Physiological responses of two contrasting desert plant species to precipitation variability are differentially regulated by soil moisture and nitrogen dynamics

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Abstract

Alterations in global and regional precipitation patterns are expected to affect plant and ecosystem productivity, especially in water-limited ecosystems. This study examined the effects of natural and supplemental (25% increase) seasonal precipitation on a sotol grassland ecosystem in Big Bend National Park in the Chihuahuan Desert. Physiological responses – leaf photosynthesis at saturating light ($A_{sat}$), stomatal conductance ($g_s$), and leaf nitrogen [N] – of two species differing in their life form and physiological strategies (Dasylirion leiophyllum, a C$_3$ shrub; Bouteloua curtipendula, a C$_4$ grass) were measured over 3 years (2004–2006) that differed greatly in their annual and seasonal precipitation patterns (2004: wet, 2005: average, 2006: dry). Precipitation inputs are likely to affect leaf-level physiology through the direct effects of altered soil water and soil nitrogen. Thus, the effects of precipitation, watering treatment, soil moisture, and nitrogen were quantified via multivariate hierarchical Bayesian models that explicitly linked the leaf and soil responses. The two species differed in their physiological responses to precipitation and were differentially controlled by soil water vs. soil nitrogen. In the relatively deeply rooted C$_3$ shrub, D. leiophyllum, $A_{sat}$ was highest in moist periods and was primarily regulated by deep (16–30 cm) soil water. In the shallow-rooted C$_4$ grass, B. curtipendula, $A_{sat}$ was only coupled to leaf [N], both of which increased in dry periods when soil [N] was highest. Supplemental watering during the wet year generally decreased $A_{sat}$ and leaf [N] in D. leiophyllum, perhaps due to nutrient limitation, and physiological responses in this species were influenced by the cumulative effects of 5 years of supplemental watering. Both species are common in this ecosystem and responded strongly, yet differently, to soil moisture and nitrogen, suggesting that changes in the timing and magnitude of precipitation may have consequences for plant carbon gain, with the potential to alter community composition.

Keywords: Bouteloua curtipendula, Chihuahuan Desert, climate change, Dasylirion leiophyllum, hierarchical Bayesian modeling, photosynthesis, precipitation manipulation

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Introduction

Global and regional climate models suggest that large precipitation events are likely to increase in frequency during the next century as a result of anthropogenic-induced climate change (IPCC, 2007). Desert ecosystems cover about 30% of the Earth’s terrestrial surface, are increasing in area globally, and are strongly controlled by water availability (Reynolds, 2001; Reynolds & Stafford-Smith, 2002). Hence, it is critical to understand how alterations in precipitation patterns will impact arid and semiarid ecosystems (Weltzin et al., 2003). Indeed, changes in the timing and frequency of precipitation over the arid and semiarid regions of the southwestern United States may directly affect ecosys-
tem processes, because the spatial and temporal availability of water regulates the vegetation productivity and soil carbon and water dynamics in these ecosystems (Weltzin & McPherson, 2003; Huxman et al., 2004; Ogle & Reynolds, 2004; Snyder et al., 2004).

Plant responses to precipitation depend on fluctuations in soil moisture related to the intensity, duration, and seasonality of precipitation events, all of which are highly variable in arid and semiarid ecosystems (McAuliffe, 2003; Loik et al., 2004). Analysis of historical precipitation records at 316 arid and semiarid sites in the western United States revealed that 24–65% of individual rain events were very small (<5 mm), and only 2–23% were large (>30 mm) (Loik et al., 2004). As a result of highly episodic and variable precipitation, natural selection in arid and semiarid environments has favored plant characteristics related to, for example, rooting distributions or physiological behavior that maximize the use of precipitation events or ‘pulses’ (Schwinning & Ehleringer, 2001; Ogle & Reynolds, 2004; Reynolds et al., 2004). Differences in such characteristics often align with plant functional type classifications (e.g., shrubs vs. grasses). For example, many desert shrubs have roots distributed in both shallow and deep soil layers, allowing for use of ephemeral soil water derived from recent small rain events, but also enabling access to deeper, stored soil water, thereby extending photosynthetic activity during extended dry periods (e.g., Brown & Archer, 1990; Ogle et al., 2004; Cheng et al., 2006). Conversely, some shallow-rooted grasses primarily use soil water in near-surface layers, which are often very dry, but these species tend to have higher water use efficiencies compared with more deeply rooted species (Schwinning et al., 2002).

An important environmental factor influencing plant responses to precipitation is plant nitrogen [N], supplied through root uptake of soil [N] that is coupled with root water acquisition. Deconstructing the relationship between plant [N] and soil [N] in arid and semiarid ecosystems under altered precipitation regimes is important for three primary reasons. First, soil [N] is inherently low in these ecosystems (Kietl et al., 1998) and thus has the potential to limit the primary productivity. Second, desert plant species have been shown to maximize the use of soil [N] reserves more than nondesert species (Carrera et al., 2000; James & Richards, 2007). Third, soil [N] availability is coupled to soil microbial activity (e.g., nitrification, mineralization, and decomposition). Microbial activity, in turn, is influenced by soil moisture availability, causing plant-available [N] to be indirectly linked to precipitation inputs through the direct responses of the microbial community to soil moisture as affected by precipitation event size, duration, and intensity (Austin et al., 2004; Barker et al., 2006; Bell et al., 2008).

In summary, it is critical to develop an improved understanding of how plant physiological processes affecting productivity, such as photosynthesis, respond to variable precipitation in arid and semiarid ecosystems (Weltzin et al., 2003). Developing this understanding requires simultaneous consideration of the effects of precipitation pulses on interannual and interseasonal fluctuations in soil moisture, soil nitrogen, and plant nitrogen. Toward this goal, this study examined the effects of natural and supplemental (25% increase) seasonal precipitation on a sotol grassland ecosystem in Big Bend National Park in the Chihuahuan Desert. Seasonal photosynthetic responses of two species representing different growth forms and physiological strategies (e.g., C₃ shrub vs. C₄ grass) were monitored over 3 years (2004–2006) that differed greatly in their annual and seasonal natural precipitation patterns. The first objective was to quantify how photosynthesis varied in response to variability in seasonal and annual precipitation associated with both natural and supplemental inputs. Significant effects of different precipitation patterns are likely due to the direct effects of altered soil water and soil nitrogen on leaf-level physiology. Thus, the second objective was to understand the mechanisms underlying plant responses to precipitation by quantifying the effects of changes in soil water and soil nitrogen on photosynthesis via a novel hierarchical Bayesian (HB) regression model that explicitly linked the leaf and soil responses.

