12-1-2014

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Recommended Citation

Petrie, Matthew. "Community ecology, climate change and ecohydrology in desert grassland and shrubland." (2014). https://digitalrepository.unm.edu/biol_etds/92

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Community ecology, climate change and ecohydrology in desert grassland and shrubland

by

Matthew Daniel Petrie

M.A. Geography, University of Kansas, 2010
B.S. Environmental Studies, University of Kansas, 2008

DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of

Doctor of Philosophy
Biology

The University of New Mexico

Albuquerque, New Mexico

December, 2014

Acknowledgments

This research was partially funded by a National Science Foundation grant to the University of New Mexico for Long Term Ecological Research at the Sevilleta LTER, by a grant from the USDA Forest Service, Western Wildland Environmental Threat Assessment Center, by NASA grant award NNX11AG91G, through an NSF-EPSCoR award for Hydrology to the University of New Mexico, and grants and scholarships from the Department of Biology at the University of New Mexico.

I wish to thank the Sevilleta LTER staff and field crew for experiment and data management support, as well as the professors and students that have made my time at UNM an enjoyable experience.

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Abstract

This dissertation explores the climate, ecology and hydrology of Chihuahuan Desert ecosystems in the context of global climate change. In coming decades, the southwestern United States is projected to experience greater temperature-driven aridity, possible small decreases in annual precipitation, and a later onset of summer monsoon rainfall. These changes may have profound consequences for ecological systems in the Chihuahuan Desert, which are intensely water-limited and respond to even small pulses of moisture availability. The first chapter (Chapter 2) compares change in the properties of monsoon season precipitation from 1910-2010 in the northern Chihuahuan Desert region to local variability in monsoon precipitation from 2001-2012 at the Desert's northern ecological boundary. From 1910-2010, monsoon precipitation events in the Chihuahuan Desert increased in frequency and decreased in magnitude, and the longest wet and dry periods increased in length. These changes may be masked locally due to high annual variation in total seasonal precipitation, however, which suggests a limited capability for small, average change in the properties of precipitation events alone to influence ecosystem processes in a changing climate. Chapter 3 explores differences in carbon exchanges between established grassland and shrubland communities at the Chihuahuan Desert's northern ecological boundary. During slightly dry years, grassland was highly sensitive to moisture limitation and was a net carbon source, while shrubland was a net carbon sink. These results support the conclusion that ecosystem carbon sequestration in the Chihuahuan Desert will increase if grassland to shrubland state transitions occur. Chapter 4 explores the importance of small rainfall events for grassland nutrient availability and aboveground net primary productivity during dry and wet monsoon seasons. In a warming environment, the residence time of small events as soil moisture will decrease, and results from this chapter show that the experimental removal of only small events during the summer monsoon in desert grassland can promote vegetation senescence and reduce soil nutrient availability, and thus inhibit grassland recovery during subsequent wet monsoons. As a whole, this dissertation research characterizes variation in monsoon season precipitation from local to regional spatial scales and from annual to inter-decadal timescales, explores the potential for greater ecosystem carbon sequestration as a consequence of grassland to shrubland state transitions, and evaluates the ecological role of very small rainfall events during the summer monsoon. While the scope of these topics is broad, this research addresses key questions regarding climate inputs and ecological processes in Chihuahuan Desert ecosystems, and also sharpens scientific understanding of how climate change may be enhanced or moderated by the sensitivity of ecological processes in aridlands to precipitation and temperature.

Contents

Chapter 1

Introduction

Aridland ecosystems depend on the availability of precipitation-derived soil moisture. Soil moisture availability exerts a strong control on the productivity and stability of vegetation communities, and also influences aridland ecosystem services including regulating atmospheric dust and pollution (Yin et al., 2005; Field et al., 2010), moderating air temperatures (D'Odorico et al., 2010, 2012), increasing rangeland quality (Baez and Collins, 2008; Knapp et al., 2008), and promoting greater terrestrial carbon sequestration (Petrie et al., 2014b; Poulter et al., 2014). While arid and semiarid systems are less productive than mesic and temperate systems, arid and semiarid ecoregions account for approximately 40% of global land area (Reynolds et al., 2007), play a sizable role in regulating global carbon exchange (Poulter et al., 2014), and may be among the most sensitive terrestrial systems to climate variability (Reynolds et al., 2007; Diffenbaugh et al., 2008; D'Odorico et al., 2012). Climate change projections for many aridlands in the southwestern United States call for increasing temperatures and possible small changes in precipitation in all or part of the year (Seager et al., 2007; Seager and Vecchi, 2010; Gutzler and Robbins, 2011). While fine scale resolution of many of these projections is uncertain, it is clear that these and most aridlands globally will experience increasing temperature-driven aridity in coming decades. Furthermore, recent ecohydrological research shows that soil moisture availability in arid and semiarid systems may be reduced by small changes to the properties of precipitation event frequency and magnitude, and by change to seasonal rainfall patterns (Heisler-White et al., 2008; Thomey et al., 2011; Petrie and Brunsell, 2012). Thus, temperature and precipitation may produce greater degrees of aridity and stronger variation in moisture availability even in cases of moderate climatic change.

To better evaluate and manage aridland resources in the context of changing climate, it is critical to understand how climate forcings vary within an ecoregion, how local systems respond to variability in these forcings, what the mechanisms shaping the ecosystem response are, and what the consequences of change in ecological functioning are likely to be. To address key components of these questions, this dissertation includes three chapters that focus on the responses of Chihuahuan Desert vegetation communities to temperature and precipitation. The first (Chapter 2) compares change in the properties of monsoon season precipitation from 1910-2010 in the northern Chihuahuan Desert region and to local variability in monsoon precipitation from 2001-2012 at the Desert's northern ecological boundary. The summer monsoon season (July-September) is the dominant feature of the growing season in this region of the Chihuahuan Desert, often accounting for 40-60% of total annual rainfall and driving more than 50% of annual net primary productivity (Muldavin et al., 2008; Collins et al., 2010; Petrie et al., 2014a). By exploring differences in precipitation patterns, variability, and issues of spatial and temporal scale, Chapter 2 provides insight on how regional precipitation has changed over the past 100 years, contrasts long-term average values of precipitation with observed annual variation in these values, and identifies how changing precipitation patterns may differ from that of the larger region at the northern boundary of the Chihuahuan Desert.

A potential response of increasing temperature and aridity globally is an increase in the rate and frequency of grassland to shrubland state transitions (Eldridge et al., 2011; D'Odorico et al., 2013a). In the Chihuahuan Desert, northward expansion of creosotebush-dominated shrubland into desert grassland has occurred over the past 100 years, and this state transition has reduced important ecosystem services provided by desert grasslands as a result (Baez and Collins, 2008; D'Odorico et al., 2010). As a beneficial change in services, the state transition of grassland to shrubland will increase the carbon sequestration capacity of many North American ecoregions, but it is unclear if and to what magnitude this change could occur in the case of creosotebush expansion in the Chihuahuan Desert (Jackson et al., 2002; Emmerich, 2007; Throop et al., 2012). Chapter 3 explores differences in vegetation productivity and carbon exchange in established, neighboring grassland and shrubland in the Chihuahuan Desert during drier than average years - these conditions provide an analog to projected future climate. In this chapter, vegetation net primary productivity and ecosystem carbon exchanges are compared between grassland and shrubland, and the responses of grassland and shrubland carbon uptake and carbon loss are correlated to growing season length, soil moisture variation, and ecosystem energy partitioning. Results from this chapter support the conclusion that grassland to shrubland state transitions will increase ecosystem carbon sequestration in the Chihuahuan Desert, but at the expense of the loss of other beneficial ecosystem services.

The last research chapter of this dissertation (Chapter 4) focuses on the importance of small rainfall events in desert grassland during the summer monsoon. In a warming environment, the residence time of small events will decrease and soil moisture availability will be reduced (Rodriguez-Iturbe et al., 1999; Robertson et al., 2009; Lauenroth and Bradford, 2012), but it is unclear if these events have a measurable impact on soil moisture, nutrient availability, or grassland productivity. We experimentally removed all small rainfall events from desert grassland plots during a dry monsoon in 2012 and added a similar magnitude of small events during a wet monsoon in 2013. Chapter 4 illustrates how the loss of small events in desert grassland can promote vegetation senescence and reduce soil nutrient availability, and thus inhibit grassland recovery during subsequent wet monsoons. As a whole, this dissertation research produces a better understanding of how climate, ecology and hydrology interact to shape Chihuahuan Desert ecosystems, and explores the potential for changing climate to influence aridlands.

Chapter 2

Monsoon precipitation in the northern Chihuahuan Desert

2.1 Introduction

Monsoon precipitation exerts a strong control on the ecology and hydrology of arid ecosystems in North America and is especially important in shaping vegetation communities in the southwestern United States (Pennington and Collins, 2007; Notaro et al., 2010). In many years, the summer monsoon is the main component of southwestern US growing seasons (Notaro et al., 2010), and produces the majority of annual vegetation productivity and ecosystem carbon uptake (Pennington and Collins, 2007; Muldavin et al., 2008). Monsoon precipitation is known to be highly variable across space and time (Higgins et al., 1999; Higgins and Shi, 2000). This variation influenced shifts in vegetation communities throughout the 20^{th} century and continues to affect the biotic and abiotic components of southwestern US ecology locally and regionally (Snyder and Tartowski, 2006). In many water-driven ecosystems, vegetation productivity is influenced by variation in total precipitation at seasonal to interannual timescales, but productivity is also influenced by precipitation at shorter timescales as well (Alessandri and Navarra, 2008; Vargas et al., 2012).

Arid and semiarid ecosystems account for approximately 40% of global land area and may be among the first affected regions in cases of strong climatic change (Diffenbaugh et al., 2008). Climate change predictions for the southwestern US call for greater regional aridity (Seager and Vecchi, 2010; Gutzler and Robbins, 2011), but it is unclear how this aridity will be manifest and at what spatial and temporal scales ecosystems will respond. It is also unclear what the driving variables of future climate will be; model simulations from Seager and Vecchi (2010) and Gutzler and Robbins (2011) agree that increased temperature will induce greater regional aridity, but the role of precipitation has not been determined. Seager and Vecchi (2010) and Gutzler and Robbins (2011) both suggest decreased total precipitation and increased annual variability could occur, but precipitation projections are quite uncertain. Furthermore, predictions for increased aridity are in themselves problematic because climate is an aggregation of environmental conditions, and the extrema of these conditions may play a large or even larger role in shaping ecological responses than average values do (Pennington and Collins, 2007; Fay et al., 2008).

The North American Monsoon System (NAMS) is a primary component of the growing season in western North America. While not clearly understood, the monsoon is influenced at annual to inter-decadal timescales by the Pacific Decadal Oscillation (PDO) and the El Niño Southern Oscillation (ENSO) (Mock, 1995). The El Niño and La Niña components of ENSO also influence NAMS rainfall, and their combination and timing can induce both wet and dry conditions (Mock, 1995; Adams and Comrie, 1997; Gochis et al., 2006). In the northern Chihuahuan Desert, one of three major deserts in North America, the summer monsoon occurs roughly from July through September (DOY 182-273) and accounts for 40-50% of annual precipitation on average (Douglas et al., 1993). In this and many other arid and semiarid systems, precipitation feeds back on soil moisture (Findell and Eltahir, 2003; Mendez-Barroso and Vivoni, 2010; Brunsell et al., 2011; Xu and Zipser, 2012), and these dynamics may vary across climatic and topographic gradients (Gebremichael et al., 2007; Vivoni et al., 2010; Taylor et al., 2012). Monsoon precipitation often accounts for a large but variable percentage of ecosystem activity locally (Muldavin et al., 2008; Mendez-Barroso et al., 2009), and variation in precipitation-vegetation dynamics may upscale to influence carbon balance (Kurc and Small, 2007; Throop et al., 2013), ecosystem state-transitions (Schlesinger et al., 1990; Van Auken, 2009), and regional precipitation and temperature anomalies (Ivanov et al., 2008; D'Odorico et al., 2012) in the Chihuahuan Desert region.

The biotic and abiotic components of local ecology, such as soil moisture and vegetation productivity, respond to climate forcings at different spatial and temporal scales (Raupach, 1995; Teuling et al., 2006; Ridolfi et al., 2000), which often makes the prediction of ecological responses to climate difficult (Koster and Suarez, 1999; Brunsell and Gillies, 2003b,a; Porporato et al., 2004). In many cases, it is possible that large-scale average values closely associated with climate, such as those of precipitation, mask the smaller scale dynamics that are most important locally. Vegetation in the Chihuahuan Desert responds strongly to monsoon precipitation totals, especially in drier locations (Pennington and Collins, 2007; Mendez-Barroso et al., 2009), but it is less clear how precipitation properties affect vegetation at ecological boundaries, which may be more sensitive to climate variation than the larger ecoregion is (Gosz, 1993; D'Odorico et al., 2013b). In response, the analysis of fine-scale precipitation data and its variability across spatial and temporal scales is becoming an important component of predicting the characteristics of global climate change and its potential effects on ecosystem state transitions (Scheffer et al., 2009; Wan et al., 2013). Model simulations and field experiments in arid and semiarid systems both show that varying the properties of precipitation at a single site may produce disparate moisture availabilities and widely varying effects on vegetation fluxes of water and carbon (Petrie et al., 2012; Vargas et al., 2012). There is value in comparing precipitation variability from different spatial scales to better ascertain its influence on ecological communities regionally, and also in within-region locations that may be highly susceptible to climate change.

To better understand precipitation in the southwestern United States in the context of global change projections, we analyzed spatial and temporal variability in monsoon precipitation for the northern Chihuahuan Desert region and locally at the Sevilleta National Wildlife Refuge (SNWR), central New Mexico, USA. Our primary goal was to determine if the properties of precipitation events have changed over the past 100 years. We address the following questions: 1) Has total monsoon precipitation changed from 1910-2010 in the northern Chihuahuan Desert region? 2) Have the properties of regional scale precipitation events changed? 3) Has precipitation become more variable over time and does this variability change from dry to wet monsoons? 4) What type of precipitation event magnitudes and event frequencies account for the majority of monsoon precipitation at the SNWR? and 5) Does the nature of monsoon precipitation at SNWR sensors provide further evidence that small-scale precipitation forcings need to be better captured by larger-scale global climate models? By exploring monsoon season precipitation between these locations, this research provides insight on how regional monsoon characteristics may contrast with local characteristics at ecological boundaries, where variability in precipitation may be most influential in a changing climate.

2.2 Sites

In this study we explored change and variability in monsoon precipitation for the United States portion of the northern Chihuahuan Desert of North America, located in the states of New Mexico, Arizona and Texas (Figure 2.1). Elevation in the desert

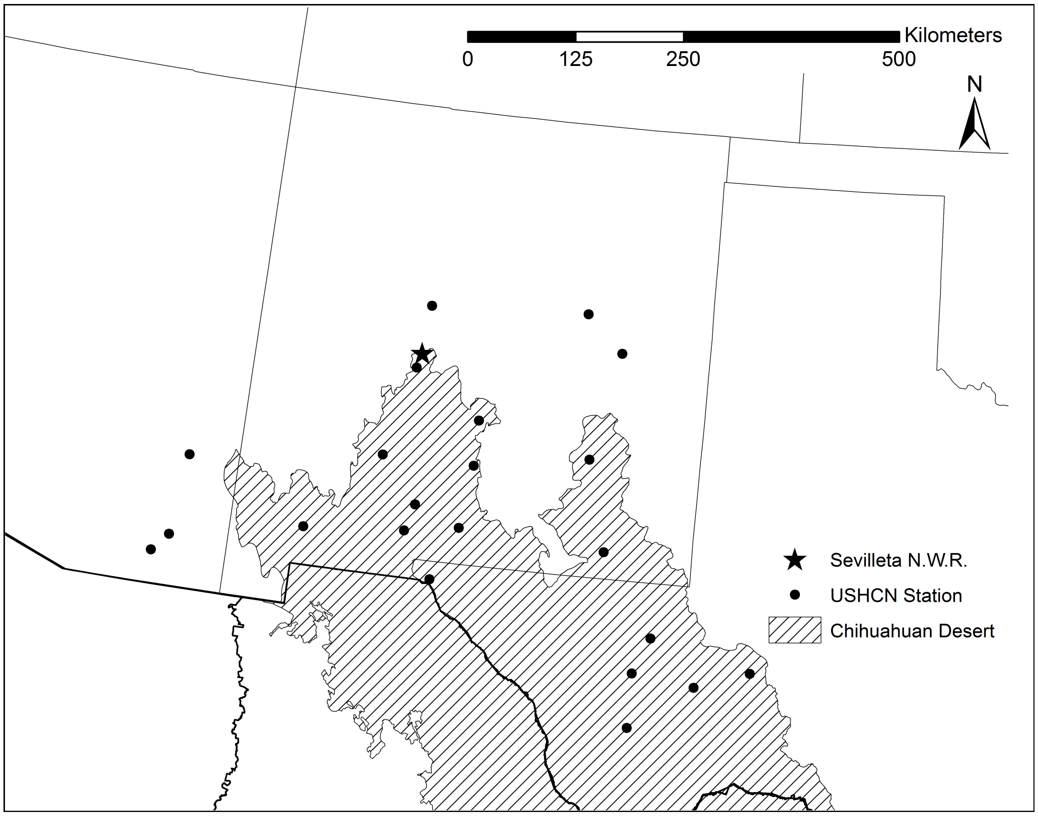

Figure 2.1: The United States Environmental Protection Agency's Chihuahuan Desert ecoregion, United States Historical Climatology Network site locations and the Sevilleta National Wildlife Refuge.

ranges from approximately 800 to 1800 meters. A large portion of annual precipitation may occur during the summer monsoon season (40-50% on average, 5.7 cm regionally from 1910-2010) (Douglas et al., 1993; Muldavin et al., 2008). Vegetation is dominated by woody species and grasses in the south (*Larrea tridentata*, *Prosopis glandulosa*, *Bouteloua eriopoda*) and desert grasslands (*Bouteloua gracilis*, *B. eriopoda*) in the north. The region exhibits an out-of-phase interaction between the spring and summer growing seasons, where precipitation events induce ecosystem pulses of vegetation productivity, nutrient cycling and fluxes of water and carbon differently between the spring and summer (Schwinning and Sala, 2004; Muldavin

Table 2.1: Summary of United States Historical Climatology Network precipitation sites from 1910-2010.

