treatments with dry-to-wet PPT transitions. Soil N concentration (mg/m^2) was estimated as the sum of N-NH_4^+ and N-NO_3^- in 10 cm deep soil samples and converted to area by multiplying by soil bulk density. For the Δ PPT effect, legacy = $-2.71 + 0.05(\Delta$ PPT), $n = 132$, $R^2 = 0.42$, $P = 0.0004$. For previous-year tiller density effect, legacy = $-25.61 + 0.019(\text{previous-year tiller density})$, $n = 66$, $R^2 = 0.38$, $P = 0.0007$. The effect of inorganic N on legacies was not significant, $P = 0.92$. Data points represent individual plot observations for unfertilized (open triangles) and fertilized (solid circles) treatments.

difference between previous and current water year PPT (Δ PPT [in millimeters]) that was created with the experimental manipulation (legacy = $-2.71 + 0.05 \Delta$ PPT; $F_{1,126} = 12.99$, $P = 0.0004$, $R^2 = 0.42$; Fig. 1A). Negative legacies resulted from dry-to-wet PPT transitions where drought-preceding treatments produced less than expected from current-year PPT. Wet-to-dry PPT transitions, in contrast, had positive legacies resulting in higher production than expected. As a result, the magnitude of the legacy was proportional to Δ PPT, with decreased ANPP in dry-to-wet PPT transitions and increased ANPP in wet to dry.

Shrubs and grasses had different responses to current and previous-year PPT (PPT_{t-1}) such that legacies resulted mostly from the response of grass ANPP to PPT transitions (Table 1). Only grass ANPP was correlated to PPT_{t-1} , and almost 80% of grass ANPP variability was accounted for by PPT and PPT_{t-1} . On the contrary, current and previous-year precipitation explained a small proportion of shrub ANPP variability (12%, Table 1).

Legacies were not asymmetric because the relationship between legacy and Δ PPT was not different between wet-to-dry and dry-to-wet PPT transitions (type of legacy \times Δ PPT, $F_{1,126} = 0.35$, $P = 0.55$). Moreover, legacies in ANPP were normally distributed (Shapiro-Wilk W Test, $P = 0.46$, $N = 132$) with a mean of $0.8 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ and 95% of the values between -56 and $57 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$.

Legacies in ANPP were positively related to the number of tillers present in the previous year (legacy = $-25.61 + 0.019$ tiller density $_{t-1}$; $F_{1,62} = 12.81$, $P = 0.0007$, $r^2 = 0.37$; Fig. 1B). Tiller density at the end of the previous-year growing season constrained ANPP in

plots with less than ~ 1600 tillers/ m^2 , and enhanced ANPP in plots with more than this tiller density. Grasses had different tiller densities depending on PPT received 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 $_{t-1} = 1292.19 + 1.2 \text{ PPT}_{t-1}$; $F_{1,127} = 19.22$, $P < 0.0001$, $R^2 = 0.13$; Fig. 2A).

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

TABLE 1. Multiple regression analysis of grass and shrub annual aboveground net primary production (ANPP) as a function of current-year precipitation (PPT_t) and previous-year precipitation (PPT_{t-1}).

Parameter estimate	Shrub ANPP		Grass ANPP	
	Estimate	P	Estimate	P
Intercept	21.901	<0.0001	-0.895	0.93
PPT_t	-0.018	0.059	0.315	<0.0001
PPT_{t-1}	-0.008	0.28	0.043	<0.01

Notes: All $N = 66$. Shrub ANPP $R^2 = 0.12$; grass ANPP $R^2 = 0.81$.

