COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Effects of experimental rainfall manipulations on Chihuahuan Desert grassland and shrubland plant communities

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Abstract Aridland ecosystems are predicted to be responsive to both increases and decreases in precipitation. In addition, chronic droughts may contribute to encroachment of native C_3 shrubs into C_4-dominated grasslands. We conducted a long-term rainfall manipulation experiment in native grassland, shrubland and the grass–shrub ecotone in the northern Chihuahuan Desert, USA. We evaluated the effects of 5 years of experimental drought and 4 years of water addition on plant community structure and dynamics. We assessed the effects of altered rainfall regimes on the abundance of dominant species as well as on species richness and subdominant grasses, forbs and shrubs. Non-metric multidimensional scaling and MANOVA were used to quantify changes in species composition in response to chronic addition or reduction of rainfall. We found that drought consistently and strongly decreased cover of *Bouteloua eriopoda*, the dominant C_4 grass in this system, whereas water addition slightly increased cover, with little variation between years. In contrast, neither chronic drought nor increased rainfall had consistent effects on the cover of *Larrea tridentata*, the dominant C_3 shrub. Species richness declined in shrub-dominated vegetation in response to drought whereas richness increased or was unaffected by water addition or drought in mixed- and grass-dominated vegetation. Cover of subdominant shrubs, grasses and forbs changed significantly over time, primarily in response to interannual rainfall variability more so than to our experimental rainfall treatments. Nevertheless, drought and water addition shifted the species composition of plant communities in all three vegetation types. Overall, we found that *B. eriopoda* responded strongly to drought and less so to irrigation, whereas *L. tridentata* showed limited response to either treatment. The strong decline in grass cover and the resistance of shrub cover to rainfall reduction suggest that chronic drought may be a key factor promoting shrub dominance during encroachment into desert grassland.

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Introduction

Climate change is expected to alter patterns of seasonal and annual precipitation locally, regionally and globally (IPCC 2007). In southwestern North America, climate models predict that annual precipitation inputs are likely to

decrease, leading to more frequent, prolonged, and extreme regional droughts especially during La Niña periods (Seager et al. 2007; Schoof et al. 2010; Gutzler and Robbins 2010). Water availability is the most critical factor regulating biological activity in aridland ecosystems (Whitford 2002; Reynolds et al. 2004; Schwinning and Sala 2004). For example, summer and winter rainfall affect species diversity (Chesson et al. 2004), net primary productivity (Knapp and Smith 2001; Muldavin et al. 2008), abundance of consumers (Brown and Ernest 2002; Yates et al. 2002; Friggens 2003; Báez et al. 2006), and cycling of carbon and nutrients (Austin et al. 2004; Huxman et al. 2004; White et al. 2004; Vargas et al. 2012; Dijkstra et al. 2012). Thus, changes in precipitation patterns are likely to have profound consequences for community structure and ecosystem functioning in arid and semiarid ecosystems.

Empirical studies demonstrate that aridland ecosystems may respond rapidly to seasonal and annual changes in precipitation (Sternberg et al. 1999; Lloret et al. 2004; Pennington and Collins 2007; Peñuelas et al. 2007). In arid and semiarid ecosystems, net primary production (NPP) responds more strongly to increased precipitation than to drought, as plants in these systems are adapted to avoid or tolerate drought (Knapp and Smith 2001; Gerten et al. 2008). However, this NPP response to altered precipitation regimes depends considerably on plant community structure, species composition and functional diversity (Reynolds et al. 2004; Collins et al. 2008; Gerten et al. 2008; Suding et al. 2008). Indeed, empirical studies indicate that species diversity can enhance community resistance to drought (Lloret et al. 2007). Drought, in turn, can act as an ecological filter that governs species composition (Chase 2007) and diversity (Lloret et al. 2004). For example, long-term water addition in grasslands either increased (Yang et al. 2011) or had little consistent effect on species diversity (Collins et al. 2012). Because plant species composition and functional diversity are critical to maintain processes such as NPP under changing climate (Chapin et al. 1997; Tilman 1999), forecasting the effects of altered precipitation in aridland ecosystems requires understanding how species, plant community structure, and plant functional types will respond to chronic drought or increases in annual precipitation.

Plant functional traits (e.g., annual/perennial, grass/forb, C_3/C_4) are generally good predictors of how species will respond to disturbances, including changes in the amount of precipitation (Knapp et al. 2002; Zavaleta et al. 2003; Wahren et al. 2005, Suding et al. 2008). Studies using long-term observations and rainfall manipulations indicate that chronic changes in rainfall regimes often lead to non-linear and unexpected responses in plant community and functional diversity (Harpole et al. 2007; Suttle et al. 2007). For example, Cleland et al. (in review) found that species

richness was positively related to interannual variation in seasonal precipitation depending on the proportion of annual species in the species pool. However, richness responses may mask functional dynamics in that cover of grasses, for example, may respond more strongly to drought than to increased precipitation, whereas annuals may do the opposite (Knapp and Smith 2001; Harpole et al. 2007; Suttle et al. 2007). Thus, generalizations about response dynamics in these systems remain nebulous.

