

DISSERTATION

**SENSITIVITY OF GRASSLAND ECOSYSTEMS ACROSS THE
GREAT PLAINS TO PRESENT AND FUTURE VARIABILITY IN
PRECIPITATION**

Submitted by

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Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Summer 2008

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED
UNDER OUR SUPERVISION BY JANA LYNN HEISLER ENTITLED SENSITIVITY
OF GRASSLAND ECOSYSTEMS ACROSS THE GREAT PLAINS TO PRESENT
AND FUTURE VARIABILITY IN PRECIPITATION BE ACCEPTED AS
FULLFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF
PHILOSOPHY.

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ABSTRACT OF DISSERTATION

SENSITIVITY OF GRASSLAND ECOSYSTEMS ACROSS THE GREAT PLAINS TO PRESENT AND FUTURE VARIABILITY IN PRECIPITATION

Patterns and controls of aboveground net primary productivity (ANPP) have been of long-standing interest to ecologists because ANPP integrates key aspects of ecosystem structure and function through time. In many terrestrial biomes, water availability is a primary constraint to ANPP, and it is an ecosystem driver that will be affected by future climate change. To understand the sensitivity of temperate grasslands to inter- and intra-annual variability in precipitation, I analyzed long-term ANPP data, conducted a multi-site experimental manipulation in which the number of growing season rainfall events was varied, and simulated the effects of altered rainfall regimes using a terrestrial ecosystem model (DAYCENT). I conducted this research within the Great Plains of North America – a region characterized by a strong west-east precipitation-productivity gradient and three distinct grassland types—the semi-arid shortgrass, the mixed-grass prairie, and the mesic tallgrass prairie.

My results demonstrate that temperate grasslands are indeed sensitive to both inter- and intra- variability in precipitation, but the ANPP response is contingent upon

ecosystem structure and typical soil water levels. Additionally, both management strategies and topographic location may interact with precipitation to enhance or diminish coherence in the ANPP response. At the dry end of the gradient (semi-arid steppe), fewer, but larger rain events led to increased periods of above-average soil water content, reduced plant water stress and increased ANPP. The opposite response was observed at the mesic end of the gradient (tallgrass prairie), where longer dry intervals between large events led to extended periods of below-average soil water content, increased plant water stress, and reduced ANPP. Mixed grass prairie was intermediate along the gradient, characterized by the greatest plant species richness, and the most sensitive to within-season variability in rainfall. Comparison of these experimental data to model simulations revealed key differences in soil water dynamics and ANPP patterns, suggesting that more experimental data is needed to parameterize biological and physical processes that drive model simulations. In conclusion, these results highlight the difficulties in extending inference from single site experiments to whole ecosystems or biomes and demonstrate the complexity inherent in predicting how terrestrial ecosystems will respond to novel climate conditions.

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ACKNOWLEDGEMENTS

While a PhD gets awarded to a single person, the degree itself is a testimony to the time, energy, and support of many people. During the past five years, I have pursued my PhD in Ecology, and I have so many people to thank for their role in my dissertation research and my life during that time. First, I would like to acknowledge the guidance and mentorship of my advisor, Alan Knapp. In a moment of brilliance, poor judgment, or perhaps both, he encouraged me to embark on a research project that would require large quantities of lumber, the courage to moonlight as a construction worker and engineer, and the insanity necessary to occupy my thoughts during the 20,000⁺ miles that I spent alone in a truck on I-70 during the summers of 2005-2006. It was no small feat to construct 45 rainout shelters and make it “rain” nearly 50 times in two years, and I thank Alan for his foresight that exciting ecological results would emerge from a project that felt like a boondoggle from the start. Alan, along with my entire graduate committee – Dr. John Blair (KSU), Dr. Eugene Kelly, and Dr. James Detling – has been generous in sharing scientific knowledge, career advice, and frequent anecdotes. I will carry much of this information with me as I move forward in my scientific career.

I have a small volunteer army to thank for their help in rainout shelter construction and the seamless execution of rainfall events. I must first acknowledge Jobie Carlisle for all the engineering and practical wisdom that he shared with me throughout this entire process. Had it not been for Jobie’s expertise and patient

disposition, high winds would have strewn bits and pieces of plastic, lumber, and assorted hardware across the Great Plains as evidence to good ideas *without* good planning. For their willingness to take orders and serve as my construction crew, I thank Priscilla Baker, Vanessa Beauchamp, Zac German, Jesse Nippert, Will Ruder, the Konza Prairie RaMPs Crew, and the SGS field crew. I called upon the help of many people in my efforts to make it rain exactly where, when, and how I wanted to. At the Saline Experimental Range, Keith Harmony assisted in locating an experimental site, strung an electric fence to exclude cattle, and provided access to water for rain events and electricity for construction. Mary Ashby located a 1000-gallon army trailer owned by the USDA-ARS and Jeff Thomas spent much time changing tires and making it reasonably roadworthy. Mark Lindquist graciously offered to drive this rig to-and-from SGS headquarters during the 2006 field season. At Konza Prairie, Jobie Carlisle designed a manifold system equipped with a generator for “rainmaking,” and Tom van Slyke and the KPBS support crew promptly delivered over 10,000 gallons of water to a storage tank throughout the field season. Megan Matonis and Will Ruder spent many hours applying water to plots at KPBS and the SER, respectively. Ian Hough carried many watering cans to plots on the SGS.

I was fortunate to have the assistance of several undergraduate students during this project. Ian Hough conducted a project on the growth response of blue grama to altered precipitation at the SGS in 2006 and Natasha Davis, Kallie Murphy, and Jake Moersen accompanied me in the field and with sample processing as NR 495 students.

During my time at CSU, I interacted with an amazing cohort of fellow students in the Knapp Lab – Jesse, Tony, Priscilla, Madeline, Zac, Greg, Karie, Amanda, and

Miriam. I thank all of you for our conversations on both scientific issues and the stuff of life.

For their patience and time in assisting me in learning to use the DAYCENT terrestrial ecosystems model, I thank Robin Kelly, Cindy Keough, Bill Parton, and Steve Del Grosso. I additionally acknowledge Dr. Jim zumBrunnen and the Statistical Laboratory at CSU for their advice on data analysis.

Finally, I wish to thank my family and friends for their continued moral support as I chased down my dream of becoming an ecologist. My most profound gratitude is extended to my husband, Daniel White. While Dan has helped me with fieldwork on several occasions, his most important contribution to my research and degree has been his constant patience, encouragement, and genuine belief in me.

This dissertation is dedicated to the memory of my father,
Joseph B. Heisler,
who always encouraged my pursuits in science, academia, and life.

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Chapter 1: Introduction

Overview

The research described in this dissertation explores precipitation as a primary driver (or control) of aboveground net primary productivity (ANPP) in both time and space, with the overarching goal of improving our ability to forecast changes in this key ecosystem process in response to ongoing global changes. Precipitation is emphasized as a driver because it has a long history of being considered a proxy for water availability in terrestrial ecosystems (Walter 1939; Leith 1975; Webb et al. 1978; Le Houerou et al. 1988), and abundant evidence supports a strong positive relationship between mean annual precipitation (MAP) and ANPP for many ecosystems around the world (Rosenzweig 1968; Rutherford 1980; Sala et al. 1988; Knapp and Smith 2001). As a limiting resource, water constrains plant productivity and soil biogeochemical processes, thereby exerting an important control on ecosystem structure and function (Sims and Singh 1978; Webb et al. 1986). A more robust understanding of the influence of this key resource on ANPP is critical because nearly all global environmental changes (i.e. elevated CO₂, rising surface temperatures, N deposition, changes in land management, or altered precipitation regimes) are predicted to influence the water balance of terrestrial ecosystems.

Patterns and controls of ANPP have been of long-standing interest to ecologists because ANPP integrates key aspects of ecosystem structure and function through time (McNaughton et al. 1989). Until recently, long-term data analyses and correlative studies

largely informed ANPP-precipitation relationships (i.e. Sala et al. 1988; Knapp and Smith 2001; Huxman et al. 2004) and focused primarily on mean annual (and to a lesser extent mean growing season) quantities of precipitation. Such analyses have been invaluable in characterizing relative water availability as it is linked to vegetation type and plant production across continents and large time scales. In reality, however, most ecosystems experience interannual variability in both precipitation and ANPP, and “average” years can be few in number. Grasslands, in particular, have tremendous potential for large variation in ANPP in response to precipitation, because of both high production potential and high rainfall variability (Knapp and Smith 2001). While precipitation quantity indeed sets upper and lower bounds for ANPP within a given ecosystem, the recent climatic history and the seasonal distribution of events impact how precipitation inputs are translated into available soil water (a more proximate control on ANPP). Antecedent conditions (wet or dry) that exist prior to a growing season or on as short of a timescale as an individual rain event have important impacts on the response potential and sensitivity of both above- and below-ground biological processes (Noy-Meir 1973; Singh et al. 1998; Reynolds et al. 2004; Yahdjian and Sala 2006). Because precipitation is the primary source of water for most terrestrial ecosystems, greater emphasis must be placed upon the timing and magnitude of inputs, dry interval length, and recent climatic history in order to improve our understanding of ANPP patterns and the underlying mechanisms for these patterns (Heisler and Weltzin 2006).

The space-for-time substitution has and continues to be a staple tool for ecologists in understanding variability in ecological processes, but it is not always an effective surrogate for characterizing the variability of individual ecosystems over time. A

primary example of the problem of space-for-time substitutions was demonstrated for the grasslands of the Great Plains of North America (Lauenroth and Sala 1992). Here, a regional analysis revealed that MAP is highly correlated with ANPP ($r^2 = 0.90$; Fig.1) across a precipitation gradient of 300-1500 mm and four distinct grassland types (Sala et al. 1988). While robust across a large region, this spatially-derived relationship fails to predict the variability in ANPP in a given site through time. Analyses of long-term data from both western semi-arid shortgrass steppe (Lauenroth and Sala 1992) and eastern mesic tallgrass prairie (Briggs and Knapp 1995) demonstrate that the response of plant production (at a single site) to interannual variability in precipitation is more buffered than the relationship across sites suggests (Fig.1). This example demonstrates two key concepts: (1) ecosystems differ in their sensitivity to interannual variability in precipitation due to buffering mechanisms and constraints (Paruelo et al. 1999); and (2) ecological gradients represent an ideal conceptual/practical framework for evaluating and comparing the response of multiple ecosystem types (within a single biome) to a common precipitation change scenario (Weltzin et al. 2003; Peñuelas et al. 2004).

Global circulation models (GCMs) forecast changes in the frequency and magnitude of precipitation events for many regions of the globe (IPCC 2007). While it is widely recognized that interannual variability in precipitation influences ANPP, a growing number of experiments affirm that many ecosystems (grasslands and arid systems, in particular) are quite sensitive to intra-annual variability in precipitation (Knapp et al. 2002; Loik et al. 2004; Sher et al. 2004; Sponseller et al. 2007). Rain event size and frequency, in addition to the seasonality of moisture inputs, influence the temporal availability of water for plant and microbial processes. While it makes intuitive

sense that plants and soil microorganisms are sensitive and responsive to the dynamics in soil water that accompany large rain events or extensive drought periods, a general understanding of the impacts of within-season variability in precipitation is lacking. A consistent prediction of GCMs is a shift to more extreme weather regimes, and ecologists must shift their focus from mean trends to modified event regimes in testing hypotheses regarding both short- and long- term ecosystem responses (Jentsch et al. 2007).

In 2006, I attended a conference in Denmark that was dedicated to the Effects of Precipitation Change on Terrestrial Ecosystems (EPRECOT). As scientists from both the European Union and the United States convened to discuss research on precipitation change (from observational, experimental, and modeling studies), the following three general questions formed the foundation for presentations and discussions at the workshop (Heisler and Weltzin 2006). I include them because they summarize my approach in designing and conducting the research in this dissertation.

- (1) How can ecologists pursue questions relating to precipitation change in terrestrial ecosystems in a synthetic way? Is it possible to achieve an understanding of precipitation as an ecosystem driver that spans multiple regions of the globe and biome types?
- (2) What are the important response variables in assessing the impacts of precipitation change? How can we conduct research that accounts for responses across ecological, spatial, and temporal scales?
- (3) How can experimental design and model development be better integrated? What are the major limitations that exist in interpreting results from both models and experimental research?

Using the Great Plains of North America as a study region, I addressed the general issue of current and future patterns and controls of ANPP by combining 1) a long-term data analysis (chapter 2), 2) an event-based study in a semi-arid grassland (chapter 3), 3) an experimental manipulation of rainfall across a regional precipitation-productivity gradient (chapter 4), 4) and a modeling study (chapter 5). Recognizing that forecast changes in climate represent novel conditions for many ecosystems (Williams et al. 2007), I imposed precipitation scenarios that were rare historically but consistent with GCM predictions. The Great Plains region (Fig. 2) encompasses major gradients in temperature and precipitation (Table 1), which are important determinants of plant community structure and ecosystem function (Borchert 1950; Weaver and Albertson 1956). From the eastern Colorado shortgrass steppe to the tallgrass prairie in eastern Kansas, annual precipitation increases nearly three-fold from 260 to 830 mm. The major grassland types in this region include semi-arid shortgrass steppe, mixed grass prairie, and mesic tallgrass prairie, each of which is described in detail at the end of this introductory chapter.

The relative importance of water as a limitation to plant production changes along this gradient, and as a result, so does the life history of plant species that dominate each distinct grassland ecosystem (Paruelo et al 1999). While temperature increases from northwest to southeast across the region, it does not account for much of the ecosystem variability (Sala et al. 1988). In semi-arid steppe, where water is the primary constraint to plant productivity (Lauenroth et al. 1978), selection has favored plant species that are slow-growing and generally drought-tolerant. Plant density is low in this semi-arid ecosystem. At the mesic end of the gradient (tallgrass prairie), plants with life history

strategies for rapid growth are limited by water, but both light and N can constrain plant production in years in which moisture limitations are minimal (Knapp and Seastedt 1986; Schimel et al. 1991). Previous research suggests that biogeochemical constraints (relating to nutrient availability) should be higher at the wet end of a precipitation gradient than a dry end (Austin and Vitousek 1998). Precipitation use efficiency peaks at intermediate locations along precipitation gradients (mixed grass prairie ecosystem; Paruelo et al. 1999) where moderate levels of both vegetational and biogeochemical constraints co-occur.

Summary of proposed research

In Chapter 2, I evaluate coherence in ANPP dynamics in a single site through time and begin to address research question 1. The primary objective of this study was to identify the overall level of synchrony or coherence of ANPP in a mesic tallgrass prairie ecosystem, where precipitation was considered constant across the region but management (fire) and topography differed. This study is important because it explicitly addresses the issue (and reality) of environmental factors that interact with precipitation (and more generally climate) in determining plant productivity. In conducting climate change research, it is critical for ecologists to consider how and why both landscape variability and management may enhance or diminish the influence of ongoing global changes (i.e. increasing CO₂, N deposition, etc.). By evaluating coherence between pairs of sampling locations subjected to similar and differing combinations of drivers, I was able to assess the relative influence of local versus regional drivers on ANPP. An understanding of coherence is important because 1) it can ultimately guide the selection

of research locations to monitor ecosystem responses to regional or global changes and 2) identify which management scenarios are likely to be most or least affected.

In Chapter 3, I evaluate the importance of small versus large events in the semi-arid short grass steppe and begin to address response variables that are critical in identifying mechanisms that drive ecosystem-level patterns such as ANPP (research question 2). This experiment also served as a springboard for the multi-site study described in chapter 4. Historically, the shortgrass steppe ecosystem was characterized by frequent, quantitatively small rainfall events that were episodically interrupted by large rain events. This precipitation regime is in marked contrast to GCM predictions, which forecast a shift to larger, but less frequent events for this region. Because the dominant plant species, *Bouteloua gracilis*, is quite responsive to frequent small pulses of moisture (Sala and Lauenroth 1982), I hypothesized that this shift in the distribution of precipitation during the growing season would result in greater plant moisture stress and a reduction in ANPP. I tested this hypothesis with an experimental manipulation of growing season rainfall that held mean rainfall constant but distributed the amount in 12-, 6-, or 4- events. Response variables for this experiment emphasized soil moisture dynamics, plant ecophysiology, and ANPP.

In Chapter 4, I extended my level of inference in assessing ecosystem response to future precipitation variability by evaluating the response of three grassland ecosystems within the Great Plains to a common GCM prediction. While GCMs differ with regard to projected changes in annual precipitation amounts in the central US, they are in agreement with predictions that the dynamics of event distribution will become more variable (Easterling et al. 2000; IPCC 2007). Evidence exists to suggest that an ongoing

shift to more extreme rainfall events (greater in magnitude, reduced in frequency) is already occurring (Karl et al. 1995; Karl and Trenberth 2003). Using the precipitation productivity gradient of the Central Plains, I conducted an experimental manipulation of growing season rainfall to assess the relative sensitivity of 3 grassland ecosystem types (semi-arid shortgrass steppe, mixed grass prairie, and tallgrass prairie) to a directional shift to more extreme rainfall patterns with no net change in growing season amounts. This multi-site experiment focused on temporal dynamics of soil moisture, plant ecophysiology, soil N availability, and ANPP – variables that were identified as important potential mechanisms for response patterns following research in chapter 3. This experimental manipulation was developed specifically to address research question 2. I used both a common methodology and a common set of response variables (Weltzin et al. 2003) to identify ecosystem sensitivities, thresholds, and local- to broad- scale mechanisms that control the response of ecosystems to changes in precipitation regimes.

In Chapter 5, I use the DAYCENT terrestrial ecosystem model to simulate responses of the shortgrass steppe and tallgrass prairie ecosystems to the precipitation regimes that I imposed in the field during the 2006 growing season. The objectives of this study were two-fold. First, I wanted to compare field versus modeled data in order to identify the relative sensitivity of this ecosystem model to within-season changes in precipitation. Second, I was interested in determining whether short-term responses to extreme precipitation events would be sustained or change over time. An additional goal of this study was to investigate research question 3 more directly and provide insight into the challenges and benefits of using a complementary model-empirical data approach to assessing the impacts of global change on ecosystem function. Because DAYCENT (and

its predecessor, CENTURY) have been developed and tested in grasslands and the Great Plains rather extensively (Kelly et al. 2000), this was an ideal opportunity to use empirical data and simulation results to further our understanding of the links between precipitation, soil moisture dynamics, and plant productivity.

Study Sites – Grasslands of the Great Plains Region of North America

Konza Prairie Biological Station

The Konza Prairie Biological Station (KNZ) is a native C₄-dominated mesic grassland in the Flint Hills of northeastern Kansas (39°05'N, 96°35'W), an area that remains the largest continuous expanse of unplowed tallgrass prairie in North America (Samson and Knopf 1994). KNZ is owned by the Nature Conservancy Kansas State University and was incorporated into the National Science Foundation's Long-Term Ecological Research Network in 1981. The Division of Biology at Kansas State University manages the research program, which emphasizes the influences of fire, grazing, and climate on plant, animal, and soil ecology of this temperate grassland ecosystem (Knapp et al. 1998).

At the eastern edge of the Great Plains Region of North America, the KPBS research station (3487-ha) is representative of the mesic tallgrass prairie ecosystem (Fig.2). Mean annual precipitation is 835 mm, 75% of which falls during the April – September growing season (Table 1; Hayden 1998). The climate is considered temperate mid-continental and characterized by periodic droughts and large seasonal and interannual variability in rainfall. Mean annual temperature is 13°C. The plant community is dominated by relatively few native perennial C₄ grasses (*Andropogon*

gerardii, *Sorghastrum nutans*, *Schizachyrium scoparium*, and *Panicum virgatum*), but considered floristically diverse, due to the abundance of C₃ herbaceous forb species (Freeman 1998).

The rain manipulation experiment described in chapter 4 was located in an area that was burned in the spring of 2005 and 2006. Prior to the initiation of this experiment, the site was burned intermittently. While grazing by native and/or domesticated ungulates has been part of the long-term site history, no grazing has occurred in this area since 1980. All 15 rainout shelters were located in a gently sloping, typical lowland prairie, where the soils are Udic Argiustolls with a soil texture of 8% sand, 60% silt, and 32% clay (Blecker 2005).

Saline Experimental Range

The Saline Experimental Range (SER; 38°53'N, 99°23'W) is a 2,400 acre contiguous tract of native mixed grass prairie (Fig.2) that was acquired and operated by the Agricultural Research Center-Hays (Kansas State University) in 1994. It is located in the Saline River Watershed, ca. 25 miles northeast of Hays, Kansas. The SER consists of a variety of upland, lowland, and breaks range sites and research emphasizes forage and beef production systems. In 2005, an electric fence was installed in order to prevent cattle grazing on the experimental plots used in my research. The plant community is dominated by the C₄ graminoids *Bouteloua curtipendula* (sideoats grama) and *Shizachyrium scoparium* (little bluestem), but C₃ forbs such as *Ambrosia psilostachya* (cuman ragweed), *Dalea purpurea* (purple prairie clover) and *Psoralea tenuiflora* (slimflower scurfpea) are abundant in cover. This mixed grass prairie site contains a diverse plant community in which species from its western (more arid) and eastern (more

mesic) grassland neighbors co-exist. Mean annual precipitation (long term average) is 576 mm (Table 1; Harmony 2007).

The rain manipulation experiment described in chapter 4 was located in an area that has historically been managed for cattle grazing and burned infrequently as a result of wildfires. The soils in this area are Typic Argiustolls with a composition of 6% sand, 69% silt, and 25% clay (Blecker 2005).

Central Plains Experimental Range

The Central Plains Experimental Range (CPER) is a semi-arid shortgrass steppe site that is located in northeastern Colorado USA (Fig.2; 40°49'N, 104°46'W). The CPER is located within the Shortgrass Steppe Long-Term Ecological Research site, which is a partnership between Colorado State University and the United States Department of Agriculture – Agricultural Research Service and Forest Service. Mean annual precipitation for this region is 321 mm (Lauenroth and Sala 1992), 70% of which occurs in the May-September growing season. Mean annual temperature is 8.6°C, but ranges from a monthly low in January (-5°C) to a monthly mean high of 22°C in July (Table 1; Milchunas and Lauenroth 1995). The plant community is dominated by the C₄ grass species, *Bouteloua gracilis* (blue grama), with other major C₃ forb species including *Artemisa frigida* (fringed sagewort), *Sphaeralcea coccinea* (scarlet globemallow) and *Opuntia polyantha* (plains pricklypear).

While site management is focused on varying intensities of cattle grazing in shortgrass steppe, the study site was located in a large exclosure from which cattle were removed in 1999. The soils of this site are considered representative of the shortgrass

steppe ecosystem and are Aridic Argiustolls (14% sand, 58% silt, 28% clay; Blecker 2005).

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Table 1. Characteristics of 3 grassland ecosystems across a precipitation gradient in the Central Plains Region of North America (USA).

	SGS	HYS	KNZ
	Shortgrass Steppe LTER Nunn, CO	Saline Experimental Range Hays, KS	Konza Prairie LTER Manhattan, KS
<i>Climate and vegetation</i>			
Latitude	40°49'N	38°53'N	39°05'N
Longitude	104°46'W	99°23'W	96°35'W
MAP (mm)	321	576	835
MAT (°C)	8.6	11.9	13
Vegetation type	semi-arid steppe	mixed grass prairie	mesic tallgrass prairie
Dominant plant species	<i>Bouteloua gracilis</i>	<i>Bouteloua curtipendula</i> <i>Schizachyrium scoparium</i>	<i>Andropogon gerardii</i> <i>Sorghastrum nutans</i>
Long-term mean ANPP (g/m ²)	97	300	425

The sites are SGS, the Shortgrass Steppe Long-Term Ecological Research (LTER) site; HYS, the Saline Experimental Range, under the management of the Kansas State University Western Agricultural Research Center; and KNZ, the Konza Prairie Biological Station LTER site. MAP = Mean Annual Precipitation; MAT = Mean Annual Temperature. Plant species nomenclature follows that of the Great Plains Floral Association (1986).

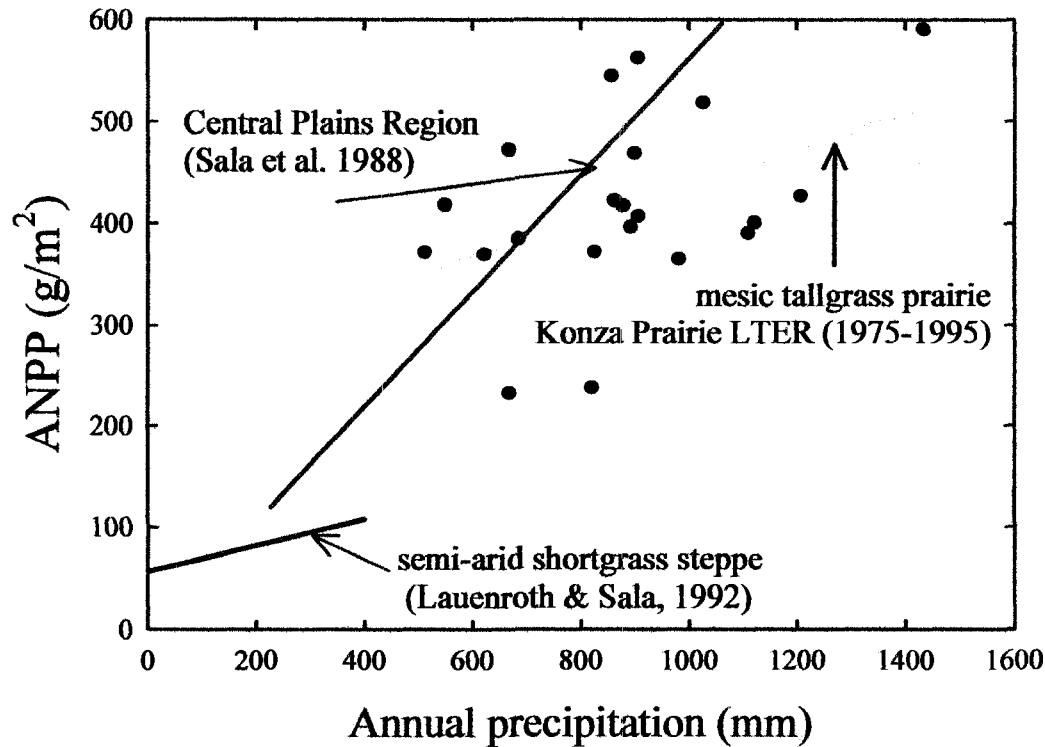


Figure 1. Spatial and temporal relationships for aboveground net primary productivity in the Great Plains and a semi-arid steppe and tallgrass prairie. Data points are from the Konza Prairie Long-Term Ecological Research site and indicate average annual aboveground net primary productivity (ANPP; g/m^2) and total annual precipitation values for 1975-1995. The yellow line depicts the relationship between annual precipitation and ANPP for this time period. The green line is adopted from Sala et al. (1988) and the red line is adopted from Lauenroth and Sala (1992).

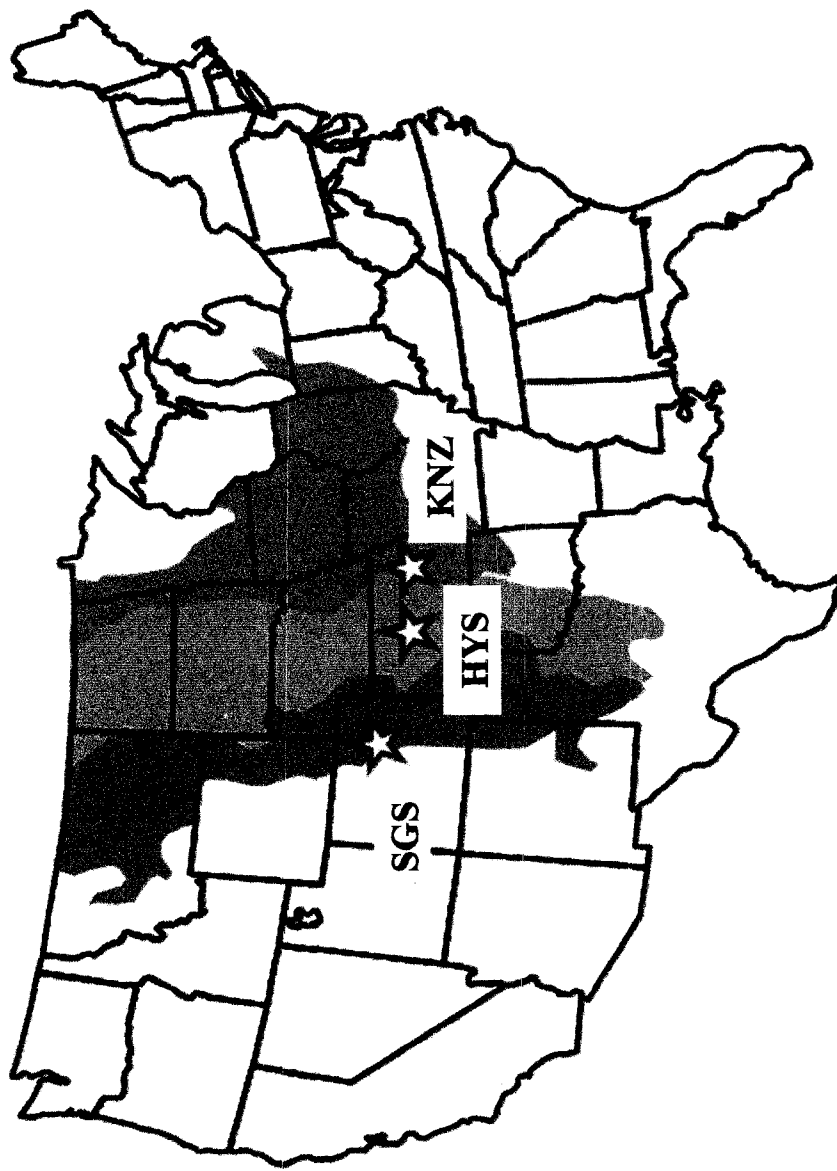


Figure 2. The Central Plains Region of North America (USA). SGS = Shortgrass Steppe LTER site (semi-arid steppe grassland) in Nunn, CO; HYS = the Saline Experimental Range in Hays, KS (mixed grass prairie); and KNZ = Konza Prairie Biological Station in Manhattan, KS (tallgrass prairie).

Chapter 2: Temporal coherence of aboveground net primary productivity in mesic grasslands

Published In: Ecography 2008, volume 31, pages 408-416

Abstract

Synchrony in ecological variables over wide geographic areas suggests that large-scale environmental factors drive the structure and function of ecosystems and override more local-scale environmental variation. Described also as coherence, this phenomenon has been documented broadly in the ecological literature and has recently received increasing attention as scientists attempt to quantify the impacts of global changes on organisms and their habitats. Using a mesic grassland site in North America, we assessed coherence in ecosystem function by quantifying similarity in aboveground net primary production (ANPP) dynamics in 48 permanent sampling locations (PSLs) over a 16-year period. Our primary objective was to characterize coherence across a broad geographic region (with similar ecosystem structure and function), and we hypothesized that precipitation and a similar fire frequency would strengthen coherence between PSLs. All 48 PSLs at our site (Konza Prairie Biological Station, Manhattan, KS, USA; KPBS) were exposed to a similar regional driver of ANPP (precipitation); however, local drivers (including differences in fire frequency and soil depth at different topographic positions) varied strongly among individual PSLs. For the purpose of this assessment, the watershed-level experimental design of KPBS was considered a model, which

represented different fire management strategies across the Great Plains Region. Our analyses revealed a site-level (KPBS) coherence in ANPP dynamics of 0.53 for the period of 1984-1999. Annual fire enhanced coherence among PSLs to 0.76, whereas less frequent fire (fire exclusion or a 4-year fire return interval) failed to further increase coherence beyond that of the KPBS site level. Soil depth also strongly influenced coherence among PSLs with shallow soils at upland sites showing strong coherence across fire regimes and annually burned uplands closely linked to annual precipitation dynamics. The lack of coherence in ecosystem function in PSLs with deep soils and low fire frequencies suggests that conservation and management efforts will need to be more location specific in such areas where biotic interactions may be more important than regional abiotic drivers.

Introduction

Within both terrestrial and aquatic ecosystems, the ability of large-scale environmental drivers to generate spatially synchronous dynamics has been documented broadly (Kratz et al. 1987; Grenfell et al. 1998; Schaubert et al. 2002; Post 2003; Cattadori et al. 2005; Patoine and Leavitt 2006). Biotic examples of spatial synchrony, such as the coupling of lynx populations with climate, were originally described by Moran (1953); however, this phenomenon has since been extended to include abiotic variables such as lake surface melting/ice break-up (Wynne et al. 1996), water chemistry (Magnuson et al. 1990; Benson et al. 2000), and lake temperature (Kratz et al. 1998; Baines et al. 2000). Such tight coupling between environmental drivers and both biological and biophysical phenomena demonstrates the sensitivity of ecosystems and

their plant and animal inhabitants to climate, land management, and resource availability – all of which are being altered via anthropogenic activities (Vitousek 1997).