Site	State	Lat [°N]	Lon [°W]	Elevation [m]	Length [yr]	$\overline{P}$ [mm]
292848	NM	33.1	107.2	1395	108	57.8
293368	NM	32.2	108.1	1365	94	61.6
298535	NM	32.3	106.8	1183	87	50.2
294426	NM	32.6	106.7	1300	92	68.1
296435	NM	32.4	106.1	1275	98	52.7
299165	NM	33.1	106.0	1350	89	53.0
291515	NM	33.6	106.0	1647	51	42.6
297610	NM	33.3	104.5	1112	93	50.9
291469	NM	32.3	104.2	951	55	54.6
298387	NM	34.1	106.9	1395	93	65.9
293294	NM	34.5	104.2	1227	105	47.1
295150	NM	34.8	106.8	1475	50	49.9
298107	NM	34.9	104.7	1405	90	48.9
415707	TX	31.1	102.2	758	76	78.6
413280	TX	30.9	102.9	926	80	59.5
416892	TX	31.4	103.5	796	62	46.3
410498	TX	31.0	103.7	982	62	52.1
410174	TX	30.4	103.7	1356	74	49.1
412797	TX	31.8	106.4	1194	70	43.9
027390	AZ	32.8	109.7	900	56	72.6
026393	AZ	31.9	109.8	1326	61	43.0
028619	AZ	31.7	110.0	1405	107	82.1

et al., 2008; Collins et al., 2008; Vargas et al., 2012). Two United States Long Term Ecological Research Network (LTER) sites are located in the region: at the Jornada Basin in southern New Mexico and the Sevilleta National Wildlife Refuge in central New Mexico [http://www.lternet.edu/].

In the first part of the study, we analyzed daily precipitation data for the US portion of the Chihuahuan Desert using United States Historical Climatology Network (USHCN) data from 1910-2010 (Williams Jr et al., 2006) [http://cdiac.ornl.gov/epubs/ndp/ushcn/usa.html] (Table 2.1). An elevation ceiling of 1650 m was employed to ensure sites were located in the Chihuahuan Desert. In total, 22 sites were included: 3 in Arizona, 13 in New Mexico and 6 in Texas (Table 2.1, Figure 2.1). Data records at these sites ranged from 50 to 108 years in length (mean = 80 years) and 16.3% of years included all 22 sites.

The second part of this study focused on the variability of monsoon precipitation at the SNWR, located at the northern boundary of the Chihuahuan Desert in central New Mexico (34.3° N latitude, 106.8° W longitude; Figure 2.1). The SNWR is located at the confluence of Colorado Plateau and Great Basin desert shrubland and grassland, Chihuahuan Desert grassland and semiarid shortgrass steppe (Gosz, 1993; Muldavin et al., 2008). Many arid ecosystems exhibit bistable dynamics between more and less-degraded ecosystem states with low reversibility (Okin et al., 2009; D'Odorico et al., 2010), and current expansion of C_3 desert shrubland dominated by creosotebush (*Larrea tridentata*) into C_4 grasslands of blue and black grama (*Bouteloua gracilis* and *Bouteloua eriopoda*, respectively) is a concern at the SNWR. We analyzed daily precipitation data for sensors at the SNWR using Sevilleta Long Term Ecological Research Network (LTER) meteorological data (SEV001) from 2001-2010, which include a range of precipitation that is illustrative of wet to dry monsoon seasons [http://sev.lternet.edu/projects.php?meid=15] (Table 2.2). These sensors roughly cover an area of 50 km^2 and sensors are located approximately within

Table 2.2: Summary of precipitation sensors at the Sevilleta National Wildlife Refuge from 2001-2012.

Sensor	Lat [°N]	Lon [°W]	Elevation [m]	Length [yr]	$\overline{P}$ [mm]
01	34.35	106.88	1466	10	92.2
40	34.36	106.68	1600	10	108.7
41	34.30	106.79	1538	10	107.4
43	34.28	107.03	1766	10	114.3
44	34.38	106.93	1503	10	102.3
45	34.38	107.00	1547	8	83.6
49	34.33	106.73	1615	10	132.4
50	34.33	106.63	1670	9	129.8

a 5 km^2 radius from any other sensor. For clarity, we refer to USHCN measurement locations as sites and SNWR measurement locations as sensors.

2.3 Methods

To determine if monsoon precipitation has changed in the Chihuahuan Desert region and to assess the variability of this precipitation at scale of individual locations, we conducted a regional analysis of precipitation variability across the northern Chihuahuan Desert (Section 2.4.1) and a local analysis at the SNWR (Section 2.4.2). The monsoon season was defined as July-September (DOY 181-273), adjusted for leap years (Adams and Comrie, 1997). USHCN sites without a full yearly monsoon record (92 days) were not included in the analysis except in calculating precipitation event timing [λ: events day^{-1}] and magnitude [α: cm event^{-1}]. In the second part of the study, we analyzed daily precipitation data from sensors at the SNWR from 2001-2010. A secondary part of this analysis included hourly data from 2006-2010, resulting in slightly better determination of event frequency compared to daily data because an event that occurs before and after midnight is not separated into 2 events. Implementing a 0.5 cm day^{-1} high-pass filter on the precipitation records (not shown) maintained the precipitation trends presented in this manuscript, suggesting that instrumentation changes through time have not influenced data quality.

2.3.1 Extreme values of precipitation

To determine how extreme wet and dry periods have changed regionally from 1910-2010, we employed a peak over threshold analysis of extreme values of groups of days with and without precipitation. Groups were defined as periods of consecutive days at a single USHCN site with or without precipitation, where the shortest possible group is one day and the longest is 92 days, corresponding to the length of the entire monsoon. For example, a USHCN station receiving 3 consecutive days without precipitation in 1910 would result in a value of 3 in the corresponding without precipitation tally for 1910. Peak over threshold analysis identifies changes to the one-tailed confidence threshold, where values above the threshold are extreme with regards to the rest of the record. The magnitude of the confidence threshold is incrementally adjusted to account for the frequency and magnitude of large values in the record using a floating baseline value. We used the technique from Coelho et al. (2008) for peak over threshold determination and present an analysis for wet and dry periods across all sites from 1912-2008 at 95% confidence ($p = 0.05$). We implemented the 5-year mean as the floating baseline value, and adjusting the length of this value between 3 and 10 years did not affect the results of our analysis.

2.3.2 Spatial kriging of precipitation

To visualize spatial variability in monsoon precipitation across the SNWR, we employed a kriging technique to estimate total mean precipitation and the mean standard deviation of precipitation at SNWR sensors from 2001-2010 ($n = 77$, Table 2.2) using the R-project gstat package (R Development Core Team, 2011), utilizing a linear variogram model in 8 directions for the kriging estimation. This technique does not account for topography in estimating total monsoon precipitation, and kriged values presented here are therefore not an accurate approximation over the non-Chihuahuan Desert eastern and western boundaries of the SNWR, which are higher in elevation and not located in the Chihuahuan Desert.

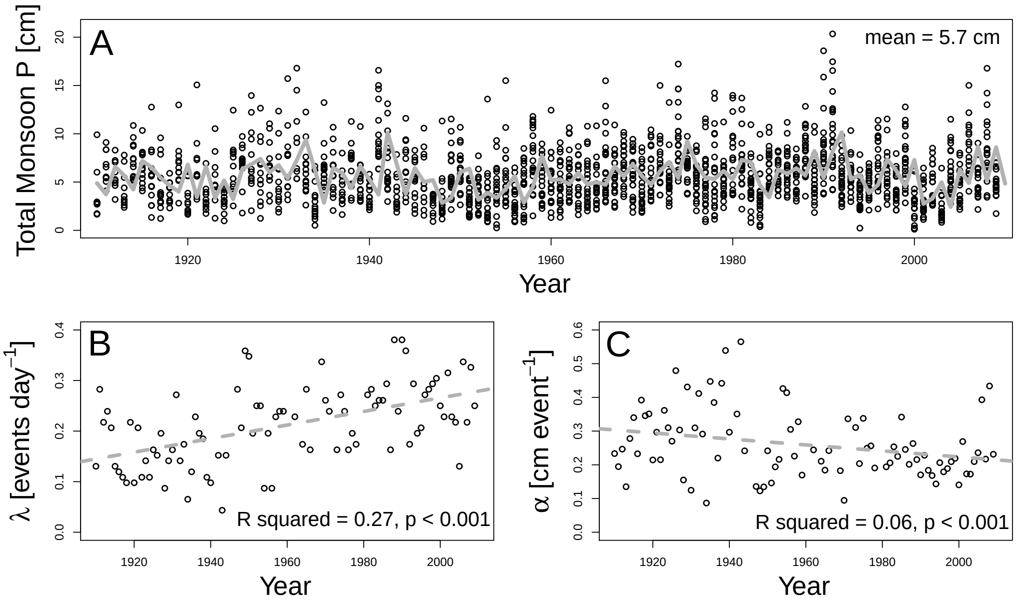

Figure 2.2: Total USHCN site precipitation (Panel A), average monsoon event timing [λ: events day^{-1}] (Panel B) and average monsoon event magnitude [α: depth event^{-1}] (Panel C) for up to 22 sites in the northern Chihuahuan Desert from 1910-2010. Mean annual monsoon precipitation from 1910-2010 is indicated by the line in Panel A.

2.4 Results

2.4.1 Regional precipitation from 1910-2010

Linear correlation of data from 1910-2010 show no trend in total USHCN site precipitation and weak trends in average event timing [λ] and average event magnitude [α], with high variability in precipitation between sites and years (Figure 2.2). Based on the slope of the regression line, average precipitation event timing has increased from 1910-2010, from a frequency of approximately one event every 7.0 days ($\lambda = 0.14$ events d^{-1}) in 1910 to approximately one event every 3.6 days ($\lambda = 0.28$ events d^{-1}) in 2010 (Panel B). The average magnitude of precipitation events has decreased to a small degree from approximately 3.0 mm per event in 1910 to 2.1 mm per event in

2010 (Panel C). These trends (more events of slightly lower magnitude) qualitatively support our determination of no trend in total monsoon precipitation.

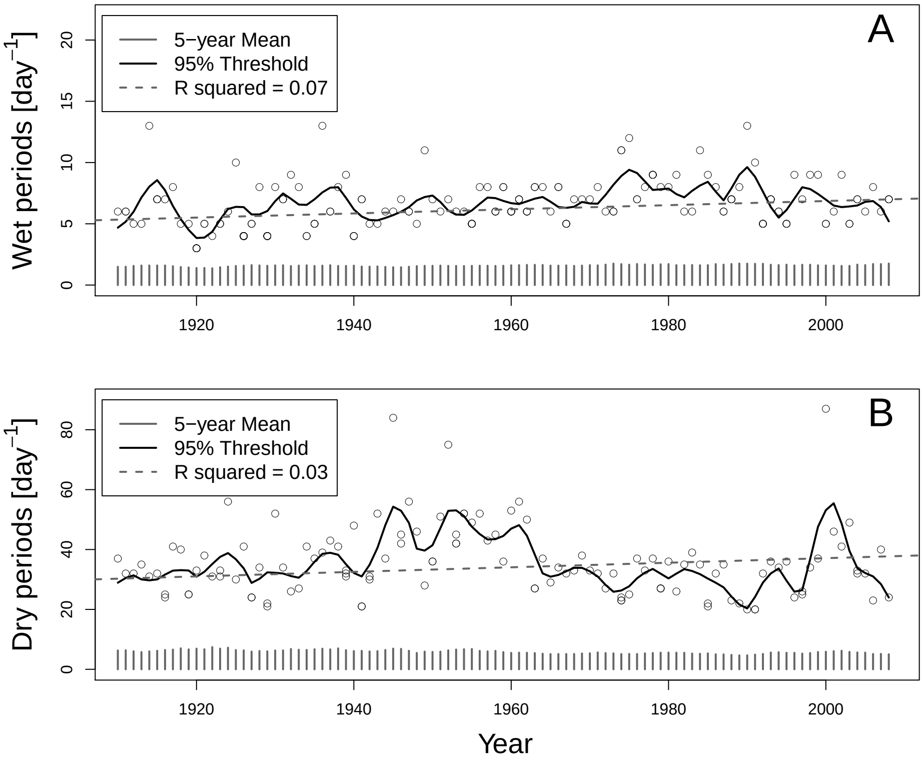

Figure 2.3: Peak over threshold analysis of consecutive days with precipitation (Panel A) and without precipitation (bottom) during the monsoon season from 1912-2008. Points denote periods above the 95% confidence threshold (p = 0.05); the threshold is lowess smoothed by 10% for illustration purposes and is denoted by a dashed line, while the 5-year mean of precipitation is illustrated as vertical lines. Extreme dry periods have increased from an average of 38 days in 1910 to 46 days in 2010, while extreme wet periods have increased from an average of 11 days to 13 days over the same period.

Peak Over Threshold (POT) analysis shows a slight increase in the 95% confidence threshold from 1910-2010 for groups of days with precipitation (R^2 = 0.07, p = 0.05, Figure 2.3A), indicating that extreme periods of continuous precipitation have increased in magnitude from approximately 11 days in 1910 to 13 days in 2010, based on the slope of the regression line. This is consistent with the observed small increase in event timing in Figure 2.2B. Conversely, POT analysis of extreme periods without precipitation also shows an increase from approximately 38 days in 1910 to 46 days in 2010 ($R^2 = 0.03$, $p = 0.05$), and also shows spikes of high values that are consistent with known dry periods for the region during the 1950s and early 2000s. Although average total precipitation has not changed over the past 100 years, monsoon precipitation events in the northern Chihuahuan Desert region have become more numerous and slightly smaller in magnitude, with greater average length of the very wettest and driest periods.

2.4.2 Monsoon precipitation at the Sevilleta NWR

From 2001-2010, average monsoon precipitation at the SNWR was higher than in the Chihuahuan Desert region, although the SNWR experienced two years with lower average precipitation than in the larger region (2007, 2009; Table 2.3). Normalized variability in total precipitation was lower at the SNWR during this period (Table 2.3), and total precipitation was slightly higher at sensors located at the east side of the refuge (Figure 2.4A). Precipitation at SNWR sensors shows no consistent spatial pattern, however, and the normalized standard deviation of monsoon precipitation at a sensor is 50% of the 10.8 cm average (Figure 2.4B). Therefore, individual sensors at the SNWR experienced precipitation totals both higher and lower than the 10.8 cm average in most years, and this high variability is characteristic of both the SNWR and the Chihuahuan Desert.