In addition to climate change, aridland ecosystems are undergoing a state transition from C_4-dominated grasslands to C_3-dominated shrublands (Van Auken 2009). In the southwestern US, for example, *Larrea tridentata* now dominates nearly 19 million ha of former grassland (Van Auken 2000). The replacement of C_4 grasses by C_3 native shrubs alters carbon storage and net primary production (Jackson et al. 2002; Knapp et al. 2008; Eldridge et al. 2011), modifies hydrological function (Bhark and Small 2003; Ravi et al. 2007; Turnbull et al. 2010a), and enhances loss of biodiversity (Báez and Collins 2008; Ratajczak et al. 2012) and soil fertility (Huenneke et al. 2002; Ravi et al. 2010; Turnbull et al. 2010b). Although shrub encroachment likely results from multiple interacting factors (Van Auken 2000, 2009), one potential driver of this state transition is climate variability (Brown et al. 1997; Van Auken 2009). Indeed, studies have shown that production in areas dominated by *L. tridentata* is more stable (Muldavin et al. 2008; Xia et al. 2010) while compositional variability is less stable than in grass-dominated areas (Báez and Collins 2008). Thus, understanding how rainfall variability affects ecosystem state transitions is critical to forecast large-scale changes in grass and shrub composition and abundance under future climate scenarios.

In general, precipitation inputs define, to a large extent, soil moisture availability and species abundances in aridland ecosystems (Reynolds et al. 2004; Muldavin et al. 2008; Collins et al. 2008). Thus, plant community composition and structure are likely to be highly sensitive to both increases and decreases in growing season rainfall (Knapp and Smith 2001; Diffenbaugh et al. 2008). To determine how altered rainfall regimes affected aridland vegetation across a grassland to shrubland transition zone, we experimentally increased annual precipitation by 42 % of the long-term average over 4 years, or decreased precipitation by 50 % of ambient rainfall over 5 years in three vegetation types in the northern Chihuahuan Desert: creosotebush (*Larrea tridentata*) shrubland, black grama (*Bouteloua eriopoda*) grassland, and mixed vegetation at the grass–shrub ecotone. Because water is the primarily limiting resource in aridland systems, we hypothesized (1) that cover of dominant and subordinate species would increase over time with chronic water addition and decrease over time under chronic drought in all three

community types, (2) species richness would increase with chronic water addition and decrease with chronic drought, and that the decrease in richness would be greatest in shrub dominated vegetation, and (3) as a consequence of (1) and (2), we hypothesized that plant community composition would differ among rainfall treatments within each of the three vegetation types.

Materials and methods

Study area

This study was conducted at the Sevilleta National Wildlife Refuge (SNWR) in central New Mexico, USA. The SNWR lies at the northern end of the Chihuahuan Desert (Kroel-Dulay et al. 2004) where a distinct transition zone occurs between desert grassland dominated by *Bouteloua eriopoda* (black grama) and shrubland dominated by *Larrea tridentata*. Other common plant species at this site include *Muhlenbergia arenicola*, *Aristida purpurea*, *Sporobolus* spp., *Guttierezia sarothrae*, and *Sphaeralcea wrightii*.

Spatial and temporal variability in precipitation is high at the SNWR, both among seasons and years (Pennington and Collins 2007; Notaro et al. 2010). As a consequence of scarce water inputs, annual aboveground net primary production is low ranging from 50 to 200 g m^{-2} (Xia et al. 2010). The SNWR receives an average of 250 mm of precipitation annually, 60 % of which occurs from July through September (Gosz et al. 1995). Average annual temperature is 13.2 °C, with a low of 1.6 °C in January and average high of 25.4 °C in July.

Experimental design

We conducted two rainfall manipulation experiments between 2002 and 2008 in *L. tridentata* shrubland, *B. eriopoda* grassland, and the grass–shrub ecotone at the SNWR. In each vegetation type, we established three blocks, within 50 m of each other, which contained three experimental 10 × 15 m plots, for a total of 27 plots. Each block contained one replicate of ambient, drought, and increased rainfall treatments, for a total of three replicates of each treatment at each site. Grassland, ecotone, and shrubland sites were less than 2 kilometers apart.

