THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

CLIMATE CHANGE INFLUENCE ON ECOHYDROLOGICAL PROCESSES

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirement for the

Degree of

DOCTOR OF PHILOSOPHY

By
JESSE EUGENE BELL
Norman, Oklahoma
2009

CLIMATE CHANGE INFLUENCE ON ECOHYDROLOGICAL PROCESSES

A DISSERTATION APPROVED FOR THE
DEPARTMENT OF BOTANY AND MICROBIOLOGY

BY

____
Dr. Yiqi Luo (chair)

____
Dr. Wayne Elisons

____
Dr. William Ortiz

____
Dr. Aondover A. Tarhule

____
Dr. Mark Meo

To my terrific wife, Elizabeth

ACKNOWLEDGEMENTS

First, I'd like to thank my advisor, Yiqi Luo, who took me in and gave me a chance to accomplish my goal. I appreciate all of the help. I would like to extend my gratitude to Wayne Elisens, William Ortiz, Aondover A. Tarhule, and Mark Meo for their support, advice, and willingness to serve on my advisory committee. I'd also wish to give a special thanks to fellow labmates Xuhui Zhou, Dafeng Hui, Shenfeng Fei, and Ensheng Weng, as well as every other member of the Luo lab. Ensheng – thanks for paving the way. Beck Sherry deserves special thanks for her helpful presence and making sure that the lab is running and functional. Everyone in the lab has been very helpful and provided a wonderful environment for my professional development. Thanks to Rod Kumimoto for his hours of entertainment, interesting scientific discussions, and friendship. I'd also like to thank Gordon Uno for putting up with me and allowing me to TA his class.

Many thanks to Mark Nanny for allowing me to become a National Science Foundation Fellow and help fund my last two years of grad school (also a wonderful trip to Thailand). My fellowship has been a fantastic experience and has really helped me develop as an educator. I've developed wonderful friendships and connections because of this fellowship. I'd also like to thank Linda Wallace for keeping Kessler Field Farm Lab in working order. I'm very grateful to Adell, Bev, Tammy, and Gail for helping me figure out how grad school works. Additionally, I'd like to express my appreciation to all the faculty and graduate students in the Botany and Microbiology department.

Finally, I would like to thank my family members who have remained my foundation during this arduous process. For their unwavering support, I'm truly grateful that I have two wonderful parents to be a part of my life and encourage me in my most difficult times. Lastly, I'd like to thank my beautiful wife, Elizabeth – you have been my greatest discovery during graduate school.

TABLE OF CONTENTS

LIST OF TABLES

Chapter 2

Chapter 3

Chapter 4

LIST OF FIGURES

Chapter 1

Chapter 2

Chapter 3

Chapter 4

ABSTRACT

Coupling of the carbon and hydrological cycles, such as the relationship between photosynthesis and transpiration, are essential global and environmental change issues, which are interrelated to future water availability, carbon and water feedback to climate, and carbon sequestration. The goal of this dissertation is to recapitulate three projects that use independent experimental, analytical, and modeling approaches to evaluate the influence of climate change on the carbon and water cycle. In the first study, I used the Terrestrial ECOsystem (TECO) model to evaluate the ecohydrological and carbon-water coupling response to single and multiple climate change scenarios – this included combinations of warming, elevated CO_2, and altered precipitation on runoff, evaporation, transpiration, rooting zone soil moisture content (RZSM), water use efficiency (WUE), and rain use efficiency (RUE) - in a North American tallgrass prairie. The 200 different scenarios, with gradual change for 100 years, showed strong responses in runoff, evaporation, transpiration, and RZSM to changes in temperature and precipitation, while effects of CO_2 changes were relatively little. For example, runoff decreased by 50% with a 10 ^{o}C increase in temperature and increased by 250% with doubled precipitation. Ecosystem-level RUE increased with CO_2, decreased with precipitation, and optimized at 4-6 ^{o}C of warming. In contrast, plant-level WUE was highest at doubled CO_2, doubled precipitation, and ambient temperature. The different response patterns of RUE and WUE signify that processes at different scales responded uniquely to climate change. Combinations of temperature, CO_2, and precipitation anomalies interactively affected response magnitude and/or patterns of ecohydrological

processes. Our results suggest that ecohydrological processes were considerably affected by global change factors and then likely regulate other ecosystem processes, such as carbon and nitrogen cycling.

The second experiment was conducted to assess the effects of warming and doubled precipitation on soil water dynamics in a tallgrass prairie ecosystem. Using a one year "pulse" experiment, with 4°C warming and a doubling in precipitation intensity, an analysis of annual soil moisture, soil moisture frequency, and water loss was done. There was a decrease in soil moisture frequency from 0–120 cm in both warming and warming with increased precipitation experiments. Different soil depths had similar patterns of change in soil moisture and soil temperature frequency. A statistical difference in soil moisture was found among the different treatment types. A correlation of evapotranspiration and soil moisture allowed for an estimate of changes in evapotranspiration from the wilting point (E_w) to maximum evapotranspiration (E_{max}). These results revealed a shift in the slope and position of E_w to E_{max} with experimental warming. Our results showed that the soil moisture dynamics and the ecohydrology were significantly changed by different global climate change scenarios.

The third study was an investigation the role of experimental warming on carbon-water coupling across multiple ecosystem types. Here I used a meta-analysis technique to evaluate the impact of experimental warming on rain use efficiency. These results indicate that increases in temperature cause a significant increase in RUE. Additionally, we show that experimental warming had the largest impact on shrubland and tundra sites, while grasslands, receiving the highest amount of

precipitation and lowest experimental temperatures, had the second lowest response to experimental warming. Wetland biomes had the lowest response to experimental warming. This research demonstrates that there are temperature limitations that span multiple ecosystems and these results are beneficial for large-scale modeling projects.

Keywords: global climate change, carbon-water coupling, ecohydrology, terrestrial ecosystem ecology, grassland, warming, precipitation, CO_2**,** rain use efficiency, runoff, evaporation, transpiration, soil moisture, water use efficiency, ecosystem modeling

Chapter 1

Introduction

1.1 Introduction

The influence of greenhouse gases on atmospheric temperature is a well understood process. Some of the earliest research on understanding the impact of greenhouse gases on Earth's temperature was done in 1820s by the French scientist Jean Baptiste Joseph Fourier. Subsequent work was done by John Tyndall, a British scientist, on characterizing the particular gases that cause the greenhouse gas effect. In the 1890s, a Swedish scientist, Svante Arrhenius, mathematically derived that an increase in carbon dioxide (CO_2) would increase the Earth's temperature. However, it was not until the 1950s that a United States' scientist, Dr. Charles Keeling, devised a method of measuring atmospheric CO_2 concentrations. Soon afterwards it was discovered that the average concentration of atmospheric CO_2 increased every year and many scientists speculated that the increase in CO_2 was related to the burning of fossil fuels (i.e. coal and oil). Since 1990, the Intergovernmental Panel on Climate Change (IPCC) has released four assessments on the anthropogenic increase in greenhouse gases (e.g. CO_2, N_2O, CH_4, and CFC) and the subsequent connection of increases in atmospheric temperatures.

In the next century, climate change is predicted to continue to change due to various human activities that will increase greenhouse gases (e.g. continued increase in dependence on fossil fuels, destruction of forests, and the increasing human population). As a consequence, CO_2 is predicted to continue to increase and the

Earth's surface temperature is expected to rise somewhere between 1.1 to 6.4 °C by the end of the 20th Century. In addition, warmer atmospheric temperature is likely to result in higher moisture demand and cause alterations in hydrological cycle (Huntington 2006). The IPCC (2007) has indicated that there could be a 0.5 to 1% change in precipitation per decade for the next century. These changes in climate conditions (i.e. temperature, CO_2, and precipitation) could have an unparalleled change in ecosystem processes and functions.

Multiple climate change scenarios have shown to alter different hydrological processes. Huntington (2006) predicted an exponential increase in specific humidity due to an increase in atmospheric temperature. Climate modeling studies estimate that a 3.4% increase in precipitation should occur per every degree Kelvin (Allen and Ingram, 2002). Additional analysis indicates that intensity and severity of precipitation will result from climate change (Easterling et al., 2000). Furthermore, site specific ecosystem studies have evaluated a multitude of possible changes in various hydrological processes under different climate change scenarios. For example, research was conducted on changes in soil moisture (Owensby et al., 1993; Gerten et al., 2007), runoff (Wetherald and Manabe 2002; Betts et al., 2007), transpiration (Nijs et al., 1997; Lockwood et al., 1999;Yang et al., 2003), and plant water use (Allen et al, 2003; Morgan et al., 2004) with different climate change scenarios. No studies, to this author's knowledge, have investigated all hydrological processes under various climate change scenarios or linked these changes with other biogeochemical cycles (e.g. carbon).

Interactions of anthropogenic climate change on ecosystem processes have become a topic of interest to ecologists seeking to scientifically evaluate changes in the Earth's biosphere. This includes investigating the changes in biogeochemical cycles (e.g. carbon, nitrogen, and water). A biogeochemical cycle is a pathway that allows a chemical element, or compound, to move through the Earth's biosphere, atmosphere, hydrosphere and lithosphere. These cycles have now been changed because of human activities. For example, the burning of coal and oil is rapidly releasing stored terrestrial carbon into the atmosphere and stored nitrogen in the atmosphere is being manufactured as agricultural fertilizer through the human-engineered Haber-Bosch process. These unprecedented changes in biogeochemical cycles and climate make it important to understand ecosystem response and its ability to withstand future perturbation.

Ecologists have used multiple methods to investigate future climate change scenarios. This research comprises of field experiments that use various warming techniques, precipitation manipulation, and increased CO_2. A few specific examples include a continuous warming experiment, using infrared heating apparatuses, for the past 9 years at The University of Oklahoma (Wan et al. 2002), a precipitation manipulation experiment, that altered the rainfall frequency and intensity, at the Konza Prairie Biological Station (Harper et al. 2005), and the Duke Forest Face site that has increased CO_2 concentrations to a loblolly pine forest (Ellsworth et al. 1995). Furthermore, a few experiments have used combinations of climate change factors to simulate multidimensional future conditions. For example, there was a one year "pulse" warming and precipitation experiment at The University of Oklahoma (Zhou et al. 2006) that was designed to evaluate the impacts of an anomalous year (or "pulse"). Although a large amount of research has addressed the interaction of climate change and ecosystem processes, there are many environmental questions that remain unanswered.

Ecohydrology is a new discipline that combines both hydrology and ecology to understand the hydrological cycle. It is well known that multiple ecosystem processes actively contribute to the terrestrial hydrological cycle (e.g. transpiration, plant uptake of water, and rainfall interception). Hence, climate change manipulation experiments on various ecosystems allow for a better understanding of the processes that govern ecohydrology. For example, transpiration increased by experimental warming (Nijs et al. 1997) was significantly altered either positively or negatively based on rainfall manipulation (Fay et al. 2003), and decreased with higher atmospheric CO_2 (Polly et al. 1999; Ferrestti et al. 2003). Furthermore, various climate change research has demonstrated that other ecohydrological processes will be changed by factors such as soil moisture (Wullschenger et al. 2002; Morgan et al 2004), runoff (Wetherald and Manabe2002; Betts et al. 2007), and evaporation (Ferretti et al. 2003). Although most of these studies have focused on single factor experiments or large scale modeling efforts, this research has proved valuable and helped in identifying changes in various processes, albeit with some limitations. Hence, climate change will occur in combination with multiple factors and could produce interactions that cannot be accounted for with single factor experiments or large scale modeling. Therefore, identification of these potential interactive processes and regional scale patterns become increasingly important.

There is little available research that focuses on the coupling of biogeochemical cycles. Historically, researchers have generally focused on specific biogeochemical cycles. These cycles, however, are not isolated from each other in nature and always work in concert. Hence, it is important to understand how biogeochemical cycles respond in unison with climate change. In order to examine multiple interactions of biogeochemical cycles and a variety of combinations of climate change scenarios it is sometimes necessary to use modeling.

The work in this dissertation addresses the response of the hydrological cycle and carbon-water cycle coupling to global climate change using three approaches: ecosystem modeling, meta-analysis, and a one year "pulse" experiment. The results of this research will help scientists, politicians, and the general public better understand the implications of global climate change on ecosystem processes especially changes in the hydrological and carbon cycle. This endeavor can help guide future scientific experimental research and, in particular, the modeling component could be very helpful in illustrating which potential climate change combinations are most beneficial for changing ecosystem processes. Additionally, these results could be useful for understanding and implementing local ecosystem processes and feedbacks into regional and global scale models. Politicians, regional planners, and natural resource managers should be interested in the response of carbon and water to different climate change scenarios.

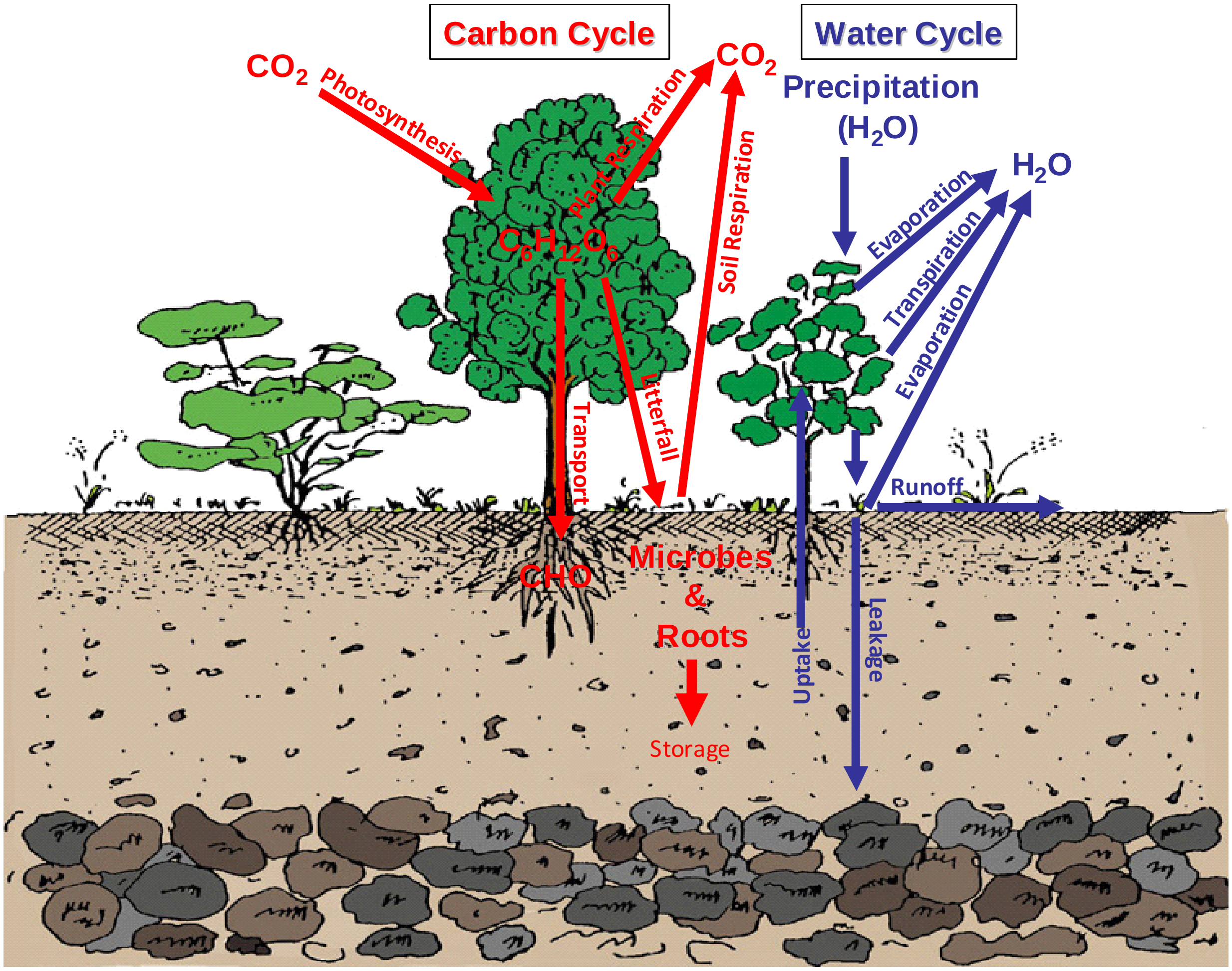


Figure 1.1 Schematic illustration of the terrestrial ecosystem carbon and hydrological cycle. Red arrows represent the transport of carbon and the blue arrows represent the transport of water; each arrow is labeled with the appropriate process. This diagram is to show the similarities between the two cycles and the atmosphere-plant-soil interaction.

In Chapter 2, I use the Terrestrial Ecosystem (TECO) model to analyze changes in the hydrological cycle and explore the relationship of carbon-water coupling at two different scales. This technique focuses on the tallgrass prairie in Oklahoma because of the availability of actual data for validation of the model. In Chapter 3, I analyze soil moisture dynamics during a one year "pulse" experiment at The University of Oklahoma. This experiment was designed to simulate both single and multiple scenarios of climate change in a tallgrass prairie. In Chapter 4, I investigate the carbon-water coupling at multiple experimental warming sites and utilized a meta-analysis statistical technique to evaluate results from individual experimental studies. Finally, Chapter 5 presents the conclusions of this dissertation and discusses future research needs in global climate change. It should be noted that Chapter 2, 3, and 4 are developed for peer-review publication.

Chapter 2

Ecohydrological Responses to Multifactor Global Change in a Tallgrass Prairie: A Modeling Analysis

---

This chapter has been submitted for publication in *JGR – Biogeoscience* (2009)

Abstract

Relative impacts of multiple global change factors on ecohydrological processes in terrestrial ecosystems have not been carefully studied. In this study, we used a terrestrial ecosystem (TECO) model to examine effects of three global change factors (i.e., climate warming, elevated CO_2, and altered precipitation) individually and in combination on runoff, evaporation, transpiration, rooting zone soil moisture content, water use efficiency (WUE), and rain use efficiency (RUE) in a North American tallgrass prairie. We conducted a total of 200 different scenarios with gradual changes of the three factors for 100 years. Our modeling results show strong responses of runoff, evaporation, transpiration, and rooting zone soil moisture to changes in temperature and precipitation, while effects of CO_2 changes were relatively minor. For example, runoff decreased by 50% with a 10 ^{o}C increase in temperature and increased by 250% with doubled precipitation. Ecosystem-level RUE increased with CO_2, decreased with precipitation, and optimized at 4-6 ^{o}C of warming. In contrast, plant-level WUE was highest at doubled CO_2, doubled precipitation, and ambient temperature. The different response patterns of RUE and WUE signify that processes at different scales responded uniquely to climate change. Combinations of temperature, CO_2, and precipitation anomalies interactively affected response magnitude and/or patterns of ecohydrological processes. Our results suggest that ecohydrological processes were considerably affected by global change factors and then likely regulate other ecosystem processes, such as carbon and nitrogen cycling. In particular, substantial changes in runoff to different climate change scenarios could have policy implications because it is a major component to

replenishing freshwater. These modeling results should be tested by and could influence design of field experiments on ecohydrological processes.

