Precipitation timing and magnitude differentially affect aboveground annual net primary productivity in three perennial species in a Chihuahuan Desert grassland

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Summary

- Plant productivity in deserts may be more directly responsive to soil water availability than to precipitation. However, measurement of soil moisture alone may not be enough to elucidate plant responses to precipitation pulses, as edaphic factors may influence productivity when soil moisture is adequate.
- The first objective of the study was to determine the responses of the aboveground annual net primary productivity (ANPP) of three perennial species (from different functional groups) in a Chihuahuan Desert grassland to variation in natural precipitation (annual and seasonal) and a 25% increase in seasonal precipitation (supplemental watering in summer and winter). Secondly, ANPP responses to other key environmental and soil parameters were explored during dry, average, and wet years over a 5-yr period.
- ANPP predictors for each species were dynamic. High ANPP in *Dasylirion leiophyllum* was positively associated with higher soil NH_4-N and frequent larger precipitation events, while that in *Bouteloua curtipendula* was positively correlated with frequent small summer precipitation events with short inter-pulse periods and supplemental winter water. *Opuntia phaeacantha* was responsive to small precipitation events with short inter-pulse periods.
- Although several studies have shown ANPP increases with increases in precipitation and soil moisture in desert systems, this was not observed here as a universal predictor of ANPP, particularly in dry years.

Introduction

Climate change scenarios predict significant alterations in the timing and magnitude of precipitation in arid and semiarid ecosystems, which may result in alterations of plant productivity (Knapp & Smith, 2001; Weltzin & Tissue, 2003; Schwinning *et al.*, 2004; Snyder & Tartowski, 2006). According to the pulse-reserve paradigm, biomass production following a precipitation event is dependent on the intervals between precipitation events and the duration necessary to obtain sufficient water to initiate biomass production (Noy-Meir, 1973). When a precipitation event is large, rapid biomass production is initiated and continues until the available water is consumed (Noy-Meir, 1973; Sala & Lauenroth, 1982). If precipitation events are small but tightly clustered, soil water may accumulate and generate a single large period of biomass production (Noy-Meir, 1973; Reynolds *et al.*, 2004). In contrast, intermediate intervals between precipitation events may trigger a series of shorter periods of biomass production as the soil begins to dry between these events; however, the available soil moisture will not become fully depleted unless the interval between precipitation events exceeds the soil moisture recharge interval. When the available soil water supply becomes fully depleted, biomass production ceases (Noy-Meir, 1973; Reynolds *et al.*, 2004).

Recently, Ogle & Reynolds (2004) developed a threshold-delay model that incorporates precipitation thresholds, lag times in response variables, resource partitioning, and plant functional type strategies to predict plant responses to variable precipitation regimes. This model suggests that productivity in deserts is a direct response not to precipitation (as suggested by the pulse-reserve model) but rather to soil water availability (Reynolds *et al.*, 2004). However, measurement of soil moisture alone may not be sufficient to determine plant responses to precipitation pulses, as nitrogen (N) availability (e.g. Whitford, 1986) and soil temperatures may also control primary production even during periods when soil moisture is adequate. Coexistence of different plant functional types in arid environments may reflect niche partitioning of soil water through plant physiological responses to seasonal temperatures and utilization of soil water in different soil layers (Guo & Brown, 1997; Reynolds *et al.*, 2004; Muldavin *et al.*, 2008).

Although many variables often affect plant aboveground annual net primary productivity (ANPP) in desert ecosystems, ANPP typically correlates strongly with annual precipitation (Knapp & Smith, 2001; Weltzin & Tissue, 2003; Huxman *et al.*, 2004b). Similarly, mesic grasslands are strongly influenced by the amount and distribution of annual precipitation, but ANPP in any given year can fluctuate depending on precipitation frequency and magnitude, as well as plant production occurring in the previous year (Sala *et al.*, 1988; Knapp *et al.*, 2001; Oesterheld *et al.*, 2001). ANPP may also be strongly influenced by the mixture of plant functional types within a community. For example, shrub ANPP was associated with annual precipitation, but ANPP in grasses was not; however, when grass and shrub ANPPs were pooled, the different functional responses to precipitation were masked (Jobbagy & Sala, 2000). Therefore, when studying community ANPP responses to precipitation, individual plant functional group responses should be considered in order to understand their unique contribution to the overall community (Jobbagy & Sala, 2000; Huenneke *et al.*, 2002; Havstad *et al.*, 2006).

In the Chihuahuan Desert, a 25% increase in winter and summer precipitation has been predicted, with most of the additional precipitation occurring in fewer, more intense precipitation events (Johns *et al.*, 1997; Flato *et al.*, 2000). Our first objective was to determine the responses of ANPP of three dominant perennial species (*Dasylirion leiophyllum*, a shrub; *Opuntia phaeacantha*, a succulent; and *Bouteloua curtipendula*, a grass) to variation in the timing and magnitude of natural precipitation (annual and seasonal) and a 25% increase in seasonal precipitation (e.g. supplemental watering in summer and winter). Secondly, we explored ANPP responses to other key environmental and soil parameters to determine the potential impact of these variables on ANPP for these three different functional plant types.

Materials and Methods

Study site

The study was conducted in a sotol grassland ecosystem (1526 m elevation) within the Pine Canyon Watershed, Big Bend National Park (BBNP), TX, USA (29°5′N, 103°10′W, 1526 m above sea level), in the Chihuahuan Desert. The dominant plant genera include *Dasylirion*, *Condalia*, *Opuntia*, *Bouteloua*, *Agave*, *Nolina*, and *Muhlenbergia*, with *Dasylirion*, *Opuntia*, and *Bouteloua* composing 30–50% of the community plant cover. This soil overlays a fractured igneous bedrock formation, also known as the Lajitas-rock outcrop complex; the soil texture is a sandy-loam within a rocky A-horizon and has little to no litter layer (Aide *et al.*, 2003). BBNP has a bimodal and highly variable seasonal rainfall regime, with the majority of annual precipitation occurring as monsoonal rain in the late summer. The average annual precipitation is *c.* 365 mm (range 170–570 mm) at Panther Junction (*c.* 6 km from the field site). Most of the seasonal precipitation (45%) occurs in the summer months (June, July, and August). The fall (September, October, and November) receives *c.* 27% of the annual rainfall, while 17% occurs in the spring (March, April, and May) and only 11% occurs in the winter (December, January, and February). Average daily air temperatures at the site in the summer range from a minimum of 18–22°C to a maximum of 32–36°C, while winter daily air temperature averages can range from a minimum of 1–6°C to a maximum of 14–20°C. Spring and fall experience similar temperatures, ranging from 9 to 30°C.

Research plots and study plants

The study focused on three dominant perennial species representing three different functional types: *Dasylirion leiophyllum* (Engelm.) (sotol; a C_3 shrub), *Opuntia phaeacantha* (Engelm.) (brownspine prickly pear; a crassulacean acid metabolism (CAM) succulent), and *Bouteloua curtipendula* ((Michx.) Torr.) (sideoats grama; a C_4 grass). In January 2002, water treatments were applied to smaller individual plots (three 1 × 0.5 m plots per treatment; one plant per plot; 12 plots per species; 36 plots in total) and larger community plots (three 3 × 3 m plots per treatment; many plants per plot; 12 plots in total) to simulate a Hadley Climate Model 2 scenario (Gordon *et al.*, 2000), as described in Patrick *et al.* (in press). Plots were distributed randomly throughout the sotol grassland site and watering was contained within each plot (Patrick *et al.*, in press). The smaller individual plots were used for ANPP measurements and the larger community plots were used for soil sampling, in order to avoid long-term damage to the ANPP plants, as previously described for this site (Bell *et al.*, 2008; Patrick *et al.*, in press). All plots had similar soil conditions, which are characteristic of this region of BBNP (Bell *et al.*, 2008; Patrick *et al.*, in press).

