

**THE EFFECTS OF PRECIPITATION VARIABILITY ON C4
PHOTOSYNTHESIS, NET PRIMARY PRODUCTION AND
SOIL RESPIRATION IN A CHIHUAHUAN DESERT
GRASSLAND**

by

MICHELL L. THOMEY

A.A., Liberal Studies, Fullerton College, 1994
B.S., Biology, California State University, Fullerton, 1998
M.S., Biology, California State University, Fullerton, 2003

DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of

Doctor of Philosophy

Biology

The University of New Mexico
Albuquerque, New Mexico

July, 2012

ACKNOWLEDGEMENTS

I want to especially acknowledge my family, Jerry, Bette, Shon, Annette for all your support and encouragement over the years; and Josiah for the joy.

I want to thank my graduate committee, Scott, Will, Bob and Jesse. Each one of you truly represents my research interests. I have learned so much from you. Scott thanks for, supporting my research, teaching me to be a better writer, pushing me beyond my self-imposed limits, and giving me a chance to pursue my dream. Will, I remember reading about your research during my Master's degree and being so intimidated when I first started working with you. Over the years, you have helped me with my research and to navigate my way through this business with common sense. Thank you.

Heather Paulsen and Cheryl Martin. You always worked everything out, always had a solution, and here I am. Thank you.

Sevilleta LTER Staff – You often stepped in and helped out even though it was likely beyond the job description. Your support of me and my research has been invaluable.

“The global C cycle is changing, so we have a long list of tantalizing, relevant questions to puzzle, amuse and bemuse us. And, like never before, we have a ready audience, waiting for our findings and insights. That may make us a little nervous, but at the same time it adds urgency and spice to the science. It may be, a century from now, when our work is done and the current turbulence of the C cycle has been calmed, that our successors will look back and say: it must have been an exciting time for scientists, back then, in the golden age of C cycle science.” - H.H. Janzen

**THE EFFECTS OF PRECIPITATION VARIABILITY ON C4
PHOTOSYNTHESIS, NET PRIMARY PRODUCTION AND SOIL
RESPIRATION IN A CHIHUAHUAN DESERT GRASSLAND**

by

Michell L. Thomey

A.A., Liberal Studies, Fullerton College, 1994

B.S., Biology, California State University, Fullerton, 1998

M.S., Biology, California State University, Fullerton, 2003

Ph.D., Biology, University of New Mexico, 2012

ABSTRACT

Although the Earth's climate system has always been inherently variable, the magnitude and rate of anthropogenic climate change is subjecting ecosystems and the populations that they contain to novel environmental conditions. Because water is the most limiting resource, arid-semiarid ecosystems are likely to be highly responsive to future climate variability. The goal of my dissertation is to understand how precipitation variability affects primary productivity and soil respiration in desert grassland ecosystems. Initially, I reviewed the literature to understand how climate change affects net ecosystem exchange (NEE) across the warm deserts of North America (Chapter 2). Next, I examined the effects of precipitation frequency and intensity on soil moisture (θ), leaf-level photosynthesis (A_{net}), predawn leaf water potential (Ψ_{pd}), aboveground net primary productivity (ANPP), and soil respiration (R_s) (Chapter 3). Last, I studied how

large (10 mm) and extreme (30 mm) rainfall events with extended dry periods affected the ecophysiological response of two co-occurring dominant perennial C₄ grasses, *Bouteloua eriopoda* and *B. gracilis* across an arid-semiarid ecotone (Chapter 4).

TABLE OF CONTENTS

Chapter 1. Introduction	1
Chapter 2. Implications of Climate Change and Future Management of the North American Warm Deserts	3
Abstract	4
Introduction	5
The Deserts of North America	6
Carbon cycling in the North American warm deserts:	
Precipitation	10
CO ₂	13
Warming	16
Environmental hurdle #1: Disturbance	17
Environmental hurdle #2: Invasive species	19
Carbon Sequestration and land management	21
Figure	22
Figure caption	23
Chapter 3. Effect of Precipitation Variability on Net Primary Production and Soil Respiration in a Chihuahuan Desert Grassland	25
Abstract	26
Introduction	27
Materials and Methods	29
Study site	29
Experimental Design	29
Gas Exchange Measurements	30

Leaf Water Potential	31
Aboveground Net Primary Productivity (ANPP)	32
Soil Moisture and Soil Respiration	32
Data Analysis	33
Results	34
Pulse-response after experimental rain events	35
Seasonal responses	36
Discussion	39
Acknowledgements	47
Tables	48
Figures	49
Figure captions	57
Chapter 4. Effects of Monsoon Precipitation Variability on the Ecophysiological Response of Two Dominant C4 Grasses Across an Arid-Semiarid Ecotone	61
Abstract	62
Introduction	63
Materials and Methods	65
Study area	65
Study sites	66
Experimental design	67
Sensor and field measurements	68
Data analysis	70
Results	71
Shelter effects	71

Soil water dynamics	71
Monsoon rainfall variability: intraspecific plant response	72
Monsoon rainfall variability: interspecific plant response	73
Discussion	74
Monsoon rainfall variability: A_{net} and soil water dynamics	74
Monsoon rainfall variability: intraspecific plant response.	75
Monsoon rainfall variability: interspecific plant response	76
Acknowledgements	80
Tables	81
Figures	84
Figure captions	88
Chapter 5. Conclusion	90
References	93
Chapter 1	93
Chapter 2	94
Chapter 3	105
Chapter 4	110
Chapter 5	116

Chapter 1

Introduction

Although Earth's climate system has always been inherently variable (Vitousek 1992), the magnitude and rate of change associated with anthropogenic climate change is subjecting ecosystems and the populations that they contain to novel environmental conditions (Seastedt et al. 2008). At present, carbon dioxide (CO₂) concentrations are increasing roughly 2 parts per million (ppm) annually and mean global temperatures are projected to increase 1.1°C – 6.4°C by the end of this century (IPCC 2007). Because primary production and soil respiration across terrestrial ecosystems can have positive or negative feedbacks on atmospheric CO₂ concentrations (Huxman et al. 2004; Bardgett et al. 2008), it is essential to understand how species, communities and ecosystems will likely respond to progressive climate change.

In North America, desert grasslands occur from Mexico north into Arizona, New Mexico and Texas (Allred 2005). While the North American Prairie has been subjected to land-use degradation, extended drought and overgrazing in desert grasslands has exacerbated the decline in herbaceous cover which is often replaced by woody species (Schlesinger et al. 1990; Van Auken 2000; Peters and Gibbens, 2006). Because water is the most limiting resource, arid ecosystems are also likely to be highly responsive to future climate variability (Diffenbaugh et al. 2008). Understanding how climate change will impact desert grasslands is important because these communities: 1) provide habitat for plants, animals and soil organisms that often live near their physiological limits (Lauenroth and Milchunas 1992), 2) provide soil stability decreasing dust production (Archer and Predick 2008; Field et al. 2010; Ravi et al. 2010) and 3) sustain grazing lands that support livestock production.

Arid-semiarid ecosystems are defined by highly variable seasonal and inter-annual precipitation, potential evapotranspiration that exceeds precipitation, and “pulsed” precipitation events that drive biotic activity until available water is depleted (Noy-Meir 1973; Reynolds et al. 2004; Collins et al. 2008). In arid and semiarid ecosystems the magnitude and frequency of pulsed events trigger a hierarchy of biotic activity (Schwinning and Sala 2004). For example, Chen et al. (2009) note that in the Mongolian steppe, pulses ≤ 5 mm stimulated heterotrophic respiration while pulses > 25 mm resulted in carbon-sequestration. Understanding how the spatial and temporal patterns in precipitation affect primary productivity and soil respiration is important because soil water availability is a primary regulator of carbon exchange (Huxman et al. 2004). The goal of my dissertation is to understand how increased precipitation variability affects soil water dynamics and C_4 photosynthesis, net primary productivity, and soil respiration in desert grassland ecosystems.

Chapter 2
Implications of Climate Change and Future Management of
The North American Warm Deserts

Michell L. Thomey¹

Paulette L. Ford²

Deborah M. Finch²

Matt C. Reeves³

Marcy E. Litvak¹

and

Scott L. Collins¹

¹Department of Biology MSC03-2020, University of New Mexico, Albuquerque,
NM 87131, USA

²Rocky Mountain Research Station, Albuquerque, New Mexico, USA

³Rocky Mountain Research Station, Missoula, Montana, USA

Key Words: Climate change, Carbon, Mojave Desert, Sonoran Desert, Chihuahuan
Desert

Abstract

The terrestrial carbon cycle functions analogous to a respiratory system where carbon dioxide (CO_2) acquired from the atmosphere through photosynthesis is assimilated in plants (gross primary productivity, GPP), while CO_2 is also emitted back to the atmosphere as the byproduct of autotrophic and heterotrophic respiration (hereafter, ecosystem respiration, R_{eco}). Because of fossil CO_2 emissions, increasing CO_2 concentrations, warmer temperatures, and changes in the frequency of extreme weather and climate events will alter the balance between GPP and R_{eco} (e.g. NEE; net ecosystem exchange) and influence the amount of CO_2 remaining in the atmosphere. The goal of this review is to summarize the literature from the warm deserts of North America and discuss how climate change might affect NEE. Furthermore, we want to investigate the potential to increase carbon sequestration across the Mojave, Sonoran and Chihuahuan Deserts. Throughout the southwestern U.S., climate models project increased aridity, seasonal shifts in precipitation along with more extreme precipitation events. In general, soil moisture and the seasonal patterns of precipitation drive the variability in NEE. In addition, increased atmospheric CO_2 concentrations may enhance carbon sequestration but only in years with above average rainfall. Last, while desert ecosystems are rarely included in warming studies, we would expect that warmer temperatures would intensify soil water limitation and decrease respiration and primary productivity. Because arid-semiarid ecosystems cover ~45% of the terrestrial surface and desertification will likely increase in the future, management strategies that increase C sequestration or decrease carbon loss are worth pursuing.

Introduction

In the terrestrial carbon cycle carbon dioxide (CO_2) acquired from the atmosphere through photosynthesis is assimilated in plants (gross primary productivity, GPP), while CO_2 is also emitted back to the atmosphere as the byproduct of autotrophic and heterotrophic respiration (hereafter, ecosystem respiration, R_{eco}) (Kondratyev et al. 2003; Adams 2010). Together, these metabolic processes serve as the engine that drives the terrestrial carbon cycle (Chapin et al. 2002). Because of fossil CO_2 emissions, ecosystems are subject to shifts in climate patterns (Allison et al. 2011). While the degree of impact may vary by latitude, increasing CO_2 concentrations, warmer temperatures, and changes in the frequency of extreme weather and climate events will alter the balance between GPP (net CO_2 uptake) and R_{eco} (CO_2 loss) or net ecosystem exchange (NEE) and influence the amount of CO_2 remaining in the atmosphere (Adams 2010).

Although arid-semiarid regions are characterized by low primary productivity, they cover $\sim 45\%$ of the land surface (Schimel 2010) and, therefore, collectively contribute significantly to the carbon cycle. This biome stores ~ 199 Pg C in vegetation and in soil organic carbon (Janzen 2004). Moreover, the soils also contain inorganic carbon as carbonate (CaCO_3) which sequesters an additional 800-1700 Pg C (Schlesinger et al. 2000). For this reason, arid-semiarid soils are considered the third largest global pool of carbon (Emmerich 2003). In these water-limited ecosystems, CO_2 loss through R_{eco} frequently exceeds GPP as net CO_2 uptake is limited to periods of favorable rainfall (Anderson-Teixeira et al. 2011). Arid-semiarid ecosystems are highly responsive to precipitation variability and, therefore, will be affected by predicted increases in extreme precipitation events, increased CO_2 concentrations and increased temperatures (Smith et

al. 1997; Heisler-White et al. 2008; Diffenbaugh et al. 2008). Therefore, it is important to understand how these elements of climate change might affect NEE.

The goal of this review is to summarize the literature from the warm deserts of North America and learn how the elements of climate change might affect NEE. We also bring in leaf (photosynthesis; A_{net}), soil (soil respiration; R_s) and plant community (aboveground net primary productivity; ANPP) studies from the Mojave, Sonoran and Chihuahuan Deserts to determine if common trends exist across measurement scales that can be utilized to effectively manage the warm deserts. Furthermore, we investigate the potential management strategies that may increase carbon sequestration or minimize carbon losses in this region. We begin by describing the warm deserts in the southwestern U.S. and consider climate change projections for this region. We then examine how climate change may affect NEE and carbon sequestration.

The Deserts of North America

The North American Desert biome is divided into cold and warm deserts. The cold desert, including the Great Basin and Colorado Plateau, is primarily located in Nevada but also extends into portions of Utah, Colorado, Arizona, New Mexico, Oregon, Washington, Idaho and Wyoming (Barbour and Billings 2000). When compared to the warm deserts, the cold deserts occur at higher elevations, have more days with temperatures that reach freezing, receive precipitation that mostly falls as snow during the winter, and maintain deeper soil water recharge due to lower evapotranspiration and the slow release of water through snowmelt (Smith et al. 1997). The warm deserts are divided into 3 types: 1) Mojave, 2) Sonoran and 3) Chihuahuan. While the largest area of the Sonoran and Chihuahuan Deserts is located in Mexico, in the United States these

desert types are distributed from Nevada into southern California (Mojave), east through southern Arizona (Sonoran), southern New Mexico (Chihuahuan), and finally into western Texas (Chihuahuan). We limit the remainder of our discussion to the warm desert types (Figure 1).

A common trait of the Mojave, Sonoran and Chihuahuan Deserts is that they are located on the leeward (e.g. rain shadow) side of the Sierra Nevada, Peninsular and Sierra Madre Occidental, and Sierra Madre Oriental mountain ranges, respectively. Another shared trait is that precipitation is spatially and temporally variable and occurs in discrete packages (e.g. “pulses”) that initiate biotic activity followed by a dry inter-pulse period when the ecosystem returns to a less biologically active state (Noy-Meir 1973). Finally, in the southwestern U.S. short-term variability in winter rainfall derived from the Pacific is largely influenced by the El Niño and La Niña phases of the Southern Oscillation (Merideth 2001). The El Niño phase is largely associated with the high pressure system over Darwin, Australia that temporarily reverses position with the low pressure system located over Tahiti (Barry and Chorley 2003). This exchange of pressure systems results in the breakdown of the trade winds, warmer sea surface temperatures (SST) along the coast of South America, and a low pressure zone of rising air and increased precipitation leading to above average rainfall across the warm deserts (Merideth 2001). In contrast, the La Niña phase is characterized by a strengthening of the trade winds that bring below normal SST along the coast of South America and above normal SST to the western Pacific (Duxbury and Duxbury 1989). This shift in SST results in the northward displacement of the subtropical and mid-latitude jet streams leading to dry winters (Duxbury and Duxbury 1989; Barry and Chorley 2003) across the warm deserts. Beyond

these similarities, the warm deserts are distinguished by climatic differences. The obvious differences include, 1) the precipitation gradient with rainfall increasing from the Mojave Desert east to the Chihuahuan Desert and 2) the seasonality of precipitation with a winter dominant rainfall in the Mojave, summer and winter rainfall dominant (bi-modal) in the Sonoran, and summer rainfall dominant in the Chihuahuan Desert with some winter precipitation inputs.

The Mojave Desert is the driest of the warm deserts. The mean annual temperature range is from 1.5 – 28.7°C and winter snowfall can occur (Beatly 1974; Rundel and Gibson 1996). Average rainfall is 137 – 168 mm/year and is characterized by a winter dominant rainfall pattern in which most rainfall occurs from October through April as a result of west-to-east frontal systems originating over the Pacific Ocean (Smith et al. 1997; Hereford 2006). This rainfall pattern is particularly important for the C_3 perennial shrubs (*Larrea tridentata*, *Ambrosia dumosa*, *Atriplex hymenelytra*, *A. polycarpa*, *Coleogyne ramosissima*) that dominate the landscape (Rundel and Gibson 1996; MacMahon 2000). The eastern margins of the Mojave can experience a winter/summer (e.g. bimodal) rainfall pattern when the North American Monsoon System (NAMS) expands into the region (Rundel and Gibson 1996). For example, Hereford et al. (2006) found a winter dominant rainfall pattern at 90% of weather stations located west of 117° W longitude (Barstow, California) while a bimodal rainfall pattern occurred at 70% of the weather stations located east of this longitude. The eastern region is also referred to as the Colorado Desert and is considered to be an extension of the Sonoran Desert (Schoenherr 1992).

The Sonoran Desert is the warmest of the desert types and is defined as subtropical in nature (Rundel and Gibson 1996). Because this desert type rarely has freezing temperatures or winter snowfall it is distinguished, in part, by cold intolerant succulents (*Carnegiea gigantea*). In addition, the Sonoran desert supports a variety of tree species (*Cercidium macrophyllum*, *Acacia greggii*, *Olneya tesota*, *Prosopis glandulosa*, *Fouquieria splendens*), perennial grasses (*Hilaria rigida*) and shrubs (*Hyptis emoryi*, *Atriplex ploycarpa*, *Larrea tridentata*) (Nielson 1987; MacMahon 2000). The annual temperatures range from 12°C – 30°C (Smith et al. 1997). While rainfall varies across the region, mean annual rainfall is 258 – 311 mm/year and occurs in a bimodal pattern (Bahre and Shelton 1993; MacMahon 2000). In contrast to the Mojave, summer rainfall in the Sonoran Desert is produced by the North American Monsoon System (NAMS; Smith et al. 1997). During the summer monsoon season, (July – September) the Bermuda high pressure cell shifts from the Atlantic coast northwest. Meanwhile, land and ocean temperatures diverge resulting in a shift in wind patterns. This brings in moisture mostly from the Gulf of Mexico and also from the Gulf of California giving way to convective storm patterns (Barry and Chorley 2003). Overall, this bi-modal precipitation pattern lends to high plant diversity including winter active as well as summer active species (Barbour and Billings 2000).

The Chihuahuan Desert is located at the wettest end of the precipitation gradient. This desert community exhibits higher elevations and cooler temperatures when compared to the Mojave and Sonoran Deserts (Smith et al. 1997). The majority of precipitation in this region falls during the summer monsoon season (July-September) as a result of the NAMS, but winter rainfall and snowfall results in a weak bimodal signal.

On average, annual precipitation is 250 mm/year (77 – 507 mm/year) and the mean annual temperature is 14.7°C (13.5°C – 16.3°C) (Wainwright 2006). These climate factors contribute to a marked increase in perennial grass dominance (*Bouteloua eriopoda*, *B. gracilis*, *Sporobolus* spp., *Pleuraphis jamesii*, *Muhlenbergia* spp., *Aristida purpurea*) (MacMahon 2000; Whitford 2002; Peters and Gibbens 2006). Other dominant species include *Larrea tridentata*, *Gutierrezia sarothrae*, and *Ephedra trifurca*.

Throughout the southwestern U.S., climate models consistently project increased aridity, seasonal shifts in precipitation along with more extreme precipitation events (Diffenbaugh et al. 2005; Seager et al. 2007; Schoof et al. 2010). Already, temperatures are increasing faster in the Southwestern U.S. than anywhere in the nation (Global Climate Change in the U.S. 2009). While droughts and megadroughts are a trait of the regional climate, a poleward shift in the subtropical dry zones, for example, would give way to a drying pattern that the southwestern U.S. has never experienced (Fawcett et al. 2011; Seager et al. 2007). Moreover, with a novel base state of aridity, these ecosystems may not be able to recover from periodic drought events (Gutzler and Robbins 2010).

Carbon cycling in the North American warm deserts: Precipitation

For each warm desert type, the majority of precipitation events are ≤ 5 mm and primarily increase microbial activity and CO₂ efflux to the atmosphere, whereas precipitation events ≥ 10 mm are required for GPP to exceed R_{eco} (Huxman et al. 2004; Loik et al. 2004; Kurc and Small 2007; Svejcar et al. 2008). Between rainfall events, GPP and microbial activity decrease although a substantial portion of deep autotrophic root respiration from > 20 - 50 cm depth can occur in desert shrublands (Breeker et al. 2012). At the soil surface inorganic nitrogen, microbial biomass, and soil organic matter

accumulate (Austin et al. 2004). When dry soil is re-wet with a large (≥ 10 mm) precipitation event, microbial activity quickly increases but net CO₂ uptake is not immediate due to plant acclimation and growth of new roots and leaves (Ogle and Reynolds 2004). In the Sonoran and Chihuahuan Deserts, there is consistently a 2-3 day lag following a precipitation event before GPP surpasses R_{eco} losses (Potts et al. 2006; Kurc and Small 2007; Scott et al. 2010; Hamerlynck et al. 2011). The delayed increase in NEE may also vary due to differences in soil moisture and the growing season. For example, Wohlfahrt et al. (2008) observed a 3-4 day lag prior to an increase in NEE following a summer rainfall event in the Mojave Desert, while NEE increased within the same day following a spring rainfall event that occurred at peak soil moisture and primary productivity.

Regardless of plant community structure, similar to ANPP, the variability in NEE is mostly driven by large rainfall events (Kurc and Benton 2010). This trend is intuitive in the Mojave Desert where deeper rooted C₃ shrubs are dominant but is less obvious in desert grasslands where the majority of C₄ roots are located in the top 30 cm of the soil (Gibbons and Lenz 2001; McCulley et al. 2004). Nevertheless, research indicates that a significant increase in A_{net} of the dominant Chihuahuan Desert grass, *Bouteloua eriopoda* in response to small (5 mm) rainfall events does not translate into a significant increase in ANPP or NEE (Kurc and Small 2007; Anderson-Teixeira et al. 2011; Thomey et al. 2011). Another factor that contributes to the variability in NEE is leaf area (Flanagan 2002; Polley et al. 2010a). At the leaf-level, research shows that native grass A_{net} development tracks leaf area in desert grasslands (Ignace et al. 2007; Hamerlynck et al. 2011). In a semiarid riparian ecosystem, the variability in GPP under drought conditions

was attributed to leaf area in grassland as opposed to stomatal adjustments in woodlands (Jenerette et al. 2009). Moreover, Comstock and Ehleringer (1986) attribute total plant canopy leaf area in *Encelia frutescens* as the main factor limiting whole-plant carbon gain. Likewise, at the community scale, Knapp and Smith (2001) also note that ANPP is constrained by leaf area and plant density in Chihuahuan Desert grassland. Thus, the variability in NEE across the warm deserts is attributed to large precipitation events that extend periods of increased soil water availability leading to improved leaf area and net CO₂ uptake. In contrast, small precipitation events can trigger a physiological response (e.g. increase A_{net}) but are quickly lost by evapotranspiration. Although water is the most limiting resource in desert ecosystems, a threshold exists such that precipitation pulses may initiate A_{net} and limited plant growth (ANPP) but net CO₂ uptake does not surpass R_{eco} (Fernández 2007; Muldavin et al. 2008; Kurc and Small 2007).

In addition to pulse size, antecedent soil moisture along with the seasonal timing of rainfall affects CO₂ uptake. In the Sonoran Desert, the magnitude of the response of A_{net} was greater when water was added to dry soil when compared to wet soils where desert grasses had already reached their physiological capacity (Ignace et al. 2007). Similarly, Patrick et al. (2007) observed that the Chihuahuan Desert shrub, *Dasyliirion leiophyllum* did not increase A_{net} when additional water was supplemented to wet soils. This trend is also reflected in NEE but for different reasons. For example, CO₂ uptake was enhanced when a large rainfall event occurred following a pre-monsoon season drought because R_{eco} was limited likely by substrate supply or nitrogen availability (Austin et al. 2004; Potts et al. 2006). The response of CO₂ uptake to the seasonal timing of rainfall is often confounded by the dominant plant type. For example, desert grassland

ANPP is strongly correlated with summer (August) precipitation and ANPP in desert shrublands responds mostly to winter precipitation (Cable 1975; Huenneke et al. 2002; Muldavin et al. 2008). This affects NEE in several ways. In desert grasslands NEE will likely not increase if above average rainfall is evenly distributed throughout the year when grasses are dormant rather than falling during the peak summer growing season (Mielnick et al. 2005). On the other hand, desert shrublands act as a strong source of CO₂ if below average rainfall occurs during the winter season (Scott et al. 2009). In general, soil moisture and seasonal patterns of precipitation affect the biotic response and drive the variability in NEE (Polley et al. 2010b).

Carbon cycling in North American warm deserts: CO₂

It is projected that arid-semiarid ecosystems will be the most responsive to elevated CO₂ concentrations largely because decreased leaf conductance (g_s) will lead to higher plant water-use efficiency (WUE; Mooney et al. 1991; Melillo et al. 1993; Smith et al. 1997). In arid environments, these physiological adjustments have the potential to decrease evapotranspiration (ET) and increase soil water content (θ) (Morgan et al. 2004). However, the effect of CO₂ extends beyond WUE (Field et al. 1995). For example, elevated CO₂ concentrations are predicted to increase primary productivity particularly in C₃ species due to the suppression of oxygenase activity of Rubisco (Lambers et al. 2008). Litter quality is another factor that may be impacted as higher CO₂ concentrations increase C:N ratios and decrease decomposition as well as soil N availability (Strain and Bazzaz 1983; Mooney et al. 1991). The impact of increased atmospheric CO₂ concentrations will vary by ecosystem (Field et al. 1995).

The most intensive experiment to study the response of arid ecosystems to elevated CO₂ occurred in the Mojave Desert at the Nevada Desert Free-Air CO₂ Enrichment (FACE) Facility (NDFF). Experimental plots were continuously exposed to CO₂ concentrations of ~ 550 μmol mol⁻¹. Following seven years of treatment, the highest mean daily NEE in elevated CO₂ plots occurred during periods of peak plant cover or high soil moisture (Jasoni et al. 2005). Soil moisture remained an important driver of the effects of CO₂ throughout all studies at the NDFF. For instance, belowground root respiration of the dominant shrubs *Larrea tridentata* and *Ambrosia dumosa* was unaffected by elevated CO₂ but, instead, reached peak rates when soils were near their maximum water content (Clark et al. 2010). Although elevated CO₂ slightly increased the C:N ratio of plant litter at the soil surface, decomposition was affected more by the proportion of non-decomposable (high lignin and secondary compounds) to decomposable species present in the litter which varied with inter-annual differences in precipitation (Weatherly et al. 2003). Additional data from the NDFF also indicate that CO₂ exposure does not affect litter quality through increased C:N ratios (Billings et al. 2003). On the other hand, leaf-level photosynthesis (A_{net}) was enhanced by elevated CO₂ (Hamerlynck et al. 2000; Naumburg et al. 2003; Houseman et al. 2003). Moreover, g_s in *L. tridentata* decreased by 25-50% in response to elevated CO₂, but these patterns were most pronounced (A_{net}) or limited (decreased g_s) to years with above average precipitation (Naumburg et al. 2003). Similarly, elevated CO₂ increased aboveground production of *L. tridentata*, *Ambrosia dumosa*, and *Krameria erecta* but this response was also limited to years with high rainfall (Smith et al. 2000; Housemen et al. 2006).

Based on these results, an increase in atmospheric CO₂ concentrations in arid ecosystems may enhance carbon sequestration but only in years with above average rainfall.