Keywords: Temperature, CO_2, precipitation, ecohydrology, rain use efficiency, water use efficiency

2.1. Introduction

The atmospheric concentration of carbon dioxide (CO_2) has increased from pre-industrial levels of 280 ppm to the present level of around 379 ppm (IPCC, 2007). Consequently, the Earth surface's temperature has increased by 0.76 ^{o}C over the last 150 years and at a rate of 0.13 ^{o}C per decade over the last fifty years (IPCC, 2007). It was predicted that Earth surface temperature will continue to increase by 1.1 to 6.4 ^{o}C over the next century (IPCC, 2007). This expected increase in temperature will likely result in alterations in the hydrological cycle at regional and global scales. Huntington (2006), for example, predicted an almost exponential increase in the specific humidity due to the increase in temperature; whereas, modeling analysis showed a 3.4% increase in precipitation per degree Kelvin (Allen and Ingram, 2002). This leads to a question: how will the hydrological cycle in terrestrial ecosystems respond to multifactor climate change?

Individual ecohydrological processes may differentially respond to global change, leading to complex patterns and changes in ecosystem water balance (Gerten et al. 2008). Wetherald and Manabe (2002) showed that modeled runoff decreased globally with an increase in temperature for a thirty year period due to increased evapotranspiration. However, an increase in precipitation in a given year results in increased runoff due to over-saturation of soil moisture. The two components of climate change (i.e., warming and altered precipitation) could interplay to affect evaporation. In addition, plant transpiration is regulated by atmospheric CO_2 concentration (Lockwood, 1999) and length of growing seasons. Sherry et al. (2007) have showed that an increase in temperature extended the growing seasons. This extension in the growing season could increase the amount of water transpired, while an increase in CO_2 can decrease the amount of transpiration from a plant due to a more efficient stomatal opening (Farquhar and Sharkey, 1982). The processes of evaporation, transpiration, and runoff all influence soil moisture content (Yang et al., 2003), The Lund-Potsdam-Jena model demonstrated varying effects of different climate change scenarios on soil moisture in different regions (Gerten et al., 2007) and consequently on biomass growth and net primary production (NPP) (Cramer et al., 2001). To improve our understanding of complex ecohydrological responses to climate change, we need to systematically examine interactions of multiple factors in influencing components of the terrestrial hydrological cycle, such as runoff, soil moisture, transpiration, and evaporation.

Additionally, the hydrological cycle in the terrestrial ecosystem is closely coupled with biogeochemical cycles. The hydrological-biogeochemical coupling may strongly respond to climate change. For example, plant water use efficiency (WUE), a major index of carbon-water coupling, usually increases with an increase in atmospheric CO_2 concentration but decreases with an increase in temperature (Allen et al., 2003) and with an increase in rainfall. It is also essential to understand how WUE responds to multi-factor global change scenarios. Carbon-water coupling at ecosystem and regional scales is usually indicated by rain-use efficiency, which, to the best of our knowledge, has not been carefully studied under different climate change scenarios using experimental approaches.

Comparative studies of ecosystem rain use efficiency (RUE) and plant WUE is helpful in revealing different processes that influence carbon and water coupling. RUE, defined by a ratio of above-ground net primary productivity (ANPP) over yearly precipitation, measures the amount of biomass production per unit of precipitation over one year. Plant-level WUE, defined by a ratio of ANPP over transpiration, measures the amount of water lost via plant transpiration for production of one unit of plant biomass. Plant WUE primarily reflects changes in leaf photosynthesis and transpiration in response to climate change; whereas ecosystem RUE measures changes in plant growth biomass in association with changes in all hydrological processes at the ecosystem scale under different climate change scenarios. An increase in precipitation, for example, usually results in increases not only in plant biomass but also in runoff and soil evaporation. Plant WUE can only measure the plant-level responses. We need ecosystem RUE, to describe changes in other ecosystem processes. Similarly, climate warming and rising atmospheric CO_2 concentration are likely to differentially influence plant WUE and ecosystem RUE.

Ecohydrological processes are influenced by climate change factors individually or in combination. There have been studies on how single-factor climate change influences ecohydrological processes. For example, Knapp et al. (2002) showed that an increase in rainfall variability resulted in a reduction of net primary production and shifts in community composition. Nilsen and Orcutt (1998) showed that decreases in soil moisture will reduce the amount of plant water potential. However, responses of ecohydrological processes to one factor are likely modified by other global change factors. A few experiments have examined ecosystem responses to multifactor global change, primarily on carbon and nutrient processes. How co-varying multifactor climate change will alter ecohydrological processes has not been carefully examined. Modeling studies have the potential to provide insight on the effects of multi-factor global change on ecohydrological processes (Knapp et al., 2007).

This study was designed to understand ecohydrological responses to global change factors (i.e., altered precipitation, warming, and elevated atmospheric CO_2 concentration) individually or in combination. We used the Terrestrial ECOsystem (TECO) model (Weng and Luo 2008) to examine changes in ecohydrological processes under 150 scenarios from 6 levels of climate warming (i.e., increases in temperature by 0, 2, 4, 6, 8, and 10 ^{o}C above the ambient), 5 levels of CO_2 concentration from ambient to doubled CO_2 with each increment of 25%, and 5 levels of precipitation from -25 to 75% of the ambient with each increment of 25%. In addition, we also examined ecosystem responses to combinations of various temperature and precipitation levels at subambient CO_2 concentration (280 ppm) for studying three-way interactions. This modeling analysis was focused on responses of runoff, evaporation, transpiration, rooting zone soil water content, water use efficiency (WUE) and rain use efficiency (RUE) to climate warming, elevated CO_2, and altered precipitation.

2.2. Materials and Methods

Model Description

The terrestrial ecosystem (TECO**)** model is a process-based ecosystem model (Weng and Luo. 2008), which evolved from the terrestrial carbon sequestration (TCS) model developed by Luo and Reynolds (1999). TECO and its precursor, TCS model, have been applied to study responses of forest ecosystems to elevated CO_2 (Luo et al. 2001, 2003, Xu et al. 2006) and examine nonlinear patterns of grassland responses to multifactor global changes (Zhou et al. 2008). The TECO model has four components: a canopy photosynthesis sub-model, a soil water dynamic sub-model, a plant growth sub-model, and a soil carbon transfer sub-model**.** The canopy photosynthesis and soil water dynamic sub-models run at hourly steps while the plant growth and soil carbon transfer sub-models run at daily steps. The TECO model was described in detail by Weng and Luo (2008). Here we provide a brief description of carbon sub-models and a full description of the soil water dynamics sub-model because the latter is the focus of this study.

The canopy sub-model is from a two-leaf photosynthesis model simulating canopy conductance, photosynthesis, transpiration, and energy partitioning (Wang and Leuning, 1998). The sub-model is composed of foliage levels that are divided in sunlit and shaded leaf area index (LAI). Leaf photosynthesis is estimated based on the Farquhar photosynthesis model (Farquhar et al., 1980) and the Ball and Berry stomatal conductance model (Ball et al., 1987). The Plant Growth sub-model simulates allocation of assimilates to plant pools, plant growth, plant respiration, and carbon transfer to litter and soil carbon pools. Allocation of assimilates depends on growth rates of leaves, stems and roots, and varies with phenology based on the ALFALFA model (Luo et al., 1995) and parameterization of litter fall by Arora and Boer (2005). Seasonal dynamics of phenology is represented by the variation of LAI. Commencement of leaf onset is regulated by growing degree days (GDD) and leaf fall is determined by low temperature and dry soil conditions. The end of the growing season occurs at LAI <0.1. The Carbon Transfer sub-model simulates carbon movement from plant pools to litter and soil pools in three layers. Carbon releases from litter and soil carbon pools are based on decomposition rates and pool sizes (Luo and Reynolds, 1999).

The soil water sub-model divides soil into ten layers as in the ALFALFA model (Luo et al., 1995) while soil carbon sub-model has three layers for carbon dynamics. The sub-model simulates dynamics of soil water content based on precipitation, runoff, evapotranspiration, and the amount of water content in the previous time step as:

$$W_{soil} = W_{soil0} + P - Runoff - ET \qquad (1)$$

where W_{soil} is soil water content, W_{soil0} is soil water content in the previous time step, P is precipitation, and ET is evapotranspiration equaling the amount of plant transpiration and soil surface evaporation. Transpiration is calculated based on the canopy model for simulating canopy conductance, photosynthesis and energy partitioning of sunlit and shade leaves separately. Evaporation (E_s) is controlled by the amount of water lost from the soil surface based on evaporative demand (Sellers et al., 1996):

$$E_s = \frac{e^*(T_{soil}) - e_a}{r_{soil} + r_d} \frac{\rho c_p}{\gamma} \frac{1}{\lambda} \qquad (2)$$

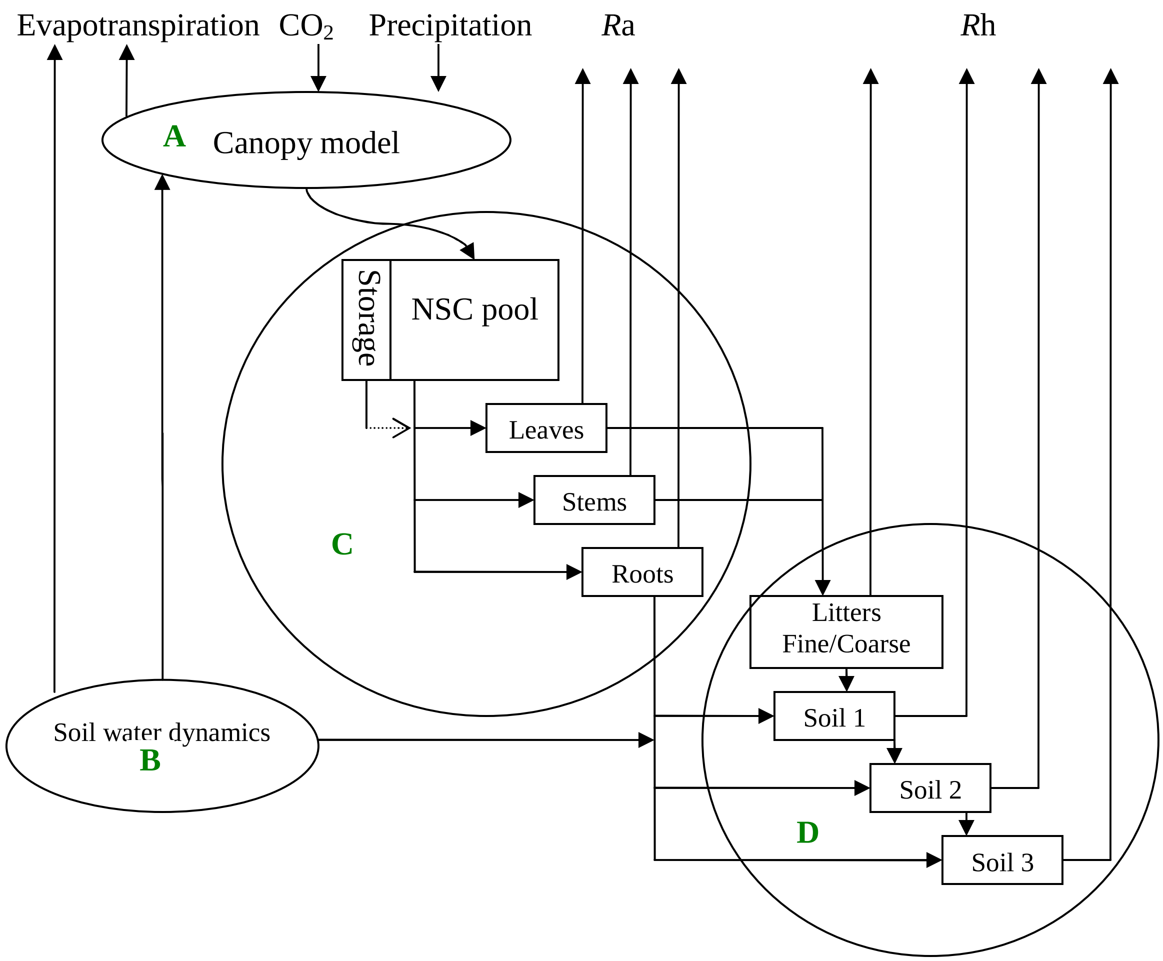


Figure 1. Structural diagram of the TECO model. (A) Canopy model; (B) Soil water dynamics model; (C) Plant growth model; (D) Carbon transfer model. Boxes represent the carbon pools. R_a is autotrophic respiration. R_h is heterotrophic respiration. NSC is non-structure carbohydrates.

The soil water sub-model divides soil into ten layers as in the ALFALFA model (Luo et al., 1995) while soil carbon sub-model has three layers for carbon dynamics. The sub-model simulates dynamics of soil water content based on precipitation, runoff, evapotranspiration, and the amount of water content in the previous time step as:

$$W_{soil} = W_{soil0} + P - Runoff - ET \tag{1}$$

where W_{soil} is soil water content, W_{soil0} is soil water content in the previous time step, P is precipitation, and ET is evapotranspiration equaling the amount of plant transpiration and soil surface evaporation. Transpiration is calculated based on the canopy model for simulating canopy conductance, photosynthesis and energy partitioning of sunlit and shade leaves separately. Evaporation (E_s) is controlled by the amount of water lost from the soil surface based on evaporative demand (Sellers et al., 1996):

$$E_s = \frac{e^*(T_{soil}) - e_a}{r_{soil} + r_d} \frac{\rho c_p}{\gamma} \frac{1}{\lambda} \tag{2}$$

where $e^*(T_{soil})$ is the saturation vapor pressure at temperature of the soil, e_a is the atmospheric vapor pressure, r_{soil} is soil resistance, r_d is the aerodynamic resistance between ground and canopy air space, ρ is the density of air, c_p is the specific heat capacity of air, γ is the psychrometric constant, λ is the latent heat of evaporation (Sellers et al., 1996).

When rainfall input into soil is more than water recharge to soil water holding capacity, runoff occurs and is estimated by the following equation:

$$Runoff = W_{soil} - W_{\max} \tag{3}$$

where, W_{max} is soil water holding capacity. The soil moisture scalar is important in regulating photosynthesis, plant growth rate, and soil carbon turnover time. We estimated the scalar by:

$$f_w = \min\left(1.0, 3.33 \cdot \left(\frac{W_{soil} - W_{\min}}{W_{\max} - W_{\min}}\right)\right) \qquad (4)$$

where, W_{min} is the permanent wilting point.

Model input data included air temperature, soil temperature, relative humidity, precipitation, and photosynthetically active radiation. Vapor pressure deficit was estimated from relative humidity and temperature. All of the daily climate data from 2000 to 2005 were from a MESONET station near Washington, Oklahoma. The model was run to an equilibrium state using 6-year repeated cycles of the climate data. The spin-up simulations were done for 100 years before we applied different scenarios.

Validation

We validated the model using data collected from a long-term warming experiment that has been ongoing at the Kessler's Farm Field Laboratory (KFFL) in McClain County, Oklahoma (34° 59' N, 97° 31' W) since November 1999. The dominant species at the site were C_4 grasses, *Schiachyrium scoparium*, *Sorghastrum nutans*, and *Eragrostis curvula*, and C_3 forbs, *Ambrosia psilostachyia* and *Xanthocephalum texanum*. Average annual rainfall is about 915mm and average annual temperature is 16.3 °C. Data sets that were used in the model validation were aboveground and belowground biomass, soil moisture, and soil respiration. The measurements of aboveground biomass were done once a year for 6 years and belowground biomass only twice (Wan et al., 2005). Measurements of soil moisture and respiration were done twice a month (Luo et al., 2001, Wan et al., 2005, Zhou et al., 2006). All of the model patterns matched closely with the observed data. A full description and graphical representation of model validation can be seen in Weng and Luo (2008).

Table 1 Scenarios for one and two factors

Factors	*Scenarios*
Temperature	ambient, +2°C, +4°C, +6°C, +8°C, +10°C
CO_2 concentration	ambient, +25%, +50%, +100%
Precipitation	ambient, -25%, +25%, +50%, +75%

Scenarios

The validated TECO model was used for this study. We developed 6 levels of climate warming (i.e., increases in temperature by 0, 2, 4, 6, 8, and 10 ^{o}C above the ambient), 5 levels of CO_2 concentration from ambient at 385 ppm to doubled CO_2 with each increment of 25%, and 5 levels of precipitation from -25 to 75% of the ambient with each increment of 25%. We used full combinations of three factors with their respective levels individually and in combinations and examined a total of 150 scenarios. The two- and three-factorial design allowed us to examine interactive effects of different combinations of climate change. For the simultaneous changes in three-factors: temperature, CO_2, and precipitation, we only show modeled results under four precipitation scenarios (-25%, ambient, 25%, and 50%) and three CO_2 concentrations (280, 385, and 780 ppm), representing preindustrial, current, and future conditions. All the combinations were run until conditions mimicked present day and then a gradual change began for the ensuing 100 years. Simulation results averaged of these 6 years were reported in the paper for comparative study of ecosystem responses to different climate change scenarios.

2.3. Results

Runoff

Runoff greatly varied with global change scenarios in precipitation, CO_2, and temperature (Fig. 2). When precipitation changed from a decrease of 25% to increases of 25, 50 and 75% from the control (i.e., ambient precipitation), there was a change in runoff by a decrease of 64% to the increases of 75, 157 and 245%, respectively (Fig. 2, A1). When temperature increased by 2 – 10 ^{o}C, runoff decreased by 25 - 73% (Fig. 2, A2). Changes in atmospheric CO_2 concentration had little impact on runoff as a single global change factor (Fig. 2, A3).

