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ABIOTIC DRIVERS OF CHIHUAHUAN DESERT PLANT COMMUNITIES

by

LAURA MARIE LADWIG

B.A., Botany, University of Wisconsin, 2004
M.S., Biology, Eastern Illinois University, 2009

DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of

Doctor of Philosophy
Biology

The University of New Mexico
Albuquerque, New Mexico

May 2014

DEDICATION

I dedicate this dissertation to my Mom, Marilyn Ladwig, for believing in me.

ACKNOWLEDGEMENTS

I have many people and organizations to thank for supporting me and my dissertation research. First and foremost I thank my advisor, Scott Collins. His direction and support throughout my graduate research helped me come to greatly appreciate the intricacies of semiarid grasslands. The lessons I learned from his patient guidance and willingness to allow me to make mistakes are priceless. I also thank the members of my graduate committee, including Bob Sinsabaugh, Diane Marshall, Paulette Ford, and Jennie McLaren. Each uniquely contributed to my success and advised me through various chapters and stages of my dissertation, and for that I thank them.

I thank my family for providing constant support and encouragement in all of my endeavors, including this dissertation. They continually show me what hard work, passion and creativity can do, and I am thankful to have them in my life. Thank you to the many graduate students who created a friendly, supportive research environment within the UNM Biology department. In particular, thank you to Sally Koerner for warmly integrating me into the UNM community and for her ever-present positive attitude that provided support on many occasions. Thank you to Amanda Boutz for her constant willingness to discuss plants and for being an unwaveringly supportive friend over the past several years. Thank you to Kayce Bell for her reliably honest perspective that helped me many times and for her realistic encouragement that we can do this. Thank you to Matt Petrie for being the voice of reason within the CERIA 308 office.

This dissertation was made possible by help from a variety of groups. Many thanks to the Sevilleta Field Station and Sevilleta Long-Term Ecological Research staff, present and past, for helping collect and manage data. In particular thank you to Amaris Swann, Don Natvig, Doug Moore, Renee Brown, John Mulhouse, Stephanie Baker, Ben Specter, Mike Friggins, and Kristin Vanderbilt. I also thank the Sevilleta National Wildlife Refuge for welcoming this research on their land. I thank the Biology department at the University of New Mexico for being a supportive community in which to be a graduate student.

Many thanks to my co-authors for helping me develop data analysis and writing skills. Co-authors include Edith Allen, Michael Allen, Scott Collins, Paulette Ford, Dan Krofcheck, Marcy Litvak, Will Pockman, Bob Sinsabaugh, Amaris Swann, Michell Thomey, Heather Tran, Laura White, and Yang Xia.

Many funding sources helped fund this research, for which I am thankful. Research was funded in part by NSF grants to the University of New Mexico for Long-term Ecological Research, Research Experience for Undergraduates, Doctoral Dissertation Improvement, and Rapid Response Research, a grant from the USDA Forest Service National Fire Plan, the U.S. Department of Energy's Office of Science through the Western Regional Center of the National Institute for Climate Change Research, T & E Inc., and several Alumni and Graduate Student Scholarships from the University of New Mexico Graduate Student Association, Department of Biology, and Biology Grad Student Association.

"It is not happy people that are thankful, but it is thankful people who are happy" (author unknown) and I am certainly very thankful.

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ABSTRACT

Within grasslands, precipitation, fire, nitrogen (N) addition, and extreme temperatures influence community composition and ecosystem function. The differential influences of these abiotic factors on Chihuahuan Desert grassland communities was examined within the Sevilleta National Wildlife Refuge, located in central New Mexico, U.S.A. Although fire is a natural disturbance in many grasslands, fire during drought temporarily increased forb cover and decreased grass cover for several years. The seasonal timing of fire was not important, rather community recovery was more influenced by the persistent drought conditions. N deposition is increasing worldwide due to human activities, and although additional N increases productivity and decreases diversity in most terrestrial systems, community responses were variable in Chihuahuan Desert grasslands. During above-average precipitation, N addition greatly increased aboveground productivity but did not influence belowground productivity or community composition. During average or below-average precipitation, no effects of N addition on the grassland community occurred. Although human activities provide grasslands with extra N, soil microorganisms help plants naturally acquire N. The activity of soil microbes, and in turn nutrient availability for plants, responded to rainfall events and the proximity to plants and varied throughout the monsoon growing season. Lastly, shrub encroachment is converting grasslands to shrublands and may possibly be reversed by extreme climate events. Following an extreme cold event at the boundary between Chihauhuan Desert grass- and shrublands, shrubs were damaged but not killed by cold temperatures. Therefore a single cold event might not be influential enough to reverse shrub encroachment. Many factors, including fire, N addition, and shrub encroachment, influence Chihauhaun Desert grasslands, but the magnitude of influence is strongly regulated by precipitation. Some factors, such as fire seasonality and N addition, were not influential during drought and only changed communities when water limitations were alleviated, while other factors, such as extreme cold temperatures, influence communities regardless of soil water status. As humans continue to change abiotic factors and natural environments, it is important to understand how plant communities respond to changing conditions.

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CHAPTER 1: INTRODUCTION

The only thing constant about nature is constant change. Humans rely on properly functioning ecosystems for survival, yet interactions between humans and nature often result in altered rates or trajectories of ecological processes (Vitousek et al. 1997a). Some consequences of human-environmental interactions are obvious, such as wide-scale deforestation, while others are more indirect or lagged in effect, including the influence of nutrient deposition or precipitation fluctuations associated with climate change (Ogle et al. 2004). Changes in species interactions and plant community composition can have cascading effects on ecosystem function. Abiotic factors influencing the environment are vast (Vitousek et al. 1997b, Trombulak and Frissell 2000, Syvitski et al. 2005) and ecological consequences of changing abiotic factors equally diverse, therefore both require further investigation.

Many abiotic and biotic components interact to shape ecological communities. At the broad scale, temperature and precipitation restrict where particular biomes can persist (Whittaker 1970). Within these climate restrictions, other abiotic factors (e.g. fire, N deposition, disturbance) shape species interactions and ecological boundaries. Humans influence the timing and intensity of abiotic components that in turn change constraints of ecological communities. My dissertation provides four examples of how Chihuahuan Desert grasslands respond to altered abiotic conditions.

Fire is a natural disturbance in many systems and an influential management tool. Fire removes dead plant material to increase light availability and release trapped nutrients, aiding in nutrient cycling and altering productivity (Knapp and Seastedt 1986, Pausas and Riberio 2013). In grasslands, fire can help maintain herbaceous, grass-dominated communities by killing or stunting young woody plants and invigorating grasses (Heisler et al. 2003). Humans have changed the fire regime in many systems, largely through suppression or altered fire frequency. As land managers schedule prescribed burns, and important question to consider is ‘When is the best time to burn?’. Within Chihuahuan Desert grasslands, natural fires occur before the monsoon season, when an increased frequency of lightning strikes ignite built up supplies of dead aboveground biomass (Parmenter 2008). Prescribed fires are frequently planned for during the natural fire season, but fire during other seasons could be equally effective and allow more flexibility in scheduling fires. In Chapter 2, I examine the influence of fire seasonality on the community composition and production of a Chihuahuan Desert grassland.

The amount of nitrogen (N) in the atmosphere is increasing due to human activities (e.g. farming, fertilizing, urbanization). Given the N limitation of many terrestrial systems (Vitousek and Howarth 1991), human-influenced N deposition alters ecosystems worldwide (Vitousek et al. 1997a, Fenn et al 2003, Galloway et al. 2004). Ecological response to N deposition includes increased plant growth and total plant productivity, but decreased diversity as more N-competitive and non-native species become favored within communities (Tilman 1987, Rajaniemi 2002, Baer et al. 2003, Suding et al. 2005, Chalcraft et al. 2008). N additions increased primary productivity in nearly all terrestrial ecosystems, but the response of desert plant communities to N deposition remains unclear (LeBauer and Treseder 2008). In Chapter 3, I examine the influence of long-term N addition on Chihuahuan Desert grassland community composition and above- and belowground productivity.

Without the addition of N from humans, desert plants rely on soil microorganisms to help obtain N. One way soil microbes help plants acquire nutrients is through extracellular enzyme activities. Soil bacteria and fungi expel enzymes into the soil to help breakdown complex molecules into smaller nutrient products that can be absorbed and utilized. Plant roots also absorb these nutrient products, thus benefiting from microbially generated activity extracellular enzymes. Plant and microbial communities interact to form properly functioning ecosystems, and each component responds differently to water availability. Timing and extent of precipitation-drought cycles are influential to ecosystem function, as small rain events with shallow infiltration stimulate soil microorganisms while plants respond to deeper infiltration following larger precipitation events (Schwinning and Sala 2004). Precipitation is a key driver of semiarid community dynamics, and microbial response to precipitation variability influences nutrient availability for plants. In Chapter 4, I examine the influence of precipitation variability on soil enzyme activity during the monsoon season.

An influential community change occurring worldwide is the conversion of grasslands into shrublands following shrub encroachment. Many factors (e.g. grazing, drought, fire suppression) interact to shift grasslands to shrublands (Van Auken 2009). A few factors have been suggested to reverse the process of shrub encroachment (e.g. cold events, increased fire frequency) but have not been thoroughly tested. *Larrea tridentata*, a dominant shrub of North American warm deserts, negatively responds to cold temperatures with xylem function and photosynthetic capacity greatly compromised as temperatures decrease (Pockman and Sperry 1997, Medeiros and Pockman 2011). Additionally, the northern boundary of *L. tridentata* is thought to be influenced by cold temperatures (Pockman and Sperry 1997, Martinez-Vilalta and Pockman 2002, Medeiros et al. 2012). Therefore, extreme cold temperatures might restrict the movement of *L. tridentata* into neighboring grasslands. In Chapter 5, I examine the influence of an extreme cold winter event on Chihuahuan Desert shrubland communities to determine if cold events can reverse shrub encroachment.

The mediator of both urban and biological growth in the southwestern U.S. is water. Precipitation varies on many scales, from timing, length, and intensity of individual events to decadal fluctuations in precipitation patterns. These variations in precipitation in turn shape communities of plants, animals, and microbes. Semiarid organisms are highly responsive to precipitation, and biotic activity is often pulsed following precipitation events (Noy-Meir 1973, Reynold et al. 2004) or expresses legacy effects from previous precipitation. Water availability interacts with other abiotic factors, including fire, additional N, and extreme cold to shape communities. The research associated with my four chapters occurred under different precipitation patterns (Figure 1.1), which presumably influenced community response. Additionally, precipitation is projected to change under future climate scenarios (Breshears et al. 2005, IPCC

2013). Regionally, future changes could include variation in rainfall distributions, later monsoon seasons, earlier winter snow melt, and interactions with increasing temperatures to result in drier conditions (Stewart et al. 2004, Seager et al. 2007). Given the continued change projected for both precipitation and other abiotic factors, it is timely to consider how abiotic factors interact with water availability to shape grassland communities.

The aforementioned projects all occurred within the Sevilleta National Wildlife Refuge (SNWR), located in central New Mexico, U.S.A. The refuge includes a variety of ecosystems and associated ecological transition zones, including short grass steppe, Chihuahuan Desert grassland and shrubland, Juniper savannah, pinyon-juniper woodlands, coniferous forest, and riparian regions. This research occurred within Chihuahuan Desert shrublands and grasslands across the refuge. The SNWR is also home to the Sevilleta Long-Term Ecological Research site, which provides data and support for long-term research (http://sev.lternet.edu).

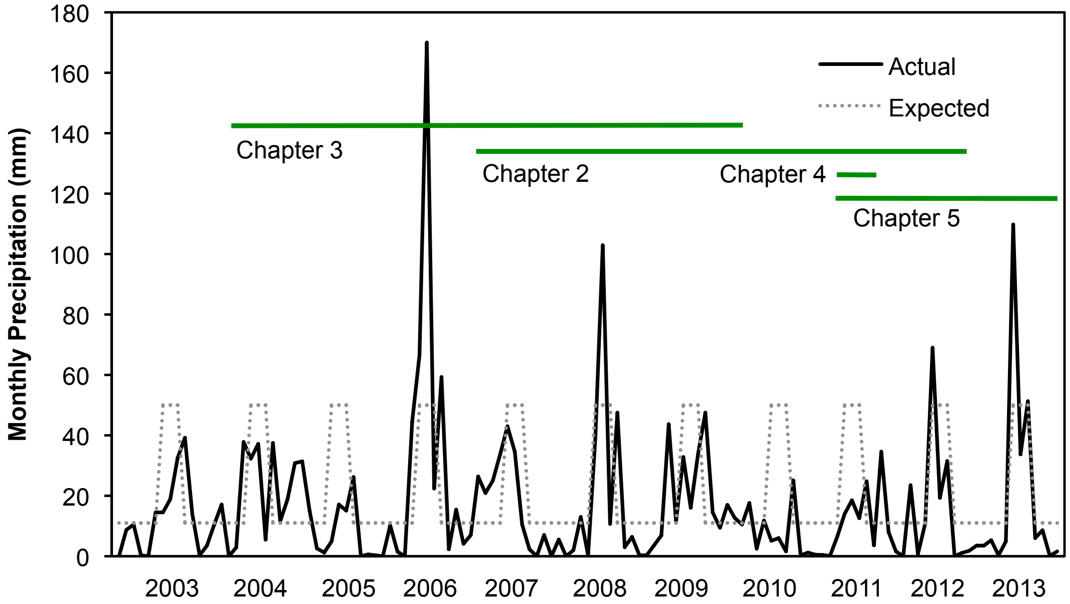


Figure 1.1 Actual (solid black) and expected (dotted grey) monthly precipitation during the extent of dissertation research. The timing of each chapter is indicated with a solid green line.

CHAPTER 2:

CHIHUAHUAN DESERT GRASSLAND RESPONDS SIMILARLY TO FALL, SPRING, AND SUMMER FIRES DURING PROLONGED DROUGHT

ABSTRACT

Land managers frequently use prescribed burning to help maintain grassland communities. Semiarid grassland dynamics following fire are linked to precipitation, with increasing soil moisture accelerating the rate of recovery. Prescribed fires are typically scheduled to follow natural fire regimes, but burning outside the natural fire season could be equally effective and more convenient for managers, depending on their management objectives. We conducted a field experiment in desert grassland to determine if fire seasonality influenced plant community recovery. Experimental burn treatments occurred in fall, spring and summer in replicate 0.24 ha plots to determine if fire seasonality affected the rate of recovery of an ungrazed Chihuahuan desert grassland in central New Mexico. Plant communities were surveyed seasonally for five years after the burns. Grassland community structure responded to fire but not fire seasonality. Grass cover in all burned treatments remained lower than unburned controls for three years after the burns. Community change through time was largely influenced by low rainfall, as grass cover in burned and unburned communities converged during a year with severe drought. In conclusion, fire seasonality did not influence rate of community recovery, but extended drought was possibly more influential than fire on grassland dynamics.

INTRODUCTION

Grasses are a critical component of rangeland function. Both natural phenomena and poor management practices can compromise grassland integrity, and maintaining semiarid grassland vegetation remains a challenge for rangeland managers. Fire frequently shapes and maintains grass-dominated communities (Pausas & Ribeiro 2013) and is often used as a management tool due to its affordability, effectiveness, and speed of treatment (Teague et al. 2001, 2008). Prescribed fires are effective in mesic grasslands where fire stimulates productivity (Knapp & Seastedt 1986), yet in semiarid grasslands lower water availability leads to decreased, patchy fuel loads and longer fire return intervals. As aridity increases, the magnitude of ecosystem benefits of fire decrease, and often semiarid plant communities are neutrally or negatively impacted by fire (Scheintaub et al. 2009). Several years may be necessary for semiarid vegetation recovery (Gosz & Gosz 1996; Parmenter 2008) and many impacts of fire on semiarid grasslands can be unpredictable (Scheintaub et al. 2009; Pastro et al. 2011). A better understanding of community response to prescribed fire is needed to help managers create optimal fire management practices within semiarid rangelands.

Water availability greatly influences desert grassland recovery (Drewa & Havstad 2001; Scheintaub et al. 2009; Pastro et al. 2011) and higher soil moisture after fire leads to faster grass recovery (Drewa et al. 2006). Total precipitation is low and variable within and between years in semiarid systems

(Dettinger et al. 2011), therefore recovery from fire is frequently inconsistent between years or sites. Since response to fire is linked to variable precipitation patterns and fire can negatively impact semiarid systems (Gosz & Gosz 1996; Scheintaub et al. 2009), studying the intricacies of semiarid community response to fire is critical for effective fire management.

The timing of fire with regard to the growing season can impact community response. Within semiarid grasslands of the Southwestern USA, perennial grasses predominantly grow during the monsoon season (Muldavin et al. 2008) and natural wildfires generally occur in early summer before the monsoon, when lightning ignites dry grasses (Parmenter 2008). In more mesic (MAP 665 mm) southern prairie grasslands of northern Texas, species respond differently to the timing of fire, with summer fires stimulating long-term growth of several co-dominant grass species and winter fires favoring others (Ansley et al. 2006; Ansley & Castellano 2007). Meanwhile, studies have found negative effects of fires during the growing season on *Bouteloua eriopoda* Torr., a dominant grass of Chihuahuan desert grasslands (Cable 1965; Drewa & Havstad 2001; Parmenter 2008; Killgore et al. 2009). However, it is unclear how prescribed fires during different times of the year affect *B. eriopoda*, particularly because a related species, *B. gracilis*, is affected by timing of prescribed fire. Cover of *Bouteloua gracilis* (Willd.ex Kunth) Lag. ex Griffiths, a dominant grass of the shortgrass steppe, shows little response to prescribed fire during the dormant-season while growing-season fires negatively impacted grass cover (Brockway et al. 2002; Ford & Johnson 2006). Current knowledge of *B. eriopoda* response to fire seasonality is based on a mix of single experimental burns and observations following natural fires, therefore a controlled experiment examining *B. eriopoda* and grassland community response to fires in different seasons is needed.

The timing of fires not only influences biotic response, but also interacts with management goals and logistics. Currently, humans control or manipulate most rangeland fires and changing socioeconomics (e.g., Dubinin et al. 2011) can indirectly influence fire regimes. In areas with an active burn crew, scheduling managed burns outside the natural fire season allows crews the ability to also deal with naturally occurring fires, yet it remains unclear if burning during other seasons influences community recovery. Understanding grassland response to a more varied seasonal burn regime may allow managers to choose the most economically and ecologically effective time for prescribed burns.

This research was conducted to provide land managers of semiarid grasslands with information about plant community recovery from fire in different seasons. Plant community response was measured for five years following a single spring, summer, or fall burn. Our specific research objective was to examine how fire seasonality influenced grass and forb cover, species richness, and community composition. We hypothesized that grassland communities and the dominant grass, *B. eriopoda*, would respond most favorably to summer burns, since that is when natural fires occur and soil moisture is more reliable because of the summer monsoon.

METHODS

Study Site

This research was conducted on the Sevilleta National Wildlife Refuge (SNWR) located in central New Mexico (34.33°N, 106.83°W). Mean (± 1 S.E.) annual precipitation is 240 (± 14) mm with roughly 60% falling during the summer monsoon season from July to September. Regional precipitation patterns in this area result in two growing seasons, a spring season following winter melt and a late summer season aligned with monsoon precipitation. Perennial grasses form the majority of aboveground net primary productivity (ANPP) and common grasses include *B. eriopoda*, *Pleuraphis jamesii* Torr., *Aristida* spp. L., and *Sporobolus* spp. R. Br.. Forb composition is interannually variable, but commonly includes *Chamaesyce* spp. Grey*, Sphaeralcea* spp*.* A. St.-Hil., *Hoffmannseggia drepanocarpa* A. Gray, and *Machaeranthera pinnatifida* (Hook.) Shinners. Prescribed burns are an active management practice at SNWR and many biotic responses to summer fires have been documented (Gosz & Gosz 1996; Parmenter 2008; Ravi et al. 2009, 2010b; Parmenter et al. 2011; White 2011) but the response of grassland communities to prescribed burns during different seasons is unknown.

Experimental Layout

Experimental burn treatments were established in a *B. eriopoda* dominated grassland located near the Deep Well area of McKenzie Flats at SNWR. The grasslands are known to have remained unburned for at least 20 years and likely were unburned for decades longer due to overgrazing during the 20th century, but fire records do not exist prior to 1989. In 2007, twenty 40 m x 60 m plots were established in a 4 x 5 grid with 10 m firebreak between plots. Fire treatments included unburned controls and a one-time fire in either fall, spring, or summer (n = 5). Replicates were randomly assigned to the 20 treatment plots. Prescribed burns occurred in November 2007 (fall), March 2008 (spring), and June 2008 (summer; Table 2.1). During each burn, fire temperature was measured at 7 to 12 points across each plot using color-changing tiles which indicated maximum fire temperature. Precipitation was measured at the Sevilleta LTER Deep Well Meteorological station (sev.lternet.edu/data).

Ten permanent 1 m x 1 m quadrats were established within each plot to monitor plant communities. Vegetation surveys were conducted in both spring (April - June) and fall (September – October) when plant cover was highest. Pre-fire vegetation surveys on all plots occurred in 2007 and percent cover of plants within quadrats was assessed twice yearly through 2012, with the exception of spring 2009 and fall 2010 when surveys were not conducted.

Several soil parameters were measured before and after fires. Pre-treatment soil samples were collected in August 2007 and post-fire samples collected in August 2008. Three 2 cm diameter by 10 cm deep soil samples were collected from each plot with a soil auger. Each soil sample was analyzed separately and averaged for mean plot measurements. Soil moisture was measured by drying soils to constant weight and organic matter content (SOM) via combustion. Field available nitrogen (NO_3 and NH_4) was measured via

Table 2.1 Climate and fire conditions during experimental burns. Climate measures are from 11:00am through 2:00pm.

Season	*Date*	*Mean air temp (°C)*	*Relative humidity*	*Mean wind speed (m/s)*	*Max wind speed (m/s)*	*Wind direction*	*Mean fire temp (°C)*	*Within plot s.d. of fire temp*
Fall	October 29, 2007	20.9	20	3.4	7.1	S to SSW	322	69
Spring	March 28, 2008	16.6	24.7	5.0	9.3	E	317	97
Summer	June 2, 2008	31.3	6.8	2.6	5.8	N, WSW	370	181

extraction with 2M KCl and analyzed with a Technicon AutoAnalyzer (Crenshaw et al. 2008). The timing of sampling may influence the soil parameters measured, as time since fire varied between treatments: 2 months since summer burns, 5 months since spring burns, and 9 months since fall burns.

Statistical Analysis

Changes in grass and forb cover through time were analyzed with a separate repeated measure analysis of variance (ANOVA) for spring and fall data to determine if seasonal cover varied among burn treatments between years. Some plants could only be identified to genus when individuals were very small or not flowering, therefore taxon richness is reported since our measure of richness was primarily based on species with a few genera level identifications. Taxa richness at the quadrat (1 m^2) and plot scale (combined 10 quadrats; 10 m^2) were analyzed separately. Differences in annual cover of the four most abundant grasses through time were assessed with a repeated measure ANOVA. Changes in community composition through time were evaluated with non-metric multidimensional scaling (NMS) ordinations using a Bray-Curtis distance matrix and 2 dimensions. A separate NMS was run for spring and fall using average percent cover of taxa within each treatment, and similar NMS were run for each year. A Permutational MANOVA (PERMANOVA) was run to determine if data groupings from each NMS were statistically different between treatments and years. To determine which species abundances varied between burn treatments, a Similarity Percentages (SIMPER) for species contributions was run for each year. Soil properties (SOM content, % moisture, NO_3, NH_4 content), pre- and post-fire and between burn treatments, were compared with a separate ANOVA for each soil property. All ANOVAs were run in SAS v.9.3 with an $\alpha = 0.05$. NMS, PERMANOVA, and SIMPER were preformed using PRIMER.

RESULTS

Above-average monsoon precipitation in 2006 stimulated grass production (Ladwig et al. 2012), increasing fuel loads prior to the experimental burns. Annual precipitation was also above-average in 2007, the year of the fall burn treatment. During all recovery years, annual precipitation was below average (Fig. 2.1). Monsoon season precipitation was also below average from 2009 to 2012, with only half the average amount of monsoon rainfall occurring in 2010 and 2011.

In the year after fire, fall grass cover decreased significantly and forbs increased in all burned plots (grasses, $p = 0.002$, $F_{12,64} = 3.04$; forbs, $p = 0.0004$, $F_{12,64} = 3.57$; Fig. 2.2). Grass cover remained significantly lower in burned plots for 3 years after fire but was generally not significantly different following spring, fall, or summer fires (Fig. 2.2). Two years after the fires, spring grass cover was lower in burned plots ($p = 0.003$, $F_{12,64} = 2.95$) and spring forbs were unaffected by fire ($p = 0.9$). The most abundant grass, *B. eriopoda*, decreased following fire ($p = 0.046$, $F_{15, 33.5} = 2.01$) and through time ($p = 0.013$, $F_{5,12} = 4.65$; Fig. 2.3). *Sporobolus* spp. and *Aristida purpurea* cover decreased with time ($p = 0.002$, $F_{5,12} = 8.02$; $p = 0.0076$, $F_{5,12} = 5.45$) but did not vary between fire treatments over time ($p = 0.7305$; $p = 0.7274$). *Pleuraphis jamesii* did not change with

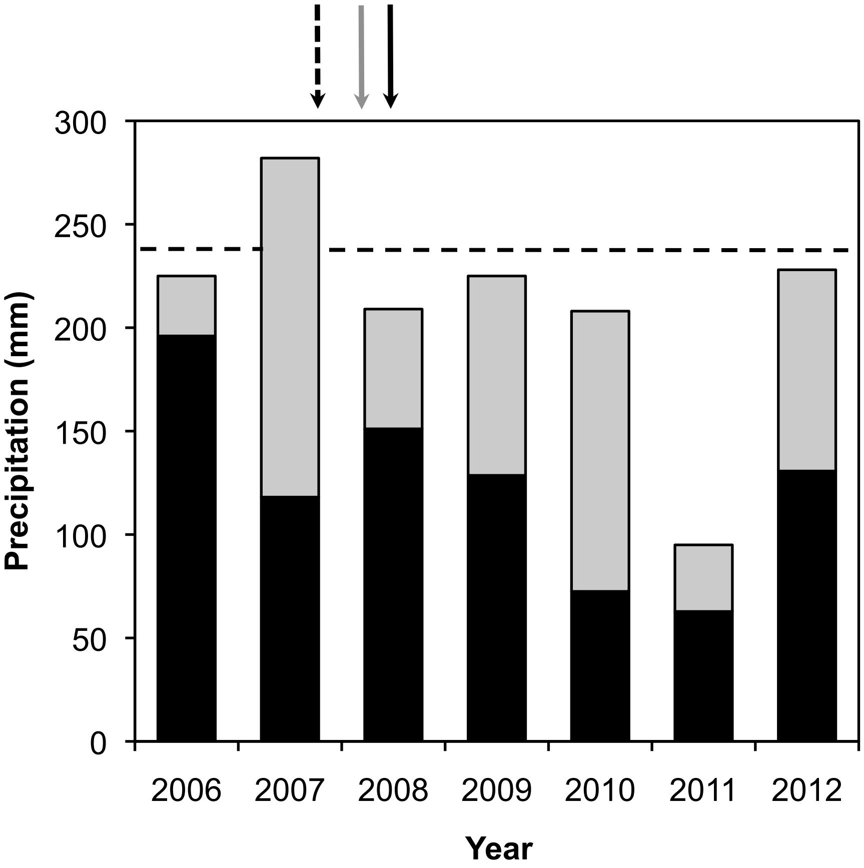


Figure 2.1 Annual precipitation for the extent of the experiment. Each bar represents total annual precipitation (mm) for the corresponding water year (October to September), with the portion of monsoon precipitation (July - September) indicated in black. The dashed line indicates long-term (22 years) average mean annual precipitation for the site. Arrows above the graph indicate when the seasonal burns occurred.