For the drought treatments, rainout shelters were constructed consisting of movable roofs that slid diagonally along rollers to cover each plot. Shelters were deployed periodically throughout the growing season (April–November) to achieve a decrease of approximately 50 % of annual inputs based on ambient rainfall measured with tipping bucket gauges at the grassland and shrubland sites. Because rainout shelters covered the sampling plots only

during rain events, their effects on other environmental variables (i.e., light, temperature) were minimal. Water addition treatment plots received ambient precipitation plus five 21 mm rainfall addition treatments (total added = 105 mm/year) over the growing season from May through October each year. The water addition treatment, using an overhead irrigation system with raindrop quality sprinkler heads, resulted in a 42 % increase in total annual precipitation based on the long-term average so that, despite interannual variation in ambient precipitation, all irrigation plots received higher than average rainfall each year. Finally, three ambient precipitation plots at each site served as controls. Chronic drought treatments were imposed for 5 years from 2002 to 2006, and water addition treatments, for 4 years, from 2005 to 2008. During our study from 2002 to 2008, annual rainfall was −22, −32, +15, +27, +30, −3, and +9 % of the long-term average., respectively As a consequence, our drought treatments resulted in total annual rainfall of 98, 85, 144, 159, and 162 mm from 2002 to 2006, respectively, and our irrigation treatments resulted in total annual rainfall amounts of 417, 425, 343, and 373 mm from 2005 to 2008, respectively. The grassland site was burned in a wildfire in 2009.

Plant community composition was measured in 30 1-m^2 permanently located quadrats evenly spaced along three transects (10 quadrats per transect) in each plot. Transects were placed at 2.5, 7.5, and 12.5 m in from the western edge of each plot to minimize edge effects. Percent cover of each species rooted in or in the case of *L. tridentata* overhanging each quadrat was visually estimated. Cover measures can add up to more than 100 % in quadrats with large cover values in multiple layers. Cover was estimated each year in May when cool season annuals were abundant, and again in September or October when peak biomass of perennials and warm season annuals occurred. We used the highest cover value for each species in each quadrat each year in all analyses.

Data analyses

Because the drought and irrigation manipulations started in different years, data were analyzed separately, and they are treated as independent experiments despite sharing control plots. We used repeated measures ANOVA to evaluate changes in plant species cover and community structure in response to the rainfall manipulations. These analyses were used to compare drought treatment plots to ambient precipitation plots from 2002 to 2006, and rainfall addition treatment plots to ambient precipitation plots from 2005 to 2008. Thus, for each experiment, the model included vegetation type (site), rainfall manipulation (treatment), time (year), and all the interactions among these factors. After the full models were run, non-significant interactions

were deleted to test for main effects. Because none of the simplified models revealed new terms that were statistically significant, the full models are presented in Supplemental Tables 1–4. Due to the small sample size and the high variability in vegetation cover from year to year, we established our initial P value as 0.10. We tested for significant differences using Tukey HSD at $P \leq 0.1$ (see Supplemental Material). Nevertheless, many differences were highly significant despite limited replication.

Response variables were total species richness, cover of the two dominant species *Bouteloua eriopoda* and *Larrea tridentata*, and combined cover of subdominant grasses (excluding *B. eriopoda*), forbs, and subdominant shrubs (excluding *Larrea tridentata*). Prior to analysis, total richness was log-transformed, and all proportional cover variables were multiplied by 0.1 and then arcsine-transformed to improve normality.

We used nonmetric multidimensional scaling (NMDS; PCOrd 4.0) to examine differences in subdominant community composition among the rainfall treatments. We used drought and ambient species composition data from 2006 and irrigation and ambient species composition data from 2008 to evaluate the cumulative effects of chronic drought and rainfall addition, respectively. We used the Jaccard Index based on a species presence/absence matrix that included all quadrat samples in all replicates of treatments and ambient rainfall plots. NMDS ranks samples in an ordination space according to their similarity and then places them in a reduced dimensional space based on their dissimilarity. A Monte Carlo randomization (1,000 randomizations) procedure was used to assign a probability value to the location of the points in the ordination space. Next, we used the treatment replicate scores in the first two axes of the NMDS as dependent variables in a MANOVA to evaluate if the treatments resulted in different subdominant communities. The MANOVA model included vegetation type (site), treatment (rainfall manipulation), and an interaction term.