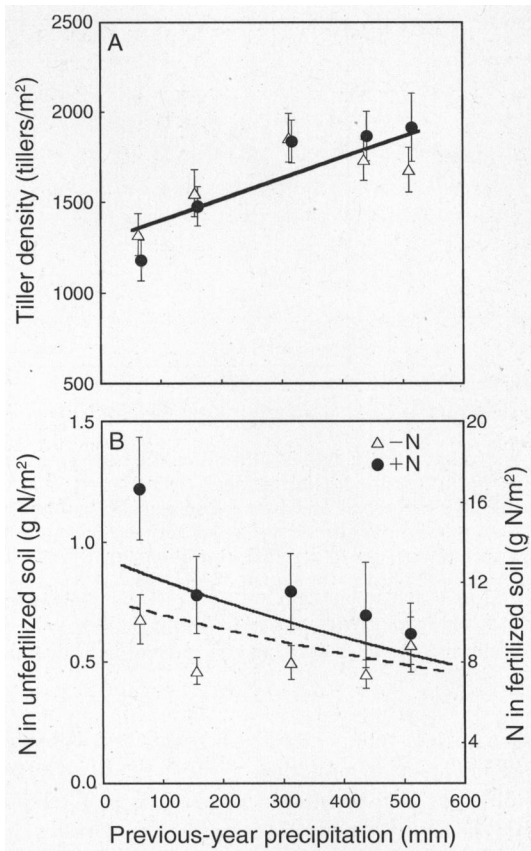


FIG. 2. (A) The effect of previous-year PPT and fertilization on tiller density. The number of tillers increased with PPT in both unfertilized (open triangles) and fertilized (solid circles) treatments (tiller density = $1292.19 + 1.2(\text{previous-year PPT})$; $F_{1,127} = 19.22$, $P < 0.0001$, $R^2 = 0.13$). Physiologically active tillers were counted at the end of the previous-year growing season. Data represent mean tiller density per treatment \pm SE, $n = 12$. (B) The effect of previous-year PPT and fertilization on available soil N. Total inorganic N at the beginning of the growing season was higher in treatments with drought history than in those that received additional PPT in the previous year, in both unfertilized (open triangles) and fertilized (solid circles) treatments (ln soil N = $6.39 - 0.0007[\text{previous-year PPT}] + 3.07N$ [where $N = 0$, unfertilized; $N = 1$, fertilized]; PPT effect $F_{1,127} = 4.14$, $P = 0.04$; N effect $F_{1,127} = 698.5$, $P < 0.0001$; whole-model $R^2 = 0.85$). Nitrogen data were ln-transformed to fit statistical assumptions. Points represent mean N concentration per treatment (g/m^2) \pm SE at 0–10 cm, $n = 12$. Lines represent significant logarithmic fits (dashed, unfertilized; solid, fertilized); $P < 0.05$. Note different y-axes for unfertilized (left) and fertilized (right) treatments.

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: $15 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (Fig. 1), which represents $\sim 20\%$ of the three-year average total productivity of ambient PPT treatments. We experimen-

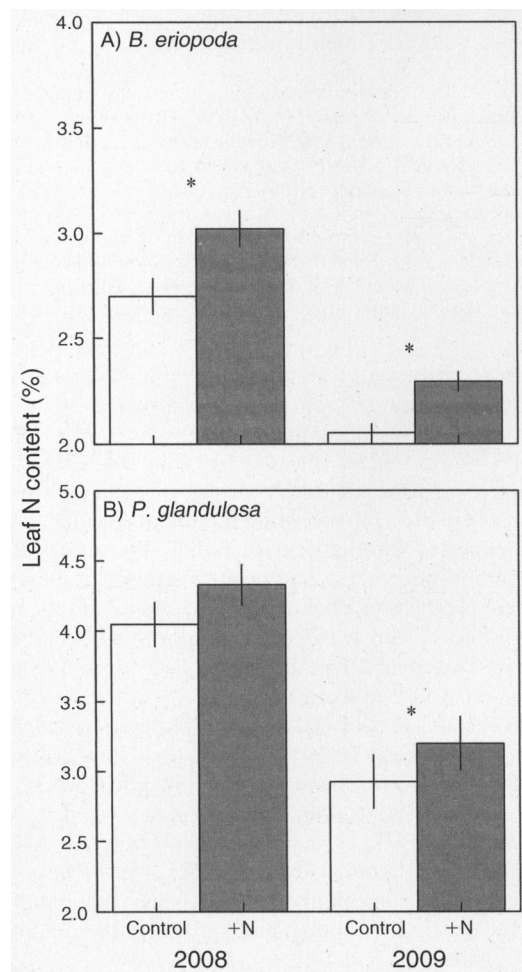


FIG. 3. (A) N concentration (as percentage mass) in *Boutelou eriopoda* leaves from control and fertilized treatments in 2008 and 2009; higher N concentration was found in fertilized treatments (gray bars) than in controls (white bars) in both years (ANOVA test: $F_{1,18} = 7.11$, $P = 0.016$; $F_{1,113} = 14.84$, $P = 0.0002$, respectively). (B) N concentration (as percentage mass) in *Prosopis glandulosa* leaves from control and fertilized treatments in 2008 and 2009; N concentration was higher, but did not significantly differ, in fertilized (gray bars) compared with unfertilized (white bars) leaves of *P. glandulosa* in 2008 (ANOVA, $F_{1,17} = 1.72$, $P = 0.2$). Significantly higher N was found in *P. glandulosa* leaves from fertilized treatments in 2009 (ANOVA, $F_{1,123} = 10.10$, $P = 0.002$). Bars represent means \pm SE, $n = 10$ (2008), and $n = 66$ (2009). Stars indicate significant differences at $P < 0.05$.

