

# Precipitation magnitude and timing differentially affect species richness and plant density in the sotol grassland of the Chihuahuan Desert

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**Abstract** Arid and semi-arid environments are dynamic ecosystems with highly variable precipitation, resulting in diverse plant communities. Changes in the timing and magnitude of precipitation due to global climate change may further alter plant community composition in desert regions. In this study, we assessed changes in species richness and plant density at the community, functional group, and species level in response to variation in the magnitude of natural seasonal precipitation and 25% increases in seasonal precipitation [e.g., supplemental watering in summer, winter, or summer and winter (SW)] over a 5-year period in a sotol grassland in the Chihuahuan Desert. Community species richness was higher with increasing winter precipitation while community plant density increased with greater amounts of winter and summer precipitation, suggesting winter precipitation was important for species recruitment and summer precipitation promoted growth of existing species. Herb and grass density increased with increasing winter and summer precipitation, but only grass density showed a significant response to supplemental

watering treatments (SW treatment plots had higher grass density). Shrubs and succulents did not exhibit changes in richness or density in response to natural or supplemental precipitation. In this 5-year study, changes in community species richness and density were driven by responses of herb and grass species that favored more frequent small precipitation events, shorter inter-pulse duration, and higher soil moisture. However, due to the long life spans of the shrub and succulent species within this community, 5 years may be insufficient to accurately evaluate their response to variable timing and magnitude of precipitation in this mid-elevation grassland.

**Keywords** Chihuahuan Desert · Grasslands · Plant density · Plant species richness · Seasonal precipitation

## Introduction

Arid and semi-arid environments are dynamic ecosystems with highly variable precipitation and diverse plant communities. Changes in precipitation and temperature due to global climate change may further alter plant community composition in desert regions, which may in turn have impacts on the constituent plant community structure (Knapp and Smith 2001; Weltzin et al. 2003). Plant responses to changes in the timing and amount of rainfall can be quite variable, depending on plant characteristics such as phenology, morphology, and physiology. Although functional types are groups of species that are ecologically similar in their effects on ecosystem processes, water acquisition is dependent on the physiology and phenology of a particular species (Reynolds et al. 2004; Buonopane et al. 2005). Therefore, individual species may respond differently

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to rainfall events of various size and frequency, resulting in variable competitive interactions among species as available resources fluctuate (Ehleringer et al. 1999).

The level of competition among plants may also be related to rainfall (pulse) frequency, resulting in greater competition during frequent water pulses while plant survival may depend more on the length of the dry intervals between pulses (inter-pulse periods) than on water competition within a pulse (Goldberg and Novoplansky 1997; Briones et al. 1998). However, different rooting depths may reduce competition for water resources, and functional types may reduce competition through differences in phenology, such that species utilize different “windows” of opportunity (Reynolds et al. 2000). Plant responses to precipitation are also influenced by soil nutrient dynamics and environmental heterogeneity (Schwinning and Ehleringer 2001; Abbott 2006; Patrick et al. 2009; Robertson et al. 2009). Soil nutrients, such as nitrogen, may become limiting or only available for plant uptake when the soil is wet for specific lengths of time (BassiriRad et al. 1999; Bell et al. 2008). None of these variables are mutually exclusive, and their interactions further complicate the distribution and abundance of plant species in arid ecosystems (Reynolds et al. 2004).

Some global climate models (e.g., Hadley Climate Model 2 and Canadian Climate Model 2) predict an increase in air temperature by 2100, which is expected to increase summer and/or winter precipitation by 25% or more in the Chihuahuan Desert, with most of the additional precipitation occurring in fewer, more intense precipitation events (Johns et al. 1997; Flato et al. 2000). The goal of this study was to determine the impact of the timing and magnitude of variable natural precipitation and supplemental seasonal water treatments on species richness and plant density at different scales: (1) community; (2) functional group (e.g., shrub, succulent, herb, grass); and (3) individual species over a 5-year period in the sotol grassland ecosystem in the Chihuahuan Desert. The roles of key environmental parameters (e.g., soil moisture, air and soil temperature, rainfall event size, duration of inter-pulse period) were assessed to determine the primary factors affecting species richness and plant density during the experimental period. Based upon differences in plant physiology, morphology and phenology, and results from our previous work in this grassland (Patrick et al. 2007; Bell et al. 2008; Patrick et al. 2009; Robertson et al. 2009), we hypothesized that:

1. Community richness and density would increase with greater precipitation in winter and summer.
2. Larger summer rainfall events would promote greater richness and density in deeper rooted shrubs and succulents.
3. Frequent, smaller rainfall events in the summer with shorter inter-pulse periods would generate greater richness and density in shallower rooted grasses and herbs.
4. Greater winter precipitation would generate greater species richness, primarily in the fast-growing, short-lived grasses and herbs.

## Materials and methods

### Study site

The study was conducted in a sotol grassland ecosystem in the Pine Canyon Watershed in Big Bend National Park (BBNP), located in the Chisos Mountains (29°5′N, 103°10′W, 1,526 m a.s.l.) of the Chihuahuan Desert. At our site, the soil type is a sandy loam (62% sand, 30% silt, 30% clay) within a rocky A-horizon with little to no litter layer and overlays a fractured igneous bedrock formation known as the Lajitas-rock outcrop complex (Bell et al. 2008). The landscape is patchy, with vegetation covering approximately 30–60% of the ground area. The dominant plant genera include *Dasylirion*, *Opuntia*, *Bouteloua*, *Nolina*, and *Aristida*, with shrubs composing 20–50% of the community plant cover, succulents 5–15%, grasses 10–30%, and herbs 10–30% (list of all species shown in Electronic supplementary material Table S1).

The Big Bend region has a bi-modal but unequal rainfall regime, with most precipitation occurring as monsoonal rain in mid to late summer. The average annual rainfall is approximately 365 mm (range of 170–570 mm) measured at the permanent meteorological station at park headquarters in Panther Junction (~6 km from the field site). Most of the precipitation occurs in the summer (45%; June, July, and August) and fall (27%; September, October, and November) (Table 1), while only 17% of the precipitation occurs in the spring (March, April, and May) and 11% in the winter (December, January, and February). During the 5-year experimental period, the magnitude and frequency of precipitation events varied widely, both seasonally and annually (Table 1). 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 during the winter average daily air temperatures range from a minimum of 1–6°C to a maximum of 14–20°C; spring and fall temperatures were similar and ranged from 9 to 30°C.