Results

Dominant species responses

The cover of *B. eriopoda* responded strongly to chronic drought and less so to water addition treatments across the three vegetation types (Figs. 1, 2; Table S1). Relative to ambient precipitation plots, drought significantly decreased the cover of *B. eriopoda* over time, and differences in cover between ambient and drought treatments were significant from 2004 to 2006 (Fig. 1). Water addition increased cover of *B. eriopoda* over time in all three vegetation types.
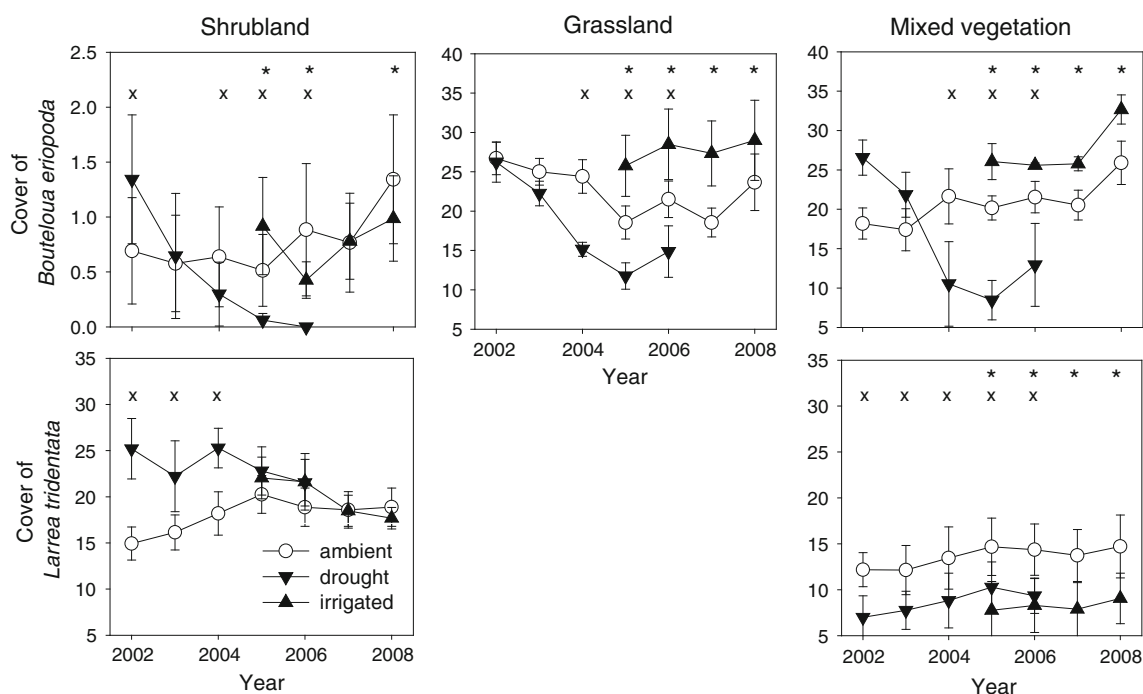

Fig. 1 Changes in percentage cover (mean ± SE) of *Bouteloua eriopoda* and *Larrea tridentata* in response to 4 years of increased (+42 % of the long-term average) and 5 years of decreased (−50 % of ambient) rainfall in central New Mexico, USA. The symbols × and

* indicate significant differences between drought treatment and ambient precipitation, and between water addition and ambient precipitation plots, respectively
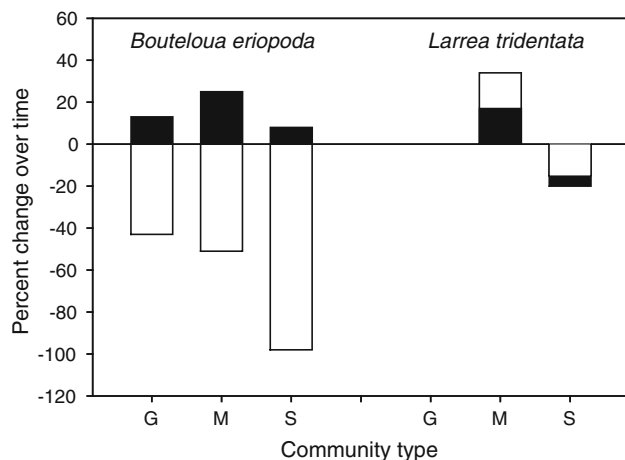
Fig. 2 Percentage change of *Bouteloua eriopoda* and *Larrea tridentata* in response to chronic drought (54 % decrease below the long-term average over 5 years) or water addition (35 % increase above the long-term average over 4 years) in grass-dominated (*G*), mixed (*M*), and shrub-dominated (*S*) areas

However, significant differences between *B. eriopoda* cover in ambient and irrigated treatments in grassland and mixed vegetation occurred at the start of the experiment, and these differences were maintained over time. Thus, cover of *B. eriopoda* mainly tracked ambient fluctuations in rainfall.

In shrublands, cover of *L. tridentata* changed little through time, thus statistically significant treatment effects reflected initial differences among sampling units (Fig. 1; Table S1). However, some trends in *L. tridentata* cover emerged over time. In both shrub and mixed vegetation, the cover of *L. tridentata* in ambient precipitation plots tended to increase from 2002 to 2005, and then remained stable. In shrublands, the cover of *L. tridentata* in drought plots varied from year to year compared to areas receiving ambient precipitation, and decreased slightly during the last 2 years of the study. In mixed vegetation, the cover of this species in drought treatments decreased slightly in 2006 only. Water addition did not increase the cover of *L. tridentata* in either shrub or mixed vegetation. In fact, *L. tridentata* cover in shrublands decreased in water addition treatment plots during 2007 and 2008.