A central goal of ecology is the elucidation of key environmental drivers and their independent and interactive influence on the structure and function of ecosystems. Of particular interest is the balance between the relative strength of regional versus local drivers. Characterizing the strength of drivers is important not only in understanding ecosystems as they exist in the present, but also in anticipating and predicting natural and human impacts on the biosphere. An effective means by which to study the relative strength of drivers is through the use of long-term dynamics in integrative ecosystem variables or population dynamics. Similar patterns of interannual fluctuations among sites distributed across the landscape suggest that external drivers strongly influence ecological processes, and in such a way that local scale differences are reduced in importance. This phenomenon has been described as temporal coherence (Magnuson et al. 1990) or spatial synchrony (Kratz et al. 1998) and may effectively guide ecologists in the selection of experimental sites as well as long-term monitoring locations. In characterizing sites as temporally coherent, the emphasis is placed on the presence of similar increases and decreases in response variables through time, rather than comparing mean values for individual years (that may exist due to differences in slope, soil fertility, plant community composition, etc.). Parmesan and Yohe (2003) used this concept to gather widespread empirical support for the coherent fingerprint of climate change across the globe. An additional application for coherence is the identification of field sites that manifest similar response patterns to large-scale changes in elevated CO₂, precipitation, or N deposition. If a number of sites (that differ in resource availability or management)

are coherent in ecosystem function, then only one of a large collection of sites can be extensively monitored in response to a regional or global driver. Acquiring the empirical support for the use of study sites as regional proxies will become essential in the development of national/international ecological monitoring networks and the selection of monitoring locations to represent different regions or ecosystems.

Mechanistic coherence underpins much of ecological research, but most studies are of too short duration or spatial extent to assess coherence explicitly. The general issue of how to make inferences from single sites or study plots to regions or biomes is paramount in ecology (Miller et al. 2004), where distinguishing between widespread vs. isolated phenomena can be a primary objective. To test for coherence of the biodiversity-ecosystem function relationship, the European BIODDEPTH network was initiated in 1997 (Spehn et al. 2005). While many well-replicated site-level studies had previously demonstrated a link between biodiversity and ecosystem function, BIODDEPTH spanned several thousand kilometers to effectively incorporate a range in climate, soil conditions, and local species pools. The results of BIODDEPTH reinforced patterns observed in other experiments and ultimately demonstrated that the biodiversity-ecosystem function relationship is coherent across large-scale environmental variation.

To date, ecologists have focused primarily on plant and animal population dynamics and their coherence with climate variables (both temperature and precipitation; Lloyd and May 1999). In many cases, this research suggests that such mechanistic linkages may result in the vulnerability of populations to climate change (Mantua et al. 1997; Post and Forchhammer 2002; Post and Forchhammer 2004; Li et al. 2006). Building on this approach, we used long-term aboveground net primary productivity

(ANPP) data from a mesic grassland in North America to assess temporal coherence across differing sampling locations in a Long-Term Ecological Research (LTER) Site. We define temporal coherence broadly as the degree to which different locations in a region behave similarly through time (Magnuson et al. 1990). Our central objective was to quantify the degree of synchrony in a fundamental ecosystem process among a variety of sampling locations in which local drivers (fire and differences in soil depth at different topographic positions) are known to be important (Gibson and Hulbert 1987; Briggs and Knapp 1995; Knapp et al. 1998). We hypothesized that ANPP dynamics at Konza Prairie Biological Station (KPBS) would be strongly coherent, with precipitation being the primary driver in generating similar dynamics through time. Additionally, we expected that a similar fire regime (i.e annual fire or the absence of fire) would lead to coherence among permanent sampling locations (PSLs) and that topographic position would not impact coherence, despite its known influence on the magnitude of ANPP over time.

Using ANPP data from a 16-year period, we assessed fire frequency, topographic position (as a surrogate for soil depth), and precipitation as candidate factors for generating or disrupting temporal coherence in ecosystem dynamics. Rather than explicitly focusing on scale, established drivers of dynamics in ANPP—climate, topographic position, and fire—were nested at spatial scales based on the watershed-level experimental design at KPBS (Knapp et al. 1998). This analysis is unique in that we explicitly focus on variability in ANPP at locations that are exposed to similar drivers (identical fire frequency and topographic position) or a combination of different drivers. For each level in the process hierarchy (precipitation at the largest scale, watershed level fire regimes at an intermediate scale, topographic position and individual sampling

locations at the local scale), we test the null hypothesis that while differences may exist in the magnitude or mean ANPP response over time, the temporal dynamics of ANPP are similar (or coherent) and driven by interannual variability in precipitation. In conducting the analysis in this way, we were able to partition the relative influence of fire and/or topographic position versus climate as key determinants of ANPP.

Specifically, we addressed the following questions: 1) Are ANPP dynamics at the site scale (KPBS), where a common regional climate is manifest, coherent? If so, this would suggest that regional climate is a driver that overrides local scale ecosystem processes across the landscape; 2) How does temporal coherence vary across differing management strategies (fire frequency), topography, and watersheds? We expected *a priori* that PSLs exposed to a common fire treatment would have strong coherence.

Material and methods

Site Description

The Konza Prairie Biological Station (KPBS) is a native C₄-dominated mesic grassland in the Flint Hills of northeastern Kansas (39°05'N, 96°35'W). KPBS is owned by the Nature Conservancy and Kansas State University and was incorporated into the National Science Foundation's Long-Term Ecological Research Network in 1981, at which time an experimental design emphasizing fire frequency was implemented. The research station is 3487 hectares in size and divided into 60 watershed-level experimental units (ca. 60 ha each on average), which are subjected to spring fire (April 10 ± 20 days) annually or at fire return intervals of two, four, ten, and 20 years ("unburned"), respectively (Knapp et al. 1998). While the experimental design incorporated grazing by both native (*Bos Bison*) and domestic (cattle) ungulates in 1987, the watersheds in this

analysis have been ungrazed for greater than 30 years. In most cases, 2-4 replicate watersheds exist for a given treatment type and they are spatially distributed throughout KPBS to allow for greater heterogeneity in both plant community composition and abiotic characteristics. To assess the influence of topography/soil type (a known ecological driver in this ecosystem) on ecosystem function, watersheds include distinct gradients with upland (maximum elevation of 444 m) to lowland (320 m) topographic positions. Uplands (benches) are formed in residuum weathered from limestones or shales and considered a unique soil pedon within KPBS (Florence pedon). The soils are characterized as fine, montmorillonitic, mesic Udertic Paleustolls and are relatively shallow and well-drained, with depth to bedrock typically < 100 cm. Because KPBS is a landscape undergoing long-term erosion, surficial deposits accumulate in valley bottoms, resulting in the distinct Tully pedon of lowland topographic positions. Lowlands are classified as fine, mixed, mesic Pachic Argiustolls, with depth to bedrock ranging from 125-200 cm (Oviatt 1998; Ransom et al. 1998).

The climate for KPBS is characterized as temperate midcontinental with 75% of annual precipitation (835 mm) falling during the growing season. Plant community composition is dominated by the warm season C₄ grasses *Andropogon gerardii* Vitman and *Sorghastrum nutans* Nash, with the bulk of plant species diversity arising through the presence of lesser abundant C₃ forbs (herbaceous dicots).

Data Description

For the purposes of this study, we chose to focus on data from watershed-level manipulations of fire regime (annual, 4-year, and unburned fire treatments), as these represent the longest continuous data available for annual ANPP. We focused on ANPP,

as it integrates many aspects of both ecosystem structure and function across the time span of a growing season. For each fire treatment, a watershed with 16 years (1984-1999) of data was included, in addition to a non-adjacent watershed with a similar fire history but 7 years (1993-1999) of data. All watersheds contained distinct upland and lowland topographic positions in which permanent sampling locations (PSLs) are located. The mean size of the six watershed experimental units was 31.2 ± 6.4 ha. The process hierarchy for our analyses included 1) precipitation (similar across all sites as confirmed with a network of rain gauges), 2) fire regime (imposed at the watershed scale), 3) topographic position, 4) the individual watershed and 5) each PSL. The reference codes and data details for each watershed are included in Table 1. Watershed codes are assigned based on the fire return interval (numerical value ranging from 1-20) and the replicate (alphanumeric value ranging from A-F). For example, watershed 1C is annually burned and the “C” replicate for that particular fire treatment (which also includes an A, B, and D replicate), whereas watershed 4B is burned once every 4 years and the “B” replicate for that fire treatment.

To estimate ANPP, all aboveground biomass within 0.10-m^2 quadrats ($n = 5$) was harvested annually along 4-50 m transects at a given upland or lowland topographic position in late August/early September. Each transect was considered to be an individual PSL. Sampling occurred at both upland and lowland PSLs ($n = 4$ PSLs per topographic position) within a given watershed, which represents the scale at which fire treatments were applied. Plant material was sorted into live graminoid and forb components, current year’s dead, and previous year’s dead (only applicable in sites and/or years in which fire did not occur), oven dried at 60°C and weighed to the nearest

0.1 g (Abrams et al. 1986). Total ANPP included all current year's production (both live and dead), whereas analyses of grass and forb ANPP included solely these components. Because we were only interested in annual production, previous years' dead was not included in any of the analyses. An annual mean value was assigned to each PSL (based on the 5 quadrats that fell along a given transect), with sites characterized by either 16 or 7 data points (depending on the number of years in which data were available).

Analytical Methods

The temporal coherence of ANPP between pairs of PSLs was calculated by taking the Pearson product-moment correlation of their 16-year (1984-1999) or 7-year (1993-1999) time series of ANPP (see example in Fig. 1). Pearson correlations are the most commonly used method to assess synchrony in ecosystems (Bjørnstad et al. 1999; Buonaccorsi et al. 2001). In cases in which correlations were calculated between a watershed with 16 years of data and a watershed with 7 years of data, the resultant correlation was based on the lesser number of years (7). This resulted in the number of pair-wise correlations indicated in Table 1. The levels of analysis included 1) management (fire frequency), 2) topographic position within a fire treatment, and 3) individual watersheds within a topographic position and fire treatment. A correlation analysis was also conducted for all PSLs for the entire research station. For a given level of analysis, the arithmetic mean of all correlation coefficients (derived from pairs of PSLs) was the measure of temporal coherence (c ; Magnuson et al. 1990). Because cross-correlation coefficients are not independent, we generated bootstrap confidence intervals for mean coherence values by sampling with replacement at each level of analysis. 1000 replicate samples were generated, with each bootstrap sample consisting of n PSLs with

replacement from the observed data. Values for n are identical to those in the analyses of raw data (Table 1) and confidence intervals were set at 95%. We consider means with non-overlapping confidence intervals to be significantly different from one another. Visual examples of both strong and weak temporal coherence are included in Fig. 1a and 1b, respectively. To evaluate correlations between ANPP and growing season precipitation, we calculated the total amount of rainfall for the months of April – September. A Pearson product-moment correlation (r) for ANPP and precipitation for each PSL was then calculated, with data aggregated at the site (KPBS) through watershed levels used in the coherence analyses. The 95% confidence intervals for each correlation were calculated in the same way as for coherence.

To differentiate 1) between pair-wise correlations between PSLs and 2) correlations between PSLs and precipitation, we refer to the former as coherence (c) and the latter as correlations (r). We make this distinction to separate general similarity in ANPP dynamics between PSLs through time from the influence of a particular driver on PSL dynamics (each PSL with annual precipitation from 1984-1999).

Assessing spatial autocorrelation

In an analysis such as this, coherent dynamics in ecosystem characteristics could be caused simply by the proximity of sample locations to one another rather than by environmental factors. To test for this spatial autocorrelation due to distance between PSLs, we used a GIS coverage for KPBS that included coordinates for each PSL. The Euclidean distance between all unique pairs of PSLs (1128) was calculated using ArcGIS, and this value was plotted against their correlation coefficient. No relationship between distance among PSLs and the degree of correlation in ANPP was detected (Fig.

2), indicating that spatial proximity did not influence coherence in ANPP in any consistent manner.

Results

ANPP Patterns

An analysis of general patterns of ANPP for this mesic grassland site revealed that the 16-yr mean for ANPP was 424 g m^{-2} . From 1984 to 1999, ANPP varied more than seven-fold at KPBS between a minimum value of 136.1 g m^{-2} and a maximum value of 1049.6 g m^{-2} (Table 2). Overall, the mean ANPP for lowland sites was greater than that observed in upland locations (487 g m^{-2} versus 362 g m^{-2} , respectively; Table 2). Annually burned sites had the greatest mean ANPP (482 g m^{-2}) and were also characterized as the most variable (CV= 33%). For the research site as a whole, the minimum value for ANPP was observed in a watershed with a 4-year fire return interval. This fire frequency also had the lowest mean ANPP of the three fire treatments (390 g m^{-2} ; Table 2). The maximum ANPP value was observed in an unburned watershed (1050 g m^{-2} ; Table 2), but in a year (1993) in which a wildfire had occurred. Annually burned lowlands were characterized as the least variable (CV=26%) and had the highest ANPP of all fire-topography aggregations.

Temporal coherence of ANPP

Are ANPP dynamics at the site scale coherent?

For this 3487 ha mesic grassland field station, our analyses revealed that temporal coherence for ANPP across the site for the years 1984-1999 averaged 0.53 (Table 3). To evaluate the role of topography as a factor, sites were grouped as either uplands or

lowlands, respectively (ignoring the role of individual fire history and watershed). This revealed that upland sites were more strongly coherent (0.67 Table 3) than lowland sites (0.50; Table 3).

How does temporal coherence vary across differing management strategies, topography, and watersheds?

Fire frequency strongly affected temporal coherence. Annual fire as an ecosystem driver was unique in that ANPP dynamics were the most strongly coherent. Mean coherence for annually burned PSLs was 0.76 (Fig. 3a; Table 3) and well above the 95% confidence intervals for the KPBS site level coherence mean (0.47 – 0.62). Further segregating the data for this fire regime by topographic position revealed an increase in coherence for upland sites (0.88; Fig. 3a) whereas the temporal coherence in lowland sites decreased (0.72; Fig. 3a). To evaluate the scale of the individual watershed, we further divided the sites into uplands and lowlands of the two annually burned watersheds (1C and 1D, respectively). The uplands of watershed 1C were identified as having the strongest coherence (0.90) of all watershed-topographic locations, followed by the upland sites of 1D (0.81). The weakest coherence for annually burned PSLs was between the PSLs of watershed 1D ($c = 0.71$; 3a); however, this value remained significantly above the KPBS site level mean and 95% confidence intervals.

As fire frequency is extended to a 4-year fire return interval, mean coherence of ANPP dynamics was strongly reduced to 0.5 (Fig. 3b; Table 3) suggesting no significant difference from analyses at the KPBS site level. Similar to the trend observed in annually burned sites, upland PSLs demonstrated stronger temporal coherence than lowland PSLs (Table 3). Mean coherence values in each topographic location were 0.67 and 0.49,

respectively (Fig. 3b). Unlike annually burned watersheds, PSLs in watersheds burned every 4 years were not strongly coherent with one another (Fig. 3b; Table 3). Coherence in watershed 4A was much stronger than in 4B, in addition to being significantly different than the KPBS site-level coherence.

The long-term unburned sites, which were exposed to only a single fire event throughout the period of data collection, were characterized by the lowest relative coherence of all fire management strategies (Fig. 3c; Table 3). Mean coherence for this fire treatment was 0.49 and not significantly different than KPBS site level coherence. When the data were segregated by topographic position, no pattern was identifiable to suggest that either uplands or lowlands had a tendency to be more or less coherent (Fig. 3c). Of all fire treatments, mean coherence was lowest in individual watersheds that were not burned.

Correlation between PSLs and precipitation

Across the KPBS site, the mean correlation between PSLs and precipitation was 0.52 (Table 3) and PSLs varied considerably in the degree to which they were correlated with interannual dynamics in precipitation. Overall, upland PSLs were more strongly correlated with precipitation (0.68) than lowland PSLs (0.37; Table 3). Similar to the PSL coherence trend for management, PSLs in annually burned areas were more strongly correlated with precipitation (0.69; Fig. 4a) as compared to PSLs in unburned areas (0.38; Fig. 4c). The 4-yr burned PSLs were intermediate to the other 2 fire treatments in mean correlation with precipitation (0.50; Fig. 4b). An interesting trend was detected in lowland transects located within watersheds that were burned every four years. In years of a fire, marked pulses in ANPP were evident and in many cases this was completely

independent of precipitation dynamics. With the exception of upland PSLs in watershed 20D, the general degree of correlation between unburned PSLs was quite low, and in many cases, correlation values were significantly lower than the KPBS site level correlation.

Temporal Coherence of ANPP: Influence of growth forms

We characterized annual ANPP values for PSLs according to growth form (graminoid versus forb) as a potential biotic mechanism for ANPP dynamics and coherence. Identifying the relative contribution of graminoid versus forb ANPP to total ANPP revealed that as the fire return interval becomes less frequent, forb ANPP increased dramatically (Appendix Fig. A.1). While grasses strongly dominate in annually burned watersheds (resulting in forb ANPP < 10%), forbs account for ca. 20-30% of the ANPP in long-term unburned watersheds. The ANPP of forbs in watersheds burned every four years was intermediate to the two extreme fire treatments (annual and unburned).

Topographic position is also important in determining the percentage of ANPP that is contributed by forb species but its effect was not consistent among fire treatments. In annually burned watersheds, forb ANPP was slightly greater in upland transects. In contrast, lowland transects of less frequently burned transects tended to have greater forb ANPP and thus less grass ANPP comparatively (Appendix Fig. A.1). Patterns of coherence in grass ANPP were similar to total ANPP, typically with slightly higher mean coherence values and levels of significance.

Discussion

Ecologists are increasingly called upon to forecast the potential impacts of global-scale phenomena such as climate and land-use change on ecosystems as well as provide management recommendations (Miller et al. 2004). While these global change drivers operate over large geographic areas and extended periods of time, the field data from which inferences are made are typically comprised of a limited number of study plots that capture only a subset of the environmental variation found across the landscape. This mismatch in the scale of the question versus the scale of data collection is considered one of the greatest challenges confronting environmental scientists (Levin 1992), but one that may be at least partially addressed through assessments of mechanistic coherence of ecological phenomena. Indeed, by demonstrating coherence in the biodiversity-productivity relationship across the European continent, ecologists within the BIODEPTH network identified the robust nature of this ecological relationship, which transcends environmental variation in both time and space (Spehn et al. 2005). In our analyses, it is important to note that while KPBS is relatively small in geographic extent, the experimental treatments within it are reflective of the many land-use/management strategies throughout the Great Plains Region. Consequently, our results have potential broader application for this region.

Across this mesic grassland site in North America, it is evident that coherence in ANPP can be either enhanced or disrupted by land management (fire frequency) and to a lesser extent by the topographic position (and resulting soil depth) of the sampling location. In grasslands, precipitation is a primary driver of ANPP; however, within a single grassland type, factors such as fire frequency and topographic position may modify

the effect of this driver directly through the removal of biomass and changes in resource availability (Knapp and Seastedt 1986; Blair 1997), and indirectly, through shifts in community structure (Collins and Gibson 1990). Our analyses revealed that the 48 PSLs within the KPBS site (3487 hectares in size) have a mean coherence of 0.53 in ANPP dynamics. While this value suggests a moderate level of consistency in ANPP dynamics through time, greater insight was gained by including fire and topography in the analyses. PSLs in annually burned upland sites were strongly coherent, with correlation values of 0.90 in several cases. This can be contrasted with the lack of coherence observed in PSLs in unburned watersheds, where values were frequently not different than the KPBS site as a whole. Because annually burned PSLs are strongly coherent both with one another and growing season precipitation, they are the most likely to respond most predictably to forecast changes in precipitation for this region, an important consideration when selecting long-term monitoring sites.

Analyses of trends or patterns of ANPP that focus on average responses and aggregate data in time or space may not be as effective in identifying the influence of a particular ecosystem driver (such as fire or topography). For example, Briggs and Knapp (1995) found that growing season precipitation explained a limited amount of the variance ($r^2 = 0.23$) in ANPP in this grassland site when data were combined across sites with differing fire regimes and/or topographic positions. The results of this study suggest that some driver combinations demonstrate strong correlations between PSLs and precipitation as well as between individual PSLs, suggesting a shared and consistent link between precipitation and ANPP. In contrast, the relative absence of coherence between

precipitation and lowland PSLs burned every 4 years, but strong coherence between individual pairs of PSLs, suggests a decoupling of this driver from ecosystem function.

How do fire frequency and topography influence temporal coherence of ANPP?

Fire frequency influences resource availability and plant community structure (Collins et al. 1995; Blair et al. 1998), both of which impact ecosystem productivity. Annual spring fire influences the structure of the plant community by favoring C₄ grass species, which competitively exclude C₃ forb species (Collins 1992; Gibson et al. 1993). In a system that is already dominated by a select suite of C₄ grasses, this creates a relatively homogeneous plant community (Collins and Smith 2006) comprised of shallow rooted species that are more dependent upon growing season rainfall for water (Nippert and Knapp 2007). A passing fire in mesic grasslands (where cover is continuous) typically destroys the previous year's accumulation of litter and makes resource availability (light, in particular) uniformly abundant (Hulbert 1969; Knapp and Seastedt 1986). In the absence of fire, vegetation becomes decoupled from precipitation as light becomes the primary limiting resource for plant growth and standing litter intercepts a greater proportion of rainfall. The resultant shift in plant community structure (as a result of competitive release) to a greater abundance of deep-rooted C₃ forbs further decouples the vegetation from growing season rainfall patterns.

Topography additionally influences coherence, due to the associated differences in soil depth and water availability. Lowland areas are characterized by deeper soils, thus reducing the reliance of the plant community on ambient rainfall patterns during the growing season. This can be compared to annually burned upland sites, where the

vegetation is more likely to be limited by moisture availability due to lower soil water storage and high evapotranspiration rates (Knapp et al. 1993).

The knowledge that ecological phenomena are spatially synchronous can be powerful, as it demonstrates the relative influence of individual and interacting drivers in ecological systems. Given that most sampling locations are nested in regions in which management and/or abiotic factors vary, coherence of ecosystem function should be more commonly assessed. Temporal coherence is a useful concept because it provides evidence that generalizing about regional responses to climate change or other global-scale phenomena is appropriate. The coherent response of primary producers to system-wide drivers has been documented in aquatic ecosystems (Li et al. 2006), where within-year dynamics of phytoplankton are coupled with bacterioplankton as a result of a trophic cascade. While beyond the scope of our analysis, it is important to note that terrestrial primary producers that are mechanistically linked to climate variables (such as precipitation or temperature) and variation may also initiate cascading effects across trophic levels. This is particularly important in regions like the Great Plains, where large tracts of rangeland support livestock, which ultimately produce important food resources for the US population as well as occupy an important role in the economy.

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Table 1. Description of the number of years of aboveground net primary productivity (ANPP; g m^{-2}) data used in analyses. Also included is the number of permanent sampling locations and correlations for each level of analyses.

	Years	Upland Sites (# of correlations)	Lowland Sites (# of correlations)	Total Sites (# of correlations)
Annual fire	1984-1999 (n=16 years)	8 (28)	8 (28)	16 (120)
1C	1993-1999 (n=7 years)	4 (6)	4 (6)	8
1D	1984-1999 (n=16 years)	4 (6)	4 (6)	8
4-year fire return interval	1984-1999 (n=16 years)	8 (28)	8 (28)	16 (120)
4A	1993-1999 (n=7 years)	4 (6)	4 (6)	8
4B	1984-1999 (n=16 years)	4 (6)	4 (6)	8
Unburned	1984-1999 (n=16 years)	8 (28)	8 (28)	16 (120)
20B	1984-1999 (n=16 years)	4 (6)	4 (6)	8
20D	1993-1999 (n=7 years)	4 (6)	4 (6)	8

To maximize the number of sites included, watersheds with 16 and 7 years of consecutive data, respectively, were selected to represent each fire treatment. In cases in which correlations were calculated between a watershed with 16 years of data and a watershed with 7 years of data, the resultant correlation was based on the lesser number of years (7). As a note, data are additive such that aggregation by each fire regime includes 2 watersheds (i.e. 1C and 1D), each of which contains an uplands and lowlands with 4 PSLS, respectively.

Table 2. Summary of aboveground net primary productivity (g m^{-2}) for Konza Prairie Biological Station from 1984-1999.

	Mean (g m^{-2})	Range (g m^{-2})	CV
Site: KPBS	424	136 – 1050	33.4
Uplands	362	136 – 1050	28.1
Lowlands	487	487 – 980	30.5
Annual Fire	482	161 – 980	33.1
Uplands	384	161 – 665	25.8
Lowlands	581	250 – 980	25.5
4-yr fire return interval	390	136 – 859	32.0
Uplands	335	136 – 566	26.8
Lowlands	444	158 – 859	29.7
Unburned	400	189 – 1050	29.7
Uplands	366	189 – 1050	30.0
Lowlands	435	217 – 841	27.1

Table 3. Mean coherence (c) of permanent sampling locations (PSLs) and correlation (r) of PSLs with precipitation at Konza Prairie Biological Station (KPBS). The 95% confidence intervals of sample means have been included for reference.

Level of data aggregation		Mean coherence (c) of PSLs	Confidence intervals	Mean correlation (r) w/precipitation	Confidence intervals
Site		0.53	0.47 – 0.62	0.52	0.43-0.62
Topography	Uplands	0.67	0.63 – 0.75	0.68	0.62 – 0.74
	Lowlands	0.50	0.44 – 0.56	0.37	0.27 – 0.47
Fire management					
Annual	Uplands	0.76	0.72 – 0.80	0.69	0.64 – 0.75
	Lowlands	0.88	0.87 – 0.89	0.80	0.87 – 0.83
4-year interval	Lowlands	0.72	0.53 – 0.64	0.58	0.53 – 0.64
	Uplands	0.50	0.47 – 0.53	0.50	0.40 – 0.61
	Lowlands	0.67	0.64 – 0.70	0.67	0.61 – 0.74
Unburned	Lowlands	0.49	0.43 – 0.55	0.34	0.22 – 0.44
	Uplands	0.49	0.42 – 0.57	0.38	0.27 – 0.48
	Lowlands	0.60	0.55 – 0.65	0.57	0.50 – 0.64
		0.52	0.44 – 0.58	0.18	0.09 – 0.27

Figure 1. Examples of (a) strong and (b) weak coherence between two different pairs of permanent sampling locations (PSLs) at the Konza Prairie Biological Station, KS, USA. Data are from PSLs in watersheds 1D and 4B (panel a) and 4B and 20B (panel b), respectively. Each line (and its component data points) depicts aboveground net primary productivity (ANPP; g m^{-2}) dynamics of an individual PSL for the time period of 1984-1999. *Inset:* An example of the relationship between ANPP at two PSLs in watershed 1D. Data points represent ANPP (g m^{-2}) for a PSL pair in a given year.

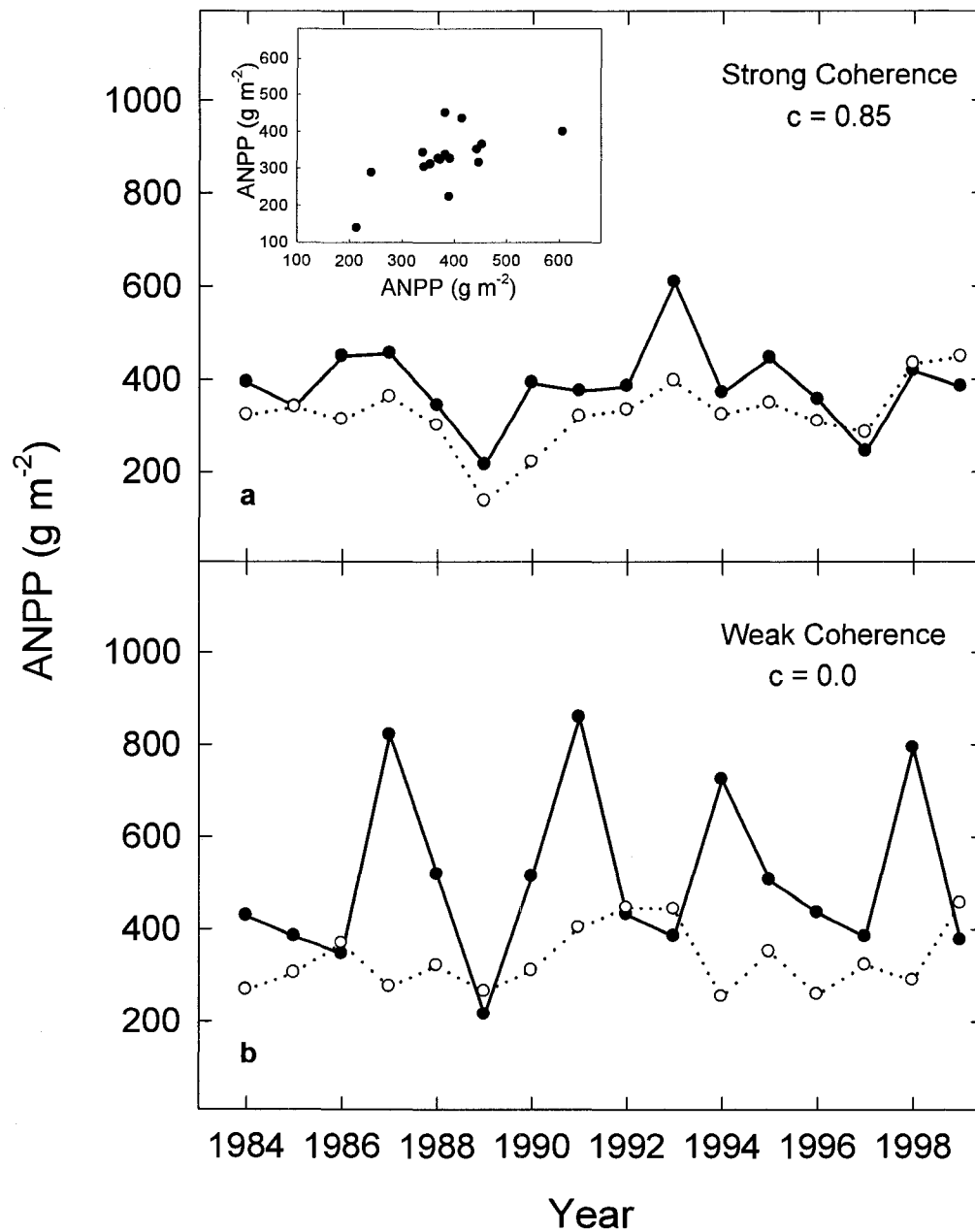


Figure 2. Distance (m) between pairs of permanent sampling locations (PSLs) versus their coherence (c) in ANPP. Data shown are for all pairs of sampling locations in six watersheds at the Konza Prairie Biological Station.

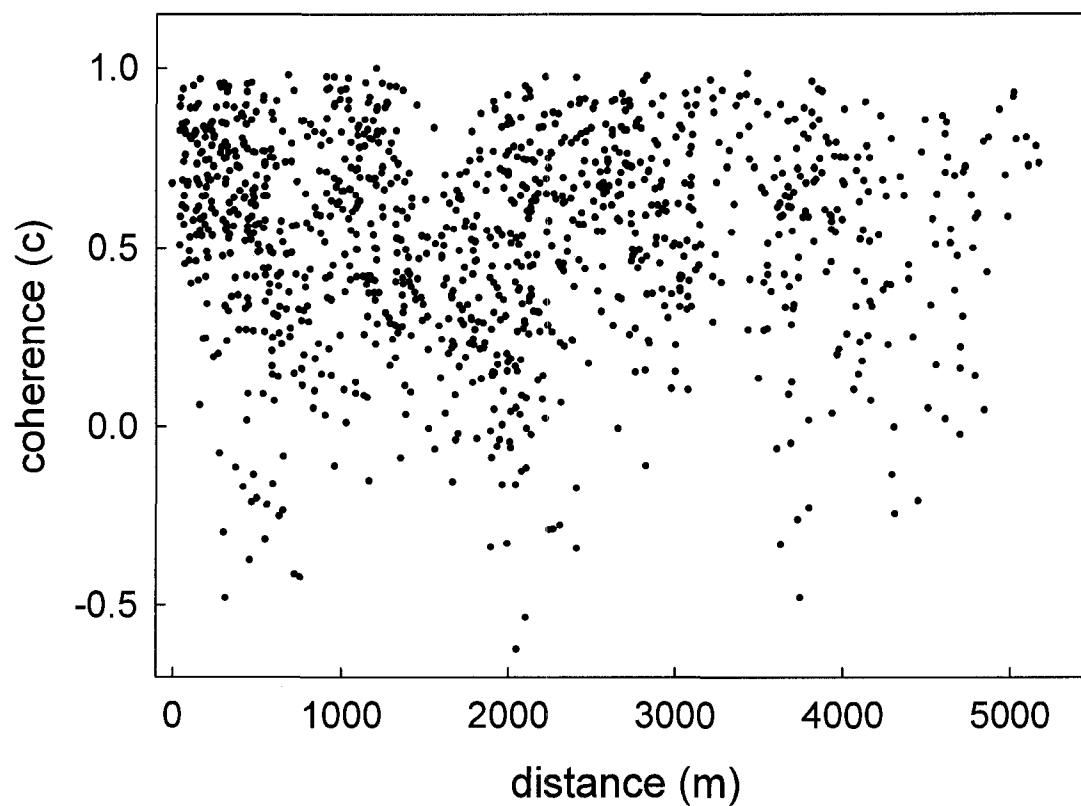


Figure 3. Mean coherence (c) in aboveground net primary productivity (ANPP; g m^{-2}) at the Konza Prairie Biological Station (KPBS). Panels represent coherence for the management regimes of annual fire (A), a 4-year fire return interval (B), and unburned conditions (C). Individual watersheds for each fire regime are indicated by alphanumeric abbreviations (i.e. 1C or 4A). Overall site level coherence (KPBS; 0.53) and 95% confidence intervals are included as references and indicated by solid and paired dash lines, respectively. U = Upland topographic position, L = Lowland topographic position.