Two-factor climate change had a varying effect on runoff (Fig. 2, B1-3). For example, when temperature increased by 10 ^{o}C with precipitation changes of -25, 25, 50 and 75%, runoff varied from -90, -35, 21 and 92%, respectively (Fig. 2, B1). Precipitation was the primary cause for a change in runoff with different combinations of CO_2 and precipitation scenarios (Fig. 2, B3). Interactive effects of

CO_2 and temperature on runoff were minor (Fig. 2, B2). Three-factor climate change also had varying changes in runoff depending on the scenario (Fig. 2, C1-3). However, changes in CO_2

Rooting Zone Soil Moisture

Simulated rooting zone soil moisture had a relatively small change in percent response to single or multi-factorial global climate change compared to other ecohydrological variables (Fig. 3). The largest change caused by a single global change factor was an 18% decrease in rooting zone soil moisture due to a temperature increase by 10 ^oC (Fig. 3, A2). When precipitation decreased by 25% from ambient, there was a decrease in rooting zone soil moisture by 3.9% (Fig. 3, A1). A precipitation increase by 75% resulted in a rooting zone soil moisture increase of 6.4%. An increase in atmospheric CO_2 concentration had the lowest impact on rooting zone soil moisture (Fig. 3, A3).

Two-factor climate change scenarios had variations in output; however, most of the variation occurred with combinations of precipitation and temperature. Hence, a combination of a 10 ^oC increase in temperature and a precipitation decrease of 25% resulted in a decrease of 22% in rooting zone soil moisture in comparison to that at ambient conditions (Fig. 3, B1). Interactive effects of CO_2 concentration with changes in either temperature or precipitation on rooting zone soil moisture were minor (Fig. 3, B2-3). The patterns of three-factor changes were similar to the patterns of two-factor

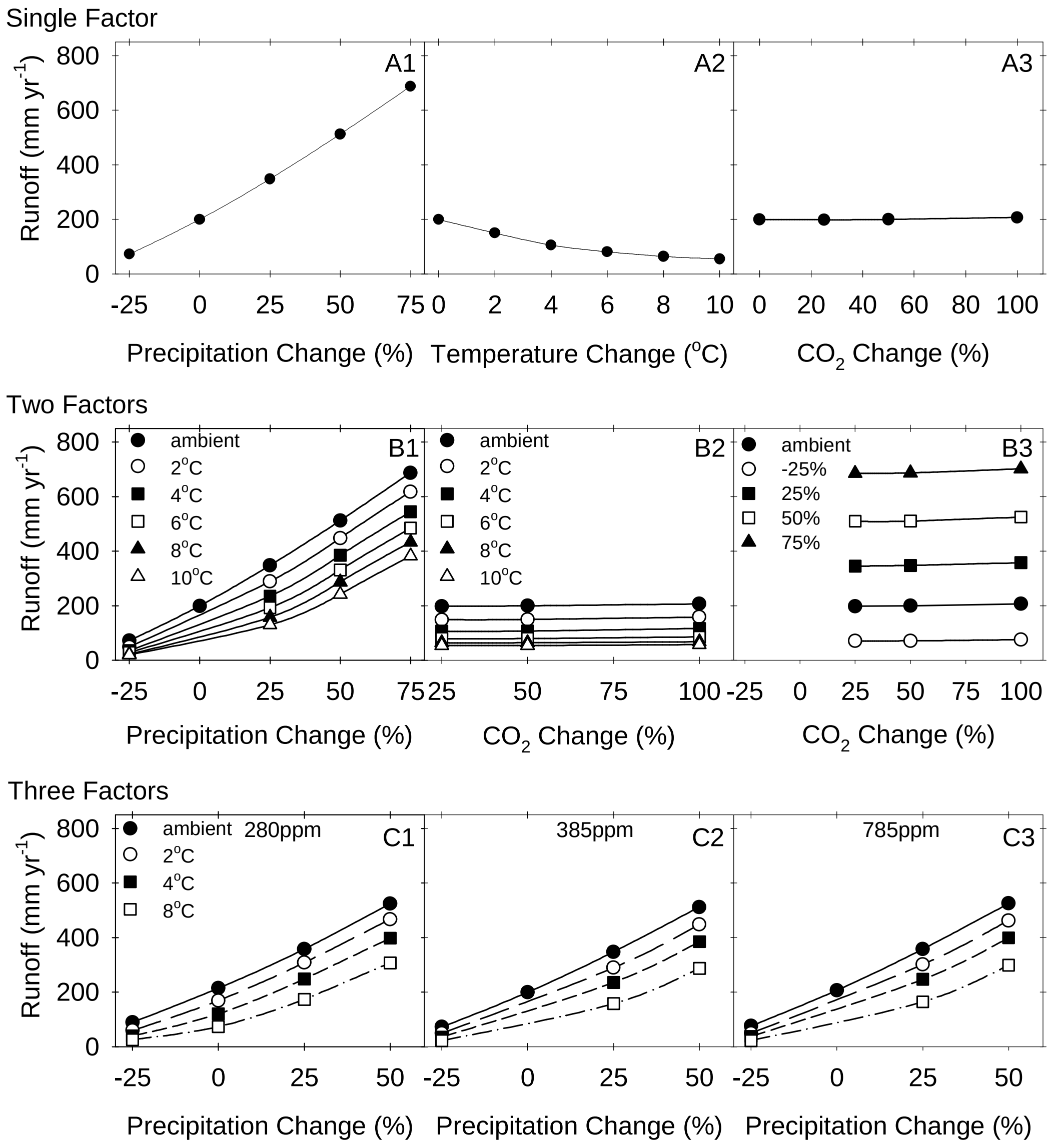


Figure 2. Runoff results from TECO model, (A1-3) single factor climate change scenarios, (B1-3) two factor combinations of precipitation, temperature and CO_2, (C1-3) three-way interactions of with multiple combinations of temperature and precipitation; under 280ppm, 385ppm and 780ppm CO_2 concentrations, respectively.

concentration were miniscule when compared to the changes in precipitation or temperature. Precipitation was the most influential on changes in runoff under three-factor change.

Rooting Zone Soil Moisture

Simulated rooting zone soil moisture had a relatively small change in percent response to single or multi-factorial global climate change compared to other ecohydrological variables (Fig. 3). The largest change caused by a single global change factor was an 18% decrease in rooting zone soil moisture due to a temperature increase by 10 ^oC (Fig. 3, A2). When precipitation decreased by 25% from ambient, there was a decrease in rooting zone soil moisture by 3.9% (Fig. 3, A1). A precipitation increase by 75% resulted in a rooting zone soil moisture increase of 6.4%. An increase in atmospheric CO_2 concentration had the lowest impact on rooting zone soil moisture (Fig. 3, A3).

Two-factor climate change scenarios had variations in output; however, most of the variation occurred with combinations of precipitation and temperature. Hence, a combination of a 10 ^oC increase in temperature and a precipitation decrease of 25% resulted in a decrease of 22% in rooting zone soil moisture in comparison to that at ambient conditions (Fig. 3, B1). Interactive effects of CO_2 concentration with changes in either temperature or precipitation on rooting zone soil moisture were minor (Fig. 3, B2-3). The patterns of three-factor changes were similar to the patterns of two-factor changes; however, there was a slight decrease in rooting zone soil moisture with an increase in CO_2 concentration (Fig. 3, C1-3).

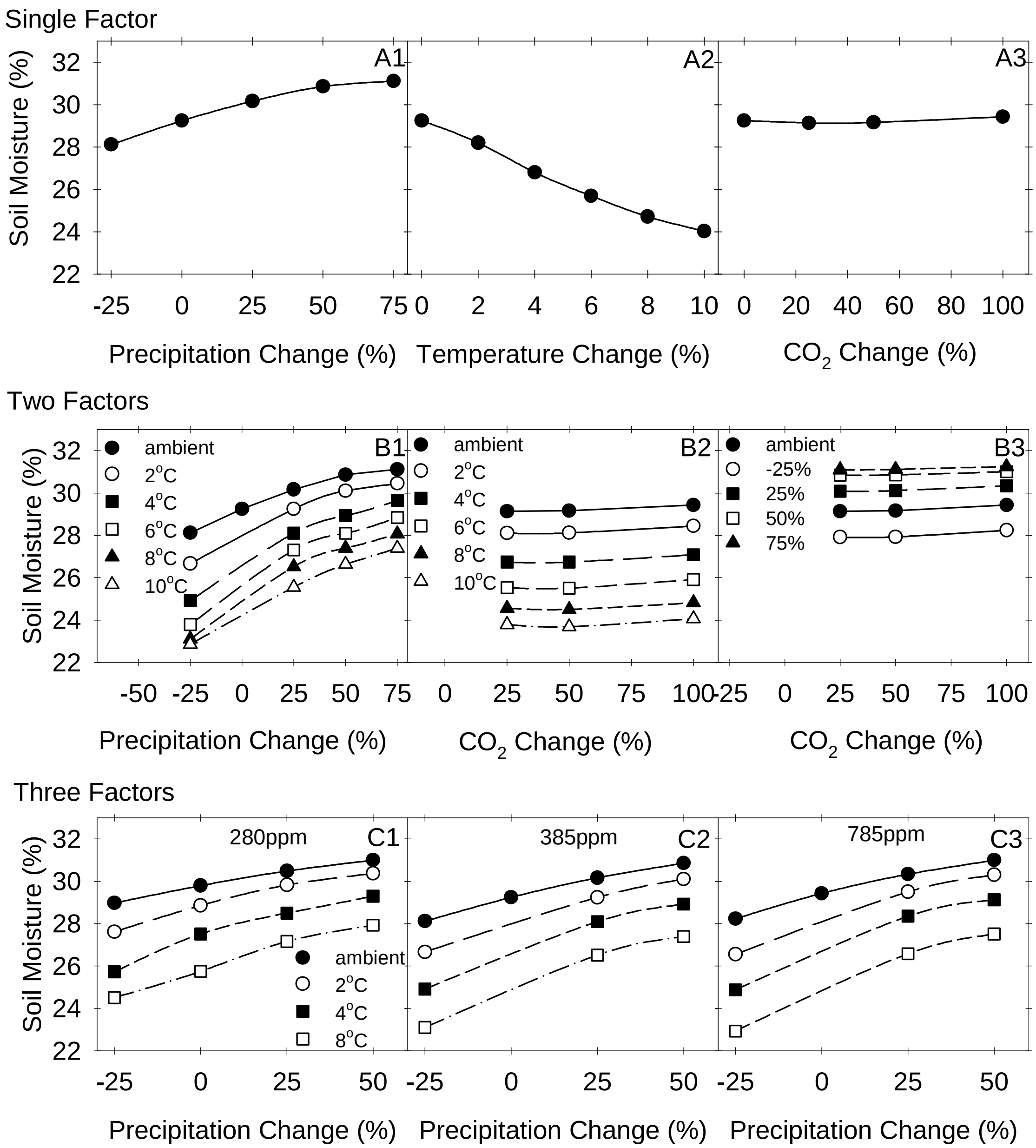


Figure 3. Rooting Zone Soil Moisture results from TECO model, (A1-3) single factor climate change scenarios, (B1-3) two factor combinations of precipitation, temperature and CO_2, (C1-3) three-way interactions of with multiple combinations of temperature and precipitation; under 280ppm, 385ppm and 780ppm CO_2 concentrations, respectively.

Evaporation and Transpiration

Simulated transpiration from the TECO model responded positively to most climate change scenarios. Single-factor precipitation change had the least impact, whereas an increase in temperature had the greatest impact on transpiration (Fig. 4, A1-2). Transpiration varied from -9 to 11% as precipitation varied from -25 to 75% from the control, whereas transpiration increased by 57% with an increase in temperature by 10^{o}C. Doubled CO_2 concentration caused a minor decrease in transpiration (Fig. 4, A3).

Two-factor climate change caused some variations under different scenarios. The greatest degree of change in transpiration occurred with different combinations of both precipitation and temperature (Fig. 4, B1). The largest percent change in transpiration came from combined increases in temperature by 10 ^{o}C and precipitation by 75%; which resulted in a simulated increase of transpiration by 101%. Two-factor change with CO_2 had little impact on the rate of transpiration (Fig. 4, B2-3). Three-factor climate change scenarios had little variation from two-factor precipitation and temperature change (Fig. 4, C1-3).

Simulations of the TECO model showed variable responses of evaporation to different single and multi-factor scenarios of climate change (Fig. 5). Single-factor precipitation had the largest impact on evaporation among the three global change factors. For example, evaporation decreased by 16% from control when precipitation was reduced by 25%, and increased by 27% when precipitation increased by 75% from the ambient level (Fig. 5, A1). Temperature caused the next largest percentage change; a

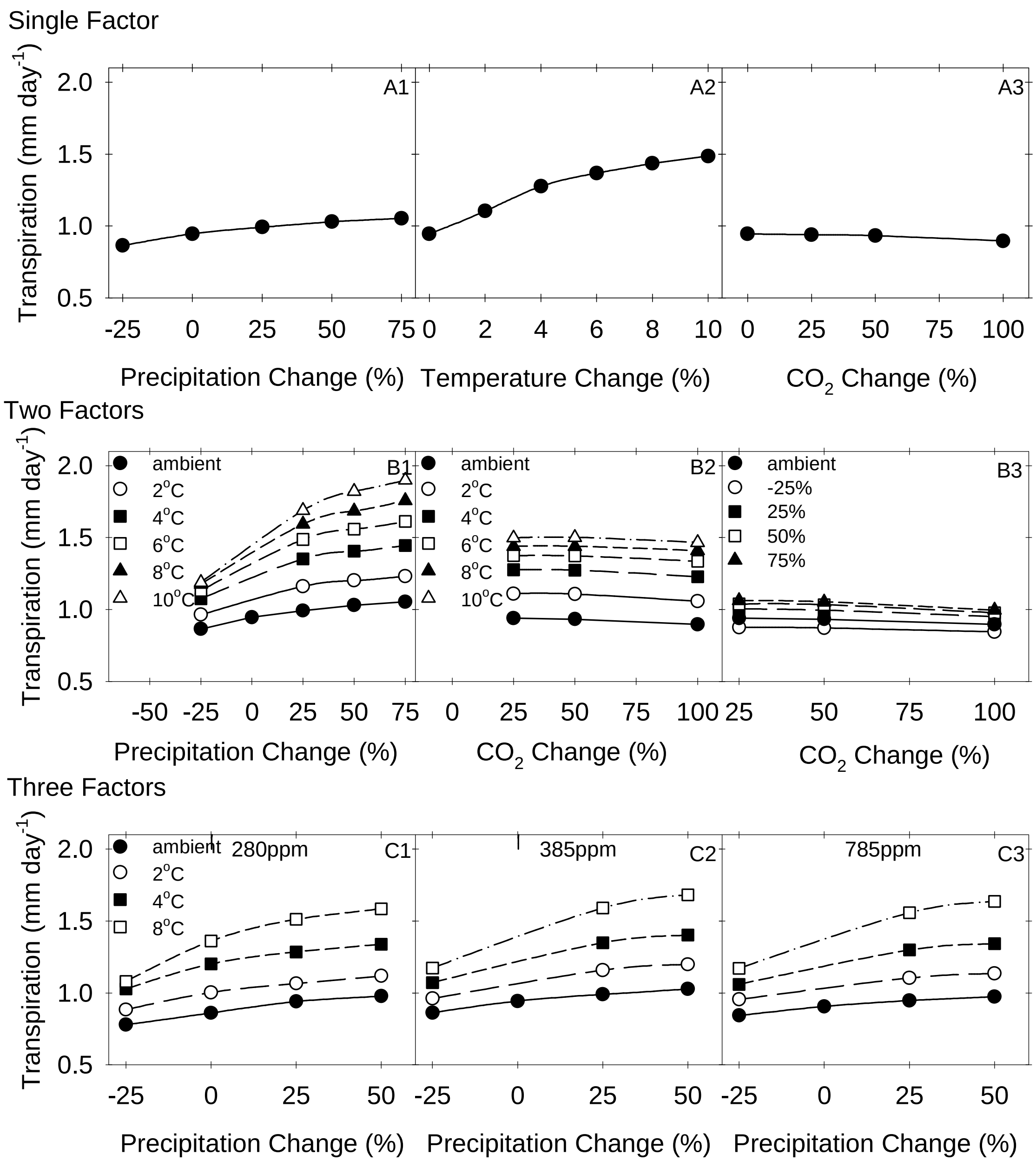


Figure 4. Transpiration results from TECO model, (A1-3) single factor climate change scenarios, (B1-3) two factor combinations of precipitation, temperature and CO_2, (C1-3) three-way interactions of with multiple combinations of temperature and precipitation; under 280ppm, 385ppm and 780ppm CO_2 concentrations, respectively.

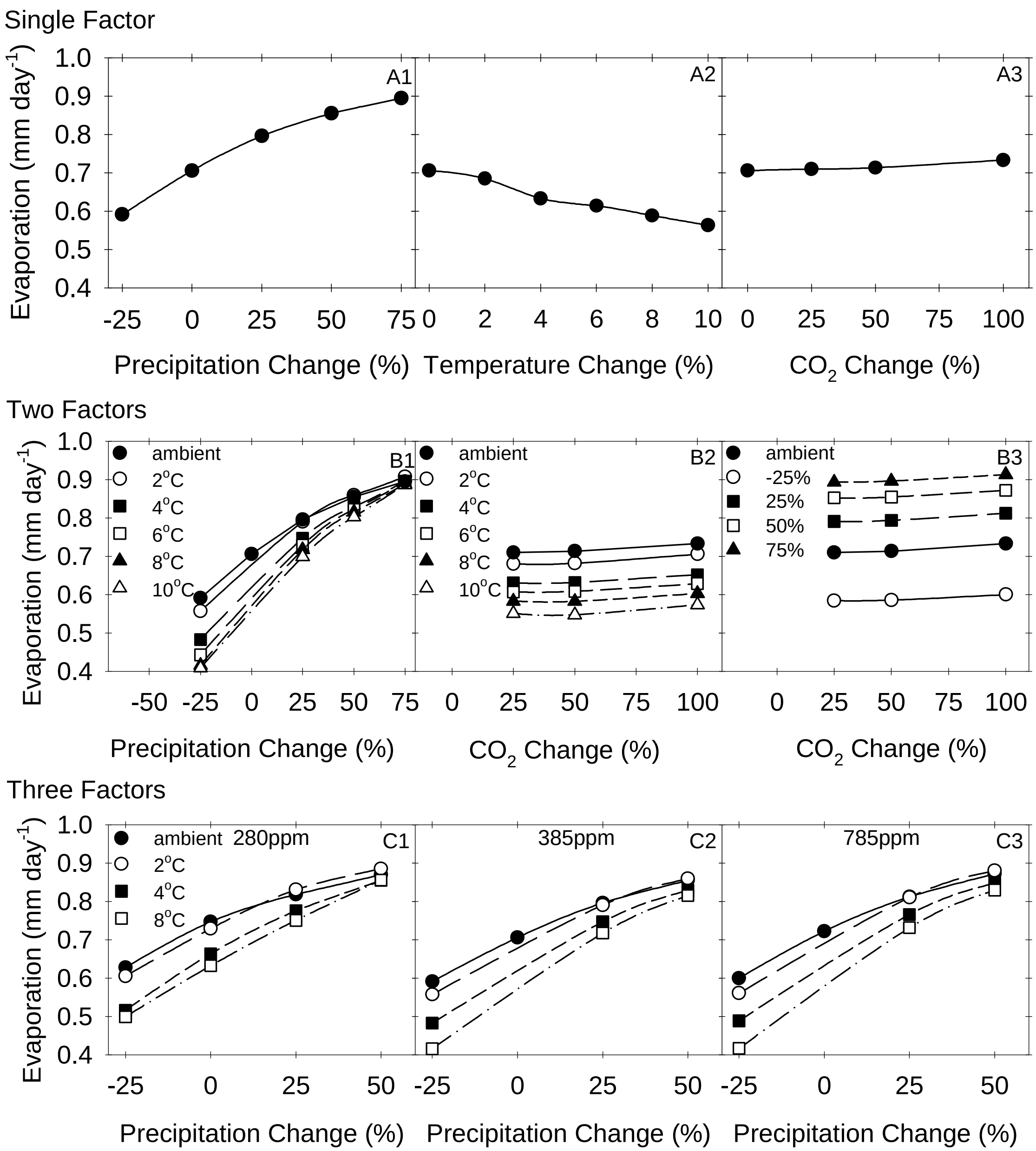


Figure 5. Evaporation results from TECO model, (A1-3) single factor climate change scenarios, (B1-3) two factor combinations of precipitation, temperature and CO_2, (C1-3) three-way interactions of with multiple combinations of temperature and precipitation; under 280ppm, 385ppm and 780ppm CO_2 concentrations, respectively.