The primary reason for high variability in monsoon precipitation at the SNWR is the occurrence of large rainfall events. In Figure 2.5, monsoons at the SNWR were organized into wet (2002, 2006, 2008; $n = 23$ sensors), average (2001, 2004, 2005, 2010; $n = 30$) and dry (2003, 2007, 2009; $n = 24$) groups based on average total precipitation. The distribution of precipitation events (mm day^{-1}) between these groupings

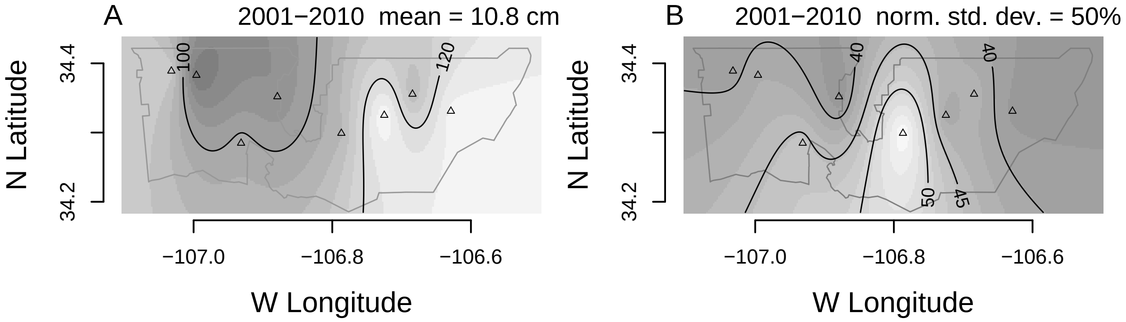

Figure 2.4: Average total monsoon precipitation (Panel A) and normalized standard deviation of monsoon precipitation (Panel B) for sensors across the Sevilleta National Wildlife Refuge from 2001-2012, kriged using a linear variogram model. Normalized standard deviation of precipitation [σ_P: %] was calculated from total annual precipitation at all sensors (n = 77). Sensors are shown as triangle symbols on the map.

shows that the primary difference between wet, average and dry monsoons is the occurrence of large events (10+ mm). Large events may account for as few as 20% of total events (Figure 2.5A), but contribute the majority of monsoon precipitation (Figure 2.5B). At the SNWR, large events accounted for 66% of total precipitation in wet years compared to 28% in dry years. Furthermore, a more sensitive analysis of hourly data at individual sensors from 2006-2010 (n = 52) shows that events of less than 3.68 mm accounted for 65% of total events at a sensor on average, but had an insignificant effect on total monsoon precipitation (One-tailed, paired t-test, $p < 0.05$).

The SNWR received higher average monsoon precipitation than the Chihuahuan Desert region from 2001-2010 (59% higher), and also experienced lower average normalized standard deviation in precipitation (34% lower, Table 2.3). While the 2001-2010 period was wetter than average across the region, the majority of the northern Chihuahuan Desert - which is located south of the SNWR - was comparatively drier and experienced higher spatial variation in rainfall. There is also a negative relationship between total precipitation and normalized variability in precipitation for

Table 2.3: Summary of precipitation at Sevilleta National Wildlife Refuge stations from 2001-2012 (n = 77) and at Chihuahuan Desert USHCN sites from 2001-2010 (n = 183). Normalized standard deviation of precipitation [σ_P: %] is shown as the average between sensors within a year (intraannual), and for as the average of mean precipitation between years (interannual).

Year	SNWR $\overline{P}$ [mm]	SNWR $\overline{\sigma_P}$ [%]	USHCN $\overline{P}$ [mm]	USHCN $\overline{\sigma_P}$ [%]
2001	96.5	22.4	27.5	63.3
2002	156.5	30.8	33.0	47.8
2003	55.4	33.2	49.7	38.5
2004	96.4	21.7	24.2	61.6
2005	104.9	40.1	63.0	37.5
2006	170.9	22.2	49.1	36.5
2007	75.4	28.7	86.6	32.3
2008	139.6	19.5	51.6	35.2
2009	82.9	21.1	86.1	40.6
2010	98.0	37.5	48.4	27.9
$\overline{x}$	107.7	27.7	67.8	42.1

all USHCN and SNWR data ($R^2 = 0.23$, $p < 0.001$, Figure 2.6). This relationship suggests that regional variability in monsoon precipitation may partly be due to differing total precipitation in spatially distinct locations (such as high precipitation at the SNWR) in many years. Also, this relationship shows that a single location within the region is likely to experience similar changes in rainfall variability in wetter or drier monsoon years that occur at the larger regional scale (Figure 2.6).

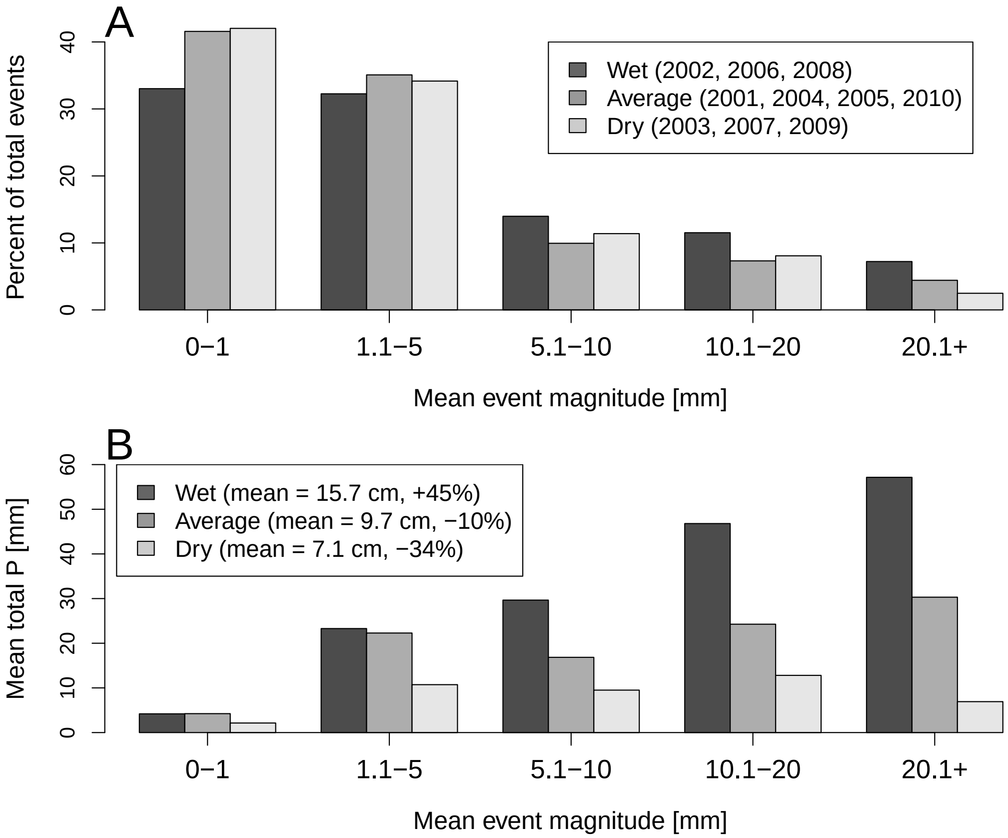

Figure 2.5: Percentage distribution of precipitation events by magnitude (Panel A) and the mean total precipitation from these events (Panel B) at the Sevilleta National Wildlife Refuge from 2001-2012 for wet (n = 23 sensors), average (n = 30) and dry (n = 24) monsoon seasons. Average monsoon precipitation during this period was 10.8 cm, and the difference between this and the wet, average and dry values is shown as a percentage (Panel B).

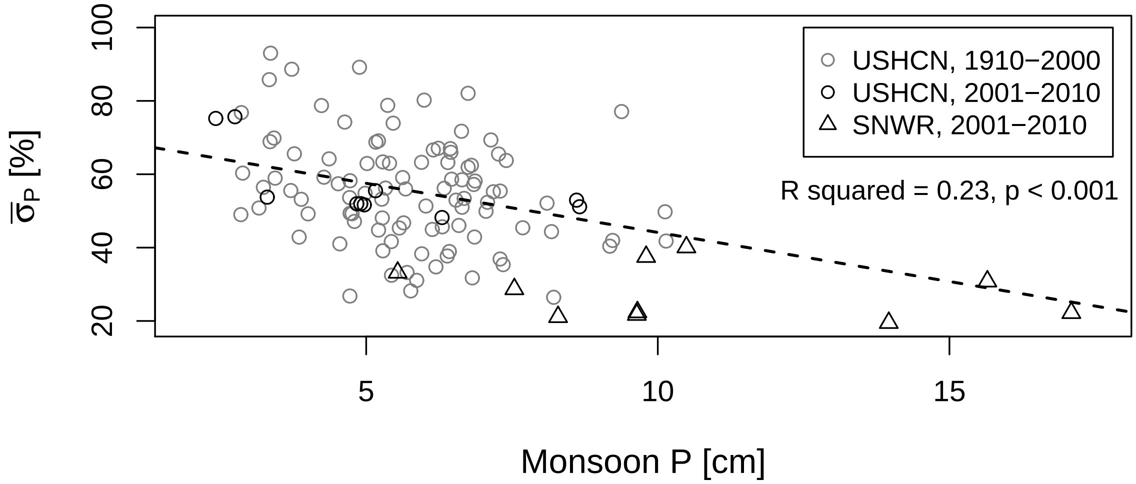

Figure 2.6: Relationship between average annual monsoon precipitation [cm] and normalized annual variability in total precipitation for USHCN sites in 1910-2010 and SNWR sensors in 2001-2010 (R^2 = 0.23, $p < 0.001$).

2.5 Discussion

2.5.1 Regional precipitation from 1910-2010

Regional precipitation exhibits trends in average event timing and magnitude (Figure 2.2), but these compensating changes have not induced change in total average monsoon precipitation at USHCN sites over the last 100 years. Although the scales of analysis differ, our results are similar to those of Anderson et al. (2010), who saw no trend in summer precipitation for much of the southwestern US, but are different than the results of Turnbull et al. (2013), who saw a slight increase in annual precipitation at a single site at the Jornada LTER from 1914-2011. The Jornada site was part of our analysis (USHCN site 294426, Table 2.1), but Turnbull et al. (2013)'s observations are muted by variability at other sites in the regional record. Furthermore, the sites presented in this study are similar in elevation (800-1800 m) and do not experience high topographical variation in precipitation that is seen in other monsoon precipitation studies (Gochis et al., 2003, 2006; Gebremichael et al., 2007; Mendez-Barroso and Vivoni, 2010). These results further emphasize issues of scale in climate data and suggest that trends occurring at single sites may be masked in larger-scale mean values; changing monsoon patterns are more likely to be localized than widespread. In our study, however, the statistical extrema of periods with and without precipitation show that precipitation is becoming more variable across the entire northern Chihuahuan Desert region during the summer monsoon (Figure 2.3) and extreme periods of wet and dry days are increasing in length (Figure 2.3A,B). The regional historical record also captures discrete, punctuated periods in the 1950s and early 2000s that correspond to known regional droughts (Figure 2.2A). Episodic dry events may occur independently from regional trends but, in the case of changing monsoon patterns (Grantz et al., 2007) and a warmer climate (Seager and Vecchi, 2010; Gutzler and Robbins, 2011), it is very unclear how change in the frequency and severity of these episodic events could affect local ecology and hydrology.

While change in the properties of precipitation is a concern for predicting the future ecology of southwestern ecosystems (Knapp et al., 2008), our analyses suggest that trends in the properties of summer precipitation did not necessarily produce greater regional aridity in the second half of the 20^{th} century. While the Chihuahuan Desert is experiencing longer wet and dry periods, illustrated by the changing length of extreme events, this variability appears to be occurring at local scales instead of occurring regionally. It is likely that individual locations may become wetter or drier with no notable change in the larger region. Unless the properties of precipitation change to a greater degree than has been observed over the past 100 years, we believe that predicted increases in surface temperature are likely to be the primary cause of increasing regional aridity in the southwestern US in coming decades. The possibility of this is not explored here, but we suspect that precipitation-driven aridity would require a large, directional shift in forcing to disrupt the inherent variability of the monsoon season. Although monsoon precipitation has changed regionally from

1910-2010, high variability in total precipitation during this period suggests that locations in the Chihuahuan Desert are more likely to experience changes in episodic events, such as drought, than they are to experience long-term, important changes in precipitation patterns. These episodic dry periods, which we observed in both the long-term record and in the analysis of extreme events during the 1950s and early 2000s (Figures 2.2A, 2.3B) are likely to be increased in frequency and magnitude by increased surface temperature as well (Gutzler and Robbins, 2011).

2.5.2 Monsoon precipitation drivers and annual dynamics

Long-term, regional climate data may often mask the change in climate at smaller scales. In our study, total precipitation at SNWR sensors and USHCN sites may correspond to regional averages, but the high annual variability observed in these data shows that both higher and lower than average precipitation is a frequent occurrence. At the SNWR, total precipitation and variability in precipitation between sensors fluctuates between wet and dry monsoons, and within year variability is very high (Table 2.2, Figure 2.4). As a result, sensors may rarely receive precipitation near mean values. This variability has important implications for climate change in aridland ecosystems; vegetation communities at scales of < 5 km^2 may experience total precipitation that varies widely from mean values at subgrid scales (roughly 50 km^2 in this case).

Figure 2.5 shows that the very largest events occur at a low frequency but produce the majority of monsoon precipitation at the SNWR. Our results corroborate with Xu and Zipser (2012) and Wall et al. (2012), who saw similar precipitation patterns across the southwestern United States using TRMM satellite data. In addition, the dominance of infrequent, large events on total site precipitation perhaps explains why changes in regional precipitation event timing and magnitude (Figure 2.2) do not affect average regional precipitation: the number of events does not necessarily correlate to total precipitation and regional decreases in average event magnitude are not very large. Thomey et al. (2011) found that a small number of large precipitation events induces a greater soil moisture response than a larger number of smaller events in Chihuahuan Desert soils, and our results, which show a reduction in the average magnitude of events, suggest that these changing patterns of precipitation warrant further attention. Furthermore, the SNWR experienced reduced normalized variability in total rainfall from 2001-2010 compared to the Chihuahuan Desert region (Figure 2.6), suggesting that regional-scale monsoon precipitation may contrast with local conditions, especially at ecosystem boundaries such as those experienced at the SNWR. Should monsoon rainfall be reduced at the SNWR, our data suggest that variability in precipitation between SNWR sensors will increase as well, likely becoming more similar to sites located farther south in the desert (Figure 2.6). These properties of precipitation are difficult to extend to local ecology, however, because small precipitation events (< 5 mm) may play a disproportionately large role in regulating nutrient availability and water balance, in addition to larger events (Sala and Lauenroth, 1982; Lauenroth and Bradford, 2012). Although our analyses point to the importance of large events, the way that statistical probabilities of all precipitation event distributions change in future climate scenarios may help assess the relationships between total precipitation, precipitation variability, and the importance of these for local ecological functioning.

2.5.3 Implications for global climate modeling

Subgrid scale precipitation data in the Chihuahuan Desert may contain information that is not resolved by global climate models (GCM). GCM outputs, often at large spatial scales ($> 10{,}000$ km^2) (Johns et al., 1997; Flato et al., 2000), do not capture the spatial heterogeneity that defines subgrid scale precipitation variability, especially at short timescales (Wan et al., 2013). In this study we provide additional evidence that regional scale precipitation statistics do not capture precipitation patterns locally, and that a high degree of variability exists in total sensor precipitation within and between years. While we are encouraged that satellite and sensor data agree on the influence of large events on total precipitation (Wall et al., 2012), the even smaller spatial resolution of GCM outputs likely does not capture this dynamic. In the case of monsoon precipitation at SNWR sensors, in which we found high within year variability, GCMs likely underestimate subgrid-scale variability total precipitation. Our data suggest that precipitation variability may increase at sites in the Chihuahuan Desert if total rainfall is reduced (Figure 2.6). Adequate soil moisture is critical for producing soil moisture-precipitation feedbacks and for large-scale vegetation activity in the Chihuahuan Desert during the summer monsoon (Mendez-Barroso et al., 2009; Mendez-Barroso and Vivoni, 2010), but it is unclear how the increased small-scale variability in precipitation that we observed also affects these processes.

The importance of capturing variability in model outputs of precipitation may also depend on the frequency that precipitation-related climatic perturbations occur. Two sub-continental drought events occurred in parts of the Chihuahuan Desert during the 1950s and early 2000s, resulting in vegetation die-offs in upland woodland ecosystems at the SNWR and in the larger southwestern US (Breshears et al., 2005). In our analysis, these droughts are distinguishable as extreme periods without precipitation (Figure 2.3B), but are not distinguishable in the regional precipitation record (Figure 2.2A). Climatic events such as these may need to encompass a very large spatial extent, affect a number of ecosystem types and occur over a number of years before they can be resolved in current GCM outputs, especially due to the difficulty of recreating climate extremes in GCMs (Wan et al., 2013). The small scale variability inherent to monsoon precipitation and the episodic nature of climatic events are both likely not accounted for in GCM outputs, and may limit analyses to the largest global change type events and trends.

2.6 Conclusions

Monsoon precipitation events in the northern Chihuahuan Desert have increased in frequency and decreased in magnitude over the past 100 years, and the length of the very wettest and driest periods have increased (Figures 2.1, 2.2). These changing patterns have not changed average total monsoon precipitation regionally. The reason for no change in average total precipitation is perhaps explained at the SNWR, where a small number of very large events can account for the majority of total precipitation and the smallest 65% of events are often insignificant in terms of total precipitation. There is great spatial and temporal variability in total monsoon precipitation at SNWR sensors within and between years. We have determined that monsoon precipitation near the regional, long-term mean rarely occurs at SNWR sensors, and variability in total precipitation at these sensors is much higher than is often accounted for in ecological analyses.