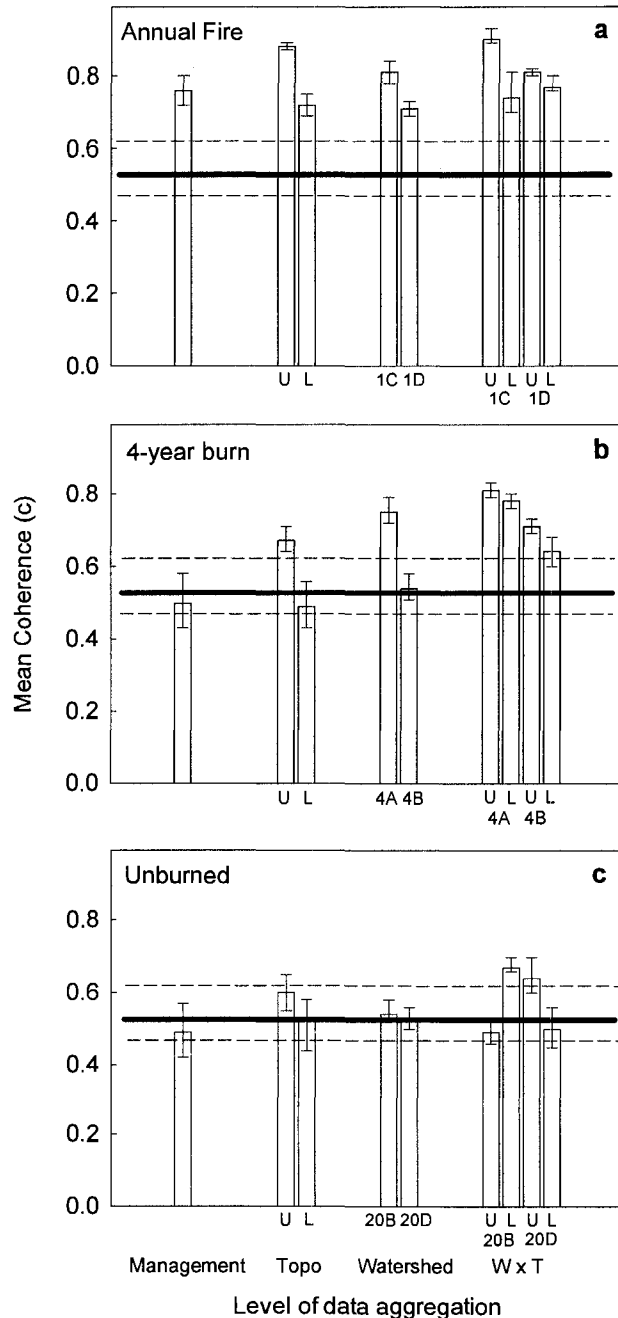
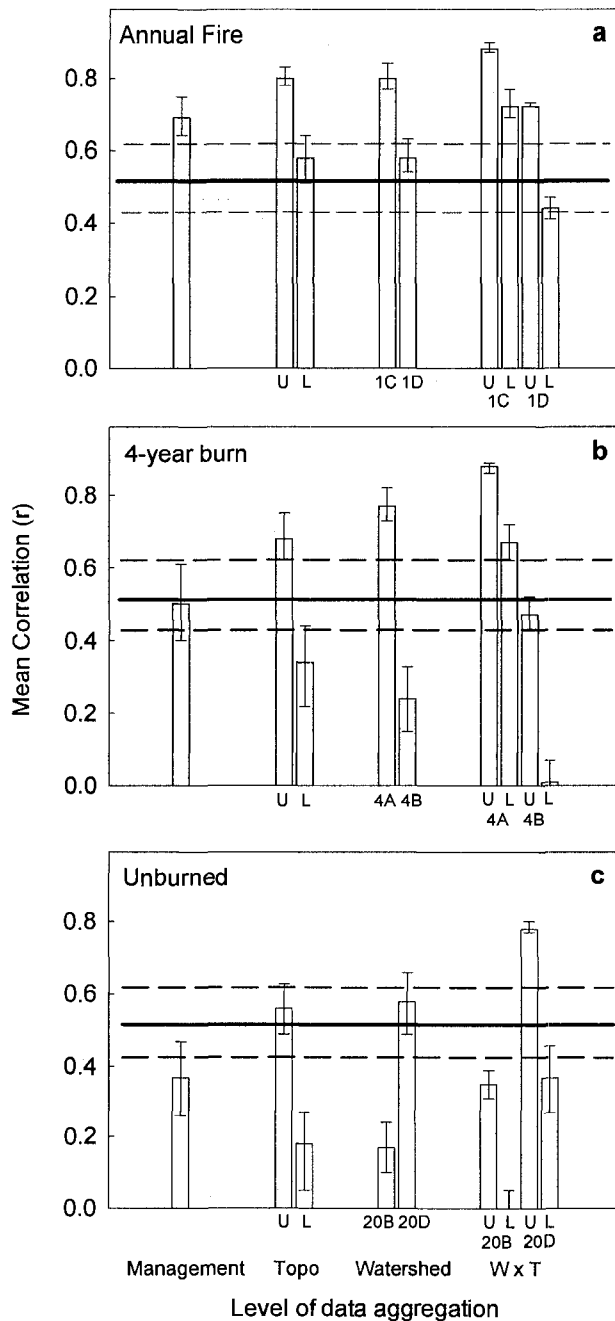


Figure 4. Mean correlation (r) between aboveground net primary productivity (ANPP; g m^{-2}) and precipitation at the Konza Prairie Biological Station (KPBS). Panels represent correlations for the management regimes of annual fire (A), a 4-year fire return interval (B) and unburned conditions (C). Individual watersheds for each fire regime are indicated by alphanumeric abbreviations (i.e. 1C or 4A). Overall site level coherence (KPBS; 0.52) and 95% confidence intervals are included as references and indicated by solid and paired dashed lines. U = Upland topographic position, L = Lowland topographic position.



Chapter 3: Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland

In press: Oecologia (2008)

Abstract

Water availability is the primary constraint to aboveground net primary productivity (ANPP) in many terrestrial biomes, and it is an ecosystem driver that will be strongly altered by future climate change. Global Circulation Models predict a shift in precipitation patterns to growing season rainfall events that are larger in size but fewer in number. This “repackaging” of rainfall into large events with long intervening dry intervals could be particularly important in semi-arid grasslands because it is in marked contrast to the frequent but small events that have historically defined this ecosystem. We investigated the effect of more extreme rainfall patterns on ANPP via the use of rainout shelters and paired this experimental manipulation with an investigation of long-term data for ANPP and precipitation. Experimental plots (n=15) received the long-term (30-yr) mean growing season precipitation quantity; however, this amount was distributed as 12-, 6-, or 4-events applied manually according to seasonal patterns for May-September. The long-term mean (1940-2005) number of rain events in this shortgrass steppe was 14 events, with a minimum of 9 events in years of average precipitation. Thus, our experimental treatments pushed this system beyond its recent historic range of variability. Plots receiving fewer, but larger rain events had the highest rates of ANPP ($184 \pm 38 \text{ g m}^{-2}$), compared to plots receiving more frequent rainfall (105

$\pm 24 \text{ g m}^{-2}$). ANPP in all experimental plots was greater than long-term mean ANPP for this system (97 g m^{-2}), which may be explained in part by the more even distribution of applied rain events. Soil moisture data indicated that larger events led to greater soil water content and likely permitted moisture penetration to deeper in the soil profile. These results indicate that semi-arid grasslands are capable of responding immediately and substantially to forecast shifts to more extreme precipitation patterns.

Introduction

Water availability is the primary constraint to plant productivity in many terrestrial biomes (Rosenzweig 1968; Webb et al. 1986; Le Houerou et al. 1988; Churkina and Running 1998), and it is an ecosystem driver that will be strongly affected by ongoing and future climate changes (Houghton et al. 2001). Shifts in precipitation patterns, along with rising surface temperatures (Karl and Trenberth 2003), will have direct effects on the hydrologic cycle and the movement of water through the atmosphere-soil-biosphere continuum (McAuliffe 2003), whereas other global change drivers such as increases in CO_2 and N levels will indirectly influence water demand and use by plants (Mooney et al 1991; Owensby et al. 1996; Shaw et al. 2002). Even if the total precipitation inputs for a given system remain unchanged, predicted changes in the distribution of precipitation events (within or between seasons) will impact the timing and quantity of soil water available for plant uptake and biogeochemical processes (Weltzin et al. 2003).

Historically, precipitation data aggregated at annual or seasonal time scales was considered a suitable proxy for soil moisture and the metric most often used to relate

water availability and aboveground net primary productivity (ANPP). At large spatial and temporal scales, abundant data support the strong predictive relationship between mean annual precipitation (MAP) and ANPP (Rosenzweig 1968; Walter 1971; Sala et al. 1988). At more local scales, however, a considerable amount of variability in ANPP remains unexplained by annual precipitation alone (Lauenroth and Sala 1992; Knapp and Smith 2001), and both experimental and observational research suggest that the within-season distribution of precipitation events has significant effects on plant and soil processes (Novoplansky and Goldberg 2001; Knapp et al. 2002; Fay et al. 2003; Schwinning and Sala 2004; Sher et al. 2004; Harper et al. 2005; Sponseller 2007). The relative partitioning of a rainfall event to runoff, infiltration, and evaporation is complex and a function of soil characteristics and topography as well as antecedent soil water conditions and the magnitude and intensity of the event (Noy-Meir 1973). Ecological processes in arid and semi-arid ecosystems are particularly sensitive to within-season dynamics, due to intense water limitations and event-driven biological response patterns (Schwinning et al. 2004).

In semi-arid grasslands, annual precipitation inputs are greatly exceeded by potential evapotranspiration, creating soil water conditions that are typically dry and only episodically relieved through discrete inputs of rainfall. Thus, chronic water limitation defines this ecosystem (Parton et al. 1981) and strongly influences the physiological characteristics and species composition of the biota (Sala et al. 1992; Chesson et al. 2004). Described originally by Noy-Meir (1973) and recently revisited by Reynolds et al. (2004), the “pulse-reserve” paradigm interprets individual rainfall events as rapidly recharging ecosystem resources, followed by the slow depletion of these resources

through biological and physical processes. This perspective 1) focuses on soil water as it becomes functionally available for plant and microbial processes and 2) emphasizes the important contribution of these moisture pulses to biological activity, which occurs in the wake of rain events of sufficient size. The biological response, both in the long- and short-term, is tightly coupled to the amount, timing, and intensity of a given pulse (Schwinning and Sala 2004) and occurs in the context of the annual precipitation regime.

The highly variable precipitation regimes that characterize semi-arid grasslands (Noy-Meir 1973) are largely composed of precipitation events that are small in size but distributed with relatively short intervals between them. For example, in the shortgrass steppe of northeastern Colorado, 65% of daily precipitation events are < 5mm (Sala and Lauenroth 1982; Sala et al. 1992) with 90% of dry intervals less than 15 days in length (Wythers et al. 1999). This historic precipitation pattern of many frequent small events differs strongly from predicted global climate change scenarios, which emphasize a shift to larger events with longer intervening dry intervals (Groisman et al. 1999; Easterling et al. 2000, IPCC 2007).

While individually small, these events represent a consistent source of water with little interannual variability in their contribution to annual moisture inputs in many semi-arid systems (Sala et al. 1992; Golluscio et al. 1998; Loik et al. 2004). Events as small as 5 mm elicit biological activity and are effective in improving water status and subsequently production processes in *Boutelous gracilis* – the dominant plant and graminoid species in the shortgrass steppe. Considered collectively, small events account for ca. 25% of growing season precipitation and are hypothesized to have a relatively larger impact (activity/mm) on ecosystem dynamics than large events (Sala and

Lauenroth 1982). The rapid physiological response time of *B. gracilis* (< 12 hours; Sala and Lauenroth 1982) to rainfall events characteristic to this growing season rainfall pattern enables this species to maximally utilize small pulses of moisture before they are lost to bare soil evaporation.

Although small events contribute considerably to ecophysiological activity of plants during the growing season, analyses of long-term data for precipitation and ANPP suggest that the single most important explanatory variable for interannual variability in ANPP is the amount of precipitation received in large events (≥ 30 mm, Lauenroth and Sala 1992). Indeed, in semi-arid grasslands, the difference between wet and dry years is related to the presence or absence of large storms, which result in greater growing season and annual moisture inputs (Parton et al. 1981; Sala et al. 1992). Because total precipitation and the number of large events are highly correlated historically, it is difficult to assess the importance of large events (independent of annual precipitation amount) on ecosystem function. Consequently, predicted scenarios that emphasize an increase in large but less frequent events, without any increase in annual precipitation totals, represent conditions that are novel to this ecosystem (Williams et al. 2007). Thus, it is important to understand the impact of this forecast shift in precipitation regime on overall ecosystem function as well as responses of the dominant grass *B. gracilis*, particularly given this species' role in providing the primary economic-based ecosystem service derived from shortgrass steppe – forage production.

To address this knowledge gap, we paired an analysis of growing season precipitation patterns during the past 65 years (1940-2005) with an experimental manipulation of growing season rainfall patterns that contrasted small, frequent events

versus large, infrequent events while maintaining total growing season precipitation amounts as equal. The focus of this experiment was growing seasonal rainfall (May-September) because precipitation inputs during this time account for greater than 70% of annual precipitation totals and large events most frequently occur during this time. Our primary goal was to determine the relative importance of small and large events during the growing season as they contribute to ecosystem function in this semi-arid short-grass steppe ecosystem. Specific research questions included the following: 1) What trends in event size and dry interval length characterize the semi-arid shortgrass steppe in recent history (past 65 years)? 2) How do event size and frequency influence ANPP in a growing season of average precipitation? 3) What is the role of event size and frequency in influencing pulse-related ecophysiological responses of the dominant grass species, *B.gracilis*, to predicted changes in precipitation patterns?

Materials and Methods

Site Description

Research was conducted at the Central Plains Experimental Range (CPER) in northeastern Colorado, USA (40° 49' N 104° 46' W). The CPER is located within the Shortgrass Steppe Long Term Ecological Research (SGS LTER) site, which is a partnership between Colorado State University and the United States Department of Agriculture – Agricultural Research Service and Forest Service. The shortgrass steppe region is a semi-arid grassland and receives an average of 321 mm of precipitation annually (Lauenroth and Sala 1992) 70% of which occurs during the May-September growing season. Mean annual temperature is 8.6°C and ranges from -5°C in January to 22°C in July (Milchunas and Lauenroth 1995). The plant community is dominated by the

C₄ grass *Bouteloua gracilis* (blue grama), with other major species including *Bucloe dactyloides* (buffalo grass), *Artemisia frigida* (fringed sagewort), *Sphaeralcea coccinea* (scarlet globemallow) and *Opuntia polykantha* (plains prickly pear). Average aboveground net primary productivity for the site is 97 g m⁻² (Lauenroth and Sala 1992) and *B. gracilis* comprises up to 90% of total aboveground grass biomass (Lauenroth et al. 1978). While site management is focused on the varying intensities of cattle grazing in shortgrass steppe, the study site was located in a large exclosure from which cattle were removed in 1999. The soils of the study site are considered representative of the shortgrass steppe ecosystem and classified as Ustollic Haplargids (Petersen et al. 1993).

Analysis of the historic precipitation record

We obtained daily precipitation data from the Central Plains Experimental Range (CPER) for the time period of 1940-2005 in order to characterize the recent historic precipitation record. Measured daily precipitation that was greater than or equal to 2 mm was considered biologically effective and included in our analyses. To make these data comparable to the period of experimental manipulation, we classified precipitation from May 26 – September 11 of each year into rain events. In many cases, an individual day of recorded precipitation constituted a rain event; however, where consecutive days of measured precipitation were identified, these were collectively considered as one rain event. In order to avoid overestimating event size or underestimating the number of rain events in a given year, in cases where > 3 consecutive days of measured precipitation occurred, these were divided into 2 events and assigned an event date according to the day in which the greatest quantity of precipitation was received.

We characterized the growing season of each year (1940-2005) according to cumulative precipitation, number of events, mean event size, mean dry interval length, and maximum event size. In addition, we analyzed separately only those years in which growing season precipitation was $\pm 15\%$ of the long-term mean (190 mm, or 161 – 218 mm). This allowed us to characterize the precipitation regime of these years for specific comparison with our experimental manipulation, which was based on average growing season rainfall amounts. To provide important context for the year in which this experiment occurred, we also calculated winter/early spring (January – April) precipitation for 2005 as well as long-term mean, maximum and minimum values.

Rainout shelter design and construction

We erected 15 5.1 m² rainout shelters, which were designed to exclude ambient rainfall in experimental plots and were located in a relatively flat grassland site with spatially homogeneous cover and no obvious signs of past disturbance. Shelter construction began with trenching the perimeter of all plots to > 1 m below ground surface and lining the trench with 6 mil plastic to minimize sub-surface water flow and prevent root and rhizome penetration into or out of the plot. The barrier enclosed a 2.25 x 2.25 m area to a depth of 1 m, which we refer to as the “sheltered area.” To eliminate surface water flow into plots, metal flashing was also installed on three sides, extending ca. 0.3 m below ground surface and ca. 0.1 m above ground surface. Metal flashing was not installed on the remaining downhill side to allow for surface runoff to occur during the application of precipitation events. Dimensions for the sheltered area were selected so that natural rainfall would be excluded from a central 1.25 x 1.25 m core plot designated for plant and soil sampling. The core plot was surrounded by a 0.5 m buffer. For rainout

shelters of comparable size, Yahdjian and Sala (2002) estimated a 0.20 m edge effect associated with ambient rainfall, and our 0.50 m buffer effectively isolated core plots from nearly all ambient precipitation (J. Heisler-White, *personal observation*).

Shelter roofs were installed on May 26, 2005 and covered the plots for the duration of the growing season. The aboveground structure consisted of 4 wooden corner posts anchored in the soil to a depth of 1 m. Each roof was detachable and consisted of a wooden frame covered in clear corrugated polycarbonate sheeting (Green-Lite). Roofs were elevated ca. 1.1 m above the ground surface and sloped slightly towards subtle topographic gradients to allow for quick drainage of ambient rainfall. Shelter sides and ends remained open in order to maximize air movement and minimize temperature and humidity effects. While this design was chosen to minimize chronic microclimatic effects, such effects are unavoidable and so we report effects on both photon flux density (PPFD) and soil temperature. This experiment was not directly tied to ambient rainfall conditions for the 2005 growing season; therefore, no unsheltered control plots (no shelter but similar rainfall patterns) were possible. We established additional plots and collected similar measurements in adjacent “nonsheltered areas.” These plots were equivalent in size to the sheltered areas and contained core plots for sampling. All senesced plant material from previous years was removed (clipped) from sheltered areas in early May to ensure that all aboveground growth was produced during the 2005 growing season.

Experimental Treatments and Protocol

The experimental period consisted of 120 days (May 26 – September 11, 2005). Because the experimental objective was solely to alter the frequency of events and the

dry interval duration, all sheltered plots received 190 mm of precipitation – the 30-year mean for the experimental period. The shelters were randomly assigned to one of the following treatments with 5 replicates each: 1) 12 events, 2) 6 events, or 3) 4 events. Rain events were spaced at 10-, 20-, or 30-days intervals, respectively, but event sizes were not constant throughout the growing season. Instead, the quantity for a given rainfall event was based on the 30-year mean for the time period preceding it in order to follow seasonal distribution patterns. For example, a rainfall event on the 14th of June for a sheltered plot with a 20-day dry interval length would be based on the 30-year mean for the period of May 26th through June 14th and this event size would be larger than one in July, a month with much less rainfall historically. Water was applied from a tank stored onsite, which was stocked from a nearby groundwater well. Chemical analysis of the groundwater revealed that key plant nutrients (N, P, K) were below detectable levels. Rain events were applied manually through the use of 8-liter watering cans at a rate of < 25 mm/hr to simulate fast-moving storm systems that characterize this region during summer months. Large events were applied over 2-3 day intervals to ensure that plots never received greater than ca. 25 mm in a single day, which also minimized run off. We chose 25 mm as the maximum daily rain event size based on a long-term data analysis by Lauenroth and Sala (1992) that identifies events > 25 mm as relatively infrequent in occurrence.

Shelter effects on microclimate

We examined shelter effects on microclimate through a series of paired measurements inside and outside the plots. Using a 1-m linear quantum light sensor (Decagon, Pullman, WA), photosynthetically active radiation (PAR) was measured both

above and below all shelter roofs (n=15) at 900, 1200, and 1400 hours MST on July 21, 2006 under full sun conditions. Four paired measurements were taken per shelter, and percent transmittance was calculated as a fraction of below roof PAR compared to the immediately above roof value. Percent transmittance was not significantly different at any of the time intervals and averaged $87 \pm 3\%$, which is similar to values observed in other permanent structures used to deflect ambient rainfall (Fay et al. 2000; Yahdjian and Sala 2002). Soil temperature was measured at 15-minute intervals during July – August 2006 using soil temperature probes attached to multi-channel Hobo dataloggers (Onset Computer Corporation, Bourne, MA, USA). Measurements were taken at 5 cm depth both inside and outside the shelters (n=2 temperature sensors per location) to allow for temperature to be directly analyzed in a pair-wise manner. This configuration was established in 3 shelters and included one shelter per treatment type. We detected a significant difference ($P < 0.01$) in daily mean, maximum, and minimum soil temperatures underneath the shelters as compared to the adjacent environment. Mean daily temperature was reduced by 1.8°C inside the shelters; however, this was likely due to shading effects of increased plant production inside the shelters rather than due to the shelters themselves. Maximum daily temperatures were also reduced inside the shelters (ca. 3.4°C), but daily minimum temperatures were only affected slightly (ca. 0.8°C). These values are similar to those reported in other rainout shelters located in arid and semi-arid environments (Yahdjian and Sala 2002).

Soil moisture measurements

Soil moisture was measured ca. every 8 days from June-September. Volumetric water content was estimated via sensors that measured dielectric permittivity of the soil

(ECH₂O soil moisture sensors, Decagon). Each sensor integrated soil moisture over the top 20 cm of soil and was placed within the core plot (ca. 0.75 m from the sheltered edge) of 4 shelters per treatment type and in all of the ambient plots. Sensor accuracy is estimated at $\pm 4\%$. Measurement dates were selected to track soil moisture dynamics in response to the most frequent experimental precipitation regime (12-events). We measured soil water content just prior to a rain event and within 2-3 days post-rain event.

Field measurements of carbon and water relations in the dominant grass B. gracilis

In order to minimize investigator impacts in the plots, we limited our measurements of plant carbon and water relations to a mid-season water addition that occurred on July 25-26, 2005. This water addition occurred on days 60-61 of the experiment and all plots received a water addition at this time. Gas exchange (net photosynthesis) of *Bouteloua gracilis* was measured post-event on July 27, 2005 at 1100-1300 hours MST under high light conditions (fixed at $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$) using an LI-6400 portable photosynthesis system (Li-Cor, Lincoln, NE, USA). In each of the 15 shelters, two measurements were taken on leaves of *B. gracilis*. Water relations of *B. gracilis* were estimated via mid-day xylem pressure potentials (XPP) using a Scholander-type pressure chamber (PMS instruments, Corvallis, OR, USA). Leaves ($n = 3$ per shelter) were collected between 1100 and 1300 hours MST on July 24, 2005 (pre-event) and July 27, 2005 (post-event).

Aboveground net primary productivity

We estimated aboveground net primary productivity at the conclusion of the experiment by clipping all plant material in two 0.25 m^2 quadrats from within the core plot of each sheltered area. Harvested plant material was oven dried at 60°C for 72

hours, sorted, and weighed to the nearest 0.01 grams. Sorted classes included *B. gracilis*, other grasses, and forbs (including sub-shrubs). Cacti were not harvested and were estimated to cover no more than 5% of the sampling area.

Statistical methods

All analyses of historic and experimental data were conducted in SAS version 9.1, with the level of significance for all statistical tests set at $P \leq 0.05$. Pearson product-moment correlations were used to test for a significant relationship between growing season mean event size, maximum event size, and mean dry interval length and ANPP. We used a single-factor generalized linear model (PROC GLM) with precipitation event number as the main effect to test for significant differences in ANPP. Because of the difference in sample size between ambient plots and experimental plots (N=3 versus N=5), the LSMEANS procedure was used to contrast group means after significant ANOVA results.

For mid-day water potentials, a two-factor generalized linear model (PROC GLM) was used to evaluate the effect of time and treatment as well as their interaction. Factor levels for time were “pre-event” and “post-event” XPP. A single factor ANOVA was used to compare leaf-level gas exchange measurements. For all statistical analyses, each shelter was considered an individual experimental unit (N=5 per treatment).

To assess minor microclimatic effects associated with the shelters, we compared PAR levels and soil temperature based on paired measurements taken inside and outside the shelters. For the light environment, we used a single factor ANOVA to compare PAR above and below all shelter roofs (n=15). Soil temperature data were characterized based on the daily mean, maximum, and minimum value measured for each of 3 shelters.

Temperature data were analyzed using an ANOVA that compared values inside and outside of the shelters across the growing season.

Results

Summary of historic precipitation trends

For the 65 year period (1940-2005), the mean rain event size during the growing season was 12.9 ± 0.4 mm, while the mean dry interval length was 8.4 ± 0.3 days. During this period, an average of 14 rain events occurred annually and the mean maximum rain event for a given year was 18.2 mm.

The number of growing season rainfall events varied from a low of 7 events (1959-1960) to a high of 23 events (1996) while total seasonal rainfall ranged from a low of 53.8 mm (1964) to 370.6 mm (1997). The most common frequency of events was 16, which occurred in 10 years of the 65-year period (Fig.1). There were no years in which 6- or 4- events occurred, but 12-events occurred in 4 years (Fig.1). The 2005 growing season was comprised of 9 rain events. It is important to note that less than 1/3 of the years in the most recent past (1940-2005) were characterized by 12 or fewer events (the focus of this experimental manipulation) and greater than 50% of the years experienced 14-18 rainfall events (Fig.1).

All years (1940-2005) of this analysis were characterized by at least one event that was ≥ 15.8 mm – the mean event size for the 12-event precipitation treatment. In 45/65 years (70%), a rain event occurred that was ≥ 31.7 mm (the average event size for the 6-event precipitation regime) whereas in 20/65 years (31%), at least one rain event in a given year exceeded 47.5 mm (the average event size for the 4-event precipitation regime).

Winter/early (January-April) spring precipitation averaged 56 ± 3.6 mm in the semi-arid steppe during the past 65 years but was highly variable ($CV = 52.5\%$). The maximum and minimum winter/early spring precipitation amounts for 1940-2005 were 154.9 mm and 16.8 mm, respectively, with ca. 70% of years falling within $\pm 50\%$ of the long-term mean (28-84 mm). In 2005, 78 mm of precipitation was received in winter/early spring.

ANPP trends during years of average rainfall

In only 15 years within the 65-year record was growing season precipitation within $\pm 15\%$ of average (Fig.1) and years in which 14-16 events occurred accounted for 8 of these years. We were able to identify only a single year in the 1940-2005 time period in which growing season precipitation was ca. average and 12 events occurred (Fig.1, Table 1). This occurred during the 1975 growing season in which 12 events occurred and 177.5 mm of rainfall were recorded. ANPP in 1975 was estimated to be 94 g m^{-2} , which was similar to ANPP in the 12-event plots of the experimental manipulation (see below). In years of average precipitation and comparable event frequency to the 12-event plots in our experimental manipulation, ANPP varied from a low of 63 g m^{-2} to a high of 118 g m^{-2} (Table 1). Neither mean event size nor mean dry interval length was significantly correlated with ANPP in the historical climate record.

Precipitation for the 2005 growing season (ambient and experimental)

Precipitation for the 2005 growing season was 189.7 mm, which was distributed in 9 rain events (Fig. 2). The total amount received was nearly identical to the 30-year mean (189.9 mm) and the amount that was applied to all sheltered plots. While completely fortuitous, this allowed us to make direct comparisons between sheltered and

unsheltered plots with regard to precipitation amount. However, the distribution of precipitation events across the 2005 growing season was quite uneven, with 103.89 mm falling in the first 10 days of the experiment (Fig. 2A). Thus, the coefficient of variation for dry interval length was highest in ambient plots (114.50%) as compared to sheltered plots, where a CV of 45.9%, 37.7%, and 4.9% was calculated for the 12-, 6-, and 4-event treatments, respectively (Fig. 2A). Two extended dry intervals occurred during the 2005 growing season, the first of which was 40 days in length and occurred from mid-June through late July. The second dry interval occurred during the final 30 days of the experiment (August-September). The majority of precipitation during the 2005 growing season fell in 3 large events, which were 49.28 mm, 40.39 mm, and 41.4 mm, respectively.

For the experimental plots, mean event size increased from 15.8 mm (12-events, range of 6.7 to 27.7 mm) to 31.7 mm (6-events, range of 14.2 to 49.4 mm) to 47.5 mm (4-events, range of 25.4 to 71.8 mm), which resulted in a two-fold difference in mean event size between the 12- and 4-event precipitation regimes (Fig. 2A). It is important to note that the largest event for the 12-event treatment (27.7 mm) was similar in amount to the smallest event in the 4-event treatment (25.4 mm), and that the largest event for the 4-event treatment (71.78 mm) was exceeded just 5 times in the 65-year period. This large event was applied over a 3 day period in our experimental plots.

Soil moisture dynamics

Mean soil moisture for the 2005 growing season was lowest in the ambient plots (3.7%) and varied between a minimum value of 1.4% and a maximum value of 6.0% (Fig. 2B). In the experimental plots, mean soil moisture was inversely related to the

number of rainfall events, with mean soil moisture values increasing from 5.2% to 7.0% to 11.2% for the 12-, 6-, and 4-event treatments, respectively (Fig. 2B). Soil moisture data for the 2005 growing season begins on day 30 of the experiment and does not capture the soil moisture associated with the large rain events in the ambient plots during the early part of the growing season. Maximum values for soil moisture were observed in the 6- and 4-event plots (18.4% and 20.4%, respectively), which were nearly two-fold higher than in the 12-event plots (11.3%). Variability in soil moisture dynamics peaked in the 6-event plots (CV = 80.0%) and was lowest in the ambient plots (CV = 30.2%).

ANPP

For the 2005 growing season, the number of precipitation events had a significant effect on ANPP. In the 12-event plots, total ANPP was $105.1 \pm 24.1 \text{ g m}^{-2}$ (Fig. 3). This was significantly lower than the 6-event and 4-event plots, where total ANPP was $177.7 \pm 37.7 \text{ g m}^{-2}$ and $183.7 \pm 37.2 \text{ g m}^{-2}$, respectively (Fig. 3). Unsheltered plots exposed to ambient conditions had the lowest total ANPP, which was $67.3 \pm 8.9 \text{ g m}^{-2}$ (Fig. 3).

Forbs comprised 5-10% of the total biomass within all rainfall treatments (both experimental and ambient) and no significant treatment effect could be identified (data not shown). The total ANPP response was driven primarily by *B. gracilis* in all treatments.