10 ^{o}C increase in temperature resulted in a decrease in evaporation by 20% from that of the control (Fig. 5, A2). Single-factor CO_2 concentration had a marginal effect on evaporation (Fig. 5, A3).

Two-factor change had a linear response with all combinations (Fig. 5, B1-3). When temperature increased by 10 ^{o}C and precipitation decreased by 25%, simulated evaporation rate was reduced by 42%. With a CO_2 increase of 100% and a precipitation increase of 75%, evaporation increased by 29%. Three-factor climate change had a response that was most similar to precipitation change. Evaporation had some slight changes under increased temperature and negligible changes under varying CO_2 concentrations.

Rain-use Efficiency

Simulated rain-use efficiency (RUE) was calculated from NPP and annual rainfall (RUE = NPP/rainfall). Single-factor climate change caused varying changes in RUE; with precipitation causing the largest percent change. The largest change in RUE, by 31%, came with a 75% increase in precipitation from ambient (Fig. 6, A1). When precipitation decreased by 25%, RUE increased by 14% in comparison to that of control. Increases in temperature caused nonlinear changes in RUE by 17, 28, 27, 21 and 13%, respectively, with temperature increases of 2, 4, 6, 8 and 10 ^{o}C from the ambient (Fig. 6, A2). When CO_2 concentration increased from ambient by 25, 50, and 100%, RUE increased by 11, 18, and 20% (Fig. 6, A3).

Two- and three-factor climate change scenarios had multiple interactive effects on RUE. For example, a temperature increase of 10^{o}C combined with multiple levels of

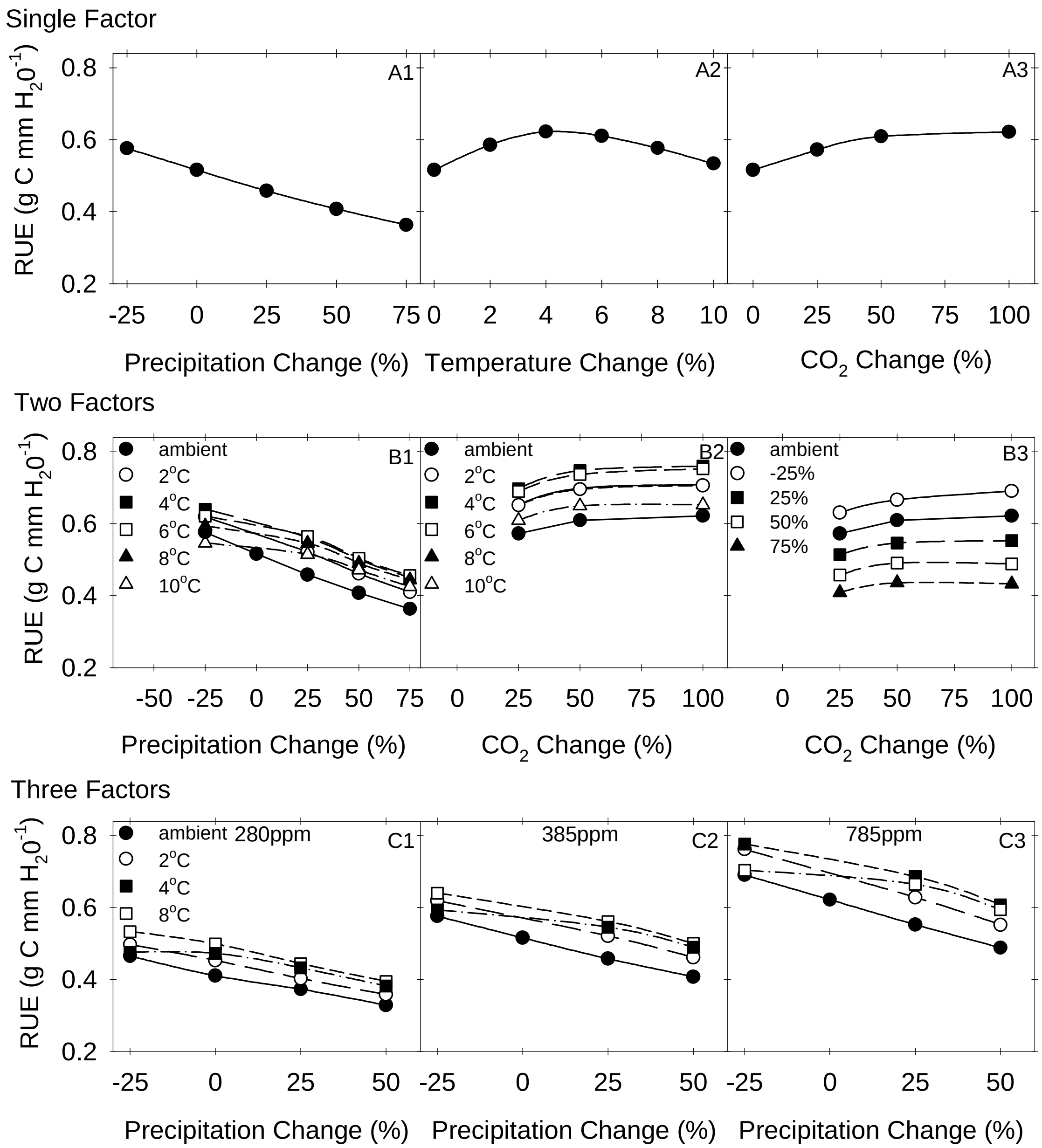


Figure 6. Rain-use efficiency results from TECO model, (A1-3) single factor climate change scenarios, (B1-3) two factor combinations of precipitation, temperature and CO_2, (C1-3) three-way interactions of with multiple combinations of temperature and precipitation; under 280ppm, 385ppm and 780ppm CO_2 concentrations, respectively.

precipitation change (decrease by 25% to increases by 25, 50 and 75%) resulted in corresponding changes in RUE by 16, 9, 0.5, and -9% (Fig. 6, B1). However, at a 10 ^{o}C increase in temperature with CO_2 increases by 25, 50, and 75% there were increases in RUE by 28, 36, and 38%, respectively (Fig. 6, B2). The optimal RUE with two-factor climate change occurred with doubled CO_2 and a 25% decrease in precipitation (Fig. 6, B3), a 4 ^{o}C increase in temperature and a 25% decrease in precipitation (Fig. 6, B1), and a 4 ^{o}C increase in temperature and doubled CO_2 (Fig. 6, B2). The responses of RUE to three-factor climate change scenarios were largely influenced by precipitation; when temperature and CO_2 concentrations also had an impact on RUE (Fig. 6, C1-3).

Water-use Efficiency

Plant-level water-use efficiency (WUE) was calculated from NPP divided by the amount of transpiration (WUE=NPP/Transpiration). Nonlinear responses in WUE were seen with single-factor changes in precipitation (Fig. 7, A1), temperature (Fig. 7, A2), and CO_2 (Fig. 7, A3). WUE increased with precipitation and CO_2 concentration but decreased with an increase in temperature. 10% stimulation in WUE occurred with a single-factor 75% increase in precipitation (Fig. 7, A1) and doubled single-factor CO_2 concentration caused an increase of 26% (Fig. 7, A3). However, WUE decreased by 34% when temperature increased by 10 ^{o}C from control (Fig. 7, A2).

Two-factor scenarios altered WUE in the same nonlinear patterns (Fig. 7, B1-3). Simulated optimal WUE occurred under the scenarios of doubled CO_2 and a 75%

increase in precipitation (Fig. 7, B3), a 75% increase in precipitation at the ambient temperature (Fig. 7, B1), and doubled CO_2 at the ambient temperature (Fig. 7, B2). However, the highest percent change in WUE, i.e., a 39% increase, occurred with a doubled CO_2 concentration and a 75% increase in precipitation. Three-factor scenarios also caused various nonlinear patterns of change in WUE with different conditions (Fig. 7, C1-3).

2.4. Discussion

Little is known about how different ecohydrological processes will respond to varying combinations of CO_2, precipitation and temperature in the future (Knapp et al, 2008). Our modeling results show that all components of the terrestrial hydrological cycle are changed under different scenarios of climate change. These results are important in explaining potential ways in which the ecosystem will respond given future alterations. Hopefully, our modeling results can be tested by and help in the design of future multi-factor experiments. To further illustrate our results, we will first explain how climate change altered ecosystem rain use and plant level water use, and then further explain effects of single- and multiple-factor climate change on the rest components of the water cycle.

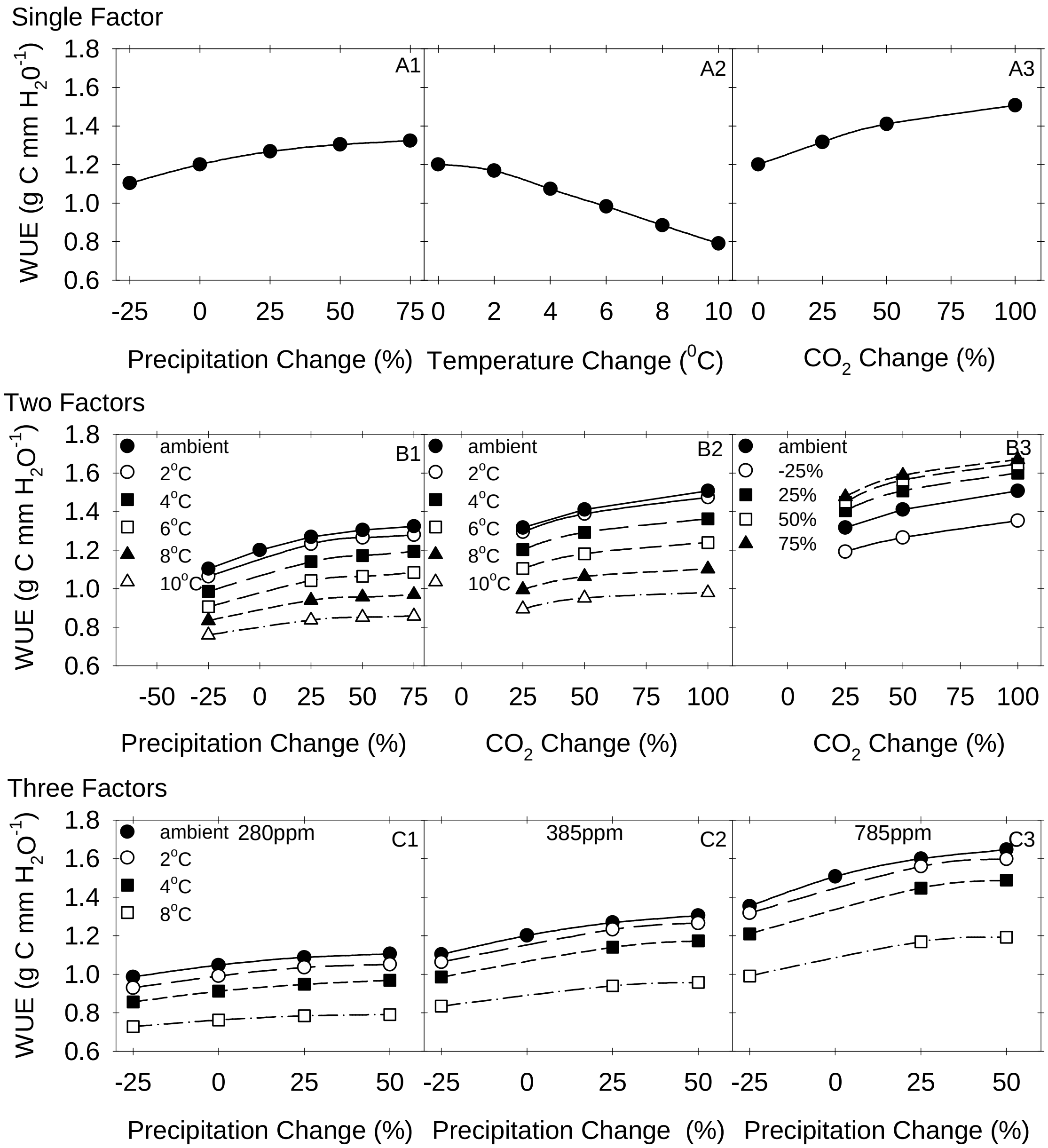


Figure 7. Water-use efficiency results from TECO model, (A1-3) single factor climate change scenarios, (B1-3) two factor combinations of precipitation, temperature and CO_2, (C1-3) three-way interactions of with multiple combinations of temperature and precipitation; under 280ppm, 385ppm and 780ppm CO_2 concentrations, respectively.

Effects of Global Change on Rain- and Water-Use Efficiency

Our simulations showed that ecosystem rain use efficiency (RUE) was dramatically different from plant water use efficiency (WUE) in response to global change. A decrease in precipitation, for example, caused an increase in RUE but a decrease in WUE (Figs. 6 and 7). Our modeled increase in RUE was consistent with the experimental results of Huxman *et al*. (2004), which showed an increase in RUE with decreased precipitation across different biomes, due to an increase in the relative amount of water used for plant production in water limited ecosystems. Our simulated responses of plant-level WUE due to changes in precipitation were similar to the modeling results by Coughenour and Chen (1997). Their results showed that WUE increased with increases in precipitation from 80 to 120% in all studied grasslands, which included Kenya, Colorado, and Kansas. It should be noted that both our modeling results and the results of Coughenour and Chen (1997) are dealing with a system level response in WUE and not leaf level responses. Meanwhile, RUE and WUE differentially responded to warming. RUE optimized at 4-6 ^{o}C temperature increase whereas WUE decreased with temperature (Fig. 6 and 7). Similarly, De Boeck *et al.* (2006) showed that plant WUE in Belgium grasslands decreased with warming. Modeled positive responses of both RUE and WUE to an increase in CO_2 (Fig. 8 and 9) were consistent with experimental results in many studies (e.g., Hui *et al*. 2001, Owensby *et al.* 1993, Morgan *et al.* 2004).

Contrasting responses of RUE and WUE to various scenarios of global change resulted from different effects of environmental factors on processes at different scales. Increased precipitation resulted in dramatic increases in runoff, substantial increases in evaporation, and little changes in transpiration. As a consequence, WUE increased as NPP increased in response to increased precipitation. However, increased precipitation resulted in water loss by evaporation and runoff at a magnitude larger than the magnitude of changes in NPP, resulting in decreased RUE. Warming caused an increase in transpiration in a larger magnitude than that for NPP, leading to decreased plant WUE. Warming increased RUE because NPP was stimulated by warming without a change in precipitation. The stimulation of NPP due to warming was partially caused by increased partitioning of precipitation to transpiration as shown by a modeling study by Weng and Luo (2008). Our modeling analysis demonstrated that plant-level processes to global climate change can not simply be scaled up to predict ecosystem-level responses, which is especially true of the hydrological cycle. Our results show that the plant level WUE is a poor determinate in explaining the total water budget for an ecosystem. However, ecosystem level RUE is more likely to illustrate changes in the rest of the water budget from alterations based on climate change.

Effects of single global change factor on ecohydrological processes

Simulated effects of single factor global change on hydrological processes in ecosystems with the TECO model were generally consistent with results from field experiments and other modeling studies. For example, our simulated runoff increased with precipitation (Fig. 2A) and rising atmospheric CO_2 but decreased with warming. At the global scale, Betts *et al.* (2007) showed that runoff increased by 6% with doubled CO_2. This increase in runoff was due to decreased stomatal conductance and transpiration under elevated CO_2. Regional modeling analysis by Cramer *et al.* (2001) showed that increased CO_2 causes an increase in WUE that will result in more runoff. These results are similar to our results, which showed that with an increase in CO_2 there was a slight increase in runoff and a large increase in WUE. Under the single factor simulation of increased temperature there was a decrease in runoff (Figure 2). There has been little research done on how single factor climate change will alter runoff. A modeling study by Wetherald and Manabe (2002) showed that with an increase in global temperatures there will be an increase in runoff. However, all of these global or regional scale modeling results do not just take warming into account, but also show that warming stimulates precipitation. This comparison of global and regional modeling efforts should be valuable in validating our ecosystem modeling results. Additionally, our ecosystem level results could illustrate possible interactions that may be overlooked by larger scale modeling analysis.