Materials and methods

Field study

The study site is located in the Pine Canyon Watershed of Big Bend National Park, Texas (BIBE, 29°5′N, 103°10′W, 1526 m a.s.l.); see Patrick et al. (2007) and Bell et al. (2008) for a detailed description of site vegetation and soil characteristics. The site receives an average of 365 mm of annual precipitation, with annual totals ranging from 149 to 578 mm for the period 1986–2006 (National Park Service, Fig. 1, Supporting information Table S1). During this period, the average number of precipitation events per year was 57; about 64% of these events were small (≤5 mm) and 71% of the inter-pulses (periods without rain) were relatively short (<5 days) (see Supporting information Table S1). Maximum daily air temperatures ranged from −4 to 41 °C, and minimum daily air temperatures ranged from −10 to 26 °C (Fig. 1).

The two dominant plants in this sotol grassland are *Dasylirion leiophyllum* (sotol; Liliaceae) and *Bouteloua*...
curtipendula (side-oats grama; Poaceae). *D. leiophyllum* is a long-lived, perennial, evergreen, C$_3$ rosette shrub (Kemp & Gardetto, 1982; MacMahon, 1997) that is photosynthetically active throughout the year. Above-ground growth occurs primarily during the spring and summer, and older plants develop a coarse fibrous root system that can extend to approximately 20–30 cm depth. In BIBE, *B. curtipendula* is only photosynthetically active from late May to early October.

Beginning in January 2002, water treatments were applied seasonally to small individual plant plots (three 1 m x 0.5 m plots per treatment, one plant per plot, 24 plots total) and large plant community plots (three 3 m x 3 m plots per treatment, multiple plants per plot, 12 plots total) to simulate a Hadley Climate Model 2 scenario (Johns et al., 1997; Gordon et al., 2000) of a 25% increase in ambient precipitation in this region (precipitation treatment details are given in Supporting Information Table S2). Plots were distributed randomly throughout the sotol grassland and spatially separated such that there was no need for subsurface water restriction, and overland flow following watering events was not an issue. The plant plots were used for leaf-level physiological measurements. The community plots were used for soil sampling because they housed both plant species, and their soils were less impacted by the effects of repeated sampling as carried out on the plant plots. The soil texture at this site is a sandy loam consisting of 62.3% sand, 29.7% silt, and 8.03% clay (Waters Agricultural Laboratories Inc., Owensboro, KY, USA). All plots had similar soil and geographic (e.g., aspect, slope) conditions characteristic of this region of BIBE.

Water treatments applied to the plots were as follows: (1) no water addition (i.e., control), (2) summer addition, (3) winter addition, and (4) both summer and winter addition. For the winter addition and summer/winter addition treatments, water was added in a single event during the winter (February), simulating a large storm event. For the summer addition and summer/winter addition treatments, water was added in three distinct events in the summer (June, July, August), simulating smaller storm events (Supporting information Table S2). Water was added manually and evenly applied within the plots over both plants and soil, so that the rate of application was similar to the rate of infiltration into the soil. In 2002, supplemental rainfall events were based on the 30-year average precipitation record. From 2003 to 2006, the amount of water added for each simulated storm was based on the ambient amount of rainfall received in the control plots before the water addition treatment during the current year. For these years, winter water addition was based on the previous 3 months of precipitation (November, December, and January), and summer water addition was based on the previous 1 month of precipitation (May, June, or July); see Supporting information Table S2 for further details.

In order to quantify ambient precipitation effects, as well as to determine if supplemental water pulses were effective in increasing soil water, volumetric soil moist-
ure content was measured throughout the experimental period using one ECH2O-10 dielectric aquameter probe (Decagon Devices, Pullman, WA, USA) placed horizontally in each plot at a soil depth of 15 cm. Measurements were logged every 2 hours and then averaged for the 24-h period to determine mean daily volumetric water content. Measured soil water content (SWC) and precipitation amounts were input to the one-dimensional, physical-based, soil water model HYDRUS 1D (Simunek et al., 2005) to calculate volumetric soil moisture content at 1-cm intervals from 2 to 30 cm for ‘representative’ plots. Application of the HYDRUS model allowed for continuous estimates of soil moisture during times of probe malfunction, as well as the ability to simulate soil moisture at additional depths relevant to all study plants (e.g., 15–30 cm).

**Leaf- and soil-level measurements**

To determine the effect of precipitation on plant photosynthesis, net assimilation rate at saturating light ($A_{sat}$) and stomatal conductance to water vapor ($g_s$) were measured with a portable, open-flow gas-exchange system (Model LI-6400, LI-COR Inc., Lincoln, NE, USA). Measurements were made on recently matured leaves, on one individual plant per species per small plot, for a total of 40 different days throughout the winter, spring, summer, and fall seasons that spanned the period from February 2004 to December 2006. On all measurement dates, data were collected in the morning when gas exchange was at its maximum rate (07:00–09:30 hours, based on diurnal measurements). Leaf-to-air vapor pressure deficit, air temperature, and CO$_2$ concentration (380μmol mol$^{-1}$) of the cuvette were set to ambient external values for each measurement period and were held constant for all measured plots. Irradiance was set at saturating light (2000 μmol m$^{-2}$s$^{-1}$). Gas exchange readings were logged three to five times within a period of about 1–3 min for each leaf and then averaged for each plant to yield an observation for each plant.

To determine if plant-available water varied annually or seasonally, leaf water potential ($\Psi$) was measured using a Scholander-type pressure chamber (3000 Series, Soilmoisture Equipment Corp., Santa Barbara, CA, USA). When possible, $\Psi$ was also measured before and after watering events to determine if plant water status changed with supplemental watering. Measurements of $\Psi$ were made mid-day to coincide with $A_{sat}$ and $g_s$ measurements; the order of plant sampling alternated between treatments to avoid time-of-day biases. The timing of measurements of $\Psi$ in *D. leiophyllum* varied between 2004 (June, July), 2005 (February, April, October, December), and 2006 (April, June, August, October). For *B. curtipendula*, $\Psi$ was measured only in 2006 (August, October). Measurements of $\Psi$ were intermittent and limited so as to not destructively sample the plants that were simultaneously being used for growth and productivity measurements. Because leaf water potential was measured infrequently, these data were not incorporated into statistical models described below.

To assess the role of nitrogen in regulating photosynthetic responses to water availability, *D. leiophyllum* and *B. curtipendula* leaves were periodically analyzed for leaf [N] throughout the study period. Recently matured leaves were harvested in the field and frozen until they could be returned to the laboratory for processing. Leaves were dried at 70°C in an oven, ground into a fine powder, and total leaf [N] was measured with a CN Analyzer (NCS 2500, Carlo Erba Inc., Milan, Italy). Leaf [N] was expressed on an area basis (mg m$^{-2}$) to compare with leaf-level photosynthesis also measured on an area basis.