Dasylirion leiophyllum is a polycarpic, dioecious perennial (C_3) with drought-resistant fibrous leaves that arise from and wrap around a woody caudex. The roots of this species are fibrous and typically spread densely through the upper 10–30 cm of soil. Older plants have roots that can extend even deeper and to further distances from the plant. Flowering usually occurs in the spring or early summer (Powell, 1998). *Opuntia phaeacantha* is a succulent CAM plant that produces green pads with 3–7-cm-long dark-brown spines and has shallow roots that are usually found in the first 5–10 cm of the soil. Most roots are in close proximity to the plant, although they can extend up to a meter away in the upper soil layers as well as downward to 30 cm in older and larger plants. Flowering generally occurs from May to June, producing either new pads or red to purple fleshy fruit in the spring (Powell & Weedin, 2004). *Bouteloua curtipendula* is a perennial bunch grass (C_4) with fibrous roots extending into the upper 10 cm of soil; flowering primarily occurs in June–November (Powell, 2000).

Precipitation manipulation and soil moisture

Seasonal precipitation treatments were applied to the research plots as follows: natural precipitation only (control (C)); natural precipitation plus supplemental summer precipitation (S); natural precipitation plus supplemental winter precipitation (W); and natural precipitation plus supplemental summer and winter precipitation (SW). Water was added as a single storm event during the winter (water application in February) and as three distinct storm events in the summer (June, July, and August). For winter and summer watering in 2002, supplemental precipitation amounts were determined as 25% of average seasonal rainfall amounts based on 30-yr rainfall data from National Park Service records. In subsequent years, supplemental water treatment amounts were determined as 25% of ambient precipitation received preceding a watering event (e.g. 3 months before the winter supplemental event, and 1 month before each summer supplemental event). Plots were slowly watered using watering cans to limit any possible surface runoff, and watering occurred on approximately the same dates in each year. Water for the tanks was provided by a local water source and transported to the site annually by the BBNP fire department.

Soil maximum and minimum temperatures were measured (15 cm depth) using HOBO ProTemp/Temp External data loggers (Onset Computer Corporation, Pocasset, MA, USA). The volumetric soil moisture content was measured from 2003 to 2006 using ECH$_2$O-10 dielectric aquameter probes (Decagon Devices, Pullman, WA, USA). One probe was placed in each plot at a soil depth of 15 cm. Measurements were logged every 2 h on Em5 data loggers (Decagon Devices) and averaged for the 24-h period. Daily high and low air temperatures and precipitation were obtained from a meteorological weather station located at Panther Junction park headquarters. Daily precipitation was used to calculate annual precipitation magnitude and inter-pulse periods (e.g. dry day events).

Soil nutrient and chemical measurements

Soil collections consisted of two composite soil samples collected from 0–15-cm depths from each community plot (12 treatment plots; 24 composite samples collected during each sample period across the study). One composite soil sample consisted of at least four subsamples within the plot to provide the best possible representation of the soil nutrient and chemical properties of the plot as a whole (Bell *et al.*, 2008). In every composite sample, soils were collected from under each dominant plant (*D. leiophyllum*, *O. phaeacantha*, and *B. curtipendula*) as well as from interplant spaces. Exchangeable soil ammonium (NH_4^+-N) was determined via colorimetric assay and was extracted 1 d after the sample collection date using a 50-ml 2M KCl solution from 5 g per dry weight equivalent soil per sample (Robertson *et al.*, 1999). Concentrations of extractable NO_3-N were determined 1 d after the sample collection date by A&L Soil Laboratories (Lubbock, TX, USA) using ion-specific probes. Soil pH was measured using a 2 : 1 paste extract, and soil organic matter (SOM) was estimated using a loss-on-ignition method (Robertson *et al.*, 1999). All soil samples were collected in March and September for each year (end of winter and summer seasons in BBNP) for each plot and analyzed within 2 wk of collection; more details on the sampling and laboratory methods are given in Bell *et al.* (2008).

Plant measurements

Total leaf area per plant (m^2) was estimated by multiplying the total number of leaves per plant with the average leaf area of each plant for 2002–2004 and 2006 (Smith & Knapp, 2001). The frequency of measurements varied depending on the species, but measurements were taken at least four times a year (once each season). Aboveground biomass (vegetative and reproductive) was determined nondestructively for each measurement period by taking off-plot destructive samples of each species to develop allometric regressions between field growth measurements (leaf area) and biomass (Retta *et al.*, 2000; Smith & Knapp, 2001). Because of the unique morphology of these plants, this provided more accurate biomass estimates than using plant volume alone (Huenneke *et al.*, 2001). Aboveground net primary production (NPP) was estimated on a plot ground area (m^2) basis for each measurement month by subtracting the total plant biomass (vegetative and reproductive) for the month from that of the previous month (Huenneke *et al.*, 2001; Muldavin *et al.*, 2008). These values were obtained for each measurement month and then totalled at the end of each year to obtain aboveground

ANPP for that year. Only positive increments were used as it was generally difficult to determine whether any negative increment values (e.g. declines in biomass) were a result of herbivory, senescence or human error (Huenneke *et al.*, 2001). The aboveground ANPP values were still an underestimate of total plant NPP because belowground productivity was not determined.

Statistical analysis

All growth and soil parameters were analyzed using repeated measures ANOVA to compare the main effects and interactive effects of water treatment and year (SPSS 11.5; SPSS Inc., Chicago, IL, USA). Parameters were considered significantly different when $P \leq 0.05$; significant effects were further analyzed using least significant difference (LSD) post hoc tests. Linear regression analyses were used to relate aboveground ANPP to natural precipitation events and supplemental precipitation treatments. Because of the nature of the data and small sample size, a Kendall's tau correlation matrix was used to detect potential correlations between species ANPP and environmental parameters (Field, 2000). These parameters included precipitation variables (annual precipitation, annual events, magnitude of precipitation event, and inter-pulse period), maximum and minimum air and soil temperatures, and soil variables (soil moisture, soil nitrate, soil ammonium, soil organic matter, and soil pH). The magnitude of the precipitation event was divided into four classes (< 5, 5–10, 10–20, and > 20 mm) and the inter-pulse period was divided into five classes (0–5, 6–10, 11–20, > 20, and > 50 d). *R* values in this matrix can range from −1.0 to 1.0 (1.0 indicates perfectly positively correlated variables and −1.0 indicates perfectly negatively correlated variables) and were considered significantly different when $P \leq 0.05$.