Future climate predictions for the southwestern United States call for increased surface temperature and altered or reduced precipitation to induce greater regional aridity (Seager and Vecchi, 2010; Gutzler and Robbins, 2011). The fact that regional monsoon precipitation totals from 1910-2010 has not changed does not contradict these predictions and instead sharpens questions on how future aridity could be realized. Increased surface temperature may induce more predictable responses in ecological functioning than altered precipitation (Petrie et al., 2012). This reality may be inconsequential, however, if the driver of ecological change in the Chihuahuan Desert is extreme dry periods, which are likely to increase in frequency and magnitude in a more arid climate (Gutzler and Robbins, 2011). If precipitation dynamics do change in the southwestern US, a shift towards larger events would likely increase soil moisture availability (Heisler-White et al., 2008) and facilitate soil moisture-precipitation feedbacks (Mendez-Barroso and Vivoni, 2010), although changing event intensity [magnitude per unit time] may alter the availability of this precipitation, especially in cases of high surface runoff due to soil texture or topography (Vivoni et al., 2010). At both local and regional scales, our analyses suggest that high annual variability will continue to characterize monsoon precipitation.

Chapter 3

Grassland to shrubland state transitions enhance carbon sequestration

3.1 Introduction

The replacement of dominant vegetation communities via ecological state transitions is occurring worldwide as a consequence of global environmental change (Scheffer and Carpenter, 2003), and these transitions may alter the quality and timing of key ecosystem services (Schlesinger et al., 1990; Maestre et al., 2012). Ecological state transitions are especially common in aridland ecoregions in response to multiple anthropogenic drivers, and the potential for climate-induced state transitions may be increasing (Reynolds et al., 2007; Diffenbaugh et al., 2008; D'Odorico et al., 2012). Climate model simulations for the southwestern United States predict greater aridity in the coming decades because of warmer temperatures and more variable precipitation regimes (Seager et al., 2007; Gutzler and Robbins, 2011), and additional projections suggest that the summer monsoon may occur later in the growing season (Seth et al., 2011). In addition to long-term change, extreme drought events in the southwestern US have had profound effects on vegetation communities regionally and locally in the past 60 years (Breshears et al., 2005). It follows that the greater aridity produced by a changing climate is likely to increase the frequency and extent of ecosystem state transitions.

One widespread ecological state transition in arid and semiarid ecosystems is from C_4-dominated grassland to C_3-dominated shrubland (Eldridge et al., 2011). As a state transition, shrub encroachment often results in permanent and measurable changes to ecosystem functioning and includes reduced plant species diversity (Baez and Collins, 2008; Knapp et al., 2008; Ratajczak et al., 2012), increased spatial heterogeneity in resource availability (Bhark and Small, 2003; Turnbull et al., 2010), increased surface temperatures (D'Odorico et al., 2010, 2012), and altered timing of ecosystem mass and energy exchange (Kurc and Small, 2007; Brunsell et al., 2011). These changes may in turn feed back to promote further state transition (D'Odorico et al., 2013b). As a beneficial change in services, some studies have shown an increase in above- or belowground ecosystem carbon sequestration as a result of grassland to shrubland state transitions (Jackson et al., 2002; Emmerich, 2007; Knapp et al., 2008). In the Chihuahuan Desert, the conditions under which grassland and shrubland may outperform each other remain unclear; Kurc and Small (2004, 2007) found grassland to be more productive than creosotebush-dominated shrubland during relatively wet growing seasons, while Throop et al. (2012) found that mesquite-dominated shrubland was more productive than grassland in a water-manipulation experiment. In other aridland systems, variables including groundwater depth (Scott et al., 2014) and soil inorganic carbon content (Emmerich, 2003) may additionally influence grassland and shrubland productivity and ecosystem C sequestration.

Understanding how carbon exchange is altered by changing ecological states is of primary importance for modeling land surface processes in GCMs (Schimel, 2010). Arid and semiarid ecoregions cover 40% of the terrestrial land surface and may have an important influence on patterns of global carbon sequestration during years of above average precipitation (Reynolds et al., 2007; Poulter et al., 2014). Although arid ecosystems exhibit relatively low net primary production, increasing lignification and aboveground carbon storage as a result of shrub encroachment may increase above- and belowground carbon sequestration (Jackson et al., 2002; Emmerich, 2007). It is unclear, however, if C sequestration is consistent through time, or can be maintained under likely scenarios of increased aridity due to global climate change (Poulter et al., 2014). By quantifying the carbon sequestration dynamics of established grassland and shrubland communities, we can elucidate the degree to which grassland to shrubland transitions impact ecosystem carbon sequestration potential.

We measured differences in production and ecosystem carbon exchange dynamics between established Chihuahuan Desert grassland and nearby creosotebush shrubland in response to interannual moisture availability, to determine if the state transition from C_4-dominated grassland to C_3-dominated shrubland resulted in increased C sequestration. During our 5-yr study, total annual precipitation was at or below average, providing an analog to the type of drier conditions that are likely to occur in coming decades (Gutzler and Robbins, 2011). We measured precipitation, soil moisture, aboveground and belowground net primary production, and ecosystem carbon and energy exchange to: 1) compare the annual production and carbon sink strength of grassland and shrubland communities; 2) characterize grassland and shrubland carbon exchange dynamics at daily, seasonal and interannual timescales; and 3) determine the sensitivity of grassland and shrubland productivity to soil moisture availability and energy partitioning during their active growing seasons. By doing so, we identified the carbon sequestration potentials of arid grassland and shrubland, and identified the biotic and abiotic variables that shaped carbon exchange in these ecosystems over multiple temporal scales.

3.2 Site

Our research was conducted at the Sevilleta National Wildlife Refuge (SNWR), New Mexico, USA (34.3° N latitude, 106.8° W longitude). At the SNWR, temperature and precipitation interact to drive a bimodal growing season that is punctuated by two periods of vegetation production (Notaro et al., 2010). The spring growing season is driven by increasing temperature and soil moisture derived from winter rainfall, and the summer growing season is driven by monsoon rainfall (Pennington and Collins, 2007; Muldavin et al., 2008). The period between these seasons (approximately May-June) is typically water-limited. Mean annual precipitation for the grassland and shrubland sites was 244 mm from 1996-2011, and 125 mm of this (51%) occurred during the summer monsoon from July-September. During our study from 2007-2011, precipitation at the grassland site averaged 208 mm annually and 93 mm during the summer monsoon (-14.8% and -25.6% compared to 1996-2011, respectively), and the shrubland site averaged 226 mm annually and 100 mm during the summer monsoon (-7.4% and -20.0%, respectively; Figure 3.1).

The northern boundary of creosotebush shrubland and the southern boundary of mixed blue and black grama grassland coexist at the SNWR, and northward expansion of creosotebush into desert grassland is ongoing in the Chihuahuan Desert region (Peters et al., 2006). We used long-term data from an eddy covariance tower in black grama (*Bouteloua eriopoda*)-dominated desert grassland (34.362° N, 106.702° W) and another tower 5 km south in creosotebush (*Larrea tridentata*)-dominated shrubland (34.335° N, 106.744° W). Elevation at both sites is approximately 1615 m. After a 2009 fire (DOY 217), a new tower was installed in a nearby unburned grassland location approximately 1.5 km away (34.355° N, 106.675° W), and we used data from this tower in 2010 and 2011. Therefore, we did not have data from 4 August 2009 until 1 January 2010 in grassland.

3.3 Methods

Aboveground production [ANPP: g C m^2 y^{-1}] was measured in spring (May) and fall (September-October) each year from 2007-2011 at the creosote shrubland and at the mixed grassland sites. Between 22 and 40, 1 m^2 permanent quadrats were located at each grassland and shrubland site for measuring ANPP using a nondestructive allometric sampling method and linear regression based on measured species volume units developed from total standing biomass measurements (Huenneke et al., 2001; Muldavin et al., 2008). Belowground production [BNPP: g C m^2 y^{-1}] was measured each year using root ingrowth "donuts" (Milchunas et al., 2005). During this period, 10 replicate ingrowth structures in mixed grassland and creosotebush shrubland were harvested annually in November at 0-15 cm and 15-30 cm depth. The majority of grassland root biomass occurs in the upper 30 cm of soil while shrub roots can penetrate much deeper (Kurc and Small, 2007). Soil were sieved (2 mm) to remove roots, which were then dried at 60°C and weighed to estimate belowground biomass (g m^{-2} $year^{-1}$). Data presented here are the combined production estimates from 0-30 cm.

Fluxes of surface carbon dioxide, water and energy were measured continuously from identical, tripod-based eddy covariance instruments at the mixed grassland and creosotebush shrubland sites from 2007-2011 (Anderson-Teixeira et al., 2011). In both sites, a three-axis sonic anemometer (Campbell Scientific CSAT-3) measured vertical wind speed, and an open-path gas analyzer (LiCor LI-7500) measured carbon and water vapor concentrations. We compiled covariances to 30 minute averages, corrected for temperature and water vapor influences (Webb et al., 1980), and sensor separation and frequency responses (Massman, 2000). We used a planar fit coordinate system to account for anemometer tilt (Anderson-Teixeira et al., 2011). We removed data in the case of instrument malfunction, when winds were coming from behind the tower, when wind speed was too low (low friction velocity), and during rainfall events. This resulted in very few data gaps and did not limit our gapfilling procedure. We gapfilled NEE, latent and sensible energy fluxes and estimated ecosystem respiration (RE) using the Max Planck Institute (Open MPI) procedure (Falge et al., 2001; Reichstein et al., 2005) [http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/index.php]. We calculated gross primary production as NEE + RE. Carbon flux data of net ecosystem exchange [NEE], gross primary production [GPP], and ecosystem respiration [RE] is presented in this study as g C m^2 $time^{-1}$.

We used daily GPP to estimate the growing season onset and vegetation senescence in grassland and shrubland, where onset was the first day of 10 consecutive days where GPP > 0.25 g C d^{-1} in spring or summer, and senescence was the last day of 10 consecutive days where GPP < 0.25 g C d^{-1} in fall or winter. This basic threshold technique was sensitive to the abrupt changes in vegetation production that occur at the beginning and end of the growing season in the Chihuahuan Desert (Kurc and Small, 2007; Collins et al., 2008).

Soils at the grassland site are classified as Turney loamy sand and soils at the shrubland site are classified as a mix between Turney loam and Nickel-Caliza very gravelly sandy loam. Differences in soil texture result in a saturated hydraulic conductivity (K_{sat}) of 1.5-5.0 cm $hour^{-1}$ at the grassland site and a K_{sat} of 2.5-8.5 cm $hour^{-1}$ at the shrubland site (United States Department of Agriculture, 2013). Volumetric soil moisture was measured from 2007-2011 at grassland and shrubland eddy covariance tower sites using soil water content probes (Campbell Scientific CS 616) buried horizontally at 2.5 cm, 12.5 cm, 22.5 cm, 37.5 cm and 52.5 cm depth in 6 pits at each site, 3 under vegetation and 3 in vegetation interspaces. These probes measure volumetric soil moisture using a time-domain technique, and are accurate at the low θ values that often occur in aridland soils. At the mixed grassland sites, data were available beginning on DOY 163 in 2007, for all of 2008, were not available in 2009, and were available beginning on DOY 56 in 2010 and for all of 2011. At the shrubland site, data were available beginning on DOY 157 in 2007, for all of 2008, beginning on DOY 176 in 2009 and for all of 2010-2011. Soil moisture was recorded as 30 minute averages and converted to mean daily soil moisture for all analyses. We calculated relative extractable soil moisture [θ_r] as:

$$\theta_r = \frac{\theta - \theta_w}{\theta_{fc} - \theta_w} \tag{3.1}$$

where θ_w is soil moisture at vegetation wilting point and θ_{fc} is soil moisture at soil field capacity. Due to the depth of the soil moisture profile data, we estimated θ_w to be the lowest observed θ value from 2007-2011 (θ_w = 0.065 shrubland; 0.061 grassland), and estimated θ_{fc} from soil water holding capacity and profile depth (θ_{fc} = 0.35 shrubland; 0.31 grassland) (United States Department of Agriculture, 2013). These values corroborated with soil moisture release curves obtained for soils at the grassland and shrubland eddy covariance tower sites. All statistics, analyses and figures were produced using R (R Development Core Team, 2011).

3.4 Results

Our study period was slightly drier than average (208 mm annually (-14.8% lower than 1996-2011 mean), 93 mm monsoon (-25.6% lower than 1996-2011 mean)). 2011 was very dry, 2006 (the year prior to our study) had an especially strong monsoon season, and 2009 had high October rainfall. From 2007-2011, total annual precipitation was similar between grassland and shrubland ($p > 0.05$), although mean daily θ_r was 6.6% higher in grassland ($p < 0.001$) (Figure 3.1). Mean daily Bowen Ratio [β] did not differ between sites ($p > 0.97$), however, indicating that grassland and shrubland experienced similar turbulent energy flux partitioning during our study.

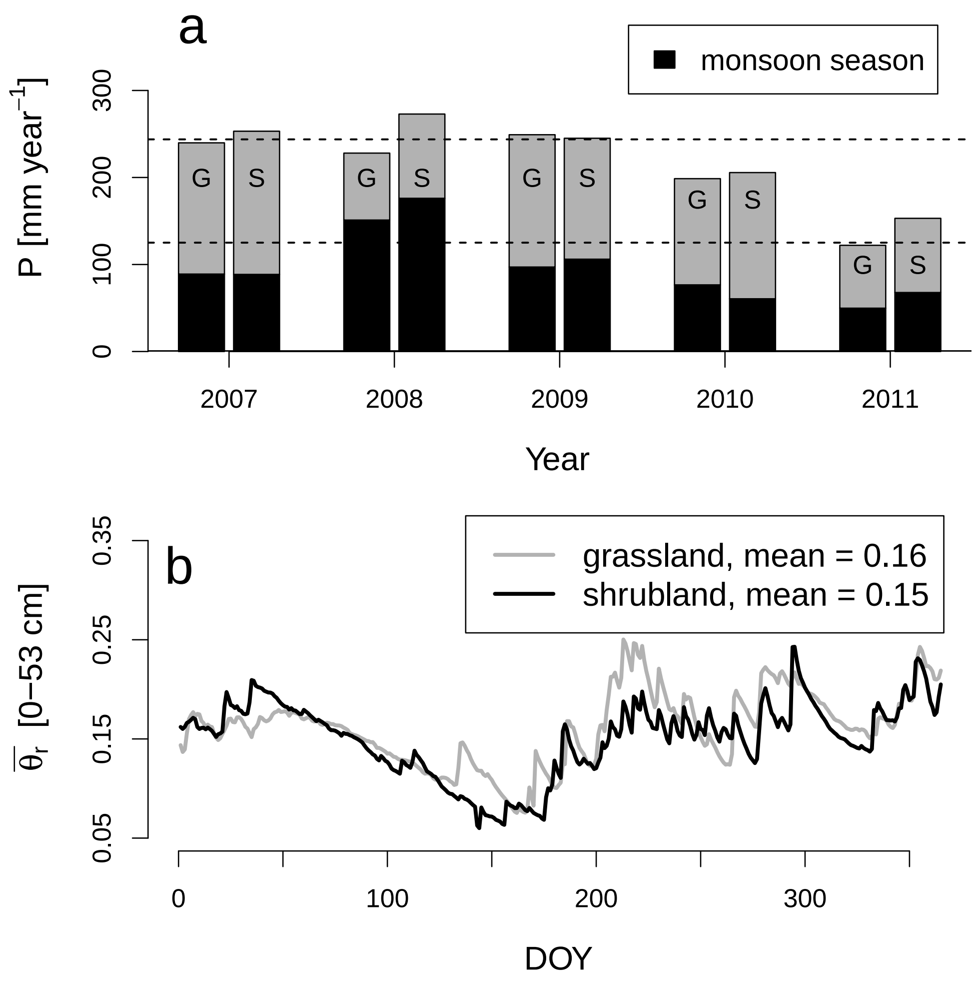

Figure 3.1: Total annual and monsoon precipitation at the creosotebush shrubland (S) and mixed grassland (G) site in 2007-2011 (Panel A) and mean daily relative extractable soil moisture [θ_r] (Panel B). Mean monsoon precipitation and mean annual precipitation from 1996-2011 are indicated by horizontal lines in Panel A. θ_r was greater on average at the grassland site ($p < 0.001$).

Despite having higher average annual net primary production than shrubland from 2007-2011, desert grassland was a net carbon source (annual positive NEE) while the adjacent shrubland was a net carbon sink (annual negative NEE; Figures 3.2 and 3.3). In general, NPP (above- plus belowground) and NEE in grassland were more variable than shrubland, resulting in a net carbon loss from grassland of 31.1

Table 3.1: Seasonal NEE and GPP.