Plant carbon-water relations

We focused our measurements of plant carbon-water relations on a precipitation event at the mid-point of the experiment (day 60; July 25, 2005) in which all treatments experienced a water application on the same day and had cumulatively received similar total precipitation inputs for the growing season. The mid-season precipitation event was

applied as 11.22 mm, 30.66 mm, and 40.38 mm for the 12-, 6-, and 4- event plots, respectively. Mid-day water potentials measured pre-event (July 24, 2005) revealed that both the ambient and 12-event plots (-2.7 ± 0.1 MPa and -2.8 ± 0.02 MPa, respectively) were significantly more water-stressed than the 6- and 4-event plots (-2.1 ± 0.09 MPa and -2.0 ± 0.1 MPa, respectively; Fig. 4). Mid-day water potentials were measured again post-event on July 27, 2005 and revealed that the 12-, 6-, and 4-event plots were no longer significantly different. Thus, while there was no significant change in mid-day water potential for the 6- and 4-event plots, water relations in the 12-event plots significantly increased (-2.0 ± 0.03 MPa; Fig. 4). Mid-day water potentials for the ambient plots remained unchanged, as no rainfall occurred during the time period between pre- and post-event measurements.

Post-event measurements of leaf-level gas exchange revealed an inverse relationship between rain event frequency and A_{net} . Sheltered plots that had received the second of 4 events had the highest photosynthetic rates ($31.6 \pm 0.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; Fig.4 inset). In contrast, the 12-event plots (which had just received event 6 of 12) had the lowest photosynthetic rates ($17.78 \pm 0.99 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; Fig.4 inset).

Discussion

In semi-arid grasslands, the temporal distribution of precipitation events strongly regulates periods of biological activity, which integrate across the growing season to determine annual rates of ANPP. While annual and seasonal precipitation patterns are key drivers of ecosystem processes, the timing, extent, and duration of precipitation pulses most directly influence how rainfall is translated into soil water that is available

for plant uptake (Loik et al. 2004). In 2005, we manipulated the number of growing season rainfall events (while holding total precipitation constant) and determined that larger, less frequent rainfall events resulted in greater ANPP and mid-season photosynthetic rates in the dominant grass, *B. gracilis*. Our goal was to expose treatment plots to predicted precipitation regimes that are largely absent from the historic record and our analyses of long-term data confirmed this. In years in which growing season precipitation was considered average, event number varied between 9 and 18, with the 2005 growing season being characterized as having the fewest number of events in the last 65 years. While a growing season precipitation pattern of 12 events (with average growing precipitation) occurred twice during the last 65 years, years with 4 or 6 events did not occur during this time period.

Given the variability that exists in event number and mean event size during growing seasons of average precipitation, it is not surprising that annual precipitation amount accounts for only 39% of the interannual variability in ANPP within this semi-arid grassland (Lauenroth and Sala 1992). In this study, all experimental plots received ca. 190 mm of rainfall, but total ANPP varied by ca. 75% from $105.1 \pm 24.1 \text{ g m}^{-2}$ to $183.7 \pm 37.2 \text{ g m}^{-2}$. Including ambient plots in the analyses further increased variation in ANPP to 173%. These results from ambient plots highlight the importance of the regularity in event distribution, and the dry interval length. Clearly this grassland is quite sensitive to rainfall event timing and amount, and a directional change in precipitation regime to fewer events that are larger in size or alterations in the timing of those events will have immediate and direct consequences on plant carbon and water relations and ecosystem function (Sala and Lauenroth 1982).

Interannual variability in winter/early spring precipitation may interact with growing season rainfall to influence annual ANPP patterns. While a relatively minor (30%) contributor to total annual precipitation, winter/early spring precipitation establishes soil moisture content at the onset of the growing season and frequently represents a peak in annual soil moisture dynamics (Lapitan and Parton 1996). In 2005, winter/early spring precipitation was 78 mm, which was slightly above the long-term mean of 56 ± 3.6 mm. Exceptionally dry or wet winter/early spring conditions, even if followed up by average growing season precipitation inputs, may modify annual rates of ANPP.

Large versus small events – biological effects

The dominant grass species at the short-grass steppe (*B. gracilis*) has been shown to respond rapidly to events as small as 5 mm through improved water relations (Sala and Lauenroth 1982). A similar result was observed in this experiment, where mid-day water potential of *B. gracilis* significantly increased following a mid-season water pulse of 11.2 mm. Our experimental results also revealed the importance of pulse intensity and antecedent conditions as primary drivers of the physiological response of *B. gracilis*. Prior to the mid-season soil moisture pulse that we monitored, XPP of *B. gracilis* in the 12-event plots was significantly lower than in the 6- and 4-event plots, respectively. This was in spite of the fact that the 12-event plots had most recently received precipitation – only 9 days before. After the precipitation event, significant responses in XPP were only observed in the frequent, small pulse event treatments (12-events), where soil moisture was considerably less prior to the pulse. This suggests that water relations of this species are 1) very dynamic in growing seasons that are dominated by small pulses with few or

no large events and 2) that under such conditions, *B. gracillis* episodically alternates between stressed and non-stressed conditions. Post-event measurements of A_{net} revealed somewhat different results, as leaf-level gas exchange remained considerably lower in grasses in the frequent, small event plots as compared to those in the infrequent, large event plots. This mismatch between water status and A_{net} suggests that the more water stressed history of these plots reduced the photosynthetic capacity of *B. gracillis* and its ability to recover when water status improved (Sala et al. 1982). The relative unresponsiveness of the 6- and 4- event plots to the mid-season water event also provides insight. Prior to the event, soil moisture was greatest in the 6 event plots and sufficient to sustain high levels of photosynthetic activity. The overall greater availability of soil moisture that resulted from the previous precipitation events likely maintained higher photosynthetic capacity in these grasses. Unfortunately, we do not have data for A_{net} prior to the pulse, so it we could not determine if *B. gracilis* in any of the plots responded with an increase in leaf-level gas exchange. Nonetheless, the ability of *B. gracilis* to maintain relatively high photosynthetic rates when there was a history of large precipitation events (within the context of average growing season amounts) is a trait consistent with the increase in ANPP in the 6 and 4-event treatments.

Large versus small events--hydrology

Two key characteristics drive the ecohydrology of semiarid grasslands: 1) evaporative demand exceeds precipitation inputs at both short- (i.e. daily) and long-term (i.e. annual) time scales (Noy-Meir 1973; Sala et al. 1992) and 2) plant cover is typically less than 50%, which results in substantial bare soil evaporation (Burke et al. 1998). Consequently, nearly all precipitation inputs during the growing season are returned to

the atmosphere by plant processes (transpiration) and/or purely physical processes (evaporation; Noy-Meir 1973; Sala et al. 1992). For this reason, the spatial and temporal availability of soil moisture for biological processes is directly linked to event size and frequency. The major consequence of a precipitation regime that is dominated by frequent, small events (semi-arid grasslands) is that the water input by individual events remains in the uppermost soil layers, which are most vulnerable to bare soil evaporation (Sala and Lauenroth 1985; Wythers et al. 1999). This results in very dynamic soil moisture patterns (Lauenroth and Bradford 2006). Growing season estimates of evaporation for the shortgrass steppe are 5-8 mm/day following a rain event (Wythers et al. 1999; Lauenroth and Bradford 2006); thus it is reasonable to assume that precipitation applied experimentally at ca. 10 day intervals (the 12-event treatment) was entirely lost to the atmosphere prior to the next event. This is consistent with the pulse-reserve paradigm. In the frequent, but small event plots, mean soil moisture was ca. 5% and never exceeded 11%. In contrast, large precipitation events (applied at 30-day intervals – 6 events) recharged soil moisture to the extent that it rarely dropped below 5%. Certainly, a considerable percentage of the water from large events would also be rapidly lost to the atmosphere via both evaporation and transpiration; however, two conditions result that make these large pulses more biologically effective between precipitation events. First, large events likely led to increased soil moisture at greater depths (not measured in this study, but see Sala et al. 1992; Parton et al. 1981) where the influence of evaporative demand is negligible. Second, large events resulted in a greater number of growing season days in which soil moisture at 0-20 cm was elevated in contrast to the 12-event plots. It is this depth in the soil profile in which ca. 50% of total fine root biomass

is located (Sala et al. 1992), allowing *B. gracilis*, in particular, to utilize both shallow and deeper soil moisture resources. This translates into important immediate effects on plant ecophysiology, which integrate into greater ANPP when considered across the time span of the growing season.

An additional aspect of hydrology not quantified in this experiment is that of hydraulic redistribution, which has been documented for several species in arid and semi-arid ecosystems (Caldwell et al. 1998). Ryel et al. (2003) demonstrated that roots of *Artemisia tridentata* can effectively move water from rainfall events < 8mm to deeper zones in the soil profile and later use this water for transpiration. This mechanism of efficient water use by plants merits further study under conditions of forecast altered rainfall regimes.

Uniform versus stochastic precipitation events

In semi-arid ecosystems, precipitation events are rarely evenly spaced in time (Loik et al. 2004), and it is unlikely that they will be in the future. For this reason, dichotomous questions addressing “frequent, small events versus infrequent, large events” encompass only one key aspect of precipitation variability while ignoring another one – stochasticity. In our analysis of the precipitation record (1940-2005), we identified 9 years in which total precipitation for the growing season was ca. average ($\pm 15\%$ of the long-term mean). While considered “average” at the aggregate temporal scale of the growing season, these 9 years differed considerably in the total number of events, mean event size, maximum event size, and the variability in event distribution. As a result, ANPP varied more than two-fold, from a low of 63 g m^{-2} to a high of 184 g m^{-2} across this range of “average amount” years. Curiously, the year in which ANPP was lowest

had the largest maximum event size (73.7 mm), during which > 40% of the growing season precipitation was received. Additionally, the remaining 90 mm was divided into 9 events with fewer than 10 mm each. In contrast, the year in which ANPP was highest had a maximum event size of 36.6 mm, with the remaining 14 growing season events sharing 180 mm. Similar to analyses in other grasslands, we were not able to identify a significant relationship between mean event size or dry interval length and ANPP (Nippert et al. 2006; Swemmer et al. 2006). Nonetheless, our results suggest that the relative evenness of event size in combination with event number may have important effects on ecosystem function. Future research focusing on these other aspects of precipitation regimes is needed to elucidate the relative importance of event size and distribution in this and other ecosystems.

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Table 1. Years in which growing season precipitation was $\pm 15\%$ of the long-term mean (1940-2005) for the Central Plains Experimental Range. Years are ordered according to increasing number of events. Data for aboveground net primary productivity are from Lauenroth and Sala 1992. In 2005 (*), ANPP was estimated by clipping ambient plots at the end of the growing season. Mean event size includes the standard error for the mean, CV = coefficient of variation calculated for the growing season.

Year	ANPP (g m^{-2})	Precipitation (mm)	Number of events	Mean event size (mm)	Max. event size (mm)	CV for event distribution	CV for event size
2005	105*	189.7	9	21.1 ± 5.8	49.3	114.5	96.5
1974	63	168.1	10	16.8 ± 6.8	73.7	33.3	127.7
1975	94	177.5	12	14.8 ± 3.3	39.9	70.4	69.9
1955	70	167.1	13	12.9 ± 2.9	34.8	250.7	80.6
1946	97	161.3	14	11.5 ± 2.4	34.0	252.3	78.4
1953	102	190.5	14	13.6 ± 3.9	53.8	47.6	105.2
1990	90	172.0	14	12.3 ± 2.4	32.8	109.0	66.5
1952	118	210.6	15	14.0 ± 3.1	36.6	90.3	85.6
1983	115	189.2	15	12.6 ± 1.5	20.3	56.8	49.2

Figure 1. Distribution of rainfall from 1940-2005 ordered according to the total number of growing season rainfall events and the frequency of years in which a given number of events occurred. Dark shaded bars indicate all years from 1940-2005, whereas light shaded bars indicate the number of rain events for only those years in which growing season precipitation was considered average ($190 \text{ mm} \pm 15\%$). For referencing the measured plots to this historical pattern, the number of rainfall events that occurred during the 2005 growing season (ambient) and the experimental treatments (12-, 6-, and 4-events) are indicated.

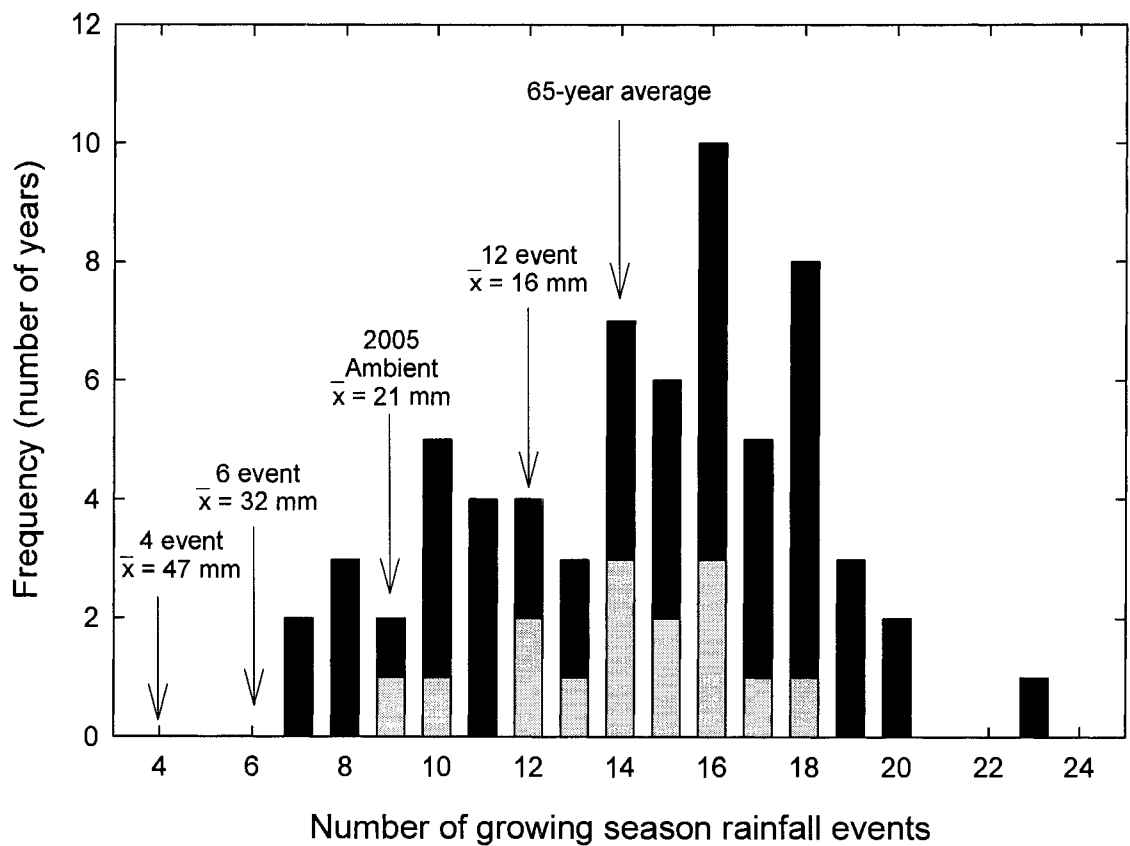


Figure 2. A. Distribution of growing season rainfall events for the ambient (unsheltered) and experimental plots during the 2005 growing season. **B.** Soil moisture dynamics (0-20 cm) for the 2005 growing season. Descriptive statistics in each panel refer to just the time period of the experiment. CV = coefficient of variation.

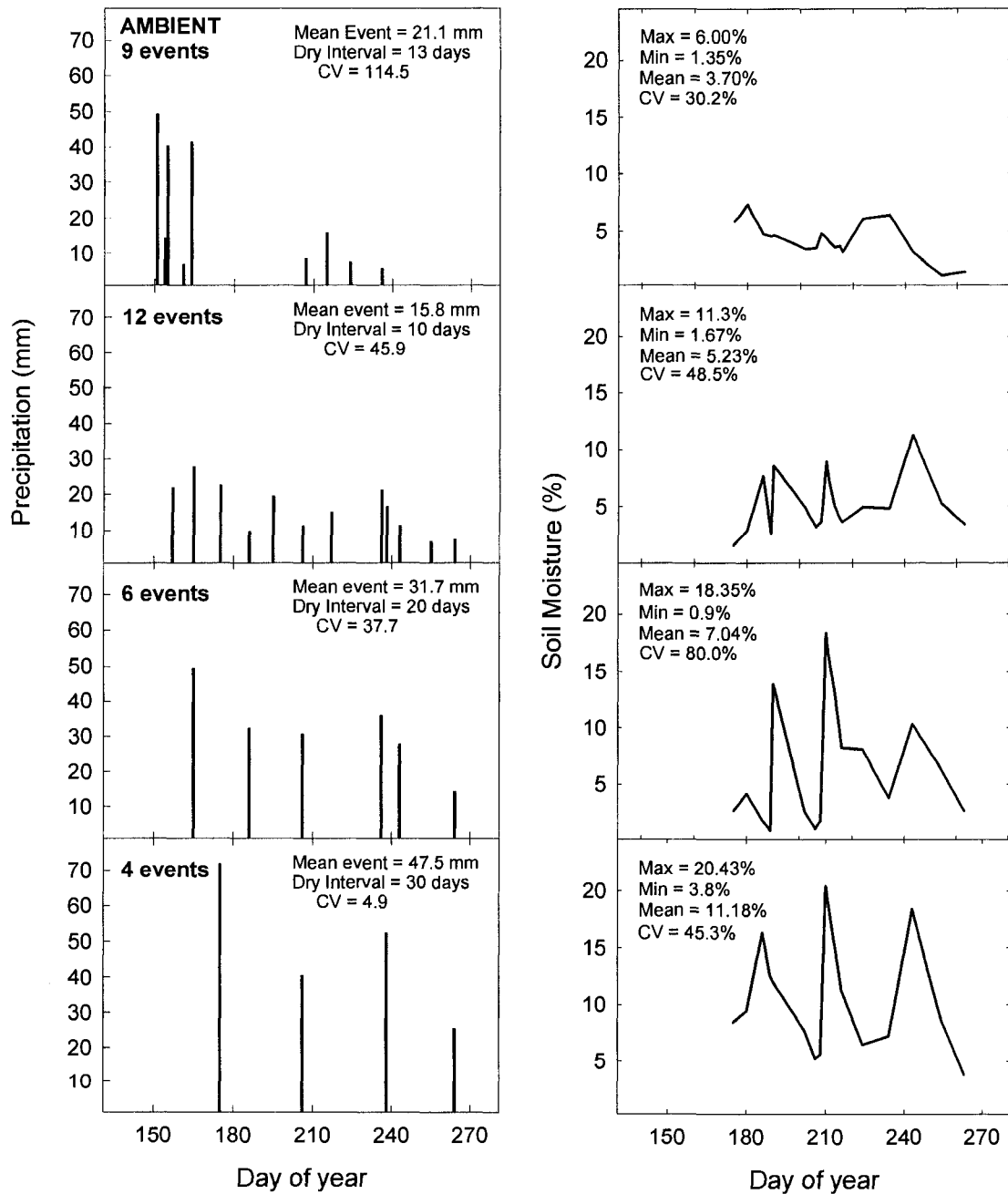


Figure 3. Total aboveground net primary productivity (ANPP; g m^{-2}) for ambient and experimental plots in 2005. Error bars denote one standard error of the mean and different letters indicate significant differences ($p < 0.05$) among treatments. The solid horizontal line indicates the long-term (39 year) mean ANPP for the Central Plains Experimental Range. The dashed horizontal lines indicate the long-term maximum (118 g m^{-2}) and minimum (63 g m^{-2}) values for ANPP in growing seasons characterized by average precipitation.

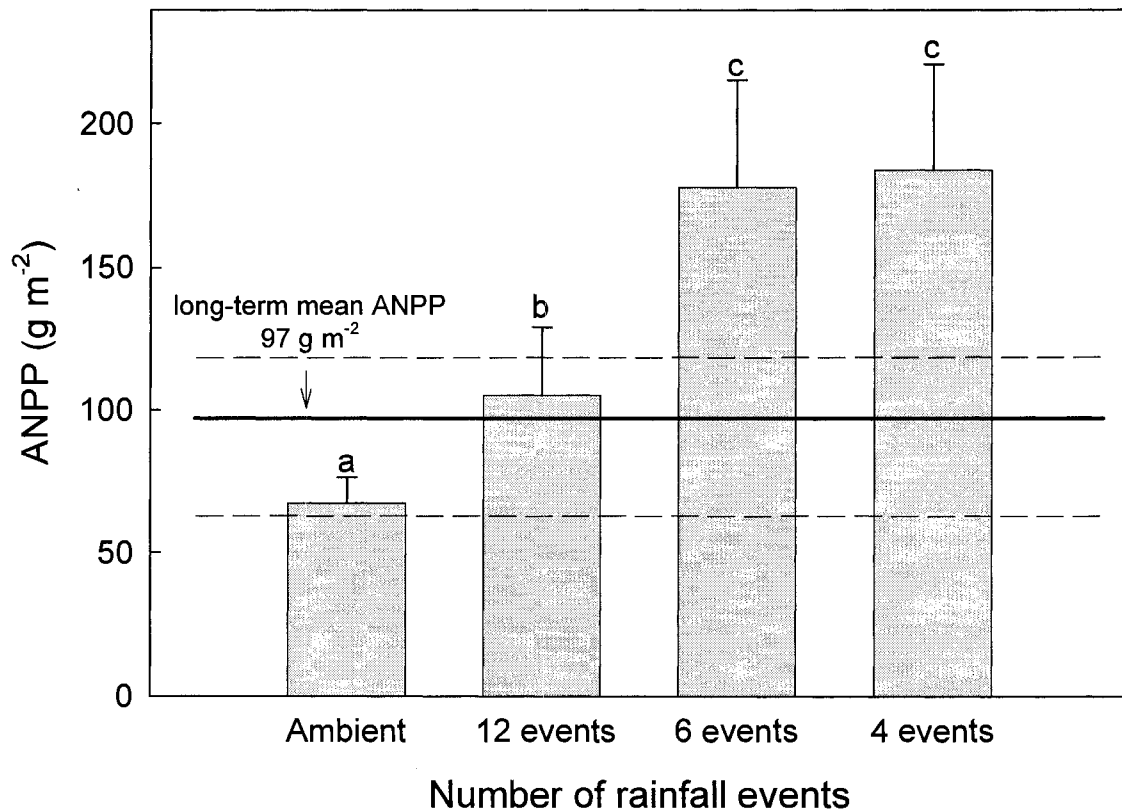
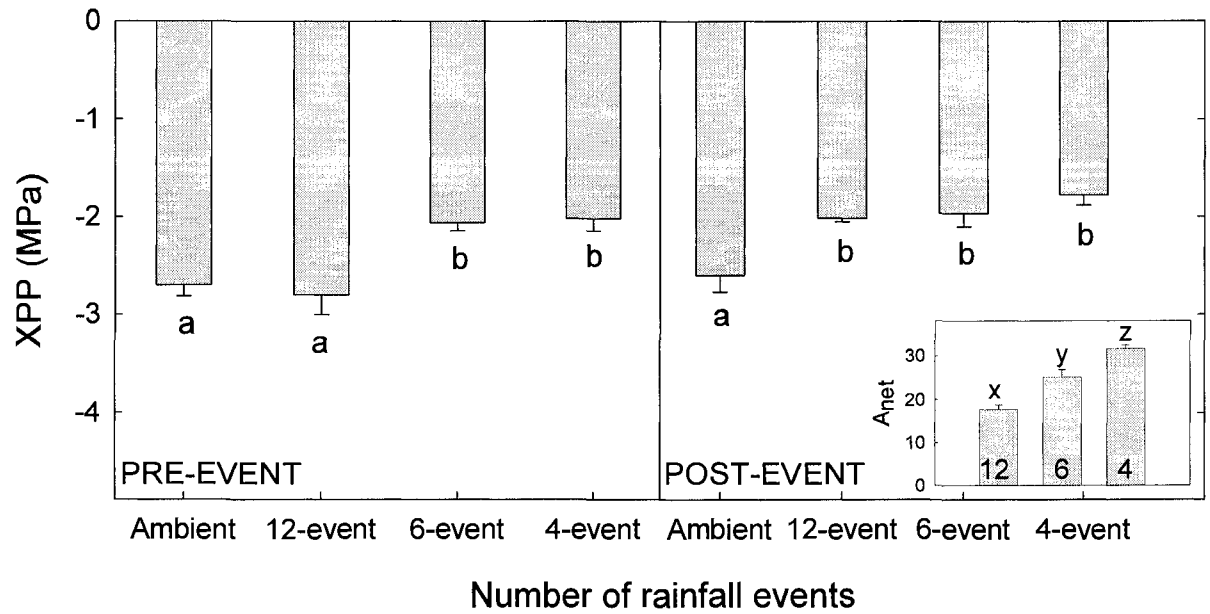


Figure 4. Mid-day leaf water potentials for *B. gracilis* before and after a mid-season precipitation event. *Inset.* Post-event measurements of leaf-level gas exchange in *B. gracilis* in the experimental plots. For each precipitation frequency, presented values are treatment means \pm 1 SE. Significant treatment differences are indicated by different letters. Units for A_{net} are $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.



Chapter 4: Contingent responses of productivity to more extreme rainfall regimes across grasslands

Abstract

Climate model simulations and empirical evidence confirm that increasing atmospheric CO₂ and warmer atmospheric temperatures are leading to more extreme precipitation regimes (Houghton et al. 2001; Karl and Trenberth 2003; Groisman and Knight 2008). These more extreme rainfall patterns are characterized by increased event size and reduced frequency and represent novel climatic conditions (Williams et al. 2007) whose consequences for different ecosystem types are largely unknown (Knapp et al 2008). Here, we present data from experimental precipitation manipulations along a 600 km precipitation-productivity gradient spanning the Central Plains Region of North America (USA) that demonstrate the strong sensitivity of temperate grassland ecosystems to more extreme growing season rainfall regimes. Further, we show that responses of aboveground net primary productivity (ANPP) to more extreme rainfall regimes are contingent on typical soil water levels for a grassland type. At the mesic end of the gradient (tallgrass prairie), longer dry intervals between events led to extended periods of below-average soil water content that increased plant water stress and reduced ANPP by 18%. The opposite response was observed at the dry end (semi-arid steppe), where a shift to fewer, but larger, events increased periods of above-average soil water content, reduced seasonal plant water stress and resulted in a 30% increase in ANPP. Plant

species richness peaked in mixed grass prairie, which was intermediate along the gradient and the most sensitive to more extreme rainfall regimes (+70% increase in ANPP).

These results highlight the difficulties in extending inference from single site experiments to whole ecosystems or biomes and demonstrate the complexity inherent in predicting how terrestrial ecosystems will respond to novel climate conditions. Even within a relatively uniform physiographic region and a single biome type, ANPP responses differed in both magnitude and direction in response to changes in event size/frequency, but no change in annual amount.

Introduction

Enhanced radiative forcing due to dramatic increases in greenhouse gas concentrations is expected to raise the mean global surface temperature 1.1 to 6.4°C by 2100 (IPCC 2007). Climate models predict that this will result in greater inter- and intra-annual variability in precipitation patterns, and evidence is mounting that growing season precipitation regimes have become more extreme globally (Easterling et al. 2000; Karl and Trenberth 2003; Groisman et al. 2005; Groisman and Knight 2008). Such an intensification of hydrologic regimes will have important impacts on ecological processes and ecosystem services, but quantifying these impacts experimentally remains a key challenge for ecologists (Weltzin et al. 2003; Heisler and Weltzin 2006).

Ecosystems differ substantially in their sensitivity to interannual variation in precipitation, largely due to differences in vegetation structure, life history traits of the dominant species, and biogeochemical mechanisms (Paruelo et al. 1999; Knapp and Smith 2001; Veron et al. 2002). These system attributes are directly linked to long-term

climatic averages and variability and effectively determine an ecosystem's potential to respond to ongoing alterations in precipitation. We took advantage of natural variation in grassland ecosystems across the strong precipitation-productivity gradient that spans the Central Plains Region of North America to evaluate the sensitivity of three distinct ecosystem types – semi-arid steppe, mixed grass prairie, and tallgrass prairie – to an increase in extreme rainfall events. This experiment enabled us to directly evaluate the interaction between means and extremes of a key limiting resource (water) that is likely to change in novel ways during the next century (Williams et al. 2007).

Compared to present conditions, a shift to more extreme rainfall regimes may increase the severity of within-season drought, significantly alter evapotranspiration from plant and soil surfaces, and generate greater runoff from saturated soils (Fay et al. 2003; McCracken et al. 2003). How will ecosystems respond to these hydrologic changes? In spite of the increase in experimental studies demonstrating important links between intra-annual precipitation patterns and biological processes in individual ecosystems (Knapp et al. 2002; Loik et al. 2004, Sher et al. 2004; Harper et al. 2005), a mechanistic understanding of the factors determining sensitivity across ecosystems is lacking.

We investigated the impacts of a shift to more extreme rainfall patterns on three distinct C₄-dominated grassland ecosystems that are arrayed across a broad precipitation gradient and characterize the Central Plains Region of North America (USA). Assessing responses across such gradients permits greater inferences regarding the short- and long-term implications of climate change at scales relevant to policymakers (Burke et al. 1991; Weltzin et al. 2003; Emmett et al. 2004). The grassland biome (as a whole) covers 1/3 of the earth's terrestrial surface, encompasses 23% of the conterminous US, and provides

important ecosystem services that include forage land for livestock and carbon sequestration. This biome displays the greatest interannual variability in ANPP under current precipitation patterns (Knapp and Smith 2001) and may be among the most responsive to future climate changes. As documented by the intense droughts of the 1930s and 1950s, this region is both socioeconomically and ecologically vulnerable to extremes in climate variability (Weaver and Albertson 1944).

We defined extreme precipitation regimes (from an intra-annual perspective) as a shift from extant rainfall patterns to regimes characterized by fewer, but larger events with extended intervening dry periods between events. Because we were interested primarily in responses to changes in the distribution of rainfall, we selected experimental treatment scenarios that were in the lower tails of long-term distribution trends (supplementary information). The Central Plains Region is an ideal location to test the generality of ecosystem responses to this predicted shift in extreme rainfall patterns because it is characterized by a strong west-east precipitation gradient that results in three moisture-driven ecosystem types – the semi-arid steppe, the mixed grass prairie, and the mesic tallgrass prairie. While MAP increases nearly three-fold (320 to 830 mm), an average of 16-18 rainfall events occur during the growing season (100-yr mean) for all three ecosystems (supplementary information).

We manipulated the distribution of rainfall during the growing season within 45 rainout shelters (15 per site) that were erected in the semi-arid shortgrass steppe (NE Colorado), mixed grass prairie (central KS), and mesic tallgrass prairie (eastern KS) of the Central Plains Region (Suppl. Fig. 3,4). The 30 yr mean quantity of growing season rainfall appropriate for each site was added to each experimental plot and distributed as

12-, 6-, or 4- events (n=5 per regime) based on normal seasonal trends (suppl. information). Duration of the dry interval between events was 10-, 20-, or 30-days, respectively.

A shift to fewer but larger events significantly altered total ANPP in all three grassland ecosystems (Fig.1). At the most arid end of the moisture gradient (shortgrass steppe; Fig. 1a), a redistribution of rainfall from 12- to 4- events resulted in a 30% increase in ANPP from 97 g m⁻² to 126 g m⁻². The largest increase (70%) in ANPP occurred in mixed grass prairie (intermediately located within the precipitation gradient), where ANPP increased from 113 g m⁻² to 193 g m⁻² in response to the shift from 12- to 4- events (Fig.1b). This positive ANPP response to a more extreme rainfall regime was reversed in the most mesic grassland (tallgrass prairie), where an 18% reduction in ANPP was observed (579 g m⁻² to 488 g m⁻²; Fig.1c). Although this broad-scale study was conducted over only 1-yr, ANPP responses in tallgrass prairie and the increase in semi-arid steppe are consistent with other short- and long-term experimental research in these grasslands (Knapp et al. 2002; Heisler-White et al. 2008).

Soil water content was strongly influenced by altered rainfall patterns (Fig.2). Because of clear inverse responses to extreme rainfall regimes, we focus on soil water content patterns observed in the semi-arid steppe and tallgrass prairie. In the upper 20 cm of the soil profile, mean soil water content in the semi-arid steppe was increased by 19%, as the number of events was decreased from 12 events (8.3%) to 4 events (10.2%). In contrast, mean soil water content was reduced by 20% (17.2% versus 13.5%) with a shift from 12- to 4-events in mesic tallgrass prairie. The most striking difference between the effect of extreme rainfall regimes along this precipitation gradient was the moisture

surpluses observed in semi-arid step versus the moisture deficits observed in tallgrass prairie (Figs.2a,2b). These conditions translated into improved water relations and elevated leaf N for the dominant grasses in semi-arid steppe. Conversely, greater water stress and reduced foliar N concentrations of the dominant species accompanied a shift to more extreme rainfall patterns in tallgrass prairie.