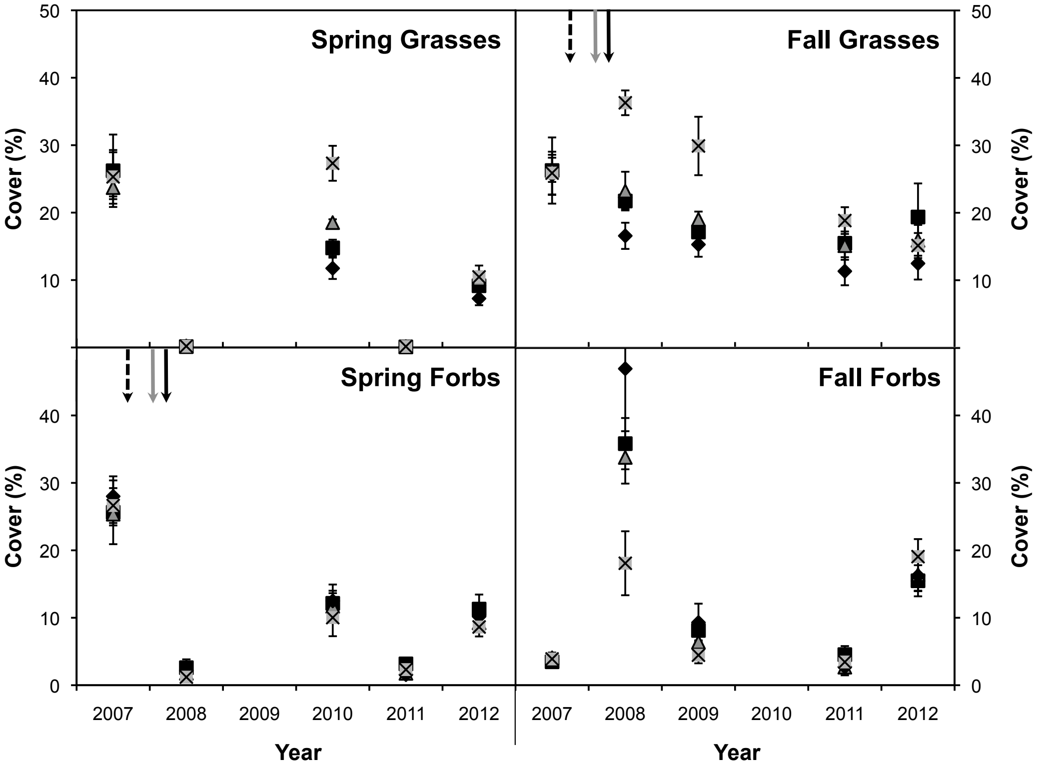


Figure 2.2 Percent cover of grasses (top) and forbs (lower) during spring (left) and fall (right) throughout the experiment. Burn treatments are depicted with different symbols and mean percent cover is graphed with error bars representing ± 1 S.E. Arrows indicate when the burn treatments occurred.

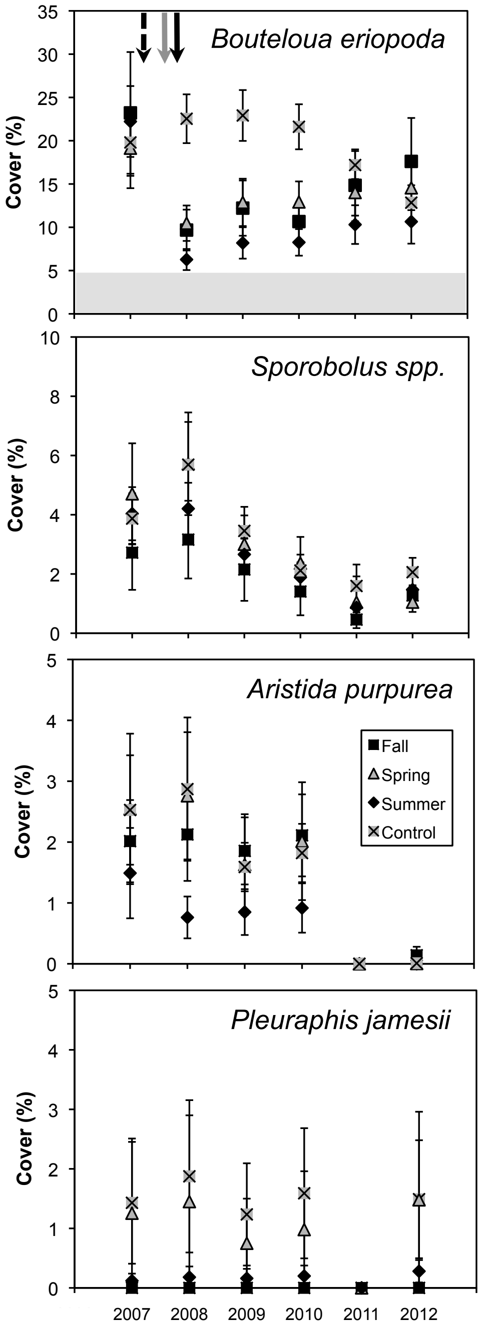


Figure 2.3 Annual percent cover of the four most abundant grasses. Burn treatments are depicted with different symbols with error bars representing ± 1 SE. The dominant grass was *B. eriopoda* (top) and the horizontal grey bar within the graph denotes the range of mean percent cover for the next most abundant grasses (lower graphs). Arrows indicate when the burn treatments occurred.

regard to time ($p = 0.41$) or fire treatments through time ($p = 0.42$; Fig. 2.3). Richness at the 1 m^2 and 10 m^2 scale decreased through time ($p < 0.001$, $F_{5,12} = 63.15$; $p < 0.001$, $F_{5,12} = 49.39$), but only varied between fire treatments at the 1 m^2 scale in 2008 ($p = 0.0054$, $F_{2.9,15} = 2.88$) and not the 10 m^2 scale ($p = 0.15$; Fig. 2.4).

Spring community composition changed and was significantly different between years ($p = 0.001$) and not different between fire treatments or the year*fire interaction ($p = 0.14$, $p = 0.99$; NMS stress = 0.16; Fig. 2.5). Fall communities varied between both years ($p = 0.001$) and fire treatments ($p = 0.001$) but not the year*fire interaction ($p = 0.98$; NMS stress = 0.19). In particular after summer burns, fall plant communities were the most different (farthest) from unburned control communities, with fall and spring burned communities being similar and generally occurring between summer and control communities (Fig. 2.5). The most abundant forbs throughout the extent of the experiment were *Dalea nana*, *Kallstroemia parviflora*, *Machaeranthera pinnatifida*, *Hoffmannseggia drepanocarpa*, and *Yucca glauca*. *Bouteloua eriopoda* was the species with most dissimilarities between control and burn plots, and comparisons between consecutive years (Table 2.2).

Fire treatments or time did not significantly influence NH_4 or NO_3 concentrations ($p = 0.5$, $p = 0.4$; Table 2.1). Soil organic matter content remained low but a significant fire*interaction indicated that SOM was only significantly different in summer plots before and after the fire (model, $p = 0.033$, $F_{7,39} = 2.55$, $r^2 = 0.357$; Fire $p = 0.19$, Year $p = 0.07$, Fire*Year $p = 0.04$; Table 2.3).

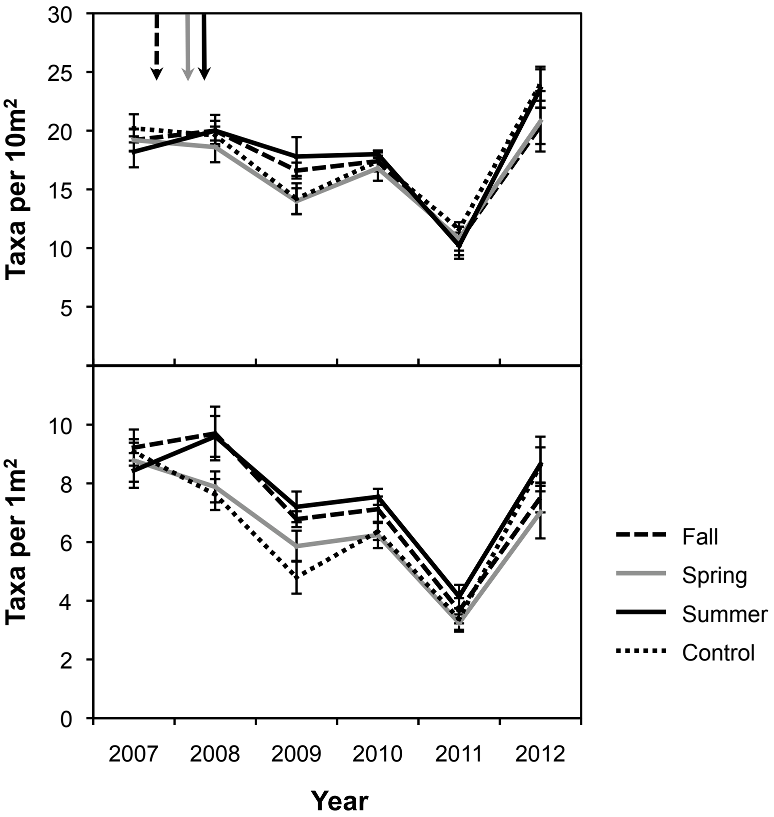
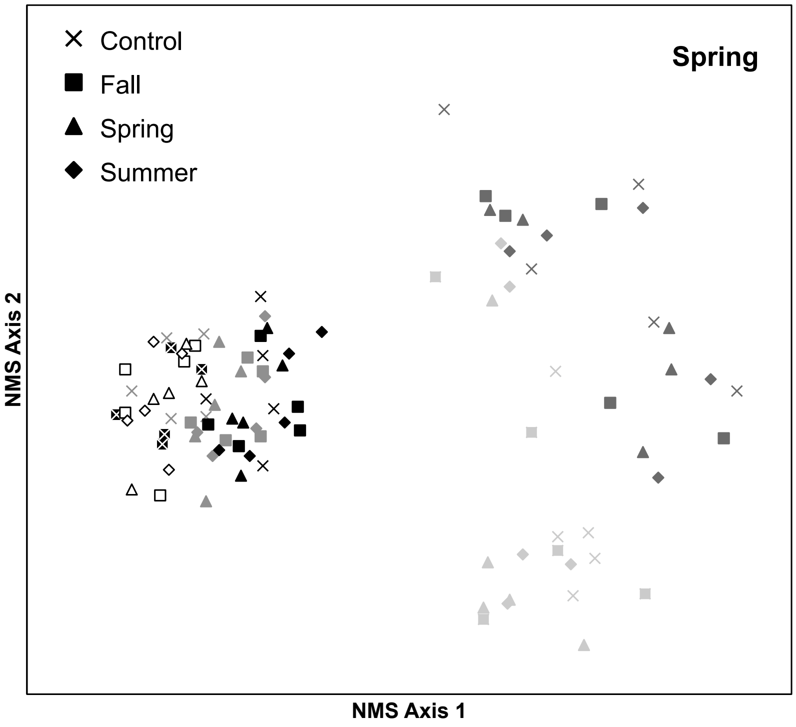


Figure 2.4 Average (± 1 S.E.) annual richness at the 10 m^2 (top) and 1 m^2 (bottom) scale. Each burn treatment is represented with a separate line: fall burn (long dashed), spring burn (solid grey), summer burn (solid black) and unburned control (short dashed). Arrows indicate when seasonal burn treatments occurred.



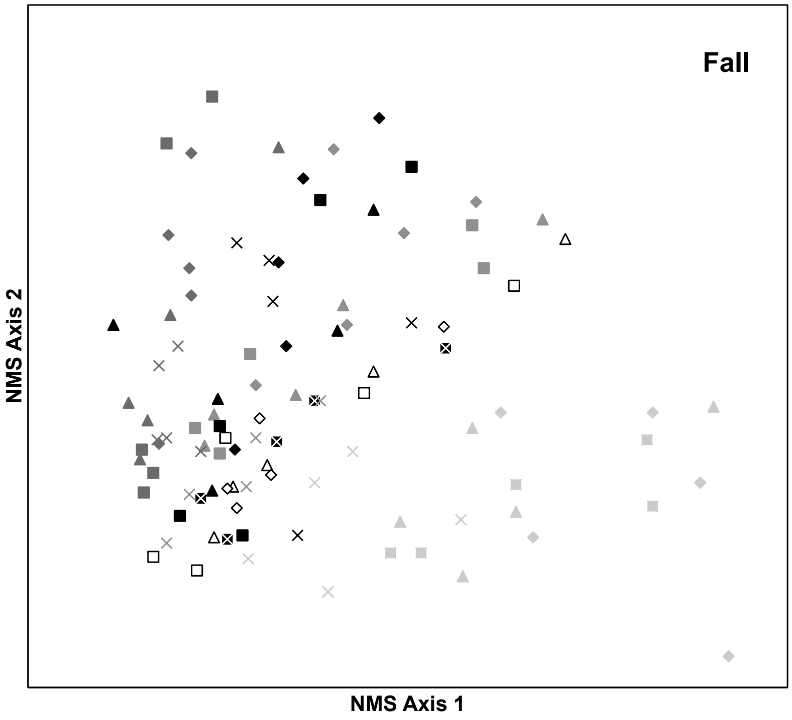


Figure 2.5 Spring (top) and fall (lower) communities based on separate NMS. Treatments are depicted with different symbols and years indicated in different shades of grey. The pre-treatment (2007) data points are white and outlined in black, and subsequent years are increasingly darker shades of grey, with the final year (2012) in black.

Table 2.2 Dissimilarity of species in fall and spring communities based on SIMPER results between consecutive years and burn treatments. Spring communities were not significantly different between fire treatment based of PERMANOVA results, therefore data are not presented.

Fall Plant Communities

2007 and 2008
(Average dissimilarity = 60.96)

Species	**Mean Abun 2007**	**Mean Abun 2008**	**Mean Diss**	**SD Diss**	**Cont%**	**Cum%**
Kallstroemia parviflora	0	13.14	12.54	1.24	20.57	20.57
Bouteloua eriopoda	19.68	12.24	12.01	1.51	19.7	40.27
Hoffmannseggia drepanocarpa	2.2	6.09	4.56	0.96	7.48	47.75
Machaeranthera pinnatifida	3.66	0.57	3.26	1.45	5.35	53.1
Sporobolus spp.	3.48	4.69	3.17	1.34	5.19	58.29
Chamaesyce spp.	0	2.44	2.46	0.64	4.04	62.34

2008 and 2009
(Average dissimilarity = 57.51)

Species	**Mean Abun 2008**	**Mean Abun 2009**	**Mean Diss**	**SD Diss**	**Cont%**	**Cum%**
Kallstroemia parviflora	13.14	0.02	14.65	1.26	25.47	25.47
Bouteloua eriopoda	12.24	14.05	6.92	1.35	12.04	37.51
Hoffmannseggia drepanocarpa	6.09	1.45	5.92	0.99	10.29	47.8
Sporobolus spp.	4.69	2.82	3.55	1.31	6.17	53.97
Chamaesyce spp.	2.44	0.01	2.9	0.64	5.03	59
Tidestromia lanuginosa	1.91	0.68	2.25	0.65	3.92	62.92

2009 and 2011
(Average dissimilarity = 45.33)

Species	**Mean Abun 2009**	**Mean Abun 2011**	**Mean Diss**	**SD Diss**	**Cont%**	**Cum%**
Bouteloua eriopoda	14.05	14.09	15.05	1.29	33.19	33.19
Sporobolus spp.	2.82	0.99	4.91	1.2	10.84	44.04
Yucca glauca	1.3	1.85	4.48	1.02	9.88	53.92
Aristida purpurea	1.48	0	3.46	1.15	7.63	61.55

2011 and 2012
(Average dissimilarity = 53.11)

Species	**Mean Abun 2011**	**Mean Abun 2012**	**Mean Diss**	**SD Diss**	**Cont%**	**Cum%**
Bouteloua eriopoda	14.09	13.51	13.64	1.24	25.68	25.68
Hoffmannseggia drepanocarpa	0.29	2.76	4.79	1.42	9.01	34.69
Yucca glauca	1.85	2.15	4.51	1	8.49	43.18
Machaeranthera pinnatifida	0.17	2.51	4.48	1.4	8.44	51.62
Sphaeralcea spp.	0.11	1.72	3.27	0.78	6.16	57.78
Salsola tragus	0	1.31	2.49	0.71	4.68	62.46

Table 2.2 (continued)

Spring Plant Communities

2007 and 2008
(Average dissimilarity = 94.39)

Species	Mean Abun 2007	Mean Abun 2008	Mean Diss	SD Diss	Cont%	Cum%
Bouteloua eriopoda	19.6	0	36.17	2.1	38.32	38.32
Dalea nana	10.42	0.11	19.03	2.03	20.17	58.49
Machaeranthera pinnatifida	3.62	0.31	6.45	1.97	6.83	65.32

2008 and 2010
(Average dissimilarity = 91.59)

Species	Mean Abun 2008	Mean Abun 2010	Mean Diss	SD Diss	Cont%	Cum%
Bouteloua eriopoda	0	13.36	41.03	2.56	44.8	44.8
Machaeranthera pinnatifida	0.31	2.85	8.46	1.21	9.23	54.03
Sporobolus spp.	0	1.94	6.5	1.22	7.1	61.13

2010 and 2011
(Average dissimilarity = 93.01)

Species	Mean Abun 2010	Mean Abun 2011	Mean Diss	SD Diss	Cont%	Cum%
Bouteloua eriopoda	13.36	0.02	40.58	2.6	43.63	43.63
Machaeranthera pinnatifida	2.85	0.22	8.7	1.23	9.36	52.98
Sporobolus spp.	1.94	0	6.48	1.21	6.96	59.95
Hoffmannseggia drepanocarpa	1.93	0	6.33	1.13	6.81	66.75

2011 and 2012
(Average dissimilarity = 90.64)

Species	Mean Abun 2011	Mean Abun 2012	Mean Diss	SD Diss	Cont%	Cum%
Bouteloua eriopoda	0.02	7.96	34.64	2.81	38.21	38.21
Hoffmannseggia drepanocarpa	0	2.53	11.37	1.46	12.54	50.76
Yucca glauca	1.43	1.75	8.39	1.01	9.26	60.01

Table 2.2 (continued)

Fall Plant Communities

Fall and Control
(Average dissimilarity = 46.01)

Species	**Mean Abun Contr**	**Mean Abun Fall**	**Mean Diss**	**SD Diss**	**Cont%**	**Cum%**
Bouteloua eriopoda	18.65	15.14	16.3	1.41	35.44	35.44
Yucca glauca	2.03	1.8	4.01	0.89	8.71	44.15
Sporobolus spp.	3.27	1.92	3.15	1.19	6.86	51.01
Hoffmannseggia drepanocarpa	1.58	2.99	2.46	0.94	5.35	56.36
Kallstroemia parviflora	1.26	2.95	2.42	0.5	5.25	61.6

Spring and Control
(Average dissimilarity = 41.66)

Species	**Mean Abun Contr**	**Mean Abun Spring**	**Mean Diss**	**SD Diss**	**Cont%**	**Cum%**
Bouteloua eriopoda	18.65	13.96	12.84	1.33	30.82	30.82
Yucca glauca	2.03	1.76	3.82	0.9	9.17	39.99
Sporobolus spp.	3.27	2.94	3.35	1.2	8.05	48.04
Kallstroemia parviflora	1.26	3.12	2.49	0.49	5.97	54.01
Hoffmannseggia drepanocarpa	1.58	2.98	2.38	0.94	5.71	59.71
Pleuraphis jamesii	1.01	0.84	1.82	0.68	4.38	64.09

Summer and Control
(Average dissimilarity = 46.97)

Species	**Mean Abun Contr**	**Mean Abun Sumr**	**Mean Diss**	**SD Diss**	**Cont%**	**Cum%**
Bouteloua eriopoda	18.65	11.12	15.91	1.44	33.87	33.87
Yucca glauca	2.03	1.13	3.56	0.83	7.59	41.46
Kallstroemia parviflora	1.26	4.1	3.05	0.39	6.48	47.94
Sporobolus spp.	3.27	2.6	2.5	1.15	5.32	53.26
Hoffmannseggia drepanocarpa	1.58	2.69	2.29	0.74	4.87	58.13
Tidestromia lanuginosa	1.1	1.38	2.18	0.54	4.63	62.76

Table 2.3 Average pre-burn (2007) and post burn (2008) soil properties. Stars indicate the values that were significantly different than each other.

Fire treatment	Organic matter (*g/g soil*)		NH_4 (*N mg/kg soil*)		NO_3 (*N mg/kg soil*)	
	Pre-burn	*Post-burn*	*Pre-burn*	*Post-burn*	*Pre-burn*	*Post-burn*
Fall	0.0133	0.0129	0.8159	1.3608	1.6376	1.8423
Spring	0.0136	0.0133	1.0487	1.1754	1.5574	1.7636
Summer	0.0129	0.0153	1.1387	0.8575	1.7924	1.6632
Control	0.0125*	0.0137*	1.3846	1.0133	1.8160	1.5360

DISCUSSION

Fire altered plant communities, lowering grass and increasing forb cover regardless of when the burn occurred. In water-stressed systems, grass cover frequently decreases during the first year post-fire (Scheintaub et al. 2009), increasing resource availability for forbs. Also, forb abundance increased in a *B. eriopoda* removal experiment suggesting a general competitive interaction between these dominant grasses and forbs (Peters & Yao 2012). Indeed, forb cover peaked initially following fire while grasses required several years to recover, leading to different recovery trajectories for fall and spring communities. Following fire, fall communities, dominated by perennial grasses, took longer to converge than spring communities, which contained more forbs. Within this grassland, changes in richness are largely dictated by forbs (Báez et al. 2006) and richness largely did not differ between burned and unburned plots. Prescribed burns can increase grassland diversity through increases in species richness (Drewa & Havstad 2001) and richness did increase following summer and fall burns at the 1 m^2 scale but not at 10 m^2. Forbs were presumably more evenly distributed across plots after summer and fall fires, leading to 1 or 2 more species at the 1 m^2 scale, but ultimately the same number of taxa remained within the larger plots. Forb abundance can be unrelated to number of taxa (Xia et al. 2010) and in this experiment increased forb cover was due to larger or more numerous individuals instead of more species.

Grass dynamics were largely attributed to the response of the dominant grass, *B. eriopoda*. *Bouteloua eriopoda*, the dominant grass of Chihuahuan desert grassland, exhibits a variable response to fire (Drewa & Havstad 2001; Parmenter 2008; Killgore et al. 2009). Natural fire return intervals may directly relate to the length of dominant grass recovery (Cable 1967). In Chihuahuan Desert grasslands dominated by *B. eriopoda*, fire return intervals are estimated around 10 years (Parmenter 2008), but remain highly variable based on moisture availability. *Bouteloua eriopoda* often shows slow or negative responses to fire (Parmenter 2008; Killgore et al. 2009; Vargas et al. 2012) and requires adequate soil moisture for full recovery (Drewa & Havstad 2001). If ample precipitation follows a fire, *B. eriopoda* can recover in one growing season (Drewa et al. 2006). During this study, drought conditions occurred throughout all years of recovery, presumably resulting in the slow recovery of *B. eriopoda*. Within mixed grasslands at SNWR, grass species respond differently to fire, and *B. eriopoda* recovers slower than neighboring grasses, including *B. gracilis*, *Sporobolus contractus*, and *Muhlenburgia arenicola* (Gosz & Gosz 1996; Ford 1999; Parmenter 2008; Augustine et al. 2010). Other grass taxa (*P. jamesii*, *Aristida* spp., and *Sporobolus* spp.) were unresponsive to fire and could have filled the niches made available by low *B. eriopoda* cover, but these sub-dominant grasses maintained low cover (1 - 5% cover), and likely contributed minimally to community recovery.