### Precipitation manipulation and soil moisture

Twelve 3-m × 3-m community plots with similar slope aspect were established in the sotol grassland site in spring

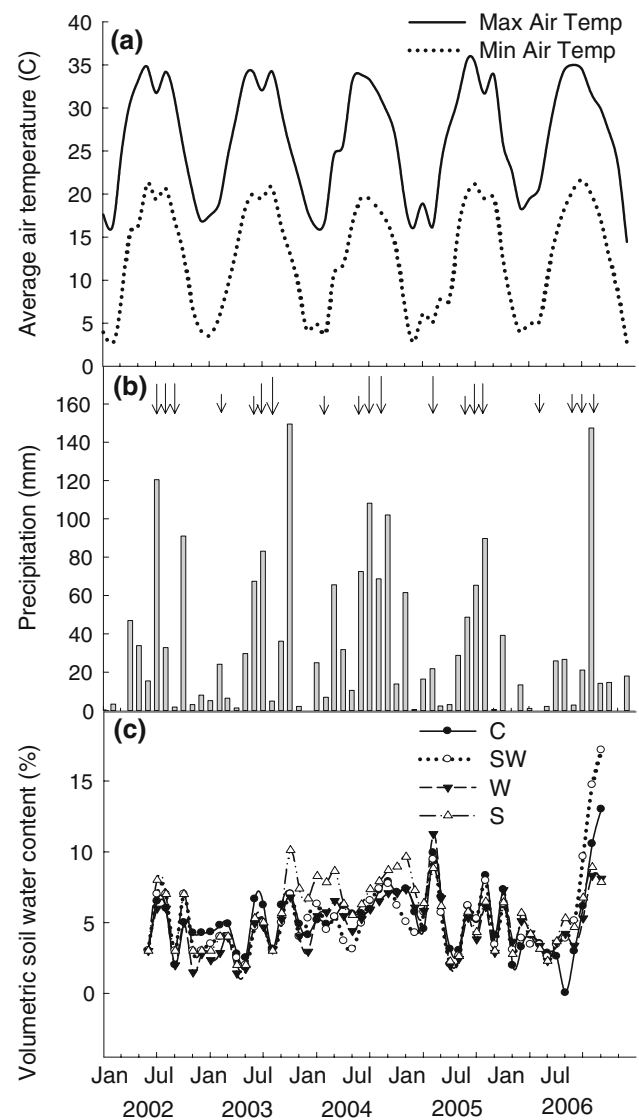
**Table 1** Seasonal precipitation for 2001–2006 and mean (1976–2006) precipitation parameters at the Panther Junction Visitor’s Center in Big Bend National Park (BBNP)

Parameter	Class	Season	2001	2002	2003	2004	2005	2006	Average
Precipitation (mm)		Winter	32 (–16)	4 (–89)	37 (–3)	32 (–15)	39 (3)	14 (–63)	38
		Spring	23 (–63)	81 (31)	37 (–40)	108 (74)	34 (–45)	55 (–11)	62
		Summer	88 (–48)	169 (0)	155 (–8)	249 (47)	204 (21)	171 (1)	169
		Fall	61 (–37)	96 (–1)	188 (94)	177 (82)	40 (–59)	29 (–70)	97
Precipitation events		Winter	10 (0)	3 (–70)	12 (20)	11 (10)	14 (40)	3 (–70)	10
		Spring	10 (–9)	10 (–9)	10 (–9)	19 (73)	10 (–9)	7 (–36)	11
		Summer	18 (–22)	26 (13)	22 (–4)	31 (35)	21 (–9)	26 (13)	23
		Fall	12 (–8)	10 (–23)	17 (31)	20 (54)	6 (–54)	10 (–23)	13
Precipitation magnitude class	<5 mm	Winter	4 (–43)	6 (–14)	7 (0)	10 (43)	9 (29)	1 (–86)	7
		Spring	9 (29)	4 (–43)	8 (14)	14 (100)	8 (14)	5 (–29)	7
		Summer	14 (0)	18 (29)	13 (–7)	19 (36)	11 (–21)	18 (29)	14
		Fall	7 (–13)	6 (–25)	10 (25)	12 (50)	4 (–50)	8 (0)	8
	5–10 mm	Winter	2 (100)	0 (–100)	1 (0)	2 (100)	6 (500)	2 (100)	1
		Spring	1 (–50)	3 (50)	1 (–50)	2 (0)	1 (–50)	0 (–200)	2
		Summer	1 (–75)	4 (0)	5 (25)	5 (25)	4 (0)	3 (–25)	4
		Fall	3 (50)	1 (–50)	1 (–50)	2 (0)	1 (–50)	0 (–200)	2
	10–20 mm	Winter	0 (–100)	0 (–100)	1 (0)	0 (–100)	0 (–100)	0 (–100)	1
		Spring	0 (–100)	3 (200)	1 (0)	1 (0)	1 (0)	0 (–100)	1
		Summer	1 (–67)	2 (–33)	2 (–33)	2 (–33)	1 (–67)	2 (–33)	3
		Fall	2 (0)	1 (–50)	3 (50)	2 (0)	0 (–200)	2 (0)	2
Precipitation magnitude class	>20 mm	Winter	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
		Spring	0 (–100)	0 (–100)	0 (–100)	2 (100)	0 (–100)	2 (100)	1
		Summer	2 (–33)	2 (–33)	2 (–33)	5 (67)	5 (67)	3 (0)	3
		Fall	0 (–100)	2 (100)	3 (200)	4 (300)	1 (0)	0 (–100)	1
Inter-pulse period class(Dry days)	0–5 days	Winter	5 (–29)	2 (–71)	7 (0)	9 (29)	10 (43)	1 (–86)	7
		Spring	6 (–25)	7 (–13)	6 (–25)	15 (88)	8 (0)	4 (–50)	8
		Summer	12 (–40)	24 (20)	18 (–10)	29 (45)	18 (–10)	24 (20)	20
		Fall	9 (–10)	6 (–40)	12 (20)	16 (60)	5 (–50)	7 (–30)	10
	6–10 days	Winter	2 (100)	0 (–100)	2 (100)	1 (0)	2 (100)	0 (–100)	1
		Spring	2 (100)	3 (200)	1 (0)	4 (300)	1 (0)	1 (0)	1
		Summer	6 (100)	2 (–33)	3 (0)	3 (0)	2 (–33)	1 (–67)	3
		Fall	1 (–100)	2 (0)	2 (0)	2 (0)	0 (–200)	2 (0)	2
	11–20 days	Winter	4 (100)	0 (–200)	2 (0)	1 (–50)	1 (–50)	2 (0)	2
		Spring	1 (0)	0 (–100)	3 (200)	1 (0)	1 (0)	1 (0)	1
		Summer	0 (–100)	1 (0)	0 (–100)	0 (–100)	2 (100)	1 (0)	1
		Fall	2 (0)	1 (–50)	4 (100)	3 (50)	0 (–100)	1 (–50)	2
	>20 days	Winter	0 (–100)	1 (0)	1 (0)	1 (0)	1 (0)	1 (0)	1
		Spring	1 (0)	1 (0)	1 (0)	0 (–100)	1 (0)	2 (100)	1
		Summer	0 (–100)	0 (–100)	1 (0)	0 (–100)	0 (–100)	1 (0)	1
		Fall	1 (0)	2 (100)	0 (–100)	0 (–100)	2 (100)	1 (0)	1
	>50 days	Winter	0 (–100)	1 (0)	0 (–100)	0 (–100)	0 (–100)	0 (–100)	1
		Spring	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
		Summer	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
		Fall	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0