The degree to which CO₂ affects ecosystem processes depends on lower g_s and ET that combine to increase soil θ (Field et al. 1995). Overall at the NDFF, higher atmospheric CO₂ concentrations did not conserve soil θ (Nowak et al. 2004). However, soil θ was higher under elevated CO₂ during wet years (Nowak et al. 2004) and this corresponded with a decrease in g_s of the dominant shrub *L. tridentata* (Naumburg et al. 2003). In addition, at the NDFF, down-regulation of photosynthesis occurred in *L. tridentata* and *Lycium andersonii* shrubs grown under elevated CO₂ concentrations (Huxman et al. 1998; Hamerlynck et al. 2002; Pataki et al. 2007). This can occur in C₃ species when carbohydrates accumulate and directly inhibit photosynthesis, or when less photosynthetic enzymes are produced (e.g. Rubisco) in response to elevated CO₂ concentrations (Stitt 1991). This response to long-term elevated CO₂ will decrease carbon sequestration capacity. Another factor to consider in a CO₂ enriched environment is that while lower g_s can lead to favorable WUE, the reduction in transpiration could increase leaf temperatures and offset reductions in g_s and affect photosynthesis (Bazzaz 1990). Higher leaf temperatures did not occur for the species that exhibited decreased g_s at the NDFF (Nowak et al. 2001). Generally, desert ecosystems may be exempt from this because, 1) small leaves track air temperature due to high convective heat transfer, and 2) in desert species heat loss by transpiration is a minimal component in leaf energy balance due to water limitations (Lambers et al. 2008). One last issue to consider is that increased primary productivity due to higher CO₂ can only be sustained with continued availability of soil nitrogen (Schaeffer et al. 2007).

Carbon cycling in North American warm deserts: Warming

In addition to precipitation and CO₂, warmer temperatures can directly affect primary productivity and respiration or indirectly affect carbon balance by altering soil moisture, nitrogen availability and species composition (Shaver et al. 2000). In a meta-analysis from 85 warming studies established around the globe, Wu et al. (2011) found that warming generally stimulated plant growth (above- and belowground net primary productivity), respiration and NEE. Moreover, a 0.3-6.0°C increase in temperature increased mean nitrogen mineralization by 46% across ecosystems ranging from tundra to grasslands (Rustad et al. 2001). Unfortunately, desert ecosystems are rarely included in warming studies. However, we would expect that warmer temperatures alone would intensify soil water limitation and, therefore, decrease respiration and primary productivity but these responses may be varied (Shaver et al. 2000; Heimann and Reichstein 2008; Shen et al. 2009). For example, in Chihuahuan Desert shrublands van Gestel et al. (2011) found that by reducing the daily range of soil temperature, soil moisture and soil respiration increased and nitrogen availability decreased while A_{net} of *Larrea tridentata* was not affected. Warmer minimum nighttime air temperatures had an opposing effect on vegetation cover in Chihuahuan Desert grassland. A 2.5°C increase in minimum nighttime air temperatures significantly increased cover of the Chihuahuan Desert grass *Bouteloua eriopoda* and of the C₃ shrub *Gutierrezia sarothrae* while warmer temperatures did not affect *B. gracilis* cover (Collins et al. 2010). Also in the Chihuahuan Desert grassland, Bell et al. (2008) found that while bacterial response tracked precipitation, soil temperature was the major determinant of fungal carbon use. Since community composition and microbial activity are sensitive to warmer temperatures in

arid ecosystems, additional research is needed to fully understand how this element of climate change may re-shape these communities.

Environmental hurdle #1: Disturbance

Many environmental hurdles limit our ability to increase carbon sequestration in arid-semiarid ecosystems. These barriers alter the carbon cycle, are often exacerbated by climate change and will affect the options available to land managers to enhance carbon sequestration. In this section, we focus on disturbance regime specifically as it relates to grazing, fire, and the carbon cycle. We define disturbance as the periodic destruction or removal of ecosystem components (Hobbs 2009).

In many ecosystems periodic disturbance is typically followed by a period of succession where an ecosystem is gradually restored to a similar pre-disturbance state (Hobbs 2009). Succession in arid-semiarid ecosystems, however, may not occur along this trajectory. Across the warm deserts, the capacity to regenerate from disturbance (e.g. resilience) is directly linked to resource availability (Brooks and Chamber 2011). As such, low primary productivity and annual rainfall in the Mojave Desert results in low resilience to disturbance whereas greater primary productivity and annual rainfall leads to increased resilience to disturbance in the Chihuahuan Desert. Moreover, novel disturbances such as increased fire frequency in the Mojave Desert results in a succession process that is varied or unknown. For example, burned *Larrea tridentata* communities converged with unburned *L. tridentata* communities over 19 years, while burned and unburned *Coleogyne ramosissima* communities lacked convergence irrespective of time since fire (Engel and Abella 2011). In contrast, the debate still continues over the role of grazing intensity and fire frequency in the Sonoran and Chihuahuan Deserts.

In general, fire and grazing can affect the carbon cycle through a variety of mechanisms that act on the components of the carbon cycle. For example, grazing or the exclusion of grazing in the Sonoran and Chihuahuan Deserts has been attributed to shrub encroachment in desert grasslands (Asner et al. 2004; Yanoff and Muldavin 2008; Browning and Archer 2011). The change in species composition from grassland to shrubland would be expected to affect soil organic carbon through changes in ANPP, belowground net primary productivity (BNPP), and nitrogen availability especially if the shrub was a legume (Piñeiro et al. 2010). Similarly, climate change is likely to increase fire frequency in the southwest and this may facilitate a change in species composition by invasive species or be perpetuated by the presence of invasive grasses across the warm deserts (Abatzoglou and Kolden 2011). Clearly, there is a positive feedback between climate, disturbance, invasive species and the carbon cycle. However, changes in carbon cycling associated with disturbance are also significant in the absence of invasive species. A study in Chihuahuan Desert grassland, consisting largely of the native perennial grass *Bouteloua eriopoda*, by Vargas et al. (2012) showed that fire, on average, decreased R_s and NPP by ~ 70%. Another study found that the native Chihuahuan Desert grasses, *B. eriopoda* and *Aristida purpurea* increased A_{net} and g_s in response to fire likely due to an increase in soil N availability (Allred and Snyder 2008). Additional studies are needed to fully understand how arid-semiarid ecosystems respond and recover from disturbance as climate change will likely increase the susceptibility of these ecosystems to disturbance and biological invasions.

Environmental hurdle #2: Invasive species

Across the Mojave, Sonoran and Chihuahuan Deserts, high temperatures, limited water availability and nutrient deficient soils create an environment where a specific suite of native plants persist (Rao et al. 2011). However, increasing CO₂ concentrations, precipitation variability, and increasing nitrogen deposition modify the availability of limiting resources and may increase invasive species success in arid-semiarid ecosystems (Davis et al. 2000). For example, when grown at elevated CO₂ concentrations plant density, biomass and seed rain was significantly higher in the non-native annual *Bromus madritensis* ssp. *rubens* when compared to native annuals during a wet year in the Mojave Desert (Smith et al. 2000). The favorable response of *B. madritensis* ssp. *rubens* is attributed to a decrease in the energetic cost of aboveground biomass construction under elevated atmospheric CO₂ concentrations (Nagel et al. 2004). In another study, Suazo et al (2012) found that non-native annual species increased in density (*Schismus* spp.) and allocated more resources to seed production (*Brassica tournefortii*) in response to disturbance as well as supplemental watering. This indicates that invasive species establishment in desert ecosystems is also favored by multiple aspects of climate change. For this review, we define invasive as any native or non-native species that causes or is likely to cause social, economic, or ecological harm (Runyon et al. USFS).

Once established, invasive species can alter ecosystem processes that feedback to the climate system (Dukes and Mooney 1999). This has been observed with shrub encroachment in the Chihuahuan and Sonoran Deserts. When experimental rainfall is -80%, -50%, +50% +80% of ambient rainfall, the C₃ shrub *Prosopis glandulosa* consistently maintains higher A_{net} and Ψ_{pd} compared with the C₄ grass *Bouteloua*

eriopoda in the Chihuahuan Desert (Throop et al. 2012). Similarly, in the Sonoran Desert, *Prosopis velutina* sustained higher A_{net} and photosynthetic function across a greater temperature range and under dry pre-monsoon conditions compared with the native C_4 grass, *Sporobolus wrightii* (Barron-Gafford et al. 2012). These results are especially interesting since C_4 species usually maintain higher rates of A_{net} and WUE under warmer and drier environmental conditions (Lambers et al. 2008). However, in the Barron-Gafford et al. (2012) study the deep rooted C_3 shrub outperformed the C_4 grass because it had access to groundwater while significantly higher A_{net} in *S. wrightii* was limited to brief periods of higher water availability during the monsoon season. Experimental results also suggest that shrub encroachment can influence soil respiration (R_s) because of shrub induced changes in microsite conditions. Research by Cable et al. (2012) show that R_s was higher near the trunk and under the canopies of large *P. velutina* but that temperature sensitivity of R_s was greatest at the canopy edge. Furthermore, R_s under large *P. velutina* canopies was more similar to R_s under grass canopies as opposed to R_s measured under the canopy of medium sized *P. velutina* (Cable et al. 2012). The differences in R_s with varied microsite conditions are likely due to higher root biomass in large *P. velutina* or to differences in heterotrophic and autotrophic response patterns from the trunk to canopy edge. At the continental-scale, shrub encroachment into Chihuahuan Desert grassland results in lower ANPP compared to mesic sites where shrubs have invaded (Huenneke et al. 2002; Knapp et al. 2008; Barger et al. 2011). These differences in primary productivity and R_s in response to shrub encroachment stand to alter the source-sink strength of warm desert ecosystems.

Carbon sequestration and land management

From this initial review we have learned that the elements of climate change will probably have contrasting effects on NEE and carbon uptake in the warm deserts. Nevertheless, increased precipitation variability will substantially affect the capacity of these water-limited ecosystems to exploit increased atmospheric CO₂ concentrations and persist during prolonged droughts. Certainly climate change mitigation in arid-semiarid ecosystems has a low potential when compared with more productive ecosystems (Brown et al. 2010). However, because arid-semiarid systems cover ~ 45% of the terrestrial surface (Schimel 2010) and desertification is projected to increase in the future (IPCC 2007) management strategies that increase C sequestration or decrease carbon loss are worth pursuing.

Among the elements of climate change precipitation variability is the least predictable but remains the most influential component in arid-semiarid ecosystems. Consequently, the most beneficial and cost-effective land management strategies should work to restore degraded lands to improve their potential for storing atmospheric CO₂ (Follet and Reed 2010 Laca et al. 2010; Piñeiro et al. 2010), maximize carbon gain during peak productivity (Svejcar et al. 2008), combine eddy co-variance techniques with field based measurements and predictive modeling to understand how arid-semiarid ecosystems function and to predict effective management strategies (Brown et al. 2010).

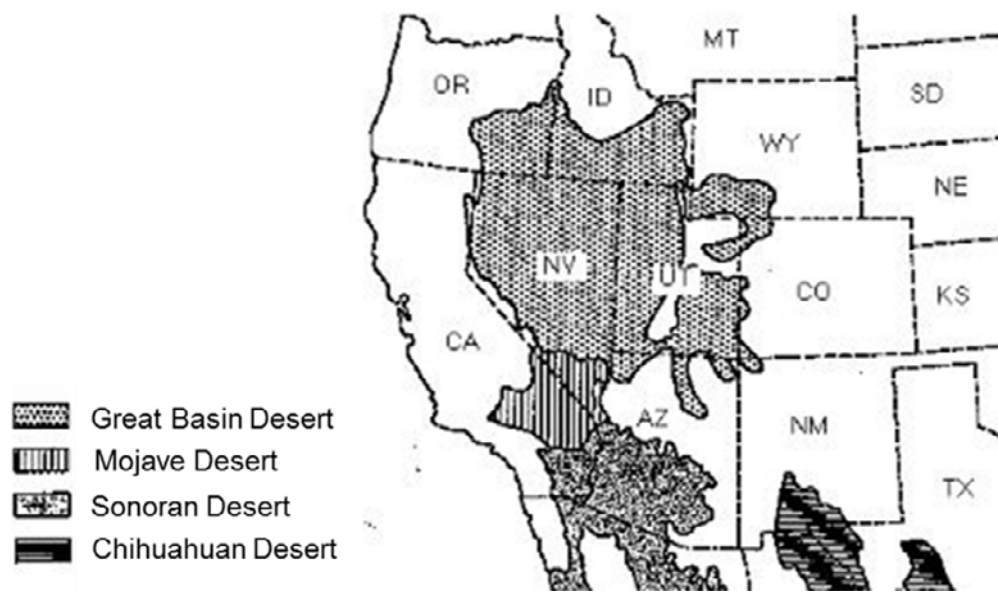


Figure 1.

Figure caption

Figure 1. The distribution of cold and warm deserts in the United States and Northern Mexico.

Chapter 3
Effect of Precipitation Variability on Net Primary Production and Soil
Respiration in a Chihuahuan Desert Grassland
Global Change Biology (2011) 17, 1505-1515

Michell L. Thomey¹

Scott L. Collins¹

Rodrigo Vargas²

Jennifer E. Johnson¹

Renee F. Brown¹

Donald O. Natvig¹

and

Michael T. Friggens¹

¹Department of Biology MSC03-2020, University of New Mexico, Albuquerque,
NM 87131, USA

²Departamento de Biología de la Conservación, Centro de Investigación Científica y de
Educación Superior de Ensenada (CICESE), BC 22860, México

Key Words: precipitation variability, desert grasslands, leaf gas exchange, primary
production, soil respiration, carbon cycle

Corresponding author: Michell L. Thomey, tel 505 277 1727, fax 505 277 5355, email
mlthomey@sevilleta.unm.edu

Abstract

Precipitation regimes are predicted to become more variable with more extreme rainfall events punctuated by longer intervening dry periods. Water-limited ecosystems are likely to be highly responsive to altered precipitation regimes. The bucket model predicts that increased precipitation variability will reduce soil moisture stress and increase primary productivity and soil respiration in aridland ecosystems. To test this hypothesis, we experimentally altered the size and frequency of precipitation events during the summer monsoon (July through September) in 2007 and 2008 in a northern Chihuahuan Desert grassland in central New Mexico, USA. Treatments included (1) ambient rain, (2) ambient rain plus one 20 mm rain event each month and (3) ambient rain plus four 5 mm rain events each month. Throughout two monsoon seasons, we measured soil temperature, soil moisture content (θ), soil respiration (R_s), along with leaf-level photosynthesis (A_{net}), predawn leaf water potential (Ψ_{pd}), and seasonal aboveground net primary productivity (ANPP) of the dominant C_4 grass, *Bouteloua eriopoda*. Treatment plots receiving a single large rainfall event each month maintained significantly higher seasonal soil θ which corresponded with a significant increase in R_s and ANPP of *B. eriopoda* when compared to plots receiving multiple small events. Because the strength of these patterns differed between years, we propose a modification of the bucket model in which both the mean and variance of soil water change as a consequence of inter-annual variability from one year to the next. Our results demonstrate that aridland ecosystems are highly sensitive to increased precipitation variability, and that more extreme precipitation events will likely have a positive impact on some aridland ecosystem processes important for the carbon cycle.

Introduction

As anthropogenic activities continue to influence drivers of global environmental change, novel abiotic conditions could shift terrestrial ecosystems outside their historical range of climate variability (Seastedt *et al.* 2008). One consequence of such change is an increase in precipitation variability characterized by more extreme precipitation events punctuated by longer intervening dry periods (Wolters *et al.* 2000; Kharin *et al.* 2007). Recently, Knapp *et al.* (2008) developed a conceptual model (hereafter referred to as the “bucket model”) to predict the response of terrestrial ecosystems to increased intra-annual precipitation variability characterized by extreme precipitation events and longer dry intervals. In this model, “the bucket” represents the uppermost soil layers with maximum root density and is characterized by upper and lower water stress thresholds. Projected changes in precipitation variability would alter soil water dynamics and biological processes depending on the existing water balance of an ecosystem. For example, in mesic systems where the bucket is moderately full, the model predicts that aboveground net primary productivity (ANPP) will decrease in response to less frequent extreme precipitation events because longer dry intervals between precipitation events increase the severity of soil water stress. In contrast, ANPP is predicted to increase in arid systems, where the soil water bucket is frequently empty, because extreme precipitation events would alleviate drought stress as deeper soil water infiltration will increase soil water content during the growing season.

Desert grasslands are distributed throughout the southwestern United States and climate models predict that these ecosystems will be highly responsive to increased climate variability in the coming decades (Diffenbaugh *et al.* 2008). These water-limited

ecosystems are defined by highly variable seasonal and inter-annual precipitation, high rates of potential evapotranspiration, and pulsed precipitation events that drive biotic activity until available water is depleted (Noy-Meir 1973; Reynolds *et al.* 2004; Collins *et al.* 2008). Climate variability and change within and between seasons will likely modify the frequency and intensity of current precipitation regimes influencing components of the carbon cycle in aridland ecosystems that may ultimately feedback to the regional climate system (Huxman *et al.* 2004; Chapin *et al.* 2009).

Grasslands are known to be highly sensitive to precipitation variability (Knapp & Smith 2001; Huxman *et al.* 2004). In mesic tallgrass prairie, increased precipitation variability decreased seasonal leaf-level photosynthesis (A_{net}), ANPP, and soil respiration (R_s ; the CO_2 efflux from soils to the atmosphere) (Knapp *et al.* 2002; Fay *et al.* 2003; Harper *et al.* 2005). Contrary to mesic grasslands, A_{net} and ANPP increased in semi-arid short grass steppe under experimentally altered precipitation patterns (Heisler-White *et al.* 2008). Yet, few studies in aridland ecosystems expand beyond single-pulsed events or seasonal changes in precipitation regimes (Huxman *et al.* 2004; Ignace *et al.* 2007; Patrick *et al.* 2007; Cable *et al.* 2008) to include the effects of increased growing season intra-annual precipitation variability (but see Heisler-White *et al.* 2009).

To determine the effects of altered precipitation regimes on an arid ecosystem, we experimentally altered precipitation frequency and intensity without changing the total amount of precipitation added in Chihuahuan Desert grassland during the summer monsoon in 2007 and 2008. Based on the bucket model, we hypothesized that a small number of large storm events would increase soil moisture availability over the growing

season leading to higher A_{net} , increased ANPP and an increase in soil respiration relative to a large number of small storm events.

Materials and methods

Study site

Our study was conducted at the Sevilleta Long Term Ecological Research (LTER) site on the Sevilleta National Wildlife Refuge (SNWR) located 80 km south of Albuquerque, New Mexico, USA (latitude 34° 20' 20", longitude 106° 43' 30"). Livestock have been excluded from the Refuge since 1973. Climate at the SNWR is arid to semiarid with dry cool winters and springs. Mean annual temperature is 13.2°C with an average low of 1.6°C in January and a high of 25.1°C in July. Precipitation is highly variable within and between years (Pennington & Collins 2007), averaging approximately 250 mm yr⁻¹ with 53%, on average, falling during the summer monsoon (July-September). More information about the site can be found at <http://sev.lternet.edu/>

Experimental design

We manipulated rainfall event size and timing using a repeated experimental design within the Monsoon Rainfall Manipulation Experiment (MRME). Vegetation at the experimental site is characterized as Chihuahuan Desert grassland dominated by *Bouteloua eriopoda*. From 1999-2008 aboveground net primary production (ANPP) ranged from 17-180 g m⁻²yr⁻¹ (Muldavin *et al.* 2008; Xia *et al.* 2010). The MRME consists of thirteen 8m x 13m plots that were established in 2006 of which ten plots were randomly assigned to one of two rainfall variability treatments (n=5 per treatment). Three ambient rain plots served as reference for comparison to treatment plots. Throughout the 2007 and 2008 monsoon seasons (July-September), each treatment plot was irrigated

using an overhead system with raindrop quality sprinkler heads that delivered water in a 360° pattern with a total flow rate of 148.20 L min⁻¹. Water used for irrigation was obtained from a reverse-osmosis system and contained 0.67 ppm NO₃-N and 1.01 ppm NH₄-N. Rainfall treatments included: 1) Large treatments that received ambient rainfall plus one 20 mm rainfall event each month (n=5; receiving 3 rainfall events July-September); and 2) Small treatments that received ambient rainfall plus four 5 mm rainfall events each month (n=5; receiving 12 rainfall events July-September). Thus, we added the same amount of precipitation (20 mm) per month over the monsoon season but we varied the size (20 mm and 5 mm) and frequency (monthly vs. weekly) of applied precipitation events. In this study, 20 mm rainfall events simulated more extreme precipitation inputs and 5 mm rainfall events represented average precipitation inputs at the Sevilleta LTER site where 71.3% of events are ≤ 5 mm and 11.6 % are between 10-20 mm (1988-2008). Throughout this manuscript, “pulse-response” refers to measurements collected 24-hours following an applied rainfall event (or water pulse), and “seasonal” refers to measurements that were integrated over each monsoon season.

Gas exchange measurements

Leaf-level gas exchange (A_{net}) was measured using a Li-6400 portable photosynthesis system (Li-Cor, Lincoln, NE, USA) with a standard leaf chamber. Throughout both monsoon seasons, weekly field campaigns in all plots occurred 24 hours following a scheduled rainfall event (i.e. pulse-response). During each field campaign, all plots in the experiment were sampled in random order. A_{net} measurements were recorded on 1-2 fully expanded leaves from three individual plants in each plot and averaged to obtain mean pulse-response A_{net} for treatment and reference plots. Irradiance (red/blue

LED light source) was set to saturating light conditions ($1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) that had been determined by light response curves. The CO_2 concentration ($400 \mu\text{mol mol}^{-1}$) and block temperature were set to ambient conditions prior to the first measurement and held constant across all plots in order to maintain consistent chamber conditions throughout the measurement period (0900-1400 hours). Leaf area was determined by multiplying the measured width of each leaf by the length of the chamber. Rates of A_{net} were corrected for leaf area using Li-6400 simulator software (Open V5.3).

Following A_{net} measurements, leaf samples were collected and returned to the laboratory to determine leaf nitrogen concentration (% N/dry mass). For each measurement date, leaves obtained from individual plots were combined by treatment, oven dried at 60°C for 24 hours, and ground for nitrogen analysis. Leaf nitrogen concentration was determined by high temperature combustion and gas chromatography. All analyses were performed using a ThermoQuest CE Instruments NC2100 Elemental Analyzer (ThermoQuest Italia S.p.A., Rodano, Italy).

Leaf water potential

Predawn leaf xylem pressure potentials (Ψ_{pd}) were measured on 5-6 leaves collected from distinct *B. eriopoda* tillers in each plot. Mean pulse-response Ψ_{pd} is reported for treatment and reference plots. Leaves were collected (pre-dawn) and put immediately into plastic bags and then stored in a cooler. Pre-dawn leaf water potentials were measured within 1-2 hours of collection with a Scholander-type pressure chamber (PMS, Model 1000. PMS Instrument Co. Corvallis, OR).

Aboveground net primary productivity (ANPP)

Across all plots, *B. eriopoda* accounted for ~ 70% of plant cover. Additional subdominant species included *Sphaeralcea wrightii*, *Sporobolus* spp., and *Gutierrezia sarothrae*. ANPP was measured in two 1 m² subplots permanently located in each plot starting in 2007. ANPP measurements were recorded in the spring and fall of 2007 and 2008 when plant species had reached peak biomass. For every subplot, the biomass of each individual of each species was determined from cover and height size classes. Regressions of weight-to-volume were developed by harvesting various sized individuals of each species from adjacent areas. A positive change in green biomass (current season's growth) from spring to fall in each subplot was used as a measure of mean seasonal ANPP (for all species) (for detailed methods see Muldavin *et al.* 2008).

Soil moisture and soil respiration

Nearly eight months before the start of the experiment, soil sensor nodes were installed in all plots to ensure soil equilibrium after installation of environmental sensors. Each sensor node consisted of ECH₂O soil temperature and soil moisture sensors (EC-TM Decagon Devices, Inc. Pullman, WA) and Vaisala CARBOCAP soil CO₂ sensors (GMM 222, Vaisala, Helsinki, Finland) that were placed under the canopy and within the rooting zone of *B. eriopoda* at three depths (2, 8 and 16 cm) as described in Vargas and Allen (2008). The CO₂ sensors were protected with Gore-Tex[®] fiber to avoid possible wetting during rainfall events while allowing free gas exchange. Soil temperature (Ts), soil moisture content (θ), and soil CO₂ concentration were measured continuously at 30 minute intervals throughout both monsoon seasons. Values of soil CO₂ concentration (ppm) were corrected for temperature and pressure using the ideal gas law according to

the manufacturer. We calculated soil respiration (R_s , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) using the flux-gradient method as has been described for multiple ecosystems (Vargas *et al.* 2010). Briefly, we used Fick's law of diffusion where the diffusivity of CO_2 was corrected for temperature and pressure (Jones 1992) and calculated as a function of soil moisture, soil porosity, and soil texture (Moldrup *et al.* 1999). Soil porosity is $0.43 \text{ m}^3 \text{ m}^{-3}$ and bulk density was 1.51 g cm^{-3} . Soils are Typic Haplargids derived from piedmont alluvium. Soil texture in the upper 20 cm is 68% sand, 22% silt and 10% clay, with 2% calcium carbonate (Kieft *et al.* 1998). Across all treatment and reference plots, we used daily mean values, calculated on a 24-hour basis, to report seasonal R_s . Mean daily soil θ , calculated as the average soil θ for measurements from 2-16 cm depth, was used to determine pulse-response and seasonal soil θ . Similarly, daily mean soil temperature (T_s) was calculated on a 24-hour basis and averaged over all depths to obtain seasonal T_s .

Throughout the study period, we used the mean absolute difference in soil θ to quantify how ambient rainfall patterns vs. ambient rainfall patterns plus small or large rainfall additions altered soil θ variability (Knapp *et al.* 2002). These values were determined using mean daily soil θ in reference ($n=3$) and treatment plots ($n=5$ each treatment). Within each plot type (reference or treatment), soil water variability was calculated as the absolute difference in mean daily soil θ between consecutive days. Data for this study are located in data sets SEV188, 191, 206, 223, 224, and 225 at <http://sev.lternet.edu>.

Data analysis

Data analysis was completed using SAS (v 9.1, Cary, NC, USA). For each measured variable, data obtained from a single plot were averaged daily such that each

plot represented an experimental unit ($n = 3$ for ambient rainfall and $n = 5$ for 5 mm and 20 mm rainfall addition plots, respectively). When the data were analyzed collectively, year by treatment interactions were not significant ($p > 0.05$), however, there was a significant ($p < 0.05$) difference between years. Therefore, years were analyzed separately rather than combined. In each year, the main effects were divided into two groups: 1) pulse-response (i.e. post wetting measurements) of A_{net} , Ψ_{pd} , soil θ , and % leaf N/dry mass and 2) seasonal measurements (i.e. across the monsoon season per year) of R_s , T_s , ANPP, soil θ , and soil θ variability. Values were compared between treatments and reference plots. Data that did not meet the assumptions of Analysis of Variance (ANOVA) were log or square root transformed and analyzed using a single-factor General Linear Model (PROC GLM). Significant treatment effects were followed by LS Means for multiple comparisons with unbalanced designs. Data that failed to meet the assumptions of ANOVA, despite transformation, were analyzed using a single-factor Kruskal-Wallis test (PROC npar1way; Wilcoxon) for treatment effects and multiple comparisons between treatments. For all analyses alpha was set to 0.05.

Results

In 2007, small and large treatment plots received 152.2 mm of rainfall (ambient + applied). Reference plots received 92.2 mm of ambient precipitation (Table 1) which measured 36% below the long-term monsoon mean (125.8 mm) at the SNWR (1988-2008). In 2008, small and large treatment plots received 239.6 mm of rainfall (ambient + applied). Reference plots received 179.6 mm of ambient precipitation (Table 1) which measured 30% above the long-term mean. For both years, the majority of ambient rainfall

events were < 5 mm, but the number of large rainfall events (>20 mm) more than doubled in 2008 (Table 1).