Redundancy analysis (RDA) was used to explore the environmental influence of precipitation (annual precipitation, annual events, magnitude of precipitation event, and inter-pulse period), temperature (maximum and minimum air and soil temperatures), and soil (moisture, nitrate, ammonium, organic matter, and pH) factors on above-ground ANPP (CANOCO 4.5; University of South Bohemia, Ceske Budejovice, Czech Republic). This constrained ordination technique is analogous to a multivariate multiple regression and was chosen because it performs well with nonorthogonal and collinear gradient data (McGarigal *et al.*, 2000). Each year was analyzed separately to determine the possible effects of specific environmental factors on ANPP over time. Almost all RDA graphs had a high species–environment correlation value, suggesting that most of the measured environmental variables were important, although there may be other unaccounted factors of equal importance (McGarigal *et al.*, 2000). Only the first and second axes were shown in the graphs, with the first axis explaining most of the variation for RDA graphs.

Results

Environmental variables

Mean high and low monthly air temperatures were similar in each year during the 5-yr study period (Fig. 1a) and within the average range of air temperatures that have been measured over a 30-yr period for BBNP (1976–2006). Annual precipitation varied among years (see Supporting Information Table S1), but, relative to the mean annual precipitation for 1976–2006 (365 mm), measurement years were designated as follows: 2001 (191 mm, dry); 2002 (357 mm, average); 2003 (410 mm, average); 2004 (567 mm, wet); 2005 (329 mm, average); and 2006 (274 mm, dry). Seasonal precipitation varied for each year (Fig. 1b; see Table S2). In general, summer received the largest amount of precipitation and exhibited the shortest inter-pulse periods, while winter (December through February) was the driest period with the longest inter-pulse periods (> 20 or 50 d). During the experimental period, winters were exceedingly dry in 2002 (89% below average) and 2006 (63% below average). Summer precipitation was average for all years except 2004, when summer precipitation was 47% above average. In the driest year (2001), precipitation was below average for all seasons (Table S2). Volumetric soil water content was higher after supplemental or natural precipitation events, particularly large events, and generally ranged from 3 to 10% (Fig. 1c). Measured soil moisture was higher in wet years than in dry years, and soil moisture differed by season, with greater soil moisture in the summer and fall compared with the winter and spring. In addition, at the same site during this period it was observed that maximum soil moisture was highest in the SW plots, lower in the S and W plots, and lowest in the C plots during the summer (Patrick *et al.*, in press).

Soil responses to natural and supplemental precipitation

Annual shifts in extractable soil NO_3-N were observed during the study period, as NO_3-N concentrations were significantly higher in 2002 and 2003 compared with 2004 and 2006 ($P \leq 0.001$; Fig. 2a). In 2002, soil NO_3-N concentrations were significantly higher in the W plots ($P = 0.05$) compared with all other treatment plots, while the S treatment had significantly higher values than the control ($P = 0.044$; Fig. 2a). In 2004, soil NO_3-N concentrations in the W treatment were significantly higher than in the control plots ($P \leq 0.05$; Fig. 2a). Extractable soil NH_4-N concentrations (Fig. 2b) and soil organic matter (Fig. 2c) showed no response to supplemental water treatments. Annually, soil NH_4-N concentrations in 2006 were significantly higher ($P \leq 0.001$) than in previous years (Fig. 2b). Soil pH was generally acidic (pH 5.6–6.0) throughout 2002–2003 for all plots (Fig. 2d). In 2004, significant differences in overall soil pH values were observed as soil in plots receiving supplemental water became more basic (Fig. 2d).

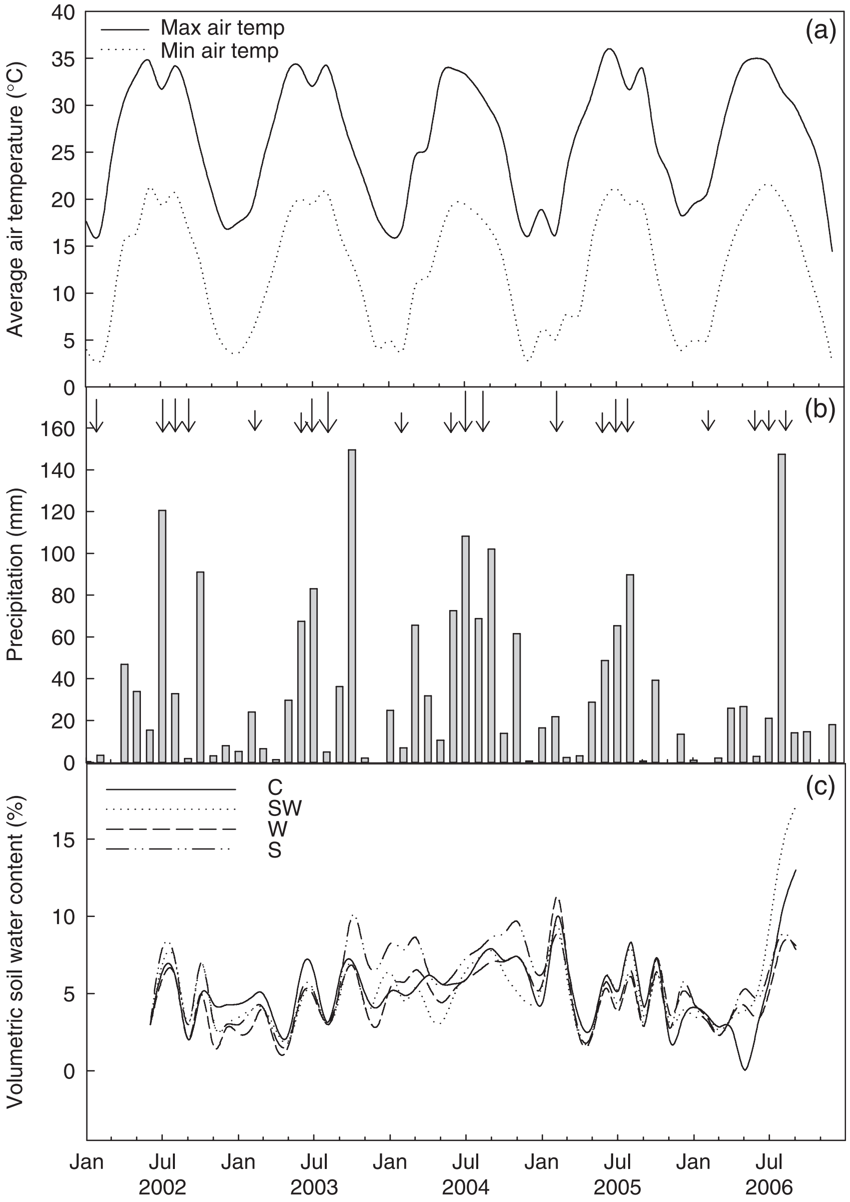

Fig. 1 Monthly environmental variables for the sotol grassland in Pine Canyon at Big Bend National Park for 2002–2006: (a) average maximum and minimum air temperatures, (b) monthly precipitation, and (c) soil moisture for each supplemental water treatment. Arrows indicate watering additions (the longer the arrow, the larger the event) and occur in this order (in mm): 2002: 11, 11, 11; 2003: 7, 7, 17, 21; 2004: 7, 3, 18, 27; 2005: 20, 7, 12, 16; and 2006: 4, 7, 0.7, and 5. C, control; SW, summer/winter; W, winter; S, summer.