To evaluate the effects of precipitation on soil nitrogen dynamics, soil samples (approximately 0–15 cm depth) were collected as composite samples from underneath study plants and inter-plant spaces in community plots (two replicate soil samples per plot, 24 total). Soils were collected one time in 2003, five times in 2004, and biannually (March and September) in 2005 and 2006; samples were stored at 4°C until processed. Levels of extractable soil nitrate (NO$_3^-$) were determined 1 day after the sample collection date by A&L Soil Laboratories (Lubbock, TX, USA) using ion-specific probes. Exchangeable soil ammonium (NH$_4^+$) was determined via colorimetric assay and was extracted 1 day after the sample collection date using a 50 mL 2M KCl solution from a 5 g field moist (oven dry equivalent) soil sample (Miller & Keeney, 1982). Greater details on sampling and laboratory methods are given in Bell et al. (2008).

**Statistical analyses**

Plant, soil, and environmental data were analyzed within an HB framework (Clark, 2005; Clark & Gelfand, 2006). This approach is advantageous for this dataset because it can (1) accommodate missing data (Gelman et al., 2004), which was encountered in this study due to temporal variation in measurements of different responses variables; (2) explicitly link plant and soil data collected over different temporal and spatial scales while simultaneously accounting for uncertainty in all response variables (e.g., Ogle & Barber, 2008); and (3) provide direct estimates of parameters – related to the effects of precipitation treatments and soil environmental drivers – that appropriately reflect uncertainty and that are straightforward to interpret (Carlin et al., 2006; Ogle & Barber, 2008).
The analysis of the leaf-level data occurred in three steps. First, an HB multivariate analysis of variance (HB-MANOVA) was conducted to estimate year, season, and watering treatment effects. Second, an HB multivariate regression (HB-MR) was conducted to explore potential mechanisms responsible for the treatment effects (or lack thereof) by modeling leaf-level responses as functions of soil and leaf covariates. Finally, the HB regression (HB-MR) was conducted to explore potential water treatment effects. Second, an HB multivariate MANOVA was conducted to estimate year, season, and watering treatment effects. Year, season, and watering treatment are essentially treated as fixed effects and plant within treatment and date within season/year are treated as nested random effects. Thus, for year y (3 years), season s (four seasons, only one for B. curtipendula), watering treatment t (four levels), plant p (three plants per watering level; 12 total), and date d (eight dates per year/season combination; 40 dates total for D. leiophyllum; 19 dates total for B. curtipendula) associated with observation i, the process model is

$$\begin{bmatrix} \hat{A}_{\text{sat}[i]} \\ \hat{g}_{s[i]} \\ \text{leaf}[N][i] \end{bmatrix} \sim \text{Normal} \left( \begin{bmatrix} \hat{A}_{\text{sat}[i]} \\ \hat{g}_{s[i]} \\ \text{leaf}[N][i] \end{bmatrix}, \Sigma_L \right),$$

where $\hat{A}_{\text{sat}}, \hat{g}_s,$ and leaf[N] are the mean (or ‘true’) values and $\Sigma_L$ is the $3 \times 3$ precision matrix (i.e., inverse of the covariance matrix) for the leaf-level data.

We assumed that the mean responses are centered on a year–season–watering treatment effect plus plant and date effects. Year, season, and watering treatment are essentially treated as fixed effects and plant within treatment and date within season/year are treated as nested random effects. Thus, for year $y$ (3 years), season $s$ (four seasons, only one for $B. curtipendula$), watering treatment $t$ (four levels), plant $p$ (three plants per watering level; 12 total), and date $d$ (eight dates per year/season combination; 40 dates total for $D. leiophyllum$; 19 dates total for $B. curtipendula$) associated with observation $i$, the process model is

$$\begin{bmatrix} \hat{A}_{\text{sat}[i]} \\ \hat{g}_{s[i]} \\ \text{leaf}[N][i] \end{bmatrix} = \begin{bmatrix} \hat{A}_{\text{sat}(y,s,t)} \\ \hat{g}_{s(y,s,t)} \\ \text{leaf}[N][y,s,t] \end{bmatrix} + \varepsilon_i + \delta_i,$$

where $\hat{A}_{\text{sat}}, \hat{g}_s,$ and leaf[N] are the treatment effects and $\varepsilon$ and $\delta$ are the nested plant and date random effects (each is a $3 \times 1$ vector), respectively. The general form of the model for each of the six groups (i.e., plant and date effects associated with each of the three leaf-level response variables) of random effects assumes that the effects are normally distributed about a zero:

$$\varepsilon \sim \text{Normal}(0, \tau),$$

where $\tau$ is the precision (1/variance) parameter that describes variability between plants or dates. The application of Eqn (3) to all six groups of random effects results in six corresponding precision terms (or variance terms).

**HB-MANOVA: leaf data.** First, the HB-MANOVA was conducted to estimate the effects of year, season, and watering treatment on plant physiological responses (i.e., $A_{\text{sat}}, g_s,$ and leaf [N]). The likelihood of all of the leaf data is based on the likelihood components of individual observations of $A_{\text{sat}}, g_s,$ and leaf [N]. Because observations of $A_{\text{sat}}, g_s,$ and leaf [N] were often made at the same time, on the same plant, and with the same instrument (e.g., $A_{\text{sat}}$ and $g_s$), it is likely that the observation errors between these three responses are correlated (e.g., Ogle & Barber, 2008). To allow for the possibility of correlated measurement errors, a multivariate normal sampling distribution is assumed such that for observation $i$ ($i = 1, 2, \ldots, 480$ for $D. leiophyllum$; $i = 1, 2, \ldots, 228$ for $B. curtipendula$):

$$\begin{bmatrix} \text{NO}_3[i] \\ \text{NH}_4[i] \end{bmatrix} \sim \text{Normal} \left( \begin{bmatrix} \text{NO}_3[i] \\ \text{NH}_4[i] \end{bmatrix}, \Sigma_S \right),$$

where $\text{NO}_3$ and $\text{NH}_4$ are the mean values and $\Sigma_S$ is the $2 \times 2$ precision matrix. The mean responses were related to fixed treatment effects, and plot random effects were incorporated to capture process error such that for plot $p$ (12 plots), treatment $t$ (four treatments), year $y$ (three
years), and season s (two seasons), the process model is

$$\begin{bmatrix} NO_3_{1(i)} \\ NH_4_{1(i)} \end{bmatrix} = \begin{bmatrix} NO_3_{1(y,s,t)} \\ NH_4_{1(y,s,t)} \end{bmatrix} + \epsilon_{(p)}, \quad (5)$$

where NO$_3$ and NH$_4$ are the treatment effects (overall population parameters or fixed effects) and \( \epsilon \) is a 2 x 1 vector of plot random effects, which was modeled like Eqn (3), introducing two additional precision terms (one for each soil nitrogen response variable).