Fire seasonality had a limited influence on grassland recovery. During the first year post-fire, grass cover was lower and forbs were more abundant following summer burns, but this difference did not persist. This seasonal pattern was contrary to our hypothesis that grasses would respond more favorably to summer fires, since summer is the natural fire season (Parmenter 2008). Although plant communities were not responsive to fire seasonality, the timing of fires could influence other factors related to grassland function. Fire can homogenize soil resources by dispersing nutrient concentrations associated with islands of fertility (White 2011; Sankey et al. 2012). Within this experiment, fire slightly increased SOM two months after fire, but increases were temporary and did not last 5 months post-fire. Additionally, several ecosystem benefits of plant cover are based on the physical presence of plant material. Standing dead or live biomass can trap soil particles and debris to help stabilize surface soil (Turnbull et al. 2008) and decrease wind (Ravi et al. 2010a) and fluvial (Bhark & Small 2003; Turnbull et al. 2008) erosion. Decreased plant cover following fire can increase run-off, lower infiltration, and lead to overall losses of water, soil and nutrients from the system (Ludwig et al. 2005; White et al. 2006). Given that standing dead plant cover is important in many abiotic processes, allowing dead cover to overwinter and burning closer to the growing season may be beneficial to ecosystem processes in Chihuahuan Desert grasslands

Belowground resources likely influence aboveground plant regrowth following fire, and although aboveground response to fire was notable, above and belowground dynamics can be uncorrelated (Burnett et al. 2012; Ladwig et al. 2012). Unlike aboveground production, belowground production by *B. eriopoda* is not influenced by fire (Burnett et al. 2012). Therefore, roots can immediately utilize available moisture following rain events. Tiller meristems, or “bud bank”, are more limited in semiarid grasslands than mesic counterparts

(Dalgleish & Hartnett 2006) and damage to the limited bud bank could prolong recovery times in more arid systems. Although fires in semiarid grasslands are frequently cooler than fires in mesic systems with greater fuel loads, soil temperatures are elevated by burning (Allen et al. 2011) and tiller damage can occur at temperatures as low as 50 - 55 °C. Given that *B. eriopoda* is rhizomatous with most buds near the soil surface, it is likely that fire during any season damages meristem tissues and slows aboveground production (Burnett et al. 2012).

The plant community was not influenced by fire seasonality, but community composition changed through time in both burned and unburned plots. Natural fire regimes in southwestern U.S.A. are predicted to change as increased temperatures and decreased humidity may lead to fires starting earlier in the spring, overall longer fire seasons, and an increased number of fire danger days (Weiss et al. 2009; Abatzoglou & Kolden 2011). Although fire had an immediate effect on plant communities, precipitation, particularly drought, had a larger overarching influence (White et al. 2006). Precipitation, the dominant driver of ecological processes in semiarid regions (Ludwig et al. 2000; Austin et al. 2004; Reynolds et al. 2004; Collins et al. 2008), influences community trajectories during fire recovery (White et al. 2006; Scheintaub et al. 2009; Vargas et al. 2012). Precipitation was low when burning occurred and remained below-average in all subsequent years, at one point reaching less than half mean annual precipitation. Drought conditions presumably slowed recovery from fire and also affected the unburned controls as all grassland communities changed, regardless of fire history. Convergence of burned and unburned communities occurred during the severe drought year. Although fire is an influential disturbance in these semiarid grasslands, soil moisture availability remains the ultimate driver of community dynamics.

IMPLICATIONS

This experiment was conducted to test whether if fires during the nontraditional burn season (spring and fall) have a different influence on community recovery than traditional summer fires. In general, fire seasonality did not influence plant communities. Burned plots, regardless of seasonal timing, experienced decreased grass cover and increased compositional variation for several years following the fire. Community response to fire was also presumably influenced by several years of drought that followed the experimental burns. Although even following extensive drought, plants respond quickly to adequate precipitation (Pennington & Collins 2007). Higher soil moisture accelerates the rate of recovery from fire and previous studies suggest an ideal time for a fire is right before a rain event (e.g., Drewa & Havstad 2001). Given the importance of soil moisture and the unpredictable nature of the timing of precipitation, it may be more feasible to burn several days after a large rain event, when plants and surface soils are dry but moisture remains in the rooting zone.

Fire did not enhance grass cover or community richness, instead overall plant cover was lower for several years following fire. Prescribed burns are often conducted to help maintain grassland integrity by returning nutrients to the soil, preventing or managing woody encroachment, or decreasing forb competitors to increase grass vigor, all of which help maintain grass dominated communities. During fire recovery, grasses were slow to respond and unburned communities changed as much as burned communities in response to several years of drought. Since semiarid grassland communities are already stressed by unpredictable drought conditions, the use of fire, particularly during drought conditions, should be carefully aligned with management goals.

CHAPTER 3:

ABOVE- AND BELOWGROUND RESPONSES TO NITROGEN ADDITION IN A CHIHUAHUAN DESERT GRASSLAND

ABSTRACT

Increased available soil nitrogen can increase biomass, lower species richness, alter soil chemistry and modify community structure in herbaceous ecosystems worldwide. Although increased nitrogen availability typically increases aboveground production and decreases species richness in mesic systems, the impacts of nitrogen additions on semiarid ecosystems remain unclear. To determine how a semiarid grassland responds to increased nitrogen availability, we examined plant community structure and above- and belowground net primary production in response to long-term nitrogen addition in a desert grassland in central New Mexico, USA. Plots were fertilized annually (10 g N m $^{-2}$) since 1995 and NPP measured from 2004 to 2009. Differences in aboveground NPP between fertilized and control treatments occurred in 2004 following a prescribed fire and in 2006 when precipitation was double the long-term average during the summer monsoon. Presumably nitrogen only became limiting once drought stress was alleviated. Belowground NPP was also related to precipitation and greatest root growth occurred the year following the wettest summer, decreasing gradually thereafter. Belowground production was unrelated to aboveground production within years and unrelated to nitrogen enrichment. Species richness changed between years in response to seasonal precipitation variability, but was not altered by nitrogen addition. Community structure did respond to nitrogen fertilization primarily through increased abundance of two dominant perennial grasses. These results were contrary to most nitrogen addition studies that find increased biomass and decreased species richness with nitrogen fertilization. Therefore, factors other than nitrogen deposition, such as fire or drought, may play a stronger role in shaping semiarid grassland communities than soil fertility.

INTRODUCTION

Human modifications to the N cycle and increased N deposition associated with urban development have altered ecosystem processes worldwide (Vitousek et al. 1997, Fenn et al. 2003a, Galloway et al. 2004). Many terrestrial ecosystems are N limited (Vitousek and Howarth 1991) and atmospheric deposition often increases nutrient availability, which typically increases aboveground net primary productivity (ANPP) and decreases species diversity (Baer et al. 2003, Chalcraft et al. 2008, Stevens et al. 2010). N deposition lowers diversity through competitive exclusion and may increase the abundance of non-native species (Tilman 1987, Rajaniemi 2002, Suding et al. 2005). Plant community responses to N addition vary across ecosystems and are often co-determined with environmental conditions (Gough et al. 2000, Clark et al. 2007). In a meta-analysis of N addition experiments, deserts were poorly represented and appeared to be the only biome that did not exhibit N limitation (LeBauer and Treseder 2008). Yet, given evidence that desert soils are notoriously nutrient poor (Peterjohn and Schlesinger 1990, Zak et al. 1994, Hall et al. 2011), further investigation is required to determine if deserts are indeed N limited or if the perceived lack of N limitation is contingent upon other environmental factors.

Aridland ecosystems are characterized by low water availability and unevenly distributed precipitation within and between years. Thus, many arid ecosystems respond primarily to precipitation pulses with greatest plant growth occurring when soil water is available (Noy-Meir 1973, Schwinning and Sala 2004). The extent of plant responses to precipitation pulses varies geographically, seasonally and as a function of plant life history traits (Ogle and Reynolds 2004). For example, within semiarid grasslands in the northern Chihuahuan Desert, peak grass production occurs following large summer rain events, whereas peak forb and shrub production, both of which are typically dominated by C_3 species, occur following winter rains (Muldavin et al. 2008, Xia et al. 2010).

Although desert plants are primarily limited by water, previous studies have indicated the potential for co-limitation by N in semiarid systems (Peterjohn and Schlesinger 1990, Hooper and Johnson 1999, Hall et al. 2011). N fertilization in other semiarid systems has lead to both decreases (Carpenter et al. 1990) and increases (Ettershank et al. 1978) in ANPP of perennial species and even within the same grassland, C_4 grasses can show variable responses to N addition (Báez et al. 2007, Collins et al. 2010). Experimental N fertilization of 3.2 to 10 g N m^{-2} yr^{-1} in Mojave, Sonoran and Chihuahuan desert communities increased

ANPP, especially by quickly responding annual plants during years of average to above average precipitation (Gutierrez and Whitford 1987, Gutierrez et al. 1988, Brooks 2003, Allen et al. 2009, Rao and Allen 2010, Rao et al. 2010). Thus, quick-growing annuals can respond to N additions yet it remains unclear how communities composed mainly of longer lived, herbaceous perennials, such as C_4 grasses, respond to chronic N addition.

Few studies have measured the effects of N addition on belowground net primary production (BNPP), yet belowground growth and storage are important components of ecosystem productivity. Increased soil N availability can alleviate N limitation, leading to a decrease or altered patterns of belowground production. In other semiarid grasslands, addition of 10 to 20 g N m^{-2} altered root growth patterns and increased shallow, fine root production (Stephens and Whitford 1993, Zeng et al. 2010). Although potentially substantial, belowground production dynamics following N fertilization in semiarid grasslands remain largely unknown because of the limited number of studies and the challenges involved with measuring belowground NPP (Milchunas 2009).

Nitrogen addition also has variable effects on plant community composition and structure in arid environments. Changes in community composition can influence ecosystem processes and alter community response to disturbances. In more mesic grasslands, N addition generally leads to a decline in species richness and community heterogeneity (Gough et al. 2000, Chalcraft et al. 2008), primarily through competitive exclusion (Rajaniemi 2002). However, N addition may increase species richness and community heterogeneity in low productivity systems (Gutierrez and Whitford 1987, Chalcraft et al. 2008) because light is rarely limiting in these systems even with an increase in aboveground NPP (but see Zeng et al. 2010). Nevertheless, it remains unclear how long-term community dynamics and structure will respond to N addition in drier semiarid grasslands.

To determine how semiarid grasslands respond to increased N availability and precipitation variability, we examined above- and belowground productivity, and plant community composition, in response to long-term N fertilization from 2004-2009 in a native northern Chihuahuan Desert plant community. We hypothesized that N addition would (1) increase ANPP only during years of average to above average precipitation, (2) decrease BNPP only during years of average to above average precipitation because of higher soil resource availability, and (3) increase species richness and diversity, and the total abundance of perennial C_4 grasses.

METHODS

Study site

This research was conducted at the Sevilleta National Wildlife Refuge (SNWR) located in central New Mexico, USA, roughly 95 km south of Albuquerque. Annual precipitation is highly variable and averages 250 mm with the majority falling as large summer monsoon events (Gosz et al. 1995, Pennington and Collins 2007). Average annual temperature is 13.2 °C with highest temperatures in June, 33.4 °C, and lowest in January, 1.6 °C (Collins et al. 2008). Several ecoregions occur within the SNWR, including the northern most extent of the Chihuahuan Desert grassland and southern extent of shortgrass steppe. Both grasslands contain a variety of forbs but are dominated by C_4 perennial grasses. Chihuahuan Desert grasslands, which occur throughout much of southern New Mexico and northern Mexico, are dominated by *Bouteloua eriopoda*. Shortgrass steppe along the Colorado plateau to the north and east of SNWR is largely dominated by *Bouteloua gracilis* as well as other perennial C_4 grasses. This research was conducted in a transition zone containing a mixture of species from both Chihuahuan Desert and shortgrass steppe vegetation.

The growing season of this semiarid grassland is closely aligned with seasonal precipitation and temperature. Over 60% of annual precipitation occurs during the summer monsoon from June to September each year while sporadic precipitation occurs throughout the winter and spring as a consequence of frontal systems from the west and northwest. This precipitation pattern results in two distinct growing seasons, spring and fall, with virtually all herbaceous plants dying or going dormant between the two seasons (Notaro et al. 2010). Since plant growth is highly dependent on water, the success of each growing season depends heavily on amount of precipitation for that season and legacy effects of previous precipitation events.

Field experiment

In 1995, twenty 10 m x 5 m plots were established within the transition between Chihuahuan Desert grassland and shortgrass steppe to examine impacts of N enrichment on above- and belowground processes (Johnson et al. 2003). Ten of the plots were randomly assigned to the fertilizer treatment and ten plots served as controls. In March and June of each year since 1995, 5 g N m^{-2} as NH_4NO_3 has been applied to the 10 treatment plots. This level of N addition was chosen to reflect potential rates of atmospheric deposition near urban areas in the US Southwest (Fenn et al. 2003b). A management fire was allowed to burn through all the plots in June 2003, a time of year when lightening strikes and natural wildfires are common (Parmenter 2008).

In 1997, cover of each species was visually estimated in two randomly located 1-m^2 subplots in each treatment and control plot. Starting in 2004, vegetation within four 1-m^2 subplots in each treatment and control plot was measured during the peak spring and fall growing seasons for species composition and ANPP. For every subplot, the biomass of each species was determined allometrically from cover and height size classes following Muldavin et al. (2008). Regressions of weight-to-volume were developed by harvesting various sizes of each species from adjacent areas. A positive change in green biomass from one season to the next in each subplot was used as a measure of ANPP.

Starting in 2005, belowground net primary production (BNPP) was measured using root ingrowth donuts following Milchunas et al. (2005). A comprehensive comparison of BNPP sampling methods determined root ingrowth donuts to be a reliable and repeatable method with limited soil disturbance that can yield conservative measurements of annual BNPP

(Milchunas 2009). One root donut was located in the center of each plot to measure annual root growth within shallow (0-15 cm) and deep (15-30 cm) soil layers. To create a root ingrowth donut, a 20 cm diameter by 30 cm deep cylinder of soil was excavated with a custom-made auger and the soil was sieved to remove all roots. The surface wall of the hole from which the soil core was removed was lined with 2 mm x 2 mm mesh plastic cross-stitch fabric. A 15 cm diameter by 30 cm tall cylinder of PVC pipe was then inserted into the center of the soil core to take up space, and filled with bags of sand to hold it in place. Root-free sieved soil was then poured into the remaining space between the PVC cylinder and the cross-stitch fabric, creating a root ingrowth donut. Donuts were harvested yearly by removing the sand bags and PVC cylinder, cutting the internal soil adjacent to the cross-stitch fabric with a sharp kitchen knife, and collecting the soil and root materials. This was done at two depths, 0-15 cm and 15-30 cm. Newly collected soil from adjacent areas from 0-30 cm depth was then sifted and used to reconstruct the root ingrowth donut for the next annual harvest. Following each sample period the volume of collected soils was measured by depth, roots were sifted and floated out of each sample, collected, dried at 60°C for 48 hours, and weighed.

Detailed meteorological data from Sevilleta LTER Meteorological station 54, located 1,200 meters from the site, were used to relate measures of community structure and dynamics to seasonal and annual climate variables.

Statistical Analysis

To test our first hypothesis, we compared ANPP between fertilizer treatments and years using a repeated measures analysis of variance (RMANOVA). To test hypothesis two, BNPP was evaluated separately at each depth (0–15 cm and 15-30 cm) and collectively for total BNPP. We used three separate RMANOVAs to compare BNPP between treatments and years. To test hypothesis three, we first examined treatment effects on species richness, evenness, and Shannon diversity through time with three separate RMANOVAs. Additionally, forb:grass ratios of ANPP were evaluated with a RMANOVA to determine if fertilizer differentially influenced functional groups. All statistical tests were run using SAS v9.2 and results reported using Wilk’s Lambda statistics with α=0.05.

We used PERMANOVA to determine if fertilized and control plots differed significantly in composition. The PERMANOVA procedure analyzes distance measures in any linear model with categorical factors, such as fertilizer treatments, and tests for significance by permutation of the distance matrix (Anderson 2001, Anderson and Ter Braak 2003). PERMANOVA procedures were run on the complete data set as well as on data from each year individually. Finally, we ran SIMPER (similarity percentage) analyses which uses Bray-Curtis dissimilarity values as a post hoc test to determine which species contributed the most to differences between treatment and control plots. SIMPER analyses were performed on the complete matrix as well as separately on data from each year. PERMANOVA and SIMPER were performed with PRIMER-e v6.

RESULTS

Common in arid systems, annual precipitation greatly varied between years. Lowest annual precipitation (153 mm) occurred in 2003, the year prior to vegetation sampling and the greatest annual precipitation (392 mm) occurred in 2006. All other years received roughly average precipitation (250 mm), based on the 20-year average from this site (Figure 3.1). Aboveground production strongly corresponded to monsoon precipitation and both were lowest in 2005 and greatest in 2006. Duration of monsoon season also varied between years with 2005 experiencing a short, late monsoon season, and a long monsoon season with consistent precipitation occurred in 2006. Fertilizer treatments began in 1995 and percent cover data from 1997 provided background information about community composition before the managed burn in 2003. Total vegetation cover was higher in fertilized plots than in control plots (57% vs. 42%). In 1997, grasses dominated both fertilized and unfertilized communities, and *Bouteloua gracilis* was the most abundant species. Collectively, grasses comprised 80% of plant cover in both fertilized and control plots.

Aboveground NPP varied between years ($p < 0.0001$, $F_{5,14} = 21.86$) and corresponded well with the current year's precipitation. Lowest ANPP occurred in 2005 when the monsoon season was late and short, and there was a several fold increase in ANPP during 2006, a year with a long and above average monsoon season (Figure 3.1 & 3.2). A significant interaction between time and fertilizer treatment indicated differences in ANPP between treatments among

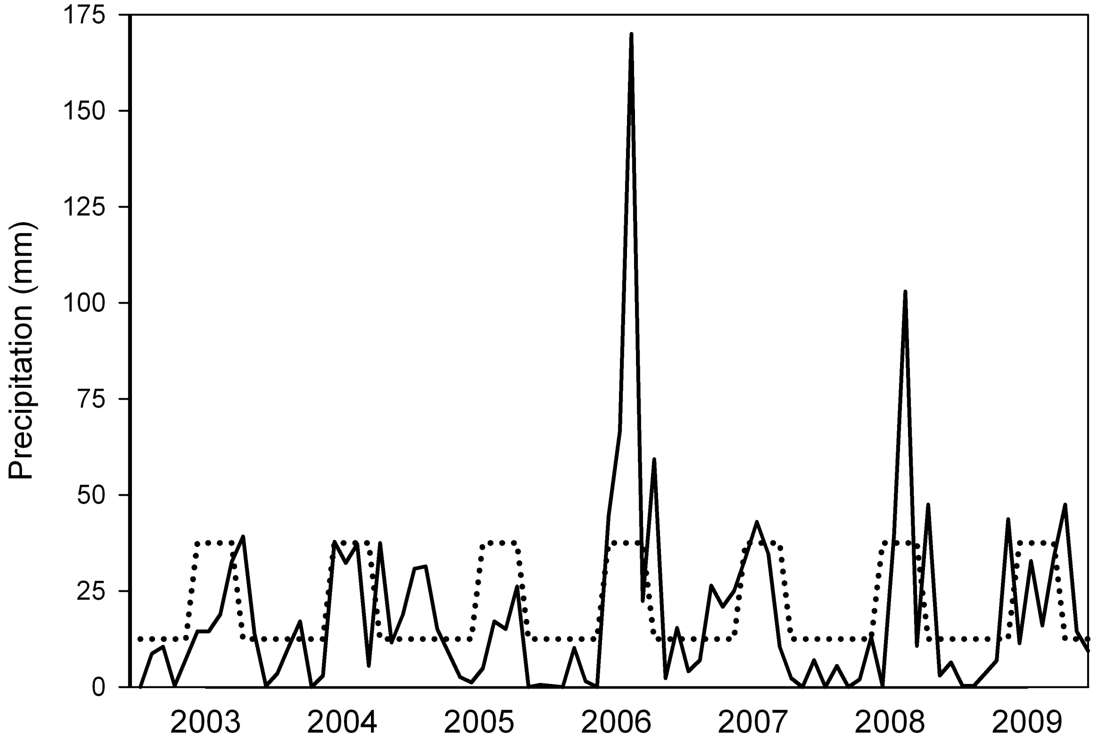


Figure 3.1 Monthly precipitation (solid line) from 2003 to 2009. Average annual precipitation (dotted line) based on the 20-year record from the Sevilleta, with 60% of annual precipitation occurring during the summer monsoon from June through September

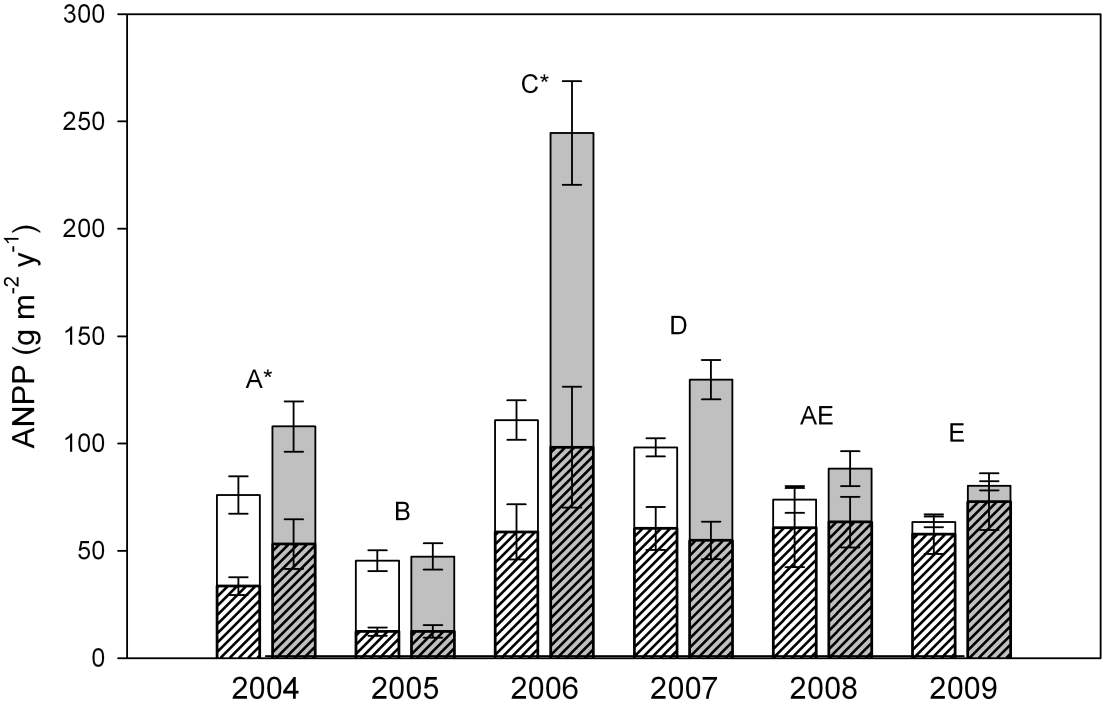


Figure 3.2 Annual ANPP in control (white) and N fertilized (grey) plots, separated into grass (striped) and forb (solid) components. With regard to total ANPP, letters indicate significant differences between years and an asterisk indicates significant differences between treatments for that year. Error bars indicate ± 1 S.E.

years ($p = 0.0452$, $F_{5,14} = 3.06$). ANPP was greater in fertilized plots during 2006 ($p = 0.0002$, $F_{1,18} = 21.02$, $r^2 = 0.539$). Nitrogen fertilization accounted for 50% of the increased production in fertilized plots. Slightly greater ANPP in fertilized plots was also present in 2004, the year following the management burn ($p = 0.0332$, $F_{1,18} = 5.32$, $r^2 = 0.228$). ANPP did not vary between fertilized and control plots in 2005, 2007, 2008 and 2009 ($p = 0.857$, $p = 0.657$, $p = 0.5335$, $p = 0.1742$; Figure 3.2).

Belowground NPP was also linked to precipitation but unlike aboveground production there was no effect of N fertilization on belowground production at shallow soils, deeper soils, or collectively ($p = 0.5528$; $p = 0.9922$; $p = 0.4792$, respectively; Figure 3.3). Both current and past annual precipitation played an equally important role in belowground production. BNPP significantly varied through time and highest BNPP occurred in 2007, a year with average precipitation following a year with above-average precipitation ($p = 0.0008$, $F_{4,12} = 10.24$; Figure 3.3). Within deeper soils (15-30 cm) BNPP did not significantly change between years ($p = 0.0712$) and variation between years was largely driven by root growth in the top 15 cm of soil ($p<0.0001$, $F_{3,14}= 26.56$).

Fertilizer effects on Shannon's diversity were only present in 2007 and diversity was higher in fertilized plots ($p=0.025$, $F_{1,18}=5.99$, $r^2=0.25$; Table 3.1). The increase in diversity was driven by increased evenness in fertilized plots ($p=0.002$, $F_{1,18}=12.91$, $r^2=0.42$) and not a change in richness between treatments. Neither total species richness, grass richness nor forb richness were

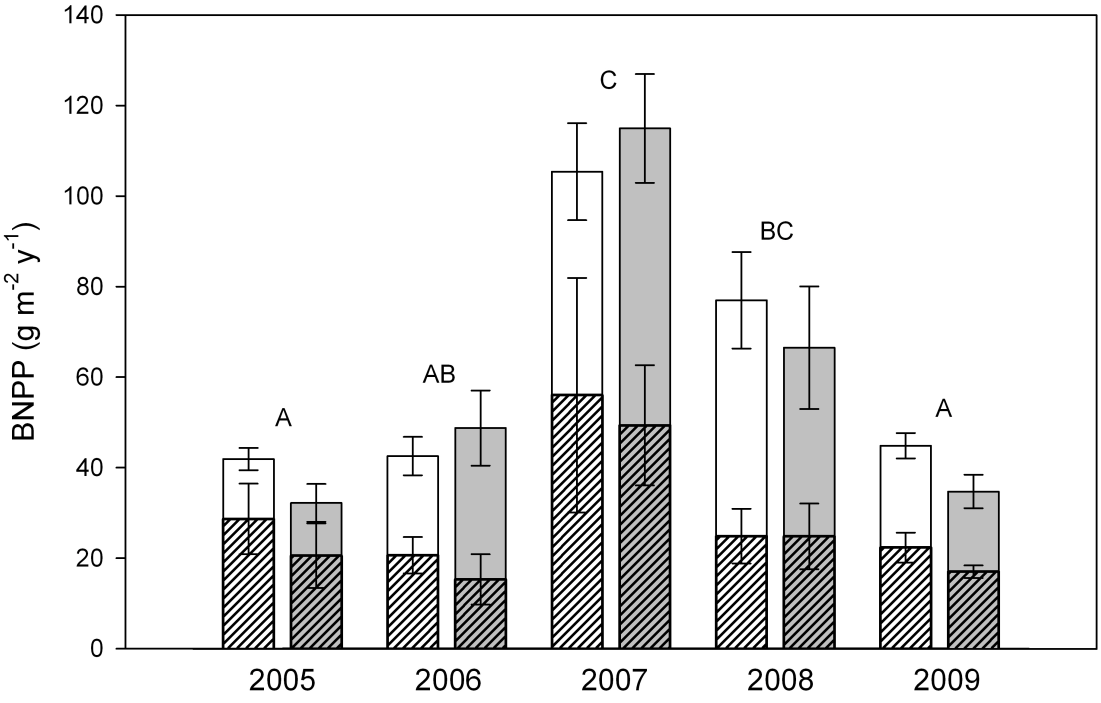


Figure 3.3 Annual BNPP within the top 30 cm of soil in control (white) and N fertilized (grey) plots. Soil profile is separated into BNPP in the top 0-15 cm of soil (striped) and 15-30 cm of soil (solid). Letters indicate years with significantly different BNPP. There was no significant difference between fertilized and control plots. Error bars indicate ± 1 S.E.