		Spring	Summer	Fall	Winter	Total
grassland	$\overline{NEE}$ [g]	7.0	9.5	4.5	10.1	31.1
grassland	$\overline{GPP}$ [g]	42.8	65.6	28.2	15.5	152.1
grassland	$\overline{RE}$ [g]	49.8	75.1	32.7	25.6	183.2
grassland	NEE [%]	23	31	14	32	100
grassland	GPP [%]	37	41	17	5	100
grassland	RE [%]	27	41	18	14	100
shrubland	$\overline{NEE}$ [g]	-21.9	-2.3	-19.4	-5.4	-49.0
shrubland	$\overline{GPP}$ [g]	39.9	55.5	46.4	17.6	159.4
shrubland	$\overline{RE}$ [g]	18.0	53.2	27.0	12.2	110.4
shrubland	NEE [%]	45	5	39	11	100
shrubland	GPP [%]	25	35	29	11	100
shrubland	RE [%]	16	48	25	11	100

g C m^{-2} year−1 on average, while the less variable, lower production shrubland had a net C uptake of 49.0 g C m^{-2} y−1. Despite measured above- and belowground plant growth, grassland was a net source of carbon in four of the five years of our study (Figure 3.2b). This pattern was particularly notable in 2007 and 2008, where grassland NPP was larger than shrubland NPP, yet grassland NEE indicated annual net carbon loss (Figures 3.2 and 3.3). NPP data from grassland and shrubland in 2005 and 2006 (two years prior to our study) were not anomalous from those of 2007-2011 (Figures 3.2a and 3.3a), suggesting that the pattern of grassland and shrubland carbon sequestration were likely similar over the seven year period.

While grassland net primary production was higher and more variable on average than shrubland (105±67 g and 77±26 g C m^{-2} y^{-1}, respectively, Figures 3.2a and 3.3a), annual shrubland GPP was 5% higher than grassland GPP (GPP = 159 g C and 152 g C m^{-2} y^{-1}, respectively, Figures 3.2c and 3.3c). The timing of maximum GPP differed seasonally between grassland and shrubland. Based on GPP, grassland was most active in spring and summer, while shrubland was most active in spring and fall (Table 3.1). Average shrubland growing season was 27 days longer than that of grassland (Figure 3.4), with shrubland notably more active later in the growing season than grassland. Therefore, ground measurements of NPP did not corroborate with eddy covariance measurements of GPP. NPP by definition cannot be negative, whereas eddy covariance measurements include total ecosystem C exchange. Also some differences result from root production below the 30 cm threshold we measured in shrubland (Jackson et al., 2002). The ratio of RE to GPP shows that RE was 20% higher than GPP in grassland ($\frac{RE}{GPP} = 1.2$), while this ratio in shrubland shows that RE was 30% lower than GPP in shrubland ($\frac{RE}{GPP} = 0.7$). Grassland RE was 66% higher than shrubland RE (RE = 183 g C and 110 g C m^{-2} $y{-}1$, respectively). Annually, slightly higher GPP in shrubland and much higher RE in grassland resulted in an average difference in carbon assimilation of 80.1 g C m^{-2} y^{-1} between grassland and shrubland during our study.

The difference in daily values of NEE between grassland and shrubland was largest during dry days (Bowen Ratio: $\beta > 5$). Bowen Ratio [β: $\frac{H}{LE}$] measurements from eddy covariance data are the ratio of partitioning between sensible energy [H] and latent energy [LE] (Bowen, 1926). We observed daily mean Bowen Ratio in this system to be more frequently influenced by the availability of water than the availability of energy, and higher β values indicate drier conditions usually caused by low LE. Average GPP in grassland and shrubland was similar at daily timescales (Figure 3.5b), but grassland RE was 0.2 g C m^{-2} day^{-1} (68%) higher than shrubland RE on average, and this difference was largest at high β values (Figure 3.5c). During the growing season, carbon exchange in grassland was more sensitive to soil moisture variation than in shrubland, and grassland often displayed higher daily GPP and lower NEE than shrubland when soil moisture was available. As θ_r increased from 10% to 20%, increasing GPP dominated the grassland carbon balance, and grassland became a net carbon sink where θ_r ~14.5% (Figure 3.6b). Grassland GPP also increased at a higher rate than RE over this interval (Figure 3.6c and 3.6d). While shrubland was a net carbon sink on average at every θ_r value, it was a notably smaller sink than grassland at $\theta \geq 15\%$ (Figure 3.6b).

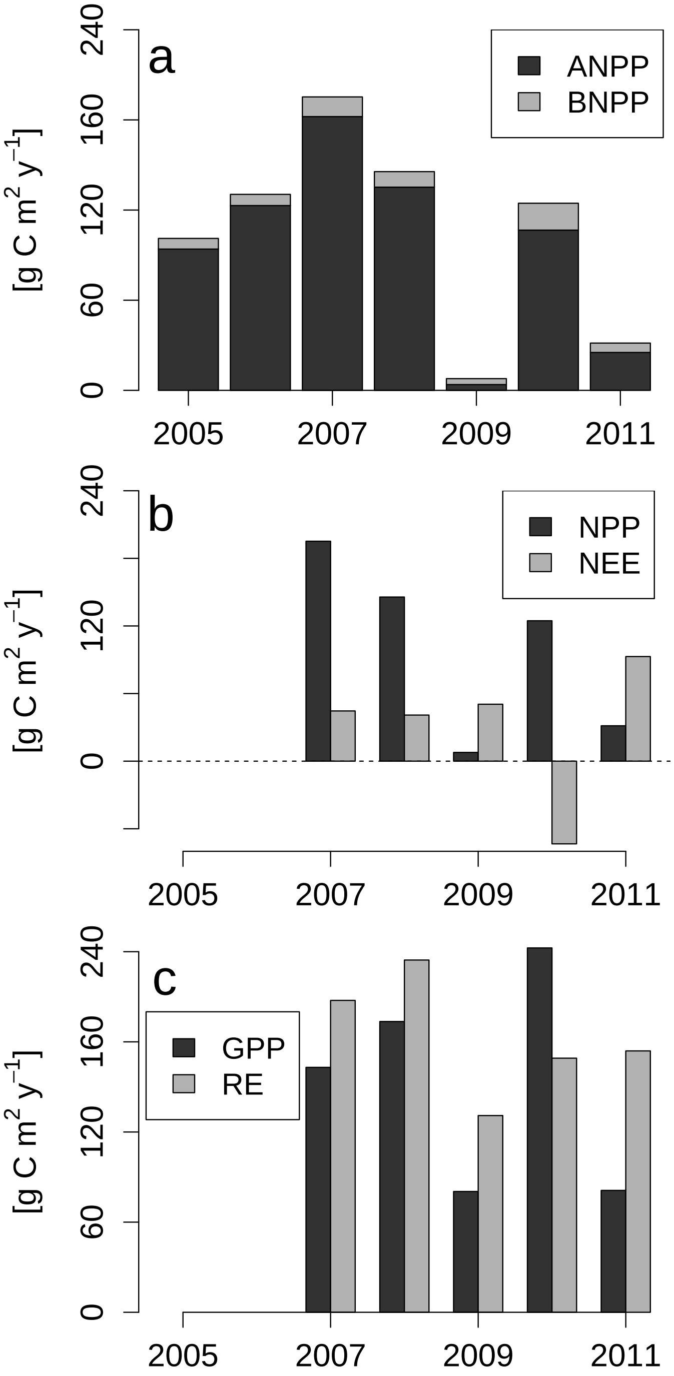

Figure 3.2: Annual aboveground [ANPP] and belowground [BNPP] production from 2005-2011 (Panel A), net primary production [NPP] and net ecosystem exchange [NEE: g m^2 y^{-1}] from 2007-2011 (Panel B) and gross primary production [GPP] and ecosystem respiration [RE] from 2007-2011 (Panel C) in desert grassland.

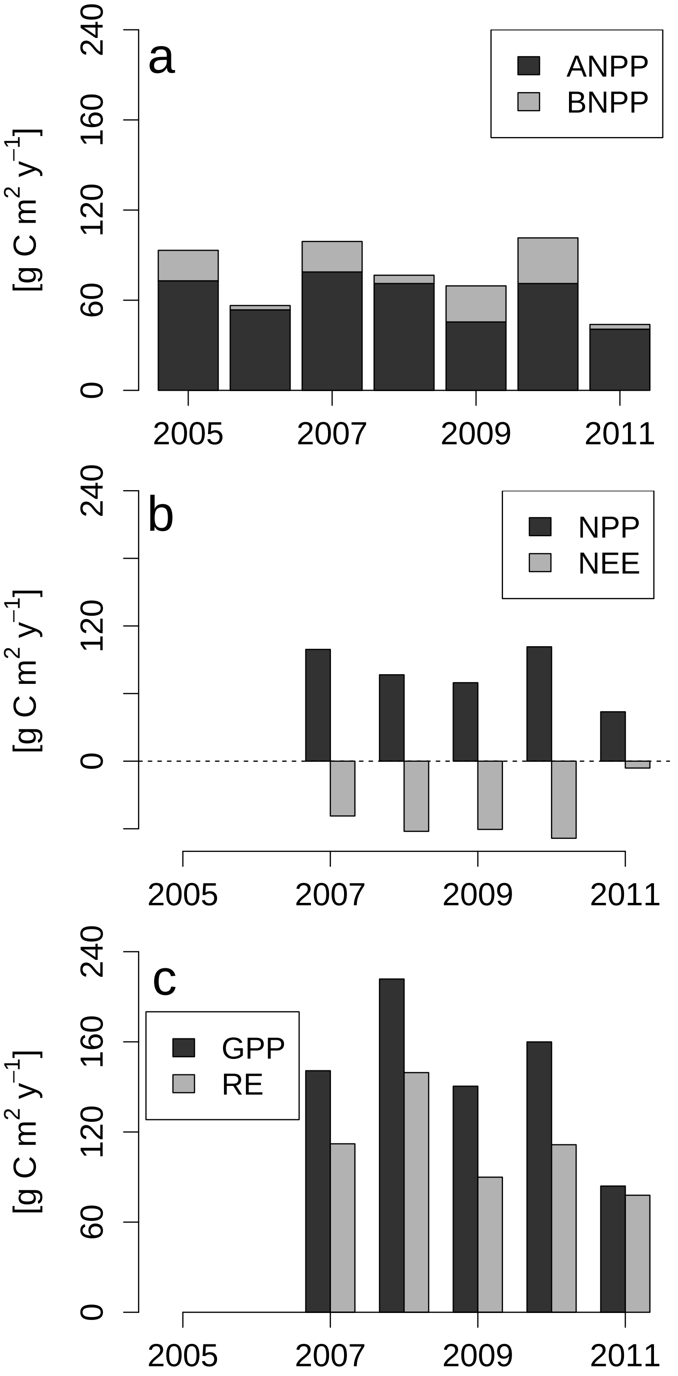

Figure 3.3: Annual aboveground [ANPP] and belowground [BNPP] production from 2005-2011 (Panel A), net primary production [NPP] and net ecosystem exchange [NEE: g m^2 y^{-1}] from 2007-2011 (Panel B) and gross primary production [GPP] and ecosystem respiration [RE] from 2007-2011 (Panel C) in creosotebush shrubland.

3.5 Discussion

3.5.1 Grassland and shrubland production and carbon sequestration

The high variability in annual grassland production observed in our study (Figure 3.2) and by others (Muldavin et al., 2008; Kurc and Small, 2007; Robertson et al., 2009) illustrates the ability of grassland vegetation to capitalize on wet years at the cost of reduced sequestration during dry years. Kurc and Small (2007)found that from 2000-2002 this grassland was a net C sink, but this occurred under a precipitation regime that was 28% higher (123 mm) than the monsoon average (96 mm) of our study (2007-2011). During the relatively drier years of our study, which more likely reflect future climate scenarios, grassland net carbon exchange was governed by the magnitude of GPP compared to that of RE in response to soil moisture availability. As a result of this interaction, which was characterized by higher RE than GPP (Figures 3.2 and 3.5, Table 3.1), grassland was a small net carbon sink only in 2010 (Figure 3.2b). We hypothesize that grassland NEE in 2010 was likely enhanced by spring production driven by rainfall that occurred in October, 2009, after the grassland had already senesced. Conversely, this grassland was a large C sink during the relatively wetter years of Kurc and Small (2004, 2007), and maximum GPP may be up to two times higher in grassland than shrubland during periods of high soil moisture availability (Kurc and Small, 2007; Robertson et al., 2009).

In contrast to grassland, shrubland displayed lower and less variable annual production (Figure 3.3), and was a small carbon sink in every year of our study. Shrubland had a longer growing season than grassland, and assimilated the majority of annual carbon during spring and fall (84%), minimizing the effect of drier than average summer conditions (Figure 3.1). The shrubland carbon sink in fall was nearly as large as in spring (Table 3.1), which has formerly been identified as the most productive period for creosotebush (Muldavin et al., 2008; Pennington and Collins, 2007). While Sponseller et al. (2012) found that creosotebush production may be highest in response to wet summers, our results suggest that dry conditions may alternately favor spring and fall production (Table 3.1). During the dry years of our study, shrubland was a small carbon sink at every timescale of analysis, and the characteristics of shrubland carbon sequestration suggest this sink will persist in a more arid future climate.

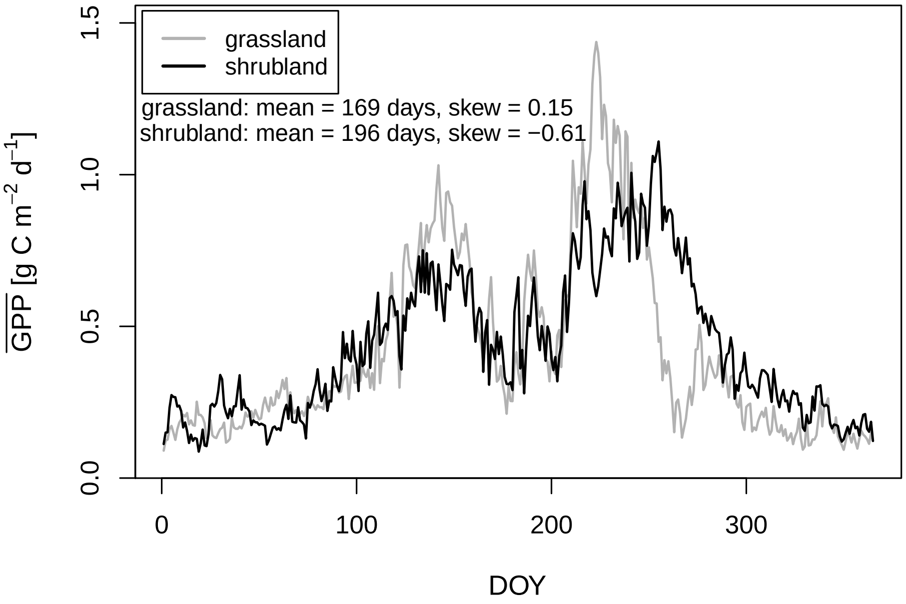

Figure 3.4: Mean daily gross primary production [GPP] from 2007-2011 shows that creosotebush shrublands have longer growing season than desert grasslands by 27 days, on average, and are notably more active late in the year.

Soil respiration in semiarid ecosystems is often dominated by heterotrophic respiration from soil biota (Belnap, 2002; Collins et al., 2014), with precipitation and θ pulses having a large influence on RE during the growing season (Belnap et al., 2004; Jenerette et al., 2008). In addition to this, we also observed RE $\sim$0.6 g C m^2 day^{-1} during the growing season in grassland at θ_r $\sim$5.0%, when biotic activity is expected to be limited (Figure 3.6d). This efflux was not observed in shrubland. While inorganic C exchange may be a large component of carbon balance in many arid and semiarid ecosystems (Emmerich, 2003; Stone, 2008), the potential for emissions from belowground petrocalcic soil horizons is low in the northern Chihuahuan Desert and not a significant source of carbon at the SNWR (Serna-Perez et al., 2006; Breecker et al., 2012). Instead, this carbon loss is likely a result of photodegradation of senesced aboveground plant biomass, which adds an additional, abiotic C flux out of the system (Rutledge et al., 2010; Lee et al., 2012). Abiotic C efflux is therefore an important component of carbon balance in this arid grassland, measurably contributing to annual grassland carbon loss.