We interpret these inverse responses in soil water content and plant physiology/leaf chemistry as contingent responses of ecosystems to average soil water conditions. Semi-arid steppe is characterized by chronically low levels of soil water availability and extended periods of intense water stress (Parton et al. 1981). Plant traits associated with stress tolerance (i.e. reduced leaf area, high WUE efficiency; Sala et al. 1992) allow the dominant species to persist. While small rain events intermittently alleviate these conditions and improve plant water relations (Sala and Lauenroth 1982), high evaporative demand rapidly returns water from bare soil to the atmosphere (Wythers et al. 1999). This pattern of precipitation input and water availability can be contrasted with a shift to larger, less frequent events (extreme rainfall patterns), where large quantities of water are distributed in relatively short periods of time, thus increasing the amount and duration of water in the soil for plant uptake. Mid-day water potentials of *Bouteloua gracilis* (dominant plant species) indicate significant reductions in plant water stress as a result of greater water availability integrated over the growing season (Fig.2a). The combination of improved plant water relations (during the peak period of photosynthetic activity) and greater foliar N content (Fig.2a) is consistent with greater leaf level carbon fixation and ultimately ANPP across the growing season. In contrast, mesic systems are defined by relatively abundant soil water availability and minimal

water stress for substantial portions of the growing season. Small, frequent events consistently recharge soil water and therefore maintain most ecosystem processes in a relatively unstressed state. A shift to more extreme events creates large periods of evapotranspiration in the absence of any moisture inputs – conditions that deplete soil water to levels below more nominal plant stress thresholds. Tradeoffs for high production potential (rapid growth rates, high leaf area, and low WUE) result in the dominant plant species *Andropogon gerardii* and *Sorghastrum nutans* possessing being highly sensitive to water stress (as evidenced by a reduction in mid-day water potentials and foliar N concentration; Fig.2b).

While we found no evidence to link responses in ANPP to changes in soil N availability with altered rainfall patterns along the precipitation gradient, the increase in N recovered from resin bags is consistent with pulsed releases of mineral N in response to soil wetting and drying (Fierer and Schimel 2002; Miller et al. 2005). N availability over the growing season was greatest in response to extreme rainfall patterns (4 events) in both semi-arid steppe and mesic tallgrass prairie (supplementary figure 2). While the temporal mismatch between limiting resources (N and water) may be an important constraint to ecosystem function over the long-term, it did not appear to influence ANPP or plant uptake in this experiment.

The 70% increase in ANPP in mixed grass prairie is consistent with predictions that suggest interannual variability in ANPP peaks at intermediate levels of precipitation (Paruelo et al. 1999; Knapp and Smith 2001). Such ecosystems are predicted to be most responsive to altered precipitation regimes, largely due to their climatic history and the plant species that inhabit them as a result. Plant species biodiversity peaked in the mixed

grass prairie (Fig. 3), where a greater abundance of both C_4 graminoids and C_3 forb species comprise the plant community. Although ecological theory and empirical evidence from other grasslands suggests that greater diversity should lead to greater temporal stability in ecosystem processes (Tilman and Downing 1994; Naeem et al. 1996; Chapin et al. 1997), this pattern is not evident at this broad geographic scale.

While considerable uncertainty surrounds the predictions of Global Circulation Models, there is abundant evidence supporting the impacts of altered precipitation regimes on terrestrial ecosystems and their plant and animal inhabitants. Our results have several important implications for predicting the magnitude and direction of change in temperate grasslands specifically, and terrestrial biomes in general, under future climates. First, it is clear that responses to extreme rainfall regimes can be rapid and independent of any change in annual precipitation amount. In this experiment, we focused on ANPP because it integrates such processes as plant physiology and microbial activity, which are closely linked to the mean and variability of soil water content. These rapid and short-term responses may ultimately lead to shifts in relative species abundance, as interspecific variability (in plant physiology, in particular) renders species more or less successful in the presence of chronic directional changes. Second, individual ecosystems will differ in their responses to temporal change in rainfall with some ecosystems experiencing greater water limitations while water stress in others will be alleviated. The ANPP responses described in this experiment have important impacts on forage quantity and quality in this region in addition to carbon cycle dynamics.

METHODS

Experimental infrastructure and design. The locations for this experiment were the Konza Prairie Long-Term Ecological Research Site (tallgrass prairie; Manhattan, KS, USA), the Saline Experimental Range (mixed grass prairie; Hays, KS), and the Shortgrass Steppe Long-Term Ecological Research Site (semi-arid steppe; Nunn, CO). Soils at each location were classified and the key physical properties of the soil that regulate water holding capacity (e.g. texture, porosity and mineralogy) as constrained by soil parent materials (residual sedimentary rocks and loess) were similar for all sites (Blecker 2005; Blecker et al. 2006). Rainout shelters (n=15 per grassland type, Suppl. Fig.4) were erected in May-June 2005 and designed to exclude ambient rainfall in 5.1 m² experimental plots. The perimeter (2.25 x 2.25 m) of each shelter was trenched to > 1m below ground surface and lined with 6 mil plastic to minimize sub-surface water flow and prevent root and rhizome penetration into or out of the plot. Dimensions for the sheltered area were selected so that natural rainfall would be excluded from a central 1.25 x 1.25 m core plot designated for plant and soil sampling. The core plot was surrounded by a 0.5 m buffer (schematic included, Suppl. Fig.3). Shelter roofs were installed ca. May 1, 2006 and covered the plots for the duration of the growing season (120 days). The aboveground structure consisted of 4 wooden corner posts anchored in the soil to a depth of 1 m. Inset roofs (clear corrugated polycarbonate sheeting) were elevated ca. 1.1 m above the ground surface and sloped slightly towards subtle topographic gradients to allow for quick drainage of ambient rainfall. Ambient plots were included in the experimental design as a reference, but are not true controls because they received ambient rainfall.

Experimental Rainfall Treatments. The shelters were randomly assigned to one of the following treatments with 5 replicates each: 1) 12 events, 2) 6 events, or 3) 4 events. Rain events were spaced at 10-, 20-, or 30-days intervals, respectively, but event sizes were not constant throughout the growing season. Instead, the quantity for a given rainfall event was based on the 30-year mean for the time period preceding it in order to follow seasonal distribution patterns. Large events were applied over 2-3 day intervals to ensure that plots never received greater than ca. 25 mm in a single day in semi-arid steppe, 38 mm in mixed grass prairie, or 50 mm in tallgrass prairie.

Data collection and analyses

Aboveground net primary productivity (ANPP). ANPP was estimated by harvesting all plant material in two 0.25 m² quadrats from within the core plot of each sheltered area. Harvested plant material was oven dried at 60°C for 72 hours, sorted, and weighed to the nearest 0.1 grams.

Plant water relations. Water relations of the dominant species in each ecosystem type were estimated via mid-day xylem pressure potentials using a Scholander-type pressure chamber (PMS Instruments, Corvallis, OR, USA). Leaves (n = 3 per shelter) were collected between 1100 and 1300 hours MST. In the semi-arid steppe, *B. gracilis* was sampled and in the tallgrass prairie, both *A. gerardii* and *S. nutans* were sampled. Mean values for XPP are based on 4 sampling dates in semi-arid steppe and 5 sampling dates in tallgrass prairie, which occurred between days 55 and 90 of the 120 experiment.

Leaf tissue N. Live foliar samples of the dominant grass species in each ecosystem were taken at the mid-point of the growing season (ca. July 5; experimental day 165) from both

sheltered and ambient plots. A composite sample of leaf tissue from 5 tillers of a given species was taken within each core plot. For the tallgrass prairie, the two dominant species *A. gerardii* and *S. nutans* were sampled. All samples were dried at 60°C for 3 days, ground on a Wiley Mill, and passed through a 2mm sieve. All samples were analyzed for total percentage C and N on a Leco elemental CHN analyzer.

Soil N availability. Available N in soils was measured May-August using mixed cation-anion resin bags. Resin bags were made from sheer nylon stockings filled with equal mixtures (10 g each) of strong anion and cation exchangers. Intact bags were soaked in 0.6 N HCl to clean them and preload the resins with H^+ and Cl^- ions. Three resins bags were placed 5 cm deep in both treatment and ambient plots at all sites. In the lab, resin bags were rinsed with deionized water and extracted with 2 mol/L KCl solution.

Available N concentrations were determined on an Alpkem Autoanalyzer (OI Corporation, College Station, TX).

Soil water content. Soil moisture was measured ca. every 5 days from May-September. Volumetric water content was estimated via sensors that measured dielectric permittivity of the soil (ECH₂O soil moisture sensors, Decagon, Pullman, WA). Each sensor integrated soil moisture over the top 20 cm of soil and was placed within the core plot of both sheltered and ambient plots at all sites.

Statistical Analyses

Statistical analysis of ANPP, water relations, leaf tissue N, and soil N availability were conducted using a mixed-effects model in Proc Mixed (SAS 9.1.3, NC, USA). The experiment was a completely randomized design, where treatment was considered a fixed

effect and shelter was considered a random effect. For several response variables, shelters were subsampled to more accurately capture shelter-level trends. Subsamples were averaged prior to any statistical analyses so that the experimental unit for all statistical analyses was “shelter” for a sample size of $n = 5$ per treatment. Because ecosystem type was also considered a fixed effect, each site was analyzed individually to determine statistically significant results among treatments. The LSMEANS procedure was used to test for significant differences among means and the Kenwood-Rogers approximation was used to calculate the denominator degrees of freedom. To calculate seasonal means for measurements of plant water relations, measurements of XPP were analyzed collectively from all days within the growing season.

Species richness was compared across sites using a mixed-effects model. Fixed effects included site and treatment, whereas shelter was included as a random effect. The LSMEANS procedure was used to test for significant differences among means. Analyses were conducted on total species richness in addition to grass and forb richness.

Values presented are means \pm 1 SE and the level of significance for all statistical tests was $P \leq 0.05$. For both foliar N and XPP, there was no significant effect of species, and we combined these data according to the main effect of treatment and report mean responses in the text and figures.

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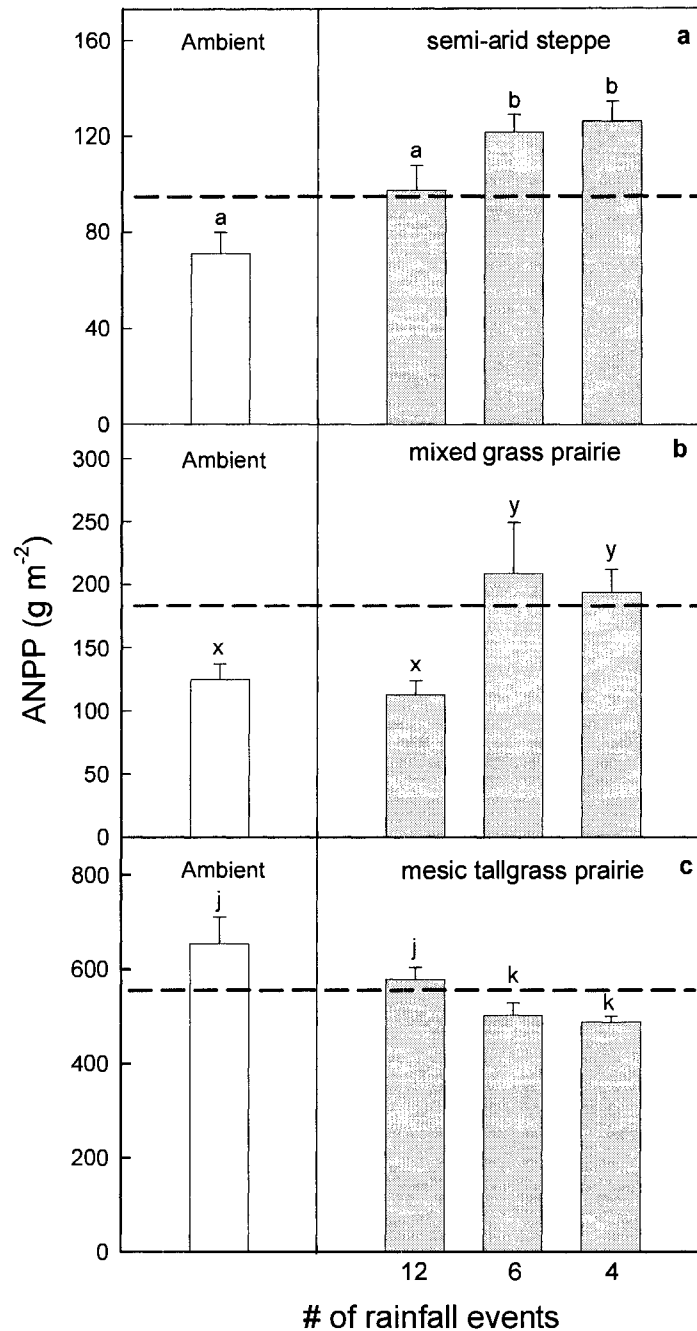


Figure 1 NPP response to extreme events across a precipitation gradient. Panels for each grassland ecosystem include ambient ANPP (white bar) in addition to the three experimental rain event regimes (grey bars). For reference, the long-term mean (Lauenroth and Sala 1992; Paruelo et al. 1999; Heisler and Knapp 2008) for each ecosystem is depicted by a horizontal dashed line. Significant differences between ANPP for a given grassland ecosystem are indicated by different letters. Mean values \pm 1 SE are included and different letters indicate statistically significant effects

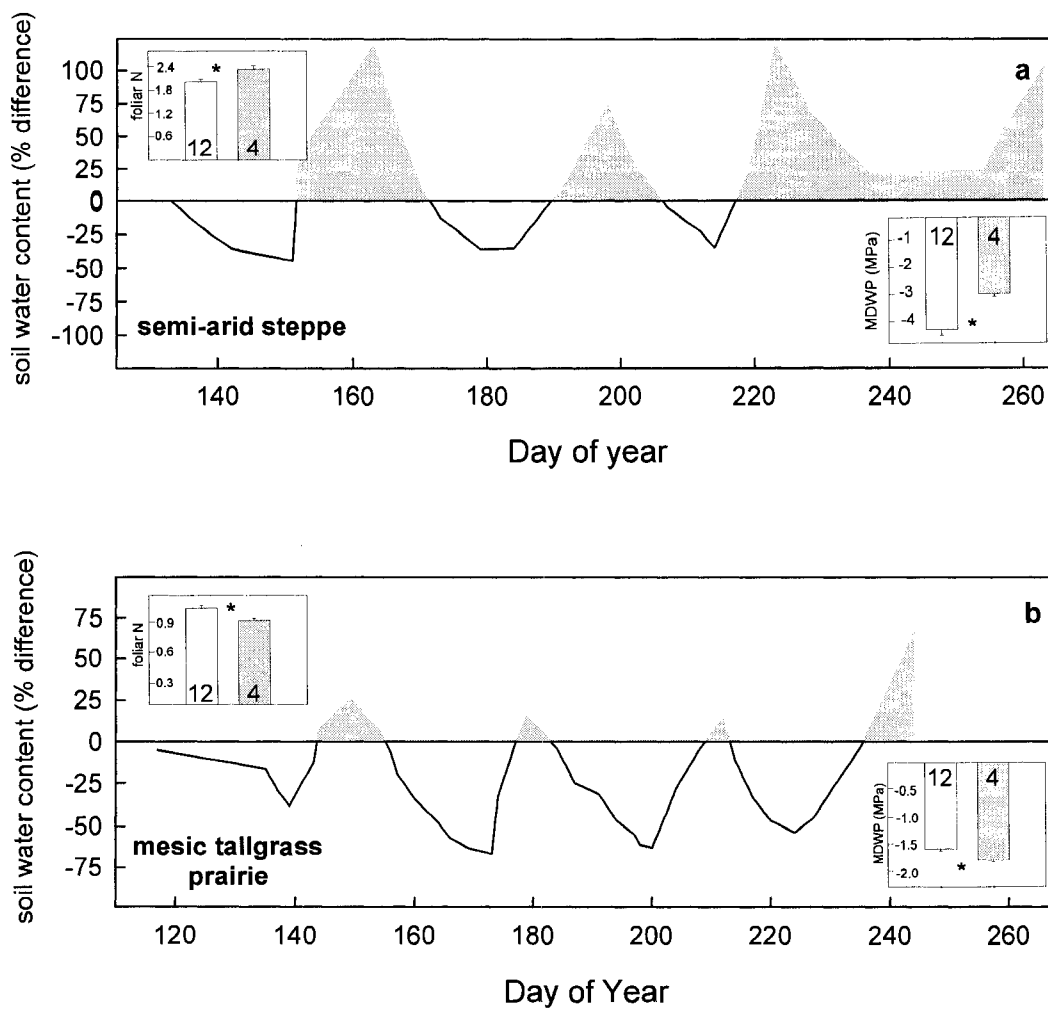


Figure 2 Temporal dynamics of soil water content under extreme rainfall patterns in semi-arid steppe (a) and mesic tallgrass prairie (b). Data for soil water content (%) are for the 4-event scenario and expressed as the percent difference from seasonal average soil moisture for the 12-event scenario. Time intervals in which soil water is above this seasonal average (moisture surpluses) are indicated by grey areas, whereas time intervals below the seasonal average (moisture deficits) are indicated by white areas. *Right Insets.* Average mid-day water potential (MDWP; MPa) for the dominant grass species in the 12- and 4-event scenarios. *Left Insets.* Mid-season foliar N levels for the dominant grass species in the 12- and 4-event scenarios. Statistically significant results are indicated by an asterisk (*). The dominant species in semi-arid steppe is *Bouteloua gracilis* while mesic tallgrass prairie is co-dominated by *Andropogon gerardii* and *Sorghastrum nutans*.

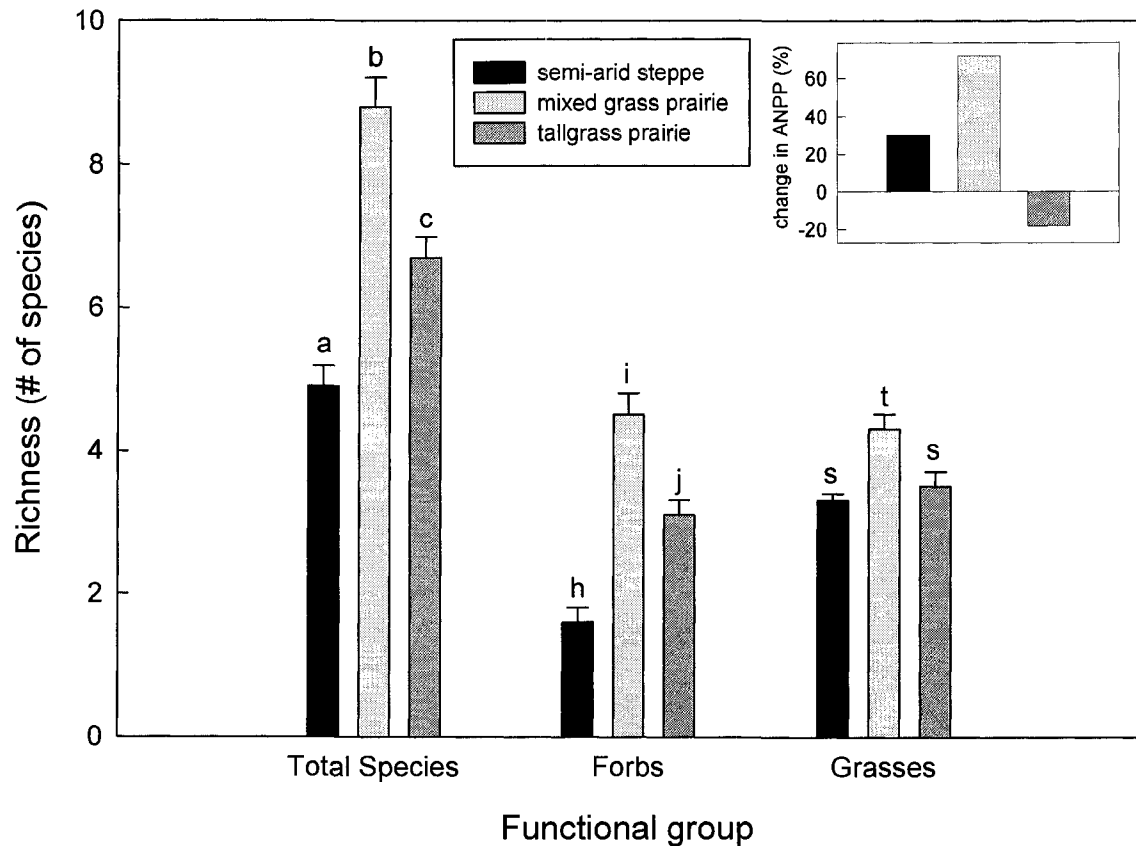
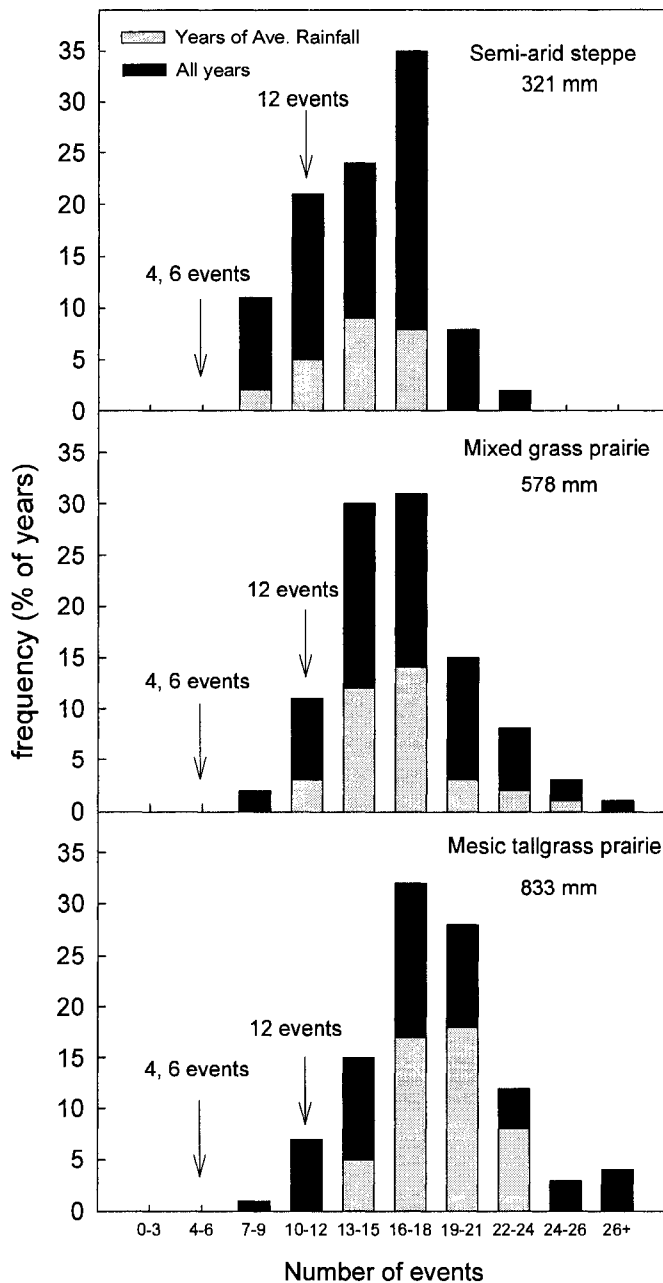


Figure 3 Plant species richness in temperate grassland ecosystems. Plant species richness in semi-arid steppe, mixed grass prairie, and tallgrass prairie ecosystems within the central Plains Region of the US. For each ecosystem type, total plant species richness was estimated in 0.25 m² quadrats that were established in all treatment plots (n=2 quadrats per plot). Data for both grass and forb functional types are also included. Significant differences are indicated by different letters. *Inset.* Change in total ANPP (%) with a shift to more extreme rainfall patterns. The greatest change in NPP (+70%) occurs in mixed grass prairie, which is characterized by greatest total plant species and functional group diversity. Mean values ± 1 SE are included and different letters indicate statistically significant effects.

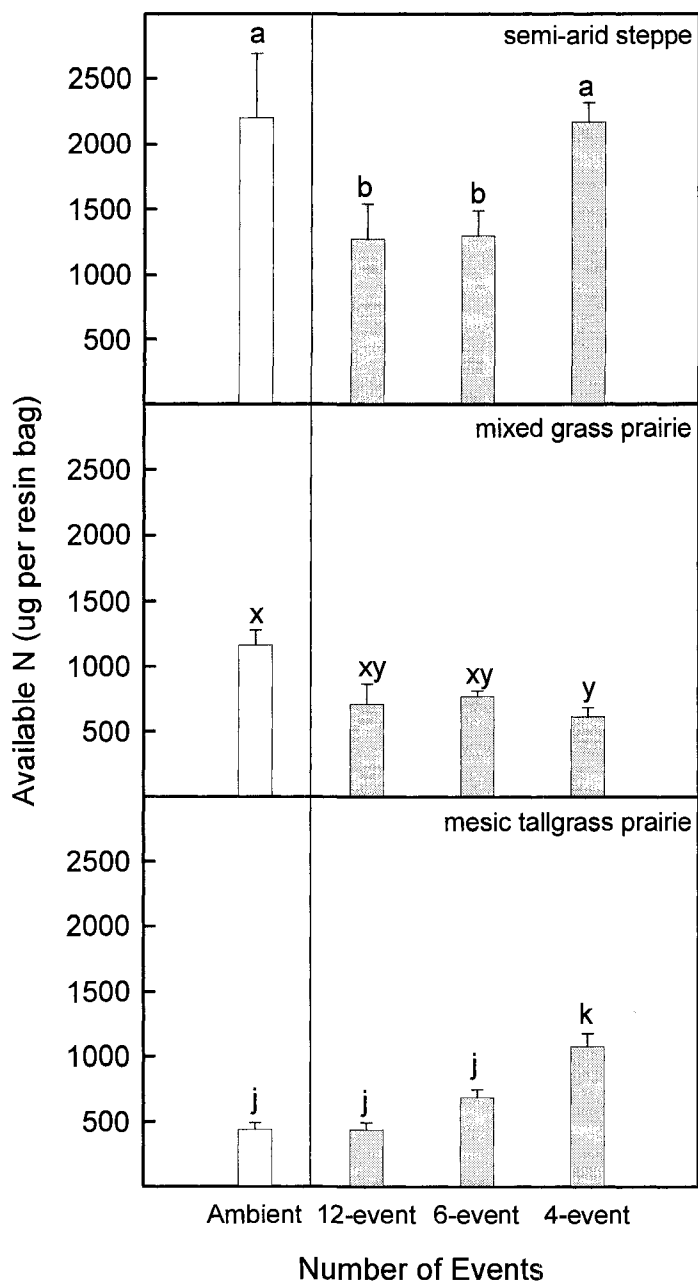
Supplementary Table 1 Key soil characteristics for grassland study sites. Data are adapted from Blecker 2005 and Blecker et al. 2006. The semi-arid steppe site is located at the Shortgrass Steppe Long-Term Ecological Research site (Central Plains Experimental Range), Nunn, CO. The mixed grass prairie site is located at the Saline Experimental Range, Hays, KS. The mesic tallgrass prairie site is located at the Konza Prairie Long-Term Ecological Research site, Manhattan, KS.

Soil Physical and Mineralogical Properties	Semi-arid Steppe, Nunn, CO	Mixed grass prairie Hays, KS	Tallgrass prairie, Manhattan, KS
A horizon Texture (% sand-silt -clay)	14-58-28	6-69-25	8-60-32
Bulk Density (g cm ⁻³)	1.2	1.2	1.4
pore space (%)	50-55	50-55	47-53
clay minerology	Mica & Smectite	Mica & Smectite	Kaolinite & Smectite
B horizon Texture (% sand-silt -clay)	12-54-34	7-50-43	4-46-50
Bulk Density (g/cm ³)	1.4	1.5	1.5
pore space (%)	47-53	44-49	44-49
clay minerology	smectite	smectite	smectite
Pedon Classification ¹	Aridic Argiustoll	Typic Argiustoll	Udic Argiustoll

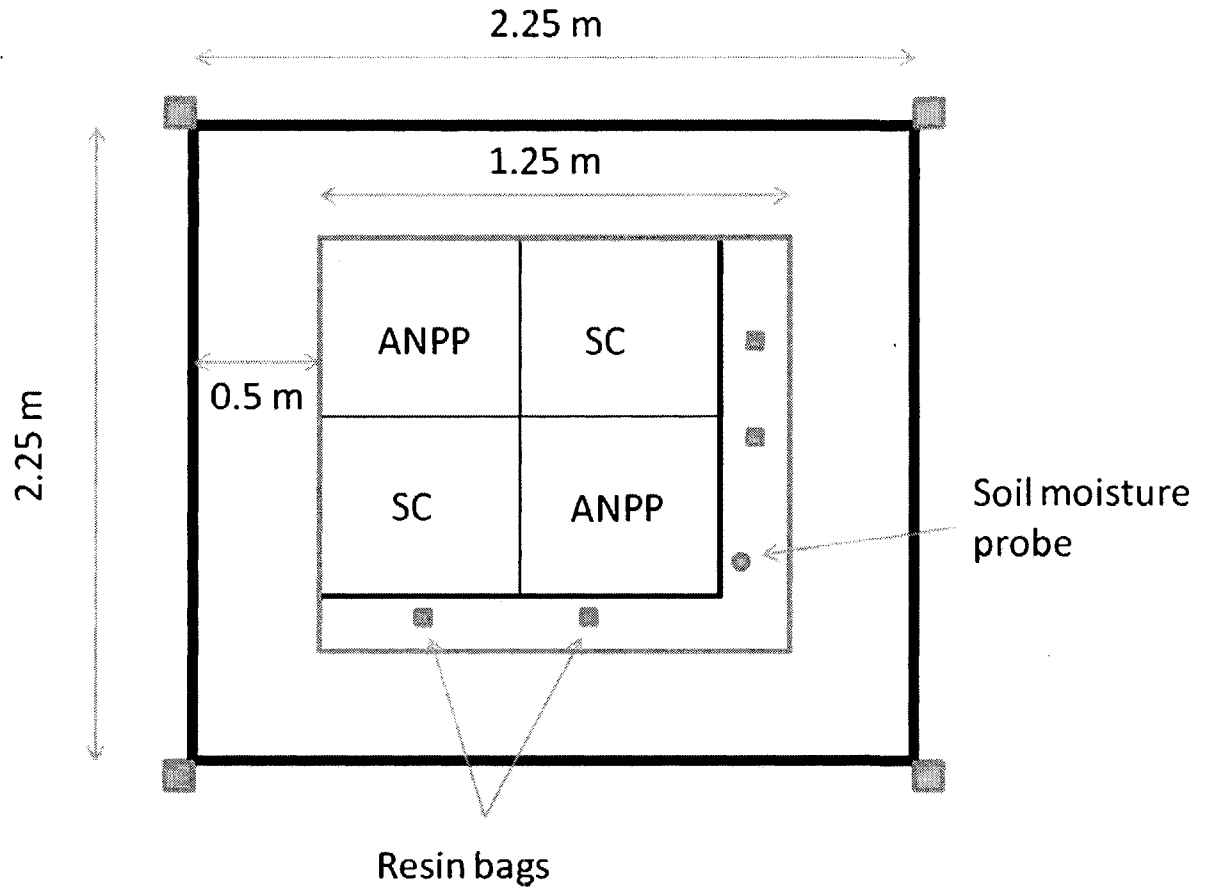
¹ *Soil Taxonomy – USDA, 200X*



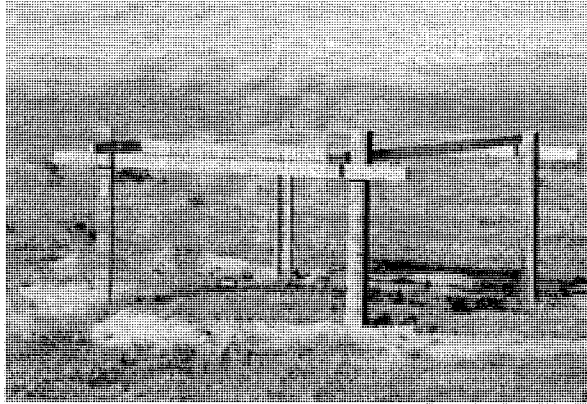
Supplementary Figure 1 Distribution patterns for growing season rainfall events across the Central Plains region. Data is from the National Climate Data Center and covers the 1896-2006 time period for Hays, KS (mixed grass prairie) and Manhattan, KS (tallgrass prairie). For the semi-arid steppe, consistent/reliable data was only available for 1948-2006 and was for Nunn, CO. The dark bars include all growing seasons, regardless of the total seasonal amount. Light colored bars only include growing seasons in which total seasonal precipitation was $\pm 15\%$ of the long-term mean.