Pulse-response after experimental rain events

Both rainfall addition treatments increased mean daily soil θ but this response was contingent on ambient rainfall (Fig. 1a, b, d, e). In 2007 and 2008, large monthly rainfall additions significantly increased pulse-response soil θ and for six consecutive days thereafter when compared to plots that received small weekly rainfall additions (Year 2007: $H = 13.22$, $p = < 0.001$; Year 2008: $H = 6.83$, $p = 0.009$) and reference plots (Year 2007: $H = 32.91$, $p = < 0.001$; Year 2008: $H = 10.28$, $p = 0.001$) (Fig. 1b, e). Mean daily soil temperature reached peak values early in the monsoon season (July-August) and decreased as the season progressed (Fig. 1c, f).

Throughout the 2007 monsoon season, plots receiving small weekly or large monthly rainfall additions significantly increased pulse-response soil θ by 89.1% and 84.7% compared to reference plots (Fig. 2a). The significant increase in pulse-response soil θ in treatment plots (small: $H = 8.80$, $p = 0.003$; large: $H = 21.56$, $p = < 0.001$) also corresponded with less negative Ψ_{pd} (small: $F = 15.35$, $p < 0.01$; large: $F = 15.35$, $p < 0.01$; Fig. 2b; Fig. S1) and a significant increase in A_{net} (small: $H = 6.74$, $p = 0.01$; large: $H = 7.74$, $p < 0.01$; Fig. 2c; Fig. S1) when compared to *B. eriopoda* in reference plots. In contrast, pulse-response soil θ had no effect on leaf nitrogen concentrations from leaves collected throughout the study period ($H = 3.92$, $p = 0.14$). Among the two rainfall addition treatments, the magnitude and frequency of rainfall additions did not significantly affect pulse-response soil θ , Ψ_{pd} , or A_{net} (Fig. 2a, b, c).

During 2008, pulse-response soil θ increased across all treatment and reference plots (Fig. 2a) likely as a result of the 95% increase in ambient precipitation compared to 2007 (Table 1). Nevertheless, plots receiving small or large rainfall additions maintained higher pulse-response soil θ than reference plots (small: $H = 5.50$, $p = 0.02$; large: $H = 7.75$, $p < 0.01$; Fig. 2a). While there was no difference in A_{net} between reference and small rainfall addition plots, A_{net} in large rainfall addition plots was significantly higher than in the reference plots ($F = 2.55$, $p = 0.03$; Fig. 2c; Fig. S1). Throughout the 2008 season, there was no treatment effect on leaf nitrogen concentrations ($F = 2.84$, $p = 0.07$) and Ψ_{pd} ($F = 2.27$, $p = 0.11$). However, leaves sampled from rainfall addition plots consistently maintained less negative Ψ_{pd} when compared to reference plots (Fig. 2b; Fig. S1).

Seasonal responses

Across the 2007 monsoon season, small weekly and large monthly rainfall additions increased seasonal soil θ relative to reference plots (small: $H = 8.25$, $p = 0.004$; large: $H = 32.91$, $p < 0.001$; mean soil θ : 0.06 ± 0.003 , 0.07 ± 0.003 , $0.08 \pm 0.003 \text{ m}^3 \text{ m}^{-3}$ reference, small and large, respectfully; Fig. 2d). In contrast to pulse-response measures of soil θ , seasonal soil θ in large rainfall addition plots increased by 20% when compared to seasonal soil θ in small rainfall addition plots. Furthermore, seasonal soil θ measured at 16 cm in large rainfall addition plots was significantly higher when compared to reference ($H = 47.49$, $p < 0.001$) and small rainfall addition plots ($H = 24.25$, $p < 0.001$) (Fig. S2).

Over the growing season, large monthly rainfall additions increased Rs 30.3% and small weekly rainfall additions increased Rs 13.5% ($F = 37.22$, $p < 0.01$; Fig. 2e) when

compared to reference plots. Overall, Rs reflected differences in seasonal soil θ (Fig. 2d, e) and treatment differences in total seasonal Rs occurred throughout the study period (838 g C m^{-2} , 726 g C m^{-2} , and 638 g C m^{-2} large, small and reference, respectively; Fig. 3a). Average diel patterns of Rs were always higher in large monthly rainfall addition plots compared to small weekly rainfall addition, and reference plots (Fig. 3c, d, e) and are consistent with the seasonal Rs results. Precipitation treatments had no significant effect on seasonal Ts (2007: $F = 4.38$, $p = 0.11$; mean seasonal Ts: 27.66 ± 0.36 , 26.73 ± 0.34 , 27.00 ± 0.34 °C reference, small and large, respectively; Fig. 1c).

Throughout the 2008 monsoon season, seasonal soil θ increased across treatment and reference plots (mean seasonal soil θ : 0.09 ± 0.004 , 0.10 ± 0.004 , $0.11 \pm 0.004 \text{ m}^3 \text{ m}^{-3}$ reference, small and large, respectfully) when compared to 2007 (Fig. 2d). This increase in precipitation along with several large ($> 20 \text{ mm}$) natural rainfall events (Table 1) diminished the difference in seasonal soil θ between reference and small rainfall addition plots. However, seasonal soil θ measured at 16 cm in large rainfall addition plots was significantly higher when compared to reference ($H = 27.81$, $p = < 0.001$) and small rainfall addition plots ($H = 7.23$, $p = < 0.001$; Fig. S2).

Total seasonal Rs was higher in large monthly rainfall addition plots compared to small weekly rainfall additions and reference plots (990 g C m^{-2} , 760 g C m^{-2} and 620 g C m^{-2} ; Fig. 3b) despite the lack of difference in mean seasonal soil θ in small and reference plots. Average diel patterns of Rs were always higher in large monthly rainfall addition plots compared to small weekly rainfall addition and reference plots (Fig. 3f, g, h) and are consistent with the seasonal Rs results (Fig. 2e). Similar to 2007, precipitation treatments had no significant effect on seasonal soil temperature (2008: $F = 2.70$, $p = 0.26$; mean

seasonal soil temperature: 25.63 ± 0.23 , 25.11 ± 0.22 , 25.30 ± 0.22 °C reference, small and large, respectively; Fig. 1f).

For both years of the study, ANPP for all species (by functional type) was dominated by graminoids with *B. eriopoda* contributing the majority to production (Fig. 4a, b). Although mean ANPP for all species increased with the magnitude of the treatment, we did not detect significant treatment differences in either year of the study. In 2007 ANPP for all species reached maximum values in plots that received large monthly rainfall additions (306.1 g m^{-2}), followed by small weekly rainfall additions (230.9 g m^{-2}) and reference plots (142.5 g m^{-2}). This trend was repeated in 2008 with values reaching 278.7 g m^{-2} , 226.3 g m^{-2} and 137.4 g m^{-2} for large, small and reference plots, respectively. In 2007 and 2008, ANPP of *B. eriopoda* was significantly higher in large monthly rainfall addition plots compared to small weekly rainfall additions (2007: 227.0 g m^{-2} vs. 162.4 g m^{-2} ; 2008: 176.6 g m^{-2} vs. 105.5 g m^{-2}). From 2007 to 2008 ANPP of *B. eriopoda* decreased while biomass production of other grasses increased in 2008 (Fig. 4a, b).

We used the mean absolute difference in mean daily soil moisture θ content to quantify the variability between treatment and reference plots. In 2007 (dry year) and 2008 (wet year) experimental rainfall additions significantly increased the variability in seasonal soil θ when compared to reference plots (2007: $F = 5.38$, $p = 0.03$; 2008: $F = 4.99$, $p = 0.04$; Fig. S3). Although soil water variability increased in 2008, the within year variability between rainfall treatments and ambient plots was dampened in the wet year (Fig. S3). When compared to reference plots, large monthly rainfall applications

increased soil water variability (Fig. S3) and this corresponded with a significant increase in pulse-response soil θ that was maintained for six consecutive days thereafter.

Discussion

Our results supported the hypothesis that increased within-season precipitation variability would increase ANPP of *B. eriopoda* and Rs (Knapp *et al.* 2008) but the magnitude of the response differed between years. These results highlight the importance of not only predicting relative changes within years, but also patterns of responses between years. Both primary productivity and Rs increased in response to small and large rainfall events, however, large rainfall events resulted in significantly higher pulse-response soil θ in the top 16 cm of soil and extended the water pulse duration for up to six days longer when compared to small rainfall event plots (Fig. 1b, e; Fig. S2). Thus, while A_{net} and Ψ_{pd} measurements of *B. eriopoda* did not reflect a difference in pulse magnitude (small vs. large), mean total seasonal Rs and ANPP of *B. eriopoda* were significantly higher in large rainfall event plots (Fig. 3; Fig. 4). Likely, *B. eriopoda* maintained high A_{net} , beyond our 1-day pulse-response sampling period, leading to higher ANPP when compared to small event plots where soil θ was ephemeral (Fig. 1b, e; Fig. S1). This interpretation is supported by: a) diel patterns of Rs were consistently higher in the large rainfall event plots compared to small event plots and ambient plots (Fig. 3c-h); and b) total seasonal Rs was related to ANPP via photosynthesis (Vargas *et al.* 2010).

Warm desert perennial grasses, such as *B. eriopoda*, are adapted to efficiently utilize episodic summer rain events by having shallow root systems and the ability to rapidly respond with high rates of photosynthesis following rainfall (Nobel 1980; Smith *et al.* 1997). At our study site, perennial grass roots are primarily distributed within the

top 20-30 cm (McCulley *et al.* 2004; Kurc & Small 2007) but *B. eriopoda* roots have also been found as deep as 45 cm (Gibbens & Lenz 2001). The 5 mm rainfall additions reached shallow depths compared to the 20 mm rainfall additions and this is reflected in the integrated daily mean soil θ reported in Figure 1. As a result, mean pulse-response soil θ in small and large rainfall addition plots was significantly higher and this corresponded with a significant increase in A_{net} and Ψ_{pd} (less negative) when compared to reference plots (Fig. 2a-c). Similar to *Bouteloua gracilis* in the shortgrass steppe (Sala & Lauenroth 1982), *B. eriopoda* also has the capacity to respond to rain events as small as 5 mm. We found that rainfall additions within the rooting zone of *B. eriopoda* initially elicited similar physiological responses independent of pulse size (Fig. 2c). Gross primary production in Mongolian semiarid grasslands responded similarly irrespective of pulse size (Chen *et al.* 2009) indicating that grassland species can utilize both shallow (~20 cm below the soil surface) and deeper (20-60 cm below the soil surface) water sources (Zhao *et al.* 2009). In arid-semiarid ecosystems, rooting depth influences the ability of plants to up-regulate photosynthesis in response to the “pulsed” precipitation regimes characteristic of this region (Williams *et al.* 1999; Schenk & Jackson 2002; Ogle & Reynolds 2004). Although we did not eliminate ambient precipitation, our results suggest that *B. eriopoda* responds to ≥ 5 mm summer rain events to maximize carbon gain during favorable periods (Smith *et al.* 1997; Schwinning *et al.* 2003).

Although we did not detect a significant difference in measures of A_{net} and Ψ_{pd} between 5 mm and 20 mm rainfall treatments (Fig. 2b, c), ANPP of *B. eriopoda* was significantly higher in plots that received large monthly (more extreme) precipitation events when compared to small weekly and ambient plots (Fig. 4). We attribute the

increase in ANPP of *B. eriopoda* to sustained levels of A_{net} that likely extended beyond our 1-day sampling period due to prolonged soil water availability in the large rainfall treatments (Fig. 1b, e). As discussed, this result is supported by higher average diel R_s patterns (Fig. 3) and because seasonal R_s has been shown to be related to photosynthetic rates in several ecosystems (Vargas *et al.* 2010). When compared to small and ambient reference plots, we found that large (20 mm) rainfall events maintained significantly higher soil θ for up to six consecutive days following an experimental addition (Fig. 1b, e). Thus, over the duration of the study, small weekly (5 mm) events were likely depleted rapidly through evapotranspiration while large monthly (20 mm) events were more effective in promoting production due to deeper soil water recharge (Schwinning & Sala 2004). Indeed, at the deepest measured depth (16 cm) we found that large rainfall additions significantly increased seasonal soil θ when compared to reference and small rainfall addition plots (Fig. S2). These findings support a soil moisture threshold for growth in *B. eriopoda* (Muldavin *et al.* 2008) in which a 5 mm rainfall event stimulates a transient physiological response that translates into a pulse of ANPP, and that larger rainfall events initiate a sustainable physiological response that results in larger increments of ANPP. Small and large rainfall events stimulate similar responses to R_s as well as those observed for ANPP.

Overall, ANPP of all plant functional types responded to the treatments, but large rainfall treatments significantly increased ANPP of the dominant C_4 grass *B. eriopoda* which contributes the majority of primary production (Fig. 4a, b). However, the magnitude of response in ANPP of *B. eriopoda* decreased from 2007 (dry year) to 2008 (wet year) across all treatments (Fig. 4a, b). Previous studies have also reported a

decrease in plant response from dry to wet years. Ignace *et al.* (2007) found that grasses in the Sonoran desert did not increase A_{net} or Ψ_{pd} in response to experimental water addition during a wet year, because favorable soil water content was already facilitating high plant performance. Using an ecosystem model, Gerten *et al.* (2008) demonstrated that NPP was most responsive during water-limited periods and least pronounced or absent in non-water limited periods. Patrick *et al.* (2009) found that photosynthesis of *Bouteloua curtipendula* in a sotol grassland decreased during a wet year due to lower leaf nitrogen concentrations. In our study, we found that leaf nitrogen concentrations increased from 2007 (reference: 1.04%, small rainfall addition: 1.11%, large rainfall addition: 0.99% N dry mass) to 2008 (reference: 1.45%, small rainfall addition: 1.36%, large rainfall addition: 1.27% N dry mass). The increase in A_{net} despite the trend towards lower leaf nitrogen concentrations in water addition plots suggests that *B. eriopoda* is primarily limited by water rather than nitrogen availability (Stephens & Whitford 1993; Báez *et al.* 2007). The decrease in ANPP of *B. eriopoda* in 2008 (Fig. 4a, b) may also have been a function of low productivity prior to the onset of the monsoon season, because winter/early spring conditions could modify ANPP in arid-semiarid grassland ecosystems (Heisler-White *et al.* 2008; Muldavin *et al.* 2008). Another factor may be the observed increase in ANPP among sub-dominant grass species (Fig. 4a, b). Jankju (2008) noted an increase in competition among perennial plant species in plots that received large infrequent rainfall events (20 mm/bi-monthly) in an arid rangeland. At local scales, other studies attribute a weak correlation between ANPP and precipitation to a potential lag in the response of ANPP to precipitation and productivity from the previous year (Osterheld *et al.* 2001; Yahdjian & Sala 2006). In our study, ANPP of *B. eriopoda* was

highest in a dry monsoon season (2007) that was preceded by record breaking wet season (2006) where monsoon precipitation measured 30% above the long-term mean, and lowest in a wet year (2008) that was preceded by a dry year (2007) where monsoon precipitation measured 36% below the long-term mean. In this study we did not collect annual root biomass data, however, the carbon gained from higher A_{net} in 2008 may have been allocated belowground rather than to aboveground biomass (ANPP) as a result of below average rainfall that occurred in the previous year (2007).

Throughout the study period, we found that significant differences in seasonal R_s reflected ANPP of *B. eriopoda*. It is widely accepted that soil respiration is largely dependent on soil temperature and moisture (Raich & Tufekcioglu 2000), but R_s is also influenced by photosynthesis and substrate supply (Craine *et al.* 1999; Wan & Luo 2003; Sponseller 2007; Vargas *et al.* 2010). We did not detect a significant difference in mean daily soil temperature between treatment and reference plots (Fig. 1c, f). However, when compared to reference plots, seasonal soil θ and ANPP of *B. eriopoda* were significantly higher in large plots and this corresponded with a significant increase in seasonal R_s (Fig. 2e). Furthermore, mean diel patterns of R_s in large rainfall additions were consistently higher than in reference and small rainfall treatment plots (Fig. 3c-h) throughout the monsoon season. Overall, our data suggest that increased R_s is related to higher soil moisture that likely increased substrate availability for R_s by: a) dissolution of substrate in soil organic matter; and b) substrate supplied by an increase in photosynthetic rates associated with large rainfall events (Vargas *et al.* unpublished). Moreover, these results support previous observations where soil moisture availability is more important than soil

temperature in regulating Rs in semiarid grasslands (Liu *et al.* 2009; Zhao *et al.* 2009; Vargas *et al.* 2010).

Grassland species are sensitive to precipitation variability due to their shallow rooting depths (< 50 cm) which limits water availability to atmospheric precipitation rather than groundwater (Shen *et al.* 2008). The bucket model (Knapp *et al.* 2008) predicts that extreme precipitation events accompanied by longer dry intervals will increase soil water availability in arid but not mesic ecosystems. As a result, arid ecosystems could experience an increase in the number of non-stressed days leading to higher primary productivity and soil respiration. We found that soil water variability was highest in large rainfall addition plots where rainfall applications significantly increased seasonal soil θ (Fig. S3). In contrast to studies from mesic grasslands (e.g. Knapp *et al.* 2002), A_{net} , ANPP and Rs were highest in large (20 mm) rainfall addition plots where higher pulse-response and seasonal soil θ and soil water variability, associated with larger pulses, increased the amount of time this system was in a non-stressed state. Similar results were also found by Heisler-White *et al.* (2009) in semi-arid steppe where a small number of large events increased soil θ leading to increased ANPP and mid-day water potential (less negative) in *Bouteloua gracilis*.

The sensitivity of this desert grassland to precipitation variability differed between years and was contingent on the amount and pattern of ambient precipitation. The bucket model (Knapp *et al.* 2008), as presented, is a static within-season model in which variance changes but the mean remains constant (Fig. 5). The bucket model does not account for year-to-year changes in precipitation that would alter the degree to which within season variability affects ecosystem response. In effect, as seasonal precipitation

varies from year-to-year, then less variability is needed to cross the stress threshold during a wet year and larger extreme events are needed in a dry year (Fig. 5). For example, during our study ambient precipitation measured 36% below (2007) and 30% above (2008) the long-term mean. Although the increase in precipitation increased soil θ and A_{net} across all plots, the magnitude of the responses between treatment and reference plots was highest in the dry year (2007) and dampened in the wet year (2008) (Fig. 2). Other studies also report an increase in the magnitude of the response of soil respiration and A_{net} when precipitation events are preceded by a dry period (Cable *et al.* 2008; Xu *et al.* 2009). By definition, variability in mean annual precipitation characterizes aridland ecosystems (Noy-Meir 1973) and thus we propose a more dynamic bucket model (Fig. 5) that takes into account inter-annual variability which pushes arid ecosystems towards or away from the non-stressed state from one year to the next.

Climate models consistently indicate a future with altered precipitation patterns and an increase in extreme precipitation events (IPCC 2007). Southwestern North America may also experience increasing aridity (Cook *et al.* 2004; Seager *et al.* 2007). Understanding how the spatial and temporal patterns in precipitation will affect ecosystem processes and carbon dynamics is important because soil water availability drives ecosystem carbon exchange in aridland ecosystems (Huxman *et al.* 2004). Moreover, models predict that arid and semiarid ecosystems are likely to be highly responsive to future climate variability (Diffenbaugh *et al.* 2008). Although production and C fluxes from aridland ecosystems are relatively small compared to mesic systems, arid and semiarid ecosystems cover 45% of the terrestrial surface (Schimel 2010) and therefore collectively contribute significantly to the global carbon budget. Therefore, it is

essential that we understand how arid and semiarid ecosystems will respond to increased precipitation variability as a consequence of global environmental change.

Acknowledgements

We thank Doug Moore for ANPP calculations, Kristin Vanderbilt for data management, Karen Wetherill, Yang Xia, Terri Koontz, and Amaris Swann for vegetation measurements, Tim Allen for sorting species, and John Craig for his assistance with leaf nitrogen analysis. Special thanks to U.S. Fish and Wildlife Service at the Sevilleta National Wildlife Refuge. Funding was provided by the University of New Mexico (GRAC and SRAC), NSF DEB-0620482 for Long-Term Ecological Research, and DoE NICCR.

Table 1. Total monsoon precipitation (July through September) and the total number of events in each rainfall event size category as observed at the Monsoon Rainfall Manipulation Experiment site at the SNWR in central New Mexico, USA. Average long-term monsoon precipitation at the SNWR is 125.8 mm (1988-2008).

Year	Total Precipitation (mm)	Rainfall Event Size Class			
		< 5 mm	5–10 mm	10–20 mm	> 20 mm
2007	92.2	18	4	1	1
2008	179.6	15	2	3	4

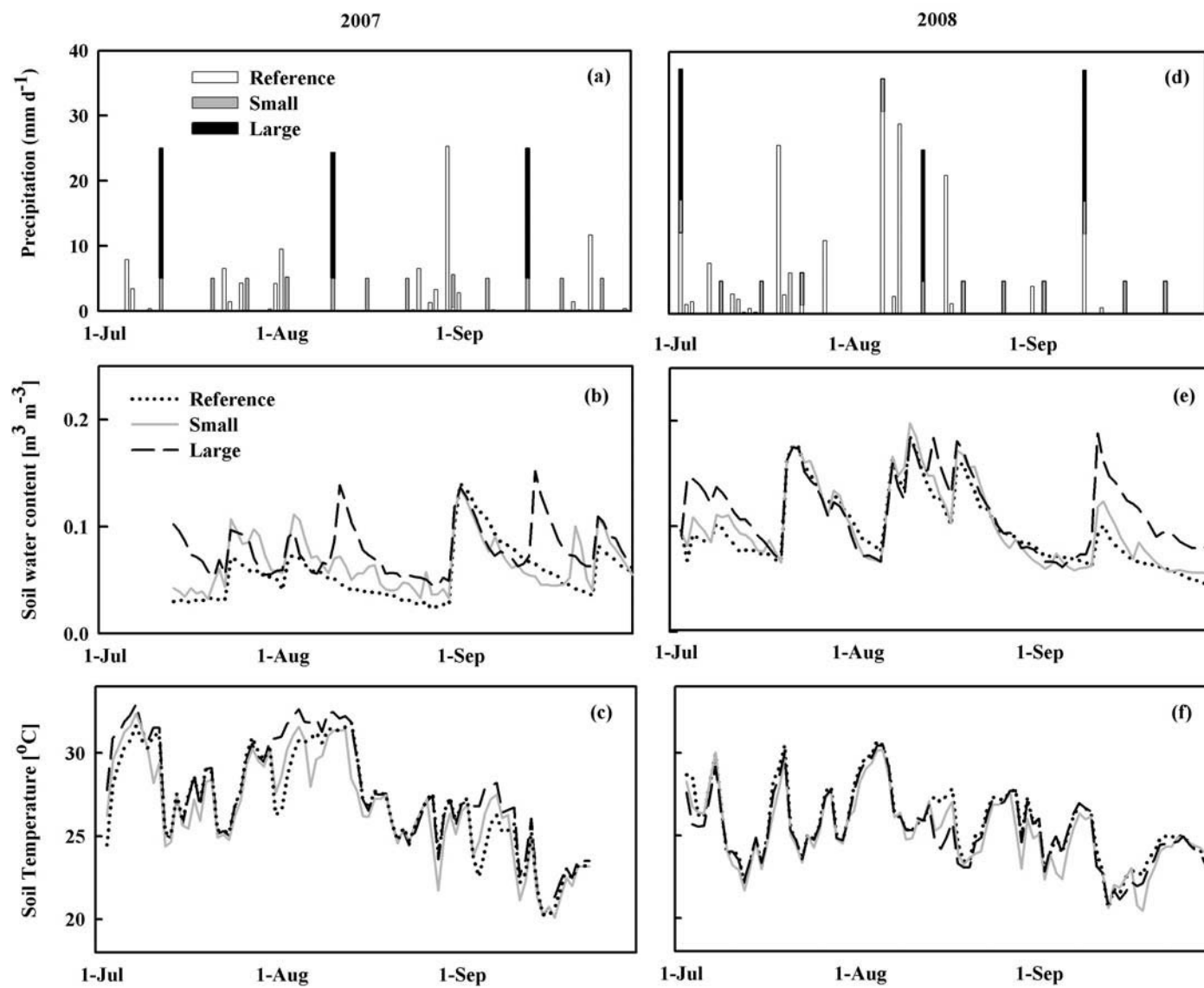


Figure 1.

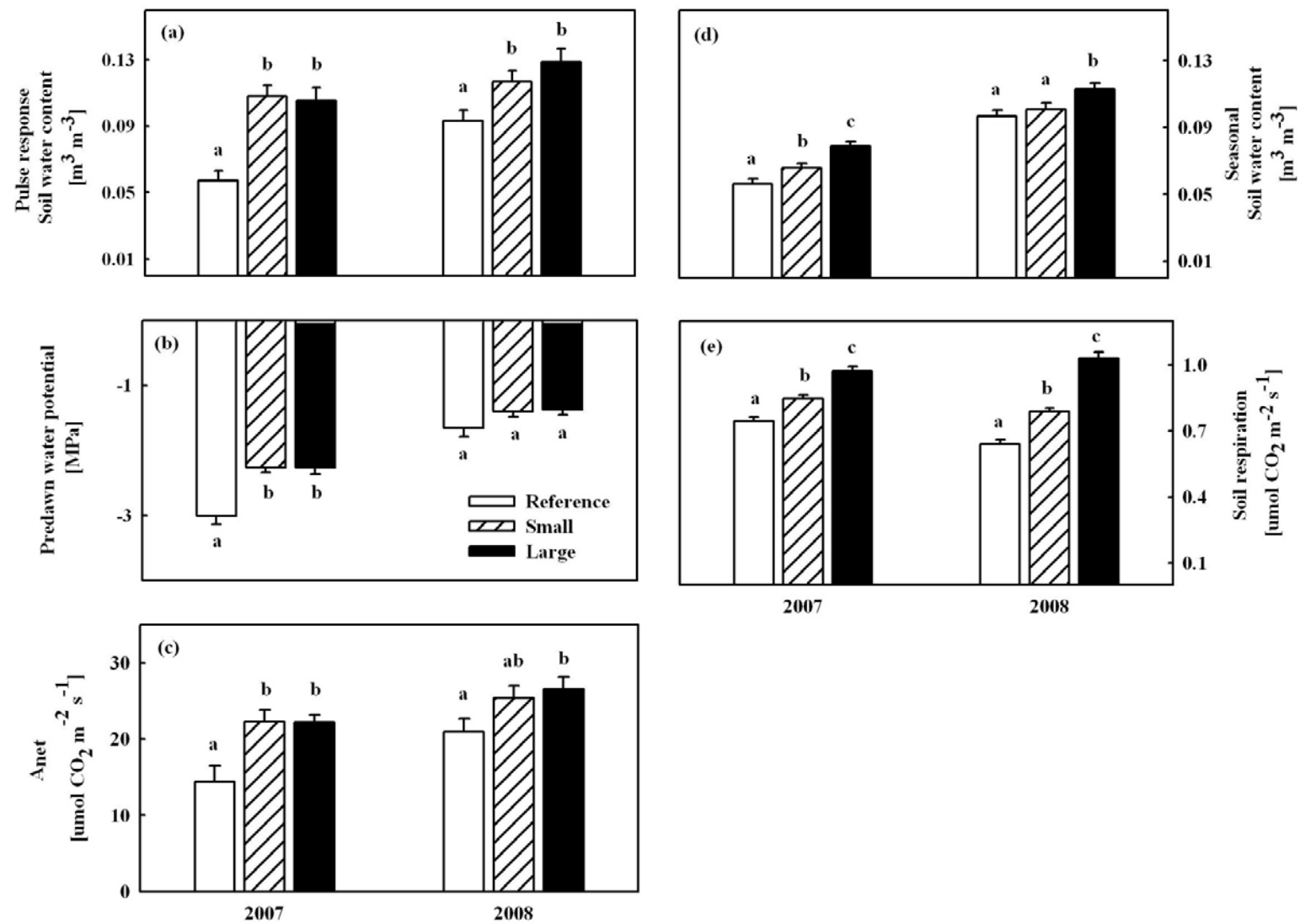


Figure 2.