The percentage difference relative to the mean values for annual and seasonal precipitation is indicated *in parentheses*

2002. All plots exhibited similar soil conditions characteristic of this region of BBNP (Bell et al. 2008; Patrick et al. 2009; Robertson et al. 2009). Seasonal precipitation treatments were applied to the research plots incorporating output from climate models (e.g., Hadley Climate Model 2 and others cited in IPCC reports) that differed in specific precipitation scenarios, but agreed that rainfall variability would increase for the Trans-Pecos region, primarily predicted to occur as a few, large storm events as described previously (Patrick et al. 2007, 2009; Robertson et al. 2009). To implement the increased variability in seasonal precipitation, we applied an amount of water that was 25% more than the natural seasonal precipitation received for that particular year (winter = December–February; summer = June–August). Precipitation treatments were as follows: (1) control with natural precipitation only (C), (2) natural precipitation plus supplemental summer precipitation (S), (3) natural precipitation plus supplemental winter precipitation (W), and (4) natural precipitation plus supplemental summer and winter precipitation (SW). Water was added as a single storm event during the generally drier winter (water application in February) and as three distinct storm events in the summer (June, July, and August), which is typically the wettest season (Fig. 1). For summer 2002 treatments, supplemental precipitation amounts were initially determined as 25% of average seasonal rainfall amounts based on 30-year rainfall data from National Park Service records. In subsequent years, supplemental water treatment amounts were determined as 25% of ambient precipitation for a period preceding a watering event (e.g., 3 months prior to the winter supplemental event, and 1 month prior to each summer supplemental event) in order to account for natural precipitation variability. Plots were slowly watered using watering cans to reduce surface runoff and watering occurred at approximately the same dates each year (Robertson et al. 2009). 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, Pocasset, Mass.). Volumetric soil moisture content was measured in 2002–2006 using ECH<sub>2</sub>O-10 dielectric aquameter probes (Decagon Devices, Pullman, Wash.). 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 seasonal precipitation magnitude and inter-pulse periods (e.g., dry day events).



**Fig. 1** Monthly environmental variables for the sotol grassland in Pine Canyon at Big Bend National Park (BBNP) for 2002–2006. **a** Average maximum and minimum air temperatures, **b** monthly precipitation, and **c** soil moisture in all water treatments. *Arrows* indicate water additions (the longer the *arrow*, the larger the event), as follows: 2002 = 11, 11, 11 mm; 2003 = 7, 7, 17, 21 mm; 2004 = 7, 3, 18, 27 mm; 2005 = 20, 7, 12, 16 mm; 2006 = 4, 7, 0.7, 5 mm. *C* Control (natural precipitation), *SW* natural precipitation plus supplemental summer/winter precipitation, *W* natural precipitation plus supplemental winter precipitation, *S* natural precipitation plus supplemental summer precipitation

#### Community composition measurements

The number of individuals of each species was counted in each 3-m × 3-m plot at the end of each winter, spring, and summer season to assess seasonal changes in species richness and plant density. If species were rhizomatous, then the existing cluster was identified as an individual; these

species were monitored for new out-shoots, which were then identified as new individuals.

Although most plants were primarily active in the spring and summer, plants were monitored in the winter (e.g., in mild winters, spring- and summer-active plants may remain active) to document plant mortality and recruitment; however, some plant characteristics (e.g., ability to dieback and reappear under favorable conditions; growth in clusters or bunches) reduced the efficacy of these measurements. Species richness was defined as the total number of species in a plot of fixed area (number of species/m<sup>2</sup>). Plant density was defined as the total number of individuals of a species per unit ground area and was used to monitor recruitment and mortality (individuals of a species/m<sup>2</sup>; Smith 1996; Gross et al. 2000). Due to the remoteness of the site, it was not possible to monitor recruitment and mortality frequently enough to assess them independently. Species richness and plant density were determined for each functional group (e.g., shrub, succulent, herb, and grass). All plants were identified to species (Correll and Johnston 1979; Powell 1998, 2000); nearly all species were perennials and non-native species were absent from the plots (Table S1).

#### Statistical analysis

All parameters were analyzed using repeated measures two-way ANOVA to compare the main effects and interactive effects of water treatment and seasons for each year, as well as the effects and interactions of water treatment and individual seasons for all years (SPSS 11.5; SPSS, Chicago, Ill.). Parameters were considered significantly different when  $P \leq 0.05$ ; significant results were further analyzed using a least significant difference post hoc test. Linear regression analyses were used to relate richness or density to natural seasonal precipitation and supplemental precipitation treatments. Due to the nature of the data and small sample size, a Kendall's  $\tau$  correlation matrix was used to detect potential correlations between species richness, density, and environmental parameters (Field 2000). These parameters included precipitation variables (seasonal precipitation, seasonal events, precipitation magnitude, and inter-pulse period), temperature (maximum and minimum air and soil temperatures), and soil moisture. Magnitude was divided into four classes (<5, 5–10, 10–20, and >20 mm) and inter-pulse period was divided into five classes (0–5, 6–10, 11–20, >20, and >50 days).  $R$ -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 environmental influence of seasonal precipitation (amount, number of events, magnitude, and inter-pulse period), temperature (maximum and minimum air and soil temperatures),

and soil moisture on community richness and density (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 non-orthogonal and co-linear gradient data (McGarigal et al. 2000). Each season was analyzed separately for all years to determine the possible seasonal effects of specific environmental factors on richness and density over time. Almost all RDA exhibited high species–environment correlation values, suggesting that most of the measured environmental variables were important, although there may be other unmeasured variables of equal importance (McGarigal et al. 2000). Only the first and second axes were displayed in each figure with the first axis explaining most of the variation in the RDA. Although all variables were analyzed, only those exhibiting a large impact are presented.

## Results

### Environmental variables

Mean high and low monthly air temperatures were similar each year during the 5-year study period (Fig. 1a) and within the average range of air temperatures that have been measured for BBNP (1976–2006). The amount of annual precipitation varied substantially among years, with most precipitation occurring during the summer and fall (Fig. 1b). Volumetric soil water content was higher after supplemental or natural precipitation events, particularly large events, and generally ranged from 3 to 10% (Fig. 1c). Soil moisture differed by season with greater soil moisture in the summer and fall compared to 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. 2009).