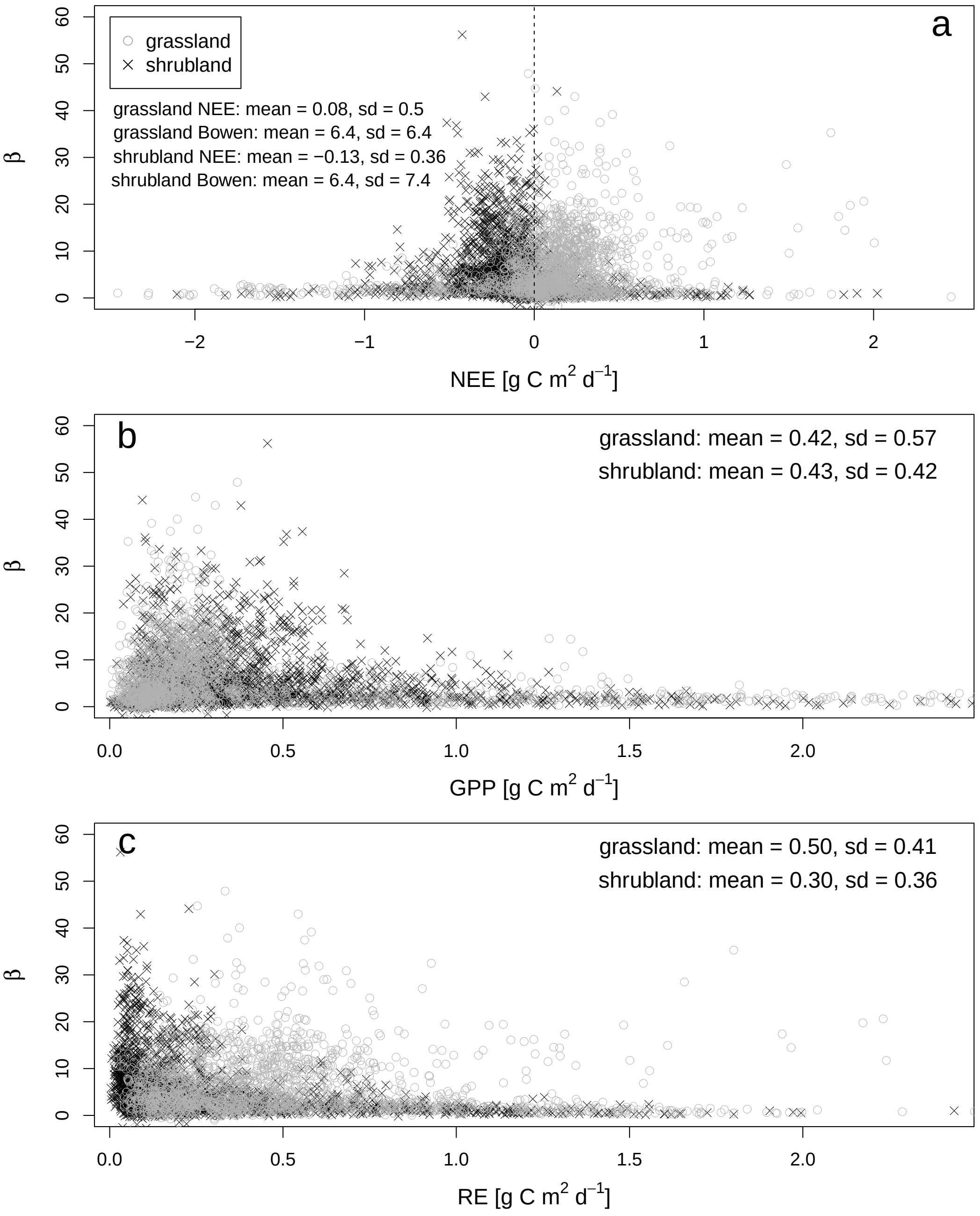

Figure 3.5: Relationship between daily Bowen Ratio [β: $\frac{H}{LE}$] to daily net ecosystem exchange [NEE] (Panel A), daily gross primary production [GPP] (Panel B) and daily ecosystem respiration [RE] (Panel C) in desert grasslands and creosotebush shrublands from 2007-2011. Summary statistics are included and carbon flux units are in g C m^2 day^{-1}.

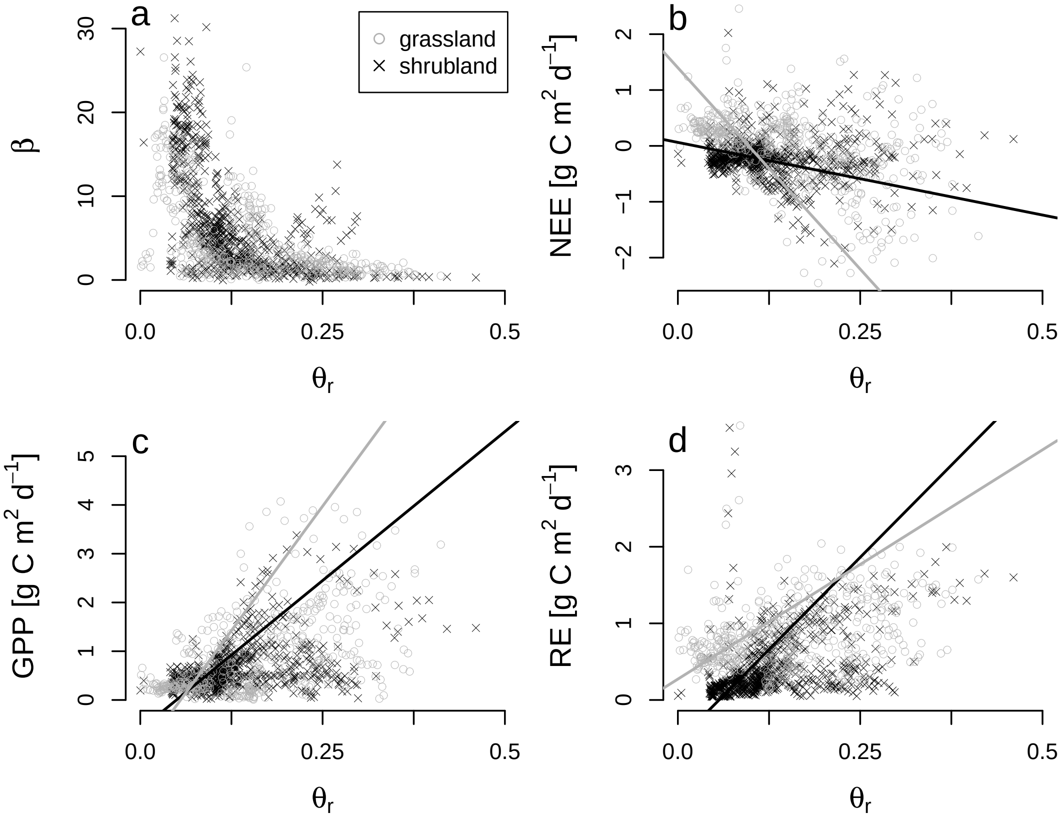

Figure 3.6: Relationship between relative extractable soil moisture [θ_r] and Bowen Ratio [β] (Panel A), Net Ecosystem Exchange [NEE] (Panel B, grassland R^2 = 0.18, shrubland R^2 = 0.01), Gross Primary Production [GPP] (Panel C, grassland R^2 = 0.29, shrubland R^2 = 0.22) and ecosystem respiration [RE] (Panel D, grassland R^2 = 0.07, shrubland R^2 = 0.17) for desert grasslands and creosotebush shrublands during their active growing seasons. All carbon flux units are in g C m^2 day^{-1}.

3.5.2 Climate change and ecological state transitions

Carbon sequestration is likely to occur as a consequence of shrub encroachment in the northern Chihuahuan Desert. Over the past 100 years, monsoon season precipitation events have increased in frequency but decreased in magnitude, and the longest wet and dry periods have increased in length (Petrie et al., 2014a). Furthermore, projected later monsoon onset in the southwestern US will reduce precipitation in

July and increase it in October, when shrubs remain active but grasses do not (Table 3.1, Figure 3.4) (Seth et al., 2011; Cook and Seager, 2013). At the SNWR, grassland was especially sensitive to dryness during summer. In the driest year of our study (2011), the grassland growing season was only 14 days long based on GPP, while that of shrubland was 48 days long. If future climate induces greater aridity in summer, and monsoon precipitation extends later into the fall, grassland will become increasingly vulnerable to further shrub encroachment.

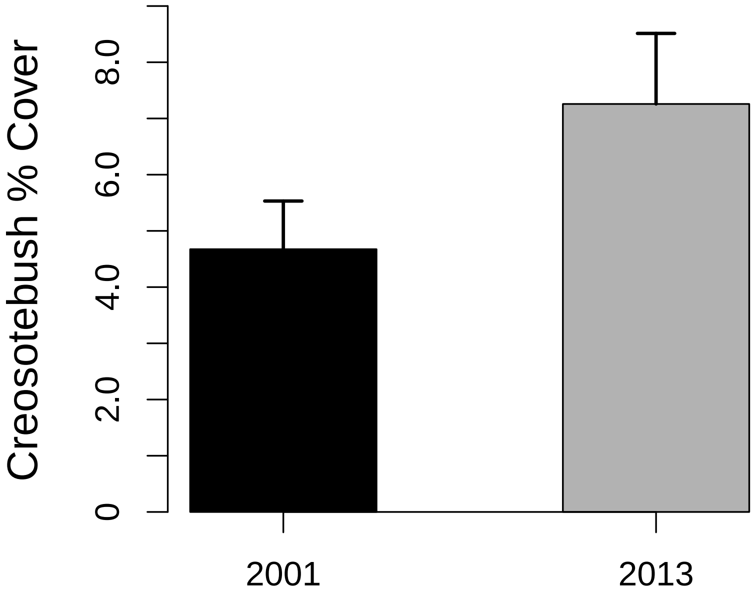

Figure 3.7: Creosotebush percent cover across two 325 m transects in creosotebush-dominated shrubland at the SNWR. Creosotebush cover [%] in 2013 was higher than in 2001 (4.7% in 2001, 7.3% in 2013, $p < 0.05$). Across two longer 1000 m transects (into blue and black grama grassland), creosotebush cover was not significantly higher in 2013 ($p > 0.13$, not shown).

While the specific mechanisms that induce grassland to shrubland state transitions in the southwestern US are complex, our results indicate that shrub encroachment will lead to increased carbon sequestration relative to grassland. If the shrubland carbon sink strength averages 49 g C m^2 $year^{-1}$, as seen in our study (Table 3.1), large-scale state transitions may increase the regional carbon sink by as much as 490 kg C hectare y^{-1} in the southwestern US. The potential for grassland to shrubland land class change is also substantial; the Southwest Regional Gap Analysis Project (SWReGAP) estimates that there are 14.9 M hectares of blue and black-grama dominated desert grassland in New Mexico alone (USGS National Gap Analysis Program, 2014). The sink potential of shrubland is produced by growth of existing individuals as well as infill, which continues to occur in areas undergoing encroachment. Indeed, creosotebush density (by sapwood area) at this site, which has been dominated by creosotebush for longer than 40 years, actually increased from 2001 to 2013 (Figure 3.7). Furthermore, Evans et al. (2014) found increases in ecosystem C sequestration over 10 years in a CO_2 enrichment experiment in the Mojave Desert. Due to these characteristics, the shrubland carbon pool is likely to both persist and increase in coming decades. Semiarid ecosystems have a strong influence on interannual variability in terrestrial carbon sequestration globally (Poulter et al., 2014), and the patterns that we observed in our study suggest that grassland carbon sequestration that occurs during wet periods (Kurc and Small, 2004, 2007) is vulnerable to decomposition during subsequent drier periods. Conversely, semiarid shrubland is notably less vulnerable to carbon losses, and our results suggest that the state transition of grassland to shrubland over large areas (> 1000 km^2) would promote lower interannual variability in terrestrial carbon sequestration.

Gains in C sequestration come at a cost to other ecosystem services provided by these desert grasslands. In addition to ecological impacts, surface soil losses that accompany land class change are a significant source of dust and pollution in the southwestern US (Yin et al., 2005; Field et al., 2010), and shrub encroachment will lead to warmer winters in nearby urban areas as well (D'Odorico et al., 2010). Land class change has been shown to influence soil moisture-precipitation feedbacks and precipitation patterns in the US Great Plains (Brunsell et al., 2011), and state transitions in the Chihuahuan Desert may alter land-atmosphere interactions that are instrumental in driving vegetation activity during the summer monsoon (Dominguez et al., 2008; Mendez-Barroso and Vivoni, 2010). In a future climate scenario where positive feedbacks may lengthen and intensify regional drought periods (Gutzler and Robbins, 2011), carbon sequestration, evaporation and changing ecosystem services will all be important components of climate change in the southwestern US.

Chapter 4

The ecological role of small rainfall events in desert grassland

4.1 Introduction

Aridland ecosystem processes are driven by the frequency and magnitude of precipitation events (Fay et al., 2000; Daly and Porporato, 2006; Fay et al., 2008; Heisler-White et al., 2008). A large proportion of these rain events are small, and it is unclear how small rain events may influence ecosystem processes. For example, vegetation productivity and soil respiration may be more responsive to a small number of large precipitation events compared to a larger number of smaller events that result in the same total amount of precipitation (Heisler-White et al., 2008; Thomey et al., 2011). In contrast, Sala and Lauenroth (1982) determined that plants may also up-regulate photosynthesis in response to rain events as small as 5 mm per day. More recently, Lauenroth and Bradford (2012) found that events < 5 mm were one of the most important controls on water balance processes in arid and semiarid ecosystems. Together these studies demonstrate the variable and inconsistent effects of small rain events on aridland ecosystem processes.

Projections of future climate in the southwestern United States call for greater temperature-driven aridity and possible change in the properties of precipitation during all or part of the year (Seager et al., 2007; Gutzler and Robbins, 2011). In a warming environment, increasing potential evaporation may reduce the residence time of precipitation derived soil moisture, even if total precipitation remains unchanged (Rodriguez-Iturbe et al., 1999; Robertson et al., 2009; Petrie et al., 2012). Although soil moisture derived from small rain events may be proportionally less influenced by increasing evaporation than that derived from large events (Lauenroth and Bradford, 2012), the effect will nonetheless be lower average soil moisture. While small precipitation events may stimulate ecosystem metabolism (Lauenroth and Bradford, 2012) and nutrient mobilization (Ivans et al., 2003), these moisture dependent process may be constrained by future evaporative demand. To evaluate the potential for climate change to impact aridland ecosystems, it is important to ascertain how small events affect ecosystem functioning under different precipitation regimes.

In aridland ecosystems, small rain events temporarily wet the soil surface and stimulate activity in the upper few centimeters of soil. In the pulse-reserve model of nutrient cycling, small precipitation events do not often stimulate vegetation activity, but they can initiate microbial processes that result in a temporary reserve of resources (such as nitrogen, carbon and phosphorus) near the soil surface. These resources may then be made available to vegetation when larger precipitation events move nutrients and water into the rooting zone (Schwinning and Sala, 2004; Reynolds et al., 2004; Austin et al., 2004; Collins et al., 2008). Most soil microbial activity occurs near the soil surface, and nutrient uptake and production by these microbes may often respond strongly to the patterns of small rain events (Belnap et al., 2004, 2005). Thus, small rain events may ultimately play a large indirect role in ecosystem productivity by driving microbial processes even during periods when plants are inactive (Huxman et al., 2004).

We experimentally manipulated monsoon season rainfall to assess the effects of small rain events on ecosystem processes in desert grasslands in the northern Chihuahuan Desert, central New Mexico, USA. The main objective of our research was to determine the effect of small rainfall events (< 3.8 mm day^{-1}) on desert grassland productivity, soil moisture availability, soil carbon (C) and nitrogen (N) content, and soil extracellular enzymatic activities (EEA) during above- and below average monsoon seasons. We hypothesized that small rainfall events would have little influence on primary productivity or soil moisture availability in wet and dry monsoons, but that microbially-driven processes (e.g., extracellular enzyme activity, soil C and N availability) would be negatively impacted by the removal of small rain events during a monsoon season with below average precipitation.

4.2 Site

Our research was conducted in a mixed *Bouteloua gracilis* and *B. eriopoda* - dominated desert grassland at the Sevilleta National Wildlife Refuge, New Mexico, USA (34.359° N, 106.736° W). Elevation at this site is approximately 1615 m. Soils are classified as Turney loamy sand, with a saturated hydraulic conductivity (K_{sat}) of 0.6-2.0 inches per hour (1.5-5.1 cm hr^{-1}) (United States Department of Agriculture, 2013). The SNWR contains a broad ecotone between Chihuahuan Desert grassland dominated by *B. eriopoda* and semiarid shortgrass steppe dominated by *B. gracilis* (Gosz, 1993; Muldavin et al., 2008).

At the SNWR, the summer monsoon from July-September may account for as much as 40-60% of total annual rainfall (approximately 110-150 mm of 250 mm total) and drive more than 50% of annual net primary productivity (Muldavin et al., 2008;

Collins et al., 2010; Petrie et al., 2014a). The years leading up to our study were slightly drier than average, and climate change projections for the region call for more variable precipitation within and between years, greater temperature-driven aridity and a later onset of the summer monsoon (Seager et al., 2007; Gutzler and Robbins, 2011; Seth et al., 2011; Cook and Seager, 2013). While total monsoon rainfall has not changed over the past 100 years, the number of precipitation events per day has increased slightly while their magnitude has decreased (Petrie et al., 2014a). In addition, sequences of the longest wet and dry periods have increased in length (Petrie et al., 2014a). Warmer average temperatures and altered rainfall patterns towards more frequent, smaller events are likely to reduce soil moisture availability in these precipitation dependent grasslands (Kurc and Small, 2004) as a consequence of higher rates of evaporation (Robertson et al., 2009; Gutzler and Robbins, 2011; Thomey et al., 2011; Vargas et al., 2012).