Our modeling results also showed that with a change in temperature alone has the largest impact on transpiration and evaporation. With a 10 ^{o}C increase in temperature there was a 20% decrease in evaporation and a 57% increase in transpiration. The simulation results on transpiration are consistent with the leaf level study by Nijs *et al.* (1997) which showed that transpiration rates increased with warming, although it should be noted that in the same document the canopy level transpiration of *Lolium perenne* decreased with warming. An increase in transpiration due to higher temperatures could be responsible for absorbing more biologically available water and decreasing the amount of soil evaporation. The next largest percent change in evaporation and transpiration was due to precipitation, followed by

CO_2. With an increase in precipitation there was a gradual increase in our simulated results for both evaporation and transpiration. These results correspond to Ferretti *et al.*'s (2003) data that an 11.90% increase in rainfall, from 2000 to 2001, over in a Colorado grassland caused a 73% increase in transpiration and a 100% increase in evaporation. They also showed that with an increase in CO_2 there was a slight increase in transpiration and a decrease or an increase in evaporation from control under different precipitation amounts (Ferretti *et al.* 2003). They attributed the increase in transpiration to an increase in total biomass in the elevated CO_2 plots. Our model results of CO_2 change were not as responsive to changes in ET as other results that have been reported. For example, Ham *et al.* (1995) showed that open-topped chambers with 2x CO_2 enrichment caused a 22% decrease in ET. However, this study was only conducted over a 34 day period during peak biomass; whereas our study was over the entire growing season. Studies over a larger spatial area show that minimal reduction in ET is due to increased leaf area under elevated CO_2 (Kergoat *et al.* 2002; Schafer *et al.* 2002).

TECO model results showed that increased temperature had the greatest impact on rooting-zone soil moisture (Figure 3). Reduced rooting zone soil moisture at increased air temperature was probably a response to an increase in transpiration and an increase in the growing season. Precipitation caused the second greatest change in percentage with an increase in rooting zone soil moisture. An increase in precipitation resulted in a strong increase in rooting zone soil moisture. Lastly, CO_2 had the least and most variable influence on rooting zone soil moisture. A doubling of CO_2 caused a slight increase in soil moisture relative to that at control. Other results have shown a similar pattern of soil moisture under elevated CO_2 (Wullschleger *et al*. 2002 and Morgan *et al.* 2004).

Some of the modeled results, however, have not yet been carefully explored by field research. This is due to the fact that not all ecohydrological components have been fully evaluated in response to climate change. Most of the experimental studies did not examine all of the ecohydrological components under climate change. This lack of data leaves a large void to be filled by future research.

Interactive effects of multifactor global change on ecohydrological processes

Multi-factor climate change resulted in both linear and nonlinear interactions of individual factors in influencing ecohydrological processes (Zhou *et al.* 2008). These results are of importance when evaluating how multifactor global change will alter ecohydrological processes. Hence, the results are likely useful for field researchers to consider the importance of multifactor global change on experimental design. The two largest influences on runoff were temperature and precipitation, while CO_2 had only a marginal effect. There were some interactive effects on runoff with simultaneous changes in precipitation and temperature. Increases in runoff, due to increased precipitation, were dampened with increases in temperature (Figure 2). Most other results have shown that future climate change will tend to increase runoff (Wetherald and Manabe 2002) but our results indicate that if there is a decrease in precipitation, or if the increase in temperature goes past the point at which precipitation can compensate, there will be a decrease in ecosystem-level runoff (Figure 2 B1).

Our model simulations showed that the interactive effect of temperature and precipitation had the most varying results on transpiration and evaporation (Figure 4 & 5). All other combinations of CO_2, temperature and precipitation varied less from control under differing conditions. However, a decrease in precipitation seemed to cause more change in ecosystem response. Knapp *et al.* (1993) explained that the impact of CO_2 will probably be more detectable during drought conditions. Their results correspond with our results of less transpiration under elevated CO_2 and decreased precipitation. The response of evaporation and transpiration are essential for understanding the potential of terrestrial hydrological feedbacks on weather patterns. Raddatz *et al.* (2003) demonstrated that regional transpiration has a positive effect on the potential energy needed to increase the probability of occurrence and intensity of severe thunderstorms. Hence, these hydrological feedbacks are also significant in regional climate modeling efforts.

Multi-factor responses produced varying alterations in rooting zone soil moisture from control. The largest percentage change in rooting zone soil moisture was the interactive effect of temperature and precipitation. Rooting zone soil moisture was highest with low temperatures and high precipitation, which was probably due to greater infiltration and decreased water loss via evapotranspiration. However, when temperatures increased and precipitation stayed constant there was a decrease in rooting zone soil moisture. This decrease was associated with higher evapotranspiration. Other combinations of climate change scenarios showed linear changes from control. Owensby *et al*. (1993) suggest that an increase in soil moisture with higher CO_2 concentrations are likely attributed to higher water use efficiency and lower rates of evapotranspiration. Our results showed similar patterns, but when compared to the effects of temperature and precipitation these changes were not as significant. These changes in soil moisture control many additional ecosystem processes. Rodriguez-Iturbe *et al*. (1999), for example, illustrated that changes in soil moisture dynamics could influence nutrient cycling, plant species composition, vegetation stress, and productivity.

Three-factor modeling with TECO was performed to show potential interactive effects of multifactor climate change on WUE and RUE. Both RUE and WUE were lower at 280ppm CO_2 (Figures 6 C1 and 7 C1) than at the other CO_2 levels (Figures 6 C2 and C3; Figure 7 C2 and C3) for each of the temperature and precipitation scenarios. At 785 ppm CO_2 both RUE (Figure 6 C3) and WUE (Figure 7 C3) had greater variability among the various climate change scenarios than at 280 and 380 ppm, suggesting that CO_2 concentration amplified responses of RUE and WUE to changes in temperature and precipitation. In addition, values of WUE themselves were larger than RUE for all the temperature, precipitation, and CO_2 scenarios.

Our results set a precedent for research on how different interactive climate change scenarios influence ecohydrological components. To our knowledge, no other modeling study has divided up specific components of ecohydrology and performed a full evaluation of how each specific component responded to different global climate change scenarios. Our study has applications for field researchers studying specific interactions in different ecosystem types under dual climate change scenarios. These results have helped identify which ecohydrological components have the greatest priority for further research. For example, combinations of temperature and precipitation had the largest interactive impacts on evaporation, runoff, transpiration, and rooting zone soil moisture. Our research also has the possibility of being applicable to regional and global climate modelers, since we have shown that two major contributing factors, transpiration and evaporation, of hydrological feedbacks to the atmosphere change under different climate change scenarios. This feedback could have some importance in understanding climatic changes (Betts 2006). Lastly, our runoff component has the potential, but should be approached with great care, in helping government agencies determine how climate change could alter the amount of freshwater in local streams and rivers.

2.5 Conclusions

Using the TECO model, we were able to distinguish ecosystem-level ecohydrological responses from that at the plant level. The model showed that combinations of precipitation and temperature had the largest impact on ecosystem-level variables (e.g., runoff, evaporation, and soil moisture), whereas CO_2 and temperature had the largest impact on plant-level variables (e.g., transpiration and WUE). We also explored how each ecohydrological process responded to different climate change scenarios. All of our results showed that the interaction of multiple climate change factors could lead to an assortment of changes in the terrestrial water cycle. Additionally, we found ecosystem-level RUE to be a better indicator of potential changes in the water cycle than plant-level WUE.

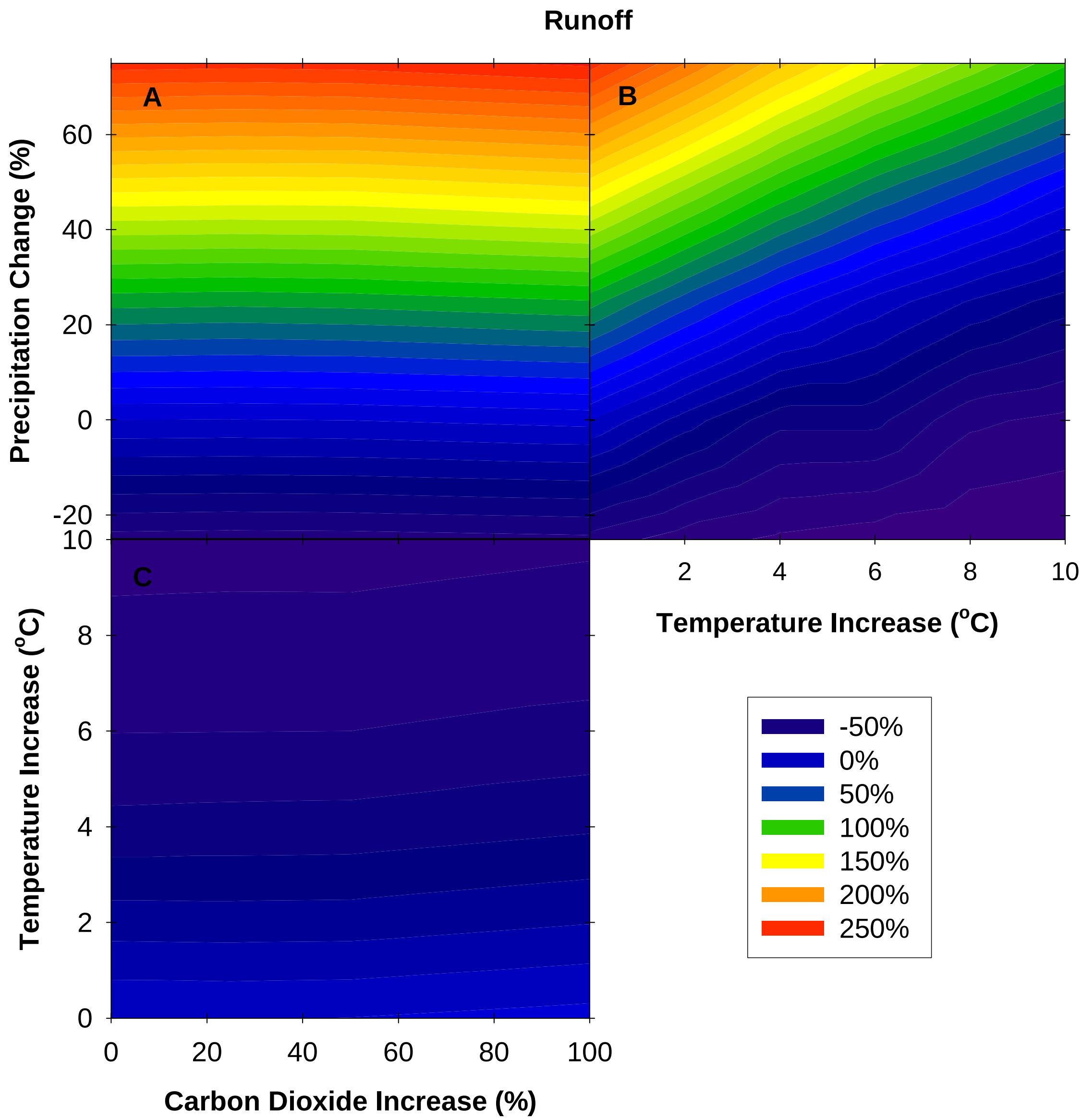
To evaluate regional evapotranspiration feedbacks to climate change under different climate change scenarios, we need to use coupled water-carbon models (e.g., TECO) in a wide variety of ecosystem types to examine if some modeled patterns in this paper can be extrapolated across multiple landscapes. Lastly, more research needs to evaluate if the patterns of runoff change are widespread (Luo *et al*. 2008); because these simulations may have a socioeconomic impact on replenishing freshwater supplies for agricultural and human use due to potential changes in the amount of runoff from different climate change scenarios.

2.6. Acknowledgements

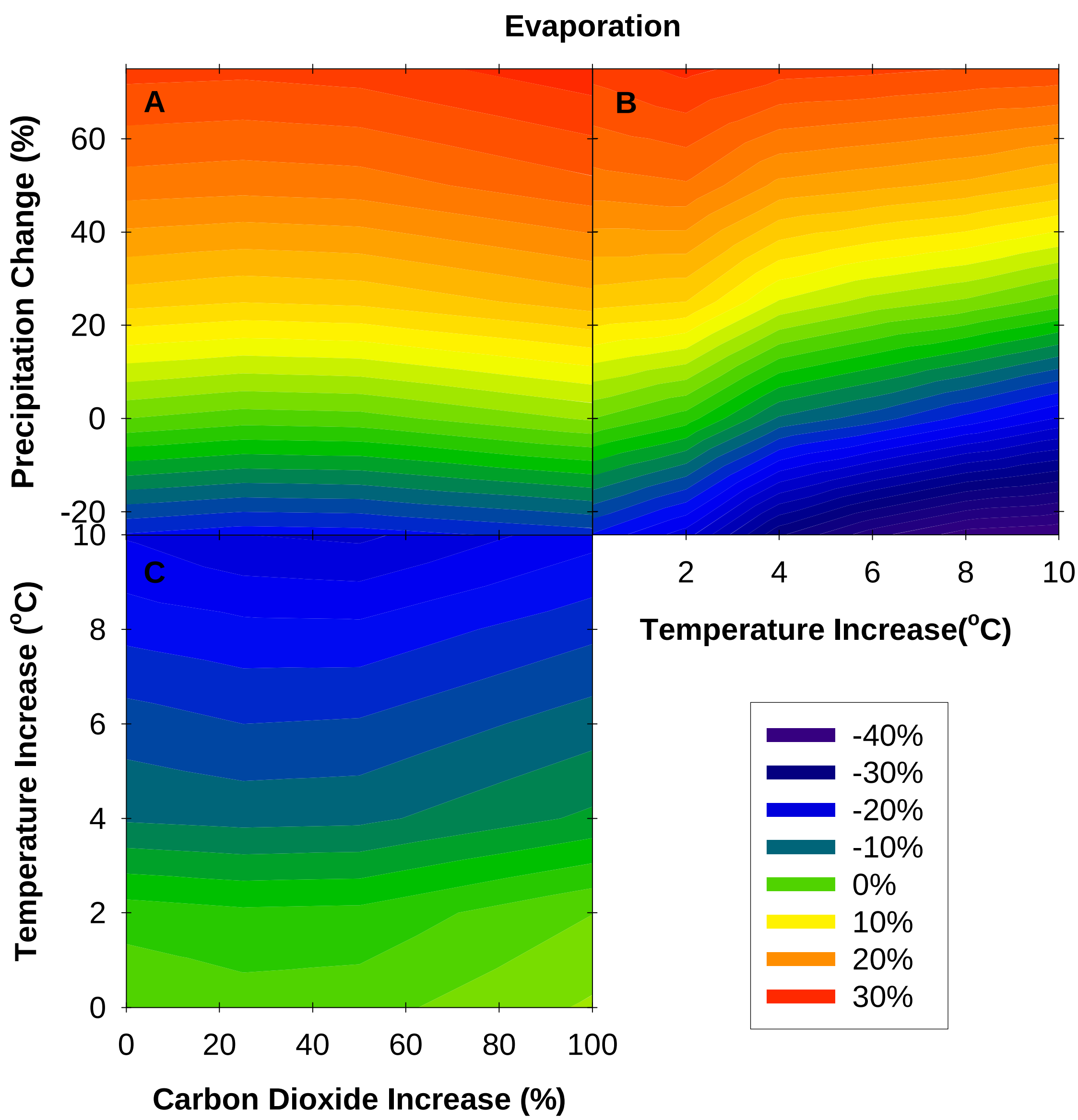
This research was supported by the National Science Foundation, under DEB 0743778 and DBI 0850290, EPS 0919446; by the Terrestrial Carbon Program at the Office of Science, United States Department of Energy, from Grant No. DE-FG02-006ER64317; United States Department of Energy through the Midwestern Regional Center of the National Institute for Climatic Change Research at Michigan Technological University, under award number DE-FC02-06ER64158. We wish to thank Xuhui Zhou for his editorial comments.

Appendix A.

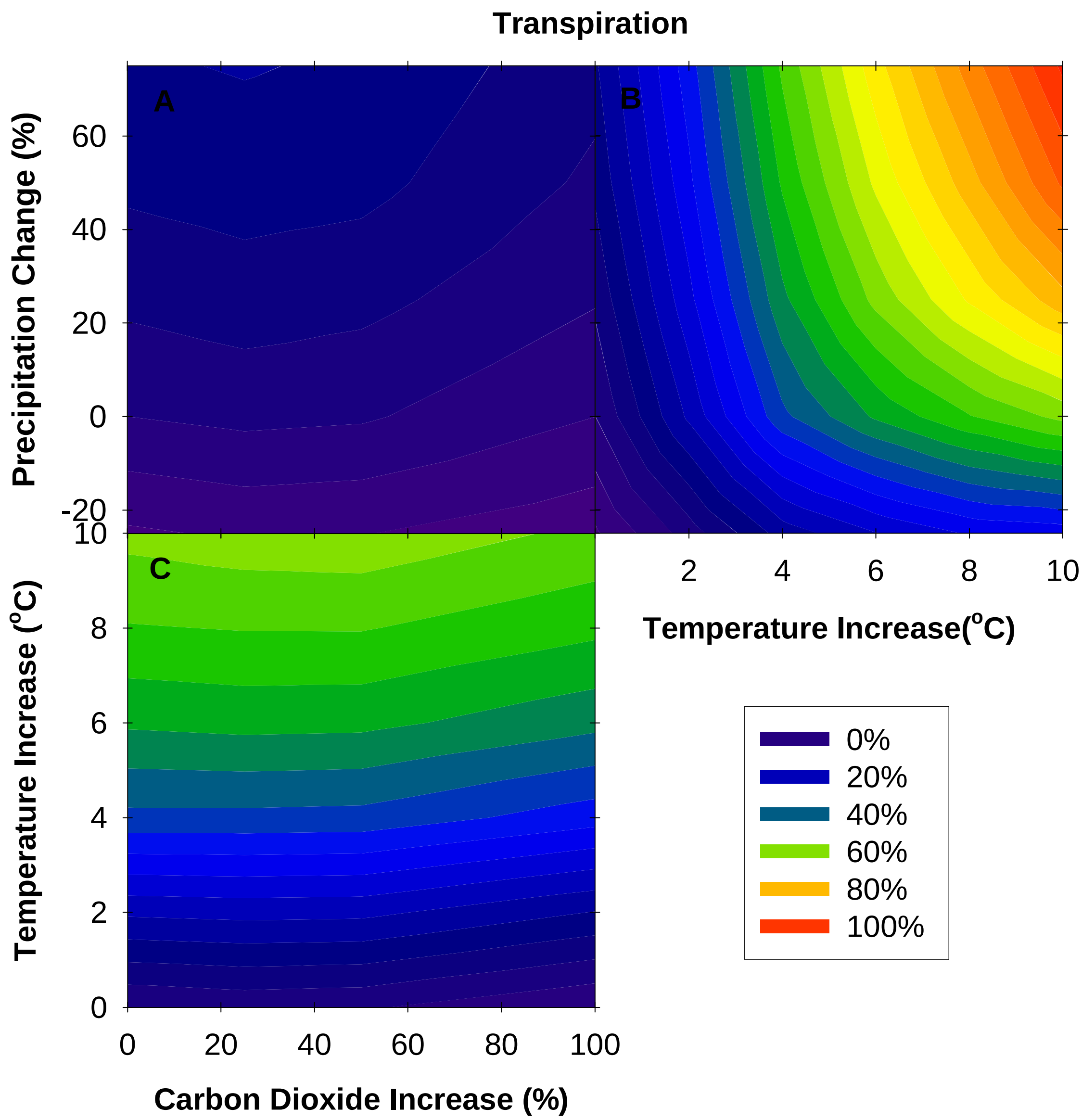
We graphed the two-factor modeled combinations of different climate change scenarios. This information should be used for determining estimated interactions between scenarios and the data could derive predictions for future experiments. All combinations are representative of percent change from control.