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 (Lauenroth 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 Δ PPT 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 $\sim 40\%$ of legacy variability. In a manner similar to other semiarid ecosystems, perennating structures are key to population persistence in the Chihuahuan Desert. In grasslands, perennating 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 ($<5\%$) (Lauenroth 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, Flemmer 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 Lauenroth 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

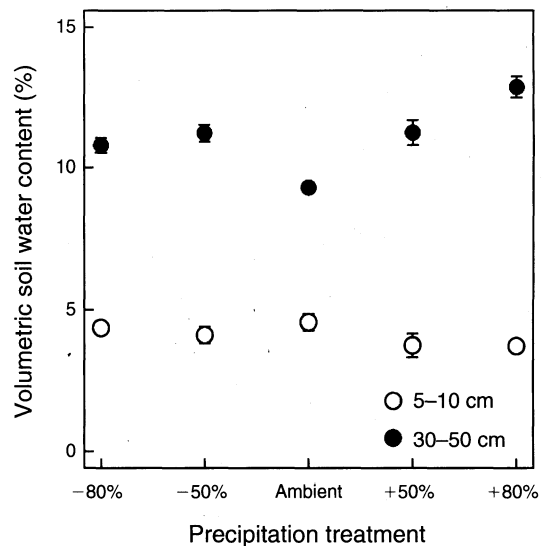


FIG. 4. The effect of precipitation treatments on soil moisture at 5–10 cm and 30–50 cm depth prior to PPT transitions. There were no significant differences in soil moisture among precipitation treatments either at shallow (open circles) or deep (solid circles) soil depth. Soil moisture was recorded 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 \pm SE, $n = 6$ (ANOVA, $F_{1,26} = 1.969$, $P = 0.172$, for soil moisture at 5–10 cm; $F_{1,28} = 0.606$, $P = 0.443$, for soil moisture at 30–50 cm).

between legacy and Δ PPT 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 ecosystem 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 Δ PPT 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

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.