Table 3.1 Shannon's Diversity (D) and evenness (E) from 2004 to 2009. Significant differences between fertilized and control plots are indicated in bold.

	2004		2005		2006		2007		2008		2009	
	D	E	D	E	D	E	D	E	D	E	D	E
Mean												
Control	1.93	0.64	1.74	0.63	1.76	0.59	**1.87**	**0.62**	1.48	0.61	1.28	0.51
Fertilized	1.65	0.56	1.70	0.63	1.71	0.60	**2.19**	**0.74**	1.44	0.58	1.36	0.55
S.E.												
Control	0.13	0.03	0.10	0.03	0.10	0.03	0.09	0.03	0.16	0.05	0.15	0.04
Fertilized	0.09	0.02	0.06	0.02	0.09	0.02	0.10	0.02	0.21	0.05	0.21	0.05

related to N fertilization (p=0.5, p=0.9, p=0.6). Species richness significantly varied between years ($p < 0.0001$, $F_{5,14} = 86.49$) and was greatest in 2004 and 2007, primarily due to an increase in annual forbs (Figure 3.4). The decline in species richness in 2008, which persisted in 2009, was largely driven by a loss of forbs. Forbs formed the majority of ANPP until 2007 when a switch in community composition resulted in grasses becoming more abundant than forbs from 2008 onwards (Figure 3.2). This switch, measured as a decrease in forb:grass ratio of ANPP, occurred in all plots and was unaffected by fertilizer treatment (p=0.4).

PERMANOVA followed by a post-hoc SIMPER analysis provided a more direct test of fertilizer effects on species composition over time. PERMANOVA on the full data set showed a significant overall difference in species composition of N fertilized and control plots (pseudo F=3.76, p=0.003) and year (pseudo F=9.21, p=0.001) but the treatment times year interaction was not significant. Yearly analyses found significant differences in composition between treatment and control plots only in 2005-2007. SIMPER results showed that overall differences in composition between treatment and control plots primarily reflected strong differences in species abundances in response to fertilization (Table 3.2). In general, the two most abundant C_4 grasses, *Bouteloua gracilis* and *Pleuraphis jamesii*, along with the annual forbs *Kallstroemia parviflora* and *Salsola tragus* had much higher abundances on fertilized compared to control plots. In contrast, the C_4 perennial grasses *B. eriopoda* and *Aristida purpurea* had higher abundances on plots that did not receive additional N.

Table 3.2 Average abundance of dominant species in fertilized and control plots from 2004 through 2009 based on SIMPER analysis.

Species	Fertilized Abundance	Control Abundance	Average Dissimilarity	Percentage Contribution	Cumulative Contribution
Pleuraphis jamesii	31.62	19.04	12.51	16.26	16.26
Bouteloua gracilis	28.12	13.97	11.22	14.58	30.84
Kallstroemia parviflora	14.53	3.31	5.00	6.51	37.35
Salsola tragus	10.84	6.19	4.98	6.48	43.83
Sphaeralcea wrightii	10.74	2.59	4.82	6.26	50.09
Cryptantha crassisepala	8.11	5.38	4.78	6.21	56.29
Gutierrezia sarothrae	3.81	9.57	4.44	5.77	62.07
Bouteloua eriopoda	3.66	9.53	4.31	5.61	67.67
Oenothera caespitosa	5.09	1.28	2.03	2.64	70.31
Aristada purpurea	1.42	5.16	2.03	2.63	72.95
Melampodium leucanthum	2.27	2.92	1.90	2.46	75.41
Tidestromia lanuginosa	4.06	0.84	1.79	2.33	77.74
Astragalus nuttallianus	2.48	2.45	1.54	2.00	79.74
Euphorbia exstipulata	1.97	2.52	1.38	1.80	81.54
Machaeranthera pinnatifida	1.37	2.12	1.19	1.55	83.09
Solanum elaeagnifolium	2.23	1.14	1.18	1.53	84.62
Chaetopappa ericoides	0.84	2.21	1.03	1.34	85.96
Sporobolus flexuosus	1.64	0.73	0.93	1.21	87.17
Sporobolus contractus	1.25	1.21	0.90	1.16	88.33
Sporobolus cryptandrus	1.36	1.17	0.79	1.03	89.36
Sphaeralcea hastulata	1.15	0.53	0.78	1.01	90.37

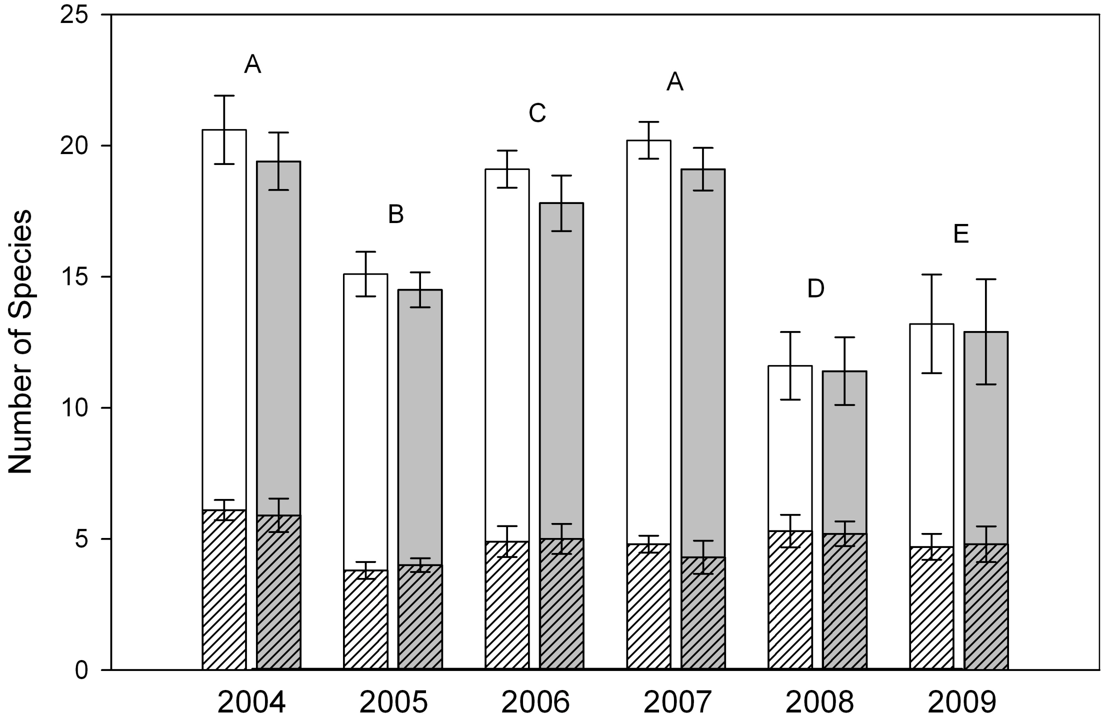


Figure 3.4 Species Richness per $4m^2$ in control (white) and N fertilized (grey) plots separated into grass (striped) and forb (open) components. Letters indicate significant differences between years. There were no significant differences between fertilizer and control treatments. Error bars indicate ±1 S.E.

DISCUSSION

Similar to many terrestrial systems (Gough et al. 2000, LeBauer and Treseder 2008), N addition resulted in increased aboveground production in some years indicating potential N limitation within this semiarid grassland. Although present, N limitation only occurred during periods of above-average precipitation, adding further support to the claim that semiarid systems are primarily water limited and secondarily N limited (Gutierrez et al. 1988, Carpenter et al. 1990, Gutierrez 1992, Brooks 2003, Allen et al. 2009, Rao and Allen 2010, Rao et al. 2010). Although apparent aboveground, N fertilization did not increase belowground production nor did it drive directional changes in plant community diversity, composition or dynamics.

Aboveground production was positively related to seasonal precipitation, with highest production (250 g m^{-2}) occurring in 2006 on fertilized plots following a summer of record high rainfall. In contrast, ANPP was <50 g m^{-2} on fertilized and control plots in 2005 when summer rains were 75% below the long-term average. Also, N addition significantly increased total aboveground production in 2004, the year following fire, when N fertilization may have restored some of the N lost through volatilization from burning. Overall, a strong N effect on ANPP only occurred during above average monsoon precipitation in 2006. Grass production was 66% higher and forb production nearly 300% higher on fertilized compared to control plots. However, greater aboveground production on fertilized plots did not persist. The results supported our first hypothesis that these desert grasslands are N limited and that N limitation only becomes evident following periods of above average rainfall as well as when N is depleted following fire. Average precipitation, however, is not sufficient to alleviate drought stress as N limitations were not present in the four years with average rainfall.

Over the five years of measurement, belowground production averaged 57.02 g m^{-2} yr^{-1}, which although low is still within the range of root production reported for other semiarid systems (30 to 443 g m^{-2} yr^{-1}; Pavon 2005). Our measurement of belowground production underestimates actual root production because fine root turnover likely occurred between annual belowground sampling periods. Nevertheless, our results are certainly comparable across plots and years, and differences in root production were apparent over time. The greatest belowground production occurred in 2007, the year following the record monsoon rainfall and declined gradually over time. A majority of increased production occurred in the top 15 cm of soil, a region of high root production (Bhark and Small 2003). Presumably BNPP increased following the wet year, supporting aboveground production from the previous year. These results demonstrate that belowground production occurs on multiple year cycles in response to above average precipitation, and provide the mechanism by which these grasslands were a net carbon source in 2007 and 2008 despite relatively high aboveground and belowground production during those years (Xia et al. 2010, Anderson-Teixeira et al. 2011). In addition, these results indicate that high aboveground production in a given year does not correspond with high belowground production.

Even when N limitation was detectable aboveground, N fertilization did not stimulate belowground production, a result counter to our second hypothesis. Instead, belowground production was most responsive to ANPP from the previous year. Although we did not see an influence of N on belowground productivity, fertilization has been shown to affect shallow root biomass and growth patterns in other desert systems. Xeric shrubs in the central valley of Mexico reduced fine root production with N enrichment (Pavon 2005), and fertilization led to shorter roots in *B. eriopoda* in another Chihuahuan Desert grassland (Stephens and Whitford 1993). In contrast, fine root biomass increased in a semiarid sand-shinnery oak ecosystem in response to water and N additions (Zhang and Zak 1998). In many terrestrial systems belowground production decreased with nitrogen addition because plants allocated more resources aboveground to compete for light (Hautier et al. 2009). In desert grasslands, however, light is generally abundant and plant cover is patchy such that aboveground competition for light is minimal even during periods of high aboveground production. Overall, our results suggest that root production in our system is driven primarily by soil water availability and not by competition for soil nitrogen.

In contrast to our third hypothesis, we observed no consistent impact of N enrichment on species composition over time. Although composition in treatment and control plots differed significantly in some years, composition of treatment and control plots did not differ during the final year of the study. Although N additions did not have large impacts on species abundances at our site, N fertilization has altered community dynamics in other desert systems. Other semiarid fertilization studies indicate decreases in species richness, a switch from C_4 to C_3 species, or influences that scale directly with amount of precipitation (Carpenter et al. 1990, Zeng et al. 2010, Hall et al. 2011). Site-specific differences may account for the differing results, as the degree of aridity and community composition varied between sites and may impact how plants respond to precipitation and N addition.

Although composition changed from a predominantly forb rich community into a grass dominated system, this change occurred on both fertilized and control plots. Thus, the increase in grass abundance relative to forbs probably reflects time since burning (Parmenter 2008). Fires occur in this system during summer months when conditions are windy and hot, and adequate dry fuel is available. Fires alter nutrient distribution locally and may promote grass dominance and reverse land degradation (Ravi et al. 2009, Ravi and D`Odorico 2009). Species abundance data collected in these plots in 1997, two years after the start of the fertilizer treatments, indicated roughly 50% cover of grass and <10% forbs. Response to fire varies among life forms (Parmenter 2008). Initially forbs dominate following fire, although *Bouteloua gracilis* recovered by the next season and it responded favorably to N addition, as well. *Bouteloua eriopoda*, on the other hand, is not well adapted to fire and can take 7-11 years to return to pre-fire abundance, depending on precipitation (Gosz and Gosz 1996, Parmenter 2008). N addition also appeared to suppress growth of *B. eriopoda*, perhaps through competition with other grasses that increased growth in fertilized plots

(Table 3.2). Above average precipitation in summer 2006 enhanced recovery of *B. eriopoda*, and the increase in abundance of competitive perennial grasses likely decreased forb abundance and diversity. Thus, fire and nitrogen combined to affect community dynamics in this desert grassland.

Although N addition may constantly shape many terrestrial communities, N addition has restricted, sporadic impacts in this semiarid system. Several factors may lead to these varied dynamics. First, when compared to other systems, N deposition is relatively low in semiarid regions, except near densely populated areas. For example, N deposition at the SNWR is currently 0.2 g N m^{-2} yr^{-1} compared to an estimated 0.4 to 3 g N m^{-2} yr^{-1} in the Phoenix metropolitan area (Fenn et al. 2003b, Báez et al. 2007, Hall et al. 2011), but N deposition at SNWR continues to increase over time. Population growth and urbanization projected for the Southwestern US will likely increase N deposition even further, making continued studies of the effects of N enrichment on aridland ecosystems necessary. Despite the potential for higher rates of deposition in the future, N retention in aridland ecosystems is low (Peterjohn and Schlesinger 1990, McCalley and Sparks 2009), suggesting that impacts of N deposition may be periodic but ephemeral. Aridland soils lose considerable N through abiotic as well as biotic processes (Peterjohn and Schlesinger 1990, Walvoord et al. 2003, McCalley and Sparks 2009). Indeed, following 9-10 years of fertilization, the soils in both control and fertilized plots in our experiment had roughly the same low N content (~0.05%; Zeglin et al. 2007) showing that nitrogen is not accumulating in these soils. Thus, even with additional inputs of N through deposition, desert soils may not retain N, and nitrogen availability may continue to limit aboveground production during years of above average precipitation.

Many press and pulse factors (Smith et al. 2009) interact to shape community dynamics in plant communities. Press factors chronically influence on the community while pulse factors occur in discrete events. In semiarid ecosystems, drought remains a persistent and frequent press disturbance, continually stressing plants and shaping community structure and ecosystem processes. Fire, although a less frequent pulse disturbance, quickly alters community composition, and leads to slow recovery by some dominant species. Nitrogen deposition is an increasing press disturbance that does not currently play a large role in shaping semiarid grassland structure and function, but has the potential to increasingly affect aridland ecosystems in the future. Currently, unlike mesic systems (Tilman 1987, Gough et al. 2000, Stevens et al. 2004), water limitation remains the key driving force in arid and semiarid vegetation with nitrogen availability as a secondary factor, but one that may temporarily favor some dominant species over others, primarily in response to periods of above average water availability during the growing season.

CHAPTER 4:

PULSE-DRIVEN DYNAMICS OF POTENTIAL ENZYME ACTIVITIES IN DRYLAND SOIL

ABSTRACT

Variable and sparse precipitation can produce pulse-reserve dynamics in dryland ecosystems. Given that soil microbes control decomposition processes, we investigated if soil microbes exhibit pulse-reserve dynamics by measuring changing potential extracellular enzyme activities within a rainfall manipulation experiment at the Sevilleta National Wildlife Refuge in central New Mexico, USA. Rainfall treatments included either three 10 mm events or one 30 mm rain event per month throughout the three month summer monsoon (July – September). Potential extracellular enzyme activities were measured immediately before and within hours after experimental rain events under plants and in unvegetated interspaces. Hydrolase enzyme activities were greater under vegetation than in interspace soils, but similar temporal patterns of enzyme activities occurred in both locations. For both rainfall treatments, extracellular enzyme activities pulsed following rain, with quick, small pulses early in the season and slower, larger pulses late in the season. Reserves of extracellular enzymes did not increase through the season, but instead remained persistant in the soil. We conclude that potential extracellular enzyme activities are pulse-driven following rain events but these pulses do not always result in accumulating reserves of extracellular enzymes in these dryland soils.

INTRODUCTION

Soil microbes control many biochemical processes in ecosystems worldwide. In semiarid grasslands, microbial nitrogen fixation can be the primary N source for plants (Evans and Ehleringer 1993). Soil microbes influence carbon cycling through considerable contributions to ecosystem respiration (Cable et al. 2008), causing grasslands to fluctuate between carbon sources and sinks based on event-scale and seasonal precipitation patterns (Huxman et al. 2004, Kurc and Small 2007, Anderson-Tiexiera et al. 2011). Although decomposition rates are often linked to microbial activity (Moorhead and Sinsabaugh 2000), abiotic factors (e.g., soil mixing, UV radiation) also drive decomposition in dryland systems (Austin and Vivanco 2006, Parton et al. 2007, Brandt et al. 2010, Hewin et al. 2013). Therefore microbial cycling helps retain nutrients and organic matter in the biotic component of dryland environments.

Although plants primarily rely on a variety of internal biochemical processes, many microbial functions are largely extracellular. In particular, microbes rely on a variety of extracellular enzymes for the breakdown of complex organic compounds into obtainable energy and nutrient sources (Sinsabaugh et al. 2002, Moorhead et al. 2012). Extracellular enzymes require soil moisture for maximum function, therefore, extended periods of drought likely decrease enzyme and microbial activities (Austin et al. 2004). During dry periods, extracellular enzymes either degrade or stabilize on soil particles, potentially preserving the utility of these nutrient-generating agents until moisture returns (Stursova and Sinsabaugh 2008). Enzyme stability varies based on the molecular structure interacting with inherent soil properties (Allison 2006, Renella et al. 2007, Dorodnikov et al. 2009, Yan et al. 2010). Soil enzyme pools in many systems respond to moisture fluctuations (Henry 2012) and pool size tends to increase following precipitation events (Munson et al. 2010).

Many environmental factors influence dryland biogeochemistry (Austin 2011), yet all biotic activity, including microbial, is limited by water availability (Huxman et al. 2004, Collins et al. 2008). Soil moisture stimulates productivity, and microbially driven processes, such as soil respiration, rapidly respond to increases in water availability (Vargas et al. 2012). Timing and magnitude of rain events alter N mineralization, transformations of organic matter, and C loss from dryland soils (Austin et al. 2004, Belnap et al. 2005, Bell et al. 2008, Munson et al. 2010, Vargas et al. 2012). Any water addition to dry soils stimulates soil microbial respiration (Ma et al. 2012) while plant activation requires a minimum soil moisture threshold (Sala and Lauenroth 1982, Reynolds et al. 2004). Therefore, small precipitation events may differentially influence plant and microbial activities, potentially separating the timing of nutrient transformation and utilization within semiarid biochemical cycles (Huxman et al. 2004, Sponseller 2007, Collins et al. 2008). Although soil moisture thresholds for plant activation can be as low as 5 mm, a 10 mm rain event can synchronize semiarid plant and microbial activity and maximize nutrient cycling efficiency (Dijkstra et al. 2012).

Soil resources and vegetation cover are highly heterogeneous in many aridland ecosytems (Schlesinger et al. 1990, 1996). These systems are characterized by patches of vegetation interspersed with unvegetated soils often occupied by biological soil crusts. Soil crusts are themselves hotspots of biological activity (Belnap and Lange 2003, Belnap et al. 2005). However, soil nutrients and organic matter are generally higher (Schlesinger et al. 1990, Keift et al. 1998, McCrackin et al. 2008), and soil moisture infiltrates deeper and remains longer in soils under plant canopies than beneath adjacent unvegetated soil patches (Bhark and Small 2003, Pockman and Small 2010). Assuming that soil resources along with root exudates influence the rate of microbial processes (e.g., Vargas et al. 2012), enzymatic activities are likely to be higher in soils beneath plant canopies than enzymatic activites beneath unvegetated patches.

Many ecological processes in desert ecosystems are characterized by pulse-reserve dynamics (Noy-Meir 1973). In this model, a precipitation pulse stimulates biological activity resulting in a biotic reserve (Noy-Meir 1973, Reynolds et al. 2004, Collins et al. 2008, Marusenko et al. 2013), such as leaf and root biomass or seed production. It is unclear, however, whether or not microbial processes, such as the production of extracellular enzymes, also exhibit pulse-reserve dynamics. If extracellular enzyme activities follow pulse-reserve dynamics, we would expect reserves (i.e. potential enzyme activities) to increase and remain high following a series of rainfall pulses.

Multiple climate change experiments have shown that temperature influences nutrient cycling processes (van Gestel et al. 2011), but microbial and enzyme dynamics responded more to precipitation variation than increased temperature (Liu et al. 2009, Castro et al. 2010, Kardol et al. 2010, Johnson et al.

2012, Henry 2012, Steinweg et al. 2012, Zelikova et al. 2012). Precipitation in the southwestern USA mainly occurs in small, pulsed events (Loik et al. 2004) and is predicted to become more variable in the future (Diffenbaugh et al. 2008, Gutzler and Robbins 2011). Given that dryland systems are sensitive to changes in precipitation (Heisler-White et al. 2009, Thomey et al. 2011, Sala et al. 2012) it is unclear how availability of soil reserves, including extracellular enzymes, will change under future patterns of precipitation. We experimentally altered the size and frequency of soil moisture inputs during the summer monsoon in a northern Chihuahuan Desert grassland and monitored extracellular enzyme potentials to ask: Do potential enzyme activities differ 1) immediately before and within hours after rain events, 2) in soils under plants vs. unvegetated patches, and 3) with differences in timing and magnitude of rainfall?

METHODS

Study site

Research was conducted on the Sevilleta National Wildlife Refuge (SNWR), in central New Mexico, USA (34.33° N, 106.83° W), also the location of the Sevilleta Long-Term Ecological Research (LTER) site. This research occurred in a mixed grassland dominated by *Bouteloua eriopoda* and *B. gracilis* representing Chihuahuan Desert and shortgrass steppe ecosystems, respectively. Soils are classified as a Typic Haplargid. Surface soils have a 3.0 - 7.5 cm deep sandy horizon composed of aeolian material and occur atop several argillic B horizons. The course texture of the A horizon allows relatively high infiltration to the B horizons, where water holding capacity is increased due to high montmorillonite content (Buxbaum and Vanderbilt 2007, Bryan-Ricketts 2012). A petrocalcic layer occurs 40 to 70 cm below the soil surface, which constrains root depth and moisture infiltration (Buxbaum and Vanderbuilt 2007). Mean annual precipitation (MAP) over the past 22 years is 240 ± 14mm, with ~60 % of MAP occurring in larger, summer monsoon events from June to September (Gosz et al. 1995, Pennington and Collins 2007). Plant production is aligned with precipitation and perennial grass production responds primarily to summer monsoon precipitation both locally and regionally (Muldavin et al. 2008, Notaro et al. 2010).

Experimental field study

From July to September 2010, potential soil enzyme activities were measured in a rainfall manipulation field study. Ten 2 m x 2 m complete rainout shelters were deployed in July 2010. Shelters had complete, clear polycarbonate roofs sloped from 1.2 to 0.9 m off the ground and were open along the sides therefore all precipitation was blocked but air easily mixed under the shelters. For complete control of precipitation in the field, natural rainfall was diverted from plots and water was experimentally applied using a hand-held garden wand during the monsoon season. Metal flashing was buried to 10 cm along the perimeter of each plot to prevent run-on. A one-time 30 mm rain event was added to all plots on 15 June 2010 to activate plants for the summer growing season. From July to September, plots were watered following one of two precipitation regimes, either one 30 mm rain event each month (n = 5) or a 10 mm rain event every 10 days (n = 5). Therefore over the course of the experiment plots received the same amount of water (120 mm) but precipitation regimes varied in frequency and magnitude of events. Soil moisture under shelters was measured in 15 minute increments from soil moisture probes (ECH$_2$O EC-5 Decagon Devices, Inc., Pullman, WA, USA) at 5 and 15 cm depths within each plot.

We collected samples from plant-associated soils at the base of grasses (referred to as plant soils hereafter) and unvegetated interspaces and analyzed these samples separately. Both plants and microbes make extracellular enzymes and our methods could not distinguish if the enzymes we measured were produced by plants or microbes. Because the majority of grass roots occur directly under aboveground biomass (Burnett et al. 2012), the much lower root biomass in interspaces allowed us to use interspace soils as a proxy for predominantly microbial-generated enzymes.

To measure soil enzymatic response to precipitation variability, surface soils from 0 – 3 cm were collected one day before and within 4 to 6 h after the first experimental rain event of each month. For each sample, four soil cores (1 cm diameter, 3 cm deep) were collected across each plot and combined for a representative assessment of soils within the plot. Surface litter and an organic layer were absent within the plots and the entire 3 cm deep sample occurred within a soil horizon composed of unconsolidated aeolian deposits (Buxman and Vanderbuilt 2007, Bryan-Ricketts 2012). The upper soil horizon at our study site was 87% sand, with a bulk density of 1.95 g/cm^3 (Bryan-Ricketts 2012). Samples were refrigerated and processed within 48 h of collection to prevent enzyme degradation. Sub-samples were weighed and dried at 60 °C to calculate field soil moisture and then burned at 500 °C for 4 h to determine percent organic matter. The potential enzyme activity levels of alkaline phosphatase (AP), beta-N-acetyl-glucosaminidase (NAG), leucine aminopeptidase (LAP), and beta-glucosidase (BG) were measured fluorometrically and phenol oxidase (PO) chlorometrically following methods of Stursova et al. (2006). AP removes phosphate groups from organic molecules. NAG degrades chitin, producing N-containing glucosamine for microbial consumption. LAP is an aminopeptidase that cleaves amino acids from proteins at the N-terminus, resulting in N-containing amines. BG catalyzes the terminal step in cellulolysis, producing glucose from cellooligosaccharides. PO uses oxygen to oxidize phenolic compounds in more recalcitrant organic matter. Oxidative activity is high in arid mineral soils where oxygen is plentiful, pH is high, and organic matter content low (Sinsabaugh 2010). Potential activity levels for all enzymes were calculated as nmol of product created per hour per gram of OM (nmol h^{-1} gOM^{-1}). Activity levels of PO during August could not be assessed due to laboratory errors. Enzyme assays provide a measure of potential enzyme activity within the soil and tend to overestimate natural activity levels since natural substrates may be larger and more complex than the smaller, uniform test substrates. Although a possible over-estimate of natural enzyme activities, enzyme potentials were uniformly measured throughout the experiment, therefore our assessment of enzyme activites is comparable across treatments and over time.