**HB-MR: linking leaf and soil responses.** Next, an HB-MR analysis was conducted to (1) estimate the effects of soil factors (e.g., soil moisture at different depths, soil nitrogen) on plant/leaf responses and (2) account for the interactions and feedbacks between different plant responses. The HB-MR model explicitly coupled the plant and soil datasets, accounted for uncertainty in all measured plant and soil data, and aligned the plant and soil data (e.g., soil and plant data were often collected at different times and different, but nearby, plots). The likelihood for the leaf data is defined as Eqn (1). The process equation models the mean responses similar to Eqn (2) by including plant and date random effects, but the mean response explicitly depends on soil and plant variables via a regression model:

$$\begin{bmatrix} \bar{A}_{sat_{(i)}} \\ \bar{g}_s \\ \bar{leaf}[N]_{(i)} \end{bmatrix} = \begin{bmatrix} \hat{A}_{sat_{(i)}} \\ \hat{g}_s \\ \hat{leaf}[N]_{(i)} \end{bmatrix} + \bar{\epsilon} + \delta_{(d)}. \quad (6)$$

The random effects \( \epsilon \) and \( \delta \) are as defined in Eqns (2) and (3). In constructing the process model, we assumed that (1) true photosynthesis at saturating light is potentially affected by SWC at two depths (SWC$_{15}$ = SWC at 15 cm; SWC$_{30}$ = SWC at 30 cm), leaf [N] content, and interactions between soil water and leaf [N]; (2) true stomatal conductance is potentially coupled to water availability at the two depths; and (3) true leaf [N] is potentially affected by soil NO$_3$ and NH$_4^+$ (and their interaction) and soil water at two depths. Thus, the regression models for the process means are

$$\begin{align*}
\hat{A}_{sat} &= a_0 + a_1 \times SWC_{15} + a_2 \times SWC_{30} + a_3 \times \text{leaf}[N] \\
&\quad + a_4 \times SWC_{15} \times \text{leaf}[N] + a_5 \times SWC_{30} \times \text{leaf}[N] \\
\hat{g}_s &= b_0 + b_1 \times SWC_{15} + b_2 \times SWC_{30} \\
\text{leaf}[N] &= c_0 + c_1 \times NO_3 + c_2 \times NH_4 + c_3 \times SWC_{15} \\
&\quad + c_4 \times SWC_{30} + c_5 \times NO_3 \times SWC_{15} \\
&\quad + c_6 \times NO_3 \times SWC_{30} \\
&\quad + c_7 \times NH_4 \times SWC_{15} + c_8 \times NH_4 \times SWC_{30} \\
&\quad + c_9 \times NO_3 \times NH_4 \quad (7)
\end{align*}$$

For ease of presentation, we have dropped the \( i, y, s, \) and \( t \) subscripts. Note though that the leaf response variables and the soil water variables are directly linked by observation (subscripted by \( i, y, s, \) and \( t \)). The leaf responses are related to latent soil nitrogen values in the corresponding year, season, and treatment (subscripted by \( y, s, t \)). The \( a, b, \) and \( c \) parameters are the regression coefficients that describe soil water, leaf [N], and soil nitrogen main effects and interactions. For more details about these parameters, see the Appendix. Note that soil moisture values for the two depths are treated as fixed (or ‘known’) covariates. Conversely, soil NO$_3$ and NH$_4^+$ are treated as random variables, and their associated means, given by the HB-MANOVA in Eqn (5), are directly related to the leaf responses in Eqn (7).

**HB-MR and HB-MANOVA: exploring remaining treatment effects.** Lastly, the amount of variation in \( \hat{A}_{sat}, \hat{g}_s, \) and leaf [N] not explained by the leaf and soil variables in the HB-MR model [see Eqn (7)] was quantified. First, the residuals obtained from the HB-MR analysis were computed by calculating the difference between the observed leaf data and the predicted values given by Eqns (6) and (7) (i.e., posterior means for \( \hat{A}_{sat}, \hat{g}_s, \) and leaf[N]). The HB-MANOVA model [Eqns (1–3)] was then rerun with the residuals treated as data (instead of the actual \( A_{sat}, g_s, \) and leaf [N] observations). Again, this HB-MANOVA was run separately for D. leiophyllum and B. curtipendula; the posterior means for the predicted residuals obtained from this model were then added to the posterior means for each \( \hat{A}_{sat}, \hat{g}_s, \) and leaf[N] obtained from the HB-MR model. These summed means (‘HB-MR + HB-MANOVA’) were compared with observed values to evaluate model goodness-of-fit and to determine the total variation explained by important covariates (i.e., soil moisture, soil nitrogen, and leaf nitrogen) and the amount of residual variation explained by remaining year, season, and watering treatment effects.

**Results**

**Annual and seasonal precipitation**

Both annual (based on a calendar year) and seasonal precipitation varied over the experimental period (Fig. 1, Supporting information Table S1). Based on the deviation from the long-term annual mean (1986–2006), 2004 was an ‘above-average’ (wet) year, 2005 was an ‘average’ year, and 2006 was a ‘below-average’ (dry) year. Differences in annual precipitation were due to differences in fall, spring, and winter precipitation amounts (Supporting information Table S1). Moreover, changes in the number of large events drove differences

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in annual rainfall amount, as observed in the wet year where large events (>20 mm) increased in the fall, summer, and spring, and the number of small events (<5 mm) increased in the winter (Supporting information Table S1). Low precipitation during the dry year was primarily a function of decreased small (<5 mm) winter precipitation events.

**Soil and plant water status**

Evaluation of measured soil moisture indicated that precipitation amount did affect SWC. Measured soil moisture differed across years and seasons, where the wet year (2004) had greater soil moisture than other years (Fig. 1), and soil moisture was higher in the summer and fall compared with the spring and winter. Water treatment also affected soil moisture: maximum soil moisture reached 14.7% in summer/winter addition plots, 11.9% in summer addition plots, and 11.3% in winter addition plots. For all treatments and plots, maximum soil moisture from the HYDRUS data was 14.5% at both depths (2–15 and 16–30 cm; Fig. 1), and the minimum was 2.8% from 2 to 15 cm and 4.7% from 16 to 30 cm. Soil moisture measured by the probes was not significantly different from the soil moisture simulated by HYDRUS (Fig. 1).