4.3 Methods

4.3.1 Experimental design

Based on daily precipitation totals from the Sevilleta Long Term Ecological Research (LTER) meteorological network (7 sensors in 2006-2007 and 8 in 2008-2010, n = 52; SEV001) located across a 50 km^2 area of the SNWR [http://sev.lternet.edu/projects.php?meid=15], we determined that precipitation events of less than 3.8 mm day^1 during the monsoon season had an insignificant effect on total seasonal precipitation (paired t-test, $p < 0.05$), accounting for 16 mm of total seasonal precipitation on average and 65% of total precipitation events.

In June 2012 prior to the start of the summer monsoon, we established 20 experimental plots in desert grassland in a 40 m by 40 m area, ten of which were randomly assigned to the small rain event removal treatment and 10 were left as ambient treatments. Removal treatments were covered by 2.2 m x 2.4 m complete rainout shelters with a maximum height of 1.2 m angled to 0.9 m. Roofing consisted of clear polycarbonate panels (SuntufPlus; Palram Americas, Kutztown, PA, USA) that eliminated UV radiation but transmitted 90% of visible light. These rainout shelters removed all rainfall from a centrally-located 1 m^2 plot in grassland co-dominated by *B. eriopoda* and *B. gracilis*.

From July 1 through September 30, 2012, we used a gas pump and sprayer hose to apply a total of seven watering treatments equal to ambient rain event size to the entire 2.2 x 2.4 m area shortly after each ambient rain event $>$ 3.8 mm (Figure 4.1). Thus, these plots only received ambient precipitation events $>$ 3.8 mm. We added an additional 3.8 mm event at the end of the monsoon season in 2012 to both ambient and treatment plots to facilitate soil enzyme analysis in conditions that would otherwise have been too dry. We used deionized water, stored in an on site tank, for watering applications. Because precipitation in 2012 was lower than average, our design resulted in a total of 87 mm of rain in ambient plots and 71 mm in treatment plots (Figure 4.1).

In 2013, we reversed the rainfall treatment. In this year, all plots received ambient precipitation and rainout shelters were not implemented. Treatment plots also received four 3.8 mm rainfall additions applied approximately once every 18 days. Thus, total added rainfall in 2013 was nearly equal to the amount of precipitation removed in 2012 (-16 mm in 2012, $+15.2$ mm in 2013). Because precipitation in 2013 was higher than average, our design resulted in a total of 143 mm of rain in ambient plots and 158 mm in the treatment plots (Figure 4.1).

To account for higher evaporation on watering days (when ambient rainfall did not occur), we used the FAO-56 Penman-Monteith equation (Suleiman and Hoogenboom, 2007) to determine how higher temperature and decreased relative humidity on these days increased potential evaporation [mm day^{-1}]. Using meteorological data, we determined that days without rainfall at the SNWR experienced 12% higher potential evaporation, on average, from 2007-2011, and this determination was corroborated by water flux data from eddy covariance. Therefore, all watering treatments were increased by 12% in our study to account for daily potential evaporation.

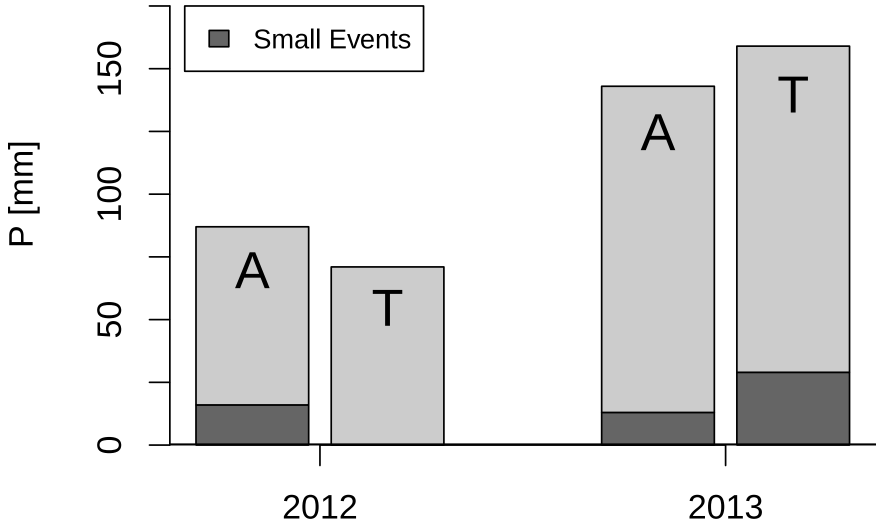

Figure 4.1: Total rainfall in ambient precipitation (A) and precipitation treatment (T) plots in 2012 and 2013. The experimental treatment in 2012 removed small rainfall events ($<$ 3.8 mm day^{-1}). In 2013, 4 small, 3.8 mm rainfall events were added incrementally to treatment plots (15.2 mm total).

4.3.2 Measurements and data analysis

Aboveground net primary productivity [ANPP: g C m^2 y^{-1}] was measured at the beginning (late June) and end (early October) of the monsoon season in 2012 and 2013. ANPP was measured using a nondestructive allometric sampling method and linear regression based on species volume units developed using total standing biomass measurements (Huenneke et al., 2001; Muldavin et al., 2008). Volumetric soil moisture content [θ: m^3 m^{-3}] was measured continuously using soil water content probes (ECH2O EC – 5 Decagon Devices, Inc., Pullman, WA, USA). Probes were buried horizontally at 5 cm depth under vegetation in 5 replicates each of ambient and treatment plots.

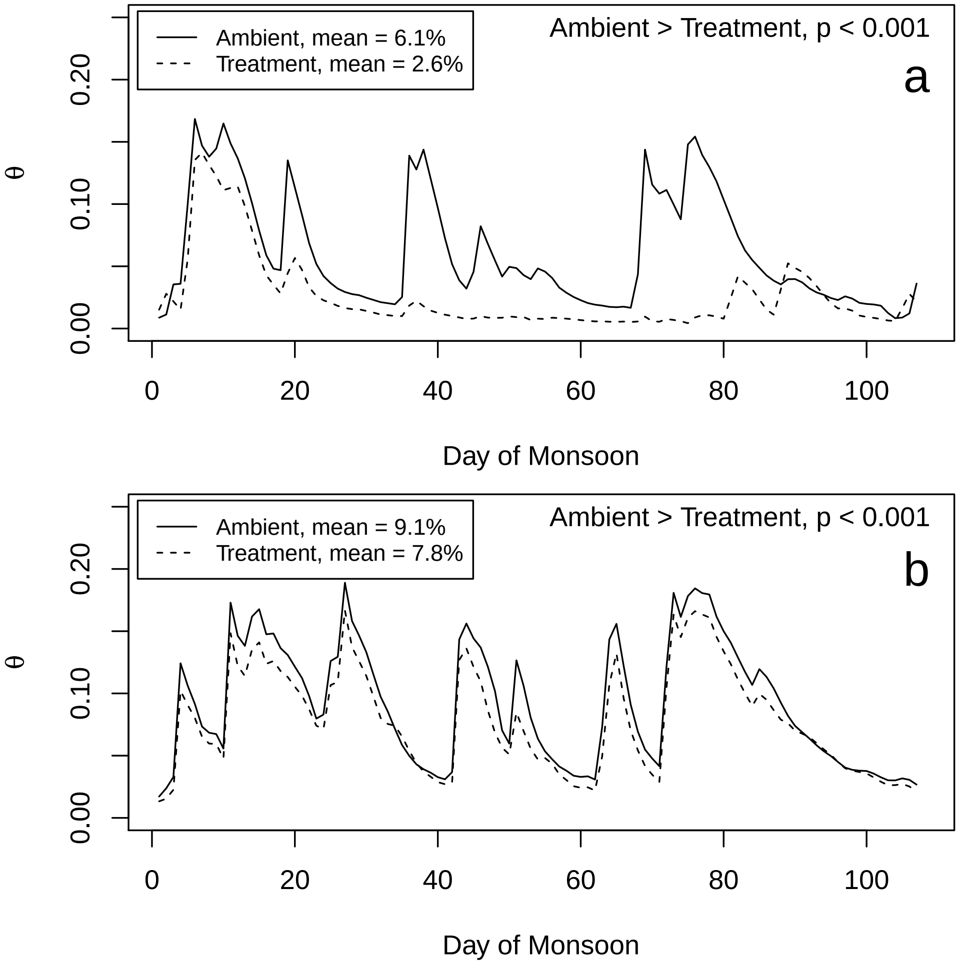

Figure 4.2: Soil moisture (0-10 cm) in ambient and treatment plots in 2012 (Panel a) and 2013 (Panel b).

Soil nitrogen content [μg 10 cm^{-2}] was measured using plant root simulator (PRS) probes, (Western Ag Global, Saskatoon, SK, Canada). One pair of cation and anion probes was located in each experimental plot (20 total pairs) at the interface of vegetation and bare soil. PRS probes provide estimates of plant available NH_4-N and NO_3-N during the monsoon season. Soil samples were taken from 0-10 cm depth at the beginning and end of each monsoon season from each treatment plot (20 total). Soil organic carbon [%] was measured using loss on ignition, where 5 g of soil was oven dried at 450°C to determine mass C loss.

The extracellular enzyme activity of soil interspaces was analyzed following Stursova et al. (2006). At the beginning (late June) and end (early October) of the monsoon season in 2012 and 2013, we measured EEA in ambient and treatment soils (0-10 cm depth) for three enzymes: 1) β-D-glucosidase; 2) Alkaline phosphatase; and 3) Alanyl aminopeptidase. Respectively, these enzymes reflect the magnitude of the ability of soil microbes and fungi to: 1) break down plant cellulose to mobilize carbon; 2) break down phosphates to mobilize phosphorus; and 3) break down the bond in alanine amino acids to mobilize nitrogen. Collectively, these assays show the net potential of soil enzymes from various sources to mobilize limiting nutrients at the beginning and end of the monsoon season (Stursova et al., 2006; Collins et al., 2008).

We explored the relationship between ecosystem carbon exchange and precipitation using data from a eddy covariance instrument located in desert grassland $<$ 1 km from our experimental site. Fluxes of surface CO_2 were measured from this eddy covariance instrument from 2007-2011 (Anderson-Teixeira et al., 2011). We used three-axis sonic anemometers (Campbell Scientific CSAT-3) to measure vertical wind speed at 10 Hz and calculate covariances. We compiled 30 minute averages of covariances, corrected for temperature and water vapor fluctuations (Webb et al., 1980) and frequency responses (Massman, 2000). Gas exchange was measured using open-path gas analyzers (LiCor LI-7500). We gapfilled NEE and estimated ecosystem respiration (RE) using the Max Planck Institute (Open MPI) procedure (Falge et al., 2001; Reichstein et al., 2005) [http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/index.php]. We calculated gross primary productivity (GPP) as NEE + RE.

4.4 Results

Precipitation during the 2012 monsoon season was 22% lower than the 2001-2010 average (87 mm, 110 mm average), and the experimental treatment was 36% lower (71 mm; Figure 4.1) than average. Removing small precipitation events resulted in significantly lower daily average soil moisture (0-10 cm) in treatment plots (3.3% treatment, 6.9% ambient, $p < 0.001$), and this difference was especially notable after day 20, when treatment plots showed a sharp decline in soil moisture retention following all rain events (Figure 4.2a). Ambient plots had significantly higher soil organic C at the end of the 2012 monsoon season ($p < 0.03$, Figure 4.3) and significantly higher total soil NO_3-N and NH_4-N (79.8 μg 10 cm^{-2} ambient, 54.6 μg treatment, $p < 0.03$, Figure 4.4a) compared to treatment plots. We observed significantly higher Alkaline phosphatase (Phosphate enzyme) activity in ambient plots at the end of the 2012 monsoon ($p < 0.05$, Figure 4.5a) and nearly significant differences in Alanyl aminopeptidase (Alanine enzyme) ($p < 0.09$), suggesting that ambient plots had a higher potential for nutrient mobilization at the end of the monsoon season. ANPP did not differ between ambient and treatment plots in 2012 (Figure 4.4b).

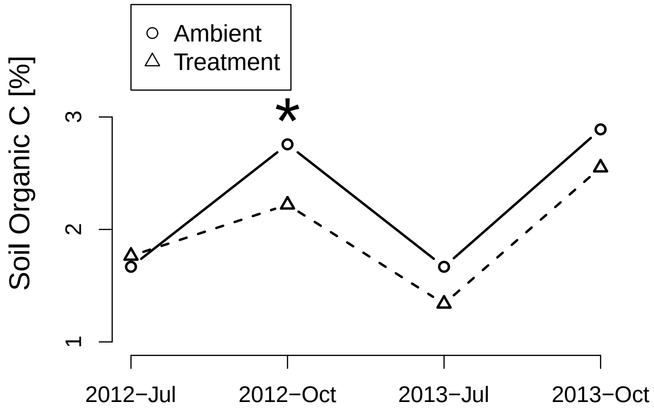

Figure 4.3: Soil organic carbon [% by mass] in ambient and treatment plots at the beginning and end of the monsoon season in 2012 and 2013. Soil C was significantly higher in ambient plots at the end of 2012 ($p < 0.03$).

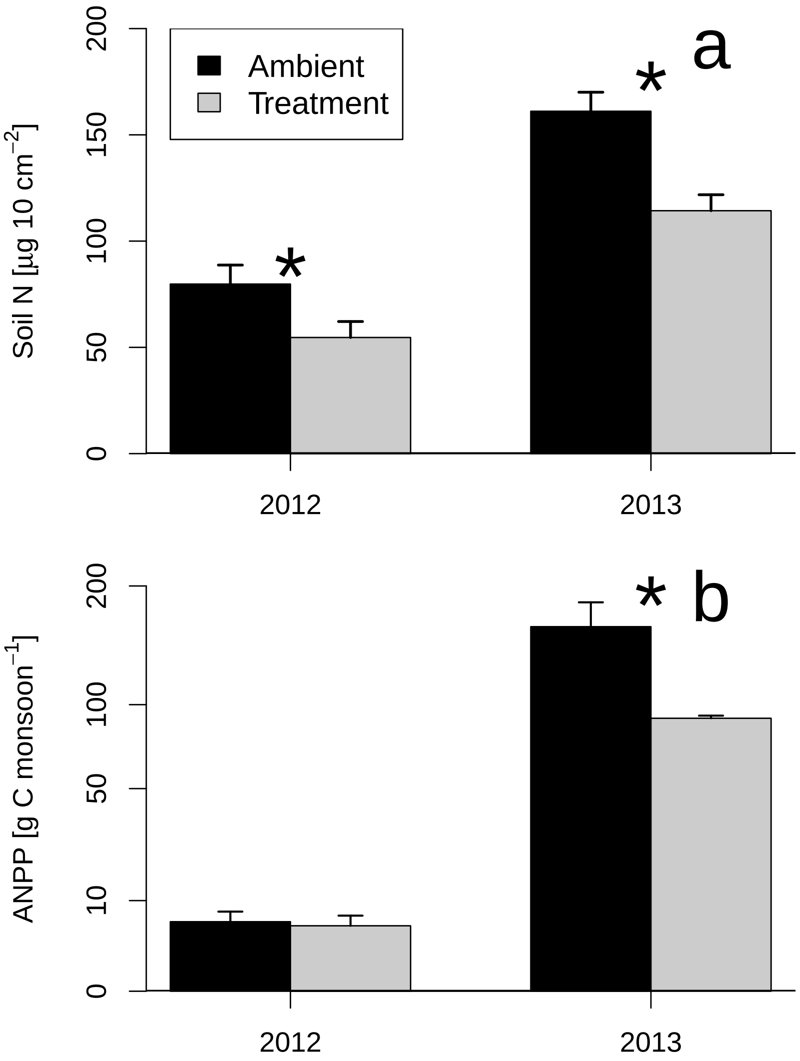

Figure 4.4: Net soil nitrogen content [μg N 10 cm^2] in ambient and treatment plots (Panel a) and Aboveground Net Primary Productivity [ANPP: mg C m^2 monsoon^{-1}] in ambient and treatment plots in 2012 and 2013 (Panel b). Soil N was significantly higher in ambient compared to treatment plots in 2012 ($p < 0.03$) and 2013 ($p < 0.05$), and ANPP in 2013 was significantly higher in ambient plots in 2013 ($p < 0.02$).