Bouteloua eriopoda responded more strongly to drought and irrigation than did *L. tridentata* (Fig. 2). *B. eriopoda* decreased 40–90 % in grass, shrub, and mixed vegetation in response to chronic drought whereas abundance increased only 12–28 % in response to irrigation. In contrast, abundance of *L. tridentata* changed from 20–38 %; however these changes were not consistent with the experimental treatments. The largest increase in abundance of *L. tridentata* occurred in response to drought in mixed vegetation whereas abundance decreased in irrigated and drought treatments in *Larrea*-dominated shrubland.

Plant functional type responses

Plant functional types responses to rainfall manipulations varied from year to year, and among vegetation types (Fig. 3; Tables S2, S3). Drought generally decreased the cover of forbs in shrublands, but forb cover generally increased over time in grassland and mixed vegetation, especially in 2006, during a year of record high monsoon precipitation. Water addition significantly increased the cover of forbs in shrub vegetation in 2007 and 2008, but had little consistent effect on forb cover in grassland and mixed vegetation. Although cover of subdominant grasses was low in drought treatments to begin with, chronic drought generally decreased cover of subdominants over time compared to ambient precipitation plots in all three sites until cover increased in response to the 2006 monsoon. However, water addition had no consistent effects on cover of subordinate grasses at any site.

Excluding *L. tridentata*, cover of subdominant shrubs decreased in shrubland in drought treatment plots compared to ambient precipitation plots (Fig. 3). Cover of subdominant shrubs increased or remained constant over time in all treatments in mixed and grass-dominated vegetation. Species richness changed significantly over time in all treatments. Total richness declined in shrub-dominated vegetation in response to chronic drought until the strong monsoon in 2006. Otherwise, total species richness generally increased or was unaffected by water addition or drought in mixed- and grass-dominated vegetation (Fig. 3).

Subdominant community responses

A three-axis solution in the NMDS ordination sufficiently represented the variation in species composition after 5 years of drought or 4 years of water addition treatments (Monte Carlo randomization, $P < 0.001$). The composition of subdominant species was significantly different between drought and ambient precipitation plots (MANOVA, Pillai's Trace values: $site_{4,26} = 0.035$, $P < 0.001$; $treatment_{2,13} = 2.33$, $P < 0.001$; site × treatment = NS), and between water addition and ambient precipitation plots (MANOVA, Pillai's Trace values: $site_{4,28} = 0.14$, $P = 0.002$; $treatment_{2,13} = 0.57$, $P = 0.051$; site × treatment = NS) (Fig. 4). The composition of subdominants was also significantly different across vegetation types. However, subdominant species composition did not differ within each vegetation type (site × $treatment_{2,12} = 0.82$, $P = 0.467$).