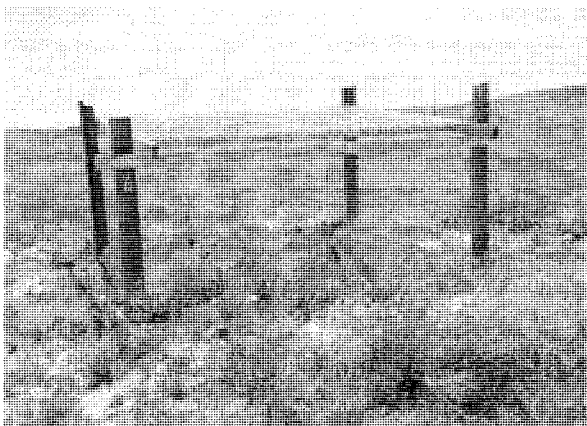
Supplementary Figure 2 Available soil N in the grassland ecosystems of the Central Plains. For each grassland, each treatment scenario (grey bars) and ambient conditions (white bars) are included. Available N in soils was measured May-August using mixed cation-anion resin bags. Mean values \pm 1 SE are included and different letters indicate statistically significant effects.



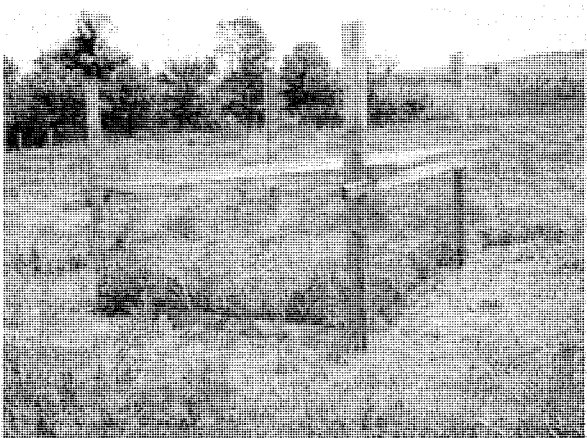
Supplementary figure 3 Schematic of a rainout shelter used during the 2005-2006 growing season. Space beneath shelters was allocated for measurements of aboveground net primary productivity, plant species composition, N availability (via resin bags), soil moisture, and plant water relations and tissue chemistry. A 0.5 m buffer surrounded the 1.25 x 1.25 m core plot that was used for sampling. ANPP = aboveground net primary productivity; SC = species composition.



Shortgrass Steppe Long-Term
Ecological Research Site
Grassland: shortgrass steppe
Nunn, Colorado, USA



Saline Experimental Range
Grassland: Mixed grass prairie
Hays, Kansas, USA



Konza Prairie Long-Term Ecological
Research Site
Grassland: tallgrass prairie
Manhattan, Kansas, USA

Supplementary Figure 4 Photographs of rainout shelters that were constructed in Great Plains Grasslands. Shelters were constructed in semi-arid steppe (top), mixed grass prairie (middle), and tallgrass prairie (bottom) in May-June 2005.

Chapter 5: Impacts of extreme rainfall events on grasslands: a modeling approach

ABSTRACT

We used a daily time step ecosystem model (DAYCENT) to simulate plant and soil water dynamics in two temperate grasslands (Central Plains, USA) under predicted precipitation change scenarios. For this region, Global Circulation Models (GCMs) forecast a shift to precipitation regimes characterized by quantitatively larger, but less frequent, events. In 2006, we experimentally manipulated growing season rainfall patterns (12-, 6-, or 4- events, respectively) in both semi-arid steppe and tallgrass prairie and compared field data for soil water dynamics and aboveground net primary productivity (ANPP) with DAYCENT output. We were interested in testing whether 1) simulated and experimental results agreed for 2006, and (2) short-term ANPP responses to altered precipitation regimes would be sustained across the time span of a century. Model output for the 2006 growing season moderately reflected observed values for soil moisture dynamics in both grassland sites (average $r^2 = 0.72$). In mesic tallgrass prairie, simulated ANPP trends were similar to field data and persisted into the future despite differing precipitation in non-growing season months. In semi-arid steppe, only slight differences in ANPP were simulated in 2006 in response to strongly differing rainfall scenarios. While DAYCENT has been parameterized for simulating the impacts of global changes on both native and agricultural ecosystems, this is the first study to

simulate ecosystem responses to extreme rainfall events. In both semi-arid steppe and tallgrass prairie, extreme rain events (and the treatments imposed in our field-based experimental manipulation) represent pulses of moisture that are novel conditions for these grasslands and therefore outside of the historic variability upon which ecosystem models are developed and validated. To more accurately forecast changes in ecological processes in response to these alterations, greater emphasis must be placed on model-data fusion exercises.

Introduction

The intensification of weather extremes is currently considered one of the most widespread facets of climate change (Jentsch et al. 2007). In the last decade, a growing number of ecological studies have focused on weather extremes, with ecologists emphasizing “events” rather than “trends” in both experimental and observational research (i.e. Allen and Breshears 1998; Smith et al. 2000; Ciais et al. 2003; Fay et al. 2008; Jankju 2008). While abundant data verify predictions that the impacts of these changes can be profound (Walther et al. 2002; Stenseth et al. 2002; Parmesan and Yohe 2003), much of the evidence focuses on short-term and immediate effects on plant and animal species (Hjelle and Glass 2000; Knapp et al 2002; Fay et al. 2003) and long-term impacts of these extremes remain largely unknown.

An increase in hurricane frequency and magnitude is a very obvious example of the intensification of weather extremes, but even more subtle changes in the frequency of extreme temperature and precipitation events can have significant effects on ecosystems and their plant and animal inhabitants. Within the United States, average annual

temperature has risen nearly 0.6°C during the last 100 years and precipitation has increased by 5-10%, the latter of which is largely due to increases in extreme precipitation events (Karl and Knight 1998; Groisman and Knight 2008). This trend of rising temperatures is expected to continue over the next decade and be associated with a further increase in the frequency of extreme precipitation events (Trenberth 1998, 1999; IPCC 2007). While the re-distribution of annual or growing season precipitation may not necessarily result in catastrophic flooding or long-term intensive drought, such “repackaging” of precipitation into larger, but less frequent, events will influence the temporal dynamics of available soil water for plant uptake (and subsequently carbon fixation), soil biogeochemical processes (i.e. nitrogen mineralization), and decomposition (Fierer and Schimel 2002; Knapp et al. 2002; Fay et al. 2003; Miller et al. 2005). Grassland ecosystems, in particular, are sensitive to both inter- and intra- annual variability in precipitation (Knapp and Smith 2001; Knapp et al. 2002). This historic sensitivity makes grasslands likely to be responsive to ongoing changes in precipitation.

Most experimental and modeling studies are exclusive in scope, and only a limited number of examples exist in which these two techniques have been used in tandem (Luo et al. 2004; Pendall et al. 2004). A recent notable exception is the work of Parton et al. (2007) where results from previous experimental manipulations of CO₂ were used to parameterize the DAYCENT terrestrial ecosystem model (Parton et al. 1998) and subsequently predict ecosystem responses to ongoing experimental manipulations in a similar ecosystem type (the Prairie Heating and Elevated CO₂ experiment). The use of empirical knowledge gained from short-term manipulative experiments to predict the

long-term responses of ecosystems is an ideal way to maximize the contributions of both research techniques.

In 2006, we conducted an experimental manipulation of growing season rainfall in two temperate grassland ecosystems located within the Great Plains of North America. More specifically, this research focused on ecosystem-level responses to a shift to more extreme rainfall events in mesic versus semi-arid ecosystems (for details, please see chapter 4 of this volume). Our results revealed that these 2 grassland ecosystems respond quite differently to extreme rainfall events. While mesic grasslands responded negatively (via a reduction in ANPP) to a growing season precipitation regime of fewer but larger events, semi-arid grasslands responded positively to this change with an increase in ANPP. Improved plant water relation was the mechanism for higher rates of plant productivity in both grasslands, despite occurring in opposite treatment scenarios.

Like the majority of experimental studies manipulating climate variables, the results of this experimental manipulation reflect ecosystems responses to key climatic changes in the short-term. To better understand potential long-term responses in the context of differing non-growing season variability in precipitation, field data can be used to parameterize and validate ecosystem models. We paired a short-term experimental study with ecosystem modeling. Our primary objective was to extend our level of inference beyond the primary responses of plants and soil processes to 100 years in the future. The specific goals of this research were to 1) first validate simulations of ANPP and soil water dynamics from the DAYCENT model with observed field data, and 2) simulate the long-term (century) or compounded effects of a shift to extreme rainfall regimes.

Model description

The DAYCENT biogeochemical model (Parton et al. 1998; Kelly et al. 2000; Del Grosso et al. 2001) is the daily time step version of the CENTURY terrestrial ecosystem model (Parton et al. 1987, 1993, 1994). The DAYCENT model simulates exchanges of carbon (C), nutrients (nitrogen, phosphorus, and sulfur), and trace gas fluxes (N_2O , NO_x , N_2 , and CH_4) among the atmosphere, soil, and vegetation. DAYCENT includes submodels for plant productivity, decomposition of dead plant material and soil organic matter, soil water and temperature dynamics, and trace gas fluxes (Fig.1). Flows of C and nutrients are controlled by the amount of C in the various pools, the nitrogen (N) concentration of the pools, temperature and soil water factors, and physical properties of the soil.

DAYCENT has been used extensively in grasslands, agricultural lands, forests, and savannas. The grassland version of the DAYCENT model has been tested with data from different grassland sites (Kelly et al. 2000; Pepper et al. 2005) and used to project the ecosystem impact of N deposition, increasing atmospheric CO_2 concentrations, and future climatic scenarios (Pepper et al. 2005). Required inputs to the model include daily maximum/minimum temperature and precipitation, site specific properties, and current and historical land use. Disturbances and management practices such as fire, grazing, cultivation and fertilizer additions can be simulated.

The plant production model simulates the growth of grasses, crops, and trees. The key processes included in the plant production model include growth of different plant parts (roots and shoots), plant death, plant phenology, and uptake of soil nutrients.

DAYCENT does not explicitly model photosynthesis; instead, plant growth is controlled primarily by water availability, temperature, solar radiation, live leaf area, and the availability of soil nutrients. The plant production submodel in DAYCENT sets monthly maximum plant production at a specific level and decreases production rates primarily in response to moisture, temperature, and nutrient constraints.

Daily soil water content and temperature for different soil layers are simulated by the soil water and temperature submodels. Key process in this model include saturated and unsaturated water flow, surface runoff, and water flow below the plant rooting zone (Parton et al. 1998). A numerical solution of the Darcy water flow equation is used to simulate water flow between soil layers using a half-hour time step. The soil temperature model simulates daily maximum, minimum, and average soil temperatures at 5-cm depth increments based on soil heat flow equations. Both the soil water and temperature submodels have been tested extensively using observed soil water and temperature data sets from a variety of sites and soil textures (Frolking et al. 1998; Eitzinger et al. 2000; Del Grosso et al. 2001).

A key improvement of DAYCENT compared with CENTURY is within the soil water and temperature algorithms (Parton et al. 1998). The new land surface submodel of DAYCENT simulates daily dynamics of soil water and temperature from a multi-layered soil system. The soil water submodel was modified to simulate above field-capacity water content, unsaturated water flow using Darcy's equation, runoff, snowpack processes, and the effect of soil freezing on saturated water flow.

Methods

Site Characteristics

We focused this study on the semi-arid steppe and mesic tallgrass prairie ecosystems of the Central Plains of North America. These two grasslands sites represent the xeric and mesic endpoints of a west-to-east moisture gradient that spans across the contiguous grassland biome of the Central Plains. We chose these grassland types because of their contrasting responses in the field to the GCM prediction of an increase in extreme rainfall events for this region. Additionally, both grasslands provide an essential ecosystem service in the form of forage production for livestock grazing. Changes in the quantity and quality of aboveground plant production will have important impacts on the ecology and economy of this region.

Semi-arid grassland. The Shortgrass Steppe (SGS) Long-Term Ecological Research site is a semi-arid steppe grassland ecosystem situated within the Pawnee National Grassland in north-central Colorado (40°49'N, 104°46'W). The site is managed by the USDA-ARS as the Central Plains Experimental Range and consists of gently rolling terrain with an average elevation of 1625 m above mean sea level. Mean annual temperature and precipitation are 8.6°C and 321 mm, respectively. Mean monthly temperatures range between -4°C to 22°C while annual precipitation has ranged from 107 and 588 mm over the last 50 years. The dominant plant species in this water and N-limited ecosystem (Sims et al. 1978) is *Bouteloua gracilis* (blue grama; Lauenroth and Dodd 1978). While soil type and development varies across the SGS, the soil type in which experimental plots were located is a coarse-loamy, mixed mesic Ustollic Haplargid (Petersen et al. 1993).

Mesic tallgrass prairie. The Konza Prairie Long-Term Ecological Research site (KNZ) is a 3,487 ha. mesic tallgrass prairie located ca. 13 km south of Manhattan, KS, USA. KNZ is located in the Flint Hills of eastern Kansas (39°05'N, 96°35'), a region characterized by a mid-continental climate consisting of cool, dry winters and warm, wet summers. Mean annual precipitation is 835 mm with 75% falling during the growing season (April-September), but is highly variable from year to year (Hayden 1998). Long-term weathering and erosion has created a non-uniform topography that is characterized by flat upland ridges, steep intermediate hillslopes, and lowlands with deep soils (Oviatt 1998). Research plots for experimental manipulations were located in lowland topographic positions, where soils are typically silty-clay loams and relatively deep (Ransom et al. 1998)

Field Experiment and data collection

The field data set used in this study was collected during the 2006 rain manipulation experiment described in chapter 4. For details on rainout shelter specifications and construction please revisit the methods of chapter 4. During the 2006 growing season, an experimental manipulation of rainfall patterns occurred at SGS and KNZ, and consisted of dividing long-term mean growing season rainfall into 12-, 6-, or 4- events that were applied at intervals of 10, 20, or 30 days, respectively. Rainfall events typically occurred over a 4-8 hour period and very large events (> 5.08 cm at KNZ; >2.54 cm at SGS) were applied over several consecutive days. Soil moisture integrated over the top 20 cm of soil was measured ca. every 3-5 days. ANPP was estimated via end-of-season biomass harvest from 2 0.25 m² quadrats that were located in a central core plot

beneath rainout shelters. ANPP values for the pair of quadrats within a shelter were averaged to produce a shelter-level response ($n = 5$ shelters per treatment type).

Model Parameterization

Because DAYCENT has been used extensively in both shortgrass steppe and tallgrass prairie ecosystems to simulate ecosystem responses to global change scenarios, we used previously parameterized and tested versions of the model. The specific parameters and model input files for both grasslands are detailed in Appendix 2.

Climate Change Simulations

DAYCENT modeling was initiated by running long-term simulations under current climate. For the SGS, we used data from 1970-2005 for a 1969-year spinup (sufficient for the model to reach equilibrium under current climate). Model output for the years 1970-1990 was used for model validation (see below). For KNZ, we used data from 1984-2005 for a 1983-year spinup and then model output for the years 1984-2005 for model validation. Beginning in 2006, treatment scenarios for growing season precipitation were included in the model. For the years 2007-2106, a 100-year daily weather set was generated by selecting years at random (with replacement) from weather data available for 1970-2005 for SGS and 1983-2005 for KNZ. As years were selected, the 130-day experimental period was substituted for the daily weather data for a particular year. For KNZ this included the time period of April 25 – September 1 and for SGS, this included the time period of May 9-September 12. To ensure that treatments were comparable for a given year, the same random selection of years was used for ambient and the 12-, 6-, and 4- event precipitation scenarios. Assembling future climatic

data in this way allowed for considerable variability in precipitation during non-growing season months. This arrangement enabled us to evaluate the relative influence of growing season patterns in the context of annual and long-term precipitation trends.

Because of the long-term nature of our simulations, we imposed moderate grazing at the SGS and a 4-year fire return interval at KNZ, which reflect typical management practices in these grassland sites.

Validation exercises

We conducted our validation with data from the Central Plains Experimental Range in northeastern Colorado and data from the Konza Prairie Long-Term Ecological Research site in Manhattan, KS. A paper by Lauenroth and Sala (1992), which included field-based data, was our source of validation data for ANPP and precipitation for the semi-arid steppe. Data from the KNZ LTER was used for the tallgrass prairie site. For both sites, we used a well-tested vegetation parametrization for semi-arid steppe and tallgrass prairie (see Appendix A.2).

In validating the model, we were unable to make direct comparisons between observations and simulations at both SGS and KNZ and had to use indirect but robust alternative methods. Because ANPP was the response variable of primary interest, we used this variable for our validation exercise. At the SGS, annual precipitation data for 1970-1990 from Lauenroth and Sala (1992) differed substantially from the climate data that we had assimilated from another source (preventing direct comparisons of ANPP data). To get around this data mismatch, we evaluated the precipitation-productivity relationship for observed data (Lauenroth and Sala 1992) and modeled data (from our

DAYCENT simulations) via regression analysis. Regression slopes for observed versus simulated data were very similar and not significantly different ($p < 0.05$), despite relatively low r^2 values for each (Fig.2). For KNZ, we used two techniques to validate our simulations, given the generally low predictive relationship between annual precipitation and ANPP in this ecosystem. First, we calculated mean, maximum, and minimum values for annual ANPP using data from both annually burned and 4-year burn treatments at KNZ. We compared simulated ANPP values for each year to observed values and agreement was $\pm 15\%$ (Table 1). Next, we evaluated the strength of the relationship between observed versus simulated ANPP. The r^2 of this relationship was 0.50 (Fig.3).

Results

Model versus manipulated rainfall comparison

Soil water. DAYCENT moderately simulated the dynamic changes in soil water content (0-20 cm) during the growing season for all precipitation scenarios in both semi-arid steppe and tallgrass prairie. The r^2 values ranged from 0.54 to 0.90 for SGS (Fig. 4) and 0.41 to 0.89 for KNZ (Fig.5), respectively. For both sites, strongest agreement was detected in the 6- and 4- event scenarios, likely due to the greater range in soil moisture that occurred as a result of quantitatively larger rainfall events.

Aboveground Net Primary Productivity. The simulated data for aboveground net primary productivity (ANPP; g/m^2) in 2006 was within normal bounds for both SGS and KNZ but relative agreement with observed data from the rainfall manipulation experiments differed between sites. For SGS, only small differences in ANPP were simulated for the

three treatment scenarios (Fig.6); this was in marked contrast to field data. Whereas a shift from 12- to 4- events led to an increase in ANPP in the field, model simulations demonstrated a small reduction in ANPP. When the treatments were simulated for the next century, differences remained low but the trend itself was sustained (Fig.6). For KNZ, considerable differences were observed among treatments (Fig. 7) and this trend was similar to that observed in the field. DAYCENT simulations of ANPP for 2007-2106 revealed that more extreme rainfall patterns can be expected to consistently reduce ANPP during the long-term, regardless of variability of precipitation during non-growing season months (Fig.7).

Water budget

We evaluated the water budget for both SGS and KNZ during the 2006 growing season to characterize the impacts of extreme events on ecosystem hydrology. While DAYCENT simulates rainfall, interception, evaporation, transpiration, and runoff on a daily timestep, we pooled the data to reflect these variables according to 10 day intervals throughout the growing season. Our primary interest was differences in water loss from soils due to both evaporation and transpiration. These variables are most likely to be affected by precipitation frequency and explain observed patterns in ANPP. It is important to note that the growing season occurs within the context of an entire year, and that moisture losses for a system may reflect moisture that has been stored in the soil from precipitation that occurred during non-growing season months (i.e. winter). Water budgets for both SGS and KNZ revealed that in 2006 moisture losses exceeded moisture inputs.

For the SGS, the most dramatic difference in water balance between the 12- and 4-event treatments was due to evaporation (Table 2). Of the ca. 20 cm of rainfall applied to plots during the growing season, nearly 20% (3.95 cm) was lost to evaporation in the 3-4 days immediately following small rain events. This amount can be contrasted with the 2.91 cm (15% of total precipitation) that evaporated from the soil surface when rainfall was applied as 4-events. Interception by the vegetation was additionally simulated as higher in the 12-event treatments (1.60 cm versus 0.6 cm). In comparing water lost via transpiration, similar losses occurred for the 2 scenarios (14.56 cm versus 14.23 cm; Table 2).

For KNZ, important differences were observed in interception, evaporation, transpiration, and runoff. The most significant difference was simulated for water loss via transpiration. Whereas 95% of water (43.56 cm) was returned to the atmosphere via plant processes (transpiration) in the 12-event plots, this amount was reduced to 87% in the 4-event plots (39.96 cm; Table 3). Additionally, large events resulted in a loss of 2 cm of rainfall to runoff. Water loss due to interception and evaporation was much greater (18% versus 13%) when precipitation was applied as more frequent, but smaller, rain events (Table 3).

Temporal patterns of soil moisture

In plotting field data for soil water content with DAYCENT model simulations, we observed several intervals throughout the growing season in which DAYCENT and field data were not in agreement. For the SGS, DAYCENT consistently simulated extended dry intervals during the periods between each large rain event (Fig.8). While

our field data support reductions in soil water content during this time, neither the magnitude nor duration was as pronounced as the model simulations (Fig.8). Additionally, the moisture pulses associated with rain events in this semi-arid grassland were simulated as very transient periods in DAYCENT while field data suggest that they were much longer in extent.

For the tallgrass prairie site, important differences in the temporal dynamics of both the 12- and 4- event scenarios were also noted. For the 12-event rainfall regime, DAYCENT consistently predicted higher values for soil moisture than field data (Fig. 9), and the moisture pulses associated with rain events for both precipitation regimes were strongly reduced (Fig. 9). The mean maximum value associated with moisture pulses was 22% (field data) for the 12-event rainfall regime, which was significantly lower than the 29% predicted by DAYCENT. For the 4-event rainfall regime, the mean maximum value associated with moisture pulses was 26%, which was significantly lower than the 33% predicted by DAYCENT. These differences in the temporal dynamics of soil water throughout the growing season are likely to influence transpiration, plant carbon fixation, and ultimately ANPP.

Discussion

Ecologists are frequently called upon to predict the impacts of global changes on the structure and function of ecosystems in addition to the essential services that native ecosystems provide. In the Great Plains of North America, the production of aboveground net primary productivity (ANPP) is a key ecosystem service of grasslands, where ranchers depend on forage for livestock grazing. To better address both the short-

term and long-term impacts of extreme precipitation events, we paired an experimental manipulation with a modeling study.

It is important to note upfront that this modeling study represents our initial attempt at simulating ANPP and soil moisture dynamics at two grassland sites using the DAYCENT terrestrial ecosystem model. DAYCENT has been extensively tested and validated for these two grassland sites, so we elected to use previously parameterized versions of the model for our initial simulations. We chose to approach the analysis in this way because we wanted to simulate ecosystem responses from the perspective of a scientist that did not have experimental data to guide parameterization. Future and follow-up simulations will seek to adjust key parameters in order to fine-tune simulated values for both ANPP and soil water dynamics.

Do simulated and experimental results for 2006 agree?

Our simulated results suggest that the DAYCENT model is indeed sensitive to intra-annual variability in precipitation but not in all ecosystems. To the best of our knowledge, this is the first comparison of experimental and simulated data that addresses ecosystem response to extreme rainfall events. While DAYCENT accurately represented field data for ANPP in the mesic grassland site, it did not simulate the observed trends for the semi-arid site. We believe that these results reflect issues with parameterization of the soil water and vegetation sub-models. Because the vegetation model is not written to be a physiological model, important limitations exist in terms of its potential to respond to variable conditions in soil moisture. Additionally, we noted important differences in

the maximum and minimum values of soil moisture surrounding the large pulses and extended dry intervals of the 4-event rainfall regime in both grassland sites.

The soil water model for DAYCENT has the capacity to simulate the movement of water through the soil profile (including such pools as runoff, evaporation, transpiration, and deep infiltration) and to incorporate important aspects of root distribution and water uptake. However, the simulation of these key processes is based on data from field experiments collected under typical environmental conditions. We believe that more field-based information on root distribution, water uptake, and hydrology would greatly improve both soil water simulations and ANPP patterns. The precipitation scenarios imposed in the field during the 2006 field season included individual rain events that are rarely encountered but predicted to occur in the future. Future experiment research will be needed to parameterize and validate DAYCENT simulations of these events.

We noted several areas of disagreement between DAYCENT simulations and field-based data for the water budget that may explain the differences in observed versus simulated ANPP for these grasslands. At the SGS, large events (4-event scenario) led to a soil water surplus for the growing season (+1.93 cm) whereas small events led to a soil water deficit (-0.44). While water loss to transpiration (a proxy for leaf-level photosynthesis) was similar for the two different rainfall scenarios, we would expect that this “extra” water might be used for increased photosynthesis rather than remaining in the soil.

For KNZ, large events led to a four-fold increase in surface runoff (0.7 cm for the 12-event regime versus 2.7 cm for the 4-event regime). While 45.7 cm of rainfall was applied during the growing season, ca. 49 cm was lost from the system via evaporation or transpiration, suggesting that stored water during non-growing season months was utilized. The reduction in transpirational water loss in the 4-event rainfall regime (ca. 40 cm versus 44 in the 12-event regime) supports lower photosynthetic rates and the ANPP response observed in the field.

Plots of soil moisture dynamics revealed that DAYCENT simulations and field measurements agreed moderately but differed in several key ways. In mesic tallgrass prairie, DAYCENT simulated greater average soil moisture for the 12-event treatment with higher maximum and minimum values for soil water content than measured in the field. Additionally, measurements of soil water content for the 4-event treatment never reached the maximum values simulated by DAYCENT. There was, however, strong agreement for minimum values. In order to more accurately simulate soil water dynamics in response to extreme events, more rigorous experimental research is needed to measure movement of water through the soil profile in addition to changes in soil water content (post-event) due to evaporation and transpiration.

The ability of DAYCENT (and other ecosystem models) to simulate ANPP in response to climate change may be enhanced by the addition of a plant physiological submodel. In Chapters 4 and 5 of this volume, we detail the ANPP responses of both the SGS and KNZ in response to extreme precipitation events that were imposed in the field during the 2005 and 2006 growing season. For the SGS in particular, extreme rainfall patterns (4-event treatment) resulted in ANPP values ($184 \pm 38 \text{ g/m}^2$) that were well-

above the long-term average value (97 g/m^2 ; Lauenroth and Sala 1992) for this semi-arid grassland ecosystem. For this reason, an ecosystem model that constrains ANPP to maximum and/or minimum values based on long-term data will likely not be responsive to extreme events in climate (precipitation or temperature) that may lead to large deviations from average values. To be effective, a plant physiology submodel must therefore be developed based on large response curves for soil moisture and plant ecophysiology and be based on data from experimental manipulations in field settings. While practically challenging to acquire, a plant physiological model should also include belowground plant processes such as belowground net primary productivity and root growth, distribution, and dynamics. Large rainfall events separated by long dry intervals will likely alter patterns of water infiltration and plant rooting patterns. Because these patterns are may be novel conditions for ecosystems, field data is required to accurately simulate them.

Short- versus long- term ANPP responses to extreme precipitation patterns

Using DAYCENT, we simulated the ANPP response of both semi-arid steppe and mesic tallgrass prairie to more extreme growing season rainfall over the long-term (2007-2106). Our results suggest that simulations for 2006 are robust to interannual variability in precipitation during non-growing season months. These results assume no net change to mean annual temperature or total growing season precipitation, which may interact with precipitation variability during the growing season to influence both soil water and plant response patterns.

Conclusion

In closing, we believe that climate change research efforts that include both experimental manipulations and ecosystem modeling are integral to understanding ecosystem responses to climate change in both the short- and long-term. Our comparison of model output versus field data from an experimental manipulation suggests that models have strong potential for predicting soil water dynamics and ANPP in response to extreme precipitation patterns but that caution must be exercised in interpreting output from models that have not been specifically parameterized to include novel climate conditions. A great number of model-data fusion efforts are needed to assist ecologists in predicting the impacts of global changes on terrestrial ecosystems.

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Table 1. Data for annual precipitation and aboveground net primary productivity (ANPP; g/m^2) for the Konza Prairie Long-Term Ecological Research site (Manhattan, KS, USA). Mean ANPP and ANPP range are from field data of annually burned and 4-year burn plots. DAYCENT simulations for ANPP (based on precipitation) are included in the last column of the table. DAYCENT simulations that do not fall within the range of ANPP for a given year are indicated by a star.

Year	Precipitation (mm)	Mean ANPP (g/m^2)	ANPP Range (g/m^2)	DAYCENT (g/m^2)
1984	941.7	440	333-551	494
1985	919.2	478	304-611	583
1986	1074.5	424	347-505	576*
1987	820.5	566	343-821	439
1988	481.0	376	238-519	424
1989	622.5	239	158-312	146*
1990	742.3	530	284-794	597
1991	605.7	572	426-859	530
1992	885.9	563	324-780	523
1993	1227.6	598	374-980	655
1994	635.6	537	369-728	602
1995	942.1	662	471-885	557
1996	737.6	505	317-743	460
1997	628.1	381	288-487	429
1998	944.0	586	352-793	528
1999	825.2	527	375-786	643

Table 2. Water balance for 12- and 4- event rainfall scenarios at the semi-arid shortgrass steppe (SGS). Data illustrate DAYCENT simulations for water inputs and outputs during the 2006 growing season. All numerical values are expressed in centimeters (cm).

Days	12-event scenario					4-event scenario				
	Precip	Intercept	Evap	Transp	Sum	Precip	Intercept	Evap	Transp	Sum
0-10				-1.15					-1.15	
10-20	1.28	-0.13	-0.28	-1.81	-0.93	0	0	0	-1.04	-1.04
20-30	2.18	-0.12	-0.32	-1.05	0.70	0	0	0	-0.27	-0.27
30-40	2.77	-0.18	-0.51	-2.00	0.08	6.23	-0.20	-0.93	-1.92	3.19
40-50	2.26	-0.17	-0.40	-2.43	-0.73	0	0	0	-2.09	-2.09
50-60	0.96	-0.12	-0.26	-1.58	-0.99	0	0	0	-0.89	-0.89
60-70	1.99	-0.15	-0.34	-0.93	0.57	5.21	-0.17	-0.67	-1.56	2.81
70-80	1.14	-0.12	-0.31	-0.91	-0.20	0	0	0	-1.50	-1.50
80-90	1.52	-0.13	-0.30	-1.28	-0.19	0	0	0	-1.08	-1.08
90-100	2.11	-0.14	-0.31	-1.28	0.39	4.78	-0.14	-0.58	-2.09	1.96
100-110	1.63	-0.13	-0.28	-0.85	0.37	0	0	0	-1.27	-1.27
110-120	1.13	-0.12	-0.34	-0.18	0.50	0	0	0	-0.18	-0.18
120-130	0.69	-0.10	-0.32	-0.26	0.01	3.45	-0.10	-0.73	-0.34	2.29
Overall Sum	19.67	-1.60	-3.95	-14.56	-0.44	19.67	-0.60	-2.91	-14.23	1.93

Abbreviations: **Precip** = precipitation; **Intercept** = amount of precipitation that was intercepted by vegetation; **Evap** = amount of water that has infiltrated the soil and later loss via the physical process of evaporative demand; **Transp** = amount of water that was transpired by vegetation; **Sum** = the balance of precipitation, interception, evaporation, and transpiration for a given 10-day period. Note: Values for a given 10-day interval are the sum of water loss or gain during the entire time period.

Table 3. Water balance for 12- and 4- event rainfall scenarios at the mesic tallgrass prairie site (KNZ). Data illustrate DAYCENT simulations for water inputs and outputs during the 2006 growing season. All numerical values are expressed in centimeters (cm).

12-event scenario							4-event scenario					
Days	Precip	Intercept	Evap	Transp	Runoff	Sum	Precip	Intercept	Evap	Transp	Runoff	Sum
0-10			-0.43	-2.15		-2.58			-0.43	-2.15		-2.58
10-20	2.95	-0.06	-0.46	-2.66	0	-0.23	0	0	-0.48	-2.71	0	-3.19
20-30	4.40	-0.90	-0.48	-3.77	0	-0.77	0	0	-0.20	-3.60	0	-3.80
30-40	4.33	-0.17	-0.48	-4.11	0	-0.43	11.68 ¹	-0.52	-0.44	-3.92	-0.78	6.02
40-50	4.49	-0.14	-0.48	-4.05	-0.02	-0.20	0	0	-0.50	-4.15	0	-4.65
50-60	4.02	-0.16	-0.48	-4.27	0	-0.89	0	0	-0.08	-2.97	0	-3.05
60-70	5.42	-0.15	-0.48	-4.48	-0.66	-0.34	13.93 ²	-0.45	-0.44	-4.27	-0.81	7.97
70-80	4.51	-0.18	-0.48	-3.98	0	-0.14	0	0	-0.50	-4.06	0	-4.56
80-90	3.15	-0.18	-0.48	-4.45	0	-1.97	0	0	-0.22	-3.70	0	-3.92
90-100	3.66	-0.17	-0.48	-4.33	0	-1.32	11.32 ³	-0.51	-0.44	-4.13	-0.79	5.45
100-110	2.73	-0.18	-0.45	-4.36	0	-2.26	0	0	-0.47	-4.50	0	-4.97
110-120	2.76	-0.16	-0.37	-2.77	0	-0.53	0	0	0	-1.64	0	-1.64
120-130	3.29	-0.13	-0.54	-0.33	0	2.28	8.78 ⁴	-0.27	-0.73	-0.31	-0.33	7.15
Sum	45.71	-2.61	-5.65	-43.56	-0.681	-9.37	45.71	-1.75	-4.48	-39.96	-2.71	-3.18

Abbreviations: **Precip** = precipitation; **Intercept** = amount of precipitation that was intercepted by vegetation; **Evap** = amount of water that has infiltrated the soil and later loss via the physical process of evaporative demand; **Transp** = amount of water that was transpired by vegetation; **Sum** = the balance of precipitation, interception, evaporation, and transpiration for a given 10-day period. Note: Values for a given 10-day interval are the sum of water loss or gain during the entire time period.