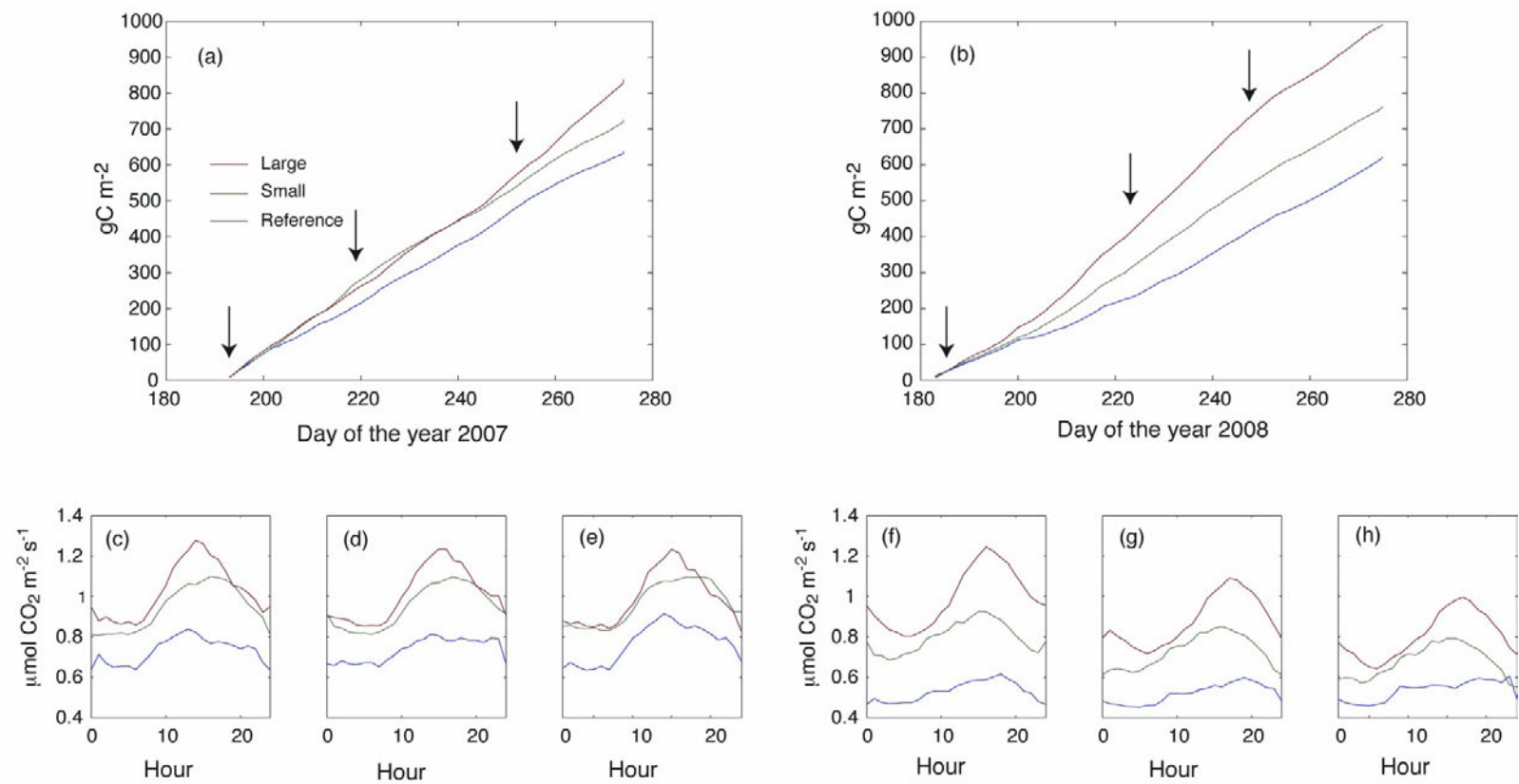


Figure 3.

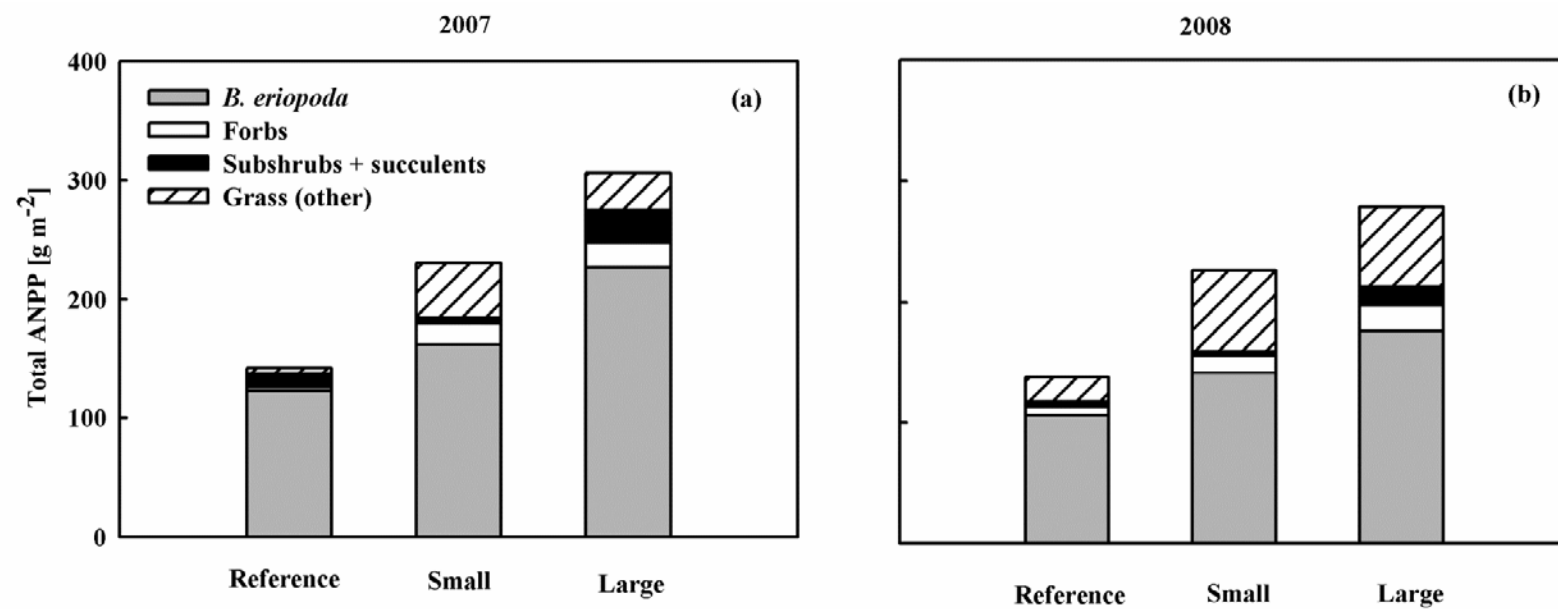


Figure 4.

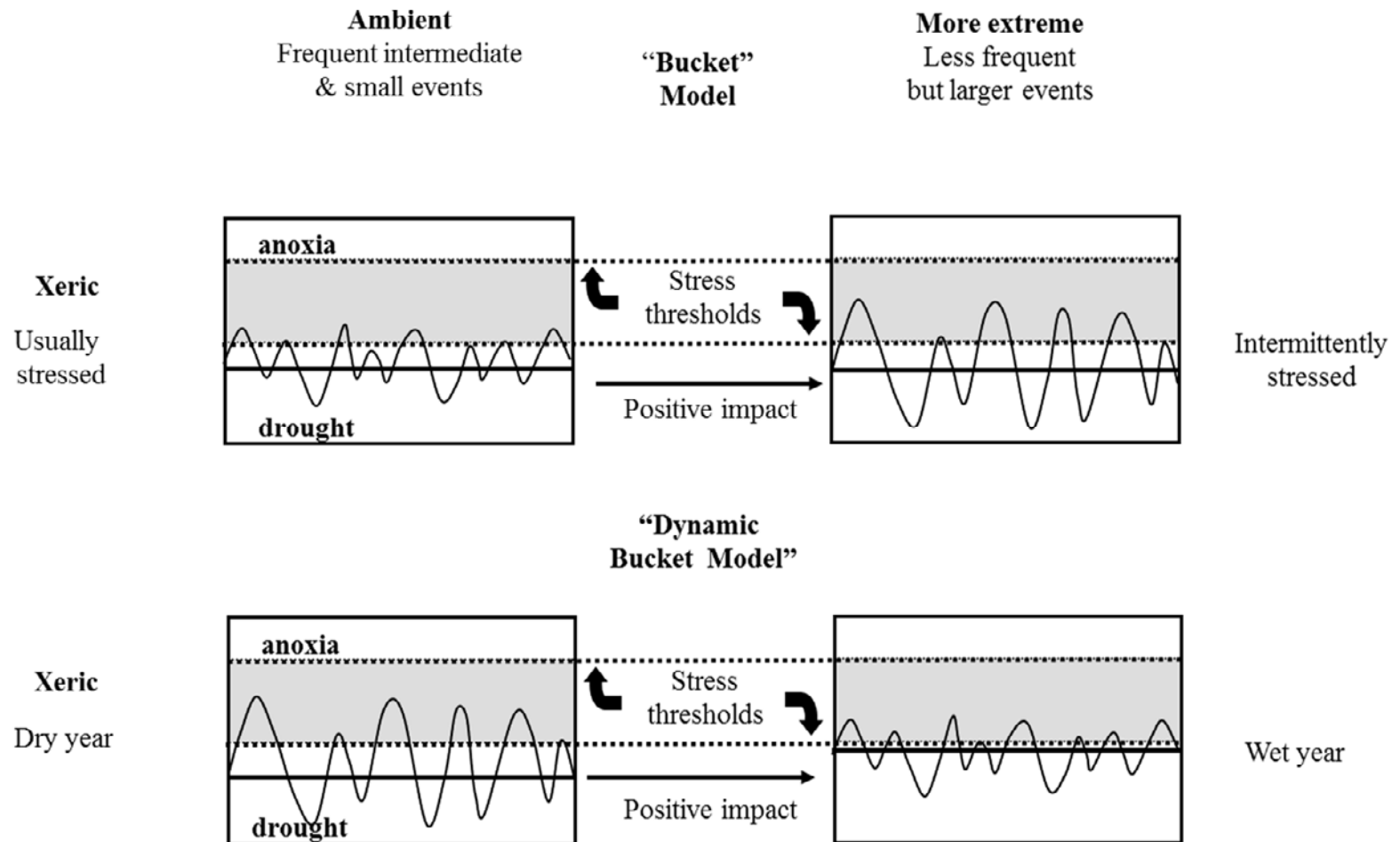


Figure 5.

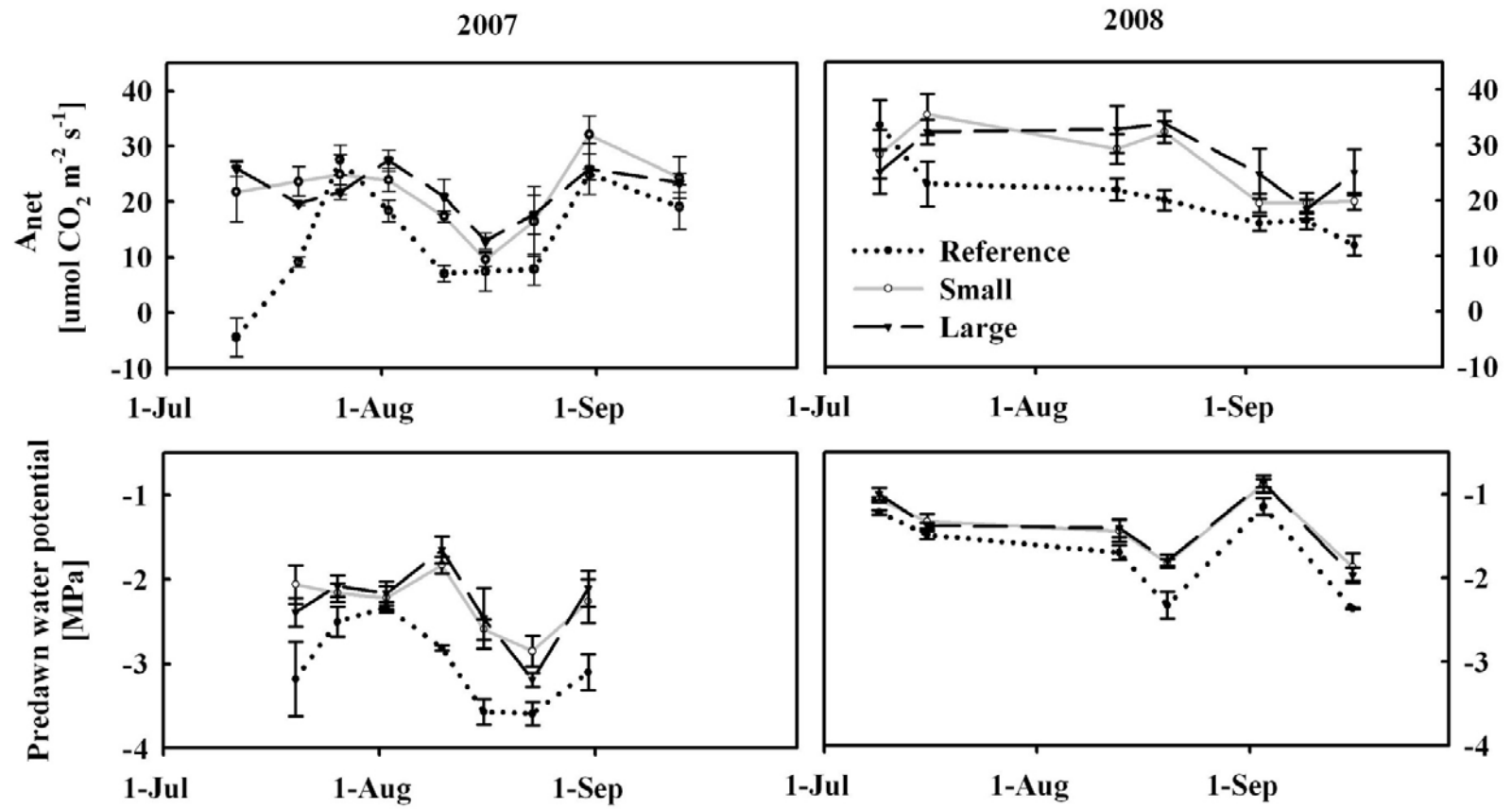


Figure S1.

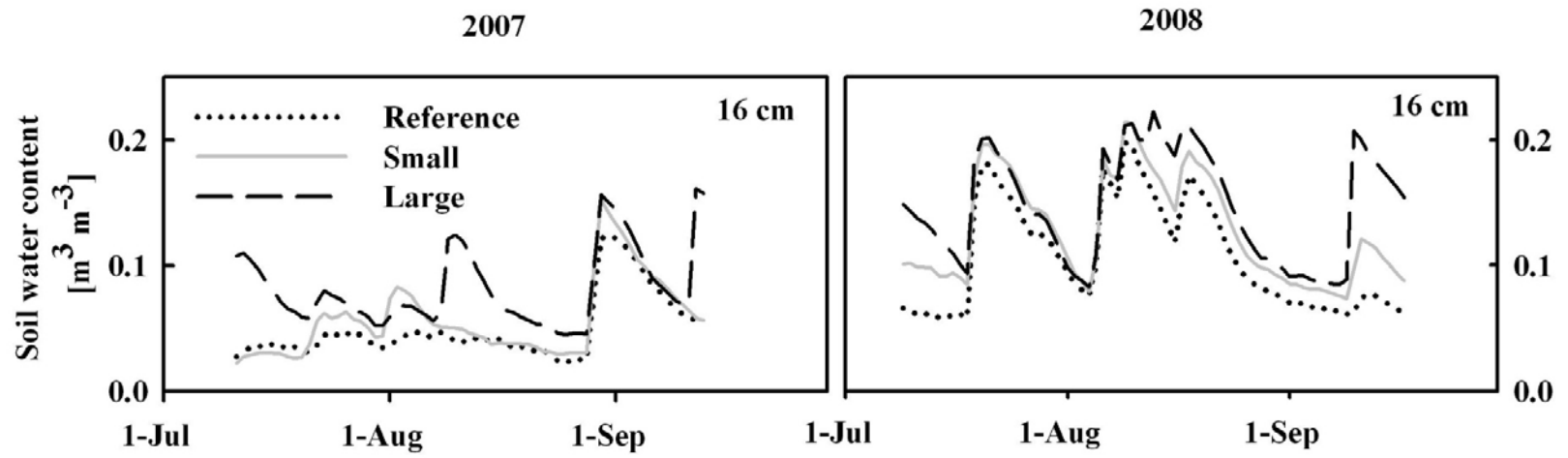


Figure S2.

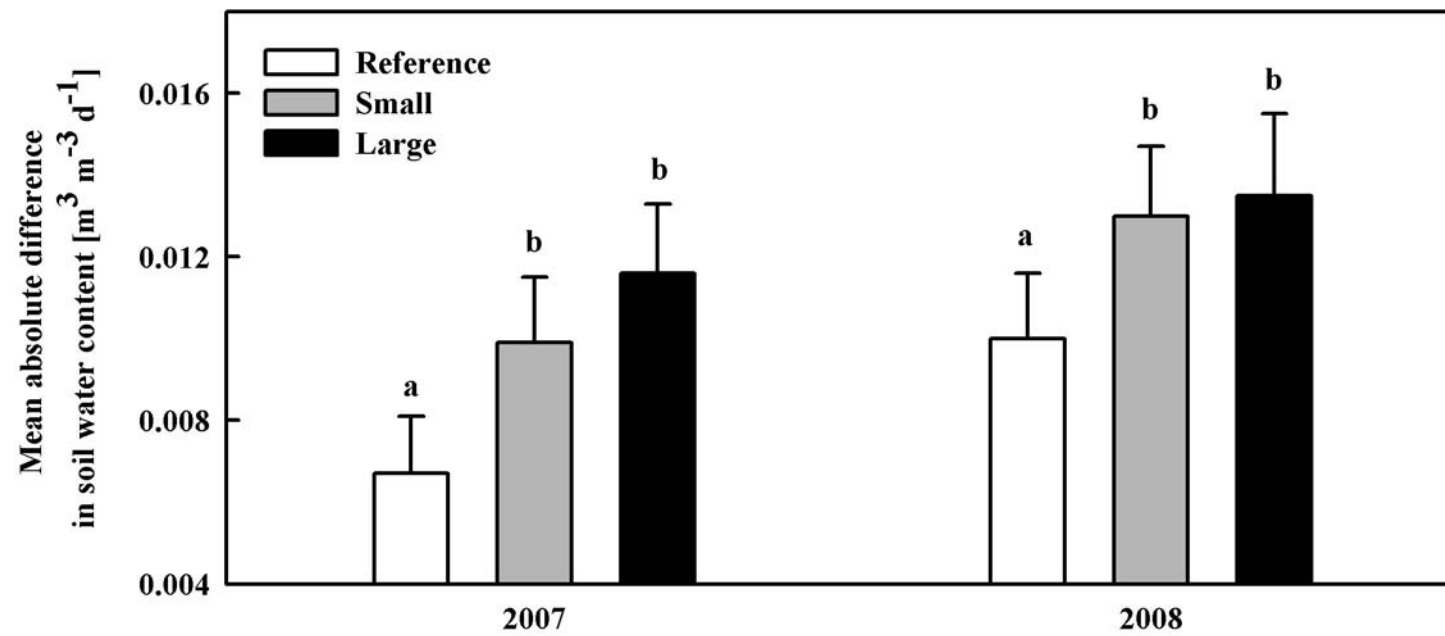


Figure S3

Figure captions

Figure 1. Daily record of physical conditions across treatment and reference plots during the 2007 and 2008 monsoon season. **(a, d)** Rainfall additions include ambient rainfall plus four 5 mm events each month (small) and ambient rainfall plus one 20 mm event each month (large). Reference plots represent ambient precipitation. Bars corresponding with rainfall additions represent the total amount of water that each plot received. **(b, e)** Daily soil moisture content (θ). Error bars were removed for clarity. The average standard error measured 8.6%, 8.5%, and 8% of the mean (2007) and 7.3%, 9.8%, and 6.5% of the mean (2008) for reference, small and large rainfall additions, respectively. **(c, f)** Soil temperature integrated over 2-16 cm depth. Error bars were removed for clarity. The average standard error measured 1.0%, 0.94%, 0.64% of the mean (2007) and 1.17%, 0.93%, 0.94% of the mean (2008) for reference, small and large rainfall additions, respectively. Lines are the mean (unweighted) for each treatment ($n=5$) integrated over 2-16 cm depth and reference ($n = 3$) plots. The mean soil θ (2007 monsoon season): 0.06, 0.11, and 0.10 $\text{m}^3 \text{m}^{-3}$ and mean soil θ (2008 monsoon season): 0.09, 0.12, and 0.13 $\text{m}^3 \text{m}^{-3}$ for reference, small, and large plots, respectively. The mean soil temperature (2007 monsoon season): 27.66, 26.73, and 27.00 $^{\circ}\text{C}$ and mean soil temperature (2008 monsoon season): 25.63, 25.11, and 25.30 $^{\circ}\text{C}$ for reference, small and large plots, respectively.

Figure 2. Components of carbon cycling and soil water dynamics for the 2007 and 2008 monsoon season. **(a)** Mean pulse-response soil θ integrated over 2-16 cm

depth (unweighted), **(b)** Mean predawn leaf water potential (Ψ_{pd}) and **(c)** Mean leaf-level photosynthesis (A_{net}) for the dominant C_4 grass *B. eriopoda* **(d)** Mean seasonal soil θ integrated over 2-16 cm depth (unweighted) and **(e)** Mean soil respiration (R_s). For all plots, different letters are significantly different ($\alpha = 0.05$) based on single factor Analysis of Variance [2008 A_{net} , 2007 & 2008 Ψ_{pd} , 2007 & 2008 ANPP, 2007 R_s] or Kruskal-Wallis test for model significance and all pair wise comparisons [2007 A_{net} , 2007 & 2008 Soil θ (pulse-response & seasonal), 2008 R_s].

Figure 3. Cumulative seasonal carbon release from soil respiration (g C m^{-2}) during the monsoon season of 2007 **(a)** and 2008 **(b)**. Arrows indicate the approximate dates when the large rainfall additions were done. Average diel patterns of soil respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) between large rainfall additions in treatment and reference plots during 2007 **(c-e)** and 2008 **(f-h)**. For example, Fig. 3c represents the average diel patterns between day of the year (DOY) 191 and 212, and Fig. 3d the average diel patterns between DOY 255 and 273.

Figure 4. Aboveground net primary productivity (ANPP) for each plant functional type in the **(a)** 2007 and **(b)** 2008 monsoon season. Bars represent mean ANPP for reference ($n=3$), small rainfall (5 mm per week), and large (20 mm per month) rainfall treatment plots ($n = 5$).

Figure 5. A revised bucket model (Knapp *et al.* 2008) based on interannual variation in mean rainfall. In each figure, the solid black line represents mean soil water content and the undulating line is the variability in soil water content. Xeric ecosystems are in a “non-stressed” state when soil water content falls within the grey area, and are in a “stressed” state when values of soil water content extend beyond the stress-threshold (outside of the grey shaded area). If annual precipitation increases, less variability is needed to reduce stress whereas if annual precipitation decreases, more extreme events are needed to reduce water stress.

Figure S1. Temporal patterns in A_{net} and predawn leaf water potential for the 2007 and 2008 monsoon seasons. Error bars indicate $\pm$ SE of the mean.

Figure S2. Mean daily soil water content at 16 cm for the 2007 and 2008 monsoon seasons. Lines are the mean for each treatment ($n = 5$) and reference ($n = 3$) plots. The mean soil θ at 16 cm (2007): 0.05, 0.06, and 0.08 $\text{m}^3 \text{m}^{-3}$ and mean soil θ (2008): 0.11, 0.13, and 0.15 $\text{m}^3 \text{m}^{-3}$ for reference, small, and large plots, respectively. The average standard error measured 6.47%, 6.56%, 4.69% of the mean (2007) and 4.86%, 3.86%, 3.54% of the mean (2008) for reference, small and large rainfall additions, respectively.

Figure S3. Seasonal mean absolute difference in mean daily soil θ used as a measure of soil water variability across all plots (the seasonal mean (unweighted)

is integrated over 2-16 cm depth). Different letters are statistically significant ($\alpha=0.05$) based on single-factor Kruskal-Wallis test for model significance and all pair wise comparisons.

Chapter 4

Effects of Monsoon Precipitation Variability on the Ecophysiological Response of Two Dominant C₄ Grasses Across an Arid-semiarid Ecotone

¹Michell L. Thomey

Scott L. Collins

William T. Pockman

Michael T. Friggens

Renee F. Brown

Department of Biology MSC03-2020, University of New Mexico, Albuquerque,
NM 87131, USA

¹Corresponding author: Michell L. Thomey, tel 505 277 1727, fax 505 277 5355,
email mlthomey@sevilleta.unm.edu

Author Contributions: MLT, SLC, WTP conceived and designed the experiment and analyses. MLT performed the experiment, analyzed the data, wrote the manuscript; all authors edited the manuscript. MTF, MLT constructed the experimental plots. RFB wrote datalogger programs and advised with installation of all sensors and solar panels.

Abstract

Anthropogenic forcing to the climate system may enhance the intensity of wet and dry periods in the southwestern U.S. We manipulated the size and frequency of precipitation events during the summer monsoon to examine how large, more extreme rainfall patterns with extended dry periods affected the ecophysiological response of two co-occurring perennial grasses, *Bouteloua eriopoda* and *B. gracilis* across an arid-semiarid ecotone. We hypothesized that both species would exhibit: 1) a positive relationship between A_{net} and soil θ because water is the most limiting resource in arid and semiarid ecosystems (Noy-Meir 1973), 2) higher A_{net} and Ψ_{pd} in 30 mm rainfall plots relative to more frequent 10 mm rainfall events because smaller events infiltrate less deeply in the soil and would be more rapidly lost to evapotranspiration. In addition, we hypothesized that 3) *B. eriopoda*, the dominant Chihuahuan Desert grass would recover from extended inter-pulse periods in less time and with higher A_{net} following 30 mm rainfall additions compared to *B. gracilis*, a dominate species in Great Plains shortgrass steppe that receives, on average, 20% more annual precipitation than Chihuahuan Desert grassland. Extreme less frequent and large rainfall events significantly increased soil θ and gave *B. gracilis* the ability to exploit water resources rapidly leading to increased A_{net} and Ψ_{pd} when compared to *B. eriopoda*. In addition, analysis of total leaf nitrogen indicated significantly higher PNUE in *B. gracilis*. A change in climate pattern to more extreme rainfall events may shift current trends such that *B. gracilis* will potentially replace *B. eriopoda* as the dominant species in this desert grassland.

Key words: Leaf gas exchange, *Bouteloua eriopoda*, *B. gracilis*, arid-semiarid grasslands

Introduction

Anthropogenic forcing to the climate system may increase climate variability leading to more extreme precipitation events as well as extended dry periods between rainfall events during the growing season (IPCC 2007; Seager et al. 2007; Diffenbaugh et al. 2008; Barnett et al. 2008; Weiss et al. 2009; Fawcett et al. 2011; Gutzler and Robbins 2010). Increased precipitation variability including more extreme precipitation events is predicted to strongly impact pulse-driven arid-semiarid ecosystems because plant community structure and local ecosystem processes are strongly tied to soil water availability (Noy-Meir 1973; Cable 1975; Schwinning and Sala 2004; Collins et al. 2008). Therefore, impending changes in precipitation regime for regions such as the southwestern U.S. will likely lead to shifts in species composition and distribution, and will alter local ecosystem processes that are strongly tied to water availability (Schlesinger et al. 1990; Williams and Albertson 2006; Pockman and Small 2010).