Discussion

Our results indicate that chronic changes in annual precipitation had significant effects on functional abundance
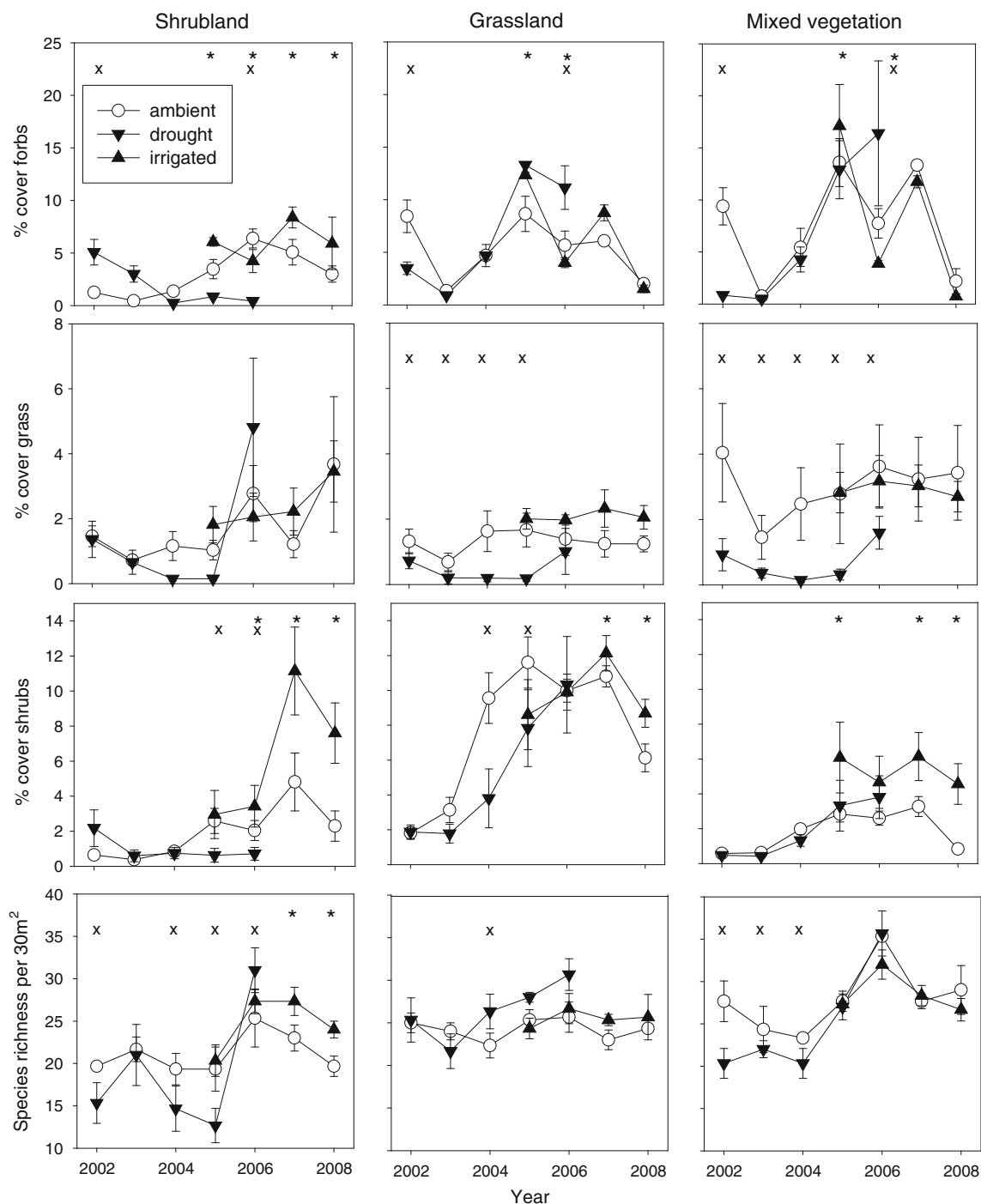
Fig. 3 Changes in cover of forbs, grasses, and shrubs (excluding *B. eriopoda* and *L. tridentata*) and total species richness (mean ± SE) in response to 4 years of experimentally increased (+42 % of the long-term average) and 5 years of decreased (−50 % of ambient) rainfall in central New Mexico, USA. The symbols × and * indicate significant differences between drought treatment and ambient precipitation; and between water addition and ambient precipitation plots, respectively

and species composition, primarily in shrub-dominated areas and less so in mixed and grass-dominated vegetation. Although some differences in cover existed at the outset, chronic drought significantly decreased the cover of the dominant native C$_4$ grass, *Bouteloua eriopoda,* in all three vegetation types (Fig. 1), whereas the cover of *Larrea*

tridentata changed over time but inconsistently with regard to our rainfall manipulations (Figs. 1, 2). In shrub-dominated areas, drought generally decreased plant cover and species richness, whereas water addition increased or had little effect on cover of *B. eriopoda,* functional types or richness, with limited inter-annual variation in responses
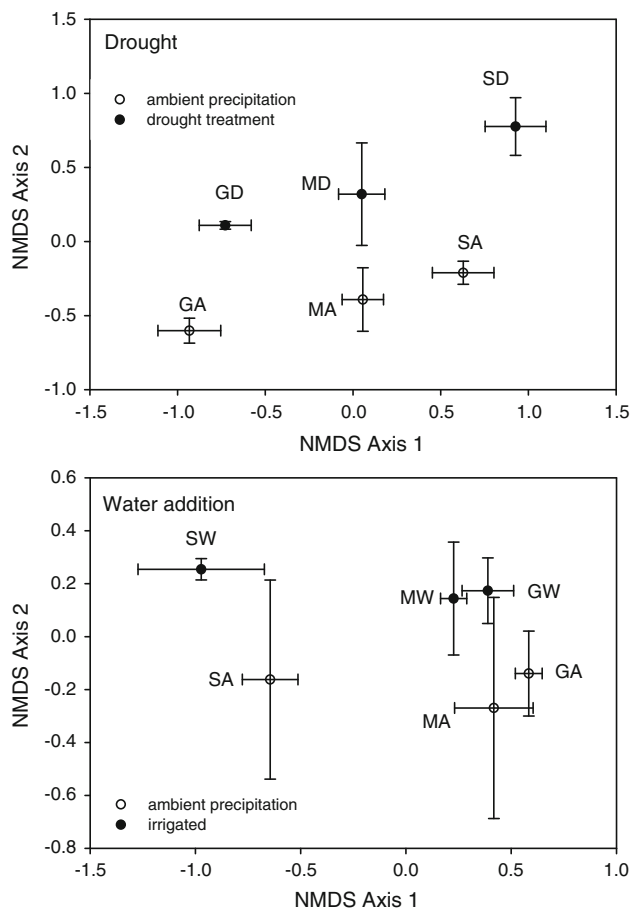
Fig. 4 Nonmetric multidimensional scaling (*NMDS*) of species composition in grassland, shrubland and mixed vegetation in response to 4 years of increased (+42 % of the long-term average) and 5 years of decreased (−50 % of ambient) rainfall in central New Mexico, USA. The mean and standard error on two axes are presented to compare drought (*D*), water addition (*W*), and ambient (*A*) precipitation plots. *S* shrubland, *G* grassland, *M* mixed vegetation