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LITERATURE CITED

- Adler, P. B., J. Leiker, and J. M. Levine. 2009. Direct and indirect effects of climate change on a prairie plant community. *PLoS ONE* 4:6 pages.
- Bai, Y., J. Wu, Q. Xing, Q. Pan, J. Huang, D. Yang, and X. Han. 2008. Primary production and rain use efficiency across a precipitation gradient on the Mongolian Plateau. *Ecology* 89:2140–2153.
- Bloom, A. J., F. S. Chapin, III, and H. A. Mooney. 1985. Resource limitation in plants: an economic analogy. *Annual Review of Ecology and Systematics* 16:363–392.
- Briggs, J. M., and A. K. Knapp. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil-moisture, topographic position, and fire as determinants of aboveground biomass. *American Journal of Botany* 82:1024–1030.
- Fay, P. A., J. D. Carlisle, B. T. Danner, M. S. Lett, J. K. McCarron, C. Stewart, A. K. Knapp, J. M. Blair, and S. L. Collins. 2002. Altered rainfall patterns, gas exchange, and growth in grasses and forbs. *International Journal of Plant Sciences* 163:549–557.
- Fay, P. A., J. D. Carlisle, A. K. Knapp, J. M. Blair, and S. L. Collins. 2003. Productivity responses to altered rainfall patterns in a C₄-dominated grassland. *Oecologia* 137:245–251.
- Fiala, K., I. Tüma, and P. Holub. 2009. Effect of manipulated rainfall on root production and plant belowground dry mass of different grassland ecosystems. *Ecosystems* 12:906–914.
- Flemmer, A. C., C. A. Busso, and O. A. Fernandez. 2002. Bud viability in perennial grasses: water stress and defoliation effects. *Journal of Range Management* 55:150.
- Flombaum, P., and O. E. Sala. 2007. A non-destructive and rapid method to estimate biomass and aboveground net primary production in arid environments. *Journal of Arid Environments* 69:352–358.
- Gao, Q., and J. F. Reynolds. 2003. Historical shrub-grass transitions in the northern Chihuahuan Desert: modeling the effects of shifting rainfall seasonality and event size over a landscape gradient. *Global Change Biology* 9:1475–1493.
- Gibbens, R. P., C. H. Herbel, H. L. Morton, W. C. Lindemann, J. A. Ryderwhite, D. B. Richman, E. W. Huddleston, W. H. Conley, C. A. Davis, J. A. Reitzel, D. M. Anderson, and A. Guiao. 1986. Some impacts of 2,4,5-T on a mesquite duneland ecosystem in southern New Mexico: a synthesis. *Journal of Range Management* 39:320–326.
- Hartnett, D. C., and P. A. Fay. 1998. Plant populations: patterns and processes. Pages 81–100 in A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. *Grassland dynamics: long-term ecological research in tallgrass prairie*. Oxford University Press, New York, New York, USA.
- Heisler-White, J. L., J. M. Blair, E. F. Kelly, K. Harmony, and A. K. Knapp. 2009. Contingent productivity responses to more extreme rainfall regimes across a grassland biome. *Global Change Biology* 15:2894–2904.
- Heisler-White, J., A. Knapp, and E. Kelly. 2008. Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland. *Oecologia* 158:129–140.
- Hendrickson, J. R., and D. D. Briske. 1997. Axillary bud banks of two semiarid perennial grasses: occurrence, longevity, and contribution to population persistence. *Oecologia* 110:584–591.
- Herbel, C. H., F. N. Ares, and R. A. Wright. 1972. Drought effects on a semidesert grassland range. *Ecology* 53:1084–1093.
- Huenneke, L. F., D. Clason, and E. Muldavin. 2001. Spatial heterogeneity in Chihuahuan Desert vegetation: implications for sampling methods in semi-arid ecosystems. *Journal of Arid Environments* 47:257–270.
- Huxman, T. E., et al. 2004. Convergence across biomes to a common rain-use efficiency. *Nature* 429:651–654.
- Jarrell, W. M., D. E. Armstrong, D. F. Grigal, E. F. Kelly, H. C. Monger, and D. A. Wedin. 1999. Soil water and temperature status. Pages 55–73 in G. P. Robertson, D. C. Coleman, C. S. Bledsoe, and P. Sollins, editors. *Standard soil methods for long-term ecological research*. Oxford University Press, New York, New York, USA.
- Jobbágy, E. G., and O. E. Sala. 2000. Controls of grass and shrub aboveground production in the Patagonian steppe. *Ecological Applications* 10:541–549.
- Jobbágy, E. G., O. E. Sala, and J. M. Paruelo. 2002. Patterns and controls of primary production in the Patagonian steppe: a remote sensing approach. *Ecology* 83:307–319.
- Knapp, A. K., P. A. Fay, J. M. Blair, S. L. Collins, M. D. Smith, J. D. Carlisle, C. W. Harper, B. T. Danner, M. S. Lett, and J. K. McCarron. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* 298:2202–2205.
- Knapp, A. K., and M. D. Smith. 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291:481–484.