Among biomes, grasslands are known to be sensitive to rainfall variability (Knapp and Smith 2001; Yang et al. 2008; Yang et al. 2011). In central New Mexico, USA, two climatically-controlled grassland ecosystems converge forming a narrow boundary (e.g., ecotone) between each biome type (Peters et al. 2006a). Chihuahuan Desert grassland (CDG) is primarily located in Mexico but extends north into Arizona, New Mexico, and Texas (Allred 2005). Great Plains shortgrass steppe (SGS) is located along the eastern side of the Rocky Mountains in Colorado with southern extensions into New Mexico and Texas and east into Oklahoma (Lauenroth et al. 2008). Vegetation change caused by climate variability should initially be detected in ecotone communities where species have potentially reached their physiological limits in distribution (Gao and Reynolds

2003). Certainly, the ecotone between CDG and SGS is, in part, influenced by large changes in temperature and precipitation (Gosz 1993; Peters et al. 2006a).

In each biome, the dominant C₄ perennial grasses *Bouteloua eriopoda* (CDG) and *Bouteloua gracilis* (SGS) have sodgrass and bunchgrass growth forms, respectively, and maintain rooting depths in the top 30 cm of the soil (McCulley et al. 2004; Gibbens and Lenz 2001). A shift in species dominance due to modified rainfall patterns could impact local ecosystem processes. For example, *B. gracilis* is generally more tolerant of grazing and fire, is less vulnerable to shrub invasion, and is highly responsive to increased nitrogen (N) availability when compared to *B. eriopoda* that responds more strongly to warmer temperatures (Senock et al. 1994; Lowe et al. 2003; Peters et al. 2006b; Báez et al. 2007; Parmenter 2008; Yanoff and Muldavin 2008; Augustine et al. 2010; Collins et al. 2010; Ladwig et al. 2012). Moreover, *B. gracilis* has also been shown to exclude water resources from seedlings and shrubs within its rooting depth (Aguilera and Lauenroth 1993; Hook and Lauenroth 1994; Lee and Lauenroth 1994; Aguilera and Lauenroth 1995). It is essential to understand how the dominant plant species respond to changes in precipitation in order to predict future boundary dynamics and species composition (Peters et al. 2009).

We examined how large (10 mm) and extreme (30 mm) precipitation events coupled with extended dry periods across an arid-semiarid grassland ecotone affected soil moisture content (θ) and the ecophysiological response of *Bouteloua eriopoda* and *Bouteloua gracilis* across an arid-semiarid ecotone. We defined 10 mm and 30 mm rainfall events as “large” and “extreme” because at our study site 70% of monsoon rainfall events are ≤ 5 mm and occur approximately every 5 days, while 14% and 2% of

monsoon rainfall events are ≥ 10 mm and ≥ 30 mm, respectively (1988-2008). We hypothesized that: 1) a positive relationship between A_{net} and soil θ would occur in both species because water is the most limiting resource in arid and semiarid ecosystems (Noy-Meir 1973), 2) within both species, A_{net} and Ψ_{pd} would be significantly higher in 30 mm rainfall plots relative to more frequent 10 mm rainfall events because smaller events infiltrate less deeply in the soil and would be more rapidly lost to evapotranspiration, and 3) *B. eriopoda*, the dominant Chihuahuan Desert grass would recover from extended inter-pulse periods in less time and with higher A_{net} following 30 mm rainfall additions when compared to *B. gracilis* that dominates in Great Plains shortgrass steppe that receives, on average, 20% more annual precipitation than Chihuahuan Desert grassland.

Materials and methods

Study area

We experimentally controlled the magnitude and frequency of rainfall events at the Sevilleta Long Term Ecological Research site (LTER) located on the Sevilleta National Wildlife Refuge (SNWR; 34.324°, -106.706° WGS84) approximately 80 km south of Albuquerque, New Mexico, USA. The SNWR occurs at a transition between Chihuahuan Desert grassland and shrubland, Great Plains shortgrass steppe, piñon-juniper woodland and riparian vegetation along the middle Rio Grande Valley. Thus, the SNWR provides an ideal setting to study changes in precipitation regime across ecotones. Grazing has been excluded from the SNWR since 1973. Climate at the SNWR is characterized as arid-semiarid with dry cool winters and springs. Mean annual temperature is 13.1°C with an average low of 1.6°C in January and a high of 25.1°C in July. Precipitation is highly variable within and between years (Pennington and Collins

2007). The SNWR receives 250 mm yr⁻¹ of precipitation of which 132 mm (53%), on average, occurs during the summer monsoon season (Muldavin et al. 2008). In this study, each experimental plot received 120 mm of monsoon precipitation (the 20 year, June-September mean; 1988-2008); a 30 mm pre-monsoon pulse in June 2010 and 90 mm delivered by the two treatments July-September 2010. The data presented here represent mean soil θ for the months that correspond with field campaigns (July-August). For the 2010 monsoon season, each site received 111 mm, 127 mm, and 102 mm of ambient rainfall for CDG, SGS and ecotone, respectively.

Study sites

Prior to the 2010 monsoon season, three study sites were established along an 8 km transect spanning the arid-semiarid grassland boundary. One site was located in CDG dominated by *B. eriopoda*, a second site was located in SGS dominated by *B. gracilis*, and a third site was located at the ecotone where *B. eriopoda* and *B. gracilis* are co-dominant. Plant cover at the CDG site consists of ~ 90% *Bouteloua eriopoda* with *Muhlenbergia arenicola*, *Sporobolus* spp., *Sphaeralcea* spp., *Gutierrezia sarothrae*, and *Hoffmannseggia drepanocarpa* as subdominant species. Plant cover at the SGS site consists of ~75% *B. gracilis* with *Muhlenbergia arenicola*, *Chamaesyce* spp., and *Hymenopappus filifolius* as subdominant species. At the ecotone site *B. eriopoda* and *B. gracilis* account for ~ 55% and ~ 38% plant cover, respectively. Subdominant species include *Pleuraphis jamesii*, *Sporobolus* spp., *Solanum elaeagnifolium*, and *Chaetopappa ericoides*.

Experimental design

In 2009, ten 2.13 m x 2.44 m complete rain-out shelters were constructed in a 10 m x 40 m area at each site for a total of 30 rain-out shelters. All sites are on level soil and in homogenous vegetation. Rain-out shelters were assembled using two angled-iron frames 2.44 m wide. Each angled-iron frame was buried in the soil for a maximum shelter height of 1.22 m (frame #1) angled to a minimum height of 0.91 m (frame #2) and anchored at each corner using galvanized cable fastened to metal posts that were driven into the soil. Roofing consisted of four 0.61 m x 2.44 m clear polycarbonate panels (Suntuf®*Plus*; Palram Americas, Kutztown, PA) that eliminated UV radiation but transmitted 90% of visible light. This roofing was successfully used in a similar rain-out shelter design (Schwinning et al. 2003). Each roofing panel was fastened to two 2.13 m x 2.44 m removable wood frames that were secured to each angled iron frame. Rain gutters were attached to each rain-out shelter with an average downspout extending 2 m – 5 m to divert ambient rainfall away from the experimental plots. In addition, aluminum flashing was buried to 10 cm along the perimeter of each rain-out shelter to avoid run-on of ambient rainfall. The majority of *B. eriopoda* and *B. gracilis* root mass radially extends no more than 30-40 cm from the plant center (Lee and Lauenroth 1994; Gibbens and Lenz 2001). Nevertheless, we limited our measurements to a 1m² subplot located in the center of each rainout shelter leaving a 50 cm buffer along the perimeter. At each site, one un-sheltered ambient plot served as a reference in order to monitor shelter effects.

One month prior to rainfall treatments (1 June 2010), ambient precipitation was excluded from all experimental plots in order to reach consistent soil moisture across all sites. This dry period was followed by a 30 mm pre-monsoon rainfall event that was

applied to all experimental plots (15 June 2010) in order to initiate the summer growing season (Ignace et al. 2007). Starting 1 July 2010, experimental plots were randomly assigned to one of two rainfall treatments (n=5 per treatment); one 30 mm rainfall event applied once per month (e.g. every 30 days) or three 10 mm rainfall events applied three times per month (e.g. every 10 days). Each experimental plot was irrigated using a hand-held garden wand that delivered water in a 360° pattern with an average flow rate of 15.7 L min⁻¹. Water used for irrigation was obtained from a reverse-osmosis (RO) system located at the University of New Mexico and transported to storage tanks located at each site. Treatment RO water contained 0.67 ppm NO₃-N and 1.01 ppm NH₄-N (Thomey et al. 2011).

Sensor and field measurements

Sensors were installed to measure soil moisture (θ) over a 15 cm depth (EC-5 Decagon, Pullman, WA) and soil temperature (Ts) at 2 cm depth using copper constantan thermocouple (Omega Engineering, Stamford, CT) in all experimental and reference plots (n=10 and n=1, respectively). At each site, air temperature (Campbell Scientific CS-107 and radiation shield, Logan, UT) and relative humidity (ibutton DS1923-F5; Maxim Integrated Products, Sunnyvale, CA) were monitored in one 10 mm and one 30 mm rainfall addition plot (n=2) and in the reference plot (n=1). Air temperature (Ta) sensors were installed 33 cm above the soil surface and relative humidity (Rh) sensors were installed 20 cm above the soil surface. Photosynthetically active radiation (PAR; LI-190 quantum sensor, LI-COR, Lincoln, NE) was measured under one rain-out shelter and compared with an ambient (unsheltered) PAR sensor located within 100 m of the

research site. Throughout the monsoon season, all measurements were recorded every 5 min and averaged every 15 minutes.

Leaf-level gas exchange (A_{net}) was measured using a Li-6400 portable photosynthesis system (Li-Cor, Lincoln, NE, USA) with a standard leaf chamber. Throughout the monsoon season (July-August), field campaigns occurred at the beginning of each month 24 hours prior (pre-pulse) to the initial 10 mm and 30 mm rainfall applications and at 1, 3, and 5 days following each rainfall addition. Additional field campaigns across all rainfall treatments occurred 24 hours prior to and following each successive 10 mm rainfall event until months end. During each field campaign, all sites and experimental plots were sampled in random order. Measurements were recorded on 1-2 fully expanded leaves of *B. eriopoda* (CDG), *B. gracilis* (SGS), and from both species at the ecotone site. Irradiance (red/blue LED light source) was set to saturating light conditions ($1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) that had been determined by light response curves. At each site, the CO_2 concentration ($400 \mu\text{mol mol}^{-1}$) and block temperature were set to ambient conditions prior to the first measurement and held constant across all experimental plots in order to maintain consistent chamber conditions throughout the measurement period (0800-1400 hours all sites). Leaf area was determined by multiplying the measured width of each leaf by the length of the chamber. Rates of A_{net} were corrected for leaf area using Li-6400 simulator software (OPEN V6).

At each field campaign, predawn leaf xylem pressure potentials (Ψ_{pd}) were measured on 2-3 leaves of *B. gracilis*, or *B. eriopoda* at the SGS and CDG sites and from both species at the ecotone site. Leaves were collected (pre-dawn) and put immediately into plastic bags, stored in a cooler and returned to the laboratory to be measured with a

Scholander-type pressure chamber (PMS, Model 1000. PMS Instrument Co. Corvallis, OR).

Following A_{net} and Ψ_{pd} measurements, leaf samples were oven dried at 60°C for 24 hours. We selected leaf samples (n=82) representing the measured range of A_{net} for each species at the ecotone site to determine leaf nitrogen concentration and photosynthetic nitrogen use efficiency (PNUE). For each leaf sample, $\text{PNUE} = A_{\text{net}} [\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}] / \text{N} [\text{mol m}^{-2}]$. Leaf nitrogen concentration was determined using a Costech ECS 4010 Elemental Analyzer coupled to a Thermo Finnigan Delta Plus mass spectrometer via a CONFLO II interface.

Data analysis

Data analysis was completed using SAS (v 9.2, Cary, NC, USA). To test for differences between treatment and species means within and across sites, we used a single-factor analysis of variance (PROC ANOVA: Ta, Rh [SGS, ecotone], A_{net} [CDG, ecotone, cross site - *B. gracilis* 10 mm SGS and *B. gracilis* 10 mm ecotone, *B. eriopoda* 10 mm CDG and *B. eriopoda* 10 mm ecotone], Ψ_{pd} [CDG, SGS, ecotone], soil θ [SGS]) with a Bonferroni test for multiple comparisons when the ANOVA model was significant at $\alpha = 0.05$ (A_{net} pre- vs. post-pulse dates). Data that did not meet normality and equal variance assumptions of ANOVA were log or square root transformed. A Kruskal-Wallis test (PROC npar1way; Wilcoxon's) was used to test for model significance and for multiple comparisons between means whenever the data failed to meet the assumptions of ANOVA despite transformation (Ts, Rh [CGD], PAR, A_{net} [SGS, cross site - *B. gracilis* 30 mm SGS and *B. gracilis* 30 mm ecotone, *B. eriopoda* 30 mm CGD and *B. eriopoda* 30 mm ecotone], soil θ [CDG, cross site], PNUE, soil texture). We used simple

linear regression (PROC REG) to analyze the relationship between A_{net} and soil θ . Because A_{net} lagged behind soil θ , we used 3-5 day post-pulse mean daily soil θ in our regression analysis depending on treatment and study site. Additional information for data analysis is as follows: 1) To verify shelter effects, the daily mean of T_a , T_s , R_h and the hourly mean for PAR were compared between rainfall treatments and reference plots throughout the study period (July-August), 2) Measures of A_{net} and Ψ_{pd} were recorded on multiple leaves within a plot and averaged such that each plot represented an experimental unit ($n=5$; 10 mm and $n=5$; 30 mm rainfall treatments), 4) For A_{net} pulse response and drought recovery, the mean pre-pulse measure of A_{net} (day -1) was analyzed as the control by which each mean post-pulse date was compared to within a species, 5) For PNUE analysis at the ecotone site we statistically tested leaf samples grouped by species because there were no significant treatment effects.

Results

Shelter effects

Within each site, mean daily T_a and R_h were not significantly different between rain-out shelter and ambient plots (Table 1). Rain-out shelters significantly increased mean daily T_s but this varied by location. At the CDG site, T_s was significantly higher in the 30 mm rainfall addition plots when compared to the 10 mm rainfall addition and ambient plots ($P = 0.005$, $H=10.66$; Table 1). At the ecotone site T_s was significantly higher under rain-out shelters ($p < 0.001$, $H=19.67$; Table 1). There was no significant shelter effect on T_s at the SGS site (Table 1). Over the course of a day, rain-out shelters reduced PAR, on average, up to $34.1 \pm 6.8\%$ (03:00 – 19:00). However, the daily peak

measure of PAR under the rain-out shelters did not fall below saturating light conditions for A_{net} ($1000 \mu\text{mol m}^{-2} \text{s}^{-1}$).

Soil water dynamics

Throughout the study period, less frequent 30 mm rainfall additions significantly increased mean seasonal soil θ when compared to plots receiving three 10 mm rainfall additions each month at the SGS ($p = 0.001$, $H=10.55$; Fig 1a) and CDG sites ($p < 0.001$, $H=13.20$; Fig. 1b). Even though there was no significant treatment effect on mean soil θ at the ecotone site, soil θ was significantly higher on the day the 30 mm rainfall addition occurred and for at least eight consecutive days thereafter when compared to the eight day post rainfall soil θ of plots that received 10 mm rainfall additions. This finding was consistent across all sites (Fig. 1a-d). Moreover, for each rainfall addition treatment we found a positive relationship between mean soil θ and A_{net} within both species except for *B. eriopoda* at the ecotone site (Fig. 2a-d).

Monsoon rainfall variability: intraspecific plant response

At the CDG site, mean A_{net} ($p = 0.0062$; $F = 7.78$) and mean Ψ_{pd} of *B. eriopoda* were significantly higher in the single 30 mm rainfall addition plots compared to the plots that received three 10 mm rainfall events per month (Table 2). At the SGS site, mean A_{net} and Ψ_{pd} of *B. gracilis* did not differ between plots that received a single 30 mm rain event versus three 10 mm rainfall events each month (Table 2). At the ecotone site, mean soil θ was not significantly different between treatments and there was no difference in mean A_{net} and Ψ_{pd} in either species between the single 30 mm and three 10 mm rainfall treatments (Table 2).

Monsoon rainfall variability: interspecific plant response

Although there was no significant difference in mean A_{net} and Ψ_{pd} within *B. eriopoda* and *B. gracilis* at the ecotone site, mean A_{net} and Ψ_{pd} differed significantly between each species even though mean soil θ was similar for each treatment (Table 2; Fig. 3a-d). When compared to *B. eriopoda*, mean A_{net} was, on average, 35% and 44% higher for *B. gracilis* leaves measured in the 10 mm and 30 mm rainfall addition plots, respectively. Moreover, *B. gracilis* maintained higher mean Ψ_{pd} in 10 mm (-3.78 ± 0.17 MPa; $p = 0.021$, $H = 5.30$; Fig. 3b) and 30 mm rainfall addition plots when compared to *B. eriopoda* although mean Ψ_{pd} was not significantly different in the 30 mm rainfall addition treatment (-3.78 ± 0.15 MPa; Fig. 3d). In addition, regardless of rainfall treatment, PNUE was significantly higher in *B. gracilis* ($325.4 \pm 30.1 \mu\text{mol CO}_2 [\text{mol N}]^{-1} \text{s}^{-1}$; $P < 0.01$, $H = 12.60$) when compared to *B. eriopoda* ($158.7 \pm 23.9 \mu\text{mol CO}_2 [\text{mol N}]^{-1} \text{s}^{-1}$) at the ecotone site.

Across all sites, pulse-response time series measurements show that *B. gracilis* rapidly recovered from drought with significantly higher daily mean A_{net} 1-day following a rainfall addition when compared to pre-pulse measures of mean A_{net} in both rainfall treatments (10 mm: $p = 0.01$, $F = 3.63$; 30 mm: $p < 0.01$, $F = 12.17$; 10 mm ecotone: $p < 0.01$, $F = 8.74$, 30 mm ecotone: $p < 0.01$, $F = 12.17$; Fig. 4a-d). In contrast, while *B. eriopoda* did respond with increased daily mean A_{net} in 10 mm rainfall addition plots, a significantly higher post-pulse response in daily mean A_{net} was only measured in 30 mm rainfall addition plots 1-5 days following a rainfall application across study sites (30 mm: $p = 0.01$, $F = 9.11$; 30 mm ecotone: $p = 0.01$, $F = 5.77$; Fig. 4a-d).

Discussion

We manipulated rainfall across an arid-semiarid grassland ecotone and measured the response of two dominant grassland species to determine how climate change may affect boundary dynamics and modify species composition. Currently, monsoon precipitation at the SNWR is dominated by rainfall events ≤ 5 mm, and the abundance of *B. eriopoda* is increasing at a greater rate than that of *B. gracilis* (1989-2007; Collins and Xia, unpublished data). Our data suggest that a shift towards large or extreme infrequent rainfall events could favor increased dominance by *B. gracilis*.

Monsoon rainfall variability: A_{net} and soil water dynamics

In arid-semiarid grasslands, water strongly controls primary productivity (Noy-Meir 1973; Cable 1975; Lauenroth and Sala, 1992; Scanlon et al. 2005; Muldavin et al. 2008). In this experiment, there was a positive relationship between A_{net} and soil θ for both species except for *B. eriopoda* measured at the ecotone site (Fig. 2). Along with pulsed rainfall events, soil texture, evaporation, run-off, and canopy interception influence soil water that is available for photosynthesis (Loik et al. 2004; McLaren et al. 2004). We did not find a significant difference in soil texture between our sites (Table 3). However, mean plant cover was highest at the ecotone site (0.55 ± 0.02 m²) when compared to the CDG (0.52 ± 0.03 m²) and SGS (0.35 ± 0.02 m²) sites. This also corresponded with increasing soil θ from ecotone < CDG < SGS (Fig. 1a-c). While we were unable to exclude a few ambient rainfall events during high winds at the SGS site, these results suggest that canopy interception or plant utilization due to increased cover may influence mean daily soil θ (Hamerlynck et al. 2010; Hamerlynck et al. 2011). In addition, rain-out shelters also significantly increased T_s at the ecotone site (Table 1)

which could increase soil water evaporation impeding plant water uptake (Huxman et al. 2004). Nevertheless, contrary to *B. eriopoda*, we did find a positive relationship between A_{net} and soil θ for *B. gracilis* at the ecotone site (Fig. 2b).

Monsoon rainfall variability: intraspecific plant response

Both *B. gracilis* and *B. eriopoda* physiologically respond to 5 mm rainfall events, but large (≥ 20 mm) rainfall events are required to significantly increase ANPP (Sala and Lauenroth 1982; Muldavin et al. 2008; Thomey et al. 2011). In our study, 30 mm rainfall events significantly increased mean soil θ when compared to 10 mm rainfall additions at the CDG and SGS sites, but significant treatment differences in mean A_{net} were only observed in *B. eriopoda* at the CDG site (Table 2). Moreover, there were no treatment differences in mean soil θ and mean A_{net} , and Ψ_{pd} within *B. gracilis* and *B. eriopoda* at the ecotone site (Table 2). As previously mentioned, the lack of treatment difference in soil θ at the ecotone site may be an artifact of canopy interception or differences in plant utilization. Across all sites, 30 mm rainfall additions significantly increased soil θ on each application date and for eight consecutive days thereafter when compared to plots receiving 10 mm rainfall additions (Fig. 1a-d). However, the magnitude of the response and the sustained difference in soil θ was highest at the CDG site and this was reflected in significant treatment effects on A_{net} for *B. eriopoda* (Table 2). This implies that shallow-rooted species such as *B. gracilis* and *B. eriopoda* do not physiologically distinguish between large and extreme rainfall events, given our application frequency, without sufficient divergence in soil θ (~ 100 % difference between treatments at the CDG site). These findings are similar to previous research where there was no difference in A_{net} and Ψ_{pd} when *B. eriopoda* was measured within 24 hours of a 5 mm and 20 mm

rainfall addition, but significant differences in end-of- season ANPP occurred because 20 mm rainfall events maintained significantly higher soil θ longer than 5 mm rainfall additions (Thomey et al. 2011). Plants may also gauge the size of rainfall events based on the magnitude of the effect on plant water potential (Schwinning et al. 2003). Our results indicate that *B. eriopoda* was increasingly drought stressed in 10 mm plots but significant treatment differences did not occur (Table 2). Overall, the degree to which the landscape and soil filters precipitation events not only affects water availability (Loik et al et al. 2004) but the duration of available soil water which serves as a measure of pulse magnitude for *B. eriopoda* and *B. gracilis*. At the local scale, this likely contributes to the weak correlation between ANPP and precipitation (Osterheld et al. 2001; Yahdjian and Sala 2006) especially considering the difference in soil θ across our 8 km transect (Table 2).

Monsoon rainfall variability: interspecific plant response

An interesting finding was the difference in mean A_{net} and Ψ_{pd} between *B. eriopoda* and *B. gracilis* at the ecotone site even though soil θ was equal across rainfall treatments. In 10 mm and 30 mm rainfall addition plots, *B. gracilis* consistently maintained higher mean A_{net} and Ψ_{pd} (less negative) compared with *B. eriopoda* (Fig. 3a-d). Since both species have similar rooting depths, it is conceivable that competition for water could occur (Goldberg and Novoplansky 1997; Gibbens and Lenz 2001). Other studies show that *B. gracilis* pre-empt water resources from seedlings and shrubs within its rooting depth (Aguilera and Lauenroth 1993; Hook and Lauenroth 1994; Lee and Lauenroth 1994; Aguilera and Lauenroth 1995), while *B. eriopoda* is less drought resistant when growing with other arid-semiarid C_4 perennial grasses (Senock et al.

1994). Although not significant, cross site mean A_{net} and Ψ_{pd} decreased on average 15% and 8%, respectively, from the CDG and SGS sites to the ecotone site (Table 2). However, the dampened ecophysiological response likely reflects the average decrease (34%) in soil θ at the ecotone site.

Similar to A_{net} and Ψ_{pd} , treatment differences did not occur in PNUE at the ecotone site. However, *B. gracilis* maintained significantly higher PNUE ($325.4 \pm 30.1 \mu\text{mol CO}_2 [\text{mol N}]^{-1} \text{s}^{-1}$; $p < 0.001$, $H = 12.6$) when compared to *B. eriopoda* ($158.7 \pm 23.9 \mu\text{mol CO}_2 [\text{mol N}]^{-1} \text{s}^{-1}$). In general, C_4 species have high PNUE due to saturating CO_2 concentrations at the site of rubisco (Sage and Pearcy 1987; Simioni et al. 2004), but PNUE can also vary within species that exhibit the C_4 pathway (Bowman 1991; Anten et al. 1995). The fact that *B. gracilis* has significantly higher PNUE than *B. eriopoda* has several implications that warrant further study. First, high PNUE in *B. gracilis* may attribute to increased photosynthetic capacity despite low nitrogen availability in arid-semiarid ecosystems (Fig. 3; Anten et al. 1998; Hooper and Johnson 1999; Gong et al. 2011). Second, *B. gracilis* could invest more nitrogen into other processes like root or leaf production (Sage and Pearcy 1987). Third, the efficient use of nitrogen suggests that *B. gracilis* may be co-limited by nitrogen when compared to *B. eriopoda* that is primarily limited by water availability (Stephens and Whitford 1993; Thomey et al. 2011). Moreover, *B. eriopoda* may be a poor competitor with a shift to large or extreme precipitation events in addition to increased nitrogen deposition at the SNWR (Báez et al. 2007).

One of the factors that contribute to increased competitive ability in plants that are equal in other regards is the timing in which each species initiates resource uptake

and growth (Mooney 1972). For example, soil water is depleted faster in plots with *Bromus tectorum* (cheatgrass) leading to reduced productivity and water status of *Chrysothamnus viscidiflorus* and *Stipa comata* when compared to plots without *B. tectorum* (Malgoza et al. 1990). We hypothesized that *B. eriopoda*, the dominant Chihuahuan Desert grass, would recover from extended dry periods (10 days and 30 days) in less time and with higher A_{net} following 10 mm and 30 mm rainfall additions when compared to *B. gracilis*. Contrary to our hypothesis, *B. eriopoda* increased A_{net} over time but the response was not significantly different from pre-pulse measures of A_{net} in the 10 mm rainfall addition plots (Fig. 4a, b). Within plots that received less frequent 30 mm rainfall additions, significantly higher post-pulse A_{net} was measured in *B. eriopoda* within 1-5 days (Fig. 4c, d). In contrast, *B. gracilis* rapidly recovered from prolonged inter-pulse periods with significantly higher A_{net} 1-day following 10 mm and 30 mm rainfall additions (Fig. 4a-d). Many arid-semiarid herbaceous plants make adjustments in resource allocation between roots and shoot growth according to water availability (Schenk and Jackson 2002). *Bouteloua eriopoda* responds to drought by allocating more biomass to roots and less to shoots (Fernández et al. 2002). This reduction in aboveground biomass conserves water loss but it also limits leaf area for photosynthetic carbon gain (Fernández and Reynolds 2000). Research by Ingace et al. (2007) and Hamerlynck et al (2011) notes A_{net} development appears to track leaf area in native desert grass species. Alternatively, in response to drought, *B. gracilis* maintains tightly curled green leaves (Ares 1976) and discards deeper suberized roots preserving shallow newly differentiated roots that are responsible for the majority of soil water uptake (Lauenroth et al. 1987). Following a rainfall event (≥ 5 mm) *B. gracilis* is able to

increase leaf water potential within 24 hours using available root mass and initiates new root growth 48 hours later to sustain increased plant water status (Sala and Lauenroth 1982; Lauenroth et al. 1987). Certainly, the higher PNUE that we found in *B. gracilis* supports rapid up-regulation of A_{net} (Lambers et al. 2008). Although beyond the scope of this study, these response patterns may also be due to differences in the rooting patterns between *B. eriopoda* and *B. gracilis* (Stephens and Whitford 1993). For example, Eissenstat and Caldwell (1988) determined that the difference in the rate of soil water extraction between two tussock grass species (*Agropyron desertorum* and *A. spicatum*) was caused by different root lengths despite similar rooting depths.