Plant water status (i.e., water potential, Ψ) was also affected by annual and seasonal variability in precipitation. Mean Ψ for *D. leiophyllum* control plants was greater in the wet year (–1.2 ± 0.3 MPa, mean ± SD) compared with the average year and the dry year (–2.2 ± 0.6 MPa; average for both years). Across all years, mean Ψ was –1.9 ± 0.6 MPa in the winter and –1.6 ± 0.5 MPa in the summer for *D. leiophyllum*. For *B. curtipendula*, mean Ψ for control plants was –1.2 ± 0.5 MPa in August of the dry year. Supplemental watering, especially in the summer, also altered plant water status. For example, 1 day after the August supplemental watering event, mean Ψ for *B. curtipendula* increased by approximately 60% in summer addition and summer/winter addition plots (–0.6 ± 0.4 MPa).

**Multivariate soil and plant responses**

Although we report results for individual response variables, recall that the statistical models were applied to multivariate responses related to soil nitrogen (i.e., NH$_4^+$ and NO$_3^-$) and leaf physiology (i.e., $A_{\text{sat}}$, $g_s$, and leaf [N]). Results from the soil HB-MANOVA indicated that the observation errors associated with NH$_4^+$ and NO$_3^-$ were mildly correlated (posterior mean for the correlation coefficient = 0.25). Likewise, the HB-MANOVA and HB-MR results indicated that the observation errors for $A_{\text{sat}}$ and $g_s$ were moderately correlated in both *D. leiophyllum* and *B. curtipendula* (mean correlation coefficient = 0.41 and 0.30, respectively), and the $A_{\text{sat}}$ and leaf [N] and the $g_s$ and leaf [N] errors were weakly correlated (mean correlation coefficient ranged from 0.02 to 0.09). Overall, a univariate analysis approach is inappropriate, and the multivariate models are necessary for accommodating correlated sources of uncertainty.

**Soil nitrogen (NO$_3^-$ and NH$_4^+$).** Results from the soil HB-MANOVA model indicated significant year, season, and treatment effects for soil nitrogen. Across all years, extractable soil NO$_3^-$ was consistently greater in the late summer compared with the late winter (Table 1, Fig. 2). Significantly greater levels of soil NH$_4^+$ occurred in the dry year compared with the wet and average years (Table 1). In the wet and average years, soil NO$_3^-$ during the summer/fall was significantly greater in winter addition plots than in other treatment plots (Fig. 2). Treatment effects for soil NH$_4^+$ were only observed in the winter/spring of the dry year, when summer/winter addition plots had the lowest amount of soil NH$_4^+$ and winter addition plots had the greatest amount of soil NH$_4^+$ (Fig. 2). These soil nitrogen results were consistent with those reported by Bell et al. (2008).

**Leaf nitrogen [N].** Sample means indicated that leaf [N] differed within and between species. Within species, leaf [N] varied by at least a factor of 2 during the

<table>
<thead>
<tr>
<th>Year</th>
<th>NO$_3^-$ (mg kg$^{-1}$ soil$^{-1}$)</th>
<th>NH$_4^+$ (mg kg$^{-1}$ soil$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean 2.5% 97.5%</td>
<td>Mean 2.5% 97.5%</td>
</tr>
<tr>
<td>2004 (wet)</td>
<td>4.06 3.60 4.54</td>
<td>6.46 4.77 8.13</td>
</tr>
<tr>
<td>2005 (average)</td>
<td>3.79 3.33 4.25</td>
<td>4.72 3.08 6.37</td>
</tr>
<tr>
<td>2006 (dry)</td>
<td>3.65 3.18 4.11</td>
<td>18.2 16.5 19.9</td>
</tr>
</tbody>
</table>

W/Sp, winter and spring seasons; Su/F, summer and fall seasons; S, summer addition treatment; W, winter addition treatment; SW, summer and winter addition treatment; C, control treatment.

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experiment (Supporting information Fig. S1). Results from the plant HB-MANOVA model indicated significant year, season, and treatment effects for leaf [N] in both species. In *D. leiophyllum*, leaf [N] increased each year, with significantly higher leaf [N] in the dry year (Table 2, Fig. 3). Also, leaf [N] was significantly greater in the fall compared with winter, spring, and summer (Table 2). Further, summer addition and control plants had significantly greater leaf [N] than winter addition plants, and summer/winter addition plants had significantly lower leaf [N] than all other treatments (Table 2). There were no significant year-by-season interactions for leaf [N], and year-by-treatment interactions showed that winter addition and summer/winter addition plants had the lowest leaf [N] across all years (Fig. 3). Leaf [N] in *B. curtipendula* also significantly increased over time, with leaf [N] in the dry year being approximately two times greater than in the wet year (Table 2). Overall in *B. curtipendula*, leaf [N] was greater in summer addition plants than in plants that received other supplemental watering treatments, and this difference was most pronounced in the wet (2004) and dry (2006) years (Fig. 4).

Results from the HB-MR model that included the effect of soil covariates on leaf [N] [see Eqn (7)] showed that in *D. leiophyllum*, 69% of the variation in leaf [N] was explained by the soil water and soil nitrogen covariates, with the strongest influence attributed to soil NH$_4^+$ and soil moisture main effects, a soil NO$_3^-$-by-soil moisture interaction, and a soil NO$_3^-$-by-soil NH$_4^+$ interaction (Table 3). In *B. curtipendula*, 92% of the variation in leaf [N] was explained by the soil water and soil nitrogen covariates, but the soil NH$_4^+$ and soil moisture main effects were the only significant terms (Table 3). When the residuals from the HB-MR were analyzed in an HB-MANOVA model, year, season, and watering treatments explained an additional 12% and a mere 2.6% of the variation in leaf [N] for *D. leiophyllum* and *B. curtipendula*, respectively. Thus, the combined model (HB-MANOVA + HB-MR) explained 81% (*D. leiophyllum*) and 95% (*B. curtipendula*) of the variation in leaf [N]. These sources of variation are summarized in Supporting information Table S3.

Stomatal conductance ($g_s$) at peak photosynthesis ($A_{sat}$). Results from the plant HB-MANOVA indicated significant year and season effects for $g_s$ in both species. In *D. leiophyllum*, $g_s$ significantly increased in the average year (2005) following the wet year (2004), and then significantly decreased in the dry year (2006) (Table 2). Summer and fall $g_s$ were not different, but were significantly higher than spring and winter $g_s$. 