Data analysis

Variation in soil organic matter content between plant and interspace soils, precipitation regimes, and months were evaluated with an ANOVA. Correlations between enzyme activity levels per gram soil and SOM determined if dynamics of these two soil resources were related. Potential enzyme activity levels through time, location of soil (plant or interspace), and between rainfall treatments were compared with a separate ANOVA for each enzyme (AP, NAG, LAP, BG, PO) for a total of 5 tests. Post-hoc tests were used to find differences when statistical tests were significant. All statistics were run in SAS v9.3 with an $\alpha = 0.05$.

RESULTS

Rainfall manipulations altered soil water content through time (Figure 4.1). Throughout the season, large (30 mm) rain events lead to deeper soil moisture but longer intervening dry periods between events than the more frequent small (10 mm) rain events. Organic matter content changed through time ($p = 0.002$, $F_{5, 101} = 4.06$) and was higher in plant soils than interspace soils ($p = 0.001$, $F_{1, 101} = 11.33$; Table 4.1). Although statistically different, the magnitude of change in OM through time was 0.002 gOM/g soil and likely not biologically significant. OM also did not differ statistically between precipitation regimes ($p = 0.3$). Enzyme

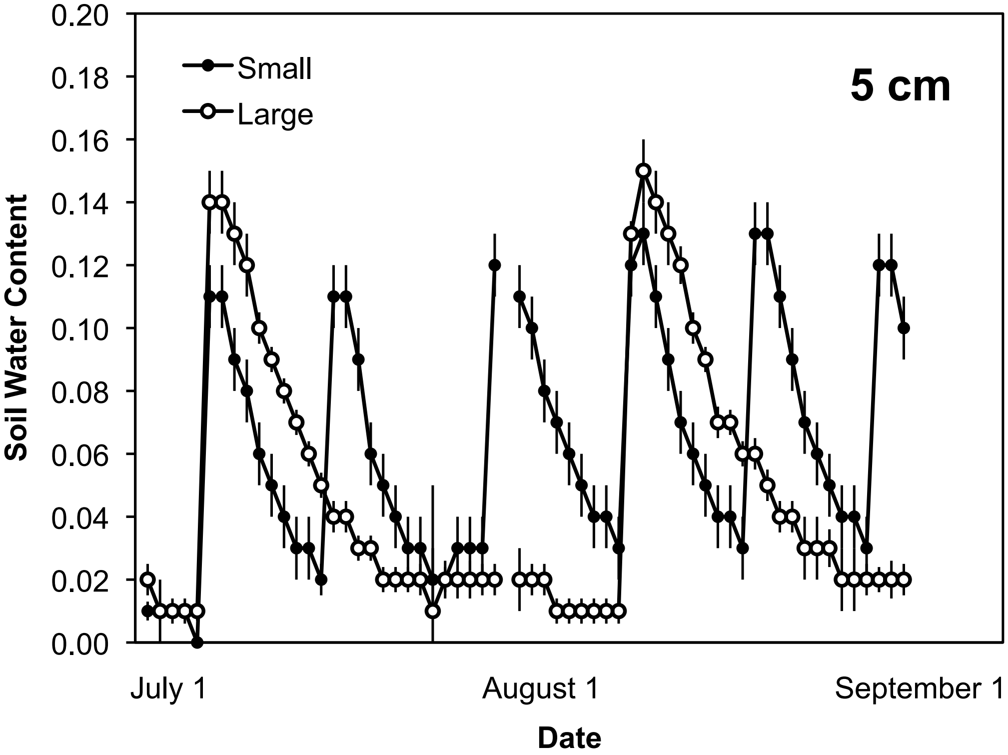


Figure 4.1 Daily soil water content of large, infrequent (30mm/month; open circles) and small, frequent (10mm/10days; black circles) rainfall treatments at 5 cm depth. Error bars indicate ± 1 S.E.

Table 4.1 Monthly mean (± 1 S.E.) soil organic matter content (g OM/g soil).

Location	Rainfall treatment	July	August	Sept	Seasonal Mean
Plant	*large, infrequent*	0.011 ± 0.001	0.013 ± 0.0009	0.010 ± 0.0007	0.011 ± 0.0007
	small, frequent	0.012 ± 0.0004	0.012 ± 0.0005	0.011 ± 0.0004	0.012 ± 0.0006
Interspace	*large, infrequent*	0.009 ± 0.001	0.011 ± 0.0009	0.008 ± 0.0006	0.009 ± 0.0003
	small, frequent	0.011 ± 0.001	0.011 ± 0.0004	0.009 ± 0.0009	0.010 ± 0.0005

activities and SOM were weakly, positively correlated in plant-associated soils and generally uncorrelated in interspace soils (Table 4.2).

Soil enzyme activities changed through time, with potential activities of each hydrolytic enzyme increasing throughout the season (Table 4.3, Figure 4.2 & 4.3). Increases in enzyme activities ranged from 35% to 400% between July and September. Hydrolytic enzyme activities were higher under plants than interspace soils, but activities followed similar temporal patterns in both soil locations. (Table 4.3, Figure 4.2 & 4.3). Enzyme activities increased following both small and large precipitation treatments (Figure 4.2 & 4.3), and temporal patterns and magnitudes of enzyme activities did not vary between precipitation regimes. The time*location interaction was not statistically significant for any enzyme, therefore changes in enzyme activites through time were not different between plant and interspace soils (Figure 4.2 & 4.3).

DISCUSSION

Seasonal dynamics of enzyme activities should reflect the availability of their substrates (Hernández and Hobbie 2010), and enzyme activities increased during the season presumably in response to both rainfall and changing plant-microbe associations. Soil OM content did not change much over the growing season, as expected, but C:N:P ratios in the soil could have changed through the season, which could also influence enzyme activities (Bell et al. 2013). Hydrolytic enzyme activities were relatively low at the beginning of the monsoon season when plants were more or less dormant. Following the onset of monsoon

Table 4.2 Correlation coefficients between extracellular enzyme activities (nmol/h/g soil) and soil OM (g/g soil) in plant associated and interspace soils. Enzymes include alkaline phosphatase (AP), beta-N-acetyl-glucosaminidase (NAG), leucine aminopeptidase (LAP), and beta-glucosidase (BG).

Enzyme	Plant	Interspace
BG	0.22	-0.07
AP	0.33	-0.05
NAG	0.32	-0.11
LAP	0.31	-0.14

Table 4.3 P-values associated with separate ANOVAs for each extracellular enzyme which compared potential enzyme activities between time (pre- and post- rain event in July, August, and September), location (plant, interspace) and Rain treatment (large infrequent, small frequent).

Enzyme	Variable		
	Time	Location	Rain trt
AP	<0.0001	<0.0001	n.s.
BG	<0.0001	<0.0001	n.s.
LAP	<0.0001	n.s.	n.s.
NAG	<0.0001	<0.0001	n.s.
PO	0.0005	0.02	n.s.

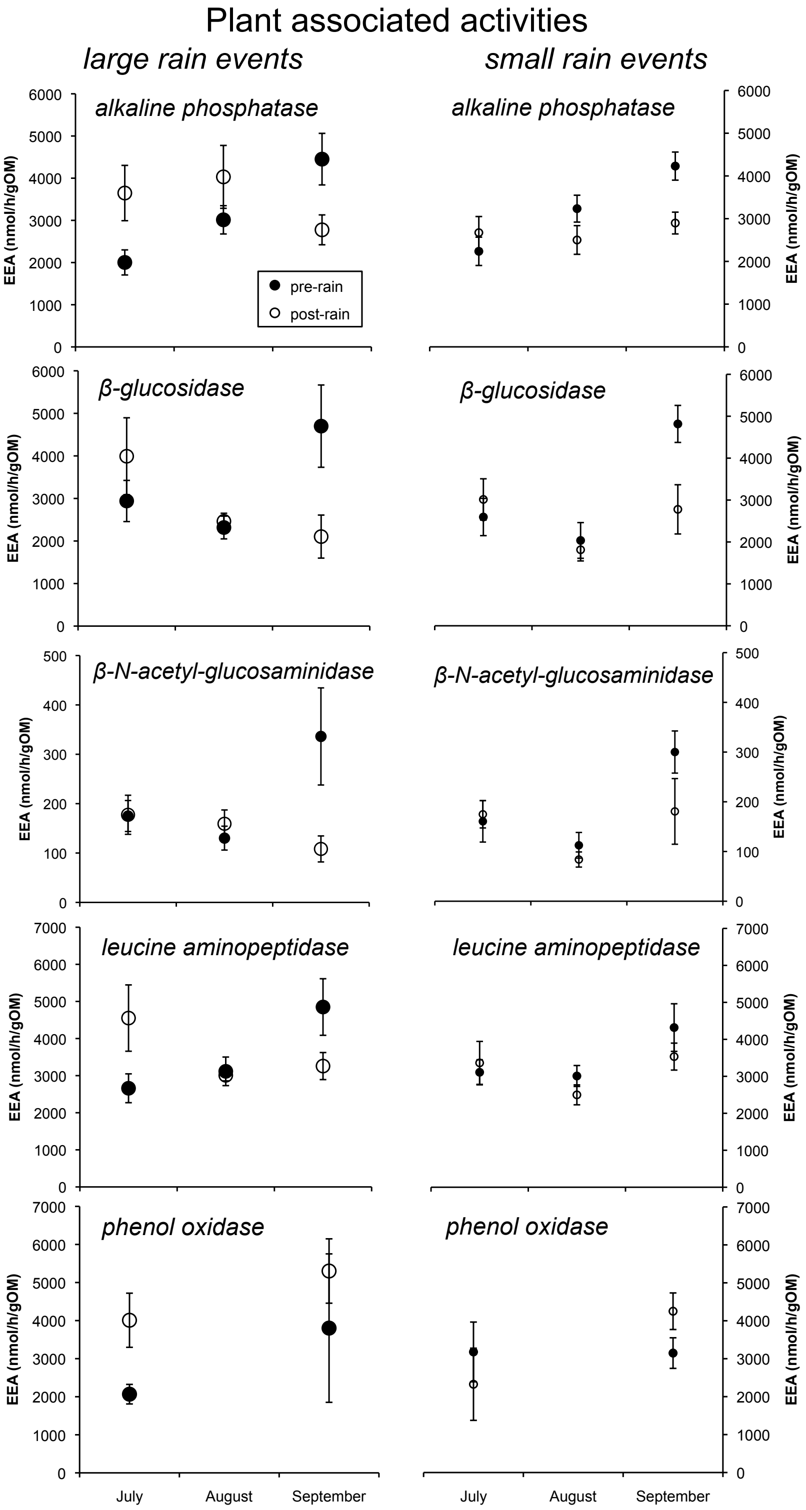


Figure 4.2 Potential enzyme activity levels for each enzyme within plant associated soils following large, infrequent (left) and small, frequent (right) precipitation events. Activity levels before (black circles) and after (open circles) rain events are graphed through time. Error bars represent ± 1 S.E.

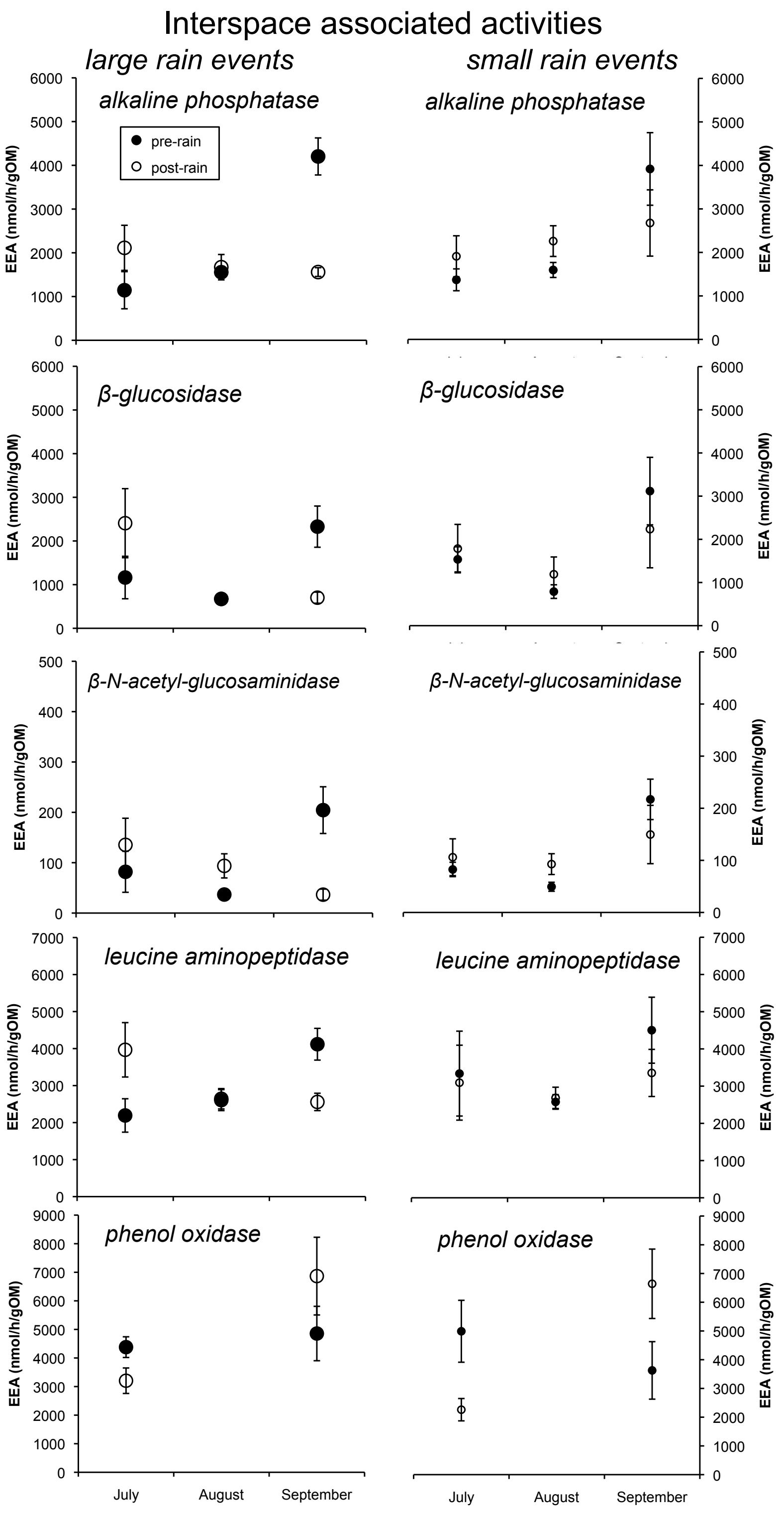


Figure 3 Potential enzyme activities within interspace soils following large, infrequent (left) and small, frequent (right) precipitation events. Activity levels before (black circles) and after (open circles) rain events are graphed through time. Error bars represent ± 1 S.E.

watering, plants rapidly upregulated photosynthesis, peaking 4 - 5 days following a rain event (Thomey 2012), and likely exuded labile compounds through roots and plant residue (Geisseler et al. 2011), which have been hypothesized to drive rapid pulses in soil respiration following rain events (Vargas et al. 2012). Increases in labile compounds and soil moisture activate microbes and stimulate enzyme production (Dorodnikov et al. 2009, Gonzales-Polo and Austin 2009), and enzyme activities increased shortly after early season rainfall. As the season progressed, enzyme activity levels were maintained and microbes also presumably had a reliable carbon source from active plants (Thomey 2012). At the end of the season, soil nutrient resources presumably change as root production of the dominant grass decreases (Burnett et al. 2012), and enzyme activities greatly decreased following the final rain event. Our assays could not determine if activities were of newly created or reused enzymes in the soil, but lower enzyme production could have contributed to the significant decrease in potential enzyme activities within hours of the final rain event. Depleted soil resources could have made it unnecessary for soil organisms to create new hydrolase enzymes late in the season. In additon to creating fewer enzymes, enzymes may have leached from the active layer or been broken-down and utilized for nutrient sources.

The temporal pattern of potential enzyme activities throughout the season was similar between plant and interspace soils, indicating that responses were not solely driven by plant interactions. Grass roots generally do not extend past the aboveground canopy (Burnett et al. 2012) and plants utilize resources in interspace soils via fungal connections between interspace soils to plant roots (Green et al. 2008, Marusenko et al. 2013). Although our methods cannot distinguish whether enzymes were created by plants or microbes, interspace enzyme activities were a proxy for primarily microbial generated enzymes due to this spatial separation in plant roots. The primary difference between plant and interspace soils was consistently higher hydrolase and lower oxidase activities under plants, presumably due to increased labile compounds under plants (Gonzales-Polo and Austin 2009). Plant-generated enzymes could also have increased total enzyme activity levels under plants, although the magnitude to which plants contribute to soil enzyme pools remains largely unknown.

Curiously, potential enzyme activities followed similar temporal patterns in both rainfall treatments. The frequency and intensity of dry-rewetting cycles can influence nutrient availability and microbial function (Chowdhury et al. 2011). Long droughts can trap nutrients in SOM or on carbonate (Ippolito et al. 2010) while frequent rain events increase nutrient availability in the soil (Fierer and Schimel 2003, Butterly et al. 2009). Longer droughts create nutrient limitations at both wetter (Tiemann and Billings 2011) and drier (Yahdjian and Sala 2010) sites, and infrequent large rain events increase soil microbial metabolism more than frequent small rain events in grasslands at the SNWR (Vargas et al. 2012). Yet temporal changes in enzyme activities were simlar under both precipitation regimes. Possibly no treatment differences occurred because our treatments delivered average monthly precipitation and soil microbes did not experience extensive drought. Microbes in arid ecosystems are not necessarily better adapted for functioning at low soil moisture relative to microbes in mesic systems. Both require adequate soil moisture to function (Manzoni et al. 2012). Total amount of monsoon precipitation may be more influential than the distribution pattern of precipitation events on potential enzyme and soil microbial activities (Herrera et al. 2011).

Desert biota respond to precipitation in a pulse-reserve manner (Reynolds et al. 2004, Collins et al. 2008) and if extracellular enzyme activities follow pulse-reserve dynamics, we would expect reserves (i.e. potential enzyme activities) to increase and remain high following a rainfall pulse. Our results are not consistent with this expectation. Instead extracellular enzyme activities followed pulse-driven dynamics, with rainfall stimulating pulses in enzyme activities but not building reserves of enzymes in the soil. Early in the season, enzyme activities had a rapid response to moisture pulses and nearly doubled activity within 4 - 6 h of July rain events. Reponses to rain events slowed mid-season, indicated by the absence of increased activities 4 - 6 h after the August rain and instead significantly higher enzyme activities 30 days later (i.e. before the September rain). Although enzyme reserves did not continually build throughout the season, enzymes remained present in the soil throughout the season. Overall, water availability increased hydrolytic enzyme activities through the first two months of the monsoon season, and as the season ended, enzyme activity levels decreased to initial seasonal levels. Similar pre- and post-monsoon season enzyme activities have been observed elsewhere in the Chihuahuan desert (Bell et al. 2009), but our enzyme measurements associated with individual rain events highlight the variable enzyme activities following rain events over the monsoon season.

CHAPTER 5:

DIFFERENTIAL RECOVERY THROUGH DESERT SHRUBLANDS FOLLOWING AN EXTREME COLD EVENT

ABSTRACT

Woody encroachment into grasslands is a worldwide phenomenon partially influenced by climate change. One component of climate change is a greater occurrence of extreme events. *Larrea tridentata* is common shrub throughout the warm deserts of North America that is currently encroaching into neighboring grasslands. The distribution of *L. tridentata* is partially limited by cold temperatures and extreme winter events might limit shrub expansion. We examined the response of *L. tridentata* to an extreme cold event when air temperatures fell to -31 °C, 20 °C below the long-term average low temperature for February. Canopy die-back and recovery were measured for 1000 individual *L. tridentata* shrubs growing at their northern range margin in Chihuahuan Desert shrublands in central New Mexico, USA. The initial response of *L. tridentata* was a nearly complete loss of canopy vegetation across shrubland and shrub-grassland ecotone regions. Although canopy loss was high, mortality was low and 99% of shrubs resprouted during the following year. Regrowth was faster in grassy ecotones than dense shrublands. After three years of recovery, *L. tridentata* canopies had regrown on average 20 to 85% of the original pre-freeze canopy sizes. Therefore, this extreme cold event temporarily decreased shrubland biomass but did not appear to slow or reverse shrub expansion.

INTRODUCTION

Throughout the world, woody vegetation is encroaching on herbaceous-dominated systems, often transforming grasslands to shrublands. Ecological impacts and social perceptions of shrub encroachment vary widely. Negative effects include decreased plant cover and diversity (Báez & Collins 2008, Ratacjzak et al. 2012), increased soil erosion and resource heterogeneity (Schlesinger et al. 1990, Turnbull et al. 2010a,b), increased nighttime temperatures (D'Odorico et al. 2012a), decreased faunal diversity (Menke 2003, Sirami et al. 2009), loss of C (Jackson et al. 2002), and less available forage for livestock (Passera et al. 1992). In contrast, positive effects of the conversion of grasslands to shrublands can include increased faunal abundance and diversity (Whitford 1997, Dettmers 2003, Fuller & DeStefano 2003, Ceballos et al. 2010), increased plant diversity (Troumbis & Memtsas 2000, Eldridge et al. 2011), reversal of desertification (Maestre et al. 2009), and more reliable C sinks during drought (Eldridge et al. 2011). Whether perceived as positive or negative, human activities interact with climate change to facilitate shrub encroachment in grasslands worldwide (Fredrickson et al. 2006, Briggs et al. 2007, Van Auken 2009). In the context of alternative stable states, conversion of grassland to shrubland is generally considered to be irreversible over ecological time frames (D'Odorico et al. 2012b).

Winter climate is changing in a variety of ways and experimental manipulations help examine the response of ecological systems (Kreyling 2010). Snow manipulations test for the ecological consequences of altered winter precipitation (Kreyling et al. 2012), and warming manipulations track ecosystem changes following gradual increases in temperature (Collins et al. 2010), yet our understanding of the response of plant communities to winter climate extremes is limited to opportunistic studies following extreme climate events, as large-scale cooling experiments are not practical. For example, ice storms in hardwood forests can temporarily increase canopy openness and shift community composition based on the shade-tolerance of species present (Rhoads et al. 2002, Arii & Lechowicz 2007, Weeks et al. 2009, Shao et al. 2011). Intensity of ice damage on individual trees can relate to the size of individuals and amount of ice accumulation (Stueve et al. 2007, Hook et al. 2011). Examples of how winter climate extremes influence natural communities are largely limited to snow and ice storm events in forests and it is unclear how rare winter events, such as extreme cold, shape community structure and functioning, especially in non-forested habitats.

Larrea tridentata (creosote bush) is an ideal species for studying relationships between shrub encroachment and changing winter climate. Native to North American warm deserts, *L. tridentata* is present throughout the southwestern U.S. and northern Mexico and alters ecosystem function as it expands into neighboring desert grasslands (Pockman & Small 2010, Turnbull et al. 2011). *Larrea tridentata* has continued to expand northward over the past two Centuries (Kelly & Goulden 2008), presumably due to increasingly warmer climate combined with altered land use practices, Warmer winter temperatures may strengthen the positive microclimate feedback between temperature and shrub cover (D’Odorico et al. 2010, He et al. 2010) and further contribute to range expansion by *L. tridentata*. Although many future global changes may support continued encroachment of *L. tridentata*, periodic extreme cold events may delay or even reverse shrub expansion. Although *L. tridentata* commonly experiences sub-freezing temperatures, low temperatures are thought to influence the northern range boundary of this species (Pockman & Sperry 1997, Martinez-Vilalta & Pockman 2002, Mederios et al. 2012). *Larrea tridentata* shrublands are year round carbon sinks (Anderson-Tiexiera et al. 2011), yet cold temperatures increase leaf folding, thus decrease leaf area, and severely reduce photosynthesis rates at temperatures below zero (Gutschick & BassiriRad 2003, Naumburg et al. 2004). Based on laboratory trials, cold temperature can be lethal to young *L. tridentata* plants, with -20 ˚C causing cell lysis and xylem cavitation in nearly all young plant stems (Pockman & Sperry 1997) and -24 ˚C causing 100% mortality of one-year old seedlings (Medeiros & Pockman 2011). Anecdotal observations following an extreme freeze in the 1930s indicated massive canopy die-back (Cottam 1937) and recovery (Fosberg 1938) of *L. tridentata* throughout the upper Sonoran Desert, yet quantitative evaluation of shrub response to natural extreme cold events is lacking.

We took advantage of a natural extreme cold event to examine how *L. tridentata* individuals responded to extreme cold at a scale unapproachable by previous lab or field manipulations. During February 2011, temperatures fell to 20°C below the 20-year average low temperature for February and remained below average for a week. A cold event of this magnitude occurs roughly every

40 years. This event allowed for the examination of naturally cold-adapted, mature plant response within both mature shrublands and shrub-grassland ecotones. Our specific research questions included: 1) Do individuals in dense shrublands and sparsely populated ecotones respond differently to an extreme cold event, and 2) if extreme cold does not kill shrubs, how long does it take shrub canopies to recover from initial cold damage?