In this study, a shift in precipitation regime towards infrequent large and extreme rainfall events gave *B. gracilis* the ability to exploit water resources rapidly leading to increased water status and carbon gain when compared to *B. eriopoda* at the ecotone site. Thus, increased dominance by *B. gracilis* is highly probable which could have profound impacts on local ecosystem processes. However, the difference in timing of A_{net} up-regulation may sustain coexistence because, by default, *B. gracilis* and *B. eriopoda* temporally partition large and extreme pulses (Chesson et al. 2004). Understanding species response as well as potential changes in species composition is important for scaling-up estimates of carbon uptake, and because species composition will affect how ecosystems respond under future climate change scenarios (Wardle et al. 2011).

Acknowledgements

Special thanks to: Lily Shuster for your tireless efforts, Doug Moore, Ben Specter, Amanda Boutz, Brenda Nieto, Scott Johnson, Sam & Rob, Michael Donovan, Tim Allen, Amaris Swann, John Mulhouse, Laura Ladwig, Alfred Garcia, Rob Pangle, Judd Hill, and the SNWR. This research was supported by the U.S. Department of Energy's Office of Science (BER) through the Western Regional Center of the National Institute for Climatic Change Research. Partial funding was also provided by a National Science Foundation grant to the University of New Mexico for Long-term Ecological Research. Additional funding for MLT was provided by the Sevilleta LTER summer fellowship, T&E Inc., UNM Department of Biology Alumni Scholarships, UNM BGSA - GRAC, UNM - SRAC, and UNM - RPT.

Table 1. Shelter effects on microclimate at each site

Chihuahuan Desert grassland	Air temperature [°C]	Relative humidity [%]	Soil temperature [°C]
Ambient	25.32 ± 0.28 [ns]	46.95 ± 2.00 [ns]	29.40 ± 0.32 [ac]
10 mm rainfall	25.33 ± 0.27 [ns]	45.49 ± 1.89 [ns]	28.81 ± 0.27 [a]
30 mm rainfall	25.37 ± 0.27 [ns]	46.01 ± 1.89 [ns]	30.12 ± 0.26 [c]
Ecotone			
Ambient	25.14 ± 0.28 [ns]	47.88 ± 1.91 [ns]	28.41 ± 0.27 [a]
10 mm rainfall	25.05 ± 0.27 [ns]	46.45 ± 1.87 [ns]	29.29 ± 0.29 [b]
30 mm rainfall	25.04 ± 0.27 [ns]	46.47 ± 1.74 [ns]	30.29 ± 0.33 [c]
Shortgrass steppe grassland			
Ambient	25.31 ± 0.30 [ns]	45.33 ± 2.27 [ns]	29.77 ± 0.37 [ns]
10 mm rainfall	25.27 ± 0.28 [ns]	47.31 ± 2.30 [ns]	29.40 ± 0.38 [ns]
30 mm rainfall	25.25 ± 0.28 [ns]	44.35 ± 1.85 [ns]	29.59 ± 0.37 [ns]

^aEach value represents the seasonal mean ± SE. For each site n = 1 for ambient and for 10 mm and 30 mm rainfall additions.

^bWithin each study site, ns = no significant difference between means; different letters note means are significantly different ($\alpha = 0.05$) based on Kruskal-Wallis test for model significance and all pairwise comparisons.

Table 2. Intraspecific response and soil moisture at each site for July-August 2010 season.

Site	A_{net} [$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$]	Leaf water potential [-Mpa]	Soil water content [$\text{m}^3 \text{ m}^{-3}$]
Endpoints	Mean [$\pm$ SE]	Mean [$\pm$ SE]	Mean [$\pm$ SE]
BOER _[CDG] 10 : BOER _[CDG] 30	7.00 [0.57] : 10.23 [0.88] *	4.03 [0.13] : 3.78 [0.15]	0.07 [0.002] : 0.10 [0.005] **
BOGR _[SGS] 10 : BOGR _[SGS] 30	11.21 [0.88] : 13.88 [1.02]	3.51 [0.12] : 3.27 [0.09]	0.10 [0.004] : 0.12 [0.005] **
Ecotone			
BOER _[E] 10 : BOER _[E] 30	7.87 [0.61] : 7.98 [0.67]	4.32 [0.15] : 3.92 [0.15]	0.07 [0.003] : 0.07 [0.005]
BOGR _[E] 10 : BOGR _[E] 30	10.62 [0.71] : 11.47 [0.72]	3.78 [0.17] : 3.72 [0.15]	same as above
Cross site			
BOER _[CDG] 10 : BOER _[E] 10	7.00 [0.57] : 7.87 [0.61]	4.03 [0.13] : 4.32 [0.15]	0.07 [0.002] : 0.07 [0.003]
BOER _[CDG] 30 : BOER _[E] 30	10.23 [0.88] : 7.98 [0.67]	3.78 [0.15] : 3.92 [0.15]	0.10 [0.005] : 0.07 [0.005] **
BOGR _[SGS] 10 : BOGR _[E] 10	11.21 [0.88] : 10.62 [0.71]	3.51 [0.12] : 3.78 [0.17]	0.10 [0.004] : 0.07 [0.003] **
BOGR _[SGS] 30 : BOGR _[E] 30	13.88 [1.02] : 11.47 [0.72]	3.27 [0.09] : 3.72 [0.15] *	0.12 [0.005] : 0.07 [0.005] **

^aFor each main effect [A_{net} , predawn leaf water potential, soil water content] statistical analyses were performed using single-factor ANOVA or Kruskal-Wallis for model significance (see methods).

* denotes model significance at $\alpha < 0.05$ and ** model significance at $\alpha = < 0.01$.

^bBOER – *B. eriopoda*, BOGR – *B. gracilis*, [CDG] – Chihuahuan Desert grassland, [SGS] – Great Plains shortgrass steppe, [E] – Ecotone, 10 and 30 = 10 mm and 30 mm – rainfall additions.

Table 3. Elevation and soil texture in the top 30 cm of soil sampled from each site.

	Desert grassland	Ecotone	Shortgrass steppe
Elevation [m]	1616	1600	1670
Sand [%]	57.5 ± 0.5	74.5 ± 0.5	59.5 ± 1.5
Silt [%]	18.5 ± 0.5	10.0 ± 1.0	17.5 ± 0.5
Clay [%]	24.0 ± 1.0	15.5 ± 0.5	23.5 ± 1.5

^aSoil texture is reported as mean ± SE (n = 2 for each site).

^bWithin each study site, soil texture means were not significantly different ($\alpha = 0.05$) based on Kruskal-Wallis test for model significance and all pairwise comparisons.

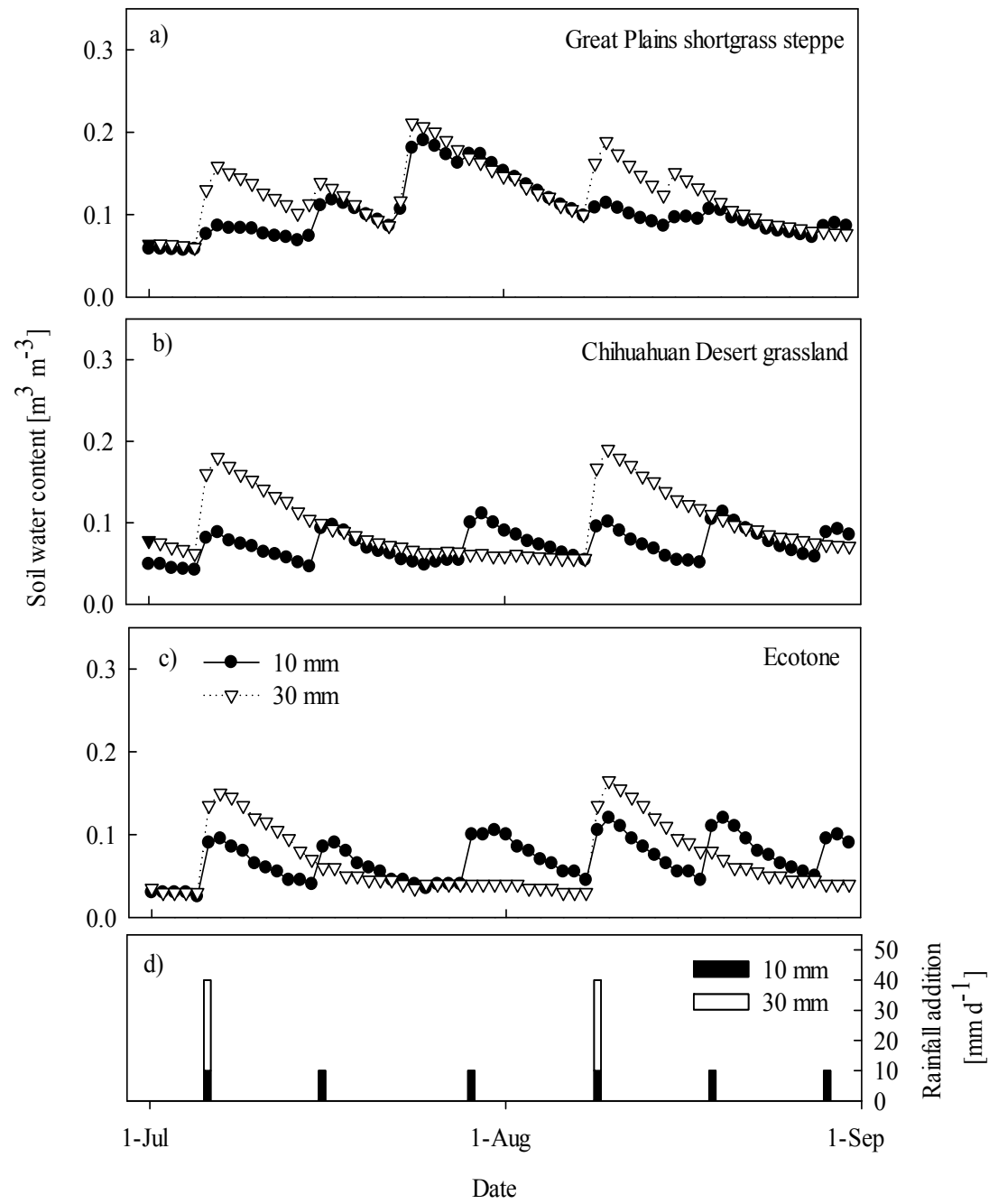


Figure 1.

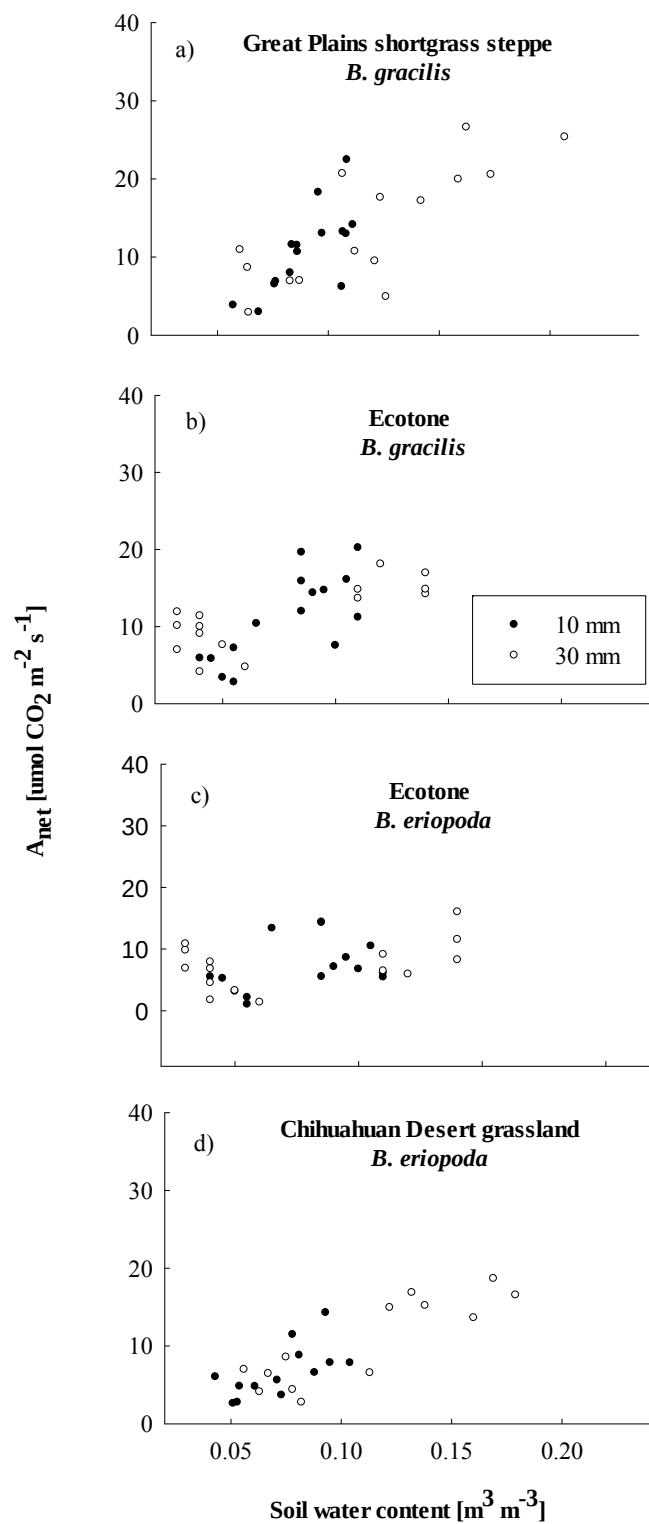


Figure 2.

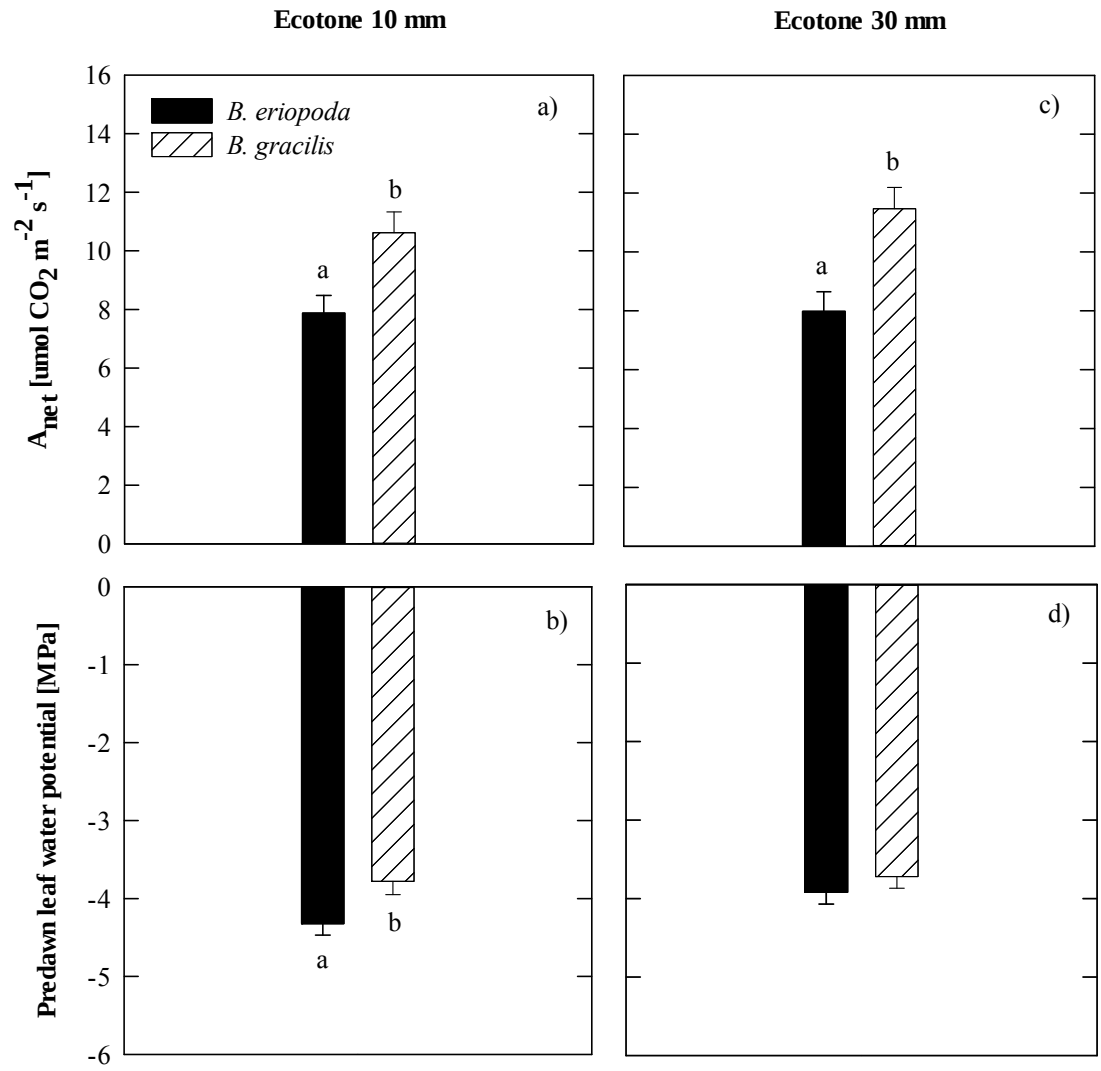


Figure 3.

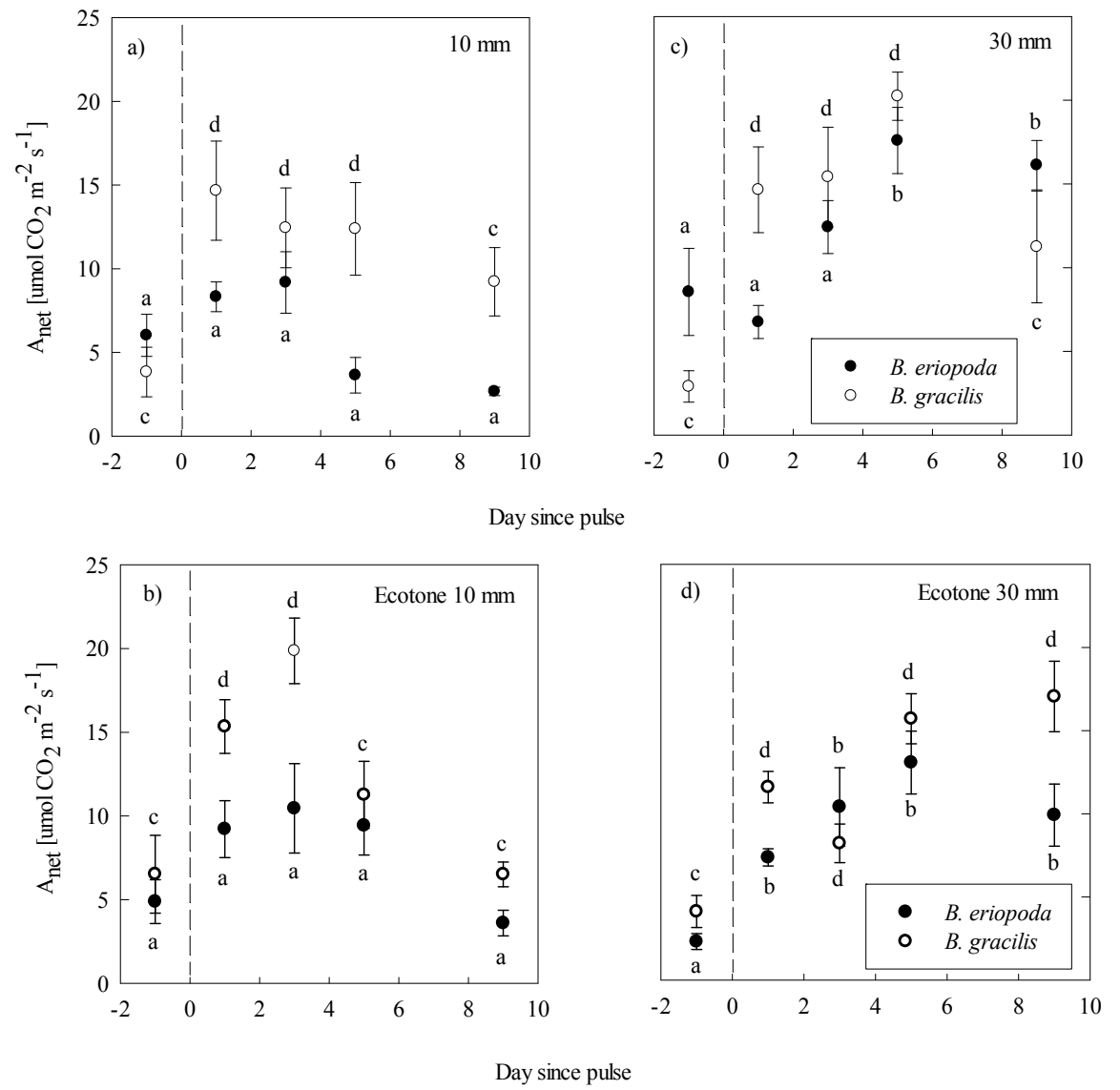


Figure 4.

Figure Captions

Figure 1. Daily mean soil water content (θ) at the Great Plains shortgrass steppe (SGS), Chihuahuan Desert grassland (GDG), and ecotone sites (a-c). Within each plot, soil θ was integrated over 5-15 cm depth and $n = 5$ for each rainfall addition type. Rainfall additions include three 10 mm events each month and one 30 mm rainfall event each month.

Standard error was omitted for clarity. For each site the mean daily standard error was: 1) 10% (10 mm) and 17% (30 mm) of the mean at SGS site, 2) 14% (10 mm) and 10% (30 mm) of the mean at CDG site and 3) 14% (10 mm) and 28% (30 mm) of the mean at the Ecotone site (d). Bars represent the total precipitation added by treatment at each site.

Figure 2. Simple linear regression of leaf gas exchange (A_{net}) and soil water content (θ) for 10 mm and 30 mm rainfall additions at each site (a-d). Data points are the daily mean A_{net} ($n = 5$) and soil θ ($n = 5$) recorded for experimental plots during each measurement campaign. For each graph, regression equations for all significant relationships at $\alpha = 0.05$ are as follows: a) *B. gracilis* SGS 10 mm; $A_{\text{net}} = -9.92 + 230 \text{ SWC}$, $R^2 = 0.513$, *B. gracilis* SGS 30 mm; $A_{\text{net}} = -2.33 + 137 \text{ SWC}$, $R^2 = 0.618$, b) *B. gracilis* Ecotone 10 mm; $A_{\text{net}} = -2.21 + 170 \text{ SWC}$, $R^2 = 0.553$, *B. gracilis* Ecotone 30 mm; $A_{\text{net}} = 5.86 + 71.8 \text{ SWC}$, $R^2 = 0.592$, d) *B. eriopoda* CDG 10 mm; $A_{\text{net}} = -1.49 + 113 \text{ SWC}$, $R^2 = 0.410$; *B. eriopoda* CDG 30 mm; $A_{\text{net}} = -2.09 + 113 \text{ SWC}$, $R^2 = 0.747$.

Figure 3. Interspecific ecophysiological response patterns for *Bouteloua eriopoda* and *B. gracilis* at the ecotone site during the 2010 monsoon season (July-August). (a, b) Mean ($\pm \text{SE}$) leaf gas exchange (A_{net}) and pre-dawn leaf water potential (Ψ_{pd}) in 10 mm rainfall addition plots (c, d) Mean ($\pm \text{SE}$) A_{net} and Ψ_{pd} in 30 mm rainfall addition plots. For all plots, significantly different means ($\alpha = 0.05$) are noted by different letters.

Figure 4. Leaf gas exchange (A_{net}) pulse response and drought recovery for each species in 10 mm and 30 mm rainfall addition plots. (a, c) Daily mean ($\pm$ SE) A_{net} pre-pulse [day -1] and post-pulse [days 1, 3, 5, 9] response for *Bouteloua eriopoda* at the Chihuahuan Desert grassland site and *B. gracilis* at the Great Plains shortgrass steppe site. (b, d) Daily mean ($\pm$ SE) A_{net} pre- and post-pulse response for *B. eriopoda* and *B. gracilis* at the ecotone site. For all plots, the dashed line indicates rainfall additions. Different letters indicate a significant difference ($\alpha = 0.05$) between means within a species based on single-factor analysis of variance and Tukey or Bonferonni tests for multiples comparisons between means.

Chapter 5

Conclusion

Throughout the southwestern U.S. climate models project increased aridity, seasonal shifts in precipitation along with more extreme precipitation events (Diffenbaugh et al. 2005; Schoof et al. 2010). Because water is the most limiting resource, arid-semiarid ecosystems are likely to be highly responsive to future climate variability (Diffenbaugh et al. 2008). The goal of this study was to understand how increased precipitation variability would affect C_4 photosynthesis (A_{net}), net primary productivity (ANPP) and soil respiration (R_s) in Chihuahuan Desert grassland.

In chapter 2, I reviewed the literature to evaluate how climate change might affect net ecosystem exchange (NEE). Furthermore, I investigated the potential to increase carbon sequestration or slow carbon loss across the Mojave, Sonoran and Chihuahuan Deserts. In general, the variability in NEE is driven by large precipitation events (≥ 10 mm; Kurc and Small 2007) that correspond with the growing season which varies by warm desert type. As such, even though water is the most limiting resource, a threshold exists where gross primary productivity (GPP) may not exceed ecosystem respiration (R_{eco}) (Fernández et al. 2007; Kurc and Small 2007; Muldavin et al. 2008). Similarly, increased atmospheric CO_2 concentrations may enhance carbon sequestration in arid-semiarid ecosystems but only in years with above average rainfall (Smith et al. 2000; Naumburg et al. 2003; Jasoni et al. 2005). Warmer temperatures can directly affect primary productivity and respiration or indirectly affect carbon balance by altering soil moisture, nitrogen availability and species composition (Shaver et al. 2000). Unfortunately, desert ecosystems are rarely included in warming studies. However,

warmer temperatures will likely intensify soil water limitation and, therefore, decrease respiration and primary productivity. Additional multi-factorial studies are needed to fully realize potential feedbacks that will occur in a world where precipitation variability, atmospheric CO₂ concentrations, and temperature increase simultaneously. Moreover, studies are also needed to understand how arid-semiarid ecosystems recover from disturbance as climate change will likely increase the susceptibility of these ecosystems to novel disturbance and biological invasions.

In chapters three and four I applied projected climate change scenarios in the field. I found that large (20 mm) less frequent rainfall events significantly increased soil moisture content leading to higher A_{net} (*Bouteloua eriopoda*), ANPP (*B. eriopoda*), and R_s . These results indicate that large less frequent rainfall events will have a positive effect on some components of the regional carbon cycle. Moreover, I found that a climate pattern characterized by extreme precipitation events (30 mm) will likely lead to a shift in species composition across a Chihuahuan Desert grassland to Great Plains shortgrass steppe ecotone. Field results from the ecotone indicate that the C₄ perennial grass *B. gracilis* maintains significantly higher A_{net} and pre-dawn water potential when compared to the perennial C₄ grass *B. eriopoda*. A potential change in species composition could affect local ecosystem processes, future estimates of carbon uptake and ecosystem response to projected climate change scenarios.