![Fig. 2](image-url) Posterior means and 95% credible intervals from the hierarchical Bayesian MANOVA analysis for soil nitrate (NO$_3^-$) and soil ammonium (NH$_4^+$) grouped by two-way interactions between year, season, and treatment. S, summer addition treatment; W, winter addition treatment; SW, summer and winter addition treatment; C, control treatment.
with spring having the lowest \( g_s \) (Table 2). Seasonal effects were present regardless of the year (Fig. 3). While \( g_s \) was slightly lower in summer/winter addition plants, water treatment did not significantly affect \( g_s \) (Table 2). Significant treatment effects were only observed in the summer and in the wet and average years (Fig. 3). In *B. curtipendula*, \( g_s \) was significantly lower in the wet year than in the average and dry years (Table 2). Year-by-treatment interactions indicated that within the average year, there was a significant treatment effect on \( g_s \) where grasses receiving summer/winter addition had the lowest \( g_s \) (Table 2, Fig. 4).

Results from the HB-MR showed that 63% and 50% of the variation in \( g_s \) of both species was explained by soil moisture at both depths for *D. leio phyllum* and *B. curtipendula*, respectively (Table 3, Supporting information Table S3). For both species, \( g_s \) was negatively correlated with shallow soil moisture (2–15 cm) and positively correlated with deeper soil moisture (16–30 cm, Table 3). The residuals from the HB-MR were analyzed with an HB-MANOVA model, which indicated that a comparatively large amount (17–18%) of the residual variation in \( g_s \) of both species was explained by year, season, and watering treatment (Supporting information Table S3). Thus, the combined model (HB-MANOVA + HB-MR) explained 80% (*D. leio phyllum*) and 68% (*B. curtipendula*) of the variation in \( g_s \) (Supporting information Table S3).

### Photosynthesis at saturating light (\( A_{sat} \))

Sample means for \( A_{sat} \) illustrate that mean \( A_{sat} \) varied by nearly an order of magnitude over the study period (Supporting information Fig. S2). Results from the plant HB-MANOVA indicated significant year, season, and treatment effects for \( A_{sat} \) in both species. In *D. leio phyllum*, \( A_{sat} \) increased in the average year (2005) following the wet year (2004) and decreased in the dry year (2006) (Table 2). Also, \( A_{sat} \) was lower in the winter and spring compared with the summer and fall (Table 2), and seasonal effects were present regardless of the year (Fig. 3). Across all years, \( A_{sat} \) was greatest in summer addition and control plants compared with winter and summer/winter addition plants (Table 2).

### Table 2

Posterior means and 95% credible intervals (CIs) (see Table 1) for year, treatment, and season main effects estimated by the hierarchical Bayesian MANOVA model (HB-MANOVA) for leaf-level responses of *Dasylirion leio phyllum* and *Bouteloua curtipendula*.

<table>
<thead>
<tr>
<th></th>
<th>( A_{sat} ) (( \mu mol \text{ m}^{-2} \text{s}^{-1} ))</th>
<th>( g_s ) (( \mu mol \text{ m}^{-2} \text{s}^{-1} ))</th>
<th>Leaf [N] (mg m(^{-2} ))</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean 2.5% 97.5%</td>
<td>Mean 2.5% 97.5%</td>
<td>Mean 2.5% 97.5%</td>
</tr>
<tr>
<td><strong>D. leio phyllum</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2004 (wet)</td>
<td>7.25 6.94 7.56</td>
<td>0.0692 0.0603 0.0780</td>
<td>1.02 0.995 1.049</td>
</tr>
<tr>
<td>2005 (average)</td>
<td>8.47 8.02 8.92</td>
<td>0.1059 0.0933 0.1185</td>
<td>1.06 1.008 1.106</td>
</tr>
<tr>
<td>2006 (dry)</td>
<td>6.11 5.65 6.57</td>
<td>0.0637 0.0510 0.0760</td>
<td>1.18 1.159 1.199</td>
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<tr>
<td>Season</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Winter</td>
<td>5.02 4.57 5.46</td>
<td>0.0506 0.0384 0.0629</td>
<td>1.08 1.048 1.121</td>
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<tr>
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<td>0.0284 0.0074 0.0488</td>
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<tr>
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<td>1.12 1.106 1.136</td>
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<tr>
<td>Treatment</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>S</td>
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<td>0.0848 0.0689 0.1016</td>
<td>1.16 1.123 1.193</td>
</tr>
<tr>
<td>W</td>
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<td>1.10 1.066 1.136</td>
</tr>
<tr>
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<tr>
<td>C</td>
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<td>0.0827 0.0665 0.0987</td>
<td>1.14 1.105 1.174</td>
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<tr>
<td><strong>B. curtipendula</strong></td>
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<td></td>
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<tr>
<td>2004</td>
<td>10.2 9.37 11.0</td>
<td>0.0724 0.0591 0.0855</td>
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<td>2006</td>
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<td>Treatment</td>
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<tr>
<td>S</td>
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<tr>
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<td>0.1204 0.0969 0.1436</td>
<td>1.62 1.580 1.665</td>
</tr>
</tbody>
</table>

S, summer addition treatment; W, winter addition treatment; SW, summer and winter addition treatment; C, control treatment.

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Treatment effects were only observed in the winter and summer seasons and were not as strong in the dry year compared with the wet and average year (Fig. 3). In *B. curtipendula*, $A_{sat}$ significantly increased with time (year) (Table 3), and plants that received supplemental water in the summer or winter – and to some extent, summer/winter – had significantly higher $A_{sat}$ than control plants (Table 2). Year affected the response to watering treatment such that significant treatment differences occurred in the average and dry years, but the direction of these effects differed between years (Fig. 4). For example, summer/winter addition plants had the lowest $A_{sat}$ in 2005 but had the highest $A_{sat}$ in 2006. Water treatment did not affect $A_{sat}$ in the wet year (Fig. 4).

Results from the HB-MR showed that in *D. leiophyllum*, $A_{sat}$ was negatively correlated with shallow soil moisture and leaf [N] (Table 3). Approximately 70% of the variation in $A_{sat}$ in *D. leiophyllum* was explained by soil moisture, leaf [N], and soil moisture-by-leaf [N] interactions (Supporting information Table S3). In *B. curtipendula*, the HB-MR model results indicated that leaf [N] was the only significant covariate in the regression for $A_{sat}$. Leaf [N], in combination with the soil moisture and soil moisture-by-leaf [N] interactions, explained 75% of the variation in $A_{sat}$ for *B. curtipendula* (Table 3, Supporting information Table S3). The HB-MANOVA analysis of the residuals indicated that 10% and a mere 4.7% of the remaining variation in $A_{sat}$ was explained by year, season, and watering treatment for *D. leiophyllum* and *B. curtipendula*, respectively (Supporting information Table S3). Thus, the combined model (HB-MANOVA + HB-MR) explained 80–81% of the variation in $A_{sat}$ for these two species (Supporting information Table S3).