(Figs. 1, 3). Overall, *B. eriopoda* responded to both drought and added rainfall (Fig. 2). Moreover, drought and water addition shifted the species composition of plant communities in the three vegetation types (Fig. 4). The distinct and rapid changes of plant functional groups suggest that adjustments in their relative importance is a potential mechanism that can maintain plant species diversity and potentially ecosystem processes (e.g., primary productivity) under altered rainfall regimes.

Our first hypothesis was partially supported. Both *B. eriopoda* and *L. tridentata* responded to water addition and chronic drought across the three vegetation types. Abundance of *B. eriopoda* declined in response to drought and increased in response to precipitation, a pattern consistent with our initial prediction. On the other hand, the response by *L. tridentata* was relatively weak and inconsistent across vegetation types. The response of *B. eriopoda* agrees with other drought and water addition experiments

in mesic grasslands (Knapp et al. 2001; Zavaleta et al. 2003; Dukes et al. 2005; Suttle et al. 2007; but see Harpole et al. 2007), and confirms that drought can dramatically decrease production in desert grasslands (Knapp and Smith 2001; Gerten et al. 2008). The response by *L. tridentata* differs from that observed in the Sonoran Desert where above average monsoon rainfall lead to significant increases in production by *L. tridentata* (Sponseller et al. 2012). Nevertheless, our findings emphasize the variable importance of water availability for plant growth in arid ecosystems (Muldavin et al. 2008; Xia et al. 2010; Thomey et al. 2011).

Plant morphological, physiological, and life history traits can be useful predictors of the capacity of species to tolerate drought and respond to precipitation inputs (Chesson and Huntly 1997; Chesson et al. 2001; Ogle and Reynolds 2004; Reynolds et al. 2004; Suding et al. 2008). Therefore, these functional characteristics can be used to model ecosystem response to climate change (Díaz and Cabido 1997; Chapin 2003). In such models, shallow-rooted species, including grasses and forbs, respond rapidly to water inputs but decline rapidly in the absence of rainfall, whereas deep-rooted plant functional types (e.g., shrubs), and C_4 species tolerate drought conditions for longer periods and exhibit lagged responses to water inputs (Ogle and Reynolds 2004). In our case, however, C_4 grasses responded strongly and quickly to chronic drought, a response common in shallow-rooted grasses (Schwinning et al. 2005).

The limited response of *B. eriopoda* to increased water availability may reflect morphological constraints on this rhizomatous grass. Knapp and Smith (2001) hypothesized that arid ecosystems would be limited by low meristem density, or the "bud bank." Dalgleish and Hartnett (2006) found that meristem densities differed across a precipitation gradient and that grasses in desert grasslands (including the SNWR) were meristem-limited. Also, *B. eriopoda* showed rapid declines in rate of net photosynthesis in a rainfall pulse experiment that controlled the size and frequency of rain events while maintaining the same total rainfall amount during the summer monsoon (Thomey 2012). Thus, the response of desert grassland species to increased rainfall may be constrained by low meristem density and photosynthetic capacity.

The slight directional cover changes of *L. tridentata* show that this species tended to increase somewhat under ambient precipitation rates, and that cover may decrease slightly after a few years of severe drought. Measures of biomass indicate that *L. tridentata* responds weakly to summer precipitation (Muldavin et al. 2008), and during droughts it depends strongly on deeper soil water that is unavailable to grasses (Schwinning et al. 2005). This response contrasts with *L. tridentata* in the Sonoran Desert

where production during the summer monsoon can greatly exceed that of growth following more predictable winter rains (Sponseller et al. 2012). Nevertheless, abundance of *L. tridentata* at our site is likely to change only after prolonged (>5 years) severe drought, or in response to other drivers, such as extreme winter cold temperatures (Pockman and Sperry 1997; Medieros and Pockman 2011).