METHODS

Study Site

This research was conducted at the Sevilleta National Wildlife Refuge (SNWR; 34.3N, 106.8W) located in central New Mexico, U.S.A. SNWR is also the site of the Sevilleta Long Term Ecological Research (LTER) program, which provided detailed long-term, site-specific climate data (http://sev.lternet.edu). Several ecosystems occur within the SNWR, including the northern extent of Chihuahuan Desert grasslands and shrublands, dominated by *Bouteloua eriopoda* and *L. tridentata*, respectively. Research was conducted in *L. tridentata* shrublands and ecotone regions co-dominated by shrubs and grasses. Annual precipitation over the past 22 years averages 240±14 mm with approximately 60% falling as large summer monsoon events (Pennington & Collins 2007; Petrie et al. 2014). Average annual temperature is 13.2 °C with highest average monthly temperatures in June, 33.4 °C, and lowest in January, 1.6 °C (Muldavin et al. 2008). Between 2001 and 2010, minimum air temperature (T_{min}) was -20 ˚C within *L. tridentata* shrublands (Figure 5.1a). Regionally, 100 year temperature

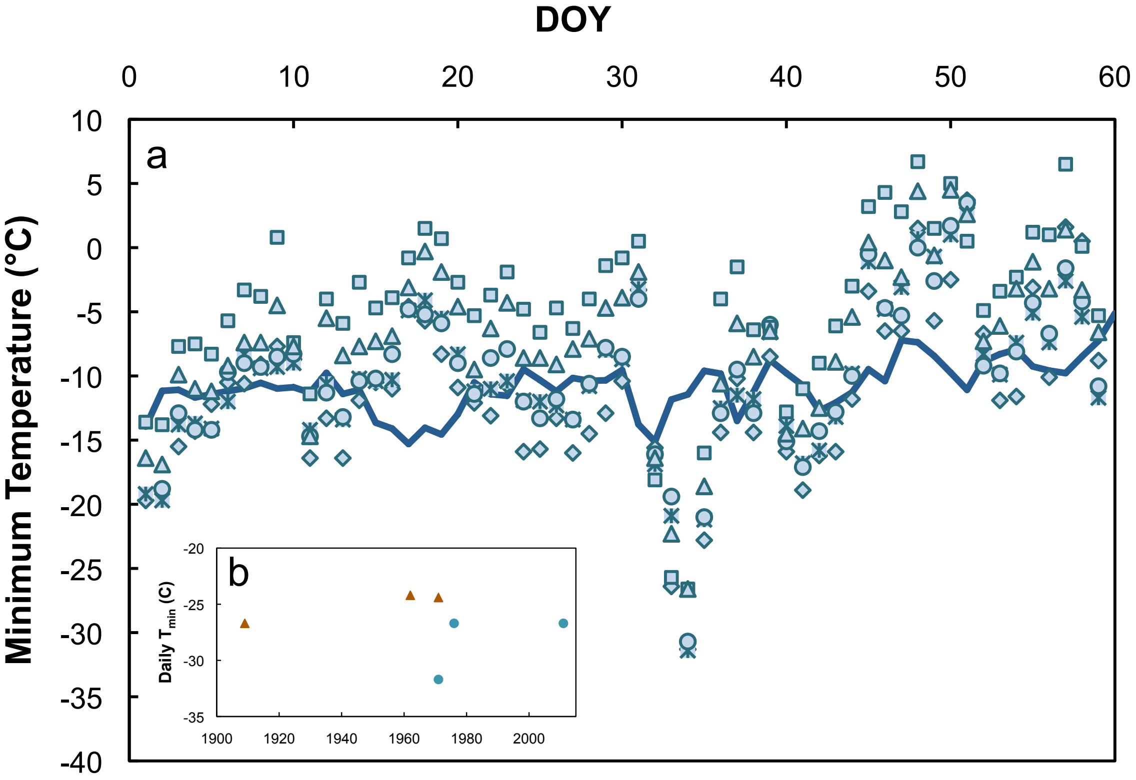


Figure 5.1 a) Average long-term daily T_{min} (solid line) across the sites for the first 60 days of the year (DOY). Points on the graph indicate daily T_{min} from each of the six survey sites, each site indicated by a different shape. b) Longer-term regional data from locations north (Los Lunas, NM; circles) and south (Soccorro, NM; triangles) of the SNWR indicating times when daily T_{min} fell below -24 °C.

records from the two closest U.S. Historical Climatology Network Data sites (http://cdiac.ornl.gov/epubs/ndp/ushcn.html; Los Lunas, NM, 60 km N and Socorro, NM, 30 km S), indicated extreme cold events below -24°C, the temperature of 100% mortality of *L. tridentata* juveniles in the greenhouse (Medeiros & Pockman 2011), occurred roughly every 25 to 40 years (Figure 5.1b). During early February 2011, minimum low temperatures fell well below average for several days, reaching the lowest levels on February 3, 2011 when T_{min} ranged from -26 to -31 °C across SNWR (Figure 5.1a).

Field surveys

Observation plots were established at five sites across SNWR to examine shrub response to extreme cold with regard to variation in T_{min} and shrub density. Criteria for site selection included the presence of *L. tridentata*, flat terrain, close proximity to existing meteorological station, and variation in both shrub density and T_{min} among sites. Circular plots (20m diameter) were established at each site and all shrubs within the plots were measured immediately following the cold event and annually for three years thereafter. At least 200 individual shrubs were evaluated at each site and the number of plots per site varied with shrub density. Five sites were established and ST and SG were within dense shrublands while Met, Mix, and West sites were in grass-shrubland ecotone sites with lower shrub density and greater grass cover.

Leaves turned brown but persisted on canopy branches for many months after the cold event, therefore I could measure pre-freeze canopy dimensions after the extreme event and estimate percent canopy death. Dead leaves were brown and broke into pieces when lightly pinched by hand. The percentage of death within the canopy was estimated in canopy death classes (no canopy death, 1-25%, 25-50%, 50-75%, 75-99% and 100% canopy death). One researcher performed all canopy estimates to increase consistency of measurements. Canopy volume, estimated by calculating the volume of an inverted cone, is correlated with biomass (Ludwig et al. 1975) and was our measure of canopy size. Canopy measurements included height, maximum horizontal width, and the perpendicular width. Presence/absence of seeds was also recorded to determine if shrubs were reproductive during recovery. Initial surveys were conducted in early spring 2011 (March and April) and annually thereafter for the following three winters.

Data Analysis

An analysis of covariance (ANCOVA) was used to examine variation in canopy die-back among sites, with pre-freeze shrub volume as a co-variate to account for differences based on size. Recovery was measured as percent change in canopy volume compared to initial conditions ($\mathrm{Volume}_{Yn}/\mathrm{Volume}_{Y0}$) and was compared between sites and years with an ANCOVA with initial pre-freeze canopy volume as a covariate. When statistical differences occurred, a Tukey post-hoc test was used to locate differences. Statistical analyses were performed using SAS v9.3 and an $\alpha=0.05$ was used to determine significance.

RESULTS

Initial canopy mortality of *L. tridentata* was extensive, and all shrubs experienced some degree of canopy die-back. Of the 995 shrub individuals surveyed, nearly all (99%) had ≥ 50% die-back. Canopy die-back varied among sites ($F_{4,952} = 59.7$, $p<0.0001$) but was unrelated to specific T_{min}. Rather, similar levels of die-back occurred at sites where T_{min} ranged from -26 to -31°C (Figure 5.2). Canopy mortality was related to shrub density, and the two sites with high shrub density experienced significantly more die-back than the three other sites (Figure 5.2). Canopy die-back was also significantly related to pre-freeze canopy volume ($F_{1, 952} = 10.46$, $p = 0.0013$). A significant interaction between site and initial volume with regard to die-back indicated shrub size was only related to canopy die-back at some sites ($F_{4, 952} = 7.63$, $p<0.0001$; model $F_{9, 952} = 55.18$, $p <0.0001$, $r^2 = 0.34$). Separate regressions between canopy die-back and initial volume were run for each site to understand this interaction and the only site with a significant regression was Mix ($F_{1, 176} = 31.71$, $p <0.0001$, $r^2 = 0.15$, $\beta = -0.85$).

Shrub mortality following the extreme cold event was exceptionally rare. During the first year of recovery, only 3 of the 995 shrubs did not have new growth. Canopy recovery varied among the sites ($F_{4, 2549} = 13.52$, $p <0.0001$) and was higher at the three ecotone sites (Met, Mix, West) which had lower shrub density and greater grass cover than shrubland sites (Figure 5.3). Recovery was also greatest during the third year of recovery ($F_{2, 2549} = 10.71$, $p <0.0001$; model $F_{15, 2549} = 6.34$, $p <0.0001$, $r^2 = 0.04$), and the year by site interaction was not statistically significant. Initial shrub size was also related to canopy regrowth

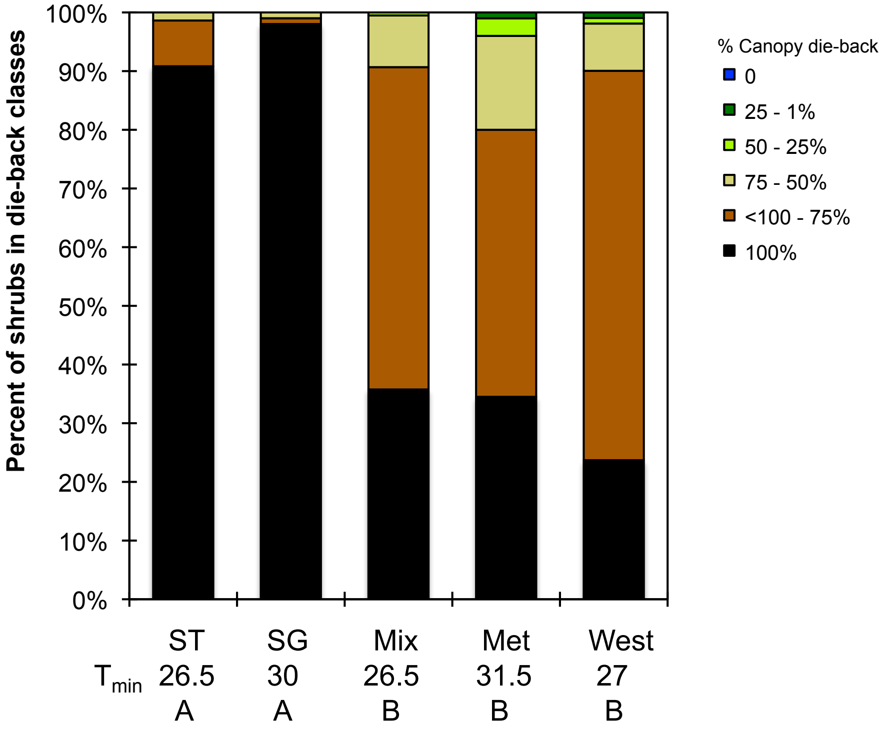


Figure 5.2 Canopy die-back based on the percentage of shrubs at each site in each canopy die-back class. Roughly 200 individuals were examined at each site. Sites are ordered based on number of plots per site, an indicator of shrub density, with shrub density decreasing from left (ST) to right (West). Low temperatures (°C) are indicated below the site names. The letters indicate significant differences in canopy death between sites.

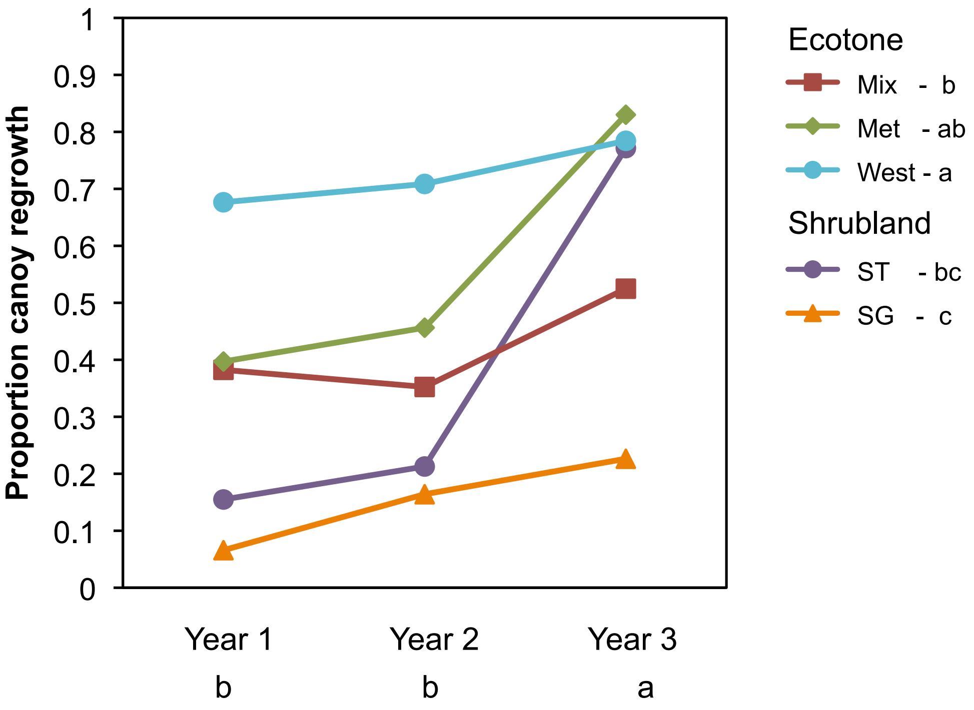


Figure 5.3 Mean proportion canopy regrowth ($Volume_{Yn}/Volume_{Y0}$) of individual shrubs for three years of recovery. Each line represents a different site. Letters next to each year or site represent statistical differences based on Tukey post-hoc tests.

($F_{1,\,2549} = 16.38$, $p<0.0001$) and based on a separate regression for each year, there was a negative relationship between size and regrowth during the second and third year of recovery (Year 2, $F_{1,\,853} = 18.0$, $p < 0.0001$, $\beta = -0.075$, $r^2 = 0.02$; Year 3, $F_{1,\,853} = 4.33$, $p = 0.03$, $\beta = -2.08$, $r^2 = 0.005$). Seed set varied among sites (Figure 5.4) and ranged from 0.5 to 82% of shrubs producing seeds during the first year of recovery. Plot level recovery was also faster in the ecotone, but average area of shrub cover was similar between all sites after three years of recovery (Figure 5.5).

DISCUSSION

Shrubs responded strikingly to the extreme cold event. Most individuals experienced nearly complete loss of canopy vegetation similar to that reported for the cold event in the 1930's (Cottam 1937, Fosberg 1938). Although below-average temperatures triggered canopy damage, minimum temperature alone did not explain the variation in degree of die-back among the surveyed populations (Figure 5.2). The site that experienced the lowest T_{min} also had relatively low canopy damage, therefore factors beyond minimum temperature influenced the degree of canopy die-back within sites.

Shrublands are generally warmer than both neighboring grasslands and ecotones (D'Odorico et al. 2010), but T_{min} during the extreme event was unrelated to shrub density. Therefore the positive feedback between shrub encroachment and temperature (D'Odorico et al. 2010, He et al. 2010), was not enough to buffer *L. tridentata* from extreme cold, and several days of extreme

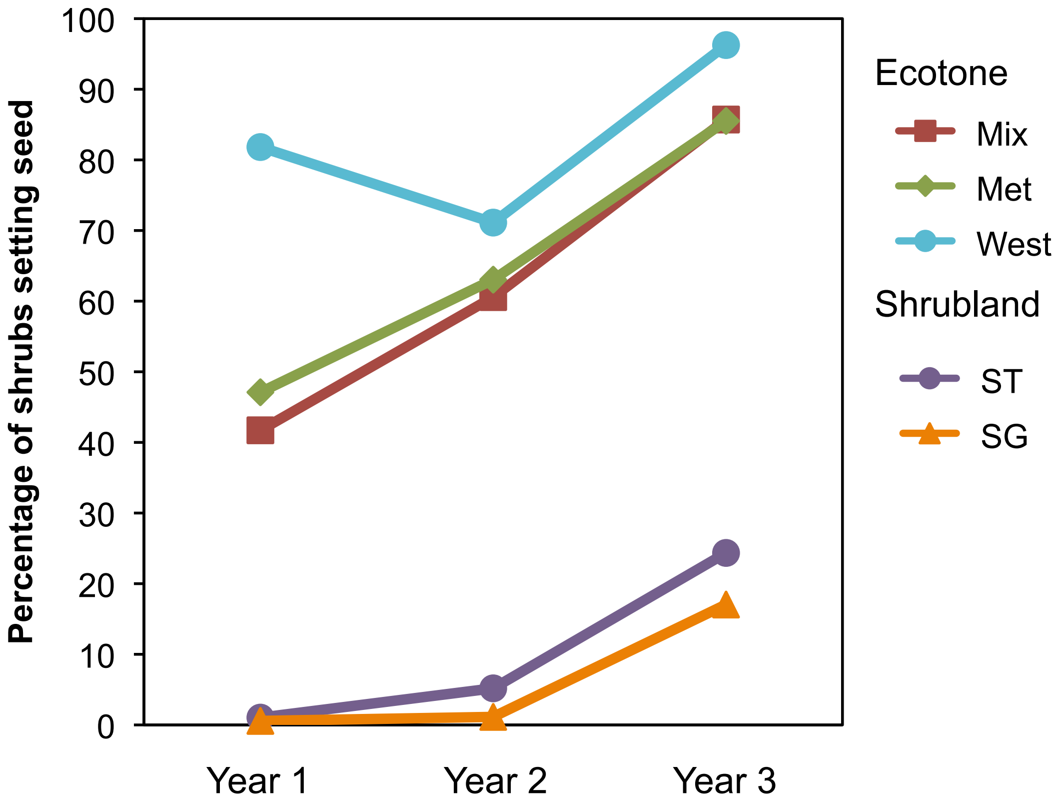


Figure 5.4 Percentage of shrubs at each site setting seeds during the three years following the extreme cold event. Each site is represented with a different line.

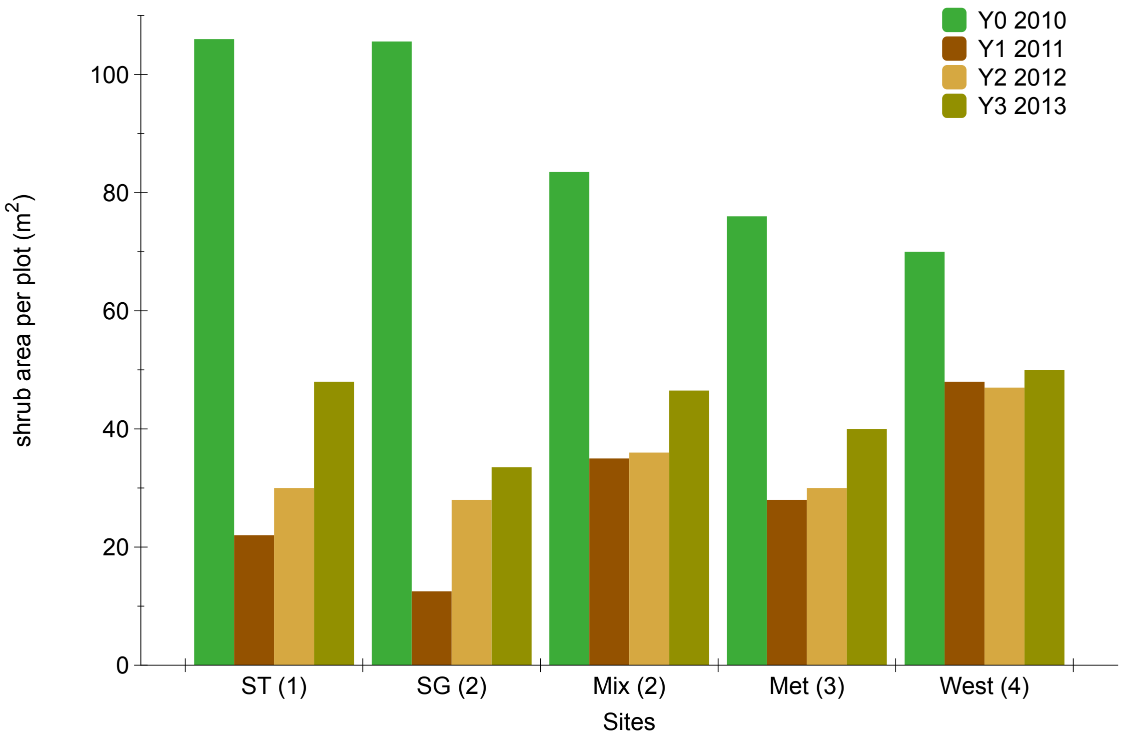


Figure 5.5 Average total cover of shrubs within each 314m^2 plot. The number of plots per site is indicated in parenthesis. Sites are ordered based on shrub density, from the most dense shrublands (ST) to least dense ecotone (West).

cold temperatures presumably overwhelmed positive temperature feedbacks within shrublands. Shrubs may benefit from temperature feedbacks during average conditions, but the advantage disappears during extreme events. Initial canopy die-back was related to shrub density, as shrubs in the high-density sites experienced more extreme die-back. Canopy size likely influenced this response, as smaller shrubs are more vulnerable to stress, such as drought (Reynolds et al. 1999). Ecotone shrubs were generally larger and had less extensive canopy mortality. However size was only negatively related to canopy die-back at one site and only accounted for a small percentage (6 - 14%) of the variation in die-back, therefore the response was not completely driven by plant size.

Cold temperatures led to extensive canopy die-back but not complete shrub mortality. After three years of recovery, shrubs covered 40% of the area they previously covered in the shrublands, and 63% of the area in ecotones (Figure 5.5). The variation in regrowth between shrublands and ecotones was likely influenced by greater stem tissue damage in shrublands. Height of green during the first year suggested if shrubs regrew via branch resprouting or basal regrowth, and the majority of new growth in shrublands was basal resprouting (mean ±S.D. height 30 ±17cm) while ecotone shrubs largely grew from existing branches in addition to basal regrowth (mean ±S.D. height 76 ±30cm). Branch resprouting individuals also tended to set seed within the first year, therefore in addition to viable vegetative buds, floral buds were also not damaged. Location of regrowth also influenced canopy dimensions as shrubs with only basal regrowth had small, dense canopies while shrubs with branch resprouting had larger, more dispersed canopies.

Canopy volumes continued to increase through time and within three years after the cold event, 12% of the shrubs had completely recovered to pre-freeze canopy volumes. It is unclear how long complete recovery will take, but the timing may be similar to recovery from other disturbances. For example, after repeated vehicle damage, *L. tridentata* experienced no mortality and canopy size recovered within 5 years (Gibson et al. 2004). Resprouting patterns of *L. tridentata* are also linked to disturbance severity (Bellingham & Sparrow 2000). Since shrubland individuals experience more severe damage, they will presumably take longer to fully recover than ecotone individuals. Rate of recovery is also presumably influenced by soil moisture availability, with greater soil moisture leading to faster recovery. The cold event occurred during a prolonged drought, and drought not only slows recovery of *L. tridentata* following disturbance (Gibson et al. 2004) but can intensify the influence of extreme temperatures (Hamerlynck et al. 2000). Even though *L. tridentata* is more drought-resistant than other desert shrubs (McAuliffe & Hamerlynck 2010), extensive drought can lead to *L. tridentata* mortality (Bowers 2005). Both drought and cold temperatures initially decrease plant performance, but can also increase the stress-tolerance of individuals to future stressful events (Medeiros & Pockman 2011). Soil moisture on average is lower in shrublands than ecotones (Bhark & Small 2003), therefore shrubland individuals may be more drought stress-adapted than ecotone shrubs, yet the opposite pattern in cold-damage was observed. Instead, the slightly cooler average temperatures in ecotones might have conditioned ecotone individuals to colder temperatures which increased their resistance to the extreme cold event.

With regard to shrub encroachment, a single extreme cold event may have limited impacts on colonization of *L. tridentata* in neighboring grasslands. Even when coupled with long-term drought, established shrubs did not die from this extreme cold event. Additionally during the first year of recovery when canopies were a fraction of their initial size, the majority of ecotone shrubs still produced seeds. High seed set during recovery was not surprising since *L. tridentata* flowers when stressed (Cunningham et al. 1979, Field & Whitford 1988, Sharifi et al 1988). Even though *L. tridentata* seed viability can be low (McGee & Marshall 1993) and successful seedling establishment is rare (Ackerman 1979), seed production following the stressful winter provided the potential for seedling establishment and shrubland expansion. Furthermore, many plant-plant interactions occur belowground, and although air temperatures greatly decreased, soil temperatures remained fairly constant throughout the cold event (unpublished data). Belowground tissues presumably experienced less, if any, damage from the extreme event and therefore would be able to continue competing with surrounding plants. Cold temperatures kill *L. tridentata* seedlings (Medeiros & Pockman 2011) and successful establishment requires ideal conditions (Ackerman 1979, Reynolds et al. 1999) therefore although one event may have limited impacts on shrub expansion, clustered cold events could both decrease mature shrub performance and negate recent establishment events.

Shrubland response to extreme cold was not accurately predicted from existing forest studies. Inherent abiotic differences between forest and shrublands may lead to differential responses of forests and shrublands to extreme winter events. Light is frequently limiting in forests and winter storms create light gaps that allow shade-tolerant species to thrive and community composition to change following the event (Arii & Lechowicz 2007). Meanwhile, light is unlimited, and often harmful, in desert shrublands and reductions in canopy cover would not alter light competition, but might influence other resources, mainly water. Forests recovery to ice storms also varies based on tree composition (Beaudet et al. 2007, Shao et al. 2011) or growth allocation of trees (Pisaric et al. 2008). The only woody species in our shrublands was *L. tridentata*, therefore variable responses between species did not contribute to recovery.

Both climate and plant communities are changing and it is important to examine how communities along ecotones respond to climate variation to understand how community boundaries may change in the future. Understanding the shrubland to grassland ecotone is particularly timely because the irreversible switch from grasslands to shrublands causes ecological and economical concern worldwide (Eldridge et al. 2011). Although periodic and short-lived, extreme events can influence shrubland dynamics differently than gradual, constant changes. Initial response of *L. tridentata* to extreme cold was much more dramatic than initial response to drought (Báez et al. 2013), yet shrubs were quick to regrow, particularly in ecotones. Understanding how influential species, such as *L. tridentata*, respond to extreme events, particularly along transition zones, will help understand the potential for shrub encroachment to continue under future climate change scenarios that include warmer winter minimum temperatures on average, but more frequent extreme events.

CHAPTER 6: CONCLUSIONS

Many abiotic factors regulate plant growth and survival, which ultimately shape plant communities through time and space. Within desert systems, abiotic factors interact with precipitation to collectively influence communities and ecosystem functioning (Figure 6.1). Humans can change the magnitude or timing of practically any abiotic factor and, whether intentional or not, are currently doing so at an unprecedented rate (Vitousek et al. 1997). Four abiotic factors currently influenced by humans were examined in this dissertation, specifically: N addition, fire seasonality, precipitation variability, and extreme cold temperatures.