In general, summer received the largest amount of precipitation and exhibited the shortest inter-pulse periods, while winter (December up to and including February) was the driest period with the longest inter-pulse periods (Table 1). 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, characterized by mostly small rainfall events.

### Richness and density responses to seasonal precipitation

Community species richness and plant density did show significant seasonal variation for all 5 years (Table 2), with the



**Table 2** Summary of  $F$ -values for repeated measures two-way ANOVA used to test supplemental water treatment for each year for the community ( $Com$ ) and each functional group

Measurement	Parameter	2002	2003	2004	2005	2006
Species richness (no. species $m^{-2}$ )	Com***	2.489	1.768	2.094	2.558	0.861
	Shrub	3.355	2.513	3.490	4.435*	2.493
	Succulent	NA	NA	NA	NA	NA
	Herb***	1.295	0.583	0.366	0.771	1.260
	Grass	0.393	0.421	0.288	0.217	0.210
Plant density (no. individuals $m^{-2}$ )	Com***	1.548	1.157	1.499	0.268	1.235
	Shrub	4.265*	3.962*	3.155	3.685	4.950*
	Succulent	3.632	5.659*	1.109	1.635	2.247
	Herb***	0.716	0.642	1.072	0.992	0.674
	Grass***	2.466	5.311*	3.768	6.057*	6.539*

For treatment,  $df = 3$ ; for season,  $df = 3$ ; for interactions,  $df = 3, 8$ . NA Not applicable

\*  $P \leq 0.05$  among treatments,

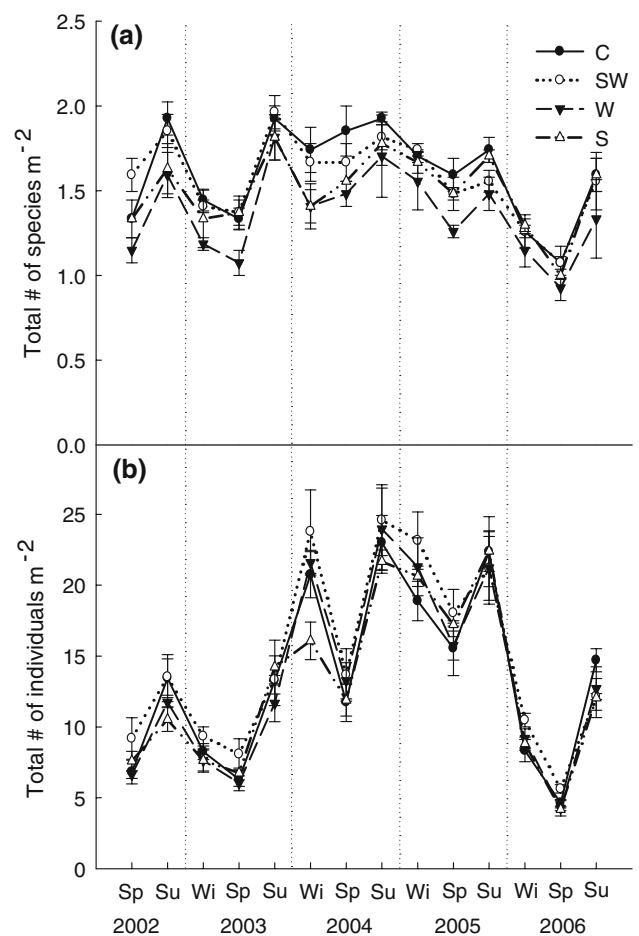
\*\*\*  $P \leq 0.001$  among seasons

greatest richness and density exhibited during the summer (Fig. 2a, b). When regressed against seasonal precipitation, community species richness exhibited a significant positive linear relationship with increasing winter precipitation ( $R^2 = 0.215$ ,  $P \leq 0.001$ ), but no response to increasing summer precipitation. Community plant density showed a significant positive linear relationship with increasing winter ( $R^2 = 0.257$ ,  $P \leq 0.001$ ) and summer ( $R^2 = 0.309$ ,  $P \leq 0.001$ ) precipitation. Seasonal precipitation explained less than 30% of the variation in community richness and density.

Shrub and succulent species richness and plant density were not affected by variation in seasonal precipitation (Table 2). However, herb and grass species richness and density varied seasonally (Table 2;  $P \leq 0.001$ ), often in the summer months, thereby affecting community species richness and plant density. Herb richness increased linearly with increasing winter precipitation ( $R^2 = 0.464$ ,  $P \leq 0.001$ ), but showed no response to increasing summer precipitation. Grass richness was not significantly related to winter or summer precipitation. Both herb density and grass density showed a significant positive linear response to increasing winter (herb,  $R^2 = 0.251$ ,  $P \leq 0.001$ ; grass,  $R^2 = 0.090$ ,  $P \leq 0.050$ ) and summer (herb,  $R^2 = 0.307$ ,  $P \leq 0.001$ ; grass,  $R^2 = 0.133$ ,  $P \leq 0.001$ ) precipitation. Seasonal precipitation explained less than 30% of the variation in herb and grass density.

#### Richness and density responses to supplemental precipitation

Community species richness and plant density were not significantly affected by supplemental water (Table 2). Succulent species richness and plant density were also not affected by supplemental water treatment. However, supplemental watering did decrease shrub richness and density, primarily due to reductions in *Artemisia ludoviciana*. Herb richness, herb density, and grass richness did not respond to supplemental water; however, grass density did show a supplemental water response (Table 2). The SW plots had



**Fig. 2** Species richness (a) and plant density (b) for 2002–2006 for the sotol grassland in BBNP. Values are mean  $\pm$  SE ( $n = 3$ ) for each water treatment. Sp Spring, Su summer, W winter; for other abbreviations, see Fig. 1

significantly greater grass density than the C and W plots ( $P \leq 0.05$ ) in 2003, 2005, and 2006 due to increases in *Bouteloua hirsuta* and *Lycurus setosus*. When analyzed separately, *B. hirsuta* was significantly greater in the SW plots than all plots in 2005 ( $F = 4.304$ ;  $P \leq 0.05$ ) and 2006