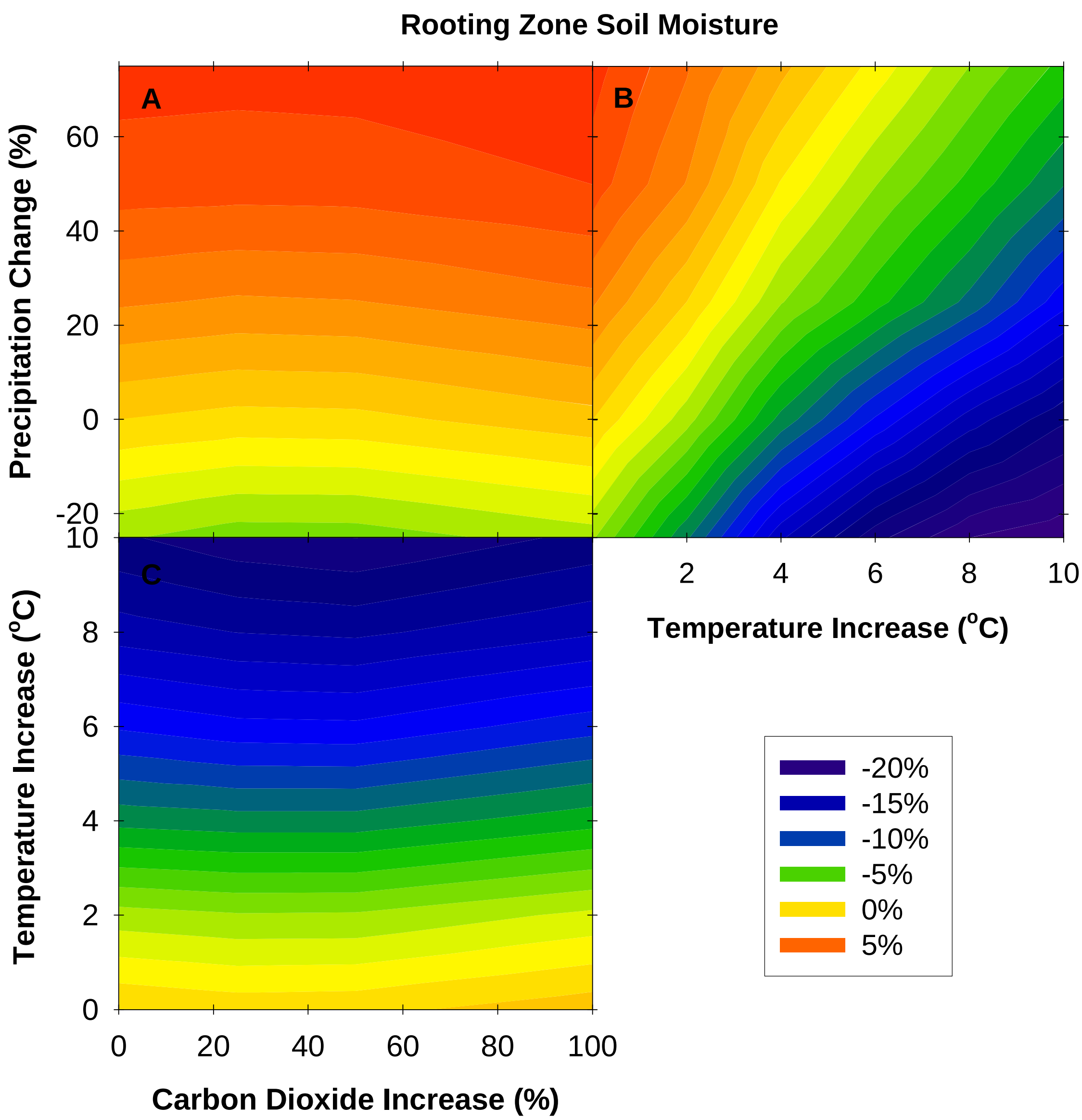
Appendix Figure 1 Model simulations of Runoff (%) in response to different multifactor co-varying scenarios of temperature, CO_2 and precipitation change. A) Precipitation change and the increase in carbon dioxide B) Temperature increase and precipitation change C) Temperature increase and carbon dioxide increase. Control was set at 0.5457 mm d-1.



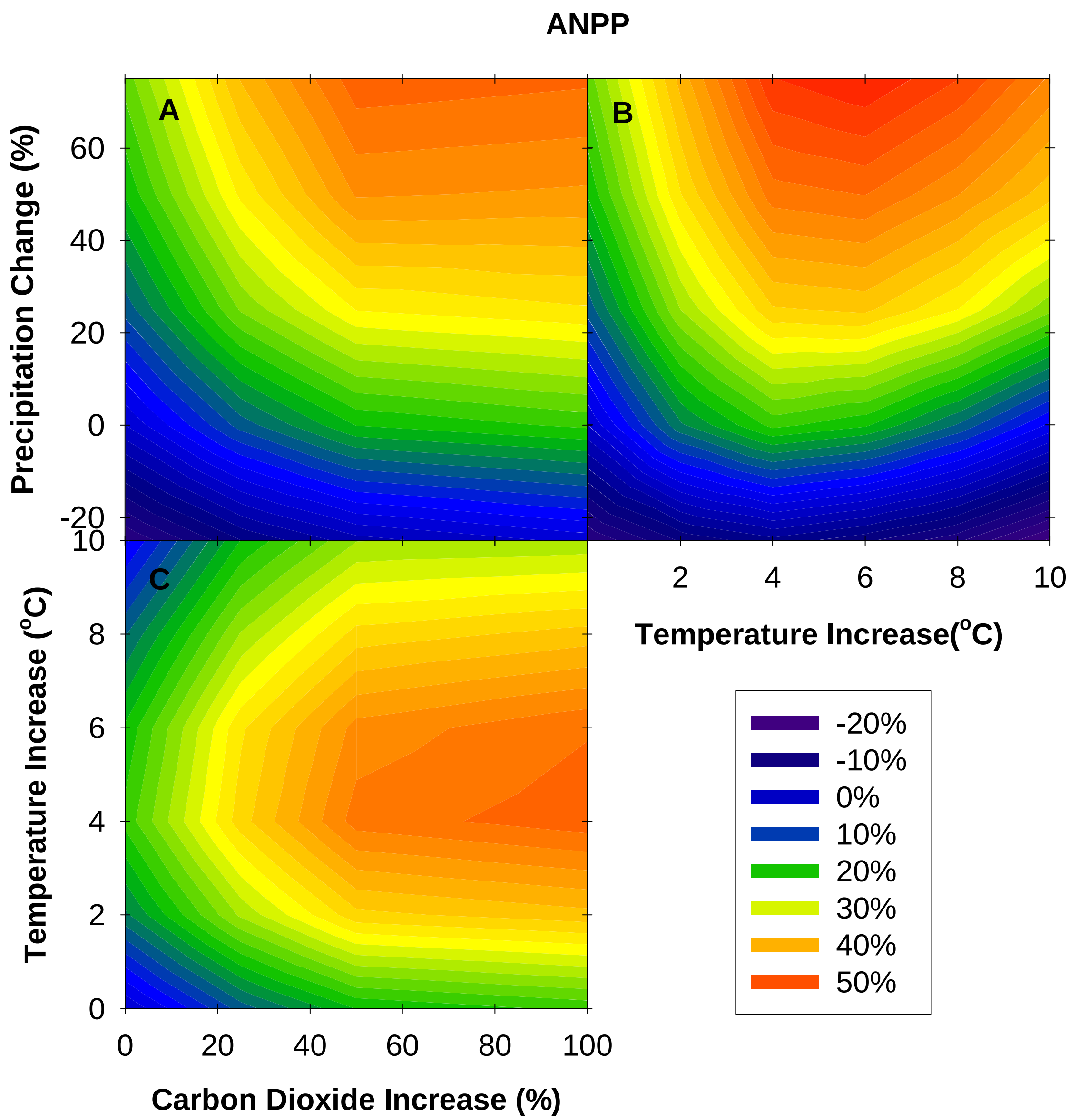
Appendix Figure 2 Model simulations of Evaporation (%) under different multifactor co-varying scenarios of temperature, CO_2 and precipitation change. A) Precipitation change and the increase in carbon dioxide B) Temperature increase and precipitation change C) Temperature increase and carbon dioxide increase. Control was 0.7060 mm d-1.



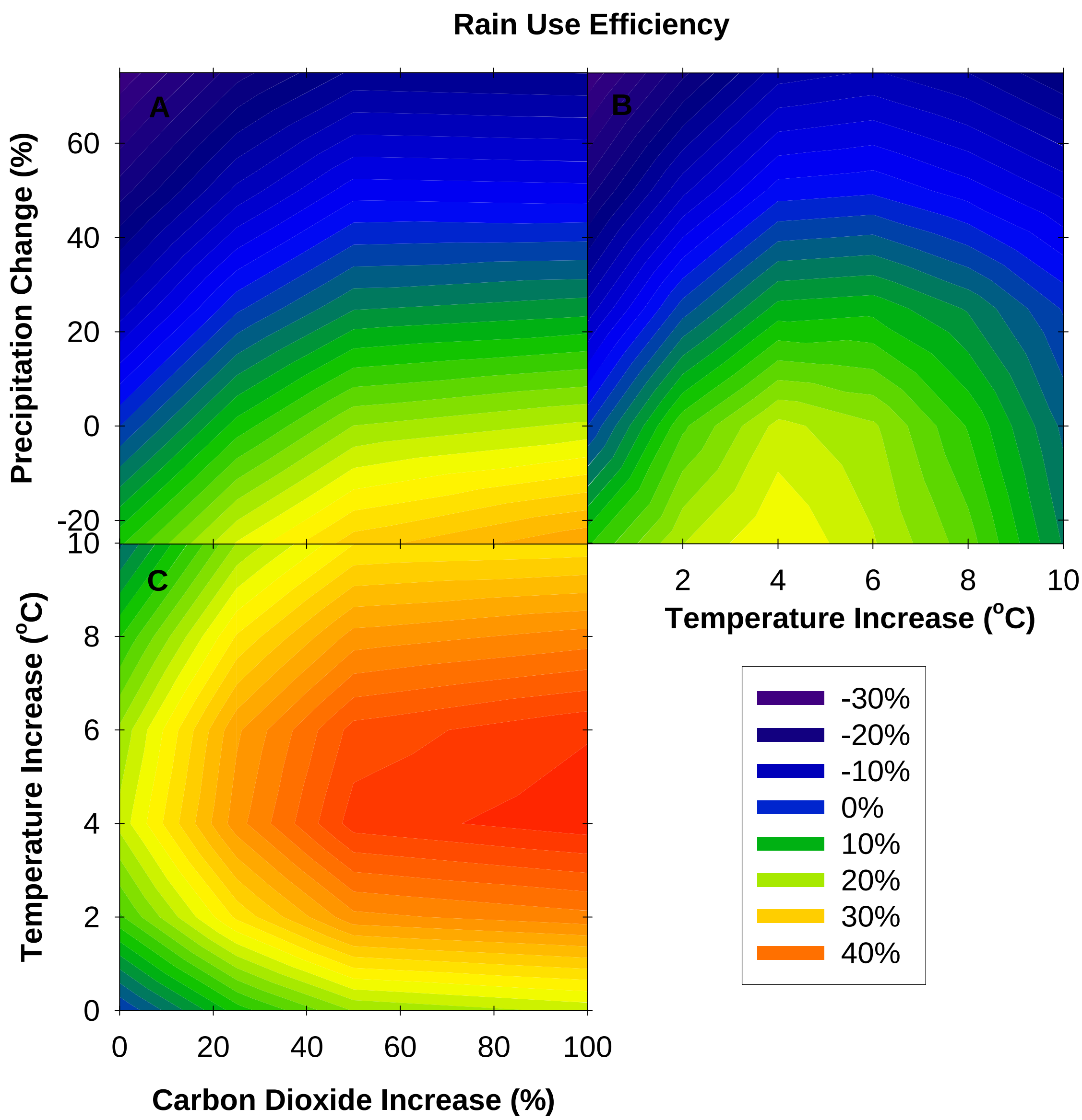
Appendix Figure 3 Model simulations of Transpiration (%) under different multifactor co-varying scenarios of temperature, CO_2 and precipitation change. A) Precipitation change and the increase in carbon dioxide B) Temperature increase and precipitation change C) Temperature increase and carbon dioxide increase. Control was 0.9435 mm d-1.



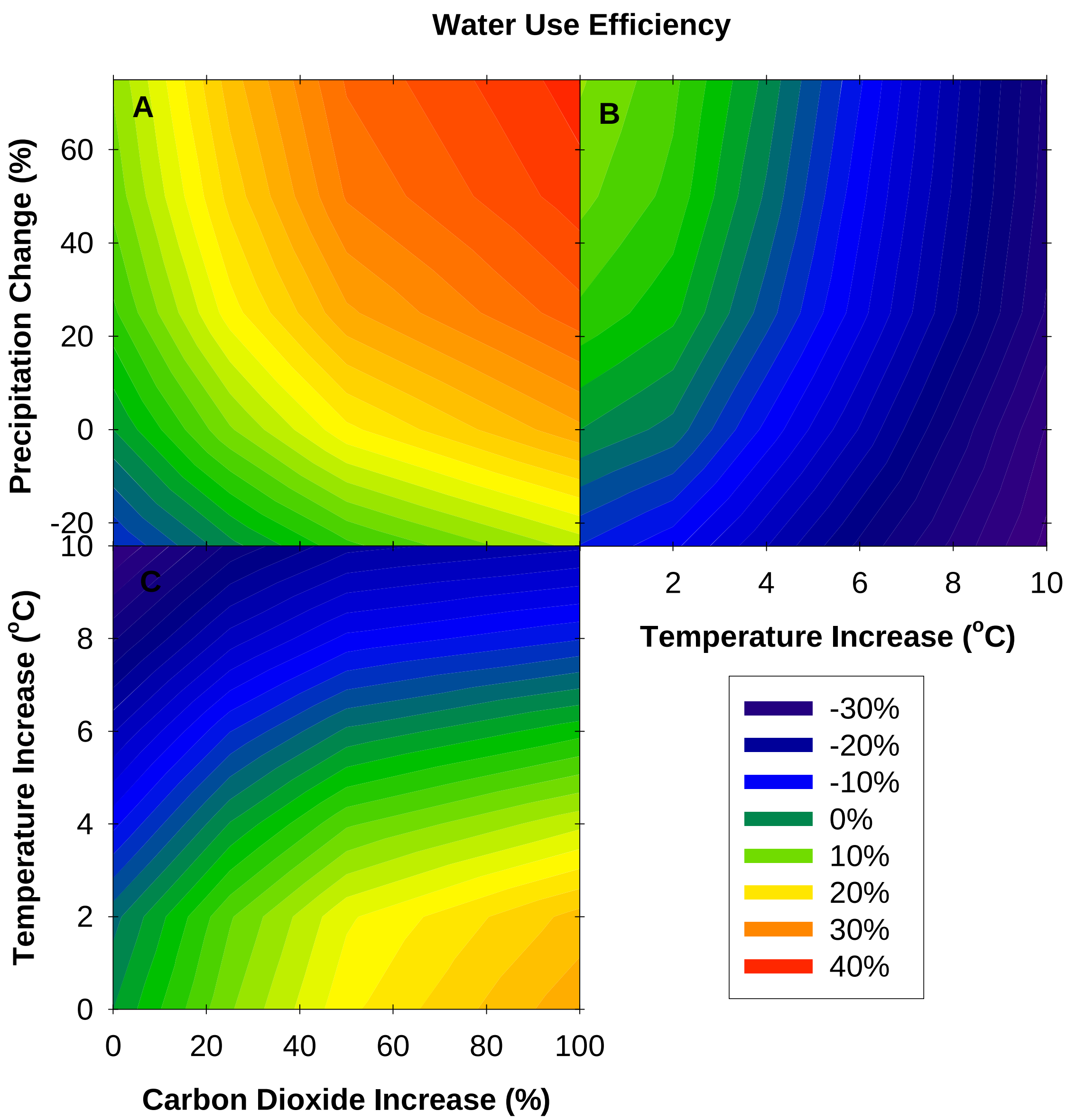
Appendix Figure 4 Modeled rooting zone soil moisture (%) under different multifactor co-varying scenarios of temperature, CO_2 and precipitation change. A) Precipitation change and the increase in carbon dioxide B) Temperature increase and precipitation change C) Temperature increase and carbon dioxide increase. Control was 29.25 % d-1.



Appendix Figure 5 Net primary production (NPP) (%) under different multifactor co-varying scenarios of temperature, CO_2 and precipitation change. A) Precipitation change and the increase in carbon dioxide B) Temperature increase and precipitation change C) Temperature increase and carbon dioxide increase. Control was 413.33 g C m-2 yr-1.



Appendix Figure 6 Modeled rain use efficiency (%) under different multifactor co-varying scenarios of temperature, CO_2 and precipitation change. A) Precipitation change and the increase in carbon dioxide B) Temperature increase and precipitation change C) Temperature increase and carbon dioxide increase. Control was 0.5159 g/mm d-1 yr-1.



Appendix Figure 7 Modeled water use efficiency (%) under different multifactor co-varying scenarios of temperature, CO_2 and precipitation change. A) Precipitation change and the increase in carbon dioxide B) Temperature increase and precipitation change C) Temperature increase and carbon dioxide increase. Control was 1.20 g/mm d-1 yr-1.

Chapter 3

Changes in soil water dynamics due to variation in precipitation and temperature: an ecohydrological analysis in a tallgrass prairie

This chapter has been accepted for publication in *Water Resource Research* (2009)

Abstract

There is considerable evidence that future global climate change will increase temperature and alter precipitation regime. To better understand how these factors will influence soil water dynamics, it is imperative to use multi-factorial experiments. A one year "pulse" experiment, with 4°C warming and a doubling in precipitation, was performed to evaluate the changes in soil moisture dynamics. Frequency distribution analyses of soil moisture and soil temperature were used to explore the consequences of climate change on ecohydrological processes at different soil depths. There was a decrease in soil moisture frequency from 0–120 cm in both warming and warming with increased precipitation experiments. Different soil depths had similar patterns of change in soil moisture and soil temperature frequency. Additionally, we correlated evapotranspiration and soil moisture to look at changes in evapotranspiration from the wilting point (E_w) to maximum evapotranspiration (E_{max}). These results revealed a shift in the slope and position of E_w to E_{max} with experimental warming. Our results showed that the soil moisture dynamics and the ecohydrology were changed by different global climate change scenarios. Understanding the effects of global warming on soil moisture dynamics will be critical for predicting changes in ecosystem level processes.