Fig. 3  Posterior means and 95% credible intervals from the hierarchical Bayesian MANOVA analysis for photosynthesis ($A_{sat}$), stomatal conductance ($g_s$), and leaf [N] for *Dasylirion leiophyllum* grouped by two-way interactions between year, season, and treatment. S, summer addition treatment; W, winter addition treatment; SW, summer and winter addition treatment; C, control treatment.
Discussion

This study aimed to examine the effects of altered precipitation on the physiological responses of plants co-occurring in a sotol grassland ecosystem in Big Bend National Park in the Chihuahuan Desert. Two species (\textit{D. leiophyllum} and \textit{B. curtipendula}) were chosen that represent different life forms (shrub vs. grass) and photosynthetic pathways (C\textsubscript{3} vs. C\textsubscript{4}), and therefore were expected to differ in their physiological responses to variable precipitation. Precipitation effects on physiological response variables are likely due to direct and indirect effects of altered soil moisture and soil nitrogen on leaf-level physiology. Thus, plant physiological responses to these soil variables were examined through a multivariate analysis of variance and a multivariate regression within an HB framework. The explicit integration of diverse data sources obtained from experimental field work via a rigorous statistical modeling framework allowed for a more holistic understanding of physiological responses in this ecosystem compared with more traditional statistical approaches (Ogle, 2008). The HB approach was particularly useful in this study because it allowed us to (1) explicitly link different types of data, some of which were misaligned in time and space; (2) partition the effects of soil and leaf covariates from categorical treatment effects; and (3) account for multiple sources of variation (or uncertainty).

The HB-MANOVA and HB-MR results suggested that mechanisms regulating plant physiological responses to annual and seasonal (both natural and supplemental) precipitation variability were primarily linked to soil moisture in the C\textsubscript{3} shrub (\textit{D. leiophyllum}) and soil nitrogen dynamics in the C\textsubscript{4} grass (\textit{B. curtipendula}). The differential importance of soil water vs. soil nitrogen to the physiological activity of these two contrasting species is likely related to their different phenologies, rooting behavior, life-history strategies, and photosynthetic pathways. Below we discuss these differences and specific predictions given by the statistical models.

Results from the HB-MANOVA showed that \textit{D. leiophyllum} exhibited heightened physiological activity under wet conditions (e.g., wet and average years) compared with dry conditions (e.g., dry year, Fig. 3). Reduced deep soil moisture during periods of low rainfall is the most likely explanation for the lower \(A_{\text{sat}}\) and \(g_s\) of this species in dry periods. Indeed, results from the HB-MR model indicated that \(A_{\text{sat}}\), \(g_s\), and leaf [N] had a positive relationship with soil moisture between 16 and 30 cm, and deep soil moisture was lowest in the dry year. In both the Sonoran Desert and Great Basin Desert, \(A_{\text{sat}}\) and \(g_s\) of deeply rooted shrubs also responded positively to increased soil moisture availability in the rooting zone (Fravolini \textit{et al.}, 2005; Loik, 2007). Because \textit{D. leiophyllum} has most of its roots in deeper soil layers (T. Robertson, personal communication), it follows that deep soil water is likely the primary factor controlling the physiological responses of this shrub to precipitation variability.
In contrast to *D. leiophyllum*, the physiological responses of *B. curtipendula* were enhanced under dry conditions. For example, *B. curtipendula* had higher photosynthesis in the dry year, and water treatment effects on $A_{\text{sat}}$ were only observed in the dry year (Fig. 4). Results from the HB-MR indicated that $A_{\text{sat}}$ in *B. curtipendula* was likely to be singularly regulated by leaf [N], and $A_{\text{sat}}$ was not directly related to soil moisture. Leaf [N], in turn, was strongly and positively correlated with soil NH$_4^+$ (Table 3), which was nearly four times higher in the dry compared with the wet and average years (Table 1). Other studies have also shown that extractable ammonium accumulates during dry periods in desert soils (Austin et al., 2004; Welter et al., 2005). Thus, it follows that reduced physiological activity in *B. curtipendula* during the wet year was most likely due to severe nitrogen limitation. Indeed, C$_4$ grasses in desert areas have been shown to translocate nitrogen from shoots to rhizomes and roots during times of stress (e.g., reduced soil [N], drought) to protect the plant from nitrogen loss when carbon assimilation is limited (Heckathorn & DeLucia, 1994). In contrast to the deeply rooted C$_3$ shrub, the relatively shallow root system of *B. curtipendula* may be an adaptation for acquiring plant available [N] from surface layers where nutrients tend to be most concentrated (Jobbagy & Jackson, 2001), especially during times of reduced soil moisture.

While photosynthesis ($A_{\text{sat}}$) was apparently regulated by different environmental drivers (i.e., deep soil water vs. soil nitrogen) in the shrub and the grass, we also observed interactions between soil moisture and nitro-

<table>
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<tr>
<th>Species</th>
<th>Dependent variable</th>
<th>Predictors</th>
<th>Parameter</th>
<th>Mean</th>
<th>2.5% CI</th>
<th>97.5% CI</th>
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<td><em>D. leiophyllum</em></td>
<td>$A_{\text{sat}}$</td>
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<td>$-246.0$</td>
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<td>a2</td>
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</table>

Table 3  Posterior means and 95% credible intervals (CIs; see Table 1) for the regression coefficients in the hierarchical Bayesian multiple regression model [HB-MR; see Eqn (7)] for Dasylirion leiophyllum and Bouteloua curtipendula.
gen dynamics that indirectly affected species physiological responses to precipitation variability. For example, although deep soil water was greatest in the wet year, especially for the water addition treatments, $A_{sat}$, $g_s$, and leaf [N] in D. leiophyllum were generally lower in the wet year compared with the average year (Fig. 3). Reduced $A_{sat}$ during the wet compared with the average year can be explained by both reduced $g_s$ (stomatal regulation of photosynthesis) and lower leaf [N] (biochemical regulation of photosynthesis), both of which were reduced by wet surface soil conditions (Table 3). In addition, consistently lower $A_{sat}$ was observed in D. leiophyllum shrubs that received the greatest frequency of increased shallow soil moisture (e.g., summer/winter addition plants). Likewise, $g_s$ and leaf [N] in B. curtipendula were also reduced by increased soil water in the top 15 cm of soil. This negative effect of surface soil water on plant physiological responses was unexpected, and could reflect an important interaction between soil water, soil nitrogen, and/or other soil nutrient dynamics that is not captured in the regression models and field data. Repeated wetting of the top 15 cm during periods of high rainfall may remove soil nutrients from layers occupied by roots through leaching or N gas losses (e.g., ammonium volatilization and NO$_x$ and N$_2$O efflux; Hall et al., 2008) or stimulate microbial growth (Bell et al., 2008) and decomposition, thereby resulting in nitrogen immobilization or mineralization (Austin et al., 2004). Thus, reduced $g_s$ during these wet, nutrient depauperate times could result from indirect effects of low leaf [N]. For example, plants may be able to maintain relatively high water use efficiency during periods of high water availability – and low nutrient availability – by reducing $g_s$ so that low photosynthetic capacity is balanced by reduced transpiration.