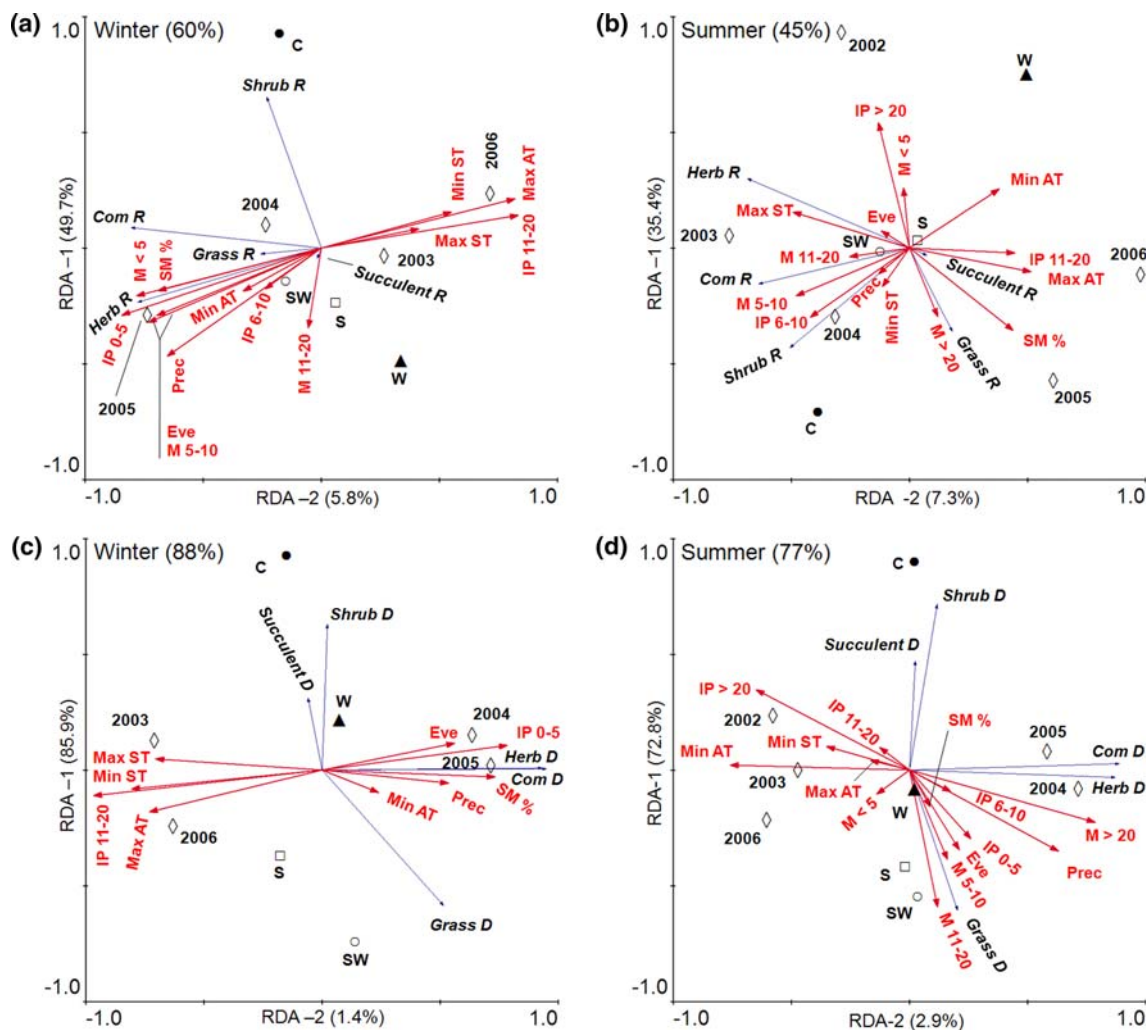
( $F = 4.892$ ;  $P \leq 0.05$ ), and the density of *L. setosus* was significantly greater in the SW plots than in the C and W plots ( $F = 3.190$ ;  $P \leq 0.05$ ) in 2006.

Factors influencing functional group richness

For each season, RDA was used to evaluate whether precipitation parameters (e.g., seasonal precipitation, magnitude, and inter-pulse duration), air and soil temperatures, and soil moisture affected community and functional group richness and density. These parameters contributed 60% of the variation in species richness in the winter and 45% in the summer (Fig. 3a, b). For both seasons, community species richness was primarily influenced by

herb and shrub richness; however, since shrub richness was fairly constant, seasonal fluctuations in community species richness were mainly due to herb richness (Fig. 3a, b). Grass richness also influenced community species richness but to a lesser degree and primarily in the winter.

Community species richness was positively correlated with the number of small magnitude events, short inter-pulse period duration, and soil moisture. Community species richness was negatively correlated with longer inter-pulse periods and air and soil temperatures, especially in the winter. Both herb and grass richness displayed relationships similar to those observed for community species richness, although herb richness showed stronger associations in the



**Fig. 3** Redundancy analysis (RDA) comparing total and functional species richness [R; community R (ComR)] and density [D; community D (ComD)] for 2002–2006 (diamonds) to measured environmental variables for the sotol grassland in BBNP. **a** Winter R, **b** summer R, **c** winter D, and **d** summer D. Values of D and R are mean  $\pm$  SE ( $n = 3$ ) for each treatment [C (filled circle), SW (open circle), W (filled triangle), S (open square)]. Environmental variables are indicated by

larger headed arrows. IP Inter-pulse period (days), M precipitation magnitude (mm), Prec seasonal precipitation (mm), Eve seasonal events, SM% soil moisture, MaxAT maximum air temperature ( $^{\circ}$ C), MinAT minimum air temperature ( $^{\circ}$ C), MaxST maximum soil temperature ( $^{\circ}$ C), MinST minimum soil temperature ( $^{\circ}$ C); for other abbreviations, see Fig. 1

winter (Fig. 3a) and grass richness showed stronger associations in the summer (Fig. 3b). Shrub richness exhibited no clear association with measured parameters except during the summer, when there were positive correlations with medium/large precipitation magnitude classes and short inter-pulse periods; there were negative correlations with longer inter-pulse durations and minimum air temperatures (Fig. 3b). Succulent richness did not exhibit a strong relationship with any of the examined parameters. In the Kendall's  $\tau$  correlation analysis, community species richness was positively correlated with herb richness for both seasons and all years, except 2005 (Table 3), and positively correlated with grass richness in summer 2006. Community and functional group richness were not correlated with any of the measured environmental parameters.

#### Factors influencing functional group density

The variation in plant density in the RDA analyses was generally well explained by the measured parameters: 88% in the winter and 77% in the summer (Fig. 3c, d). Community plant density was primarily influenced by herb density in all seasons and to a lesser degree by grass and shrub density. Both community plant density and herb density exhibited positive associations with the number of small and medium magnitude events, soil moisture, and shorter inter-pulse periods; they exhibited negative correlations with long inter-pulse duration and air and soil temperatures for all seasons (Fig. 3c, d). In summer, grass density was positively associated with the number of small and medium magnitude events, short and medium inter-pulse periods, and soil moisture (Fig. 3d). Grass density was negatively correlated with long inter-pulse duration and higher air and soil temperatures. In addition, grass density was positively correlated with supplemental SW water in all seasons and S water during the summer (Fig. 3c, d). Both shrub and succulent density were minimally affected by the measured environmental variables, but exhibited a positive correlation with each other and a negative correlation with grass density (Fig. 3c, d).