Key words: soil moisture dynamics, climate change, ecohydrology, tallgrass prairie, warming, precipitation

3.1 Introduction

Over the past century the global mean temperature has increased by about 0.6 °C and is predicted to increase 1.1–6.4 °C in the 21st century (IPCC, 2007). With this warming there is a predicted acceleration in the water cycle due to an exponential increase in specific humidity (Huntington 2006) and an associated increase in the intensity and severity of precipitation events (Easterling et al., 2000). Changes in temperature and alterations in the precipitation patterns have been shown to cause multiple changes to ecosystem processes (e.g. net primary production, root biomass, and soil respiration) Knapp et al., 2008. A central component controlling ecosystem processes is soil water balance. However, our understanding of the response to climate change on ecosystem water balance is largely limited.

A National Ecological Observatory Network (NEON) report (2004) stated that is important to understand how biologically available water in terrestrial ecosystems will respond to climate change. Evidence has shown that changes in climate variables (e.g. rainfall) will cause shifts in net primary production and community composition, which will likely impact soil water balance (Knapp 2002; Sherry et al. 2008; Sherry et al. unpublished data). Other plant responses (e.g. photosynthesis) and biogeochemical cycling (e.g. carbon and nitrogen) are also closely linked to changes in soil water balance (Knapp et al., 2008). For example, a change in plant-level response can be seen when there is a reduction in biologically available soil moisture that causes a loss in turgor, xylem cavitation, stomatal closure and a decrease in photosynthesis (Nilsen and Orcutt 1998; Porporato et al. 2001; Porporato et al. 2004).

A multitude of factors can influence soil water loss due to climate change. The most explicit cause of reduced soil moisture is higher rates of soil water evaporation due to increased thermal radiation. Further decrease in soil moisture could also occur as increased temperatures influence plant-level processes (Mellander et al. 2004), although this may vary in specific circumstances (Jones 1992; Daly et al. 2004). However, greater amounts of precipitation as a result of climatic change should in general increase the amount of soil moisture present. This contradiction leads to interesting and perplexing questions about how multiple climate change factors will contribute to changes in soil moisture dynamics.

It is important to understand how climate change will alter soil moisture given its importance for vegetation growth, plant physiological processes and biogeochemical cycles (Stephenson et al., 1990). One global modeling study suggested a decrease in soil moisture in semiarid regions under future climate change (Wetherald and Manabe, 2002). Whereas, a modeling study by Gerten et al. (2007) found varying soil moisture changes in different regions, with a predominant pattern of decreased soil moisture with increased temperatures. However, different model scenarios have shown vast differences in soil water balance (Cramer et al., 2001; Gordon and Famiglietti 2004). According to actual long-term soil moisture measurements from the Global Soil Moisture Data Bank, soil moisture has increased over the last half-century (Robock et al., 2000).

A copious amount of research has looked at different ways of manipulating an ecosystems' climate (Harte et al., 1995, Marion et al., 1997, Hobbie & Chapin, 1998, Melillo et al, 2002, and Wan et al., 2002). Warming has had different magnitudes of effect on soil moisture with each of these experiments. For example, Wan et al. (2002) saw little to no change in soil moisture with a 2^{o}C increase in temperature alone; but with clipping and warming there was an 11% decrease in soil moisture. Whereas, an experimental warming site in a montane meadow showed a reduction in soil moisture as a result of an increased physiological response of the vegetation (Saleska et al., 1999). This large amount of variability in soil moisture response to climate change among individual ecosystem makes it important to understand how different systems will respond if predictions are to be made at regional and global scales.

In this study, we examine the effects of two different climate change variables including increased temperature and precipitation intensity, and their combination, on the soil water balance of a prairie ecosystem. Not only do we consider the potential change in soil moisture, but also, the change in soil temperature. This is one of the first studies focusing on the extent to which biologically available soil moisture is altered under single and multi-factor scenarios of climate change. Also, our evaluation is one of the first to analyze the response of soil temperature and soil moisture to different climate scenarios in multiple soil-layers. Included in our analyses is an evaluation of the effects of experimental climate change on evapotranspiration/leakage (water loss) at wilting point (E_w) and at maximum evapotranspiration/leakage (E_{max}) (Rodriguez-Iturbe 2000). Shifts in E_w and E_{max} provide insight on the impact climate conditions have on an ecosystem's ability to use and conserve water (Rodriguez-Iturbe 2000).

Our study used a multifactor experiment with levels of change in warming and precipitation consistent with those predicted for the region (Wan et al. 2002). We hypothesized (1) increase in temperature would decrease soil moisture, (2) increase in precipitation would increase soil moisture (3) treatment of increased temperature and doubled precipitation would have an intermediate effect. The experiment was a short-term, one year “pulse” experiment using a probabilistic/frequency approach to evaluate changes in soil moisture dynamics and fully incorporate the stochastic nature of soil moisture dynamics.

3.2 Methods

Study Site

The experiment was located at the Kessler’s Farm Field Laboratory in McClain County, Oklahoma (34 59’ N, 97 31’ W), approximately 40km southwest of the University of Oklahoma. The area is a 137.6-ha field station positioned in the Central Redbed Plains (Tarr et al., 1980). The study site is predominately a tallgrass prairie mix of *Panicum virgatum, Schizchyrium scoparium, Andropogon gerardii, Sorgastrum nutans, Ambrosia psilostachyia*, and *Bromus japonicus*. Mean annual temperature is 16.3 °C, with monthly air temperature ranging from 3.3 °C in January to 28.1 °C in July. Mean annual precipitation is 915 mm, with monthly precipitation ranging from 30 mm in January to 135 mm in May (average values from 1948 to 1998, via the Oklahoma Climatological Survey) (Figure 1). The soil is part of the Nash-Lucian complex with a neutral pH, a high available water capacity, and a deep, moderately penetrable root zone (USDA, 1979).

2.2 Experimental Design

The one year pulse experiment was set at a target treatment of a 4.0 °C increase in soil temperature at a depth of 2cm. Twenty plots were placed in two rows that were separated by approximately 3m and each plot was 3 x 2 m. The distance between plots

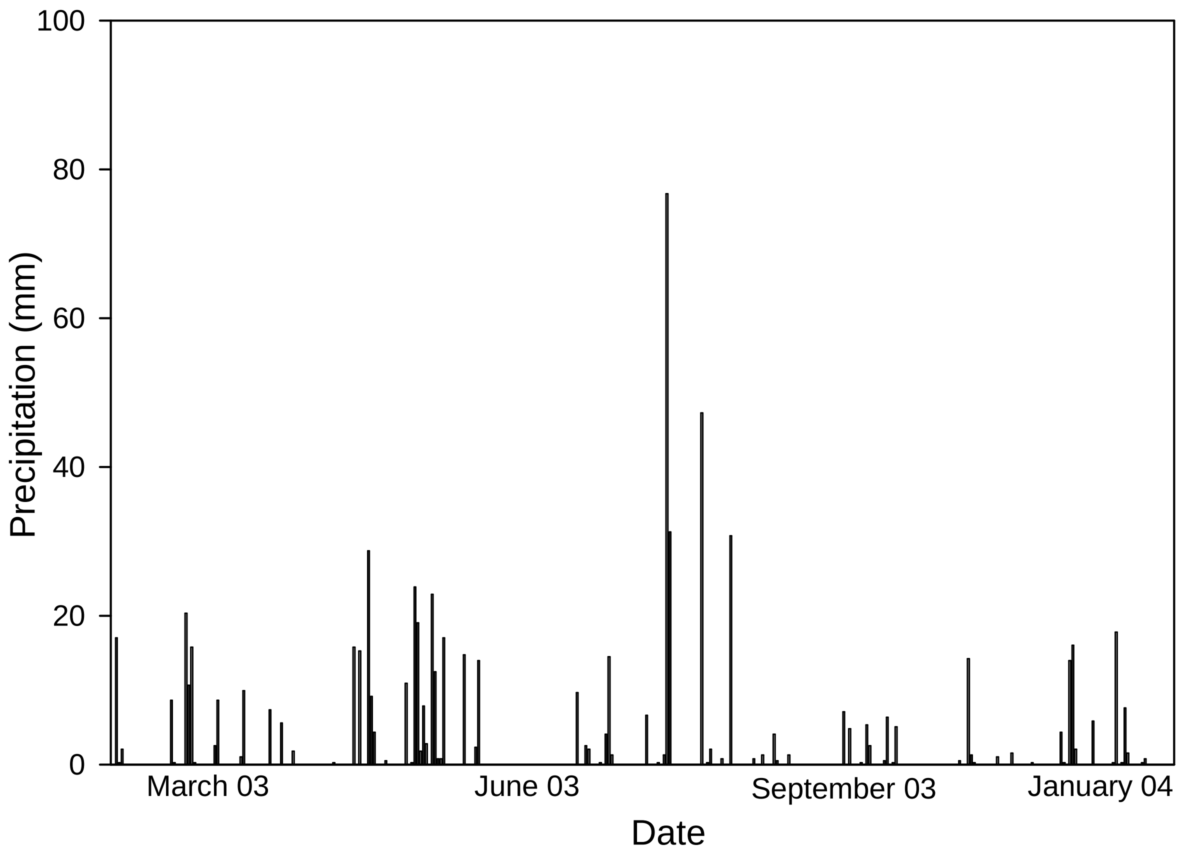


Figure 1. Daily precipitation amount during the experimental season from February 2003 to February 2004. (Mesonet, Oklahoma Climatological Survey)

within one row was 1.5 m. Ten out of the twenty plots were randomly selected to receive warming treatments and had 2 infrared heaters suspended in the middle of the plots at the height of 1.5m above the ground. The other 10 plots had "dummy" heaters made of metal flashing suspended at the same height as in the warmed plots. Five of both the warmed and unwarmed plots were randomly selected to receive doubled precipitation using a "rain-catchment" device, which is an angled catchment the same size as the plot. The "rain-catchment" device was designed to funnel water onto these plots to provide an additional amount of precipitation that would normally fall on the control. Piping was used to evenly distribute the rainwater across the plots. Several variations were tested before the final design was selected for the experiment based on the most even distribution of precipitation. It should be noted that this experiment was designed to increase rainfall intensity and had no impact on the frequency of rainfall. There were four treatments of control (C), warmed (W), precipitation doubling (PPT), and warmed plus precipitation doubling (W+PPT), and each treatment had five replicates. The duration of the experiment was from 20 February 2003 to 20 February 2004.

Soil Moisture and Temperature Measurements

Soil Moisture was measured using automatic TDR probes (time domain reflectometry; E.S.I. Equipment, Environmental Sensors Inc. Sidney, Canada). Each probe recorded hourly measurements at 5 different depths 0–15 cm, 15–30 cm, 30–60 cm, 60–90 cm, and 90–120 cm (Figure 2a). Data were logged through a CR10X measurement and control system (Campbell Scientific, Inc., Logan, Utah). Nine of the TDR probes experienced damage or malfunction during the study. Complete data sets were available for only 11 of the 20 plots.

Soil Temperature was measured hourly at six depths using thermocouple wires attached to a 25 channel solid state multiplexor (AM25T) (Campbell Scientific, Inc., Logan, Utah). Each measurement was automatically measured at six depths starting at the soil surface, 7.5 cm, 22.5 cm, 45 cm, 75 cm, and 105 cm (Figure 2b).

To show changes in soil moisture and temperature at different depths, we constructed graphs of yearly average soil moisture and temperature. The data was collected from the entire experimental period. Additionally, similar graphs were configured for seasonal variation. The four seasons of winter (December 22 – March 19), spring (March 20 – June 20), summer (June 21 – September 20), and fall (September 21 – December 21) were based on the standard division of a temperate zone in the Northern Hemisphere.

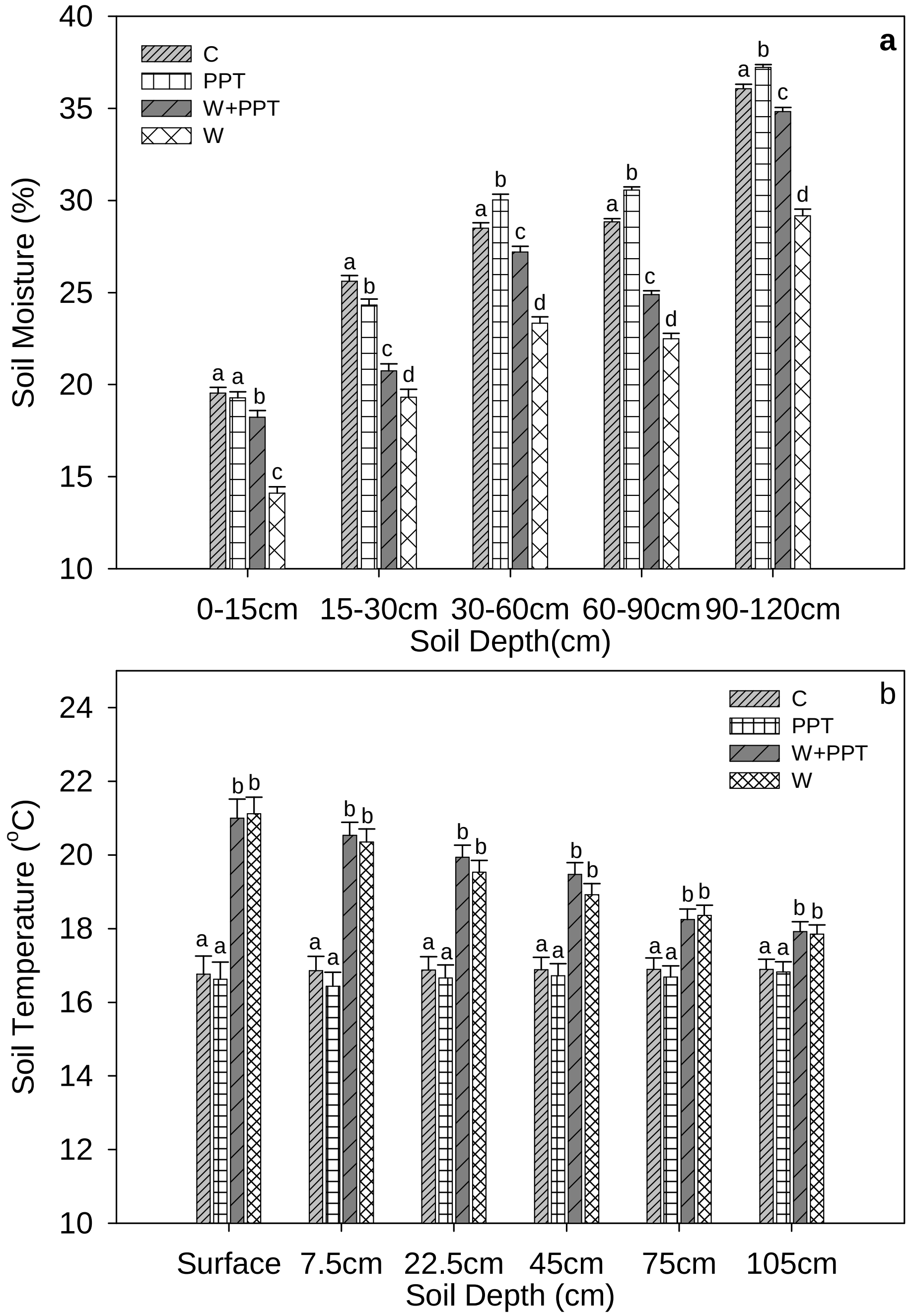


Figure 2. a) Soil moisture responses to different climate change treatments (C, PPT, W+PPT, and W). Depth of soil is divided into different segments. Each treatment was statistically compared with other treatment types (mean ± SE n=365). Statistical difference was shown with *a, b, c*, and *d*. b) Soil temperature responses to different climate change treatments (C, PPT, W+PPT, and W). Depth of soil is divided into different segments. Each treatment was statistically compared with other treatment types (mean ± SE n=365). Statistical difference was shown with *a, b, c*, and *d*.

Water loss (Evapotranspiration and Leakage)

Water loss ($\mathbf{W}_{l}$), an estimate of evapotranspiration and leakage, was calculated using the daily average of bulk soil moisture at a given day ($\mathbf{S}_{t}$) minus the daily average of bulk soil moisture from the following day ($\mathbf{S}_{t+1}$). Rainfall (**R**) was then added as a water input:

$$\mathbf{W}_{l} = (\mathbf{S}_{t} - \mathbf{S}_{t+1}) + \mathbf{R}$$

Soil moisture measurements were taken from the TDR probes and rainfall data were collected from the Oklahoma Mesonet. Our analysis used bulk soil moisture to account for the entire root profile.

Points were collected between an estimated E_{w} and E_{max} to analyze changes in the different experiment conditions on water loss. Estimations of E_{w} and E_{max} were derived from the calculations of ($\mathbf{W}_{l}$) during the longest dry period in the summer of the experiment year. This rainless period occurred during a twenty-one day stretch from day 139 to day 160 after the beginning of the experiment. $\mathbf{W}_{l}$ was then correlated with daily average bulk soil moisture for days 139 to 160. From the data, a graphical representation was made of the correlation between the points within E_{w} and E_{max} with the sequential bulk soil moisture to show changes in the four climate change scenarios. Rodriguez-Iturbe (2000) gave an illustrative diagram of the relationship between soil moisture and water loss.

Statistical Analysis

The analysis of variance (ANOVA) was conducted using the Statistical Analysis System (SAS) software (SAS Institute Inc., Cary, NC, USA). The One-way

ANOVAs were performed for a comparison of soil moisture and temperature between the four treatments (C, PPT, W, and W+PPT) for the entire experimental period (Table 1 and 2). A post hoc of multiple comparisons was done using the least significant difference (LSD) method for both moisture and temperature across the four different treatment types (Figure 2). Additionally, soil moisture and temperature dynamics, at multiple depths, were evaluated by analyzing frequency distributions using histograms in Statistical Analysis System (SAS, SAS Institute Inc., Cary, NC, USA) (Figure 3 and 4). The bins for the histograms were designated by 5°C segments for temperature and 5% segments for soil moisture.