While this study suggests that large less frequent rainfall events would increase primary productivity, it is important to remember that R_s will also increase. Whether R_s (soil CO₂ efflux to the atmosphere) will exceed CO₂ fixed by increased primary productivity is unknown. Moreover, additional studies are needed to understand how

changes in precipitation patterns may impact belowground net primary productivity in arid-semiarid ecosystems.

References

Chapter 1

- Allred KW (2005) A field guide to the grasses of New Mexico. Agricultural Experiment Station, New Mexico State University Las Cruces, NM.
- Archer SR, Predick KI (2008) Climate change and ecosystems of the southwestern United States. *Rangelands* 30:23-28.
- Bardgett RD, Freeman C, Ostle NJ (2008) Microbial contributions to climate change through carbon cycle feedbacks. *The ISME Journal* 2:805-814.
- Chen S, Lin G, Huang J, Jenerette GD (2009) Dependence of carbon sequestration on the differential responses of ecosystem photosynthesis and respiration to rain pulses in a semiarid steppe. *Global Change Biology* 15:2450-2461.
- Collins SL, Sinsabaugh RL, Crenshaw C, Green L, Porras-Alfaro A, Stursova M, Zeglin LH (2008) Pulse dynamics and microbial processes in aridland ecosystems. *Journal of Ecology* 96:413-420.
- Diffenbaugh NS, Giorgi F, Pal JS (2008) Climate change hotspots in the United States. *Geophysical Research Letters* 35 L16709.
- Field JP, Belnap J, Breshears DD, Neff JC, Okin GS, Whicker JJ, Painter TH, Ravi S, Reheis MC, Reynolds RL (2010) The ecology of dust. *Frontiers in Ecology and the Environment* doi:10.1890/090050.
- Huxman TE, Snyder KA, Tissue D, Leffler AJ, Pockman WT, Ogle K, Sandquist D, Potts DL, Schwinning S. (2004) Precipitation pulses and carbon balance in semi-arid and arid ecosystems. *Oecologia* 141:254-268.
- [IPCC] Intergovernmental Panel on Climate Change (2007) *Climate Change 2007: The Physical Science Basis. Summary for Policymakers*. Cambridge University Press, New York.
- Lauenroth WK, Milchunas DG. (1992) Short-Grass Steppe. In: Coupland RT (ed) *Ecosystems of The World: Natural Grassland*. Elsevier, Amsterdam.
- Noy-Meir I (1973) Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4:25-52.

- Peters DPC, Gibbens RP (2006) Plant communities in the Jornada basin: the dynamic landscape. In: Havstad KM, Huenneke LF, Schlesinger WH (eds) *Structure and function of a Chihuahuan Desert ecosystem*. Oxford University Press, New York, pp. 211-231.
- Ravi S, Breshers DD, Huxman TE, D'Odorico P (2010) Land degradation in drylands: interactions among hydrologic Aeolian erosion and vegetation dynamics. *Geomorphology* 116:236-245.
- Reynolds JF, Kemp PR, Ogle K, Fernandez RJ (2004) Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia* 141:194-210.
- Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG (1990) Biological feedbacks in global desertification. *Science* 247:1043-1048.
- Schwinning S and Sala OE (2004) Hierarchy of responses to resource pulses in arid And semi-arid ecosystems. *Oecologia* 141:211-220.
- Seastedt TR, Hobbs RJ, Suding KN (2008) Management of novel ecosystems: are novel approaches required? *Frontiers in Ecology and the Environment* 6:547-553.
- Van Auken OW (2000) Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics* 31:197-215.
- Vitousek PM. (1992) Global environmental change: An introduction. *Annual Review of Ecology and Systematics* 23:1-14.

Chapter 2

- Abatzoglou, J.T., Kolden, C.A., 2011. Climate change in western U.S. deserts: potential for increased wildfire and invasive annual grasses. *Rangeland Ecology and Management*.64, 417-478.
- Adams, J., 2010. *Vegetation-Climate Interaction: How Plants Make The Global Environment*. Praxis Publishing, UK.
- Allison, I., Bindoff, N., Bindshadler, R., Cox, P., de Noblet-Ducoudré, N., England, M., Francis, J., Gruber, N., Haywood, A., Karoly, D., Kaser, G., Le Quéré, C., Lenton, T., Mann, M., McNeil, B., Pitman, A., Rahmstorf, S., Rignot, E., Schellnhuber, H.J., Schneider, S., Sherwood, S., Somerville, R., Steffen, K., Steig, E., Visbeck, M., Weaver, A., 2011. *The Copenhagen Diagnosis: Updating the World on the Latest Climate Science*. Elsevier, UK.

- Allred, B.W., Snyder, K.A., 2008. Ecophysiological responses of Chihuahuan Desert grasses to fire. *Journal of Arid Environments*. 72, 1989-1996.
- Anderson-Teixeira, K.J., Delong, J.P., Fox, A.M., Brese, D.A., Litvak, M.E., 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.
- Asner, G.P., Elmore, A.J., Olander, L.P., Martin, R.E., Harris, A.T., 2004. Grazing systems, ecosystem responses, and global change. *Annual Review of Environmental Resources*. 29, 261-299.
- Austin, A.T., Yahdjian, L., Stark, J.M., Belnap, J., Porporato, A., Norton, U., Ravetta, D.A., Schaeffer, S.M., 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia*. 141, 221-235.
- Bahre, C.J., Shelton, M.L., 1993. Historic vegetation change, mesquite increases, and climate in southeastern Arizona. *Journal of Biogeography*. 20, 489-504.
- Barbour, M.G., Billings, W.D., 2000. *North American Terrestrial Vegetation*. Cambridge University Press, UK.
- Barger, N.N., Archer, S.R., Campbell, J.L., Huang, C-y, Morton, J.A., Knapp, A.K., 2011. Woody plant proliferation in North American drylands: A synthesis of impacts on ecosystem carbon balance. *Journal of Geophysical Research*. 116, G00K07, doi: 10.1029/2010JG001506.
- Barron-Gafford, G.A., Scott, R.L., Jenerette, G.D., Hamerlynck, E.P., Huxman, T.E., 2012. Temperature and precipitation controls over leaf- and ecosystem-level CO₂ flux along a woody plant encroachment gradient. *Global Change Biology*. 18, 1389-1400.
- Barry, R.G., Chorley, R.J., 2003. *Atmosphere, Weather and Climate*. Routledge, New York, NY.
- Bazzaz, F.A., 1990. The response of natural ecosystems to the rising global CO₂ levels. *Annual Review of Ecology and Systematics*. 21, 167-196.
- Beatley, J.C., 1974. Effects of rainfall and temperature on the distribution and behavior of *Larrea tridentata* (Creosote-bush) in the Mojave Desert of Nevada. *Ecology*. 55, 245-261.
- Bell, C., McIntyre, N., Cox, S., Tissue, D., Zak, J., 2008. Soil microbial responses to temporal variations of moisture and temperature in a Chihuahuan Desert grassland. *Microbial Ecology*. 56, 153-167.

- Billings, S.A., Zitzer, S.F., Weatherly, H.E., Schaeffer, S.M., Charlet, T.N., Arnone, J.A., Evans, R.D., 2003. Effects of elevated CO₂ on green tissue and litter quality in an intact Mojave Desert ecosystem. *Global Change Biology*. 9, 729-736.
- Breecker, D.O., McFadden, L.O., Sharp, Z.D., Martinez, M., Litvak, M.E., 2012. Deep autotrophic soil respiration in shrubland and woodland ecosystems in central New Mexico. *Ecosystems*. 15, 83-96.
- Brooks, M.L., Chambers, J.C., 2011. Resistance to invasion and resilience to fire in desert shrublands of North America. *Rangeland Ecology and Management*. 64, 431-438.
- Brown J., Angerer, J., Salley, S.W., Blaisdell, R., Stuth, J.W., 2010. Improving estimates of rangeland carbon sequestration potential in the U.S. southwest *Rangeland Ecology and Management*. 63, 147-154.
- Browning, D.M., Archer, S.R., 2011. Protection from livestock fails to deter shrub proliferation in a desert landscape with a history of heavy grazing. *Ecological Applications*. 21, 1629-1642.
- Cable, D.R., 1975. Influence of precipitation on perennial grass production in the semi-desert southwest. *Ecology*. 56, 981-986.
- Cable, J.M., Barron-Gafford, G.A., Ogle, K., Pavao-Zuckerman, M., Scott, R.L., Williams, D.G., Huxman, T.E., 2012. Shrub encroachment alters sensitivity of soil respiration to temperature and moisture. *Journal of Geophysical Research*. 117, G01001, doi: 10.1029/2011JG001757.
- Chapin III, F.S., Matson, P.A., Mooney, H.A., 2002. *Principles of Terrestrial Ecosystem Ecology*. Springer-Verlag, New York, NY USA.
- Clark, N.M., Apple, M.E., Nowak, R.S., 2010. The effects of elevated CO₂ on root respiration rates of two Mojave Desert shrubs. *Global Change Biology*. 16, 1566-1575.
- Collins, S.L., Fargione, J.E., Crenshaw, C.L., Nonaka, E., Elliot, J.R., Xia, Y., Pockman, W.T., 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.
- Comstock, J., Ehleringer J., 1986. Canopy dynamics and carbon gain in response to soil water availability in *Encelia frutescens* gray, a drought-deciduous shrub. *Oecologia*. 68, 271-278.

- Davis, M.A., Grime, J.P., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of invisibility. *Journal of Ecology*. 88, 528-534.
- Diffenbaugh, N.S., Giorgi, F., Pal, J.S., 2008. Climate change hotspots in the United States. *Geophysical Research Letters*. 35, L16709.
- Diffenbaugh, N.S., Pal, J.S., Trapp, R.J., Giorgi, F., 2005. Fine-scale processes regulate the response of extreme events to global climate change. *Proceedings of the National Academy of Science*. 102, 15774-15778.
- Dukes, J.S., Mooney, H.A., 1999. Does global change increase the success of biological invaders. *TREE*. 14, 135-139.
- Duxbury, A.C., Duxbury, A.B., 1989. *An Introduction to the World's Oceans*. Wm. C. Brown Publishers, Dubuque, IA.
- Emmerich, W.E., 2003. Carbon dioxide fluxes in a semiarid environment with high carbonate soils. *Agricultural and Forest Meteorology*. 116, 91-102.
- Engel, E.C., Abella, S.R., 2011. Vegetation recovery in a desert landscape after wildfires: influences of community type, time since fire and contingency effects. *Journal of Applied Ecology*. 48, 1401-1410.
- Fawcett, P.J., Werne, J.P., Anderson, R.S., Heikoop, J.M., Brown, E.T., Berke, M.A., Smith, S.J., Goff, F., Donohoo-Hurley, L., Cisneros-Dozal, L.M., Schouten, S., Sinnige Damsté, J.S., Huang, Y., Toney, J., Fessenden, J., WoldeGabriel, G., Atudorei, V., Geissman, J.W., Allen, C.D., 2011. Extended megadroughts in the southwestern United States during pleistocene interglacials. *Nature*. 470, 518-521.
- Field, C.B., Jackson, R.B., Mooney, H.A., 1995. Stomatal responses to increased CO₂: Implications from the plant to the global scale. *Plant, Cell and Environment*. 18, 1214-1225.
- Flanagan, L.B., Wever, L.A., Carlson, P.J., 2002. Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperature grassland. *Global Change Biology*. 8, 599-615.
- Fernández, R.J., 2007. On the frequent lack of response of plants to rainfall events in arid areas. *Journal of Arid Environments*. 68, 688-691.
- Follett, R.F., Reed, D.A., 2010. Soil carbon sequestration in grazing lands: societal benefits and policy implications. *Rangeland Ecology and Management*. 63, 4-15.
- Gibbens, R.P. and Lenz, J.M., 2001. Root systems of some Chihuahuan Desert plants. *Journal of Arid Environments*. 49, 221-263.

- Global Climate Change Impacts in the United States. 2009. In: Karl, T.R., Melillo, J.M., Peterson, T.C. (eds). Cambridge University, New York, NY.
- Gutzler, D.S., Robbins, T.O., 2010. Climate variability and projected change in the western United States: regional downscaling and drought statistics. *Climate Dynamics*. doi: 10.1007/s00382-010-0838-7.
- Hamerlynck, E.P., Huxman, T.E., Charlet, T.N., Smith, S.D., 2002. Effects of elevated CO₂ (FACE) on the functional ecology of the drought-deciduous Mojave Desert shrub, *Lycium andersonii*. *Environmental and Experimental Botany*. 48, 93-106.
- Hamerlynck, E.P., Huxman, T.E., Nowak, R.S., Redar, S., Loik, M.E., Jordan, D.N., Zitzer, S.F., Coleman, J.S., Seemann, J.R., Smith, S.D., 2000. Photosynthetic responses of *Larrea tridentata* to a step-increase in atmospheric CO₂ at the Nevada Desert FACE Facility. *Journal of Arid Environments*. 44, 425-436.
- Hamerlynck, E.P., Scott, R.L., Stone, J.J. 2011. Soil moisture and ecosystem function responses of desert grassland varying in vegetative cover to a saturating precipitation pulse. *Ecohydrology*. doi:10.1002/eco.214.
- Heimann, M., Reichstein, M., 2008. Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature*. 451, 289-292.
- Hereford, R., Webb, R.H., Longpré, C.I., 2006. Precipitation history and ecosystem response to multidecadal precipitation variability in the Mojave Desert region, 1893-2001. *Journal of Arid Environments*. 67, 13-34.
- Heisler-White, J.L., Knapp, A.K., Kelly, E.F., 2008. Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland. *Oecologia*. 158, 129-140.
- Hobbs, R.J., 2009. Restoration Ecology, in: Levin, S.A. (Ed.), *The Princeton Guide to Ecology*. Princeton University Press, Princeton, N.J.
- Housman, D.C., Naumburg, E., Huxman, T.E., Charlet, T.N., Nowak, R.S., Smith, S.D., 2006. Increases in desert shrub productivity under elevated carbon dioxide vary with water availability. *Ecosystems*. 9, 374-385.
- Housman, D.C., Zitzer, S.F., Huxman, T.E., Smith, S.D., 2003. Functional ecology of shrub seedlings after a natural recruitment event at the Nevada Desert FACE Facility. *Global Change Biology*. 9, 718-728.
- Huenneke, L.F., Anderson, J.P., Remenga, M., Schlelesinger, W.H., 2002. Desertification alters patterns of aboveground net primary production in Chihuahuan ecosystems. *Global Change Biology*. 8, 247-264.

- Huxman, T.E., Hamerlynck, E.P., Moore, B.D., Smith, S.D., Jordan, D.N., Zitzer, S.F., Nowak, R.S., Coleman, J.S., Seemann, J.R., 1998. Photosynthetic down-regulation in *Larrea tridentata* exposed to elevated atmospheric CO₂: interaction with drought under glasshouse and field (FACE) exposure. *Plant, Cell and Environment*. 21, 1153-1161.
- Huxman, T.E., Snyder, K.A., Tissue, D., Leffler, A.J., Pockman, W.T., Ogle, K., Sandquist, D., Potts, D.L., Schwinning, S., 2004. Precipitation pulses and carbon balance in semi-arid and arid ecosystems. *Oecologia*. 141, 254-268.
- Ignace, D.D., Huxman, T.E., Weltzin, J.F., Williams, D.G., 2007. Leaf gas exchange and water status responses of a native and non-native grass to precipitation across contrasting soil surfaces in the Sonoran Desert. *Oecologia*. 152, 401-413.
- [IPCC] Intergovernmental Panel on Climate Change. 2007. *Climate Change 2007: The Physical Science Basis. Summary for Policymakers*. Cambridge University Press, New York.
- Janzen, H.H., 2004. Carbon cycling in earth systems – a soil science perspective. *Agriculture Ecosystems and Environment*. 104, 399-417.
- Jasoni, R.L., Smith, S.D., Arnone, J.A., 2005. Net ecosystem CO₂ exchange in Mojave Desert shrublands during the eighth year of exposure to elevated CO₂. *Global Change Biology*. 11, 749-756.
- Jenerette, G.D., Scott, R.L., Barron-Gafford, G.A., Huxman, T.E., 2009. Gross primary production variability associated with meteorology, physiology, leaf area, and water supply in contrasting woodland and grassland semiarid riparian ecosystems. *Journal of Geophysical Research*. 114, G04010, doi: 10.1029/2009JG001074.
- Knapp, A.K., Briggs, J.M., Collins, S.L., Archer, S.R., Bret-Harte, M.S., Ewers, B.E., Peters, D.P., Young, D.R., Shaver, G.R., Pendall, E., Cleary, M.B., 2008. Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Global Change Biology*. 14, 615-623.
- Knapp, A.K., Smith, M.D., 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science*. 291, 481-484.
- Kondratyev, K.Y., Krapivin, V.F., Varotsos, C.A., 2003. *Global Carbon Cycle and Climate Change*. Springer-Praxis, Germany.

- Kurc, S.A., Benton, L.M., 2010. Digital image-derived greenness links deep soil moisture to carbon uptake in a creosotebush-dominated shrubland. *Journal of Arid Environments*. 74, 585-594.
- Kurc, S.A., Small, E.E., 2007. Soil moisture variations and ecosystem-scale fluxes of water and carbon in semiarid grassland and shrubland. *Water Resources Research*. 43, W06416.
- Laca, E.A., McEachern, M-B., Demment, M.W., 2010. Global grazinglands and greenhouse gas fluxes. *Rangeland Ecology and Management*. 63, 1-3.
- Lambers, H., Chapin, F.S., Pons, T.L., 2008. *Plant physiological ecology*, 2nd edn. Springer, New York.
- Loik, M.E., Breshears, D.D., Lauenroth, W.K., Belnap, J., 2004. A multi-scale perspective on water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. *Oecologia*. 141, 269-281.
- McCulley, R.L., Jobbagy, E.G., Pockman, W.T., Jackson, R.B., 2004. Nutrient uptake as a contributing explanation for deep rooting in arid and semi-arid ecosystems. *Oecologia*. 141, 620-628.
- Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Moore, B., Vorosmarty, C.J., Schloss A.L., 1993. Global climate change and terrestrial net primary production. *Nature*. 363, 234-240.
- Merideth R., 2001. *A Primer on Climatic Variability and Change in the Southwest*. Udall Center for Studies in Public Policy, The University of Arizona.
- Mielnick, P., Dugas, W.A., Mitchell, K., Havstad, K. 2005. Long-term measurements of CO₂ flux and evapotranspiration in a Chihuahuan Desert grassland. *Journal of Arid Environments*. 60, 423-436.
- Mooney, H.A., Drake, B.G., Luxmore, R.J., Oechel, W.C., Pitelka, L.F., 1991. Predicting ecosystem responses to elevated CO₂ concentrations. *Bioscience*. 41, 96-104.
- Morgan, J.A., Pataki, D.E., Körner, C., Clark, H., Del Grosso, S.J., Grünzweig, J.M., Knapp, A.K., Mosier, A.R., Newton, P.C.D., Niklaus, P.A., Nippert, J.B., Nowak, R.S., Parton, W.J., Polley, H.W., Shaw, M.R., 2004. Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO₂. *Oecologia*. 140, 11-25.
- Muldavin, E.H., Moore, D.I., Collins, S.L., Wetherill, K.R., Lightfoot, D.C., 2008. Aboveground net primary production dynamics in a northern Chihuahuan Desert ecosystem. *Oecologia*. 155, 123-132.

- Nagel, J.M., Huxman, T.E., Griffen, K.L., Smith, S.D., 2004. CO₂ enrichment reduces the energetic cost of biomass construction in an invasive desert grass. *Ecology*. 85, 100-106.
- Naumburg, E., Housman, D.C., Huxman, T.E., Charlet, T.N., Loik, M.E., Smith, S.D., 2003. Photosynthetic responses of Mojave Desert shrubs to free air CO₂ enrichment are greatest during wet years. *Global Change Biology*. 9, 276-285.
- Nielson, R.P., 1987. Biotic regionalization and climatic controls in western North America. *Vegetatio*. 70, 135-147.
- Nowak, R.S., DeFalco, L.A., Wilcox, C.S., Jordan, D.N., Coleman, J.S., Seemann, J.R., Smith, S.D., 2001. Leaf conductance decreased under free-air CO₂ enrichment (FACE) for three perennials in the Nevada desert. *New Phytologist*. 150, 449-458.
- Nowak, R.S., Zitzer, S.F., Babcock, D., Smith-Longozo, V., Charlet, T.N., Coleman, J.S., Seemann, J.R., Smith, S.D., 2004. Elevated atmospheric CO₂ does not conserve soil water in the Mojave Desert. *Ecology*. 85, 93-99.
- Noy-Meir, I., 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*. 4, 25-52.
- Ogle, K., Reynolds, J.F., 2004. Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds and delays. *Oecologia*. 141, 282-294.
- Pataki, D.E., Huxman, T.E., Jordan, D.N., Zitzer, S.F., Coleman, J.S., Smith, S.D., Nowak, R.S., Seemann, J.R., 2000. Water use of two Mojave Desert shrubs under elevated CO₂. *Global Change Biology*. 6, 889-897.
- Patrick, L.D., Ogle, K., Bell, C.W., Zak, J., Tissue, D., 2009. Physiological responses of two contrasting desert plant species to precipitation variability are differentially regulated by soil moisture and nitrogen dynamics. *Global Change Biology*. 15, 1214-1229.
- Peters, D.P.C., Gibbens, R.P., 2006. Plant communities in the Jornada basin: the dynamic landscape, in: Havstad, K.M., Huenneke, L.F., Schlesinger, W.H. (Eds.), *Structure and Function of a Chihuahuan Desert Ecosystem: The Jornada Basin Long-Term Ecological Research Site*. Oxford University Press, New York, NY.
- Piñeiro, G., Paruelo, J.M., Oesterheld, M., Jobbágy, E.G., 2010. Pathways of grazing effects on soil organic carbon and nitrogen. *Rangeland Ecology and Management*. 63, 109-119.

- Polley, H.W., Emmerich, W., Bradford, J.A., Sims, P.L., Johnson, D.A., Saliendra, N.Z., Svejcar, T., Angell, R., Frank, A.B., Phillips, R.L., Snyder, K.A., Morgan, J.A., 2010a. Physiological and environmental regulation of interannual variability of CO₂ exchange on rangelands in the western United States. *Global Change Biology*. 16, 990-1002.
- Polly, H.W., Emmerich, W., Bradford, J.A., Sims, P.L., Johnson, D.A., Saliendra, N.Z., Svejcar, T., Angell, R., Frank, A.B., Phillips, R.L., Snyder, K.A., Morgan, J.A., Sanabria, J., Mielnick, P.C., Dugas, W.A., 2010b. Precipitation regulates the response of net ecosystem CO₂ exchange to environmental variation on United States rangelands. *Rangeland Ecology and Management*. 63, 176-186.
- Potts, D.L., Huxman, T.E., Cable, J.M., English, N.B., Ignace, D.D., Eilts, J.A., Mason, M.J., Weltzin, J.F., Williams, D.G., 2006. Antecedent moisture and seasonal precipitation influence the response of canopy-scale carbon and water exchange to rainfall pulses in a semi-arid grassland. *New Phytologist*. 170, 849-860.
- Rao, L.E., Steers, R.J., Allen, E.B., 2011. Effects of natural and anthropogenic gradients on native and exotic winter annuals in a southern California Desert. *Plant Ecology*. 212, 1079-1089.
- Rundel, P.W., Gibson, A.C., 1996. *Ecological Communities and Processes in a Mojave Desert Ecosystem: Rock Valley, Nevada*. Cambridge University Press, Great Britain.
- Runyon, J.B., Butler, J.L., Friggens, M., Meyer, S., Sing, S., *Invasive Species and Climate Change: executive Summary*. Forest Service, Rocky Mountain Research Station, Bozeman, MT.
- Rustad, L.E., Campbell, J.L., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartley, A.E., Cornelissen, J.H.C., Gurevitch, J., GCTE-NEWS, 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*. 126, 543-562.
- Schaeffer, S.M., Billings, S.A., Evans, R.D., 2007. Laboratory incubations reveal potential responses of soil nitrogen cycling to changes in soil C and N availability in Mojave Desert soils exposed to elevated atmospheric CO₂. *Global Change Biology*. 13, 854-865.
- Schimel, D.S., 2010. Drylands in the Earth system. *Science*. 327, 418-419.
- Schlesinger, W.H., Winkler, J.P., Megonigal, J.P., 2000. Soil and the global carbon cycle, in: Waglely, T.M.L., Schimel, D.S. (Eds.), *The Carbon Cycle*. Cambridge University Press, United Kingdom, pp 95-101.

- Schoenherr, A.A., 1992. A Natural History of California. University of California Press, Berkeley, California.
- Schoof, J.T., Pryor, S.C., Surprenant J., 2010. Development of daily precipitation projections for the United States based on probabilistic downscaling. *Journal of Geophysical Research*. 115, D13106, doi:10.1029/2009JD013030.
- Scott, R.L., Hamerlynck, E.P., Jenerette, G.D., Moran, M.S., Barron-Gafford, G.A., 2010. Carbon dioxide exchange in a semidesert grassland through drought-induced vegetation change. *Journal of Geophysical Research*. doi:10.1029/2010JG001348
- Scott, R.L., Jenerette, G.D., Potts, D.L., Huxman, T.E., 2009. Effects of seasonal drought on net carbon dioxide exchange from a woody-plant-encroached semiarid grassland. *Journal of Geophysical Research*. doi:10.1029/2008JG000900.
- Seager, R., Ting, M., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H-P., Harnik, N., Leetmaa, A., Lau, N-C., Li, C., Velez, J., Naik, N., 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science*. 316:1181-1184.
- Shaver, G.R., Canadell, J., Chapin, F.S., Guirevitch, J., Harte, J., Henry, G., Ineson, P., Jonasson, S., Melillo, J., Pitelka, L., Rustad, L., 2000. Global warming and terrestrial ecosystems: a conceptual framework for analysis. *BioScience*. 50, 871-882.
- Shen, W., Reynolds, J.F., Hui, D., 2009. Responses of dryland soil respiration and soil carbon pool size to abrupt vs. gradual and individual vs. combined changes in soil temperature, precipitation, and atmospheric [CO₂]: a simulation analysis. *Global Change Biology*. 15, 2274-2294.
- Smith, S.D., Huxman, T.E., Zitzer, S.F., Charlet, T.N., Housman, D.C., Coleman, J.S., Fenstermaker, L.K., Seemann, J.R., Nowak, R.S., 2000. Elevated CO₂ increases productivity and invasive species success in an arid ecosystem. *Nature*. 408, 79-82.
- Smith, S.D., Monson, R.K., Anderson, J.E., 1997. *Physiological Ecology of North American Desert Plants*. Springer, Germany.
- Stitt, M., 1991. Rising CO₂ levels and their potential significance for carbon flow in photosynthetic cells. *Plant, Cell and Environment*. 14, 741-762.
- Strain, B.R., Bazzaz, F.A., 1983. Terrestrial plant communities, in: Lemon, E.R., (Ed), CO₂ and Plants: The Response of Plants to Rising Levels of Atmospheric Carbon Dioxide, Westview, Boulder, CO.