Aboveground ANPP responses to natural and supplemental precipitation

Dasylirion leiophyllum did not exhibit an overall response in ANPP to increasing annual precipitation ($R^2 = 0.013$; $P = 0.211$), although there was a significant difference in ANPP among years (Fig. 3a; Table 1). *Bouteloua curtipendula* exhibited a significant ($R^2 = 0.058$; $P \leq 0.05$) decline in aboveground ANPP with increasing annual precipitation, but only 6% of the variation in ANPP could be explained by annual precipitation (Fig. 3b; Table 1). No relationship between ANPP and annual precipitation was observed in *O. phaeacantha* during this study ($R^2 = 0.000$; $P \leq 0.1$; Fig. 3c; Table 1). However, *O. phaeacantha* did exhibit a significant increase in ANPP as a result of increasing precipitation in an average year (2003) ($R^2 = 0.381$, $P \leq 0.05$). Seasonally, *D. leiophyllum* produced higher biomass during the summer, *B. curtipendula* in mid and late summer, and *O. phaeacantha* during the spring and early summer (data not shown).

Dasylirion leiophyllum showed no significant response of ANPP to seasonal supplemental precipitation during the 5-yr period (Fig. 3a; Table 1). Supplemental water additions increased ANPP in W plants of *B. curtipendula* compared with all treatments in an average year (2002; $P \leq 0.05$; Fig. 3b). ANPP of W plants was only significantly greater than that of S plants in 2003 ($P \leq 0.05$), with no treatment differences in other years. *Opuntia phaeacantha* did not exhibit a significant ANPP response to supplemental precipitation (Fig. 3c), except

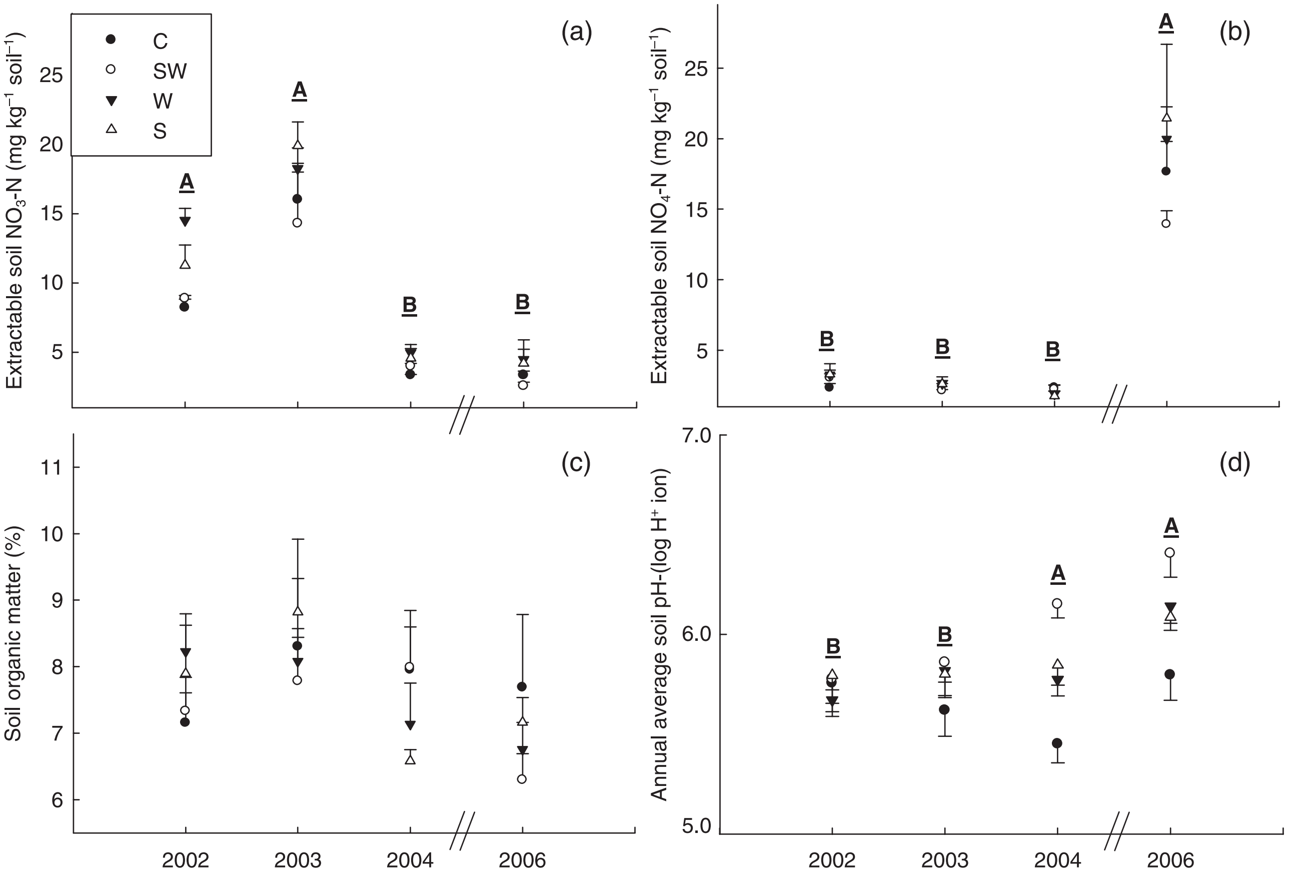

Fig. 2 Annual averages for (a) extractable soil NO_3-N, (b) extractable soil NH_4-N, (c) soil organic matter, and (d) soil pH for the sotol grassland in Pine Canyon at Big Bend National Park for 2002–2006. Values are plotted as means ± SEM (2002, $n = 15$; 2003, $n = 12$; 2004, $n = 30$, 2006, $n = 12$) for each supplemental water treatment (C, control; SW, summer/winter; W, winter; and S, summer). Values designated with letters exhibit a statistical difference at $P \leq 0.05$ for each year.

in 2003, where SW plants had significantly higher ANPP than W plants ($P \leq 0.05$).

Redundancy and Kendall tau analyses

When each year was analyzed separately using RDA, a different tri-plot arrangement emerged (Fig. 4a–d); only significant environmental and soil variables are shown for each year. One consistent pattern was that concentrations of NH_4-N, NO_3-N, and soil organic matter, followed by inter-pulse duration and magnitude of precipitation event, were typically of high importance in predicting ANPP for *D. leiophyllum* and *B. curtipendula*. In the first 3 yr (2002–2004), when annual precipitation amounts were average or above average, 70–90% of the variability in ANPP of the different species could be explained by these soil and environmental variables. In a dry year (2006), only 32% of the variability in ANPP could be explained by these same factors.

For *D. leiophyllum*, ANPP was highly correlated with concentrations of NH_4-N, NO_3-N, and soil organic matter during average to wet years (Fig. 4a–c), but not during a dry year (2006), when ANPP was more highly correlated with climatic variables, specifically small precipitation events and short inter-pulse periods (Fig. 4d). However, *D. leiophyllum* ANPP also exhibited a negative correlation with soil moisture and NO_3-N during a wet year (2004) (Fig. 4c). ANPP in *D. leiophyllum* showed a positive correlation with S treatment during average (2002) and dry (2006) precipitation periods. In the Kendall tau correlation analysis, *D. leiophyllum* showed a significant positive correlation with NH_4-N ($R = 0.595$) but only in 2004 (Table 2); there was no significant correlation with any precipitation variable (data not shown).