In the Kendall's  $\tau$  correlation analysis, community plant density was positively correlated with herb density for both seasons in all years and with grass density in winter 2005 and 2006 (Table 3). Shrub density was negatively correlated with grass density in winter 2003, summer 2005, and winter 2006; shrub density was also negatively correlated with herb density in summer 2003 and winter 2005. Grass density was negatively correlated with herb density in summer 2006, following low precipitation in the winter and previous fall.

Plant density was significantly correlated with precipitation variables (Table 3). Grass density was positively correlated with summer precipitation in 2003, 2005, and 2006, which also corresponded with positive correlations with small to medium precipitation magnitude classes

**Table 3** Kendall  $\tau$  correlation values among plant richness ( $R$ ), density ( $D$ ), and environmental parameters measured in the sotol grasslands in BBNP for winter and summer (2002–2006)

Year	Winter		Summer	
	Variable	$R$ -value <sup>a</sup>	Variable	$R$ -value <sup>a</sup>
2002	NA	NA	Com $R$ /herb $R$	+0.738
			Com $R$ /com $D$	+0.493
			Com $D$ /herb $D$	+0.626
			SM/prec	+0.816
2003	Com $R$ /herb $R$	+0.581	Com $R$ /herb $R$	+0.539
	Com $D$ /herb $D$	+0.488	Com $D$ /herb $D$	+0.565
	Shrub $D$ /grass $D$	−0.484	Shrub $D$ /herb $D$	−0.512
2004			Grass $D$ /prec	+0.542
	Com $R$ /herb $R$	+0.669	Com $R$ /herb $R$	+0.631
	Com $D$ /herb $D$	+0.879	Com $R$ /com $D$	+0.524
			Com $D$ /herb $R$	+0.435
			Herb $R$ /herb $D$	+0.472
			Com $D$ /herb $D$	+0.565
			Shrub $D$ /prec	−0.563
			Grass $D$ /SM	−0.625
			SM/prec	+0.671
	2005	Com $D$ /herb $D$	+0.504	Com $R$ /shrub $D$
Com $D$ /grass $D$		+0.481	Shrub $R$ /shrub $D$	+0.481
Shrub $D$ /herb $D$		−0.481	Shrub $D$ /SM	+0.548
			Com $D$ /herb $D$	+0.718
2006			Shrub $D$ /grass $D$	−0.534
	Com $R$ /herb $R$	+0.557	Grass $D$ /prec	+0.739
	Shrub $R$ /shrub $D$	+0.598	Com $R$ /herb $R$	+0.696
	Shrub $R$ /prec	−0.669	Com $R$ /grass $R$	+0.590
	Com $D$ /herb $D$	+0.520	Com $D$ /herb $D$	+0.585
	Com $D$ /grass $D$	+0.500	Herb $D$ /grass $D$	−0.667
	Shrub $D$ /grass $D$	−0.531	Grass $D$ /prec	+0.662
Herb $D$ /prec	+0.651	Grass $D$ /SM	+0.625	
		SM/prec	+0.816	

Prec Seasonal precipitation, SM volumetric soil moisture percentage; for other abbreviations, see Tables 1 and 2

<sup>a</sup>  $R$ -values listed have  $P \leq 0.05$

( $R = 0.500$ – $0.740$ ) and short inter-pulse periods ( $R = 0.500$ – $0.740$ ). Grass density was also negatively correlated with long inter-pulse periods in 2003, 2005 and 2006 ( $R = 0.540$ – $0.740$ ). Herb density showed a positive correlation with winter precipitation in 2006, probably due to low precipitation in the winter and previous fall. Soil moisture was positively correlated with precipitation in the summers of 2002, 2004, and 2006.

#### Factors influencing grass and herb species density

Herbs and grasses were a significant component of the community. Subsequently, we analyzed the densities of



eight herb species (*Croton pottsii*, *Dalea aurea*, *Erigeron flagellaris*, *Eriogonum wrightii*, *Euphorbia cinerascens*, *Sisymbrium linearifolium*, *Tragia ramosa*, and *Gnaphalium wrightii*) and five grass species (*Aristida purpurea*, *Bouteloua curtipendula*, *Bouteloua hirsuta*, *Andropogon gerardi*, and *L. setosus*) that were present in all of our plots (Table S1). These species are perennials except for *G. wrightii* which is an annual; *G. wrightii* was present in all plots at the beginning of the experiment in 2002, but progressively declined in abundance until it disappeared after the 2004 growing season. When these individual species were analyzed using RDA, our measured parameters contributed 86% of the variation in grass and herb species density in the winter and 79% in the summer (Fig. 4a, b).

Herb density was primarily influenced by *E. flagellaris* in all seasons. Almost all herb species were positively correlated with soil moisture, total seasonal precipitation, number of small-magnitude precipitation events, and short inter-pulse duration; they were negatively correlated with long inter-pulse periods, and air and soil temperatures for all seasons, although there was greater variability in the summer (Fig. 4a, b). An exception was *C. pottsii* which was negatively correlated with grass species densities in the winter and summer (Fig. 4a, b). *L. setosus* and *B. hirsuta* were the main contributors to the variation in total grass density for all seasons (Fig. 4a, b). Grass density in the summer was positively correlated with short inter-pulse periods, small and medium magnitude classes, and soil moisture and negatively correlated with longer inter-pulse durations (Fig. 4b). Total grass density and the density of two grass species

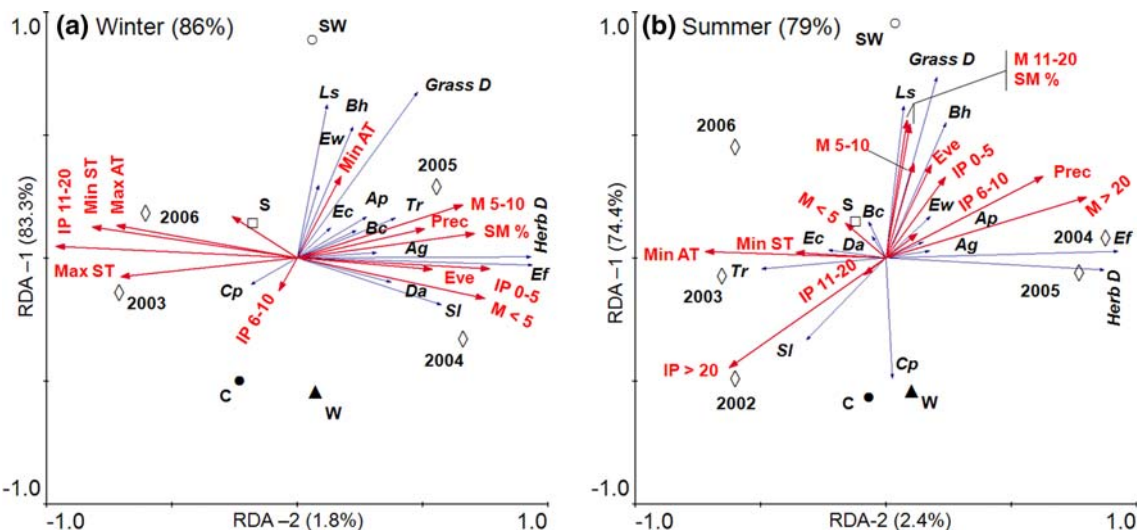
(*L. setosus* and *B. hirsuta*) were positively correlated with minimum air temperatures in the winter (Fig. 4a).