- Suazo, A.A., Spencer, J.E., Engel, E.C., Abella, S.R., 2012. Responses of native and non-native Mojave Desert winter annuals to soil disturbance and water additions. *Biological Invasions*. 14, 215-227.
- Svejcar, T., Raymond, A., Bradford, J.A., Dugas, W., Emmerich, W., Frank, A.B., Gilmanov, T., Haferkamp, M., Johnson, D.A., Mayeux, H., Mielnick, P., Morgan, J., Saliendra, N.Z., Schuman, G.E., Sims, P.L., Snyder, K., 2008. Carbon fluxes on North American Rangelands. *Rangeland Ecology and Management*. 61, 465-474.
- Thomey, M.L., Collins, S.L., Vargas, R., Johnson, J.E., Brown, R.F., Natvig, D.O., Friggens, M.T., 2011. Effect of precipitation variability on net primary production and soil respiration in a Chihuahuan Desert grassland. *Global Change Biology*. 17, 1505-1515.
- Throop, H.L., Reichman, L.G., Sala, O.E., Archer, S.R., 2012. Response of dominant grass and shrub species to water manipulation: an ecophysiological basis for shrub invasion in a Chihuahuan Desert Grassland. *Oecologia*. doi: 10.1007/s00442-011-2217-4.
- Van Gestel, N.C., Schwilk, D.W., Tissue, D.T., Zak, J.C., 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., Collins, S.L., Thomey, M.L., Johnson, J.E., Brown, R.F., Natvig, D.O., Friggens, M.T., 2012. Precipitation variability and fire influence the temporal dynamics of soil CO₂ efflux in an arid grassland. *Global Change Biology*. 18, 1401-1411.
- Wainwright, J., 2006. Climate and climatological variations in the Jornada Basin, in: Havstad, K.M., Huenneke, L.F., Schlesinger, W.H. (Eds.), *Structure and Function of a Chihuahuan Desert Ecosystem: The Jornada Basin Long-Term Ecological Research Site*, Oxford University Press, New York, NY.
- Weatherly, H.E., Zitzer, S.F., Coleman, J.S., Aronone, J.A., 2003. *In situ* litter decomposition and litter quality in a Mojave Desert ecosystem: effects of elevated atmospheric CO₂ and interannual climate variability. *Global Change Biology*. 9, 1223-1233.
- Whitford, W.G., 2002. *Ecology of Desert Systems*. Academic Press. UK.
- Wohlfahrt, G., Fenstermaker, L.F., Arnone, J.A., 2008. Large annual net ecosystem CO₂ uptake of a Mojave Desert ecosystem. *Global Change Biology*. 14, 1475-1487.

Wu, Z., Dijkstra P., Koch, G.W., Peñuelas, J., Hungate, B.A., 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biology*, **17**, 927-942.

Yanoff S., Muldavin E., 2008. Grassland-shrubland transformation and grazing: a century-scale view of northern Chihuahuan Desert grassland. *Journal of Arid Environments*, **72**, 1594-1605.

Chapter 3

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

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

Chapin FS, McFarland J, McGuire AD, Euskirchen ES, Ruess RW, Kielland K (2009) The changing global carbon cycle: linking plant-soil carbon dynamics to global consequences. *Journal of Ecology*, **97**, 840-850.

Chen S, Lin G, Huang J, Jenerette GD (2009) Dependence of carbon sequestration on the differential responses of ecosystem photosynthesis and respiration to rain pulses in a semiarid steppe. *Global Change Biology*, **15**, 2450-2461.

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

Cook ER, Woodhouse CA, Eakin CM, Meko DM, Stahle DW (2004) Long-term aridity changes in the Western United States. *Science*, **306**, 1015-1018.

Craine JM, Wedin DA, Chapin FS (1999) Predominance of ecophysiological controls on soil CO₂ flux in a Minnesota grassland. *Plant and Soil*, **207**, 77-86.

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

Fay PA, Carlisle JD, Knapp AK, Blair JM, Collins SL (2003) Productivity responses to altered rainfall patterns in a C₄-dominated grassland. *Oecologia*, **137**, 245-251.

- Gerten D, Luo Y, LeMarie G, *et al.* (2008) Modelled effects of precipitation on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biology*, **14**, 2365-2379.
- Gibbens RP and Lenz JM (2001) Root systems of some Chihuahuan Desert plants. *Journal of Arid Environments*, **49**, 221-263.
- Harper CW, Blair JM, Fay PA, Knapp AK, Carlisle JD (2005) Increased rainfall variability and reduced rainfall amount decreases soil CO₂ flux in a grassland ecosystem. *Global Change Biology*, **11**, 322-334.
- Heisler-White JL, Blair JM, Kelly EF, Harmony K, Knapp AK (2009) Contingent productivity responses to more extreme rainfall regimes across a grassland biome. *Global Change Biology*, **15**, 2894-2904.
- Heisler-White JL, Knapp AK, Kelly EF (2008) Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland. *Oecologia*, **158**, 129-140.
- Huxman TE, Cable JM, Ignace DD, Eilts JA, English NB, Weltzin J, Williams DG (2004) Response of net ecosystem gas exchange to a simulated precipitation pulse in a semi-arid grassland: the role of native versus non-native grasses and soil texture. *Oecologia*, **141**, 295-305.
- Huxman, TE, Snyder KA, Tissue D *et al.* (2004) Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia*, **141**, 254-268.
- Ignace DD, Huxman TE, Weltzin JF, Williams DG (2007) Leaf gas exchange and water status responses of a native and non-native grass to precipitation across contrasting soil surfaces in the Sonoran Desert. *Oecologia*, **152**, 401-413.
- [IPCC] Intergovernmental Panel on Climate Change (2007) *Climate Change 2007: The Physical Science Basis. Summary for Policymakers*. Cambridge University Press, New York.
- Jankju M (2008) Individual performances and the interaction between arid land plants affected by the growth season water pulses. *Arid Land Research and Management*, **22**, 123-133.
- Jones, HG (1992) *Plants and Microclimate: A Quantitative Approach to Environmental Plant Physiology*. Cambridge University Press, New York.
- Kharin VV, Zwiers FW, Zhang X, Hegerl GC (2007) Changes in temperature and precipitation extremes in the IPCC ensemble of global coupled model simulations. *Journal of Climate*, **20**, 1419-1443.

- Kieft, TL, White CS, Loftin SR, Aguilar R, Craig JA, Skaar DA. (1998) Temporal dynamics in soil carbon and nitrogen resources at a grassland-shrubland ecotone. *Ecology*, **79**, 671-683.
- Knapp AK, Beier C, Briske DD *et al.* (2008) Consequences of more extreme precipitation regimes for terrestrial ecosystems. *BioScience*, **58**, 811-821.
- Knapp AK, Fay PA, Blair JM *et al.* (2002) Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science*, **298**, 2202-2205.
- Knapp AK and Smith MD (2001) Variation among biomes in temporal dynamics of aboveground primary production. *Science*, **291**, 481-484.
- Kurc SA and Small EE (2007) Soil moisture variations and ecosystem-scale fluxes of water and carbon in semiarid grassland and shrubland. *Water Resources Research*, **43**, W06416.
- Liu W, Zhang Z, Wan S (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.
- McCulley RL, Jobbagy EG, Pockman WT, Jackson RB (2004) Nutrient uptake as a contributing explanation for deep rooting in arid and semi-arid ecosystems. *Oecologia*, **141**, 620-628.
- Moldrup P, Olesen T, Yamaguchi T, Schjoning P, Rolston DE (1999) Modeling diffusion and reaction in soils. IX. The bucking-ham-burdine-campbell equation for gas diffusivity in undisturbed soil. *Soil Science*, **164**, 542-551.
- Muldavin EH, Moore DI, Collins SL, Wetherill KR, Lightfoot DC (2008) Aboveground net Production dynamics in a northern Chihuahuan Desert ecosystem. *Oecologia*, **155**, 123-132.
- Nobel PS (1980) Water vapor conductance and CO₂ uptake for leaves of C₄ desert grass, *Hilaria rigida*. *Ecology*, **61**, 252-258.
- Noy-Meir I (1973) Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*, **4**, 25-52.
- Ogle K and Reynolds JF (2004) Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds and delays. *Oecologia*, **141**, 282-294.

- Osterheld M, Juan L, Semmartin M, Sala OE (2001) Inter-annual variation in primary production of semi-arid grassland related to previous-year production. *Journal of Vegetation Science*, **12**, 137-142.
- Patrick LD, Ogle K, Bell CW, Zak J, Tissue D (2009) Physiological responses of two contrasting desert plant species to precipitation variability are differentially regulated by soil moisture and nitrogen dynamics. *Global Change Biology*, **15**, 1214-1229.
- Patrick L, Cable J, Potts D *et al.* (2007) Effects of an increase in summer precipitation on leaf, soil, and ecosystem fluxes of CO₂ and H₂O in a sotol grassland in Big Bend National Park, Texas. *Oecologia*, **151**, 704-718.
- Pennington DD and Collins SL (2007) Response of an aridland ecosystem to interannual climate variability and prolonged drought. *Landscape Ecology*, **22**, 897-910.
- Raich JW and Tufekcioglu A (2000) Vegetation and soil respiration: correlations and controls. *Biogeochemistry*, **48**, 71-90.
- Reynolds JF, Kemp PR, Ogle K, Fernandez RJ (2004) Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia*, **141**, 194-210.
- Sala OE and Lauenroth WK (1982) Small rainfall events: an ecological role in semiarid regions. *Oecologia*, **53**, 301-304.
- Schenk HJ and Jackson RB (2002) Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology*, **90**, 480-494.
- Schimel DS (2010) Drylands in the Earth system. *Science*, **327**, 418-419.
- Schwinning S and Sala OE (2004) Hierarchy of responses to resource pulses in arid And semi-arid ecosystems. *Oecologia*, **141**, 211-220.
- Schwinning S, Starr BI, Ehleringer JR (2003) Dominant cold desert plants do not partition warm season precipitation by event size. *Oecologia*, **136**, 252-260.
- Seager R, Ting M, Held I *et al.* (2007) Model projections of an imminent transition to a more arid climate in southwestern North America. *Science*, **316**, 1181-1184.
- Seastedt TR, Hobbs RJ, Suding KN (2008) Management of novel ecosystems: are novel approaches required? *Frontiers in Ecology and the Environment*, **6**, 547-553.

- Shen W, Reynolds JF, Hui D (2009) Responses of dryland soil respiration and soil carbon pool size to abrupt vs. gradual and individual vs. combined changes in soil temperature, precipitation, and atmospheric [CO₂]: a simulation analysis. *Global Change Biology*, **15**, 2274-2294.
- Smith, SD, Monson RK, Anderson JE (1997) *Physiological Ecology of North American Desert Plants*. Springer, Berlin, Germany.
- Sponseller RA (2007) Precipitation pulses and soil CO₂ flux in a Sonoran Desert ecosystem. *Global Change Biology*, **13**, 426-436.
- Stephens G and Whitford WG (1993) Responses of *Bouteloua eriopoda* to irrigation and nitrogen fertilization in a Chihuahuan Desert grassland. *Journal of Arid Environments*, **24**, 415-421.
- Vargas R and Allen MF (2008) Dynamics of fine root, fungal rhizomorphs, and soil respiration in a mixed temperate forest: Integrating sensors and observations. *Vadose Zone Journal*, **7**, 1055-1064.
- Vargas R, Baldocchi D, Allen M *et al.* (2010) Looking deeper into the soil: biophysical controls and seasonal lags of soil CO₂ production and efflux across multiple vegetation types. *Ecological Applications*, **20**, 1569-1582 doi: 10.1890/09-0693.
- Wan S and Luo Y (2003) Substrate regulation of soil respiration in a tallgrass prairie: results of a clipping and shading experiment. *Global Biogeochemical Cycles*, **17**, 1-12.
- Williams DG, McPerson GR, Weltzin JF (1999) Stress in wildland plants: implications for ecosystem structure and function. In: *Handbook of Plant and Crop Stress*. (ed Pessarakli M), pp. 907-929. Marcel Dekker, Inc. New York, USA.
- Wolters V, Silver WL, Bignell DE *et al.* (2000). Effects of global changes on above- and belowground biodiversity in terrestrial ecosystems: implications for ecosystem functioning. *BioScience*, **50**, 1089-1098.
- Xia Y, Moore DI, Collins SL, Muldavin EH (2010) Aboveground production and species richness of annuals in Chihuahuan Desert grassland and shrubland plant communities. *Journal of Arid Environments*, **74**, 378-385.
- Xu Z, Zhou G, Shimizu H (2009) Are plant growth and photosynthesis limited by pre-drought following rewatering in grass? *Journal of Experimental Botany*, **60**, 3737-3749.
- Yahdjian L and Sala OE (2006) Vegetation structure constrains primary production response to water availability in the Patagonian steppe. *Ecology*, **87**, 952-962.

Zhao J, Yuchun QI, Yunshe D, Domroes M (2009) Seasonal patterns of soil respiration in three types of communities along grass-desert shrub transition in inner Mongolia, China. *Advances in Atmospheric Sciences*, **26**, 503-512.

Zhao W, Shi-Ping C, Xing-Guo H, Guang-Hui L (2009) Effects of long-term grazing on the morphological and functional traits of *Leymus chinensis* in the semiarid grassland of inner Mongolia, China. *Ecological Research*, **24**, 99-108.

Chapter 4

Aguilera MO, Lauenroth WK (1993) Seedling establishment in adult neighborhoods intraspecific constraints in the regeneration of the bunchgrass *Bouteloua gracilis*. *Journal of Ecology* 81:253-261

Aguilera MO, Lauenroth WK (1995) Influence of gap disturbances and type of microsites on seedling establishment in *Bouteloua gracilis*. *Journal of Ecology* 83:87-97

Allred KW (2005) A field guide to the grasses of New Mexico. Agricultural Experiment Station, New Mexico State University Las Cruces, NM

Anten NPR, Schieving F, Werger MJA (1995) Patterns of light and nitrogen distribution in relation to whole canopy carbon gain in C3 and C4 mono- and dicotyledonous species. *Oecologia* 101:504-513

Anten NPR, Werger MJA, Medina E (1998) Nitrogen distribution and leaf area indices in relation to photosynthetic nitrogen use efficiency in savanna grasses. *Plant Ecology* 138:63-75

Ares J (1976) Dynamics of the root system of blue grama. *Journal of Range Management* 29:208-213

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

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

Barnett TP, Pierce DW, Hidalgo HG, Bonfils C, Santer BD, Das T, Bala G, Wood AW, Nozawa T, Mirin AA, Cayan DR, Dettinger MD (2008) Human-induced changes in the hydrology of the western United States. *Science* 319:1080-1083

- Bowman WD (1991) Effect of nitrogen nutrition on photosynthesis and growth in C₄ *Panicum* species. *Plant, Cell and Environment* 14:295-301
- Cable DR (1975) Influence of precipitation on perennial grass production in the semi-desert southwest. *Ecology* 56:981-986
- Chesson P, Gebauer RLE, Schwinning S, Huntly N, Wiegand K, Ernest MSK, Sher A, Novoplansky A, Weltzin JF (2004) Resource pulse, species, interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia* 141:236-253
- Collins SL, Fargione JE, Crenshaw CL, Nonaka E, Elliot JR, Xia Y, Pockman WT (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
- Collins SL, Sinsabaugh RL, Crenshaw C, Green L, Porras-Alfaro A, Stursova M, Zeglin LH (2008) Pulse dynamics and microbial processes in aridland ecosystems. *Journal of Ecology* 96:413-420
- Diffenbaugh NS, Giorgi F, Pal JS (2008) Climate change hotspots in the United States. *Geophysical Research Letters* 35:L16709
- Eissenstat DM, Caldwell MM (1988) Competitive ability is linked to rates of water extraction: a field study of two aridland tussock grasses. *Oecologia* 75:1-7
- Fawcett PJ, Werne JP, Anderson RS, Heikoop JM, Brown ET, Berke MA, Smith SJ, Goff F, Donohoo-Hurley L, Cisneros-Dozal LM, Schouten S, Sinnige Damsté JS, Huang Y, Toney J, Fessenden J, WoldeGabriel G, Atudorei V, Geissman JW, Allen CD (2011) Extended megadroughts in the southwestern United States during pleistocene interglacials. *Nature* 470:518-521
- Fernández RJ (2007) On the frequent lack of response of plants to rainfall events in arid areas. *Journal of Arid Environments* 68 688-691
- Fernández RJ, Reynolds JF (2000) Potential growth and drought tolerance of eight desert grasses: lack of trade-off? *Oecologia* 123:90-98
- Fernández RJ, Wang M, Reynolds JF (2002) Do morphological changes mediate plant responses to water stress? A steady-state experiment with two C₄ grasses. *New Phytologist* 155:79-88
- Gao Q, Reynolds JF (2003) Historical shrub-grass transitions in the northern Chihuahuan Desert: modeling the effects of shifting rainfall seasonality and event size over a landscape gradient. *Global Change Biology* 9:1475-1493

- Gibbens RP, Lenz JM (2001) Root systems of some Chihuahuan Desert plants. *Journal Of Arid Environments* 49:221-263
- Goldberg D, Novoplansky A (1997) On the relative importance of competition in unproductive environments. *Journal of Ecology* 85:409-418
- Gong XY, Chen Q, Lin S, Brueck H, Dittert K, Taube F, Schnyder H (2011) Tradeoffs between nitrogen- and water-use efficiency in dominant species of the semiarid steppe of Inner Mongolia. 340:227-238
- Gosz JR (1993) Ecotone hierarchies. *Ecological Applications* 3:369-376
- Gutzler DS, Robbins TO (2010) Climate variability and projected change in the western United States: regional downscaling and drought statistics. *Climate Dynamics* doi: 10.1007/s00382-010-0838-7
- Hamerlynck EP, Scott RL, Moran MS, Keefer TO, Huxman TE (2010) Growing season ecosystem and leaf-level gas exchange of an exotic and native semiarid bunchgrass. *Oecologia* 163:561-570
- Hamerlynck EP, Scott RL, Stone JJ (2011) Soil moisture and ecosystem function responses of desert grassland varying in vegetative cover to a saturating precipitation pulse. *Ecohydrology* doi:10.1002/eco.214
- Hook PB, Lauenroth WK (1994) Root system response of a perennial bunchgrass to neighborhood-scale soil water heterogeneity. *Functional Ecology* 8:738-745
- Hooper DU, Johnson L (1999) Nitrogen limitation in dryland ecosystems: responses to geographical and temporal variation in precipitation. *Biogeochemistry* 46:247-293
- Huxman TE, Snyder KA, Tissue D, Leffler AJ, Pockman WT, Ogle K, Sandquist D, Potts DL, Schwinning S. (2004) Precipitation pulses and carbon balance in semi-arid and arid ecosystems. *Oecologia* 141:254-268
- Ignace DD, Huxman TE, Weltzin JF, Williams DG (2007) Leaf gas exchange and water status responses of a native and non-native grass to precipitation across contrasting soil surfaces in the Sonoran Desert. *Oecologia* 152:401-413
- [IPCC] Intergovernmental Panel on Climate Change (2007) *Climate change 2007: the physical science basis. Summary for policymakers*. Cambridge University Press, New York
- Knapp AK, Smith MD (2001) Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291:481-484

- Ladwig LM, Collins SL, Swann AL, Xia Y, Allen MF, Allen EB (2012) Above- and belowground responses to nitrogen addition in a Chihuahuan Desert grassland. *Oecologia* DOI: 10.1007/s00442-011-2173-z
- Lambers H, Chapin III FS, Pons TL (2008) Plant physiological ecology, 2nd edition. Springer, New York
- Lauenroth WK, Burke IC, Morgan JA (2008) The shortgrass steppe: the region and research sites. In: Lauenroth WK, Burke IC (eds) *Ecology of the shortgrass steppe*. Oxford University Press, New York, pp 3-13
- Lauenroth WK, Sala OE (1992) Long-term forage production of North American shortgrass steppe. *Ecological Applications* 2:397-403
- Lauenroth WK, Sala OE, Milchunas DG, Lathrop RW (1987) Root dynamics of *Bouteloua gracilis* during short-term recovery from drought. *Functional Ecology* 1:117-124
- Lee CA, Lauenroth WK (1994) Spatial distributions of grass and shrub root systems in the shortgrass steppe. *American Midland Naturalist* 132:117-123
- Loik ME, Breshears DD, Lauenroth WK, Belnap J (2004) A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. *Oecologia* 141:269-281
- Lowe PN, Lauenroth WK, Burke IC (2003) Effects of nitrogen availability on competition between *Bromus tectorum* and *Bouteloua gracilis*. *Plant Ecology* 167:247-254
- McCulley RL, Jobbagy EG, Pockman WT, Jackson RB (2004) Nutrient uptake as a contributing explanation for deep rooting in arid and semiarid ecosystems. *Oecologia* 141:620-628
- McLaren JR, Wilson SD, Peltzer DA (2004) Plant feedbacks increase the temporal heterogeneity of soil moisture. *Oikos* 107:199-205
- Melgoza G, Nowak RS, Tausch RJ (1990) Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* 83:7-13
- Mooney HA (1972) The carbon balance of plants. *Annual Review of Ecology and Systematics* 3:315-346
- Muldavin EH, Moore DI, Collins SL, Wetherill KR, Lightfoot DC (2008) Aboveground net production dynamics in a northern Chihuahuan Desert ecosystem. *Oecologia* 155:123-132

- Noy-Meir I (1973) Desert ecosystems: environment and procedures. *Annual Review of Ecology and Systematics* 4:25-52
- Osterheld M, Juan L, Semmartin M, Sala OE (2001) Inter-annual variation in primary production of semiarid grassland related to previous-year production. *Journal of Vegetation Science* 12:137-142
- 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
- Pennington DD, Collins SL (2007) Response of an aridland ecosystem to interannual climate variability and prolonged drought. *Landscape Ecology* 22:897-910
- Peters DPC, Gosz JR, Pockman WT, Small EE, Parmenter RR, Collins SL, Muldavin E (2006a) Integrating patch and boundary dynamics to understand and predict biotic transitions at multiple scales. *Landscape Ecology* 21:19-33
- Peters DPC, Yao J, Gosz JR (2006b) Woody plant invasion at a semi-arid/arid transition zone: importance of ecosystem type to colonization and patch expansion. *Journal of Vegetation Science* 17:389-396
- Peters DPC, Gosz JR, Collins SL (2009) Boundary dynamics in landscapes. In: Levin SA (ed) *The Princeton guide to ecology*. Princeton University Press, Princeton, New Jersey, pp 458-463
- Pockman WT, Small EE (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
- Sage RF and Pearcy RW (1987) The nitrogen use efficiency of C₃ and C₄ plants. *Plant Physiology* 84:959-963
- Sala OE, Lauenroth WK (1982) Small rainfall events: an ecological role in semi-arid regions. *Oecologia* 53:301-304
- Scanlon BR, Levitt DG, Reedy RC, Keese KE, Sully MJ (2005) Ecological controls on water-cycle response to climate variability in deserts. *Proceedings of the National Academy of Sciences* 102:6033-6038
- Schenk H.J. and Jackson R.B. 2002. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology* 90:480-494

- Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG (1990) Biological feedbacks in global desertification. *Science* 247:1043-1048
- Schwinning S, Sala OE (2004) Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. *Oecologia* 141:211-220
- Schwinning S, Starr BI, Ehleringer JR (2003) Dominant cold desert plants do not partition warm season precipitation by event size. *Oecologia* 136:252-260
- Seager R, Ting M, Held I, Kushnir Y, Lu J, Vecchi G, Huang H-P, Harnik N, Leetmaa A, Lau N-C, Li C, Velez J, Naik N (2007) Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316:1181-1184
- Senock RS, Devine DL, Sisson WB, Donart GB (1994) Ecophysiology of three C₄ perennial grasses in the northern Chihuahuan Desert. *The Southwestern Naturalist* 39: 122-127
- Simioni G, LeRoux X, Gignoux J, Walcroft AS (2004) Leaf gas exchange characteristics and water- and nitrogen-use efficiencies of dominant grass and tree species in a west African savanna. *Plant Ecology* 173:233-246
- Stephens G, Whitford WG (1993) Responses of *Bouteloua eriopoda* to irrigation and nitrogen fertilization in a Chihuahuan Desert grassland. *Journal of Arid Environments* 24: 415-421
- Thomey ML, Collins SL, Vargas R, Johnson JE, Brown RF, Natvig DO, Friggs MT (2011) Effect of precipitation variability on net primary production and soil respiration in a Chihuahuan Desert grassland. *Global Change Biology* 17:1505-1515
- Wardle DA, Bardgett RD, Callaway RM, Van der Putten WH (2011) Terrestrial ecosystem responses to species gains and losses. *Science* 332:1273-1277
- Weiss JL, Castro CL, Overpeck JT (2009) Distinguishing pronounced droughts in the southwestern United States: seasonality and effects of warmer temperatures. *Journal of Climate* 22:5918-5932
- Williams CA, Albertson JD (2006) Dynamical effects of the statistical structure of annual rainfall on dryland vegetation. *Global Change Biology* 12:777-792
- Yahdjian L, Sala OE (2006) Vegetation structure constrains primary production response to water variability in the Patagonian steppe. *Ecology* 87:952-962

- Yang H, Wu M, Liu W, Zhang Z, Zhang N, Wan S (2011) Community structure and composition in response to climate change in a temperate steppe. *Global Change Biology* 17:452-465
- Yang Y, Fang J, Ma W, Wang W (2008) Relationship between variability in aboveground net primary production and precipitation in global grasslands. *Geophysical Research Letters* 35: L23710 doi:10.1029/2008GL035408
- Yanoff S, Muldavin E (2008) Grassland-shrubland transformation and grazing: a century-scale view of a northern Chihuahuan Desert grassland. *Journal of Arid Environments* 72:1594-1605

Chapter 5

- Diffenbaugh NS, Giorgi F, Pal JS (2008) Climate change hotspots in the United States. *Geophysical Research Letters* 35 L16709
- Diffenbaugh NS, Pal JS, Trapp RJ, Giorgi F (2005) Fine-scale processes regulate the response of extreme events to global climate change. *Proceedings of the National Academy of Sciences* 102:15774-15773
- Fernández RJ (2007) On the frequent lack of response of plants to rainfall events in arid areas. *Journal of Arid Environments* 68:688-691
- Jasoni RL, Smith SD, Arnone JA (2005) Net ecosystem CO₂ exchange in Mojave Desert shrublands during the eighth year of exposure to elevated CO₂. *Global Change Biology* 11:749-756
- Kurc SA and Small EE (2007) Soil moisture variations and ecosystem-scale fluxes of water and carbon in semiarid grassland and shrubland. *Water Resources Research* 43:W06416
- Muldavin EH, Moore DI, Collins SL, Wetherill KR, Lightfoot DC (2008) Aboveground net production dynamics in a northern Chihuahuan Desert ecosystem. *Oecologia* 155:123-132
- Naumburg E, Housman DC, Huxman TE, Charlet TN, Loik ME, Smith SD (2003) Photosynthetic responses of Mojave Desert shrubs to free air CO₂ enrichment are greatest during wet years. *Global Change Biology* 9: 276-285
- Schoof JT, Pryor SC, Surprenant J (2010) Development of daily precipitation projections for the United States based on probabilistic downscaling. *Journal of Geophysical Research* 115, D13106, doi:10.1029/2009JD013030

Shaver GR, Canadell J, Chapin FS, Guirevitch J, Harte J, Henry G, Ineson P, Jonasson S, Melillo J, Pitelka L, Rustad L (2000) Global warming and terrestrial ecosystems: a conceptual framework for analysis. *BioScience* 50:871-882

Smith SD, Huxman TE, Zitzer SF, Charlet TN, Housman DC, Coleman JS, Fenstermaker LK, Seeman JR, Nowak RS (2000) Elevated CO₂ increases productivity and invasive species success in an arid ecosystem. *Nature* 408:79-82