The importance of the interactions between variation in soil moisture and soil nitrogen was also expressed during periods of reduced or less frequent rainfall in B. curtipendula. During the dry year, $A_{sat}$ of B. curtipendula was highest in the three water addition treatments and lowest – but still high compared with the wet and average years – in the control treatment. Lower $A_{sat}$ in the control plants during the dry year appears to be due to reduced $g_s$ and lower leaf [N]. Both $g_s$ and leaf [N] are positively correlated with deep soil water, and both may have decreased in response to reduced availability of deep soil water under the driest scenario examined in this study.

While our results suggest that plant physiological responses to precipitation could be directly and indirectly linked to soil moisture and soil nitrogen dynamics, it should be noted that these covariates did not explain all the variation in the observed plant responses. To address this issue, combined results from the ‘HB-MR + HB-MANOVA’ analysis served to describe (1) potential long-term cumulative effects of altered precipitation and/or (2) effects of other unmeasured factors correlated with year, season, and treatment that could have affected short-term and/or long-term physiological responses. Our results indicated that other factors and/or cumulative effects of precipitation affected the physiological responses of both species. Furthermore, these effects were stronger in D. leiophyllum compared with B. curtipendula (Supporting information Table S3). D. leiophyllum is a more deeply rooted, longer lived, evergreen, woody plant, and thus it may be more influenced by the cumulative effects of precipitation through processes such as shifts in carbon allocation between stem, leaf, and root tissues. Further, it is possible that D. leiophyllum is more limited by other environmental factors than B. curtipendula. While leaf [N] increased in a dry year in D. leiophyllum, $A_{sat}$ did not simultaneously increase. This could be due to, for example, seasonal temperature controls, constraints associated with longer lived leaves, or limitations by other nutrients such as phosphorus. For example, Ghanoum & Conroy (2007) showed that phosphorus deficiency inhibited growth in C$_3$ and not C$_4$ plants, indicating that phosphorous availability could have been important for D. leiophyllum but less so for B. curtipendula. In general, the limited number of leaf and soil variables considered in this study, in addition to season, year, and treatment effects, explained a significant amount (78–95%) of the variation in leaf-level physiological properties of these two species.

Conclusions

The combination of an extensive dataset associated with a relatively long-term precipitation manipulation and rigorous statistical modeling provided important insight into the impacts of precipitation change on desert plant physiology. The effects of precipitation on plant photosynthetic responses differed between species (i.e., plant functional types) due to differential limitation by soil moisture vs. soil nitrogen. The deeply rooted C$_3$ shrub (D. leiophyllum) only increased photosynthesis under conditions of both increased soil water at depth (16–30 cm) and sufficient leaf and soil [N], with deep soil water being the primary regulator of its physiological responses. In contrast, photosynthesis in the shallow rooted C$_4$ grass (B. curtipendula) was primarily dependent on leaf and soil [N], but soil moisture availability became important during extended periods of low rainfall.

A 25% increase in precipitation had significant effects on plant photosynthetic responses that were driven by plant–soil interactions. Although photosynthesis in
D. leiophyllum was generally higher when deep soil water was high, photosynthesis decreased under wet conditions associated with (1) an increase in both summer and winter precipitation during an average year or (2) the addition of summer precipitation in a wet year. In both cases, the negative effect of additional water is potentially due to competitive plant and soil processes limiting shrub access to nutrients. In B. curtipendula, supplemental seasonal precipitation in the winter and the summer had positive impacts on photosynthesis in an average and dry year due to increased leaf [N] driven by increased soil NH₄⁺. Further, cumulative effects of supplemental precipitation regulated physiological responses to a greater degree in the shrub than in the grass.

In conclusion, plant interactions with the soil microbial community are an important driver of photosynthetic responses in this ecosystem. Hence, the impacts of shifts in seasonal precipitation on plant carbon gain in this sotol grassland community will be controlled by close linkages between soil variables and plant physiology. Other global change factors such as nitrogen deposition will likely interact with altered precipitation to affect plant growth and survival in the future.

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References


Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1.

Fig. S1. Observed leaf [N] on an area basis in (a) Dasyliirion leiophyllum and (b) Bouteloua curtipendula from 2004 to 2006. Values are sample means ± SE, based on N = 3 for each treatment. S, summer addition treatment; W, winter addition treatment; SW, summer and winter addition treatment; C, control treatment.

Fig. S2. Observed photosynthesis at saturating light ($A_{sat}$) for Dasyliirion leiophyllum and Bouteloua curtipendula from 2004 to 2006. Values are sample mean ± SE, based on N = 3 for each treatment. S, summer addition treatment; W, winter addition treatment; SW, summer and winter addition treatment; C, control treatment.

Table S1. Seasonal precipitation amounts, number of precipitation events, and event size (or magnitude) received at the sotol grassland site during the study period (2004–2006) compared with the long-term seasonal mean (1986–2006). The percentage difference from the 20-year mean is indicated in parentheses. Winter: DJF, spring: MAM, summer: JJA, fall: SON.

Table S2. Supplemental seasonal precipitation amounts (mm) from the initiation of the experimental manipulation to the end of the study period (2002–2006). In 2002, supplemental amounts were based on the 30-year seasonal mean. From 2003 to 2006, supplemental winter amounts were 25% of the previous 3 months’ precipitation, and supplemental summer amounts were 25% of the previous 1 month’s precipitation.

Table S3. Observed vs. predicted $r^2$ values for the hierarchical Bayesian multiple regression model (HB-MR) [see Eqn (7) and Table 3]. Values are also shown for the HB-MR model that evaluates the residuals from that HB-MR in an HB-MANOVA model with year, season, and treatment effects (HB-MR + HB-MANOVA).

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