During wet years, ANPP in *B. curtipendula* was correlated with soil variables and long inter-pulse periods, while in a dry year greater control of ANPP was exerted by climatic variables and soil NH_4-N concentrations. In an average year (2002), ANPP was positively correlated with soil organic matter and negatively correlated with the occurrence of an inter-pulse period of 6–10 d and precipitation magnitudes of 10–20 mm (Fig. 4a). As precipitation increased, *B. curtipendula* ANPP was positively correlated with NH_4-N and NO_3-N concentrations, soil moisture, and inter-pulse periods > 20 d (Fig. 4b,c). However, ANPP was negatively correlated with small precipitation magnitudes of 5–10 mm in a wet year (2004). In a dry year (2006), which had an extensive drought period at the beginning of the year followed by large moisture pulses in the summer, variation in ANPP of *B. curtipendula* was not strongly correlated with the measured environmental variables (Fig. 4d). *Bouteloua curtipendula* ANPP did show significant correlations in the Kendall tau correlation matrix for 2002 and 2003 (Table 2). *Bouteloua curtipendula* was positively correlated with NO_3-N ($R = 0.788$) in 2002 and negatively correlated with soil pH ($R = -0.455$) in 2003. There was no significant correlation with any precipitation variables (data not shown).

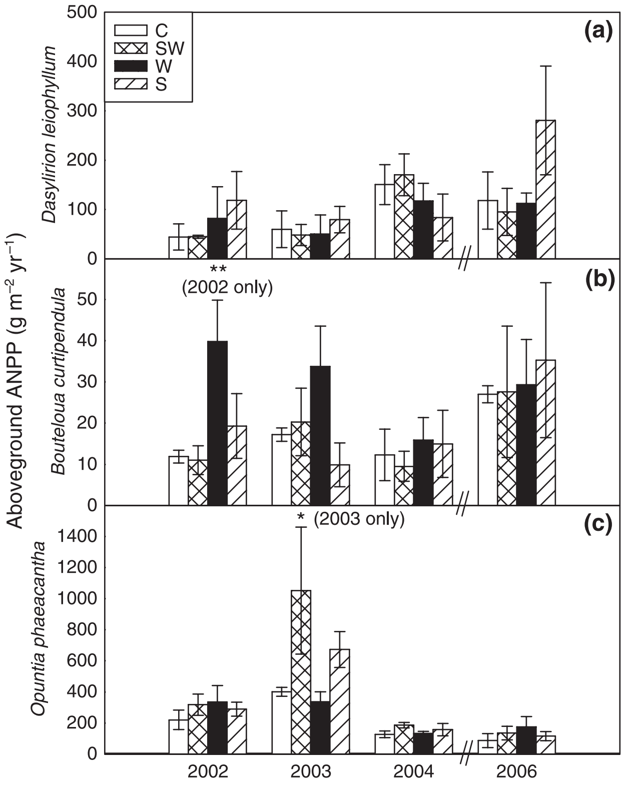

Fig. 3 Aboveground annual net primary productivity (ANPP) for (a) *Dasylirion leiophyllum*, (b) *Opuntia phaeacantha*, and (c) *Bouteloua curtipendula* for 2002–2004 and 2006 from the sotol grassland in Big Bend National Park. Values are plotted as means ± SEM ($n = 3$) for each supplemental water treatment (C, control; SW, summer/winter; W, winter; and S, summer). Statistical difference: *, $P \leq 0.1$; **, $P \leq 0.05$.

Variability in *O. phaeacantha* ANPP was more highly correlated with climatic variables (magnitude of precipitation event and inter-pulse period) than soil variables, although the response varied depending on moisture inputs during the specific year. During average and wet years, ANPP was correlated with annual precipitation, number of precipitation events, small and medium precipitation magnitude events, and shorter inter-pulse periods (Fig. 4a–c). During a dry year, variation in *O. phaeacantha* ANPP was correlated with soil pH, small precipitation magnitude events, and medium inter-pulse periods (Fig. 4d). In *O. phaeacantha*, ANPP was negatively correlated with inter-pulse periods > 50 d during average years (2002 and 2003), soil NO_3-N in a wet year (2004), and soil organic matter in a dry year (2006). ANPP in *O. phaeacantha* was correlated with the W treatment in average (2002) and dry (2006) years. *Opuntia phaeacantha* ANPP also showed correlations for each year in the Kendall tau correlation analysis (Table 2). *Opuntia phaeacantha* ANPP was positively correlated with NH_4-N ($R = 0.473$) and soil pH ($R = 0.515$) in 2002 and annual precipitation in 2003 ($R = 0.570$) and 2004 ($R = 0.503$). It was negatively correlated with soil organic matter ($R = -0.455$) in 2004. *Opuntia phaeacantha* was the only species that also showed correlations of ANPP with inter-pulse period and magnitude intervals, but only for 2003 and 2004. In 2003, ANPP was positively correlated with precipitation magnitude classes 5–10 mm ($R = 0.532$), 10–20 mm ($R = 0.698$), and > 20 mm ($R = 0.698$), as well as

Table 1 *F*-values for repeated measures and one-way ANOVAs used to test supplemental water treatment, year, and their interactions for annual net primary productivity (ANPP) for each species

Statistics	*Dasylirion leiophyllum*	*Bouteloua curtipendula*	*Opuntia phaeacantha*
Repeated measures			
Year	4.683**	3.958*	17.597***
Treatment	0.572	0.832	1.751 (SW > C*)
Year × treatment	1.561	1.123	2.186
One-way			
2002	0.608	4.054** (W > C,SW,S)	0.474
2003	0.201	2.049 (W > S**)	2.293 (SW > C*,W**)
2004	0.835	0.221	1.152
2006	1.644 (S > SW*)	0.078	0.586

Statistical difference: *, $P \leq 0.1$; **, $P \leq 0.05$; ***, $P \leq 0.001$.
C, control; SW, summer/winter; W, winter; S, summer.