The Kendall's  $\tau$  correlation analyses were similar to RDA, although observed differences between years were more common. *E. flagellaris* was positively correlated with herb density for winter and summer in all years ( $R = 0.515\text{--}0.780$ ). However, grass density was positively correlated with various grass species, depending on year: *L. setosus* from 2003 to 2006 ( $R = 0.480\text{--}0.640$ ); *Andropogon gerardi* in 2004 ( $R = 0.500$ ); *B. hirsuta* from 2004 to 2005 ( $R = 0.480\text{--}0.520$ ); and *Aristida purpurea* in 2005 ( $R = 0.504$ ). *L. setosus* and *B. hirsuta* were positively correlated with each other for winter and summer in all years ( $R = 0.500\text{--}0.600$ ). Only *L. setosus* density in the summer (2004 and 2005) was positively correlated with precipitation, specifically short inter-pulse periods, small- and medium-magnitude classes, and soil moisture ( $R = 0.550\text{--}0.610$ ) and negatively correlated with longer inter-pulse durations ( $R = 0.550\text{--}0.610$ ). *C. pottsii* appeared to prefer drier summer conditions (2003 and 2005), exhibiting negative correlations with precipitation ( $R = 0.600\text{--}0.750$ ) and positive correlations with longer inter-pulse periods ( $R = 0.630\text{--}0.745$ ).

### Discussion

Community responses to seasonal and supplemental precipitation

Community species richness and plant density increased with increasing winter precipitation, but only plant density



**Fig. 4** RDA comparing functional and individual *D* for 2002–2006 (diamond) to measured environmental variables for the sotol grassland in BBNP for **a** winter and **b** summer. Density values are mean  $\pm$  SE ( $n = 3$ ) for each treatment [C (filled circle), SW (open circle), W (filled triangle), S (open square)]. Environmental variables are indicated by

large-headed arrows. Cp *Croton pottsii*, Da *Dalea aurea*, Ef *Erigeron flagellaris*, Ew *Eriogonum wrightii*, Ec *Euphorbia cinerascens*, Sl *Sisymbrium linearifolium*, Tr *Tragia ramosa*, Ap *Aristida purpurea*, Bc *Bouteloua curtipendula*, Bh *Bouteloua hirsuta*, Ag *Andropogon gerardi*, Ls *Lycurus setosus*; for other abbreviations, see Figs. 1 and 3

increased with increasing summer precipitation. Although most plants in the Chihuahuan Desert are primarily active in the spring and summer, Muldavin et al. (2008) demonstrated that winter precipitation contributed substantially to the accumulation of soil moisture due to low evaporative water loss. If winter soil moisture is maintained into the spring, then a greater variety of species may emerge and survive during the early growing season, thereby increasing species richness. For some species, adequate winter and spring precipitation may provide more biologically useful seasonal pulses than summer precipitation by initiating or maintaining root development, allowing these plants to utilize water expediently when physiologically active during the late spring and summer months (Reynolds et al. 2004). For example, in a related project at our site in the Chihuahuan Desert, Robertson et al. (2009) observed that the summer-active,  $C_4$  grass *B. curtipendula* produced greater biomass when receiving supplemental winter precipitation during a very dry winter and following a very dry year. These results demonstrated that precipitation events during periods of negligible above-ground physiological activity may be very important for subsequent plant activity and establishment. The lack of an impact of higher summer precipitation on species richness may reflect limitations on recruitment from the current seed bank and competition from established vegetation and adverse environmental conditions (Housman et al. 2003; Zeiter et al. 2006). However, these factors do not negatively affect plant density which is generally positively affected by increased resource availability, such as summer precipitation.

Supplemental precipitation did not significantly affect community species richness or plant density in the sotol grassland within our 5-year study period. In a sagebrush steppe community, changes in vegetation structure after the extended drought period of 1933–1957 required 10–20 years to become evident (Anderson and Inouye 2001). Similarly, a 5-year period in the sotol grassland may be insufficient to observe significant differences in vegetation structure due to supplemental precipitation. In our study, summer precipitation was average or above average (2004), with soil moisture adequate to support normal growth and physiological responses (Patrick et al. 2009; Robertson et al. 2009). If the upper soils had approached water-holding capacity, supplemental precipitation would have been insufficient to generate additional plant response, as has been observed in the Chihuahuan Desert (Muldavin et al. 2008; Robertson et al. 2009). It is also possible that there may be a memory or lag effect initiated by past precipitation events for some species, as well as differences in allocation of water to storage, which makes it difficult to clearly distinguish between treatment effects (Schwinning et al. 2004; Cleland et al. 2006).

#### Functional group responses to seasonal and supplemental precipitation

Changes in community composition are often dependent on the differential impact of variable precipitation on component functional groups (Jobbagy and Sala 2000; Huenneke et al. 2002). In this study, herbs and grasses, but not shrubs and succulents, were generally responsive to changes in precipitation. Subsequently, changes in herb and grass richness and density were primarily responsible for changes in community richness and density in the sotol grassland.

Herb species richness and density increased ca. 30% with increasing natural seasonal precipitation and were positively associated with more frequent small/medium-magnitude events and short inter-pulse periods. Herb density, but not herb species richness, increased with increasing summer precipitation. In summer, changes in herb richness may be limited due to the available seed bank as well as other factors, such as biotic and abiotic competition (Zeiter et al. 2006). Herb density may be more responsive to water availability than herb richness during the growing season due to greater competition for resources in order to attain reproductive capacity before the end of the season (Cleland et al. 2006). Herb species richness and density did not respond to supplemental water treatments, although precipitation is often the primary regulator of herb abundance (Buonopane et al. 2005). Adequate summer precipitation during the study period may have precluded a supplemental water treatment effect. Furthermore, many of these herbs species may “die back” when conditions are unfavorable and “reappear” when conditions are favorable, making it difficult to clearly distinguish the impact of supplement water treatments on mortality and recruitment.