The lack of a clear response of subdominant grasses to water addition suggests that their establishment and performance could be negatively affected by competition with *B. eriopoda*, as its cover increased in this treatment. Peters and Yao (2012) found that subdominant grasses and forbs increased following the experimental removal of *B. eriopoda*. Indeed, under high resource availability, small statured plants can be overshadowed by taller plants (Zavaleta et al. 2003; Suding et al. 2005), and are limited by the availability of sites for establishment (Milton and Dean 2000; Bakker et al. 2006). Other results suggest that water addition may or may not substantially increase the cover of subdominant grasses (White et al. 2000; Zavaleta et al. 2003; Yao et al. 2006; Harpole et al. 2007; Suttle et al. 2007) at least in part because of competition from dominant species (Peters and Yao 2012). Finally, the interannual variability in the drought treatments (from 35 to 66 %) may have contributed to the variable response by the subdominant species. Thus, interspecific competition and idiosyncratic responses by subdominant grasses seem to constrain the potential for this functional group to decline under drought or increase substantially under elevated rainfall regimes.

It has been suggested that strong responses to high precipitation and mild declines under drought conditions are due to buffering mechanisms that reduce the impact of drought on plant production in arid and semiarid systems (Knapp and Smith 2001; Gerten et al. 2008). For example, C_4 grasses have the physiological capacity to tolerate drought (Fay et al. 2003), and *L. tridentata* can use water stored in deep soil layers (Schwinning et al. 2005; Muldavin et al. 2008). *B. eriopoda* declined significantly and quickly in response to rainfall reduction, indicating that this C_4 perennial grass is not particularly drought tolerant, a result that is counter to assumptions about C_4 grasses in some climate change models (Chapin 2003; Gerten et al. 2008). Thus, more accurate models, which allow for rapid vegetation changes within and among functional types (e.g., Collins et al. 2012) under altered rainfall regimes should be developed to incorporate differences in species tolerance to drought and compensation within plant functional types and plant life history traits (Reynolds et al. 2004; Collins et al. 2008).

How altered rainfall regimes will affect the abundance of species has important implications for predicting species composition and community structure at regional scales

(Chase 2007; Phillips et al. 2009). In our study, in each vegetation type, rainfall manipulations led to the formation of plant communities with different species composition compared to areas receiving ambient precipitation (Fig. 4). Possibly, drought acted as a filter to promote the survival and colonization of drought tolerant species, whereas drought-intolerant species were eliminated from the community (Kneitel and Chase 2004; Chase 2007). In contrast, water addition enhanced the growth of drought-intolerant species, which may have displaced small-statured species, including annuals (Suttle et al. 2007). Previous studies have not found such marked directional changes in plant species composition under drought conditions, although sensitivity at the seedling stage and idiosyncratic responses have been reported (Lloret et al. 2004, 2009). Moreover, we found no indication of convergence toward a single community composition across vegetation types. As a consequence, these vegetation types could maintain different species composition under spatially variable rainfall regimes, thus maintaining high levels of regional diversity (Kneitel and Chase 2004; Chase 2007).

Changes of *B. eriopoda* cover due to rainfall manipulations contradicted previous studies conducted in the northern Chihuahuan Desert, in that rates of summer precipitation strongly influence *B. eriopoda* density and primary productivity at small and large spatial scales (Huenneke et al. 2002; Báez et al. 2006; Yao et al. 2006). Others have reported that production of *B. eriopoda* was poorly correlated with summer precipitation (Muldavin et al. 2008). In this study, *B. eriopoda* was eliminated from drought treatment plots in shrub vegetation due to its initial low densities. However, drought can greatly reduce abundance of *B. eriopoda* throughout the grassland to shrubland gradient (Fig. 1), which may accelerate shrub dominance in mixed vegetation, especially when rainfall increases again. Increased dominance by *L. tridentata* at the expense of *B. eriopoda* has been shown to contribute to high species turnover and low temporal stability of subdominant communities in shrub-dominated areas compared to grassland (Báez and Collins 2008).

In this study, examining the responses of individual plant functional types to rainfall manipulations shed light on the mechanisms that buffer community responses to drought, and those that constrain responses to rainfall (Knapp and Smith 2001; Gerten et al. 2004; Dalgleish and Hartnett 2006). Our results demonstrated that plant community dynamics were mediated by complex and at times idiosyncratic responses among dominant species and plant functional types. Hence, more accurate forecasts of the effects of altered rainfall regimes may be achieved by recognizing that differential responses will likely occur among plant functional types in aridland plant communities as a consequence of plant species richness and diversity,

plant life histories, and interspecific competition. These differential responses to altered rainfall regimes may contribute to shrub dominance during the process of shrub encroachment into grasslands.

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