¹This rain event occurred over 3 days, during which 5.08 cm, 5.08 cm, and 1.51 cm were applied, respectively.

²This rain event occurred over 3 days, during which 5.08 cm, 5.08 cm, and 3.76 cm were applied, respectively.

³This rain event occurred over 3 days, during which 5.08 cm, 5.08 cm, and 1.16 cm were applied, respectively.

⁴This rain event occurred over 2 days, during which 5.08 and 3.70 were applied, respectively.

DAYCENT MODEL

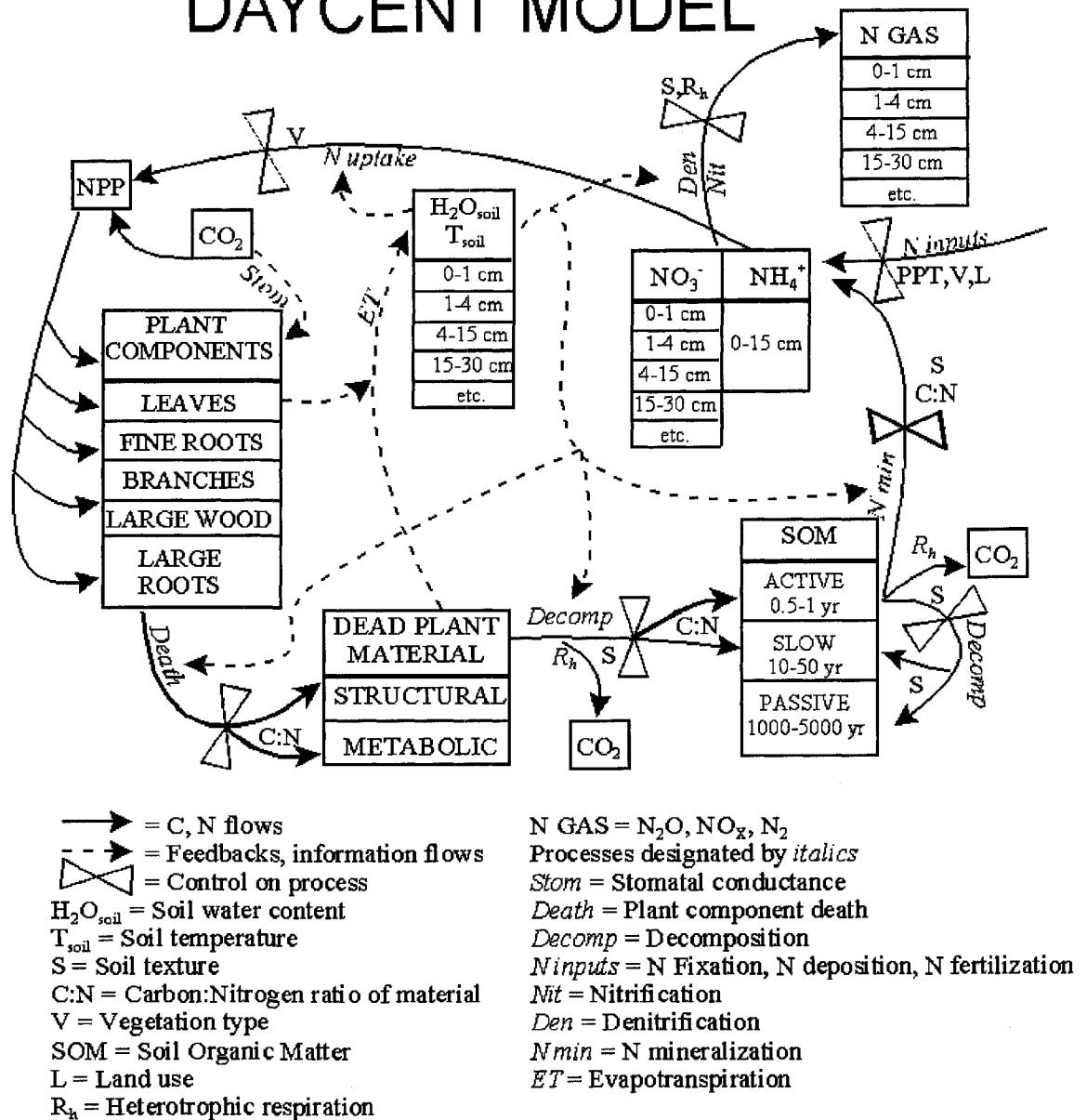


Figure 1. Diagram for the DAYCENT terrestrial ecosystem model illustrating the major carbon and nitrogen flows and the controls for them (Parton et al. 1998; Kelly et al. 2000; Del Grosso et al. 2001).

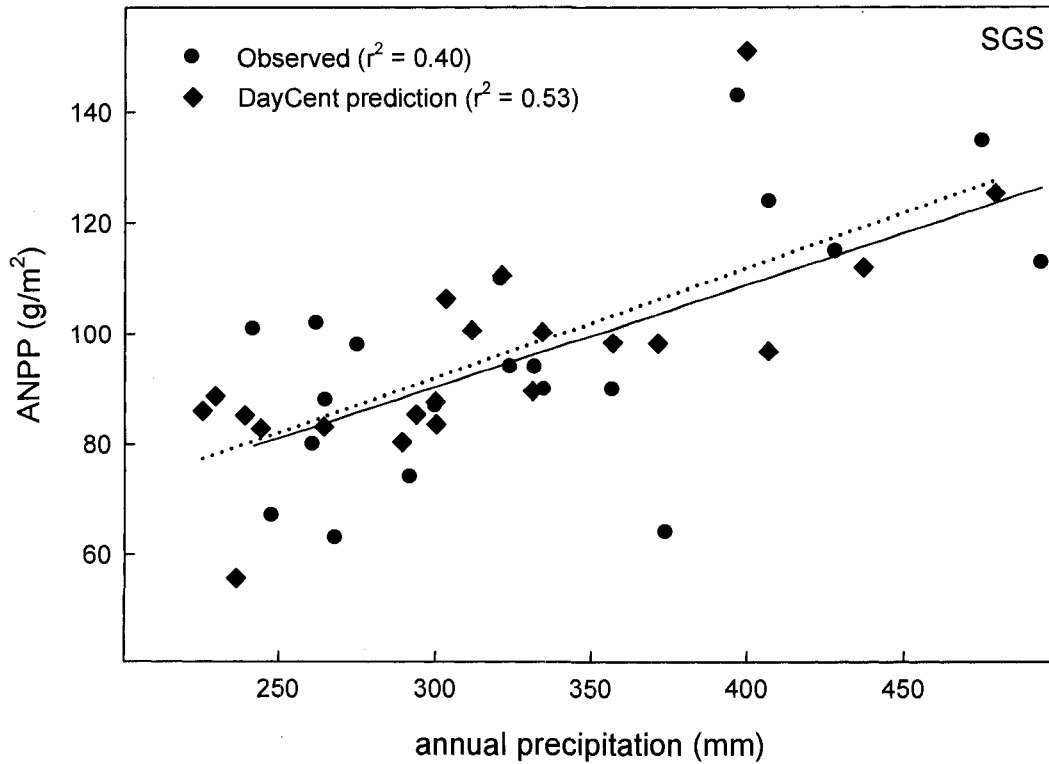


Figure 2. Model validation of aboveground net primary productivity (ANPP; g/m²) data for the semi-arid grassland (SGS). Observed data (both precipitation and ANPP) is from Lauenroth and Sala 1992 and field data are DAYCENT simulations for the same time period (1970-1990). The solid line represents the precipitation-ANPP relationship based on observed data whereas the dotted line represents observed weather data and DAYCENT simulations. There is no significant difference between the linear equations that describe this relationship. The equation based on data from Lauenroth and Sala is $ANPP = 0.19(\text{annual precipitation}) + 34.7$. The equation based on DAYCENT simulations is $ANPP = 0.20(\text{annual precipitation}) + 32.4$.

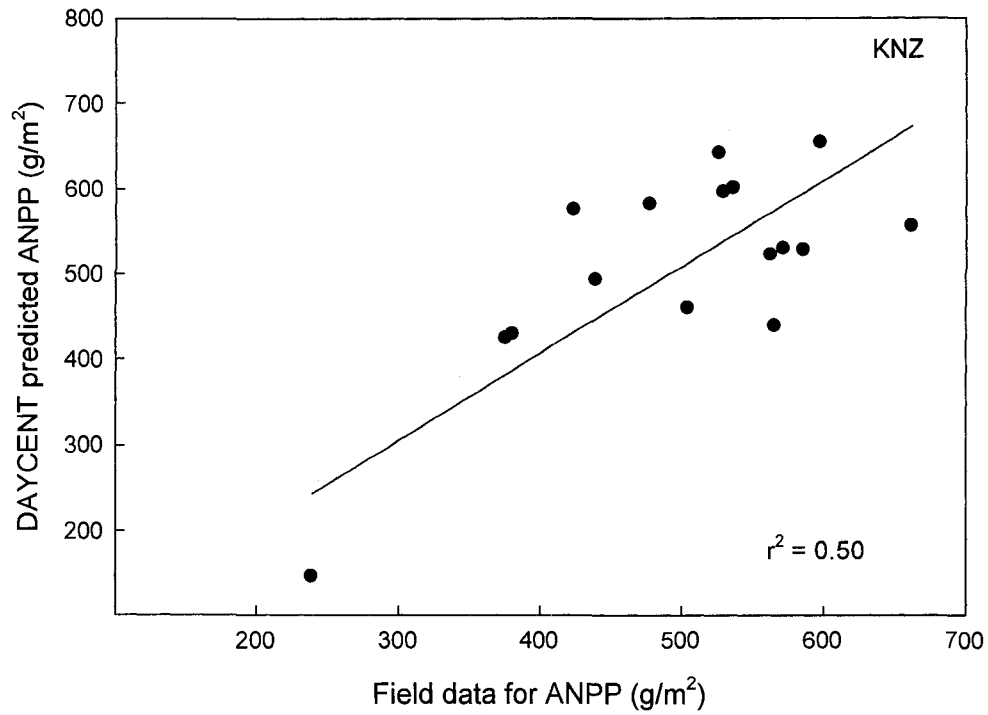


Figure 3. Model validation of aboveground net primary productivity (ANPP; g/m²) data for the tallgrass prairie site (KNZ).

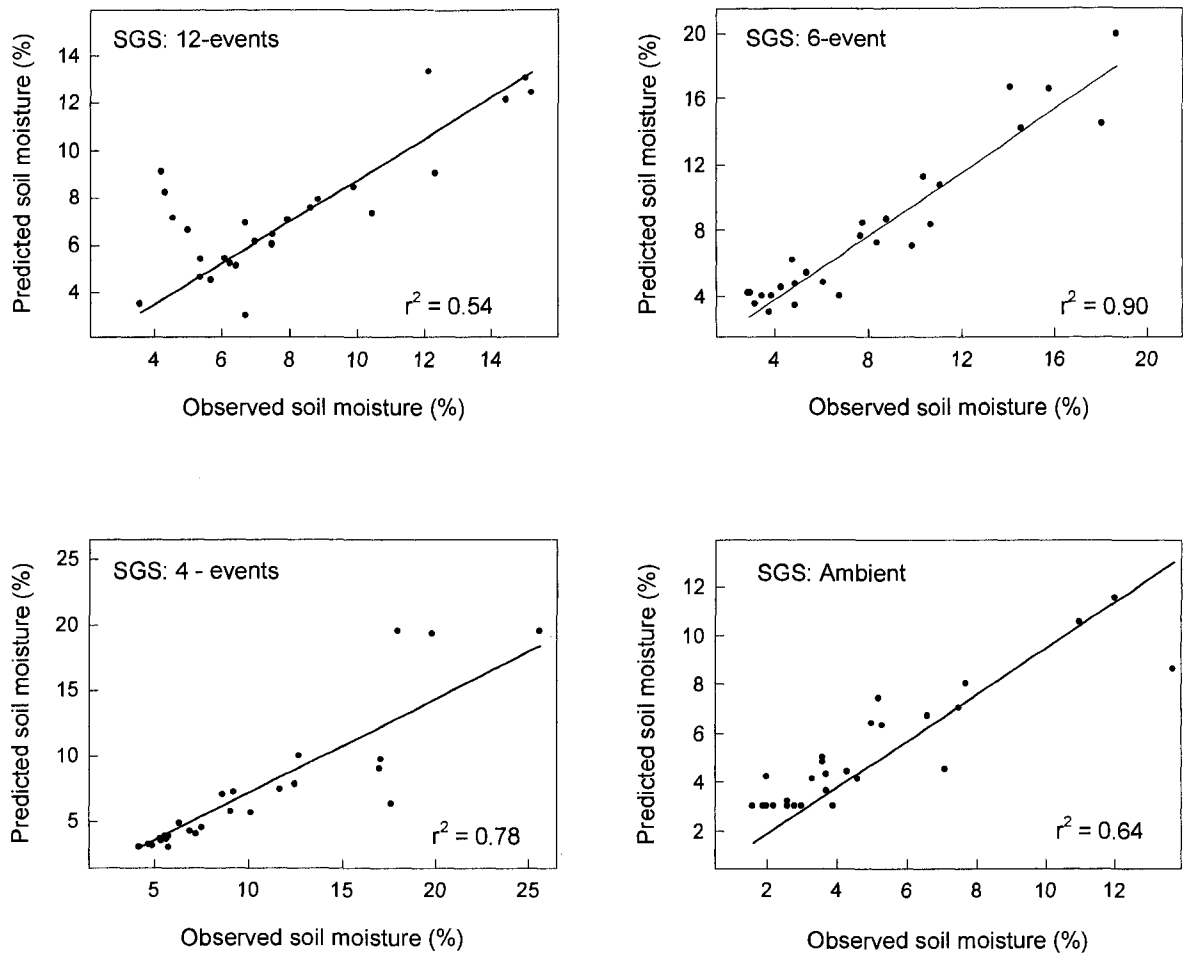


Figure 4. Relative agreement between observed and simulated soil moisture (%) for the semi-arid steppe ecosystem (SGS). All three treatment scenarios (12-, 6-, and 4-events) are included as well as data from plots exposed to ambient rainfall in 2006. Data points indicate individual days during the growing season in which soil moisture was measured in the field and could be compared to DAYCENT simulations.

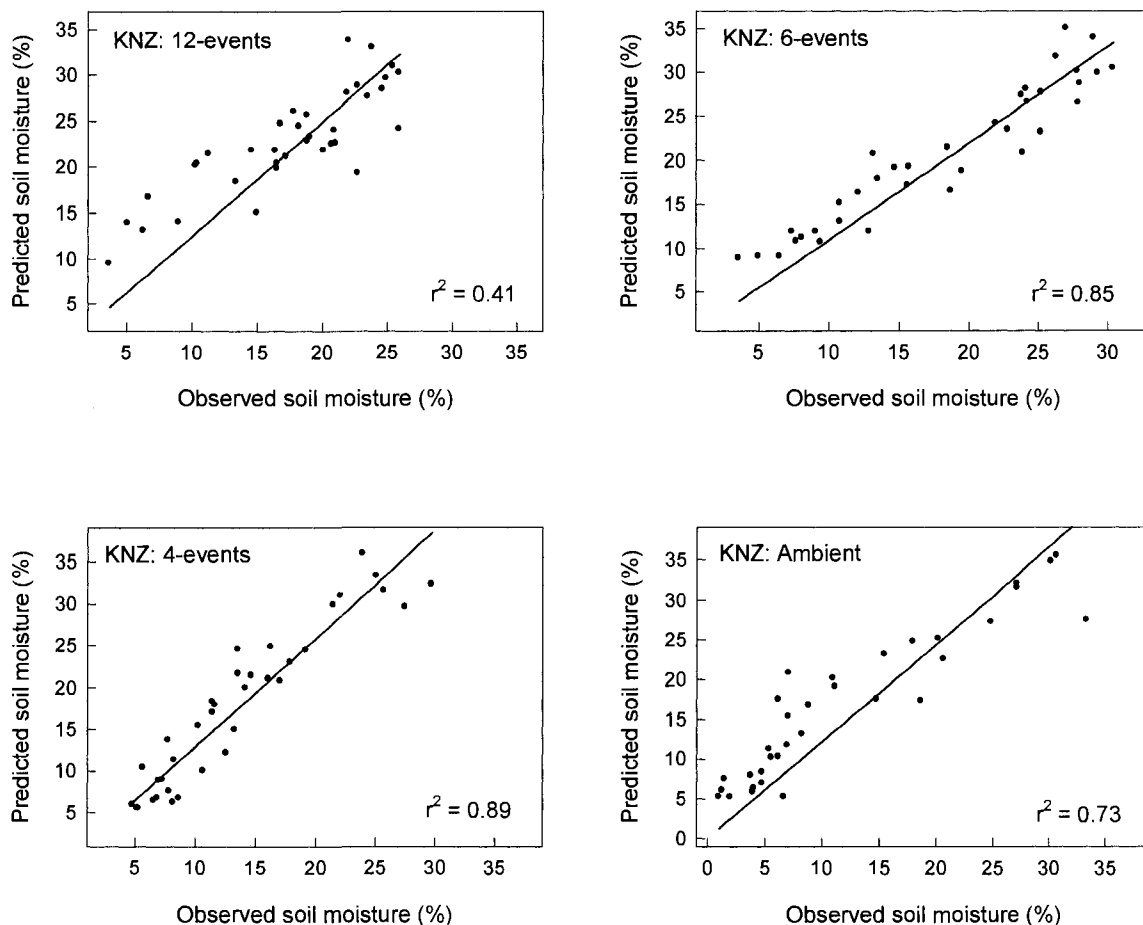


Figure 5. Relative agreement between observed and simulated soil moisture (%) for the tallgrass prairie ecosystem (KNZ). All three treatment scenarios (12-, 6-, and 4-events) are included as well as data from plots exposed to ambient rainfall in 2006. Data points indicate individual days during the growing season in which soil moisture was measured in the field and could be compared to DAYCENT simulations.

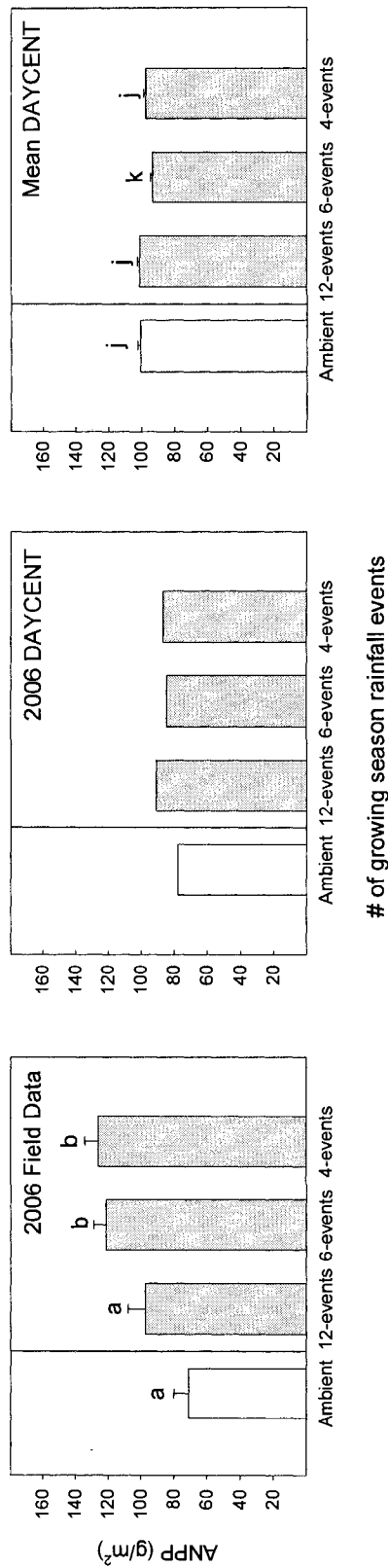


Figure 6. Aboveground net primary productivity (ANPP: g/m^2) data for the semi-arid shortgrass steppe (SGS) during the 2006 growing season and averaged over the next century. Data from both ambient precipitation and imposed rainfall scenarios are included. Statistically significant ($p < 0.05$) differences in ANPP between scenarios are indicated by different letters.

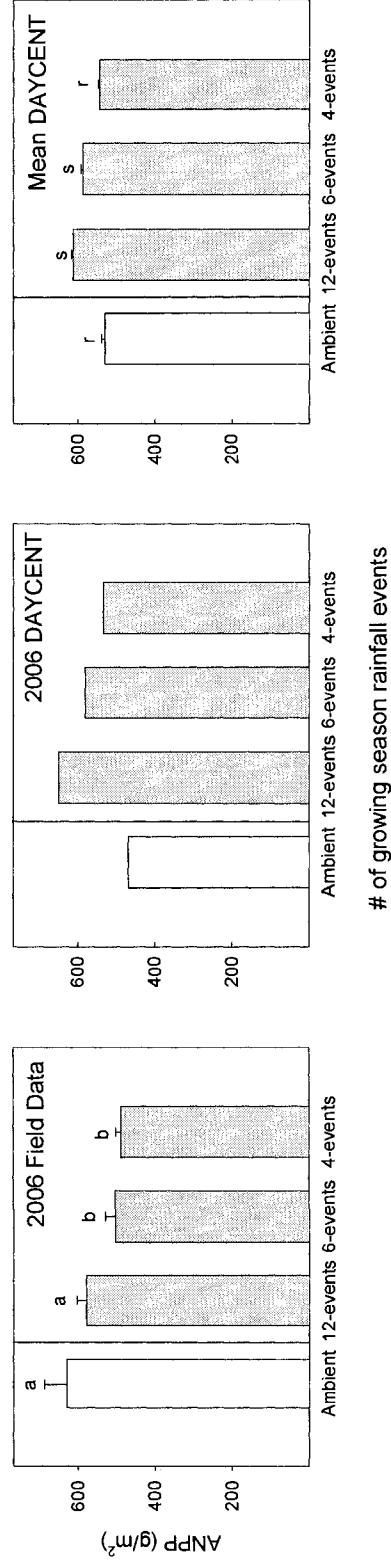


Figure 7. Aboveground net primary productivity (ANPP: g/m²) data for the tallgrass prairie ecosystem (KNZ) during the 2006 growing season and averaged over the next century. Data from both ambient precipitation and imposed rainfall scenarios are included. Statistically significant ($p < 0.05$) differences in ANPP between scenarios are indicated by different letters.

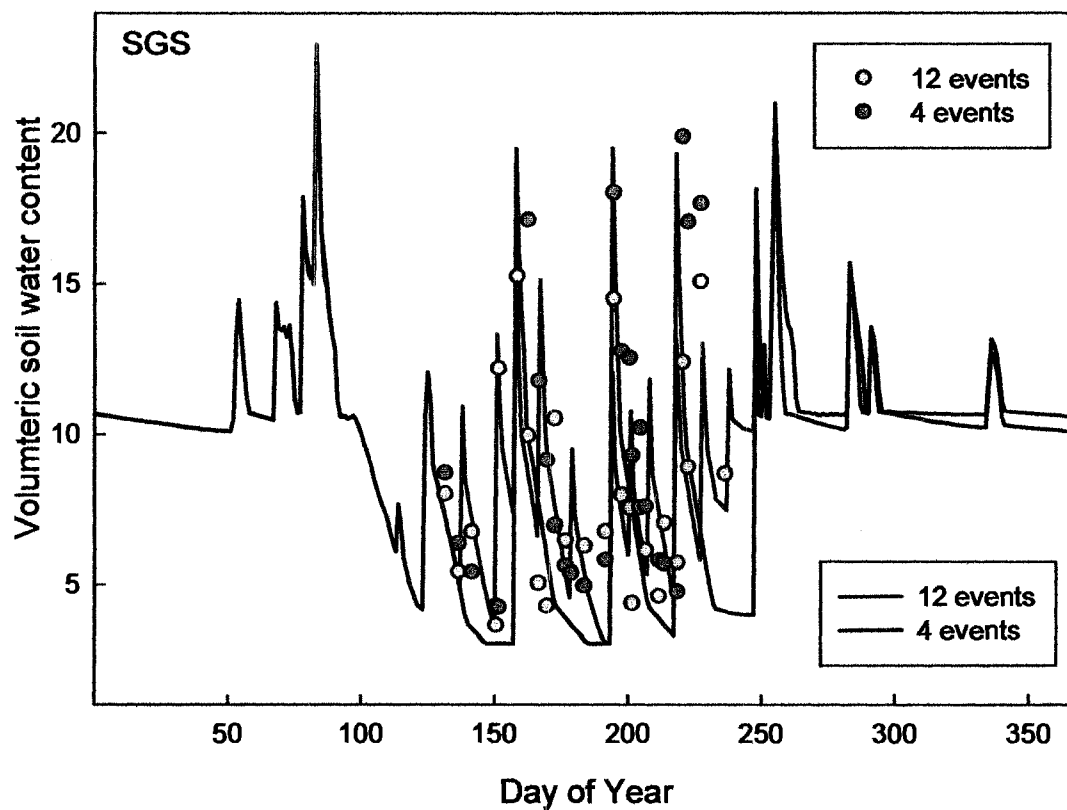


Figure 8. Soil moisture dynamics (%) for the semi-arid shortgrass steppe ecosystem (SGS). Data points were collected in the field during the 2006 growing season. DAYCENT simulations of daily soil moisture for the 12- and 4- event precipitation scenarios are indicated by the colored lines.

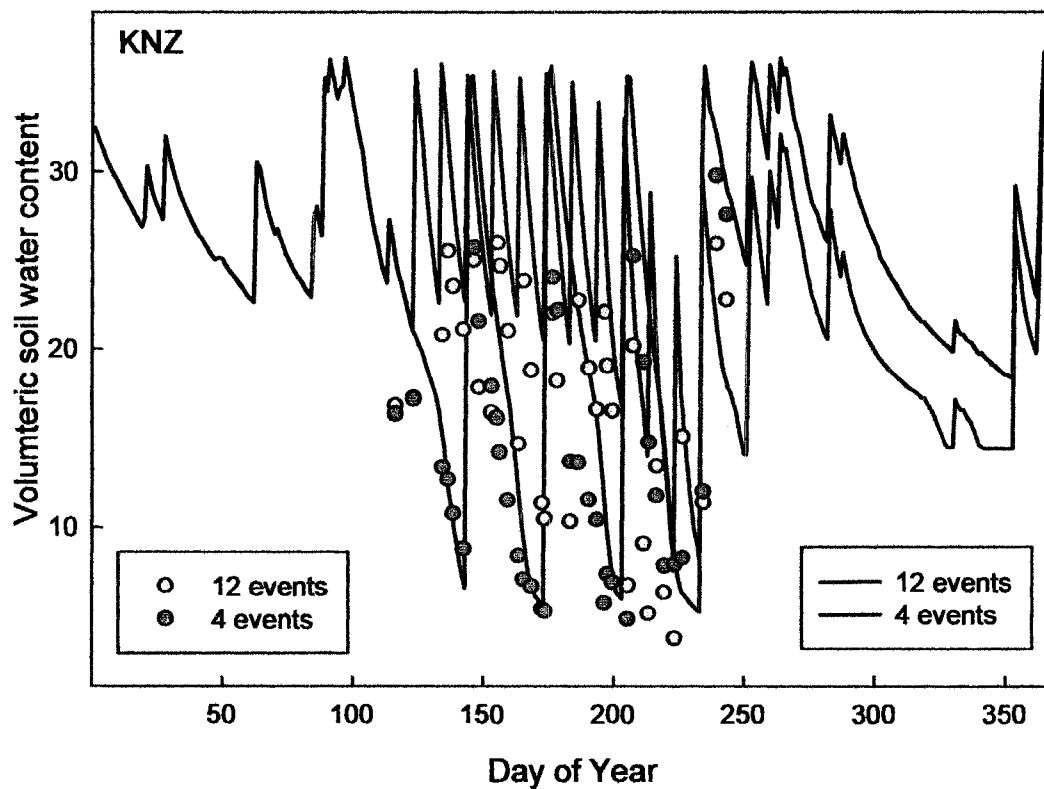


Figure 9. Soil moisture dynamics (%) for the tallgrass prairie ecosystem (KNZ). Data points were collected in the field during the 2006 growing season. DAYCENT simulations of daily soil moisture for the 12- and 4- event precipitation scenarios are indicated by the colored lines.

Chapter 6: Summary and Conclusions

The research described in this dissertation explores precipitation as a primary driver of aboveground net primary productivity (ANPP) in both time and space, with the overarching goal of improving our ability to forecast changes in this key ecosystem process in response to ongoing global changes. I conducted this research within the Great Plains of North America and combined an analysis of long-term data, experimental manipulations of growing season rainfall, and terrestrial ecosystem modeling to pursue my research goal. The Great Plains region contains a 600 km west-east precipitation gradient that results in three distinct grassland ecosystems, the semi-arid shortgrass steppe of northeastern Colorado, the mixed grass prairie of central Kansas, and the tallgrass prairie of eastern Kansas. Within this region, ANPP is tightly linked to long-term average and interannual precipitation patterns, and increasing evidence suggests that intra-annual precipitation patterns are additionally important in determining ANPP.

During the last decade, an increasing number of ecological experiments have focused on identifying the influence of global changes on ecosystem structure and function. Few, however, have explicitly quantified the coherence of response variables across differing management strategies, soil types, or topographic positions. Using the watershed-level experimental design of Konza Prairie Biological Station (KNZ), I assessed coherence in ANPP dynamics from 1984-1999. I tested the hypothesis that despite differences in mean ANPP, permanent sampling locations across KNZ would be

similar in ANPP dynamics and that fire frequency, in particular, would strengthen coherence. For the KNZ site as a whole, coherence (c) was 0.53. Strongest coherence was observed in annually burned upland sites ($c = 0.88$), which were strongly correlated (r) with annual precipitation ($r = 0.80$). In contrast, unburned sites were only weakly coherent ($c = 0.49$) and decoupled from interannual precipitation dynamics. This research suggests that both land management and topography interact to strengthen or diminish the coherent response of ecosystems to large-scale drivers such as climate.

To compare the influence of large versus small rain events on ANPP in the semi-arid shortgrass steppe, I manipulated the frequency of rain events during the 2005 growing season through the use of moderate-sized rainout shelters. The long-term mean rainfall amount was applied to all experimental plots, which received 12, 6, or 4 events, respectively ($n = 5$ per treatment). I discovered that ANPP peaked in plots where rain events were large and less frequent (4 events; $184 \pm 38 \text{ g/m}^2$), as compared to a growing season rainfall regime characterized by frequent, small events (12 events; $105 \pm 24 \text{ g/m}^2$). Soil moisture data from the plots indicated that large events led to greater mean, maximum, and minimum soil water content, which may explain the improved carbon-water relations of the dominant species (*Bouteloua gracilis*) at the mid-point of the growing season. These results indicate that the quantity and temporal distribution of rain events in semi-arid grasslands strongly influences biological activity and annual rates of ANPP.

In 2006, I conducted a multi-site experimental manipulation of rainfall to evaluate the relative responsiveness and sensitivity of differing grassland types to more extreme precipitation patterns. Rainout shelters were constructed in semi-arid steppe, mixed grass

prairie, and mesic tallgrass prairie ecosystems ($n = 15$ per grassland type) and growing season rainfall was distributed as 12-, 6-, or 4-events according to long-term average seasonal trends. At the mesic end of the gradient (tallgrass prairie), longer dry intervals between events led to extended periods of below-average soil water content that increased plant water stress and reduced ANPP by 18%. The opposite response was observed at the dry end (semi-arid steppe), where a shift to fewer, but larger, events increased periods of above-average soil water content, reduced seasonal plant water stress and resulted in a 30% increase in ANPP. Plant species richness peaked in mixed grass prairie, which was intermediate and the most sensitive to more extreme rainfall regimes (+70% increase in ANPP). These results highlight the difficulties in extending inference from single site experiments to whole ecosystems or biomes and demonstrate the complexity inherent in predicting how terrestrial ecosystems will respond to novel climate conditions.