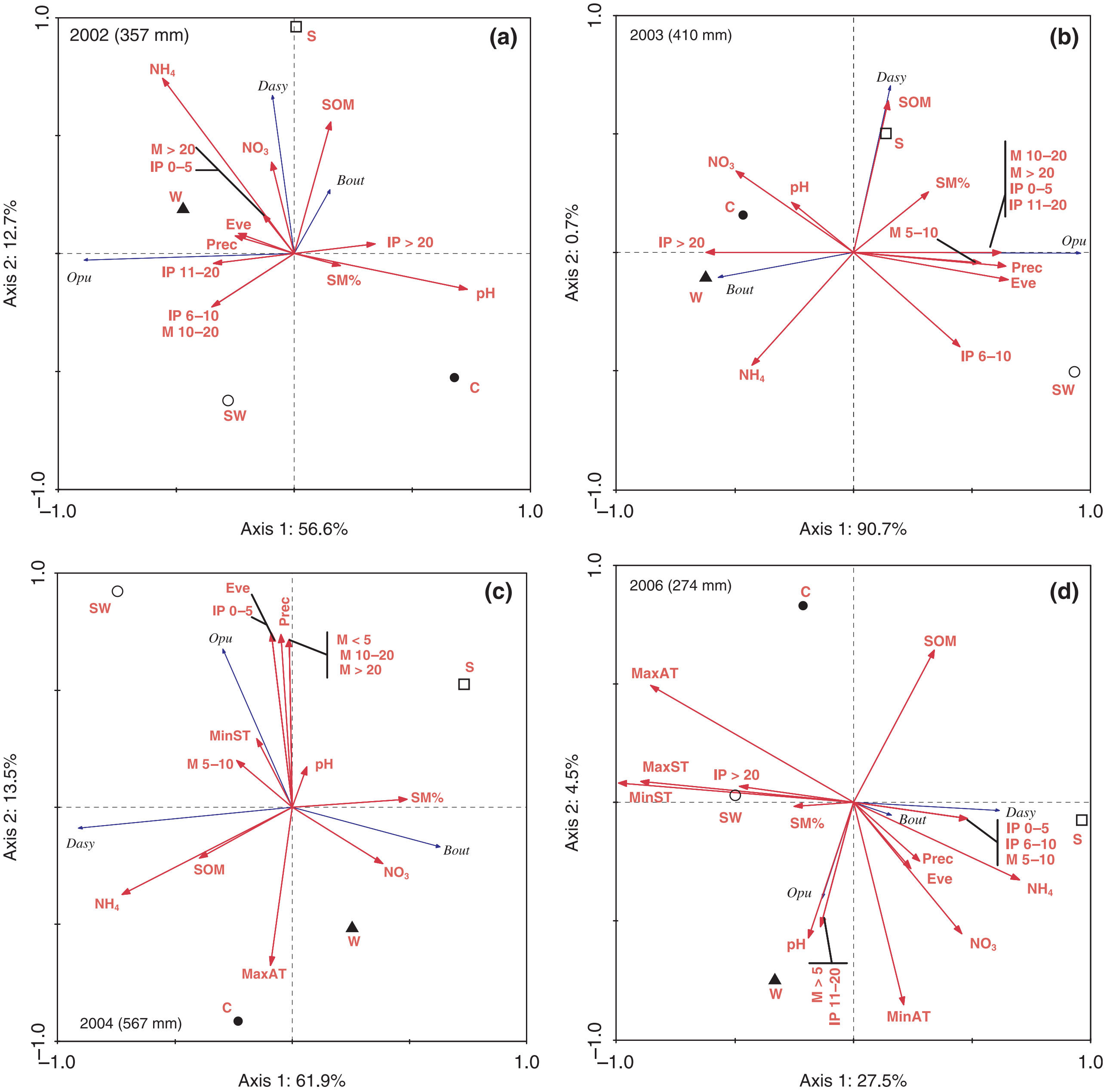

Fig. 4 Redundancy analysis (RDA) comparing aboveground annual net primary productivity (ANPP) of *Dasylirion leiophyllum* (Dasy), *Opuntia phaeacantha* (Opu), and *Bouteloua curtipendula* (Bout) with measured environmental variables for the sotol grassland in Big Bend National Park for each year: (a) 2002, (b) 2003, (c) 2004, and (d) 2006. ANPP values are means ± SEM ($n = 3$) and soil values (extractable soil NO_3-N, extractable soil NH_4-N, soil organic matter, and soil pH) are means ± SEM (2002, $n = 15$; 2003, $n = 12$; 2004, $n = 30$; 2006, $n = 12$) for each treatment. Treatments: closed circles, control (C); open circles, summer and winter (SW); triangles, winter (W); squares, summer (S). Environmental variables: IP, inter-pulse period (d); M, precipitation magnitude (mm); Prec, annual precipitation; Eve, annual events; SOM, soil organic matter; SM%, soil moisture; MaxAT, maximum air temperature; MinAT, minimum air temperature; MaxST, maximum soil temperature; MinST, minimum soil temperature.

inter-pulse period class 11–20 d ($R = 0.698$). It was negatively correlated with inter-pulse period class > 20 d ($R = -0.698$). For 2004, *O. phaeacantha* ANPP was positively correlated with precipitation magnitude classes < 5 mm ($R = 0.533$), 10–20 mm ($R = 0.533$), and > 20 mm ($R = 0.533$), as well as the inter-pulse period class 0–5 d ($R = 0.503$).

Discussion

Aboveground ANPP responses to natural precipitation

The responses of ANPP of our three dominant perennial species (*D. leiophyllum*, a shrub; *O. phaeacantha*, a succulent;

Table 2 Kendall tau correlation matrix among species annual net primary productivity (ANPP) and environmental parameters measured in the sotol grasslands in Big Bend National Park (BBNP) for each year

2002	Bout	Dasy	Opu	$\mathrm{NO_3}$-N	$\mathrm{NH_4}$-N	SOM	pH	Prec	SM%
Bout	1.000								
Dasy	0.091	1.000							
Opu	–0.182	–0.061	1.000						
$\mathrm{NO_3}$-N	**0.788**	0.061	–0.030	1.000					
$\mathrm{NH_4}$-N	0.260	0.137	**0.473**	0.351	1.000				
SOM	0.182	0.121	–0.152	0.333	0.107	1.000			
pH	0.061	0.000	**0.515**	0.212	**0.595**	–0.091	1.000		
Prec	–0.067	0.168	0.235	–0.034	0.186	0.000	–0.067	1.000	
SM%	–0.268	0.235	0.034	–0.168	–0.017	–0.067	–0.268	0.333	1.000
2003	Bout	Dasy	Opu	$\mathrm{NO_3}$-N	$\mathrm{NH_4}$-N	SOM	pH	Prec	SM%
Bout	1.000								
Dasy	–0.121	1.000							
Opu	–0.424	0.273	1.000						
$\mathrm{NO_3}$-N	0.242	0.030	–0.152	1.000					
$\mathrm{NH_4}$-N	0.107	–0.198	–0.321	0.260	1.000				
SOM	–0.061	0.273	0.091	0.333	–0.015	1.000			
pH	**–0.455**	–0.121	0.121	–0.061	0.076	0.303	1.000		
Prec	–0.067	0.034	**0.570**	–0.034	–0.084	–0.134	–0.168	1.000	
SM%	–0.436	0.268	0.268	0.134	–0.152	0.168	0.134	0.000	1.000
2004	Bout	Dasy	Opu	$\mathrm{NO_3}$-N	$\mathrm{NH_4}$-N	SOM	pH	Prec	SM%
Bout	1.000								
Dasy	–0.382	1.000							
Opu	–0.030	0.107	1.000						
$\mathrm{NO_3}$-N	0.046	–0.092	–0.076	1.000					
$\mathrm{NH_4}$-N	–0.333	**0.595**	0.030	–0.046	1.000				
SOM	0.030	0.229	–0.091	–0.290	0.030	1.000			
pH	–0.242	0.046	–0.121	0.046	0.121	–0.242	1.000		
Prec	–0.034	0.051	**0.503**	0.338	–0.101	–0.101	**–0.469**	1.000	
SM%	0.101	–0.321	–0.235	–0.068	–0.168	–0.302	0.268	–0.333	1.000
2006	Bout	Dasy	Opu	$\mathrm{NO_3}$-N	$\mathrm{NH_4}$-N	SOM	pH	Prec	SM%
Bout	1.000								
Dasy	0.303	1.000							
Opu	–0.212	0.061	1.000						
$\mathrm{NO_3}$-N	–0.061	–0.333	0.061	1.000					
$\mathrm{NH_4}$-N	0.242	–0.030	0.061	**0.576**	1.000				
SOM	–0.030	0.182	**–0.455**	0.182	0.121	1.000			
pH	0.333	0.182	0.030	0.061	0.000	–0.091	1.000		
Prec	–0.201	0.067	0.101	–0.335	–0.268	–0.201	–0.436	1.000	
SM%	–0.101	0.101	–0.067	**–0.570**	–0.369	–0.168	–0.268	**0.667**	1.000