- Langer, R. H. M. 1972. How grasses grow. Edward Arnold, London, UK.
- Lauenroth, W. K. 1979. Grassland primary production: North American grasslands in perspective. Pages 3–24 in N. R. French, editor. Perspectives in grassland ecology. Ecological studies. Springer-Verlag, New York, New York, USA.
- Lauenroth, W. K., and O. E. Sala. 1992. Long-term forage production of North American shortgrass steppe. Ecological Applications 2:397–403.
- Lauenroth, W. K., O. E. Sala, D. P. Coffin, and T. B. Kirchner. 1994. The importance of soil-water in the recruitment of *Bouteloua gracilis* in the shortgrass steppe. Ecological Applications 4:741–749.
- Lauenroth, W., O. Sala, D. Milchunas, and R. Lathrop. 1987. Root dynamics of *Bouteloua gracilis* during short-term recovery from drought. Functional Ecology 1:117–124.
- Levine, J. M., A. K. McEachern, and C. Cowan. 2010. Do competitors modulate rare plant response to precipitation change? Ecology 91:130–140.
- Matías, L., J. Castro, and R. Zamora. 2011. Soil-nutrient availability under a global-change scenario in a Mediterranean mountain ecosystem. Global Change Biology 17:1646–1657.
- McNaughton, S. J., O. E. Sala, and M. Oesterheld. 1993. Comparative ecology of African and South American arid to subhumid ecosystems. Chapter 18 in P. Goldblatt, editor. Biological relationships between Africa and South America. Yale University Press, New Haven, Connecticut, USA.
- Neilson, R. P. 1986. High-resolution climatic analysis and Southwest biogeography. Science 232:27–34.
- Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4:25–52.
- Peters, D. P. C., J. Yao, O. E. Sala, and J. P. Anderson. 2012. Directional climate change and potential reversal of desertification in arid and semiarid ecosystems. Global Change Biology 18:151–163.
- Potts, D. L., T. E. Huxman, J. M. Cable, N. B. English, D. D. Ignace, J. A. Eilts, M. J. Mason, J. F. Weltzin, and D. G. Williams. 2006. Antecedent moisture and seasonal precipitation influence the response of canopy-scale carbon and water exchange to rainfall pulses in a semi-arid grassland. New Phytologist 170:849–860.
- Rao, L., and E. Allen. 2010. Combined effects of precipitation and nitrogen deposition on native and invasive winter annual production in California deserts. Oecologia 162:1035–1046.
- Reichmann, L. G., O. E. Sala, and D. P. C. Peters. 2013. Water controls on nitrogen transformations and stocks in an arid ecosystem. Ecosphere 4:11.
- Richards, J. H., and M. M. Caldwell. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. Oecologia 73:486–489.
- Sala, O. E., and A. T. Austin. 2000. Methods of estimating aboveground net primary productivity. Pages 31–43 in O. E. Sala, R. B. Jackson, H. A. Mooney, and R. W. Howarth, editors. Methods in ecosystem science. Springer, New York, New York, USA.
- Sala, O. E., L. A. Gherardi, L. G. Reichmann, E. G. Jobbagy, and D. P. Peters. 2012. Legacies of precipitation fluctuations on primary production: theory and data synthesis. Proceedings of the Royal Society B 367:3135–3144.
- Sala, O., W. Lauenroth, and W. Parton. 1992. Long-term soil water dynamics in the shortgrass steppe. Ecology 73:1175–1181.
- Sala, O. E., W. J. Parton, W. K. Lauenroth, and L. A. Joyce. 1988. Primary production of the central grassland region of the United States. Ecology 69:40–45.
- SAS Institute. 2009. JMP version 9.0.2. SAS Institute, Cary, North Carolina, USA.
- Schwinning, S., and O. E. Sala. 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141:211–220.
- Seager, R., et al. 2007. Model projections of an imminent transition to a more arid climate in Southwestern North America. Science 316:1181–1184.
- Sheppard, P. R., A. C. Comrie, G. D. Packin, K. Angersbach, and M. K. Hughes. 2002. The climate of the US Southwest. Climate Research 21:219–238.
- Sherry, R. A., E. S. Weng, J. A. Arnone, D. W. Johnson, D. S. Schimel, P. S. Verburg, L. L. Wallace, and Y. Q. Luo. 2008. Lagged effects of experimental warming and doubled precipitation on annual and seasonal aboveground biomass production in a tallgrass prairie. Global Change Biology 14:2923–2936.
- Shinoda, M., G. U. Nachinshonhor, and M. Nemoto. 2010. Impact of drought on vegetation dynamics of the Mongolian steppe: a field experiment. Journal of Arid Environments 74:63–69.
- Soil Survey Staff. 1999. Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys. Second edition. U.S. Government Printing Office, Washington, D.C., USA.
- Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. Averyt, M. Tignor, and H. Miller. 2007. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Suttle, K. B., M. A. Thomsen, and M. E. Power. 2007. Species interactions reverse grassland responses to changing climate. Science 315:640–642.
- Throop, H., L. Reichmann, O. Sala, and S. Archer. 2012. Response of dominant grass and shrub species to water manipulation: an ecophysiological basis for shrub invasion in a Chihuahuan Desert grassland. Oecologia 169:373–383.
- Xiao, J., and A. Moody. 2004. Photosynthetic activity of US biomes: responses to the spatial variability and seasonality of precipitation and temperature. Global Change Biology 10:437–451.
- Yahdjian, L., and O. E. Sala. 2002. A rainout shelter design for intercepting different amounts of rainfall. Oecologia 133:95–101.
- Yahdjian, L., and O. E. Sala. 2006. Vegetation structure constrains primary production response to increased water availability in the Patagonian Steppe of Argentina. Ecology 87:952–962.
- Yahdjian, L., and O. Sala. 2010. Size of precipitation pulses controls nitrogen transformation and losses in an arid Patagonian ecosystem. Ecosystems 13:575–585.