Finally, I compared field-based experimental results for ANPP and soil moisture from shortgrass steppe and tallgrass prairie ecosystems with simulated results from DAYCENT – a terrestrial ecosystem model. The DAYCENT model contains soil water, plant productivity, and biogeochemical sub-models that operate on a daily time step and has been used extensively for predicting ecosystem responses to global changes. For both ecosystems, I simulated the 2006 growing season and then incorporated the treatment scenarios (12-, 6-, or 4-events, respectively) into annual precipitation regimes for 100 years into the future. While trends for field-based and simulated ANPP data were similar in tallgrass prairie, DAYCENT simulated minimal ANPP differences for the semi-arid steppe. Comparisons of observed versus simulated soil water dynamics for

both ecosystems revealed relatively high r^2 values; however, strong agreement was limited to intermediate values for soil water content. Experimental data suggest that large rain events result in extended periods of elevated soil water content, conditions that were not simulated by DAYCENT. Because extreme rainfall patterns represent novel climate conditions for many ecosystems, models will require additional data from field experiments to accurately parameterize the physical and biogeochemical consequences of conditions that have not been historically experienced by ecosystems.

The results of this dissertation highlight variability in ANPP within grasslands and the independent and interactive drivers that control this variability in both time and space. Grassland structure and function is strongly influenced by water availability, which makes this ecosystem particularly sensitive to ongoing changes in precipitation patterns and rising atmospheric temperatures. In 1992, Sala and Lauenroth demonstrated that the productivity response of individual grassland ecosystems to interannual variability in precipitation cannot be easily predicted by the spatial relationship for the grassland region as a whole. Results from this dissertation further suggest that individual ecosystems differ in their response to intra-annual variability in precipitation – a general prediction of Global Circulation Models. Whereas mesic tallgrass prairie responded negatively (via a reduction in ANPP) to a shift to larger or more extreme rainfall events, semi-arid shortgrass steppe responded positively (with an increase in ANPP) to this predicted climate change scenario. Mixed grass prairie, intermediately located between semi-arid and mesic grasslands, was most responsive to this forecast change in precipitation. Changes in climate will occur against a backdrop of environmental variation that includes differences in land management, soil structure/development, and

landscape heterogeneity. Evidence from an analysis of long-term data in mesic tallgrass prairie revealed that annual fire strengthened coherence in interannual dynamics of ANPP between sampling locations and that this management strategy also resulted in the close coupling of ANPP dynamics with precipitation. The lack of coherence in unburned sampling locations (both with one another and annual precipitation) suggests that climate change will impact landscapes in different ways. This is an important consideration in the selection of study sites as regional proxies and/or monitoring locations to represent different regions or ecosystems to global change. In closing, the results of this dissertation emphasize the integral part of retrospective analysis coupled with experimental and modeling studies in forecasting the impacts of global changes on ecosystems.

Appendix:

1. Figure A.1. Forb ANPP in response to fire frequency in mesic tallgrass prairie
2. Input files and parameterization for the DAYCENT terrestrial ecosystem model

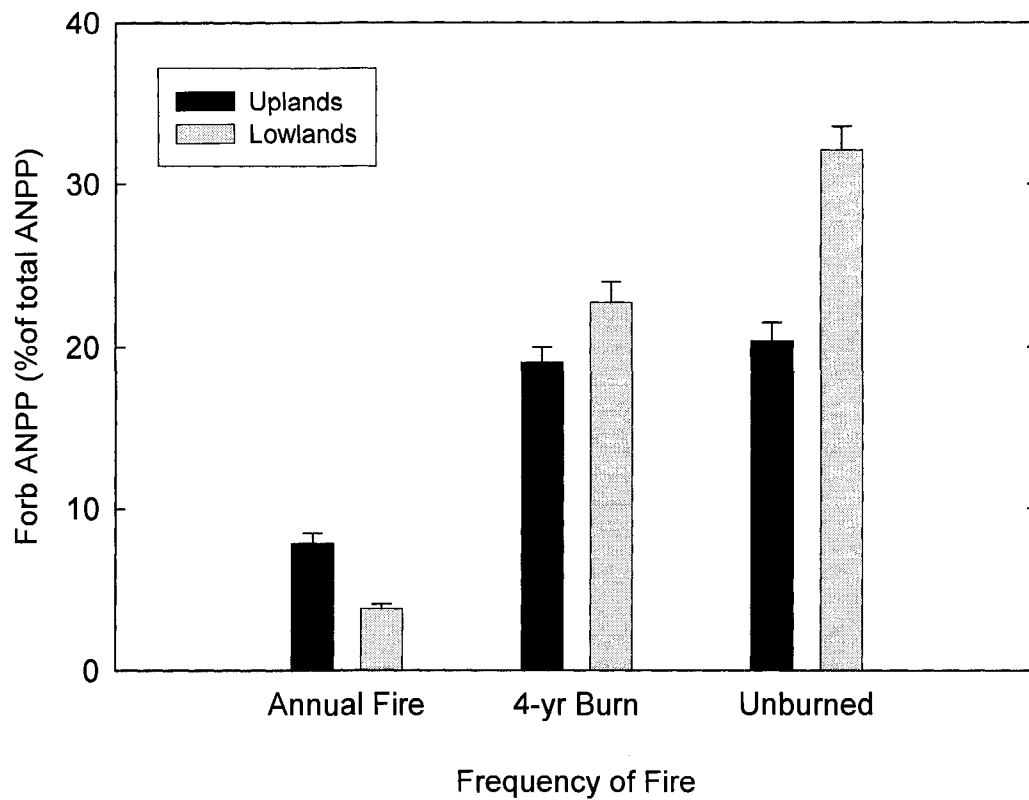


Figure A.1. Forb aboveground net primary productivity (ANPP, percentage of total ANPP) in annually burned, 4-yr burned, and unburned watersheds at the Konza Prairie Long-Term Ecological Research site. Data have been divided into upland and lowland topographic positions and long-term mean values ± 1 SE are presented.

Appendix 2

Key input files for the DAYCENT terrestrial ecosystem model

KNZ (mesic tallgrass prairie site)

fire.100 file

M MEDIUM (Konza Fire)

0.7	'FLFREM'
0.7	'FDFREM(1)'
0.3	'FDFREM(2)'
0.700	'FDFREM(3)'
0.600	'FDFREM(4)'
0.100	'FRET(1,1)'
0.1	'FRET(1,2)'
1.0	'FRET(1,3)'
1.0	'FRET(1,4)'
0.003	'FRET(2,1)'
0.200	'FRET(2,2)'
0.000	'FRET(2,3)'
0.000	'FRET(2,4)'
0.003	'FRET(3,1)'
0.200	'FRET(3,2)'
0.000	'FRET(3,3)'
0.000	'FRET(3,4)'
0.2	'FRTSH'
10.0	'FNUE(1)'
30.0	'FNUE(2)'

knz.100 file

*** Climate parameters

1.6963	'PRECIP(1)'
2.8421	'PRECIP(2)'
4.9473	'PRECIP(3)'
7.6479	'PRECIP(4)'
10.5565	'PRECIP(5)'
12.5073	'PRECIP(6)'
10.2487	'PRECIP(7)'
11.0042	'PRECIP(8)'
6.6331	'PRECIP(9)'
6.1983	'PRECIP(10)'
3.6865	'PRECIP(11)'
2.2896	'PRECIP(12)'
0.9646	'PRCSTD(1)'

2.4361	'PRCSTD(2)'
3.3296	'PRCSTD(3)'
4.5631	'PRCSTD(4)'
7.5814	'PRCSTD(5)'
6.9471	'PRCSTD(6)'
8.8229	'PRCSTD(7)'
5.7783	'PRCSTD(8)'
4.0105	'PRCSTD(9)'
4.4311	'PRCSTD(10)'
2.7815	'PRCSTD(11)'
2.0921	'PRCSTD(12)'
0.0209	'PRCSKW(1)'
1.1358	'PRCSKW(2)'
0.5136	'PRCSKW(3)'
1.4465	'PRCSKW(4)'
1.5984	'PRCSKW(5)'
0.5994	'PRCSKW(6)'
1.8349	'PRCSKW(7)'
0.2883	'PRCSKW(8)'
0.7664	'PRCSKW(9)'
0.6308	'PRCSKW(10)'
0.8765	'PRCSKW(11)'
1.0536	'PRCSKW(12)'
-6.8475	'TMN2M(1)'
-4.7229	'TMN2M(2)'
0.0061	'TMN2M(3)'
5.9690	'TMN2M(4)'
11.5071	'TMN2M(5)'
16.5691	'TMN2M(6)'
19.7996	'TMN2M(7)'
18.8719	'TMN2M(8)'
13.3660	'TMN2M(9)'
6.7743	'TMN2M(10)'
0.1054	'TMN2M(11)'
-5.8127	'TMN2M(12)'
4.9079	'TMX2M(1)'
7.9232	'TMX2M(2)'
13.6313	'TMX2M(3)'
19.6680	'TMX2M(4)'
24.4809	'TMX2M(5)'
29.1133	'TMX2M(6)'
32.6892	'TMX2M(7)'
32.0074	'TMX2M(8)'
27.1766	'TMX2M(9)'
20.4007	'TMX2M(10)'
12.2783	'TMX2M(11)'

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5.0386      'TMX2M(12)'
*** Site and control parameters
0.00000     'IVAUTO'
1.00000     'NELEM'
39.06000    'SITLAT'
96.32000    'SITLNG'
0.08000     'SAND'
0.60000     'SILT'
0.32000     'CLAY'
0.00000     'ROCK'
1.40000     'BULKD'
7.00000     'NLAYER'
4.00000     'NLAYPG'
1.00000     'DRAIN'
0.00000     'BASEF'
0.00000     'STORMF'
8.00000     'PRECRO'
0.15000     'FRACRO'
0.00000     'SWFLAG'
0.20000     'AWILT(1)'
0.20000     'AWILT(2)'
0.20000     'AWILT(3)'
0.20000     'AWILT(4)'
0.20000     'AWILT(5)'
0.20000     'AWILT(6)'
0.20000     'AWILT(7)'
0.20000     'AWILT(8)'
0.20000     'AWILT(9)'
0.30000     'AWILT(10)'
0.30000     'AFIEL(1)'
0.30000     'AFIEL(2)'
0.30000     'AFIEL(3)'
0.30000     'AFIEL(4)'
0.30000     'AFIEL(5)'
0.30000     'AFIEL(6)'
0.30000     'AFIEL(7)'
0.30000     'AFIEL(8)'
0.30000     'AFIEL(9)'
0.00000     'AFIEL(10)'
6.30000     'PH'
1.00000     'PSLSRB'
2.00000     'SORPMX'
*** External nutrient input parameters
1.10000     'EPNFA(1)'
0.00700     'EPNFA(2)'
30.0000     'EPNFS(1)'

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0.01000	'EPNFS(2)'
0.00000	'SATMOS(1)'
0.00000	'SATMOS(2)'
0.00000	'SIRRI'
*** Organic matter initial values	
20.00000	'SOM1CI(1,1)'
0.00000	'SOM1CI(1,2)'
60.0000	'SOM1CI(2,1)'
0.00000	'SOM1CI(2,2)'
3200.000	'SOM2CI(1)'
0.00000	'SOM2CI(2)'
1700.0000	'SOM3CI(1)'
0.00000	'SOM3CI(2)'
16.00000	'RCES1(1,1)'
50.00000	'RCES1(1,2)'
50.00000	'RCES1(1,3)'
12.00000	'RCES1(2,1)'
50.00000	'RCES1(2,2)'
50.00000	'RCES1(2,3)'
17.00000	'RCES2(1)'
117.0000	'RCES2(2)'
117.0000	'RCES2(3)'
8.00000	'RCES3(1)'
62.0000	'RCES3(2)'
62.0000	'RCES3(3)'
100.0000	'CLITTR(1,1)'
0.00000	'CLITTR(1,2)'
100.0000	'CLITTR(2,1)'
0.00000	'CLITTR(2,2)'
66.0000	'RCELIT(1,1)'
300.0000	'RCELIT(1,2)'
300.0000	'RCELIT(1,3)'
66.0000	'RCELIT(2,1)'
300.0000	'RCELIT(2,2)'
300.0000	'RCELIT(2,3)'
0.00000	'AGLCIS(1)'
0.00000	'AGLCIS(2)'
0.00000	'AGLIVE(1)'
0.00000	'AGLIVE(2)'
0.00000	'AGLIVE(3)'
150.0000	'BGLCIS(1)'
0.00000	'BGLCIS(2)'
3.00000	'BGLIVE(1)'
0.40000	'BGLIVE(2)'
0.40000	'BGLIVE(3)'
50.0000	'STDCIS(1)'

0.00000	'STDCIS(2)'
0.80000	'STDEDE(1)'
0.20000	'STDEDE(2)'
0.20000	'STDEDE(3)'
*** Forest organic matter initial parameters	
0.00000	'RLVCIS(1)'
0.00000	'RLVCIS(2)'
0.00000	'RLEAVE(1)'
0.00000	'RLEAVE(2)'
0.00000	'RLEAVE(3)'
0.00000	'FBRCIS(1)'
0.00000	'FBRCIS(2)'
0.00000	'FBRCHE(1)'
0.00000	'FBRCHE(2)'
0.00000	'FBRCHE(3)'
7000.00	'RLWCIS(1)'
0.00000	'RLWCIS(2)'
50.0000	'RLWODE(1)'
0.00000	'RLWODE(2)'
0.00000	'RLWODE(3)'
250.000	'FRTCIS(1)'
0.00000	'FRTCIS(2)'
3.00000	'FROOTE(1)'
0.00000	'FROOTE(2)'
0.00000	'FROOTE(3)'
300.000	'CRTCIS(1)'
0.00000	'CRTCIS(2)'
3.60000	'CROOTE(1)'
0.00000	'CROOTE(2)'
0.00000	'CROOTE(3)'
105.000	'WD1CIS(1)'
0.00000	'WD1CIS(2)'
1400.00	'WD2CIS(1)'
0.00000	'WD2CIS(2)'
180.000	'WD3CIS(1)'
0.00000	'WD3CIS(2)'
*** Mineral initial parameters	
0.25000	'MINERL(1,1)'
0.00000	'MINERL(2,1)'
0.00000	'MINERL(3,1)'
0.00000	'MINERL(4,1)'
0.00000	'MINERL(5,1)'
0.00000	'MINERL(6,1)'
0.00000	'MINERL(7,1)'
0.00000	'MINERL(8,1)'
0.00000	'MINERL(9,1)'

0.00000	'MINERL(10,1)'
0.50000	'MINERL(1,2)'
0.00000	'MINERL(2,2)'
0.00000	'MINERL(3,2)'
0.00000	'MINERL(4,2)'
0.00000	'MINERL(5,2)'
0.00000	'MINERL(6,2)'
0.00000	'MINERL(7,2)'
0.00000	'MINERL(8,2)'
0.00000	'MINERL(9,2)'
0.00000	'MINERL(10,2)'
0.50000	'MINERL(1,3)'
0.00000	'MINERL(2,3)'
0.00000	'MINERL(3,3)'
0.00000	'MINERL(4,3)'
0.00000	'MINERL(5,3)'
0.00000	'MINERL(6,3)'
0.00000	'MINERL(7,3)'
0.00000	'MINERL(8,3)'
0.00000	'MINERL(9,3)'
0.00000	'MINERL(10,3)'
0.00000	'PARENT(1)'
50.0000	'PARENT(2)'
50.0000	'PARENT(3)'
0.00000	'SECNDY(1)'
15.0000	'SECNDY(2)'
2.00000	'SECNDY(3)'
0.00000	'OCCLUD'
*** Water initial parameters	
0.00000	'RWCF(1)'
0.00000	'RWCF(2)'
0.00000	'RWCF(3)'
0.00000	'RWCF(4)'
0.00000	'RWCF(5)'
0.00000	'RWCF(6)'
0.00000	'RWCF(7)'
0.00000	'RWCF(8)'
0.00000	'RWCF(9)'
0.00000	'RWCF(10)'
0.00000	'SNLQ'
0.00000	'SNOW'

crop.100 file

TMC4 Temperate_Tallgrass_[Konza_tallgrass]
0.50000 'PRDX(1)'

22.0000	'PPDF(1)'
38.0000	'PPDF(2)'
1.00000	'PPDF(3)'
2.50000	'PPDF(4)'
1.00000	'BIOFLG'
60.0000	'BIOK5'
1.00000	'PLTMRF'
100.0000	'FULCAN'
1.00000	'FRTCINDX'
0.70000	'FRTC(1)'
0.35000	'FRTC(2)'
3.00000	'FRTC(3)'
0.20000	'FRTC(4)'
0.1	'FRTC(5)'
0.50	'CFRTC(1)'
0.25	'CFRTC(2)'
0.70	'CFRTCW(1)'
0.30	'CFRTCW(2)'
200.00000	'BIOMAX'
20.00000	'PRAMN(1,1)'
390.00000	'PRAMN(2,1)'
340.00000	'PRAMN(3,1)'
30.00000	'PRAMN(1,2)'
390.00000	'PRAMN(2,2)'
340.00000	'PRAMN(3,2)'
40.00000	'PRAMX(1,1)'
440.0000	'PRAMX(2,1)'
440.0000	'PRAMX(3,1)'
80.0000	'PRAMX(1,2)'
440.0000	'PRAMX(2,2)'
440.0000	'PRAMX(3,2)'
60.0000	'PRBMN(1,1)'
390.0000	'PRBMN(2,1)'
340.0000	'PRBMN(3,1)'
0.00000	'PRBMN(1,2)'
0.00000	'PRBMN(2,2)'
0.00000	'PRBMN(3,2)'
60.0000	'PRBMX(1,1)'
420.0000	'PRBMX(2,1)'
420.0000	'PRBMX(3,1)'
0.00000	'PRBMX(1,2)'
0.00000	'PRBMX(2,2)'
0.00000	'PRBMX(3,2)'
0.02000	'FLIGNI(1,1)'
0.00120	'FLIGNI(2,1)'
0.26000	'FLIGNI(1,2)'

-0.00150	'FLIGNI(2,2)'
0.00000	'HIMAX'
0.00000	'HIWSF'
0.00000	'HIMON(1)'
0.00000	'HIMON(2)'
0.50000	'EFRGRN(1)'
0.50000	'EFRGRN(2)'
0.50000	'EFRGRN(3)'
0.04000	'VLOSSP'
0.20000	'FSDETH(1)'
0.95000	'FSDETH(2)'
0.20000	'FSDETH(3)'
150.0000	'FSDETH(4)'
0.15000	'FALLRT'
0.07000	'RDR'
2.00000	'RTDTMP'
0.50000	'CRPRTF(1)'
0.00000	'CRPRTF(2)'
0.00000	'CRPRTF(3)'
0.00000	'SNFXMX(1)'
27.0000	'DEL13C'
1.25000	'CO2IPR'
0.75000	'CO2ITR'
1.25000	'CO2ICE(1,1,1)'
1.00000	'CO2ICE(1,1,2)'
1.00000	'CO2ICE(1,1,3)'
1.25000	'CO2ICE(1,2,1)'
1.00000	'CO2ICE(1,2,2)'
1.00000	'CO2ICE(1,2,3)'
1.00000	'CO2IRS(1)'
0.00000	'KMRSP(1)'
0.00000	'CKMRSPMX(1)'
0.00000	'CKMRSPMX(2)'
0.25000	'NO3PREF(1)'
4.00000	'CLAYPG'
10.0000	'TMPGERM'
1500.00	'DDBASE'
7.0	'TMPKILL'
10	'BASETEMP'
100	'MNDDHRV'
200	'MXDDHRV'

SGS – Semi-arid Shortgrass Steppe Site

graz.100 file

G20 Medium_intensity__no_effect_on_production

.2	'FLGREM'
0.05	'FDGREM'
0.3	'GFCRET'
0.8	'GRET(1)'
0.95	'GRET(2)'
0.95	'GRET(3)'
0	'GRZEFF'
0.5	'FECF(1)'
0.9	'FECF(2)'
0.5	'FECF(3)'
0.25	'FECLIG'

sgs.100

CPR CPER

*** Climate parameters

0.60000	'PRECIP(1)'
0.60000	'PRECIP(2)'
1.70000	'PRECIP(3)'
3.20000	'PRECIP(4)'
5.60000	'PRECIP(5)'
5.20000	'PRECIP(6)'
5.80000	'PRECIP(7)'
3.80000	'PRECIP(8)'
3.00000	'PRECIP(9)'
2.00000	'PRECIP(10)'
0.80000	'PRECIP(11)'
0.30000	'PRECIP(12)'
0.68000	'PRCSTD(1)'
0.78000	'PRCSTD(2)'
1.77000	'PRCSTD(3)'
2.73000	'PRCSTD(4)'
4.98000	'PRCSTD(5)'
4.17000	'PRCSTD(6)'
2.57000	'PRCSTD(7)'
2.58000	'PRCSTD(8)'
2.91000	'PRCSTD(9)'
1.99000	'PRCSTD(10)'
1.07000	'PRCSTD(11)'
0.97000	'PRCSTD(12)'
0.00000	'PRCSKW(1)'
0.00000	'PRCSKW(2)'
0.00000	'PRCSKW(3)'
0.00000	'PRCSKW(4)'
0.00000	'PRCSKW(5)'

0.00000	'PRCSKW(6)'
0.00000	'PRCSKW(7)'
0.00000	'PRCSKW(8)'
0.00000	'PRCSKW(9)'
0.00000	'PRCSKW(10)'
0.00000	'PRCSKW(11)'
0.00000	'PRCSKW(12)'
-6.27000	'TMN2M(1)'
-9.80000	'TMN2M(2)'
-5.39000	'TMN2M(3)'
-3.11000	'TMN2M(4)'
4.12000	'TMN2M(5)'
10.5700	'TMN2M(6)'
13.55000	'TMN2M(7)'
12.46000	'TMN2M(8)'
7.15000	'TMN2M(9)'
1.18000	'TMN2M(10)'
-2.35000	'TMN2M(11)'
-7.58000	'TMN2M(12)'
11.7200	'TMX2M(1)'
8.15000	'TMX2M(2)'
14.71000	'TMX2M(3)'
12.98000	'TMX2M(4)'
18.32000	'TMX2M(5)'
28.52000	'TMX2M(6)'
30.65000	'TMX2M(7)'
29.84000	'TMX2M(8)'
27.19000	'TMX2M(9)'
21.04000	'TMX2M(10)'
14.50000	'TMX2M(11)'
7.47000	'TMX2M(12)'
*** Site and control parameters	
0.00000	'IVAUTO'
1.00000	'NELEM'
40.5200	'SITLAT'
104.410	'SITLNG'
0.14000	'SAND'
0.58000	'SILT'
0.28000	'CLAY'
0.00000	'ROCK'
1.20000	'BULKD'
7.00000	'NLAYER'
4.00000	'NLAYPG'
1.00000	'DRAIN'
0.50000	'BASEF'
0.50000	'STORMF'

8.00000	'PRECRO'
0.15000	'FRACRO'
0.00000	'SWFLAG'
0.20000	'AWILT(1)'
0.20000	'AWILT(2)'
0.20000	'AWILT(3)'
0.20000	'AWILT(4)'
0.20000	'AWILT(5)'
0.20000	'AWILT(6)'
0.20000	'AWILT(7)'
0.20000	'AWILT(8)'
0.20000	'AWILT(9)'
0.30000	'AWILT(10)'
0.30000	'AFIEL(1)'
0.30000	'AFIEL(2)'
0.30000	'AFIEL(3)'
0.30000	'AFIEL(4)'
0.30000	'AFIEL(5)'
0.30000	'AFIEL(6)'
0.30000	'AFIEL(7)'
0.30000	'AFIEL(8)'
0.30000	'AFIEL(9)'
0.00000	'AFIEL(10)'
6.30000	'PH'
1.00000	'PSLSRB'
2.00000	'SORPMX'
*** External nutrient input parameters	
0.05000	'EPNFA(1)'
0.00700	'EPNFA(2)'
30.0000	'EPNFS(1)'
0.01000	'EPNFS(2)'
0.00000	'SATMOS(1)'
0.00000	'SATMOS(2)'
0.00000	'SIRRI'
*** Organic matter initial values	
40.00000	'SOM1CI(1,1)'
0.000000	'SOM1CI(1,2)'
450.0000	'SOM1CI(2,1)'
0.000000	'SOM1CI(2,2)'
1000.000	'SOM2CI(1)'
0.000000	'SOM2CI(2)'
1200.000	'SOM3CI(1)'
0.000000	'SOM3CI(2)'
8.000000	'RCES1(1,1)'
25.00000	'RCES1(1,2)'
25.00000	'RCES1(1,3)'

8.000000	'RCES1(2,1)'
25.00000	'RCES1(2,2)'
25.00000	'RCES1(2,3)'
15.00000	'RCES2(1)'
60.00000	'RCES2(2)'
60.00000	'RCES2(3)'
8.000000	'RCES3(1)'
31.00000	'RCES3(2)'
31.00000	'RCES3(3)'
50.00000	'CLITTR(1,1)'
0.000000	'CLITTR(1,2)'
50.00000	'CLITTR(2,1)'
0.000000	'CLITTR(2,2)'
33.00000	'RCELIT(1,1)'
150.0000	'RCELIT(1,2)'
150.0000	'RCELIT(1,3)'
33.00000	'RCELIT(2,1)'
150.0000	'RCELIT(2,2)'
150.0000	'RCELIT(2,3)'
0.000000	'AGLCIS(1)'
0.000000	'AGLCIS(2)'
0.000000	'AGLIVE(1)'
0.000000	'AGLIVE(2)'
0.000000	'AGLIVE(3)'
150.0000	'BGLCIS(1)'
0.000000	'BGLCIS(2)'
3.000000	'BGLIVE(1)'
0.400000	'BGLIVE(2)'
0.400000	'BGLIVE(3)'
50.00000	'STDCIS(1)'
0.000000	'STDCIS(2)'
0.800000	'STDEDE(1)'
0.200000	'STDEDE(2)'
0.200000	'STDEDE(3)'
*** Forest organic matter initial parameters	
0.00000	'RLVCIS(1)'
0.00000	'RLVCIS(2)'
0.00000	'RLEAVE(1)'
0.00000	'RLEAVE(2)'
0.00000	'RLEAVE(3)'
0.00000	'FBRCIS(1)'
0.00000	'FBRCIS(2)'
0.00000	'FBRCHE(1)'
0.00000	'FBRCHE(2)'
0.00000	'FBRCHE(3)'
0.00000	'RLWCIS(1)'

0.00000	'RLWCIS(2)'
0.00000	'RLWODE(1)'
0.00000	'RLWODE(2)'
0.00000	'RLWODE(3)'
0.00000	'FRTCIS(1)'
0.00000	'FRTCIS(2)'
0.00000	'FROOTE(1)'
0.00000	'FROOTE(2)'
0.00000	'FROOTE(3)'
0.00000	'CRTCIS(1)'
0.00000	'CRTCIS(2)'
0.00000	'CROOTE(1)'
0.00000	'CROOTE(2)'
0.00000	'CROOTE(3)'
0.00000	'WD1CIS(1)'
0.00000	'WD1CIS(2)'
0.00000	'WD2CIS(1)'
0.00000	'WD2CIS(2)'
0.00000	'WD3CIS(1)'
0.00000	'WD3CIS(2)'
*** Mineral initial parameters	
0.25000	'MINERL(1,1)'
0.00000	'MINERL(2,1)'
0.00000	'MINERL(3,1)'
0.00000	'MINERL(4,1)'
0.00000	'MINERL(5,1)'
0.00000	'MINERL(6,1)'
0.00000	'MINERL(7,1)'
0.00000	'MINERL(8,1)'
0.00000	'MINERL(9,1)'
0.00000	'MINERL(10,1)'
0.50000	'MINERL(1,2)'
0.00000	'MINERL(2,2)'
0.00000	'MINERL(3,2)'
0.00000	'MINERL(4,2)'
0.00000	'MINERL(5,2)'
0.00000	'MINERL(6,2)'
0.00000	'MINERL(7,2)'
0.00000	'MINERL(8,2)'
0.00000	'MINERL(9,2)'
0.00000	'MINERL(10,2)'
0.50000	'MINERL(1,3)'
0.00000	'MINERL(2,3)'
0.00000	'MINERL(3,3)'
0.00000	'MINERL(4,3)'
0.00000	'MINERL(5,3)'

0.00000	'MINERL(6,3)'
0.00000	'MINERL(7,3)'
0.00000	'MINERL(8,3)'
0.00000	'MINERL(9,3)'
0.00000	'MINERL(10,3)'
0.00000	'PARENT(1)'
50.0000	'PARENT(2)'
50.0000	'PARENT(3)'
0.00000	'SECNDY(1)'
15.0000	'SECNDY(2)'
2.00000	'SECNDY(3)'
0.00000	'OCCLUD'
*** Water initial parameters	
0.00000	'RWCF(1)'
0.00000	'RWCF(2)'
0.00000	'RWCF(3)'
0.00000	'RWCF(4)'
0.00000	'RWCF(5)'
0.00000	'RWCF(6)'
0.00000	'RWCF(7)'
0.00000	'RWCF(8)'
0.00000	'RWCF(9)'
0.00000	'RWCF(10)'
0.00000	'SNLQ'
0.00000	'SNOW'

crop.100 file

CPR	Shortgrass_(steppe_or_desert)
0.500000	'PRDX(1)'
30.00000	'PPDF(1)'
45.00000	'PPDF(2)'
1.000000	'PPDF(3)'
2.500000	'PPDF(4)'
1.000000	'BIOFLG'
60.00000	'BIOK5'
1.000000	'PLTMRF'
100.0000	'FULCAN'
1.000000	'FRTCINDEX'
0.700000	'FRTC(1)'
0.300000	'FRTC(2)'
3.000000	'FRTC(3)'
0.200000	'FRTC(4)'
0.100000	'FRTC(5)'
0.400000	'CFRTCEN(1)'
0.250000	'CFRTCEN(2)'

0.700000	'CFRTCW(1)'
0.300000	'CFRTCW(2)'
200.0000	'BIOMAX'
20.00000	'PRAMN(1,1)'
390.0000	'PRAMN(2,1)'
340.0000	'PRAMN(3,1)'
60.00000	'PRAMN(1,2)'
390.0000	'PRAMN(2,2)'
340.0000	'PRAMN(3,2)'
30.00000	'PRAMX(1,1)'
440.0000	'PRAMX(2,1)'
440.0000	'PRAMX(3,1)'
80.00000	'PRAMX(1,2)'
440.0000	'PRAMX(2,2)'
440.0000	'PRAMX(3,2)'
40.00000	'PRBMN(1,1)'
390.0000	'PRBMN(2,1)'
340.0000	'PRBMN(3,1)'
0.000000	'PRBMN(1,2)'
0.000000	'PRBMN(2,2)'
0.000000	'PRBMN(3,2)'
50.00000	'PRBMX(1,1)'
420.0000	'PRBMX(2,1)'
420.0000	'PRBMX(3,1)'
0.000000	'PRBMX(1,2)'
0.000000	'PRBMX(2,2)'
0.000000	'PRBMX(3,2)'
0.020000	'FLIGNI(1,1)'
0.001200	'FLIGNI(2,1)'
0.260000	'FLIGNI(1,2)'
-0.00150	'FLIGNI(2,2)'
0.000000	'HIMAX'
0.000000	'HIWSF'
0.000000	'HIMON(1)'
0.000000	'HIMON(2)'
0.500000	'EFRGRN(1)'
0.500000	'EFRGRN(2)'
0.500000	'EFRGRN(3)'
0.040000	'VLOSSP'
0.200000	'FSDETH(1)'
0.950000	'FSDETH(2)'
0.200000	'FSDETH(3)'
150.0000	'FSDETH(4)'
0.200000	'FALLRT'
0.050000	'RDR'
2.000000	'RTDTMP'

0.300000	'CRPRTF(1)'
0.000000	'CRPRTF(2)'
0.000000	'CRPRTF(3)'
0.000000	'SNFXMX(1)'
27.00000	'DEL13C'
1.100000	'CO2IPR'
0.650000	'CO2ITR'
1.300000	'CO2ICE(1,1,1)'
1.000000	'CO2ICE(1,1,2)'
1.000000	'CO2ICE(1,1,3)'
1.300000	'CO2ICE(1,2,1)'
1.000000	'CO2ICE(1,2,2)'
1.000000	'CO2ICE(1,2,3)'
1.000000	'CO2IRS'
0.000000	'KMRSP(1)'
0.000000	'CKMRSPMX(1)'
0.000000	'CKMRSPMX(2)'
0.500000	'NO3PREF(1)'
4.000000	'CLAYPG'
10.00000	'TMPGERM'
1500.000	'DDBASE'
7.000000	'TMPKILL'
10.00000	'BASETEMP'
100.0000	'MNDDHRV'
200.0000	'MXDDHRV'