In 2013, monsoon rainfall was 29% higher than the 2001-2010 average (143 mm, 110 mm average), and treatment plots received 43% higher rainfall (159 mm; Figure 4.1). We observed significantly higher daily average soil moisture (0-10 cm) in ambient plots (7.8%, 9.1% ambient, $p < 0.001$), although the difference between treatment and ambient plots was not as large as in 2012 (Figure 4.2b). Soil organic C did not differ between ambient and treatment plots at either the beginning or end of the 2013 monsoon (Figure 4.3), nor did soil enzyme activities (Figure 4.5). Soil NO_3-N and NH_4-N was significantly higher in ambient compared to treatment plots (161.1 μg 10 cm^{-2} ambient, 114.3 μg treatment, $p < 0.05$, Figure 4.4a). We observed significantly higher ANPP in ambient compared to treatment plots (161.8 g m^{-2} ambient, 90.7 g m^{-2} treatment, $p < 0.02$; Figure 4.4b).

Using five years of eddy covariance data (2007-2011), we found that daily gross primary productivity [GPP: g C m^{-2} day^{-1}] at a nearby grassland site was more sensitive to the average magnitude of rainfall events [α: mm event^{-1}] over a prior period of 14 days than it was to the average number of events [λ: events day^{-1}] over the same period (Figure 4.6). Furthermore, GPP responded strongly as α increased from 2-3 mm, suggesting that even a small number of these events was sufficient to stimulate grassland carbon uptake.

4.5 Discussion

In this study, we experimentally removed small rainfall events from grassland plots during a dry monsoon in 2012 and added a similar magnitude of precipitation in four small events to treatment plots during a wet monsoon the following year. In 2012, treatment plots experienced lower θ, soil NO_3-N and NH_4-N, soil organic C and Alkaline phosphatase enzyme activity compared to ambient plots, but did not experience lower ANPP. This treatment may also have contributed to earlier vegetation senescence, which did not occur to the same degree in ambient plots. In 2013, seasonal averaged θ was higher in treatment and control plots compared to 2012, but treatment plots experienced somewhat lower seasonal averaged soil NO_3-N and

NH_4-N, and ANPP than ambient plots, despite receiving supplemented precipitation in the form of small rain events.

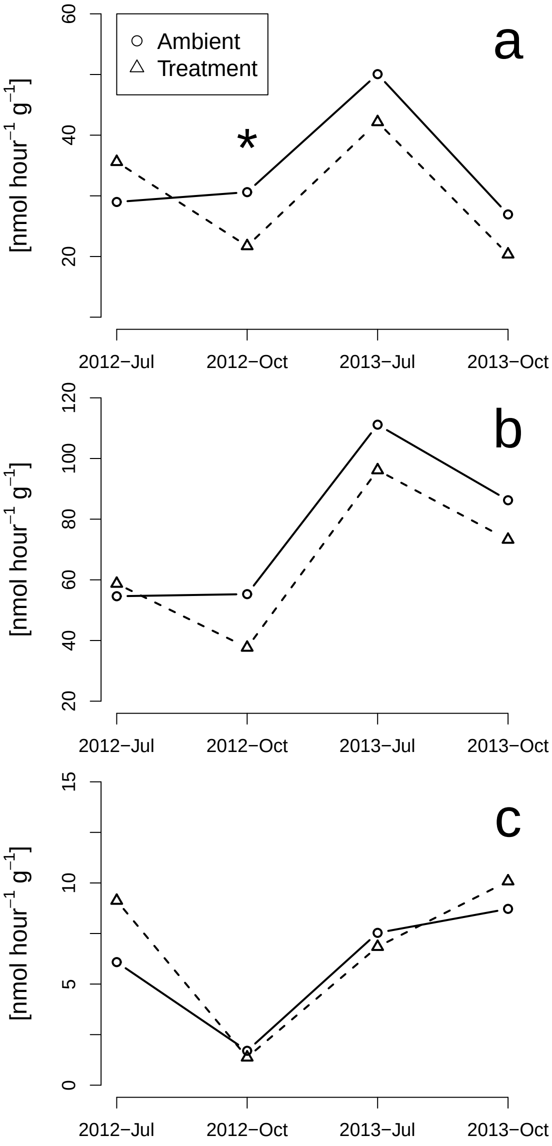

Figure 4.5: Net extracellular enzyme activity [EEA: nmol hour^{-1} g soil^{-1}] of soil interspaces (0-10 cm depth) in ambient and treatment plots at the beginning and end of the monsoon season in 2012 and 2013. EEA data includes analysis of Alkaline phosphatase (Panel a), Alanyl aminopeptidase (Panel b) and β-D-glucosidase (Panel c). Extracellular activity of Alkaline phosphatase was significantly higher in ambient plots at the end of the 2012 monsoon ($p < 0.05$, Panel a).

Eddy covariance data from 2007-2011 show that daily gross primary productivity in this grassland is more sensitive to increasing magnitude of precipitation events than increasing number of precipitation events. For both gross primary productivity and ecosystem respiration (not shown), measured fluxes increased substantially at ~2.5 mm day^{-1} (Figure 4.6). Studies by Schwinning and Sala (2004) and Reynolds et al. (2004) have observed similar patterns of C and N fluxes in the Chihuahuan Desert. Therefore, we hypothesize that the nutrient status of ambient plots was increased relative to treatment plots in 2012 by at least three events between 2.5 mm and 3.8 mm. Once water limitation has been removed, N and P are the most limiting nutrients in this ecosystem (Yandjian et al., 2011; Mueller et al., 2008; Turnbull et al., 2011), and nitrogen addition in SNWR grassland has been shown to increase aboveground productivity during wet years (Ladwig et al., 2012).

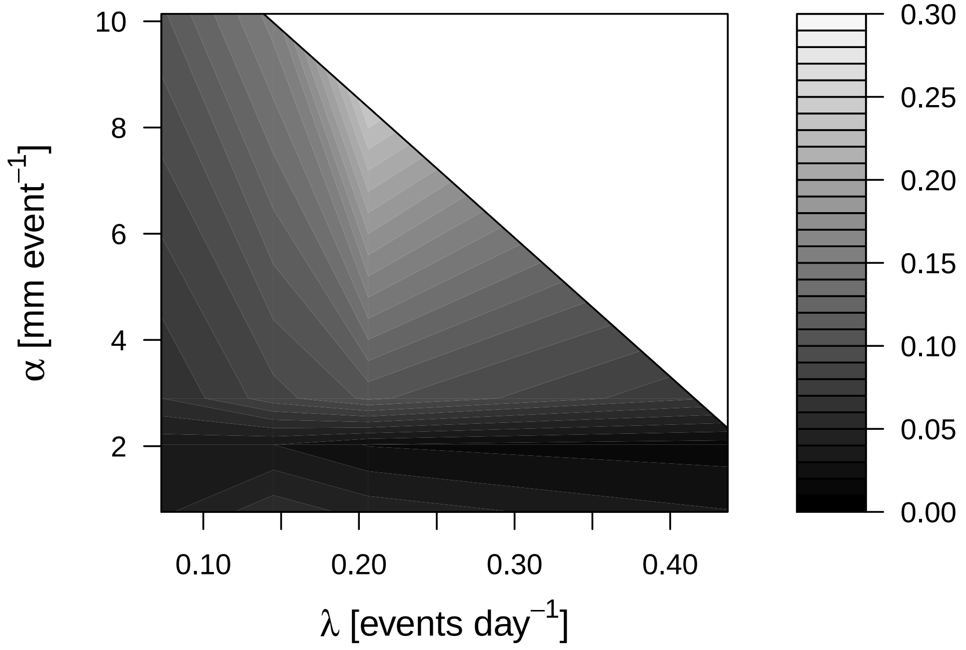

Figure 4.6: Response of daily gross primary productivity [GPP: g C m^2 day^{-1}] to prior 14-day precipitation timing [λ: events day^{-1}] and magnitude [α: mm event^{-1}] statistics. GPP responds strongly to α, especially as α increases from 2 to 3 mm event^{-1}.

Compared to average or wet years, below average precipitation in the northern Chihuahuan Desert may result from a similar number of small rain events but fewer large rain events (Petrie et al., 2014a). In dry years, ANPP is limited by water availability rather than soil nutrients, which likely explains the similar ANPP between treatment and ambient plots in our study, and the fact that total precipitation between treatment and ambient plots differed by only 16 mm. Available soil N may accumulate during dry years because small events stimulate microbial mineralization but limit plant uptake (Huxman et al., 2004; Collins et al., 2008). Reichmann et al. (2013) found lower available soil N in irrigated plots compared to drought treatments as a function of higher leaching and immobilization by plants and microbes. In contrast, we found lower plant available N in plots where small rain events were removed during a year of below average precipitation. These are the events that would otherwise stimulate microbial mineralization as well as N fixation by crusts (Austin et al., 2004; Belnap, 2002). As a consequence, plants may have had access to less available nitrogen, which may have limited their ability to respond to higher rainfall in the following year.

We hypothesize that the reason for higher ANPP in ambient plots in 2013 is that the small event removal treatment in 2012 - which significantly reduced nutrient pools - hindered the ability for treatment plots to respond to a subsequent monsoon season with high rainfall. During 2012, vegetative cover in treatment plots decreased from 21.4% to 16.4% (paired, one-tailed t-test, $p < 0.035$). Early senescence in dry years has previously been observed in this grassland (Petrie et al., 2014b), and bare soil evaporation is the largest component of θ losses from upper soil horizons in many semiarid grasslands (Lauenroth and Bradford, 2012). We attribute lower average daily θ in treatment plots in 2012 (Figure 4.2a) to this loss of vegetative cover and increase in bare soil fraction, which likely increased the rate of evaporation in treatment plots compared to ambient plots. At the beginning of the 2013 monsoon season, neither vegetative cover (18.6% ambient, 15.9% treatment, $p >$

0.14) nor spring biomass (5.3 g m^{-2} ambient, 3.9 g m^{-2} treatment, $p > 0.53$) was greater in ambient compared to treatment plots. By the end of the season, however, both vegetative cover (41.0% ambient, 26.3% treatment, $p < 0.02$) and ANPP were significantly higher in ambient plots (Figure 4.4b). The emerging difference in growth and vegetative cover during the 2013 monsoon is consistent with higher θ in ambient compared to treatment plots (Figure 4.2b). Due to these differences, we attribute ANPP differences in 2013 to higher soil nutrient availability in ambient plots, and possibly lower meristem density in treatment compared to control plots which allowed grasses in ambient plots to respond more favorably to higher rainfall than treatment plots in 2013.

Previous research has shown that grassland productivity at the Sevilleta is meristem limited (Dalgleish and Hartnett, 2006), and meristem density is hypothesized to be a key mechanism by which ANPP responds to interannual variability in rainfall (Knapp and Smith, 2001) and nitrogen availability (Dalgleish et al., 2008). Sala et al. (2012) reported that interannual variability in ANPP at a site over time is often poorly correlated with mean annual precipitation suggesting that legacy effects are prominent in arid grasslands. Indeed, Reichmann et al. (2013) found strong legacy effects on ANPP in a northern Chihuahuan Desert grassland. Specifically, the ANPP response in plots during a wet year that followed two years of experimental drought was lower than the ANPP response in plots that did not experience drought. This legacy was explained by lower tiller density, a function of meristem availability, following the drought treatments. Our experiment is consistent with these findings and suggests that small rain events may be important sources of shallow soil moisture for production and maintenance of meristems in this desert grassland.

The legacy effects of small events may facilitate grassland recovery in the year following a dry monsoon season and, conversely, the lack of small events may hinder grassland recovery under the same conditions. At the SNWR, the average monsoon season from 2001-2010 produced 110 mm of precipitation, and drier than average monsoons like in 2012 (71 mm) are a common occurrence in the Chihuahuan Desert region, and may increase in the future (Gutzler and Robbins, 2011). In a warming climate, higher evaporative demand is likely to reduce the soil moisture residence time of small precipitation events (Laio et al., 2002; Austin et al., 2004; Porporato et al., 2004). In our study, the greater loss of small events promoted more frequent grassland senescence and loss of vegetative cover, lower availability of soil C, soil NO_3-N and NH_4-N, and P mobilization potential, and reduced ANPP response in years following a dry monsoon. Based on eddy covariance data, the threshold between effective and ineffective rainfall events may be $\sim$2.5 mm. The loss of soil nutrients is a precursor to grassland degradation in this region (Turnbull et al., 2011), and may contribute to the state transition of grassland to shrubland in dryland ecosystems (D'Odorico et al., 2013b). Overall, our results show that small precipitation events may have significant legacy effects on productivity of desert grassland following dry years, and the increased rate of evaporation of these events in a warmer climate may further influence how desert grassland responds to and recovers from moisture limitation in the future.

Chapter 5

Conclusions

Through the research described in this dissertation, I explored the climate, ecology and hydrology of the northern Chihuahuan Desert to better constrain understanding of how climate inputs and projections of increasing aridity will affect grassland and shrubland ecosystems in this region. This research reflects the multidisciplinary nature and direction of contemporary ecological research. There is great opportunity to utilize differing scientific perspectives and techniques to produce information that is more comprehensive and is also more useable by resource managers and decisionmakers. The ecological sciences continue to be pressed towards applicability and economy instead of specialization, and this dissertation was developed with this direction in mind.

The main goal of this dissertation was to illuminate key components of grassland and shrubland productivity and stability in the northern Chihuahuan Desert in the context of global climate change. Chapter 2 focused on historical and current variability in monsoon precipitation across the northern Chihuahuan Desert, and also at the desert's ecologically sensitive northern boundary. Results from this chapter suggest that both local and regional variability in rainfall is higher than what is normally attributed to the summer monsoon. Furthermore, the type of changes in rainfall that are projected to occur in the southwestern United States in coming decades do not fall outside the range of precipitation totals commonly experienced in the Chihuahuan Desert, suggesting that ecosystems in this region may not be highly sensitive to changing average values of precipitation alone. Using statistics of monsoon precipitation at the SNWR that were determined in Chapter 2, this dissertation research evaluated the potential for small rainfall events - which I hypothesized would be ecologically unimportant - to influence nutrient availability and vegetation productivity in Chihuahuan Desert grasslands in Chapter 4. The statistically-based experimental design of Chapter 4 was the basis for uncovering a particular case where the loss of small rainfall events was detrimental to grassland nutrient availability and produced a legacy effect that inhibited grassland recovery from drought. In Chapter 3, I compared vegetation productivity and carbon exchanges in neighboring grassland and shrubland communities during a drier than average 5-year period, and determined that grassland to shrubland state transitions are likely to increase ecosystem carbon sequestration across the Chihuahuan Desert, even in a more arid future climate. By developing new research on the characteristics of climate and ecosystem ecology, and also by building on prior research in a directed manner, the chapters of this dissertation provide insight on key components of climate change, precipitation variability, and ecohydrological functioning in Chihuahuan Desert grassland and shrubland communities.

The relationships between climate and ecological functioning in aridland systems are somewhat intuitive yet also complex. In the case of climate change, deleterious results of climate change such as ecosystem degradation and loss of services are of primary interest, not necessarily the patterns and characteristics of biophysical processes themselves. Therefore, the value of my dissertation research is in identifying patterns and characteristics of climate and ecological functioning that are known correlates to important phenomena such as increasing aridity, carbon sequestration and land degradation. This dissertation sharpens understanding of the inherent variability of monsoon precipitation (Chapter 2), of the mechanisms by which desert shrubland carbon sequestration is favored over that of grassland during dry years (Chapter 3), and of how small changes in precipitation can influence nutrient availability and productivity in desert grasslands (Chapter 4). Climate change in the Chihuahuan Desert region is likely to promote more frequent dry summers (Gutzler and Robbins, 2011), which may be intensified by changing precipitation patterns and the more rapid evaporation of small rainfall events (Robertson et al., 2009; Seager and Vecchi, 2010; Lauenroth and Bradford, 2012). Increasing summer aridity is likely to have more deleterious consequences on grassland than shrubland, and it is possible that grassland to shrubland state transitions will increase in frequency under this future climate regime.

Quantifying how ecosystems and the services they provide respond and feed back on climate inputs is one of the great challenges of ecologic research, and this dissertation attempts to address key components of a larger body of research. Aridland ecoregions, despite constituting a sizable proportion of global land area, are grossly underrepresented in the scientific literature. In the case of the Chihuahuan Desert, large deficiencies include understanding the mechanisms of grassland degradation and ecological transitions, the temporal structure and statistical probabilities of ecologically-significant drought events, the connection between microbial communities and vegetation functioning, and the potential for climate change to alter soil moisture-precipitation feedbacks and regional precipitation patterns. The northern Chihuahuan Desert exists at the confluence of many ecological boundaries, and this location promotes the assessment of ecological changes at the locations where ecosystems are most sensitive. By focusing on ecological change in this region, it will continue to be possible to gain valuable insight on the functioning of Chihuahuan Desert ecosystems and also explore the dynamics of similar underrepresented aridland ecoregions globally.

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