Grass density increased with increasing seasonal precipitation, but seasonal precipitation explained <15% of the variation. Grass density appeared to favor small/medium-magnitude events and small/medium inter-pulse periods, thus exhibiting high variability from year to year, especially due to inter-annual variation in precipitation (Huenneke et al. 2002) or when other resources (e.g., nitrogen) were limiting (Hooper and Johnson 1999; Eviner et al. 2006). In studies by Buonopane et al. (2005) and Yahdjian and Sala (2006), grasses were more productive in wet years following a dry year. In the sotol grassland, grass density also responded to 3 relatively wet years, especially in summer, following a very dry year (2001; 50% below average). However, the increase in grass richness and density in the sotol grassland may also be due to other environmental cues for higher growth or germination following dry years (Adler and Levine 2007), but they were not identified in this study. Grass density was negatively correlated with herb density in summer 2006 (following a dry winter and spring), suggesting greater competition for similar resources.

Grass species richness did not respond to supplemental water treatments, but grass density increased in SW plots at the end of the 5-year study. Additional winter precipitation may facilitate root development, promoting fast growth during the early growing season, while additional summer precipitation may aid survival, especially when inter-pulse periods are long (Bates et al. 2006; Muldavin et al. 2008; Robertson et al. 2009). The delayed treatment response may have been due to lags between grass recruitment and maturation from previous drought conditions (Anderson and Inouye 2001).

Shrubs and succulents did not exhibit changes in richness or density in response to natural variation in seasonal precipitation or to supplemental precipitation. Typically, long-lived and deep-rooted shrubs such as those in the sotol grassland respond slowly to alterations in precipitation and water availability (Huenneke et al. 2002; Yahdjian and Sala 2006; Robertson et al. 2009). Similarly, the water storage capacity of succulents confounds their responses to increased seasonal precipitation due to the potentially long lag periods between precipitation events (Dougherty et al. 1996; Adler and Levine 2007; Robertson et al. 2009). Buonopane et al. (2005) conducted a 5-year experiment on the response of a Chihuahuan Desert shrubland community to the removal of different plant functional groups and found that shrubs and succulents were generally not responsive; this suggests recovery from alterations in the environment could take decades. Shrub density did show a negative correlation with herb and grass densities, especially during dry conditions, reflecting the capacity of shrubs to access deep soil moisture when herbs and grasses were limited to shallower, much drier soils (Gibbens et al. 2005).

The effect of variable precipitation on soil nutrients, particularly nitrogen, may also exert significant control on species richness and plant density. For example, in a concurrent study at our site, Patrick et al. (2009) observed that photosynthetic rates in *Dasyliirion leiophyllum* were lower in plants receiving supplemental precipitation during a wet year, due in part to reductions in soil N availability. Similarly, Robertson et al. (2009) observed that above-ground annual net primary productivity (ANPP) of *D. leiophyllum*, *B. curtipendula*, and *Opuntia phaeacantha* was dependent upon the interactive effects of precipitation and soil N. In wet years, it was observed that ANPP of *D. leiophyllum* and *B. curtipendula* was positively correlated with soil ammonium-nitrogen and nitrate-nitrogen but not precipitation (Robertson et al. 2009). Since soil nitrogen is commonly limiting in desert grasslands, especially in wet years due to declines in nitrogen availability and immobilization, limited nitrogen availability may have a stronger impact on functional group species richness and plant density than precipitation (Havstad et al. 2006; Muldavin et al. 2008; Robertson et al. 2009).

#### Individual species contributions to richness and density

Although the magnitude of seasonal precipitation plays an important role in regulating plant richness and density, RDA and Kendall  $\tau$  analyses suggest storm frequency and intensity may also be important regulators, especially for herbs and grasses. Herb and grass richness and density were positively influenced by higher frequency of small- and medium-sized pulses, resulting in shorter inter-pulse durations and higher soil moisture. These plants are shallow-rooted, allowing them to quickly utilize precipitation in the upper soil layers, particularly in the upper 40 cm where plants may obtain more than 60% of their annual water (Reynolds et al. 2004; Muldavin et al. 2008). This is especially true for two small, short-lived perennial herb species, *E. flagellaris* and *T. ramosa*, which contribute substantially to herb density. Although small, *E. flagellaris* can produce long trailing branches that form mats on the desert floor (Correll and Johnston 1979), especially during periods of high precipitation; in the wet year of 2004, *E. flagellaris* increased by >60% in all plots. Interestingly one of the few annuals at the site, *G. wrightii*, declined in all plots by 2004, possibly due to increased competition by *Erigeron* and/or increased grass densities, but reappeared in 2007 (data not shown). *C. pottsii*, which favors dry open areas and disturbed habitats (Correll and Johnston 1979), may also be negatively impacted by increased precipitation and grass densities.

For grasses, *Bouteloua curtipendula* and *Aristida purpurea* demonstrated little or no change in density during the 5-year study, while *Bouteloua hirsuta*, *Andropogon gerardi*, and *L. setosus* increased in density, thereby increasing grass density, especially in the SW treatment plots. Whether this increase was due to greater water use efficiency, higher reproductive output and survivorship, or natural recovery from past grazing pressures was beyond the scope of this study. It is unclear whether these three species will survive future dry years and eventually out-compete *B. curtipendula* and *A. purpurea*.

#### Conclusion

The coexistence of different species within an arid ecosystem depends upon numerous variables, including the timing and magnitude of precipitation and plant strategies in accessing water (Walter 1971; Schenk and Jackson 2002). Revisiting our hypotheses, we did find that community richness and density increased with increasing seasonal precipitation; richness increased with greater winter precipitation and density increased with greater summer precipitation. However, we did not observe that large summer rainfall events promoted greater shrub and succulent richness or density; in general, shrub and succulent richness

and density were not responsive to changes in seasonal precipitation. Herb and grass density and richness were increased by more frequent, small and medium precipitation events, generating shorter inter-pulse periods. Herb and grass density exhibited positive responses to both increased summer and winter precipitation. However, the richness response varied depending upon season: herb richness increased with increasing winter precipitation while grass richness increased with increasing summer precipitation. Furthermore, other environmental factors (e.g., soil moisture, soil nitrogen, pulse magnitude and duration, etc.) may interact in multiple, nonlinear ways making it difficult to determine plant responses to precipitation pulses (Reynolds et al. 2004).

In the future, increasing precipitation may lead to increased grass and herb species richness and density but established shrublands are unlikely to be quickly replaced, especially if precipitation patterns do shift to fewer but more intense storm events (Guo and Reynolds 2003; Havstad et al. 2006). Increased grass biomass in a dry year, following high productivity in wet years, may increase fuel load and fire frequency that could reduce shrub persistence if fires occur in the community (Kirkman et al. 2001; Heisler et al. 2003). Although we did not observe changes in succulent species richness and density over the 5-year period, they may decline if future precipitation regimes favor higher grass densities, which have been shown to reduce succulent establishment (Dougherty et al. 1996; Powell and Weedon 2004).

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