Bout, *Bouteloua curtipendula*; Dasy, *Dasylirion leiophyllum*; Opu, *Opuntia phaeacantha*; SOM, soil organic matter; Prec, annual precipitation; SM%, volumetric soil moisture.
R values in bold indicate a statistical difference of $P \leq 0.05$.

and *B. curtipendula*, a grass) to variation in the timing and magnitude of natural precipitation (annual and seasonal) during the 5-yr study period varied for each species. *Dasylirion leiophyllum* exhibited its highest ANPP during the wettest year (2004) when precipitation was 55% above average, precipitation events were 44% above average, and large precipitation events (> 20 mm) were 140% more frequent than average. These frequent large precipitation events, combined with frequent smaller events, wet the upper and lower soil layers for long periods of time, allowing roots in both zones to utilize soil moisture for most of the growing season, thereby promoting plant growth (Gibbens & Lenz, 2001). Apparently, frequent large precipitation events in the wet year, in which these events were twice as frequent as in any other year, were key determinants of productivity in this deeper rooted shrub. Fravolini *et al.* (2005) found similar results with another deep-rooted shrub, mesquite (*Prosopis velutina*), where large rain events during wet summers resulted in increased water uptake and photosynthesis, especially in course-textured soils, leading to increased biomass.

In *B. curtipendula*, ANPP was highest in an average precipitation year following a dry year, which suggests that total annual precipitation was not a major determinant of productivity in this species. The winter precipitation was below average, but summer precipitation was average, with most of the precipitation occurring in small (< 5 mm) events during this period of high physiological activity. During the summer, there were also very few inter-pulse periods > 10 d, indicating that the soil was rarely dry for extended periods of time. These data suggest that frequent, small precipitation events with relatively few extended dry inter-pulse periods promote productivity in this shallow-rooted bunchgrass. Similarly, Jobbagy & Sala (2000) observed a weak correlation of ANPP with annual precipitation in several grass species in the Patagonian steppe, as ANPP was more strongly correlated with seasonal precipitation amounts and temperature. This suggests that grass ANPP was primarily responsive to the seasonal timing and magnitude of precipitation and subsequent soil moisture, rather than to the amount of precipitation received annually. In our study, ANPP in *B. curtipendula* may be more influenced by seasonal precipitation patterns, mainly summer precipitation with frequent precipitation events and few long inter-pulse periods, rather than total summer precipitation amounts. In addition, adequate winter and spring precipitation may maintain root development, allowing these plants to fully exploit water availability when physiologically active during the late spring and summer months (Bates *et al.*, 2006; Muldavin *et al.*, 2008). Furthermore, the decline of ANPP during wetter years (2003–2004) may be attributable to other limiting factors (e.g. NH_4-N and NO_3-N) or increased competition as a result of greater plant density (Yahdjian & Sala, 2006; Muldavin *et al.*, 2008).

In *O. phaeacantha*, ANPP was highest in an average precipitation year (2003), when plants received average winter precipitation, as well as average fall precipitation in the previous year. This precipitation pattern differed from that in other study years, when plants were exposed to either dry winters, or both a dry winter and a dry fall in the previous year. In the spring of 2003, precipitation magnitude was below average, but most precipitation events were small (< 5 mm) with most inter-pulse periods < 20 d, indicating that soil moisture was probably adequate at shallow rooting depths (5–10 cm), where *O. phaeacantha* roots are most abundant and can readily utilize water (Dougherty *et al.*, 1996). Pad production occurs in mid/late spring (Powell, 1998) and is largely dependent on prior fall and winter precipitation, when water is stored in the soil and in the succulent pads of *O. phaeacantha*, rather than only current spring precipitation events (Muldavin *et al.*, 2008).

Aboveground ANPP response to supplemental precipitation

ANPP responses to increased supplemental seasonal precipitation also varied depending on the species. Supplemental seasonal precipitation did not influence ANPP in *D. leiophyllum*, but greater ANPP was observed for *B. curtipendula*. In *B. curtipendula*, supplemental winter precipitation in an average year (2002), following a very dry year, generated a large positive ANPP response in our winter watering treatment. The large pulse of supplemental water (e.g. 25 mm, which constituted more than half of the natural winter precipitation) plus the very dry conditions preceding the supplemental winter precipitation event was sufficient to initiate plant growth when temperatures increased in the spring. The significant impact of this large single rainfall event indicates the critical importance of winter precipitation in this grass species. In subsequent years, winter precipitation was generally average and the impact of the W treatment was no longer observed. The SW treatments in 2002 did not generate the same response as the W treatment, suggesting that summer additions altered the impact of the winter precipitation treatment. Bates *et al.* (2006) observed a similar response during a 7-yr study in the northern Great Basin where shallow-rooted grasses produced greater biomass when the majority of the precipitation was shifted from spring to winter. Furthermore, it is possible that the upper soils may have approached water-holding capacity during the summers of 2003 and 2004, resulting in the treatments being less effective in triggering individual growth responses (Muldavin *et al.*, 2008).

In *O. phaeacantha*, SW treatments increased ANPP following two consecutive years of average precipitation. Pad production in *O. phaeacantha* depends largely on water that is available before mid-spring, when new pads are produced. Therefore, supplemental water in 2002 for the SW treatment in the summer during an average summer and fall rainfall period and in the winter during an average winter followed by a dry spring may have delivered sufficient additional water for increased pad production in 2003. However, because *O. phaeacantha* pads store water, it is unclear if increased winter precipitation could also significantly contribute to increased pad production the following summer.

Best predictors of ANPP

Past studies have shown that annual precipitation may only partially explain differences in ANPP (Knapp & Smith, 2001; Huenneke *et al.*, 2002). Storm frequency and intensity may also be important regulators of plant productivity (Knapp *et al.*, 2002; Schwinning *et al.*, 2004; Fravolini *et al.*, 2005). In slow-growing species, such as commonly occur in desert environments, growth responses to precipitation events may be delayed or not affected to a significant degree (Huxman *et al.*, 2004a; Sher *et al.*, 2004).

When we further explored ANPP responses to other key environmental and soil parameters to determine the potential impact of these variables on the ANPP of each species, we found that the responses varied for each species and between sampling years. For *D. leiophyllum*, soil organic matter (RDA analysis) and soil NH_4-N (Kendall tau correlation) may have strong impacts on aboveground ANPP during wet years. However, during drier years, ANPP was mainly affected by climatic variables (e.g. small precipitation events and shorter inter-pulse periods) rather than soil variables (e.g. NH_4-N and NO_3-N). The importance of the woody caudex of this species to plant growth dynamics has never been fully investigated, but it may allow the plant to store sufficient quantities of water and nutrients in wetter years. The ability to store water in some shrubs allows survival through long drought periods (Barker *et al.*, 2006). *Dasylirion leiophyllum* is a very long-lived and slow-growing plant, potentially establishing an 'island of fertility' which may provide the plant with a localized nutrient supply when soil moisture is not limiting (Schlesinger & Pilmanis, 1998; Reynolds *et al.*, 1999). *Dasylirion leiophyllum* also had roots within the upper soil horizons, allowing it to compete with grasses for soil moisture, as well as having deeper roots giving it access to water in lower soil horizons (Scott *et al.*, 2000; Gibbens & Lenz, 2001). Because of this extensive root system, it is difficult to clearly distinguish which climatic variables have a greater impact on ANPP as indicated by the Kendall tau correlation.