During drought, grassland communities were influenced by fire but not the timing of fire. Fire reduced plant cover, which took three years to recover to unburned conditions. The recovery of plant cover was largely influenced by the dominant grass, *Bouteloua eriopoda*, which has variable fire recovery response rates linked to water availability (Cable 1965, Drewa and Havstad 2001, Parmenter 2008, Killgore et al. 2009). Regardless of when fire occurred (spring, fall, or summer), fire decreased *B. eriopoda* cover for three years. Fire also temporarily altered community composition. Following fire, forb cover greatly increased and an additional one or two species occurred within the 1 m^2 plots. Although significant, both changes were temporary and only occurred during the year immediately following fire. Overall, fire seasonality did not influence community response to fire. Although, fires were followed by four years of below-average precipitation which likely influenced recovery. Therefore recovery from fire was likely linked to drought, as recovery from fire is often unpredictable and slow in water limited systems (Scheintaub et al. 2009).

The influence of N addition on Chihuahuan Desert grassland communities varied between years and had limited long-term impacts. N additions increased plant productivity during a year with above-average precipitation and led to an almost tripling of forb productivity. Although apparent when present, the impacts of N deposition on aboveground production were absent in years with average or below-average precipitation. Furthermore, belowground productivity, species richness, and community composition were not influenced by N addition, regardless of water availability. In the majority of terrestrial systems, N deposition leads to directional and persistent changes in plant community production (Baer et al. 2003, Stevens et al. 2004, Chalcraft et al. 2008, LeBauer and Treseder 2008) and diversity (Tilman 1987, Rajaniemi 2002, Suding et al. 2005). Yet within this Chihuahuan Desert grassland, N addition did not consistently influence the community, instead N was a secondary limitation and additional N only increased grassland productivity during above-average precipitation.

Although water is the primary limiting factor in semiarid systems, not all communities respond similarly to precipitation fluctuations. Plants are responsive to timing and intensities of current and past precipitation (Ogle et al. 2004), but soil microorganisms may be more responsive to total precipitation rather than distribution patterns, at least with regards to soil extracellular enzyme activities (EEA). Under two different precipitation regimes (many, small rain events or few, large events) EEA changed similarly throughout the monsoon season, increasing after early-season rain and decreasing after late-season rain. Soil enzyme activities were also tied to plant activity, and higher enzyme activities occurred in rhizosphere soils relative to interspace soils. Throughout the season, enzyme activities varied more between rhizosphere and interspace soils than between rain events. Presumably both indirect effects of altered precipitation on plants plus direct effects of precipitation variation influence soil microorganisms. Given the highly connected nature of plant and soil communities (Reynolds et al. 2003, Wardle 2004, Collins et al. 2008, van der Heijden et al 2008) in pulse-driven systems, it is important to understand how soil microorganisms respond to precipitation events.

Shrub encroachment turns grasslands into shrublands, and although an extreme cold event damaged *L. tridentata* shurbs throughout grass- to shrubland transitions, it did not kill shrubs. Therefore, a single cold event had limited impacts on reversing shrub encroachment within this Chihuahuan Desert grassland. Following the cold event, most *L. tridentata* individuals experienced near complete loss of canopy vegetation, but within 6 months most had begun producing new leaves. Less initial damage and faster recovery occurred within grass-shrubland ecotone sites when compared to dense shrublands, therefore providing further support that this single cold event had a limited influence on reversing shrub encroachment. Response of shrubs to extreme cold was likely influenced by water availability (Medeiros and Pockman 2011), but the influence of water availability could not be tested since the cold event occurred during the middle of an extensive, 4-year drought. Although one extreme cold event had limited long-term impacts on shrub encroachment into grasslands, several cold events clustered in time may more effectively restrict shrub encroachment.

Precipitation influences community response to disturbance in dryland systems (Swetman and Betancourt 1998), and the interactive effects of precipitation with other abiotic factors was obvious throughout my dissertation chapters. The primary abiotic limitation to desert productivity is water, and community responses to the fluctuation of other factors, including N addition and fire seasonality, were regulated by water availability. With adequate water availability, secondary resource limitations became apparent. For example, forbs were more responsive than grasses to the combined effects of water and N (Chapter 3) and sub-dominant grasses were less affected than the dominant grass (*B. eriopoda*) by fire during drought (Chapter 2). Although Chihuahuan Desert communities are largely driven by precipitation, some abiotic facters can impact communities regardless of water availability. For example, the response of *L. tridentata* shrubs to an extreme cold event was extensive during drought and, although not directly tested, extreme cold would presumably also damage *L. tridenata* during times of abundant soil moisture. Many abiotic factors influence semiarid plant communities, but water availability plays an important role in the response of Chihuahuan Desert communities to any abiotic disturbance (Figure 6.1).

The natural world is changing in many ways, through climate change and a variety of direct human influences. Community change is inevitable following human alterations therefore it is important to study how communities respond to altered abiotic conditions to help understand current and future natural communities. Semiarid systems are tough systems, composed of species evolved to handle harsh conditions yet they are not impervious to change.

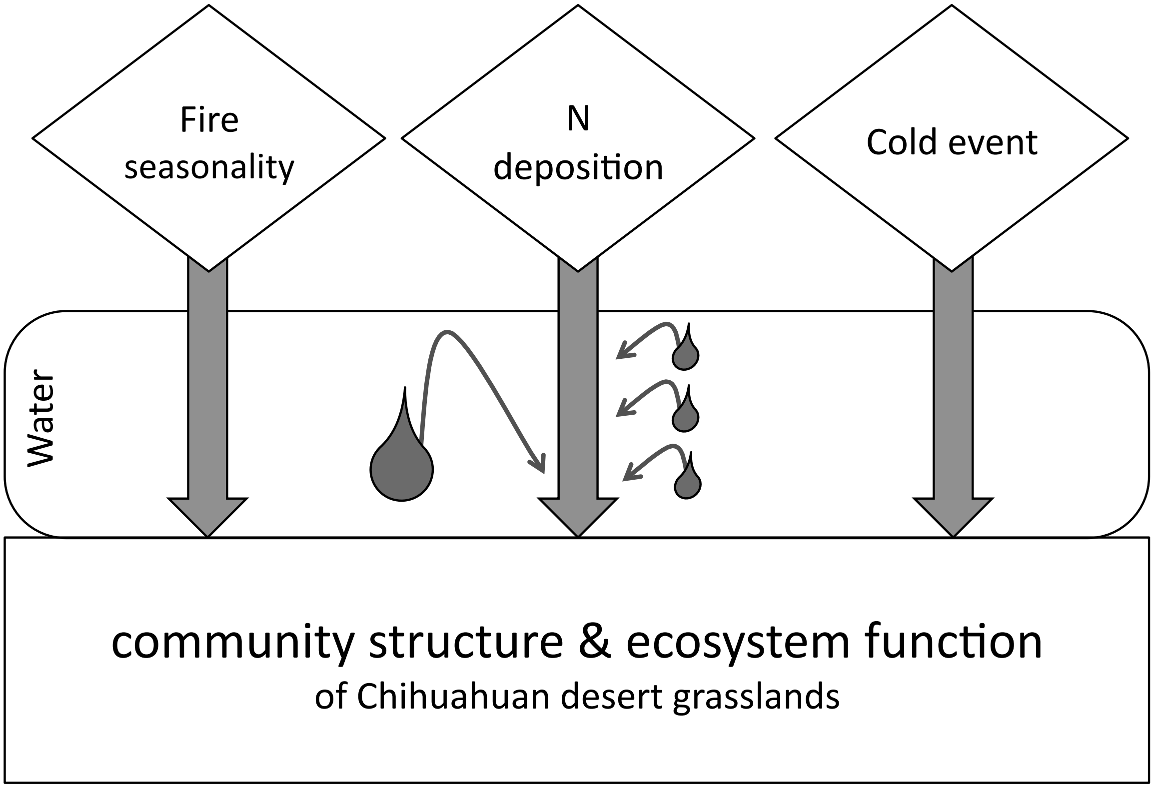


Figure 6.1 Conceptual diagram for how several abiotic factors (diamonds) interact with water availability to influence Chihuahuan Desert grassland community structure and ecosystem function. Water availability changes within and between years. The raindrops and arrows indicate varying effects of within-season precipitation. Some abiotic factors (fire seasonality, N addition) do not influence the community during drought, while other factors (extreme cold) impact communities regardless of soil water condition.

REFERENCES

Abatzoglou JT, and CA Kolden. 2011. Climate change in western US deserts: potential for increased wildfire and invasive annual grasses. Rangeland Ecology and Management **64**:471-478.

Ackerman, TL. 1979. Germination and survival of perennial plant species in the Mojave Desert. The Southwest Naturalist **24**: 399-408.

Allen EB, LE Rao, RJ Steers, A Bytnerowicz, and ME Fenn. 2009. Impacts of atmospheric nitrogen deposition on vegetation and soils in Joshua Tree National Park. *in* Webb RH, Fenstermaker LF, Heaton JS, Hughson DL, McDonald EV, and Miller DM, eds. The Mojave Desert: Ecosystem Processes and Sustainability. Pages 78-100. University of Nevada Press, Las Vegas.

Allen EB, RJ Steers, and SJ Dickens. 2011. Impacts of fire and invasive species on desert soil ecology. Rangeland Ecology and Management **64**:450-462.

Allison SD. 2006. Soil minerals and humic acids alter enzyme stability: implications for ecosystem processes. Biogeochemistry. **81**:361-373.

Anderson MJ. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology **26**:32-46.

Anderson MJ, and CJF Ter Braak. 2003. Permutation tests for multi-factorial analysis of variance. Journal of Statistical Computation and Simulation **73**:85-113.

Anderson-Teixeira KJ, JP Delong, AM Fox, DA Brese, and ME Litvak. 2011. Differential responses of production and respiration to temperature and moisture drive the carbon balance across a climatic gradient in New Mexico. Global Change Biology **17**: 410-424.

Ansley RJ, and MJ Castellano. 2007. Texas wintergrass and buffalograss response to seasonal fires and clipping. Rangeland Ecology and Management **60**:154-164.

Ansley RJ, MJ Castellano, and WE Pinchak. 2006. Sideoats grama growth responses to seasonal fires and clipping. Rangeland Ecology and Management **59**:258-266.

Arii K, and MJ Lechowicz. 2007. Changes in understory light regime in a beech-maple forest after a severe ice storm. Canadian Journal of Forest Research **37**: 1770-1776.

Augustine DJ, JD Derner, and DG Milchunas. 2010. Prescribed fire, grazing, and herbaceous plant production in shortgrass steppe. Rangeland Ecology and Management **63**:317-323.

Austin AT, L Yahdjian, JM Stark, J Belnap, A Porporato, U Norton, DA Ravetta, and SM Schaeffer. 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia **141**:221-235.

Austin AT, and L Vivanco. 2006. Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. Nature **422**:555-558.

Austin AT. 2011. Has water limited our imagination for aridland biogeography? Trends in Ecology and Evolution **26**: 229-235.

Baer SG, JM Blair, SL Collins, and AK Knapp. 2003. Soil resources regulate productivity and diversity in newly established tallgrass prairie. Ecology

84:724-735.

Báez S, SL Collins, D Lightfoot, and TL Koontz. 2006. Bottom-up regulation of plant community structure in an aridland ecosystem. Ecology **87**:2746-2754.

Báez S, J Fargione, DI Moore, SL Collins, and JR Gosz. 2007. Atmospheric nitrogen deposition in the northern Chihuahuan desert: Temporal trends and potential consequences. Journal of Arid Environments **68**:640-651.

Báez S, and SL Collins. 2008. Shrub invasion decreases diversity and alters community stability in Northern Chihuahuan Desert plant communities. Plos One **3**:8.

Báez S, SL Collins, WT Pockman, JE Johnson, and EE Small. 2013. Effects of experimental rainfall manipulations on Chihuahuan Desert grassland and shrubland plant communities. Oecologia **172**:1117-1127.

Beaudet M, J Brisson, C Messier, and D Gravel. 2007. Effects of a major ice storm on understory light conditions in an old-growth *Acer-Fagus* forest: Patterns of recovery over seven years. Forest Ecology and Management **242**: 553-557.

Bell C, N McIntyre, S Cox, D Tissue, and J Zak. 2008. Soil microbial responses to temporal variations of moisture and temperature in a Chihuahuan Desert grassland. Microbial Ecology **56**:153-167.

Bell CW, V Acosta-Martinez, NE McIntyre, S Cox, DT Tissue, and JC Zak. 2009. Linking microbial community structure and function to seasonal differences in soil moisture and temperature in a Chihuahuan Desert grassland. Microbial Ecology **58**:827-842.

Bell C, Y Carrillo, CM Boot, JD Rocca, E Pendall, and D Wallenstein. 2013. Rhizosphere stoichiometry: are C : N : P ratios of plants, soils, and enzymes conserved at the plant species-level? New Phytologist. DOI:10.1111/nph.12531

Bellingham PJ, and AD Sparrow. 2000. Resprouting as a life history strategy in woody plant communities. Oikos **89**:409-416.

Belnap J, and OL Lange. *eds* 2003. Biological soil crusts: structure, function, and management. Springer, Berlin Heidelberg, New York.

Belnap J, JR Welter, NB Grimm, N Barger, and JA Ludwig. 2005. Linkages between microbial and hydrologic processes in arid and semiarid watersheds. Ecology **86**:298-307.

Bhark EW, and EE Small. 2003. Association between plant canopies and the spatial patterns of infiltration in shrubland and grassland of the Chihuahuan Desert, New Mexico. Ecosystems **6**:185-196.

Brandt LA, JY King, SE Hobbie, DG Milchunas, and RL Sinsabaugh. 2010. The role of photodegradation in surface litter decomposition across a grassland ecosystem precipitation gradient. Ecosystems **13**:765-781.

Breshears DD, NS Cobb, PM Rich, KP Price, CD Allen, RG Balice, WH Romme, JH Kastens j, ML Floyd, J Belnap, JJ Anderson, OB Myers, and CW Meyer. 2005. Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Sciences **102**:15144-15148.

Briggs JM, H Schaafsma, and D Trenkov. 2007. Woody vegetation expansion in a desert grassland: Prehistoric human impacts? Journal of Arid

Environments **69**:458-472.

Brockway DG, RG Gatewood, and RB Paris. 2002. Restoring fire as an ecological process in shortgrass prairie ecosystems: initial effects of prescribed burning during the dormant and growing seasons. Journal of Environmental Management **65**:135-152.

Brooks ML. 2003. Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. Journal of Applied Ecology **40**:344-353.

Bowers JE. 2005. Effects of drought on shrub survival and longevity in the Northern Sonoran Desert. Journal of the Torrey Botanical Society **132**:421-431.

Bryan-Ricketts D. 2012. Soil geomorphology of the eastern Sevilleta Long Term Ecological Research site. PhD Dissertation. University of New Mexico.

Burnett SA, JA Hattey, JE Johnson, AL Swann, DI Moore, and SL Collins. 2012. Effects of fire on belowground biomass in Chihuahuan desert grassland. Ecosphere **3**:Article 107.

Butterly CR, EK Bünemann, AM McNeill, JA Baldock, and P Marschner. 2009. Carbon pulses but not phosphorus pulses are related to decreases in microbial biomass during repeated drying and rewetting of soils. Soil Biology and Biochemistry **41**:1406-1416.

Buxman CAZ, and K Vanderbilt. 2007. Soil heterogeneity and the distribution of desert and steppe plant species across a desert-grassland ecotone. Journal of Arid Environments **69**:617-632.

Cable DR. 1965. Damage to mesquite (*Prosopis juliflora)*, Lehmann lovegrass

(*Eragrostis lehmanniana)*, and black grama (*Bouteloua eriopoda)* by a hot June fire. Journal of Rangeland Management **18**:326-329.

Cable DR. 1967. Fire effects on semidesert grasses and shrubs. Journal of Range Management **20**:170-176.

Cable JM, K Ogle, DG Williams, JF Weltzin, and TE Huxman. 2008. Soil texture drives responses of soil respiration to precipitation pulses in the Sonoran Desert: Implications for climate change. Ecosystems **11**:961-979.

Carpenter AT, JC Moore, EF Redente, and JC Stark. 1990. Plant community dynamics in a semiarid ecosystem in relation to nutrient addition following a major disturbance. Plant and Soil **126**:91-99.

Castro HF, AT Classen, EE Austin, RJ Norby, and CW Schadt. 2010. Soil microbial community response to multiple experimental climate change drivers. Applied and Environmental Microbiology **76**:999-1007.

Ceballos G, A Davidson, R List, J Pacheco, P Manzano-Fischer, G Santos-Barrera, and J Cruzado. 2010. Rapid decline of a grassland system and its ecological and conservation implications. Plos One **5**: e8562.

Chalcraft DR, SB Cox, C Clark, EE Cleland, KN Suding, E Weiher, and E Pennington. 2008. Scale-dependent responses of plant biodiversity to nitrogen enrichment. Ecology **89**:2165-2171.

Chowdhury N, RG Burns, and P Marschner. 2011. Recovery of soil respiration after drying. Plant and Soil **348**:269-279.

Clark CM, EE Cleland, SL Collins, JE Fargione, L Gough, KL Gross, SC Pennings, KN Suding, and JB Grace. 2007. Environmental and plant community determinants of species loss following nitrogen enrichment. Ecology Letters **10**:596-607.

Collins SL, RL Sinsabaugh, C Crenshaw, L Green, A Porras-Alfaro, M Stursova, and LH Zeglin. 2008. Pulse dynamics and microbial processes in aridland ecosystems. Journal of Ecology **96**:413-420.

Collins SL, JE Fargione, CL Crenshaw, E Nonaka, JR Elliot, Y Xia, and WT Pockman. 2010. Rapid plant community responses during the summer monsoon to nighttime warming in a northern Chihuahuan Desert grassland. Journal of Arid Environments **74**:611-617.

Cottam WP. 1937. Has Utah lost claim to the lower Sonoran zone? Science **85**:563-564.

Crenshaw CL, C Lauber, RL Sinsabaugh, and LK Stavely. 2008. Fungal control of nitrous oxide production in semiarid grassland. Biogeochemistry **87**:17-27.

Cunningham GL, JP Syvertsen, JF Reynolds, and JM Willson. 1979. Some effects of soil-moisture availability on above-ground production and reproductive allocation in *Larrea tridentata* (DC) Cov. Oecologia **40**:113-123.

Dalgleish HJ, and DC Hartnett. 2006. Below-ground bud banks increase along a precipitation gradient of the North American Great Plains: a test of the meristem limitation hypothesis. New Phytologist **171**:81-89.

Dettinger MD, FM Ralph, T Das, PJ Neiman, and DR Cayan. 2011. Atmospheric rivers, floods and the water resources of California. Water **3**:445-478.

Dettmers R. 2003. Status and conservation of shrubland birds in the northeast US. Forest Ecology and Management **185**:81-93.

Diffenbaugh NS, F Giorgi, and JS Pal. 2008. Climate change hotspots in the United States. Geophysical Research Letters **35**:L16709.

Dijkstra FA, DJ Augustine, P Brewer, and JC von Fischer. 2012. Nitrogen cycling and water pulses in semiarid grasslands: are microbial and plant processes temporally asynchronous? Oecologia **170**:799-808.

D'Odorico P, J Fuentes, WT Pockman, SL Collins, Y He, JS Medeiros, S DeWekker, and ME Litvak. 2010. Positive feedback between microclimate and shrub encroachment in the northern Chihuahuan desert. Ecosphere **1**:Article 17.

D'Odorico P, GS Okin, and B Bestelmeyer. 2012. A synthetic review of feedbacks and drivers of shrub encroachment in arid grasslands. Ecohydrology **5**:520-530.

Donrodnikov M, E Blagodatskaya, S Blagodatsky, S Marhans, A Fangmeier, and Y Kuzyakov. 2009. Stimulation of microbial extracellular enzyme activities by elevated CO_2 depends on soil aggregate size. Global Change Biology **15**:1603-1614.

Drewa PB, and KM Havstad. 2001. Effects of fire, grazing, and the presence of shrubs on Chihuahuan desert grasslands. Journal of Arid Environments **48**:429-443.

Drewa PB, DPC Peters, and KM Havstad. 2006. Population and clonal level responses of a perennial grass following fire in the northern Chihuahuan Desert. Oecologia **150**:29-39.

Dubinin M, A Luschekina, and VC Radeloff. 2011. Climate, livestock, and vegetation: what drives fire increase in the arid ecosystems of southern Russia? Ecosystems **14**:547-562.

Eldridge DJ, MA Bowker, FT Maestre, E Roger, JF Reynolds, and WG Whitford. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecology Letters **14**:709-722.

Ettershank G, J Ettershank, M Bryant, and W Whitford. 1978. Effects of nitrogen fertilization on primary production in a Chichuahuan desert ecosystem. Journal of Arid Environments **1**:135-139.

Evans RD, and JR Ehleringer. 1993. A break in the nitrogen cycle in aridlands? Evidence from δ15N of soils. Oecologia **94**:314-317.

Fenn ME, JS Baron, EB Allen, HM Rueth, KR Nydick, L Geiser, WD Bowman, JO Sickman, T Meixner, DW Johnson, and P Neitlich. 2003a. Ecological effects of nitrogen deposition in the western United States. Bioscience **53**:404-420.

Fenn ME, R Haeuber, GS Tonnesen, JS Baron, S Grossman-Clarke, D Hope, DA Jaffe, S Copeland, L Geiser, HM Rueth, and JO Sickman. 2003b. Nitrogen emissions, deposition, and monitoring in the western United States. Bioscience **53**:391-403.

Fierer N, and JP Schimel. 2003. A proposed mechanism for the pulse in carbon dioxide production commonly observed following the rapid rewetting of a dry soil. Soil Science Society of America Journal **67**:798-805.

Ford PL. 1999. Response of buffalograss (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*) to fire. Great Plains Research **9**:261-276.

Ford PL, and GV Johnson. 2006. Effects of dormant- vs. growing-season fire in shortgrass steppe: biological soil crust and perennial grass responses. Journal of Arid Environments **67**:1-14.

Fosberg FR. 1938. The lower Sonoran in Utah. Science **87**:39-40.

Fredrickson EL, RE Estell, A Laliberte, and DM Anderson. 2006. Mesquite recruitment in the Chihuahuan Desert: Historic and prehistoric patterns with long-germ impacts. Journal of Arid Environments **65**:285-295.

Fuller TK, and S DeStefano. 2003. Relative importance of early-successional forests and shrubland habits to mammals in the northeastern United States. Forest Ecology and Management **185**:75-79.

Galloway JN, FJ Dentener, DG Capone, EW Boyer, RW Howarth, SP Seitzinger, GP Asner, CC Cleveland, PA Green, EA Holland, DM Kari, AF Michaels, JH Porter, AR Townsend, and CJ Vorosmarty. 2004. Nitrogen cycles: past, present, and future. Biogeochemistry **70**:153-226.

Geisseler D, WR Horwath, and KM Scow. 2011. Soil moisture and plant residue addition interact in their effect on extracellular enzyme activity. Pedobiologia **54**:71-78.

Gibson AC, MR Sharifi, and PW Rundel. 2004. Resprout characteristics of creosote bush (*Larrea tridentata*) when subjected to repeated vehicle damage. Journal of Arid Environments **57**:411-429.

Gonzalez-Polo M, and AT Austin. 2009. Spatial heterogeneity provides organic matter refuges for soil microbial activity in the Patagonian steppe, Argentina. Soil Biology and Biochemistry **41**:1348-1351.

Gosz RJ, and JR Gosz. 1996. Species interactions on the biome transition zone in New Mexico: Response of blue grama (*Bouteloua gracilis*) and black grama (*Bouteloua eripoda*) to fire and herbivory. Journal of Arid Environments **34**:101-114.

Gosz JR, DI Moore, GA Shore, HD Grover, W Rison, and C Rison. 1995. Lightning estimates of precipitation location and quality on the Sevilleta LTER, New Mexico. Ecological Applications **5**:1141-1150.

Gough L, CW Osenberg, KL Gross, and SL Collins. 2000. Fertilization effects on species density and primary productivity in herbaceous plant communities. Oikos **89**:428-439.

Green LE, A Porras-Alfaro, and RL Sinsabaugh. 2008. Translocation of nitrogen and carbon integrates biotic crust and grass production in desert grassland. Journal of Ecology **96**:1076-1085.

Gutierrez JR. 1992. Effects of low water supplementation and nutrient addition on the aboveground biomass production of annual plants in a Chilean coastal desert site. Oecologia **90**:556-559.

Gutierrez JR, and WG Whitford. 1987. Chihuahuan Desert annuals – Importance of water and nitrogen. Ecology **68**:2032-2045.

Gutierrez JR, OA Dasilva, MI Pagani, D Weems, and WG Whitford. 1988. Effects of different patterns of supplemental water and nitrogen-fertilization on productivity and composition of Chihuahuan Desert annual plants. American Midland Naturalist **119**:336-343.

Gutschick VP, and H BassiriRad. 2003. Extreme events as shaping physiology, ecology, and evolution of plants: toward a unified definition and evaluation of their consequences. New Phytologist **160**:21-42.

Gutzler DS, and TO Robbins. 2011. Climate variability and projected change in the western United States: regional downscaling and drought statistics. Climate Dynamics **37**:835-849.

Hall SJ, RA Sponseller, NB Grimm, D Huber, JP Kay, C Clark, and S Collins. 2011. Ecosystem response to nutrient enrichment in the Sonoran Desert. Ecological Applications **21**:640-660.

Hamerlynck EP, TE Huxman, ME Loik, and SD Smith. 2000. Effects of extreme high temperature, drought and elevated CO_2 on photosynthesis of the Mojave Desert evergreen shrub, *Larrea tridentata*. Plant Ecology **148**:183-193.

Hautier Y, PA Niklaus, and A Hector. 2009. Competition for light causes plant biodiversity loss after eutrophication. Science **324**:636-638.

He Y, P D'Odorico, SFJ De Wekker, JD Fuentes, and M Litvak. 2010. On the impact of shrub encroachment on microclimate conditions in the northern Chihuahuan desert. Journal of Geophysical Research-Atmospheres **115**:D21120.

Heisler JL, JM Briggs, and AK Knapp. 2003. Long-term patterns of shrub expansion in a C4-dominated grassland: fire frequency and the dynamics of shrub cover and abundance. American Journal of Botany **90**:423-428.