For *B. curtipendula*, soil organic matter (RDA analysis) and NO_3-N (Kendall tau correlation) had strong impacts on ANPP in an average precipitation year, suggesting that nitrogen mineralization rates may be a significant regulator of ANPP when soil moisture is sufficient for growth. In above-average precipitation years, soil NH_4-N and NO_3-N concentrations had stronger impacts on ANPP than in average rainfall years (RDA analysis), perhaps as a result of changes in available nitrogen. During a dry year, climatic variables and soil NH_4-N had a greater impact on ANPP because soil moisture was apparently scarcer in the upper soil horizons. It is possible that seasonal precipitation, in particular winter precipitation, and longer inter-pulse duration may have a greater impact on ANPP in *B. curtipendula*, especially during a dry season when soil moisture is less available (Bates *et al.*, 2006; Yahdjian & Sala, 2006; Muldavin *et al.*, 2008).

ANPP in *O. phaecantha* appears to be primarily regulated by climatic variables rather than soil variables, particularly precipitation magnitude and length of inter-pulse periods (RDA analysis and Kendall tau correlation). Following an average precipitation year, ANPP may be affected more strongly by shorter inter-pulse period duration (11–20 d) than by annual precipitation; however, when annual precipitation was above-average, both precipitation magnitude and the frequency of shorter inter-pulse periods had a greater impact on ANPP. An exception to this may occur with winter precipitation (e.g. when there was greater winter precipitation in 2003 and 2004, but ANPP in *O. phaeacantha* still declined in 2004). This may be a result of changes in soil NO_3-N, because ANPP in *O. phaeacantha* was negatively correlated with NO_3-N concentrations, suggesting that increased nitrogen availability may limit ANPP (Whitford, 1986; Austin *et al.*, 2004; Havstad *et al.*, 2006).

It is possible that there may be a memory or lag effect caused by past precipitation events as a result of pad water storage in *O. phaeacantha* (Dougherty *et al.*, 1996; Schwinning *et al.*, 2004). During a dry year, soil pH, small precipitation magnitude events, and inter-pulse periods of 11–20 d had significant impacts on ANPP in *O. phaeacantha*. There was almost no new pad production during the dry spring of a dry year (2006). During dry winters and springs, *O. phaeacantha* may maintain current pads rather than promote vegetative and sexual reproduction, resulting in very little detectable change in ANPP (Powell & Weedin, 2004). In the RDA analysis, *O. phaeacantha* ANPP was positively correlated with inter-pulse periods of 11–20 d and negatively related to inter-pulse periods > 20 d for all years except 2004, which experienced more frequent shorter inter-pulse periods. Therefore, medium inter-pulse periods are apparently greater regulators of ANPP in *O. phaeacantha* than precipitation magnitude and amount.

In this Chihuahuan Desert grassland ecosystem in Big Bend National Park, ANPP is limited not only by soil moisture and temperature constraints, but also by soil NO_3-N and NH_4-N concentrations. During consecutive years of average and above-average precipitation, extractable nitrogen pools were negatively correlated with annual precipitation, intermediate magnitude events, and shorter inter-pulse periods (RDA analysis). This may suggest that soil N is assimilated as soil moisture becomes available via precipitation events (Bell *et al.*, 2008). However, during an average rainfall year following a dry year (2002) or a dry year following an average rainfall year (2006), extractable nitrogen pools were positively correlated with annual precipitation, intermediate magnitude events, and shorter inter-pulse periods (Muldavin *et al.*, 2008). This may indicate a seasonal soil N build-up during seasons with sporadic precipitation. Furthermore, as soil moisture becomes available via successive precipitation events, soil nitrogen becomes soluble and readily available for plant and microbial uptake.

Soil nitrogen is commonly limiting in desert grasslands, especially in wet years as a result of declines in nitrogen availability and immobilization from previous year ANPP (Whitford, 1986; Austin *et al.*, 2004; Havstad *et al.*, 2006). Wind and water erosion, especially in sites of low plant cover, may also cause shifts in available nitrogen in wetter years (Schlesinger & Pilmanis, 1998; Havstad *et al.*, 2006). Plant cover in the sotol grassland site is *c.* 50%, resulting in a patchy landscape. Consequently, the bare soil-patches could experience soil nitrogen loss through runoff during wetter years, which may cause vegetation shifts in arid ecosystems as a result of limited N availability (Schlesinger *et al.*, 2000; Muldavin *et al.*, 2008).

Conclusions

Many studies have shown that ANPP increases with greater annual precipitation. In this sotol grassland site in the Chihuahuan Desert, there was no universal predictor of ANPP, as the response of each species to precipitation and other environmental factors (e.g. soil NH_4-N and NO_3-N concentrations) was highly variable over the 5-yr study period. In the more deeply rooted shrub *D. leiophyllum*, annual precipitation was important in predicting ANPP, which was highest in the wettest year as a result of frequent large precipitation events. In the more shallow-rooted grass *B. curtipendula*, the magnitude of annual precipitation was not a key determinant of ANPP as frequent small precipitation events in the summer with relatively few long dry inter-pulse periods seemed to regulate periods of active growth. Supplemental winter water during a very dry winter also stimulated ANPP in *B. curtipendula*, suggesting the critical importance of winter precipitation in this grass, especially during a dry year. In the succulent *O. phaeacantha*, there was no relationship between ANPP and annual precipitation, but small precipitation events with short inter-pulse periods during the winter and fall may have generated the greatest productivity.

ANPP was regulated by soil NO_3-N and NH_4-N concentrations, particularly in wet years. In *D. leiophyllum*, soil NH_4-N was positively correlated with ANPP in wet years but not in average or dry years. In *B. curtipendula*, soil NO_3-N and NH_4-N were positively correlated with ANPP in wet years compared with dry years. In *O. phaecantha*, precipitation magnitude and inter-pulse duration were positively correlated with ANPP. In average and wet years, *c.* 70–90% of the variability of ANPP could be explained by climatic and soil factors. In dry years, only 32% of the variability in ANPP could be explained by these same factors. Therefore, in dry years, other factors (e.g. herbivory, aboveground and belowground competition, and the pattern of plant recovery from drought stress) apparently have important impacts on plant productivity. Consequently, because of the diversity of environmental factors regulating ANPP in these three representative species, and their interactive effects, it may be difficult to accurately predict plant response in this desert ecosystem to variable timing and magnitude of precipitation, especially in dry years.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 Annual precipitation, number of precipitation events, precipitation magnitude class, and inter-pulse period class for 2001–2006 at the Panther Junction Visitor's Center in Big Bend National Park.

Table S2 Seasonal precipitation, number of precipitation events, precipitation magnitude class, and inter-pulse period class for 2001–2006 at the Panther Junction Visitor's Center in Big Bend National Park.