Heisler-White JL, JM Blair, EF Kelly, K Harmoney, and AK Knapp. 2009. Contingent productivity responses to more extreme rainfall regimes across a grassland biome. Global Change Biology **15**:2894-2904.

Henry HAL. 2012. Soil extracellular enzyme dynamics in a changing climate. Soil Biology and Biochemistry **47**:53-59.

Hernández DL, and SE Hobbie. 2010. The effects of substrate composition, quality, and diversity on microbial activity. Plant and Soil **335**:397-411.

Herrera J, R Pouldel, KA Nebel, and SL Collins. 2011. Precipitation increases the abundance of some groups of root-associated fungal endophytes in a semiarid grassland. Ecosphere **2**:Article 50.

Hewin DB, SR Archer, GS Okin, RL McCulley, and HL Throop. 2013. Soil-litter mixing accelerates decomposition in a Chihuahuan desert grassland. Ecosystems **16**:183-195.

Hook BA, CA Copenheaver, and A Zink-Sharp. 2011. Compression wood formation in *Pinus strobus* L. following ice storm damage in southwestern Virginia, USA. Journal of the Torrey Botanical Society **138**:52-61.

Hooper DU, and L Johnson. 1999. Nitrogen limitation in dryland ecosystems: Responses to geographical and temporal variation in precipitation. Biogeochemistry **46**:247-293.

Huxman TE, KA Snyder, D Tissue, AJ Laffler, K Ogle, WT Pockman, DR Sandquist, DL Potts, and S Schwinning. 2004. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. Oecologia **141**:254-268.

IPCC. 2013. Climate change 2013: The physical science basis. Contribution of working group I to the firth assessment report of the intergovernmental panel on climate change. eds, TF Stocker, D Qin, GK Plattner, M Tignor, SK Allen, J Boschung, A Nauels, Y Xia, V Bex, and Midgley. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535 p.

Ippolito JA, SW Blecker, CL Freeman, RL McCulley, JM Blair, and EF Kelly. 2010. Phosphorus biogeochemistry across a precipitation gradient in grasslands of central North America. Journal of Arid Environments **74**:954-961.

Jackson RB, JL Banner, EG Jobbagy, WT Pockman, and DH Wall. 2002. Ecosystem carbon loss with woody plant invasion of grasslands. Nature **418**:623-626.

Johnson NC, DL Rowland, L Corkidi, LM Egerton-Warburton, and EB Allen. 2003. Nitrogen enrichment alters mycorrhizal allocation at five mesic to semiarid grasslands. Ecology **84**:1895-1908.

Johnson SL, CR Kuske, TD Carney, DC Housman, L Gallegos-Graves, and J Belnap. 2012. Increased temperature and altered summer precipitation have differential effects on biological soil crusts in a dryland ecosystem. Global Change Biology **18**:2583-2593.

Kardol P, MA Cregger, CE Campany, and AT Classen. 2010. Soil ecosystem functioning under climate change: plant species and community effects. Ecology **91**:767-781.

Kelly AE, and ML Goulden. 2008. Rapid shifts in plant distribution with recent climate change. Proceedings of the National Academy of Sciences **105**:11823-11826.

Kieft TL, CS White, SR Loftin, R Aguilar, JA Craig, and DA Skaar. 1998. Temporal dynamics insoil carbon and nitrogen resources at a grassland-shrubland ecotone. Ecology **79**:671-683.

Killgore A, E Jackson, and WG Whitford. 2009. Fire in Chihuahuan Desert grassland: short-term effects on vegetation, small mammal populations, and faunal perturbation. Journal of Arid Environments **73**:1029-1034.

Knapp AK, and TR Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. Bioscience **36**:662-668.

Kreyling J. 2010. Winter climate change: a critical factor for temperate vegetation performance. Ecology **91**:1939-1948.

Kreyling J, M Haei, and H Laudon. 2012. Absence of snow cover reduces understory plant cover and alters plant community composition in boreal forests. Oecologia **168**:577-587.

Kurc SA, and EE Small. 2007. Soil moisture variations and ecosystem-scale fluxes of water and carbon in semiarid grassland and shrubland. Water Resources Research **43**:W06416.

Ladwig LM, SL Collins, AL Swann, Y Xia, MF Allen, and EB Allen. 2012. Above- and belowground responses to nitrogen addition in a Chihuahuan Desert grassland. Oecologia **169**:177-185.

LeBauer DS, Treseder KK (2008) Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology **89**:371-379

Liu W, Z Zhang, and S Wan. 2009. Predominant role of water in regulating soil and microbial respiration and their responses to climate change in a semiarid grassland. Global Change Biology **15**:184-195.

Loik ME, DD Breshears, WK Lauenroth, and J Belnap. 2004. A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. Oecologia **141**:269-281.

Ludwig JA, JF Reynolds, and PD Whitson. 1975. Size-biomass relationships of several Chihuahuan Desert shrubs. American Midland Naturalist **94**:451-461.

Ludwig JA, E Muldavin, and KR Blanche. 2000. Vegetation change and surface erosion in desert grasslands of Otero Mesa, Southern New Mexico: 1982 to 1995. American Midland Naturalist **144**:273-286.

Ludwig JA, BP Wilcox, DD Breshears, DJ Tongway, and AC Imeson. 2005. Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes. Ecology **86**:288-297.

Ma S, DD Baldocchi, JA Hatala, M Detto, and JC Yuste. 2012. Are rain-induced ecosystem respiration pulses enhanced by legacies of antecedent photodegradation in semi-arid environments? Agricultural and Forest Meteorology **154-155**:203-213.

Maestre FT, MA Bowker, MD Puche, MB Hinojosa, I Martinez, P Garcia-Palacios, AP Castillo, S Soliveres, AL Luzuriaga, AM Sanchez, JA Carreira, A Gallardo, and A Escudero. 2009. Shrub encroachment can reverse desertification in semi-arid Mediterranean grasslands. Ecology Letters **12**:930-941.

Manzoni S, JP Schimel, and A Porporato. 2012. Responses of soil microbial communities to water stress: results from a meta-analysis. Ecology **93**:930-938.

Martínez-Vilalta J, and WT Pockman. 2002. The vulnerability of freeze-induced xylem cavitation of *Larrea tridentata* (Zygophyllaceae) in the Chihuahuan Desert. American Journal of Botany **89**:1916-1924.

Marusenko Y, DP Huber, and SJ Hall. 2013. Fungi mediate nitrous oxide production but not ammonia oxidation in aridland soils of the southwestern US. Soil Biology and Biochemistry **63**:24-36.

McAuliffe JR, and EP Hamerlynck. 2010. Perennial plant mortality in the Sonoran and Mojave deserts in response to severe, multi-year drought. Journal of Arid Environments **74**:885-896.

McCalley CK, and JP Sparks. 2009. Abiotic gas formation drives nitrogen loss from a desert ecosystem. Science **326**:837-840.

McCrackin ML, TK Harms, NB Grimm, SJ Hall, and JP Kaye. 2008. Responses of soil microorganisms to resource availability in urban, desert soils. Biogeochemistry **87**:143-155.

McGee KP, and DL Marshall. 1993. Effects of variable moisture availability on seed germination in three populations of *Larrea tridentata*. American Midland Naturalist **130**:75-82.

Medeiros JS, DL Marshall, H Maherali, and WT Pockman. 2012. Variation in seedling freezing response is associated with climate in *Larrea*. Oecologia **169**:73-84.

Medeiros JS, and WT Pockman. 2011. Drought increases freezing tolerance of both leaves and xylem of *Larrea tridentata*. Plant Cell and Environment **34**:34-51.

Menke SB. 2003. Lizard community structure across a grassland-creosote bush ecotone in the Chihuahuan Desert. Canadian Journal of Zoology **81**:1829-1838.

Milchunas DG. 2009. Estimating root production: Comparison of 11 methods in shortgrass steppe and review of biases. Ecosystems **12**:1381-1402.

Milchunas DG, AR Mosier, JA Morgan, DR LeCain, JY King, and JA Nelson. 2005. Root production and tissue quality in a shortgrass steppe exposed to elevated CO_2: Using a new ingrowth method. Plant and Soil **268**:111-122.

Moorhead DL, and RL Sinsabaugh. 2000. Simulated patterns of litter decay predict patterns of extracellular enzyme activities. Applied Soil Ecology **14**:71-79.

Moorhead DL, G Lashermes, and RL Sinsabaugh. 2012. A theoretical model of C- and N-acquiring exoenzyme activities, which balances microbial demands during decomposition. Soil Biology and Biochemistry **53**:133-141.

Muldavin EH, DI Moore, SL Collins, KR Wetherill, and DC Lightfoot. 2008. Aboveground net primary production dynamics in a northern Chihuahuan Desert ecosystem. Oecologia **155**:123-132.

Munson SM, TJ Bento, WK Lauenroth, and IC Burke. 2010. Soil carbon flux following pulse precipitation events in the shortgrass steppe. Ecological Restoration **25**:205-211.

Naumburg E, ME Loik, and SD Smith. 2004. Photosynthetic responses of *Larrea tridentata* to seasonal temperature extremes under elevated CO_2. New Phytologist **162**:323-330.

Notaro M, Z Lui, RG Gallimore, JW Williams, DS Gutzler, and S Collins. 2010. Complex seasonal cycle of ecohydrology in the Southwest United States. Journal of Geophysical Research **115**:G04034.

Noy-Meir I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics **4**:25-51.

Ogle K, JF Reynolds. 2004. Plant responses to precipitation in desert ecosystems: Integrating functional types, pulses, thresholds, and delays. Oecologia **141**:282-294.

Parmenter RR. 2008. Long-term effects of a summer fire on desert grassland plant demographics in New Mexico. Rangeland Ecology and Management **61**:156-168.

Parmenter RR, M Kreutzian, DI Moore, and DC Lightfoot. 2011. Short-term effects of a summer wildfire on a desert grassland arthropod community in New Mexico. Environmental Entomology **40**:1051-1066.

Passera CB, O Borsetto, RJ Candia, and CR Stasi. 1992. Shrub control and seedling influences on grazing capacity in Argentina. Journal of Range Management **45**:480-482.

Pastro LA, CR Dickman, and M Letnic. 2011. Burning for biodiversity or burning biodiversity? Prescribed burn vs. wildfire impacts on plants, lizards, and mammals. Ecological Applications **21**:3238-3253.

Pausas JG, and E Ribeiro. 2013. The global fire-productivity relationship. Global Ecology and Biogeography **22**:728-736.

Pavon NP. 2005. Biomass and root production of two plant life forms in a semiarid Mexican scrub: Response to soil nitrogen availability. Canadian Journal of Botany **83**:1317-1321.

Parton W, WL Silver, IC Burke, L Grassens, ME Harmon, WS Currie, JY King, EC Adair, LA Brandt, SC Hart, and B Fasth. 2007. Global-scale similarities in nitrogen release patterns during long-term decomposition. Science **315**:361-364.

Pennington DD, and SL Collins. 2007. Response of an aridland ecosystem to interannual climate variability and prolonged drought. Landscape Ecology **22**:897-910.

Peterjohn WT, and WH Schlesinger. 1990. Nitrogen loss from deserts in the southwestern United States. Biogeochemistry **10**:67-79.

Peters DPC, and J Yao. 2012. Long-term experimental loss of foundation species: consequences for dynamics at ecotones across heterogeneous landscapes. Ecosphere **3**:Article 27.

Pisaric MFJ, DJ King, AJM MacIntosh, and R Bemrose. 2008. Impacts of the 1998 ice storm on the health and growth of Sugar maple (*Acer saccharum* Marsh.) dominated forests in Gatineau Park, Quebec. Journal of the Torrey Botanical Society **135**:530-539.

Pockman WT, and JS Sperry. 1997. Freezing-induced xylem cavitation and the northern limit of *Larrea tridentata*. Oecologia **109**:19-27.

Pockman WT, and EE Small. 2010. The influence of spatial patterns of soil moisture on the grass and shrub responses to a summer rainstorm in a Chihuahuan Desert ecotone. Ecosystems **13**:511-525.

Rajaniemi TK. 2002. Why does fertilization reduce plant species diversity? Testing three competition-based hypotheses. Journal of Ecology **90**:316-324.

Rao LE, Allen EB (2010) Combined effects of precipitation and nitrogen deposition on native and invasive winter annual production in California deserts. Oecologia **62**:1035-1046.

Rao LE, EB Allen, and T Meixner. 2010. Risk-based determination of critical nitrogen deposition loads for fire spread in southern California deserts. Ecological Applications **20**:1320-1335.

Ratajczak Z, JB Nippert, and SL Collins. 2012. Woody encroachment decreases diversity across North American grasslands and savannas. Ecology **93**:697-703.

Ravi S, and P D'Odorico. 2009. Post-fire resource redistribution and fertility island dynamics in shrub encroached desert grasslands: a modeling approach. Landscape Ecology **24**:325-335.

Ravi S, P D’Odorico, LX Wang, CS White, GS Okin, SA Macko, and SL Collins. 2009. Post-fire resource redistribution in desert grasslands: A possible negative feedback on land degradation. Ecosystems **12**:434-444.

Ravi S, DD Breshears, TE Huxman, and P D'Odorico. 2010a. Land degradation in drylands: interactions among hydrologic-aeolian erosion and vegetation dynamics. Geomorphology **116**:236-245.

Ravi S, P D'Odorico, TE Huxman, and SL Collins. 2010b. Interactions between soil erosion processes and fires: implications for the dynamics of fertility islands. Rangeland Ecology and Management **63**:267-274.

Renella G, L Landi, F Valori, and P Nannipieri. 2007. Microbial and hydrolase activity after release of low molecular weight organic compounds by a model root surface in a clayey and a sandy soil. Applied Soil Ecology **36**:124-129.

Reynolds JF, RA Virginia, PR Kemp, AG de Soyza, and DC Tremmel. 1999. Impacts of drought on desert shrubs: Effects of seasonality and degree of resource island development. Ecological Monographs **69**:69-106.

Reynolds HL, A Packer, JD Bever, and K Clay. 2003. Grassroots ecology: Plant-microbe-soil interactions as drivers of plant community structure and dynamics. Ecology **84**:2281-2291.

Reynolds JF, PR Kemp, K Ogle, and RJ Fernández. 2004. Modifying the 'pulse-reserve' paradigm for deserts of North America: Precipitation pulses, soil water, and plant responses. Oecologia **141**:194-210.

Rhoads AG, SP Hamburg, TJ Fahey, TG Siccama, EN Hane, J Battles, C Cogbill, J Randall, and G Wilson. 2002. Effects of an intense ice storm on the structure of a northern hardwood forest. Canadian Journal of Forest Research **32**:1763-1775.

Sala OE, and WK Laurenroth. 1982. Small rainfall events: an ecological role in semiarid regions. Oecologia **52**:301-304.

Sala OE, LA Gherardi, L Reichmann, E Jobbágy, and D Peters. 2012. Legacies of precipitation fluctuations on primary production: theory and data synthesis. Philosophical Transactions of the Royal Society B **367**:3135-3144.

Sankey JB., S Ravi, CSA Wallace, RH Webb, and TE Huxman. 2012. Quantifying soil surface change in degraded drylands: shrub encroachment and effects of fire and vegetation removal in a desert grassland. Journal of Geophysical Research-Biogeosciences **117**:G02025.

Scheintaub MR, JD Derner, EF Kelly, and AK Knapp. 2009. Response of the shortgrass steppe plant community to fire. Journal of Arid Environments **73**:1136-1143.

Schlesinger WH, JF Reynolds, GL Cunningham, LF Huenneke, WM Jarrell, RA Virginia, and WG Whitford. 1990. Biological feedbacks in global desertification. Science **247**:1043-1048.

Schlesinger WH, JA Raikes, AE Hartley, and AF Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology **77**:364-374.

Schwinning S, and OE Sala. 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia **141**:211-220.

Seager R, M Ting, I Held, Y Kushnir, J Lu, G Vecchi, H Huang, N Harnik, A Leetmaa, N Lau, C Li, J Velez, and N Naik. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science **316**:1181-1184.

Shao QQ, L Huang, JY Liu, WH Kuang, and J Li. 2011. Analysis of forest damage caused by the snow and ice chaos along a transect across southern

China in spring 2008. Journal of Geographical Sciences **21**:219-234.

Sharifi MR, FC Meinzer, ET Nilsen, PW Rundel, RA Virginia, WM Jarrell, DJ Herman, and PC Clark. 1988. Effects of manipulation of water and nitrogen supplies on the quantitative phenology of *Larrea tridentata* (creosote bush) in the Sonoran Desert of California. American Journal of Botany **75**:1163-1174.

Sinsabaugh RL, MM Carreiro, and S Alvarez. 2002. Enzyme and microbial dynamics of litter decomposition. *in* Enzymes in the environment: activity, ecology, and applications. *eds*. RG Burns & RP Dick, Marcel Dekker, New York.

Sinsabaugh RL. 2010. Phenol oxidase, peroxidase and organic matter dynamics of soil. Soil Biology and Biochemistry **42**:391-404.

Sirami C, C Seymour, G Midgley, and P Barnard. 2009. The impacts of shrub encroachment on savanna bird diversity from local to regional scale. Diversity and Distributions **15**:948-957.

Smith MD, AK Knapp, and SL Collins. 2009. A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. Ecology **90**:3279-3289.

Sperry JS, and MT Tyree. 1988. Mechanisms of water stress-induced xylem embolisms. Plant Physiology **88**:581-587.

Sponseller RA. 2007. Precipitation pulses and soil CO_2 flux in a Sonoran Desert ecosystem. Global Change Biology **13**:426-436.

Steinweg JM, JS Dukes, and MD Wallenstein. 2012. Modeling the effects of temperature and moisture on soil enzyme activity: Linking laboratory assays to continuous field data. Soil Biology and Biochemistry **55**:85-92.

Stephens G, and WG Whitford. 1993. Responses of Bouteloua eriopoda to irrigation and nitrogen fertilization in a Chihuahuan Desert grassland. Journal of Arid Environments **24**:415-421.

Stevens CJ, NB Dise, JO Mountford, and DJ Gowing. 2004. Impact of nitrogen deposition on the species richness of grasslands. Science **303**:1876-1879.

Stevens CJ, C Duprè, E Dorland, C Gaudnik, DJG Gowing, A Bleeker, M Diekmann, D Alard, R Bobbink, D Fowler, E Corcket, JO Mountford, V Vandvik, PA Aarrestad, S Muller, and NB Dise. 2010. Nitrogen deposition threatens species richness of grasslands across Europe. Environmental Pollution **158**:2940-2945.

Stewart IT, DR Cayan, and MD Dettinger. 2004 Changes in snowmelt runoff timing in western North America under a 'business and usual' climate change scenario. Climate Change **62**:217-232.

Stueve KM, CW Lafon, and RE Isaacs. 2007. Spatial patterns of ice storm disturbance on a forested landscape in the Appalachian Mountains, Virginia. Are*a* **39**:20-30.

Stursova M, CL Crenshaw, and RL Sinsabaugh. 2006. Microbial responses to long-term N deposition in a semiarid grassland. Microbial Ecology **51**:90-98.

Stursova M, and RL Sinsabaugh. 2008. Stabilization of oxidative enzymes in desert soil may limit organic matter accumulation. Soil Biology and Biochemistry **40**:550-553.

Suding KN, SL Collins, L Gough, C Clark, EE Cleland, KL Gross, DG Milchunas, and S Pennings. 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. Proceedings of the National Academy of Science **102**:4387-4392.

Swetnam TW, and JL Betancourt. 1998. Mesoscale disturbance and ecological response to decadal climate variability in the American Southwest. Journal of Climate **11**:3128-3147.

Syvitski JPM, CJ Vörösmarty, AJ Kettner, and P Green. 2005. Impacts of humans on the flux of terrestrial sediment into the global coastal ocean. Science **308**:376-380.

Teague WR, RJ Ansley, UP Kreuter, WE Pinchak, and JM McGrann. 2001. Economics of managing mesquite in north Texas: a sensitivity analysis. Journal of Range Management **54**:553-560.

Teaque WR, WE Grant, UP Kreuter, H Diaz-Solis, S Dube, MM Kothmann, WE Pinchak, and RJ Ansley. 2008. An ecological economic simulation model for assessing fire and grazing management effects on mesquite rangelands in Texas. Ecological Economics **64**:611-624.

Thomey ML, SL Collins, R Vargas, JE Johnson, RF Brown, DO Natvig, and MT Friggens. 2011. Effects of precipitation variability on net primary production and soil respiration on a Chihuahuan Desert grassland. Global Change Biology **17**:1505-1515.

Thomey ML. 2012. The effects of precipitation variability on C4 photosynthesis, net primary production and soil respiration in a Chihuahuan Desert grassland. PhD Dissertation. University of New Mexico.

Tienman LK, and SA Billings. 2011. Changes in variability of soil moisture alter microbial community C and N resource use. Soil Biology and Biochemistry **43**:1837-1847.

Tilman D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecological Monographs **57**:189-214.

Tilman D, and C Lehman. 2001. Human-caused environmental change: Impacts on plant diversity and evolution. Proceedings of the National Academy of Science **98**:5433-5440.

Trombulak SC, and CA Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology **14**:18-30.

Troumbis AY, and D Memtsas. 2000. Observational evidence that diversity may increase productivity in Mediterranean shrublands. Oecologia **125**:101-108.

Turnbull L, J Wainwright, and RE Brazier. 2008. A conceptual framework for understanding semi-arid land degradation: ecohydrological interactions across multiple-space and time scales. Ecohydrology **1**:23-34.

Turnbull L, J Wainwright, and RE Brazier. 2010a. Hydrology, erosion and nutrient transfers over a transition from semi-arid grassland to shrubland in the South-Western USA: A modelling assessment. Journal of Hydrology

388:258-272.

Turnbull L, J Wainwright, RE Brazier, and R Bol. 2010b. Biotic and abiotic changes in ecosystem structure over a shrub-encroachment gradient in the Southwestern USA. Ecosystem*s* **13**:1239-1255.

Turnbull L, J Wainwright, and RE Brazier. 2011. Nitrogen and phosphorus dynamics during runoff events over a transition from grassland to shrubland in the south-western United States. Hydrological Processes **25**:1-17.

Van Auken OW. 2009. Causes and consequences of woody plant encroachment into western North American grasslands. Journal of Environmental Management **90**:2931-2942.

van der Heijden MGA, RD Bardgett, and NM van Straalen. 2008. The undseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecology Letters **11**:296-310.

van Gestel NC, DW Schwilk, DT Tissue, and JC Zak. 2011. Reductions in daily soil temperature variability increase soil microbial biomass C and decrease soil N availability in the Chihuahuan Desert: potential implications for ecosystem C and N fluxes. Global Change Biology **17**:3564-3576.

Vargas R, SL Collins, ML Thomey, JE Johnson, RF Brown, DO Natvig, and MT Friggens. 2012. Precipitation variability and fire influence the temporal dynamics of soil CO_2 efflux in an arid grassland. Global Change Biology **18**:1401-1411.

Vitousek PM, RW Howarth. 1991. Nitrogen limitation on land and in the sea: How can it occur? Biogeochemistry **13**:87-115.

Vitousek PM, JD Aber, RW Howarth, GE Likens, PA Matson, DW Schindler, WH Schlesinger, and GD Tilman. 1997. Human alteration of the global nitrogen cycle: Sources and consequences. Ecological Applications **7**:737-750.

Vitousek PM, HA Mooney, J Lubchenco, and JM Melillo. 1997. Human domination of Earth's ecosystems. Science **227**:494-499.

Walvoord MA, FM Phillips, DA Stonestorm, RD Evans, PC Hartsough, BD Newman, and RG Striegl. 2003. A reservoir of nitrate beneath desert soils. Science **302**:1021-1024.

Wardle DA, RD Bardgett, JN Klironomos, H Setälä, WH van der Putten, and DH Wall. 2004. Ecological linkages between aboveground and belowground biota. Science **304**:1629-1633.

Weeks BC, SP Hamburg, and MA Vadeboncoeur. 2009. Ice storm effects on the canopy structure of a northern hardwood forest after 8 years. Canadian Journal of Forest Research **39**:1475-1483.

Weiss JL, CL Castro, and JT Overpeck. 2009. Distinguishing pronounced droughts in the Southwestern United States: seasonality and effects of warmer temperatures. Journal of Climate **22**:5918-5932.

White CS. 2011. Homogenization of the soil surface following fire in semiarid grasslands. Rangeland Ecology & Management **64**:414-418.

White CS, RL Pendleton, and BK Pendleton. 2006. Response of two semiarid grasslands to a second fire application. Rangeland Ecology and Management **59**:98-106.

Whitford WG. 1997. Desertification and animal biodiversity in the desert grasslands of North America. Journal of Arid Environments **37**:709-720.

Whittaker RH. 1970. Communities and Ecosystems. Macmillan, New York. 385 p.

Xia Y, DI Moore, SL Collins, and EH Muldavin. 2010. Aboveground production and species richness of annuals in Chihuahuan Desert grassland and shrubland plant communities. Journal of Arid Environments **74**:378-385.

Yahdjian L, and OE Sala. 2010. Size of precipitation pulses controls nitrogen transformation and losses in an arid Patagonian ecosystem. Ecosystems **13**:575-585.

Yan J, G Pan, L Li, G Quan, C Ding, and A Luo. 2010. Adsorption, immobilization, and activity of β-glucosidase on different soil colloids. Journal of Colloid and Interface Science **348**:565-570.

Zak JC, MR Willig, DL Moorhead, and HG Wildman. 1994. Functional diversity of microbial communities – A quantitative approach. Soil Biology Biochemistry **26**:1101-1108.

Zeglin LH, M Stursova, RL Sinsabaugh, and SL Collins. 2007. Microbial responses to nitrogen addition in three contrasting grassland ecosystems. Oecologia **154**:349-359.

Zelikova TJ, DC Housman, EE Grote, DA Neher, and J Belnap. 2012. Warming and increased precipitation frequency on the Colorado Plateau: implications for biological soil crusts and soil processes. Plant and Soil **355**:265-282.

Zeng DH, LJ Li, TJ Fahey, ZY Yu, ZP Fan, and FS Chen. 2010. Effects of nitrogen addition on vegetation and ecosystem carbon in a semi-arid grassland. Biogeochemistry **98**:185-193.

Zhang QH, and JC Zak. 1998. Effects of water and nitrogen amendment on soil microbial biomass and fine root production in a semi-arid environment in West Texas. Soil Biology Biochemistry **30**:39-45.