Table 1. ANOVA of soil moisture content at different depths

Source	df	SS	F-ratio	P-value
Surface	3	6965.799	27.36	<.0001
7.5cm	3	5322.511	35.99	<.0001
22.5cm	3	3267.211	25.55	<.0001
45cm	3	2166.116	19.33	<.0001
75cm	3	846.8216	9.14	<.0001
105cm	3	389.741	4.98	0.0019

(α = 0.05)

3.3 Results

Soil Moisture

We found that soil moisture varied between different experimental conditions for the investigational period. Within each treatment (C, PPT, W, and W+PPT), a statistically significant difference in soil moisture was found at all soil depths (0–15, 15–30, 30–60, 60–90, and 90–120 cm) (Table 1) (Figure 2). PPT and C plots had the wettest soil moisture conditions at all depths; furthermore, C plots had slightly wetter soil moisture values in 0-30cm while PPT plots had higher values in 30-120cm. W+PPT and W plots had the driest soil moisture values in all levels, with W consistently having the lowest value. Furthermore, an increase in soil moisture with depth was also seen under all experimental conditions (Figure 5a). Likewise, the same patterns were observed when soil moisture was analyzed over seasons (Figure 5b-e).

Frequency distributions of soil moisture were constructed at multiple soil depths to demonstrate the probabilistic changes in available soil moisture among the different experiment treatment types (Figure 3). Patterns of change in the frequency distributions closely resembled the mean soil moisture results in Figure 2a. However, frequency distributions allow for a better illustration of the actual probabilistic nature of soil moisture dynamics with each experimental treatment type. C and PPT had the wettest soil moisture frequency distributions at all depths while W+PPT and W had the driest soil moisture frequencies. Overall, the driest soil moisture frequency distributions were found in the W plots.

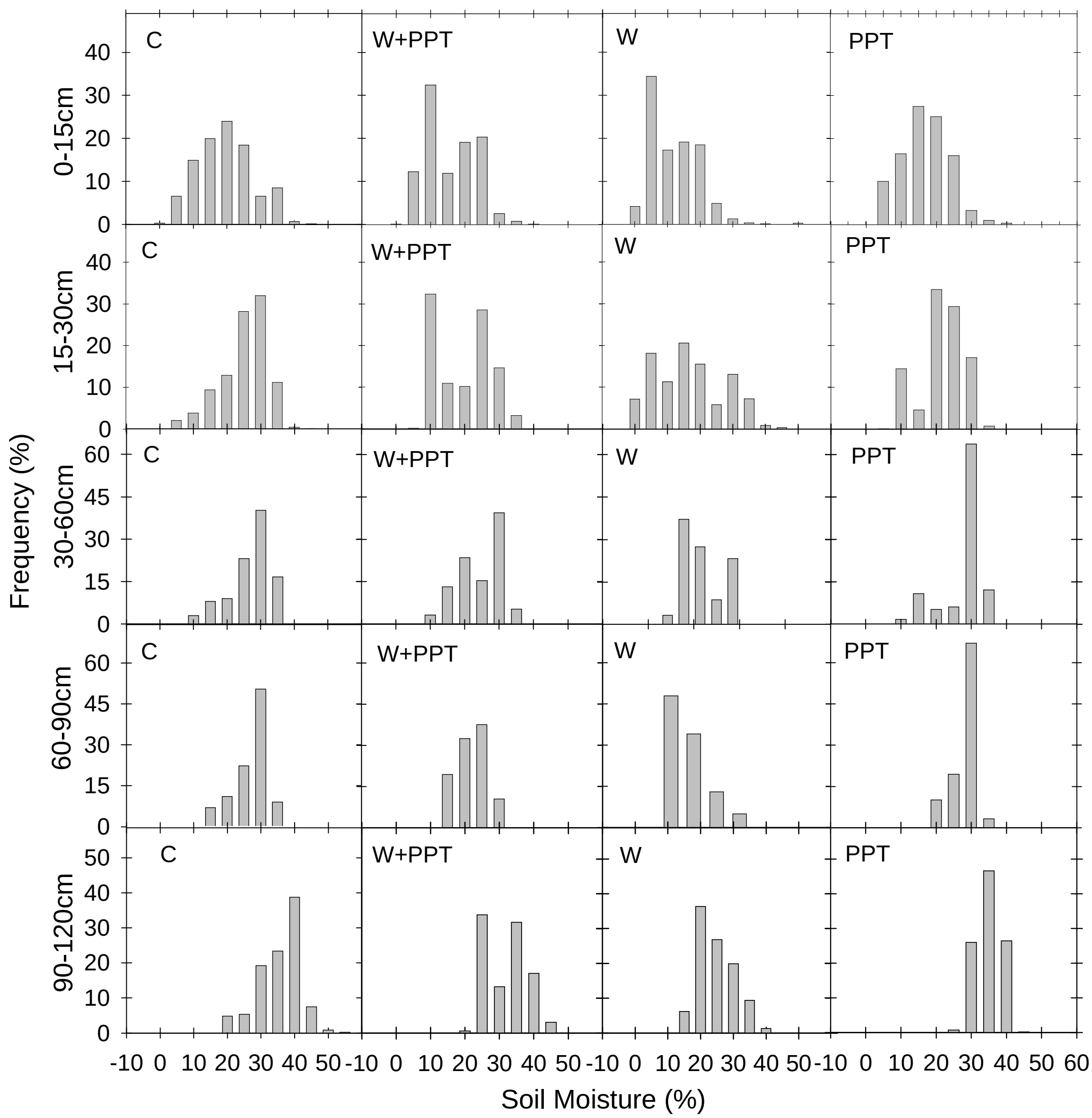


Figure 3. Soil moisture change in frequency at different soil depths. Each treatment type, C; control, W+PPT; warmed and doubled precipitation, W; warmed, PPT; doubled precipitation.

Soil Temperature

Both experimental warming treatments (W and W+PPT) showed significantly higher temperatures at all depths (Soil Surface, 7.5, 22.5, 45, 75, and 105cm) compared to non-warming treatments (C and PPT) (Table 2). No significant difference was found on soil temperature between C and PPT at any depth and a similar non-significant pattern was also established between W and W+PPT (Figure 2b). PPT and C plots had little to no change in temperature with depth; however, W and W+PPT had nearly a 3°C decrease in temperature from the soil surface to 105cm. W+PPT and W plots had the lowest soil temperature values in all levels, with W having consistently the lowest value. This is further illustrated with Figure 6a, showing the average yearly soil temperature for the different treatment types. Additionally, there were similar patterns when the treatments were divided into seasons (Figure 6b-e).

Frequency distributions of soil temperature were plotted at multiple soil depths to illustrate the probabilistic nature of soil temperature within the different experimental treatment types (Figure 4). Frequency distributions were similar to the mean soil temperature patterns seen in Table 2. Furthermore, C and PPT had the lowest temperature frequencies distributions at all depths while W+PPT and W had the highest temperature frequencies distributions.

Table 2. ANOVA of soil temperature content at different depths

Source	df	SS	F-ratio	P-value
Segment 0-15cm	3	6834.217	54.35	<0.0001
Segment 15-30cm	3	9343.574	62.24	<0.0001
Segment 30-60cm	3	8578.948	77.34	<0.0001
Segment 60-90cm	3	14132.709	281.56	<0.0001
Segment 90-120cm	3	13371.408	186.74	<0.0001

(α=0.05)

E_w and E_{max}

We found that the points between the estimated E_w and E_{max} showed changes in both slope and position, based on the different experimental conditions (Figure 7). The experimental warming plots had the greatest change, of any experimental treatment, with E_w to E_{max} occurring in the driest soil moisture conditions (Figure 7). Thus, the wilting point in the experimental warming plots occurred at a soil moisture percentage around 7%. However, little to no change occurred in the soil moisture between E_w to E_{max} with the PPT plots and C plots and the wilting point was occurring in soil moisture conditions of around 10%. There was also a change in the position of the points between E_w to E_{max} for the W+PPT plots, resulting in the area between the wilting point and maximum evaporation to occur in wetter soil moisture conditions (around 12%).

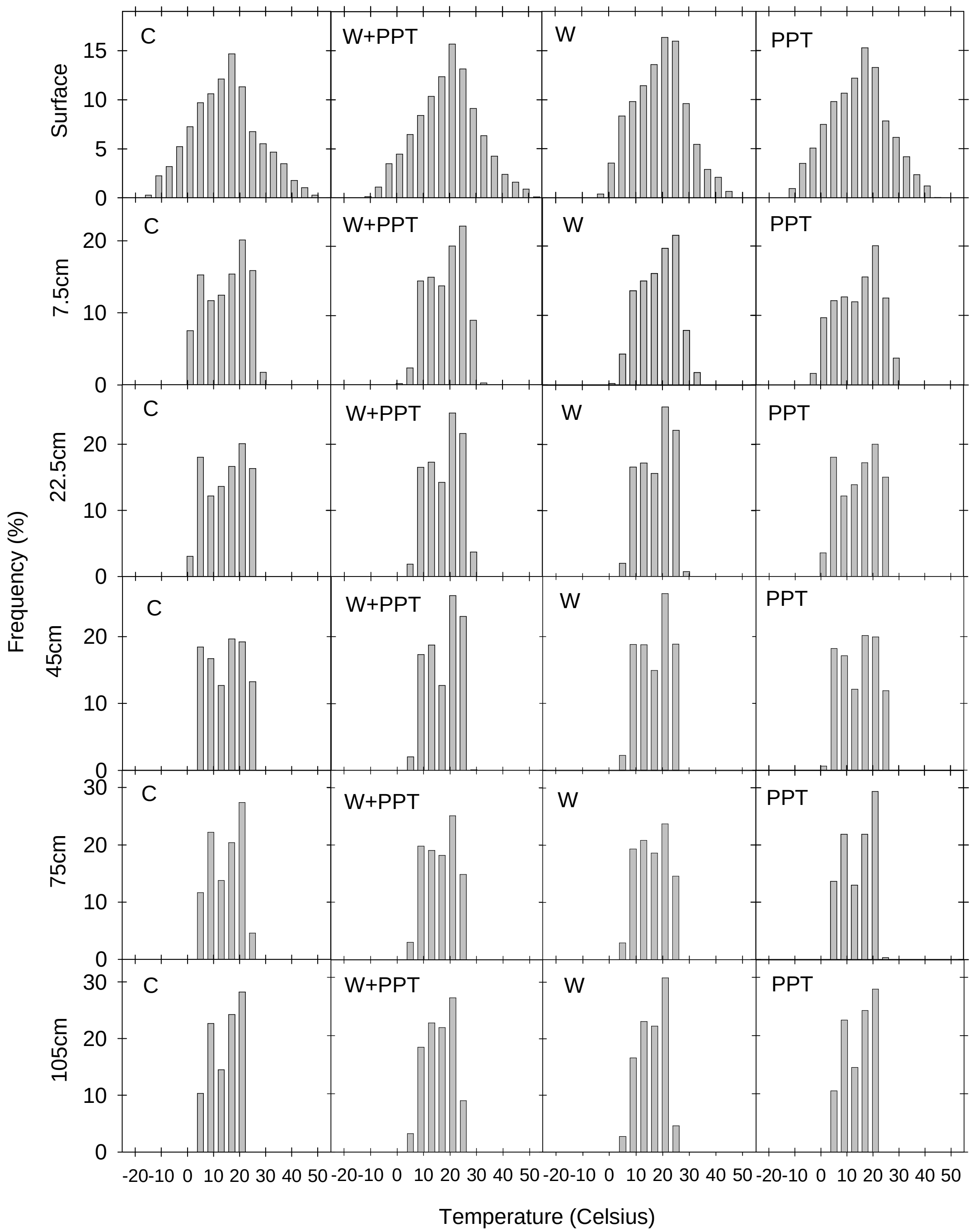


Figure 4. Soil temperature change in frequency at different soil depths. Each treatment type, C; control, W+PPT; warmed and doubled precipitation, W; warmed, PPT; doubled precipitation.

3.4 Discussion

To our knowledge, this is the first study conducted with the goal to understand the impacts of different climate change scenarios on soil conditions at multiple depths. Furthermore, the data presented here clearly show that warming and precipitation change alters soil moisture dynamics and change soil moisture frequency in a tallgrass prairie ecosystem. The changes in soil moisture and temperature are particularly significant for understanding the consequences of climate change for belowground plant and soil processes. For example, Day et al. (1991) showed that changes in soil temperature alter the ability of roots to uptake water and nutrients; furthermore, increase in soil water, or lack there of, directly affects their ability to access water. Other studies also coincide with changes in root biomass and function with changes in temperature (Bowen 1991; Li et al. 1994; Majdi & Ohrvik 2004)

Observed patters of change in soil moisture and temperature

Our results confirm earlier experimental findings that climate change will have an impact on belowground soil hydrological conditions (Harte et al, 1995, Saleska et al, 1999, Melillo et al 2002, Wan et al, 2002). However, these previous studies have not explained the extent to which different climate change scenarios would alter soil hydrological conditions at multiple depths. Our study focused on the impacts on soil moisture dynamics and changes in temperature in deep soil, with different climate change scenarios (warming, warming and increased precipitation, increased precipitation). There were significant changes in soil temperature and moisture with all experimental conditions. Soil moisture measurements were highest in both the C and PPT plots followed by the PPT+W plots and then W plots. Therefore, more biologically available water is accessible by plants in the C and PPT plots and compared to both of the warming plots. The deeper layers of the PPT plots showed the highest amount of soil moisture. This could be attributed to increased movement of water to deeper layers as a result of the higher precipitation, and less evaporative demand because of the lower temperatures. Both W and W+PPT had the lowest soil moisture at all depths, and this could be a response mechanism of plants to higher temperatures. Two factors could interplay to cause more moisture uptake in the warming plots. First, more water could be lost to the atmosphere from an increase in transpiration and evaporation. Plants could then increase the amount of water uptake to compensate for the additional transpirational loss. Second, there is a significant increase in temperature at the lower soil depths due to warming and this should increase root activity (Bowen 1991). Previously, experimental evidence showed that there was an increase in root biomass under warming in the experimental plots (Fei, Zhou, Sherry, and Luo, unpublished data). Both of these factors could together explain the decrease in soil moisture with an increase in temperature from experimental warming.

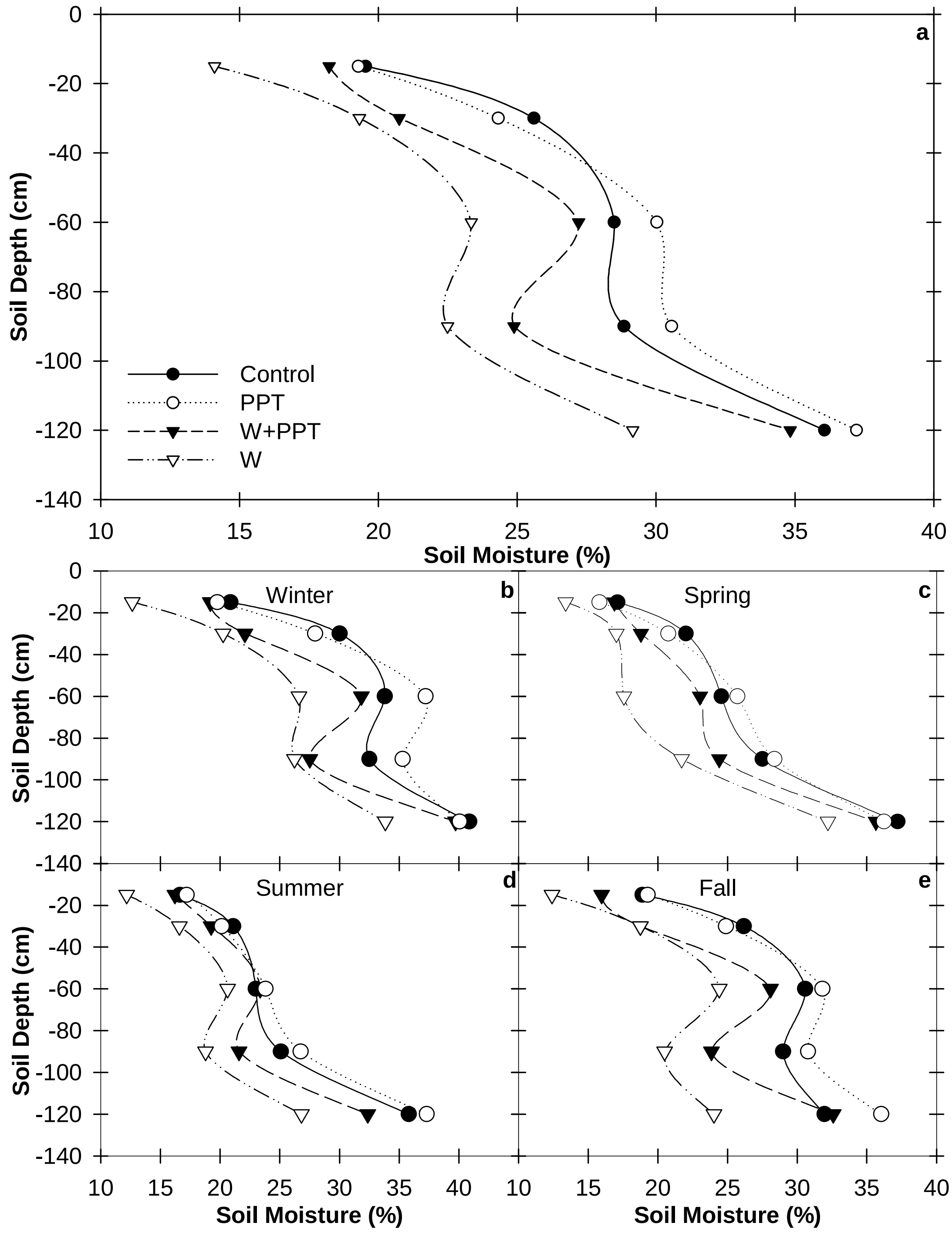


Figure 5. Average soil moisture profile; (a) yearly average, (b) winter, (c) spring, (d) summer, and (e) fall for the different experimental treatments.

Increase in deep soil temperature from higher atmospheric temperatures could result in unexpected changes. Changes in temperature around deep roots have been shown to change moisture uptake (Day et al, 1991) and there is evidence that higher soil temperatures can increase transpiration (Mellander et al. 2004). Additionally, evapotranspiration is a driving force for changing atmospheric weather patterns and has been cited in causing changes in storm severity (Raddatz and Cummine 2003). Questions on how climate change alters soil moisture in different systems and how these feedbacks impact ET's ability to change boundary layer conditions, need to be addressed.

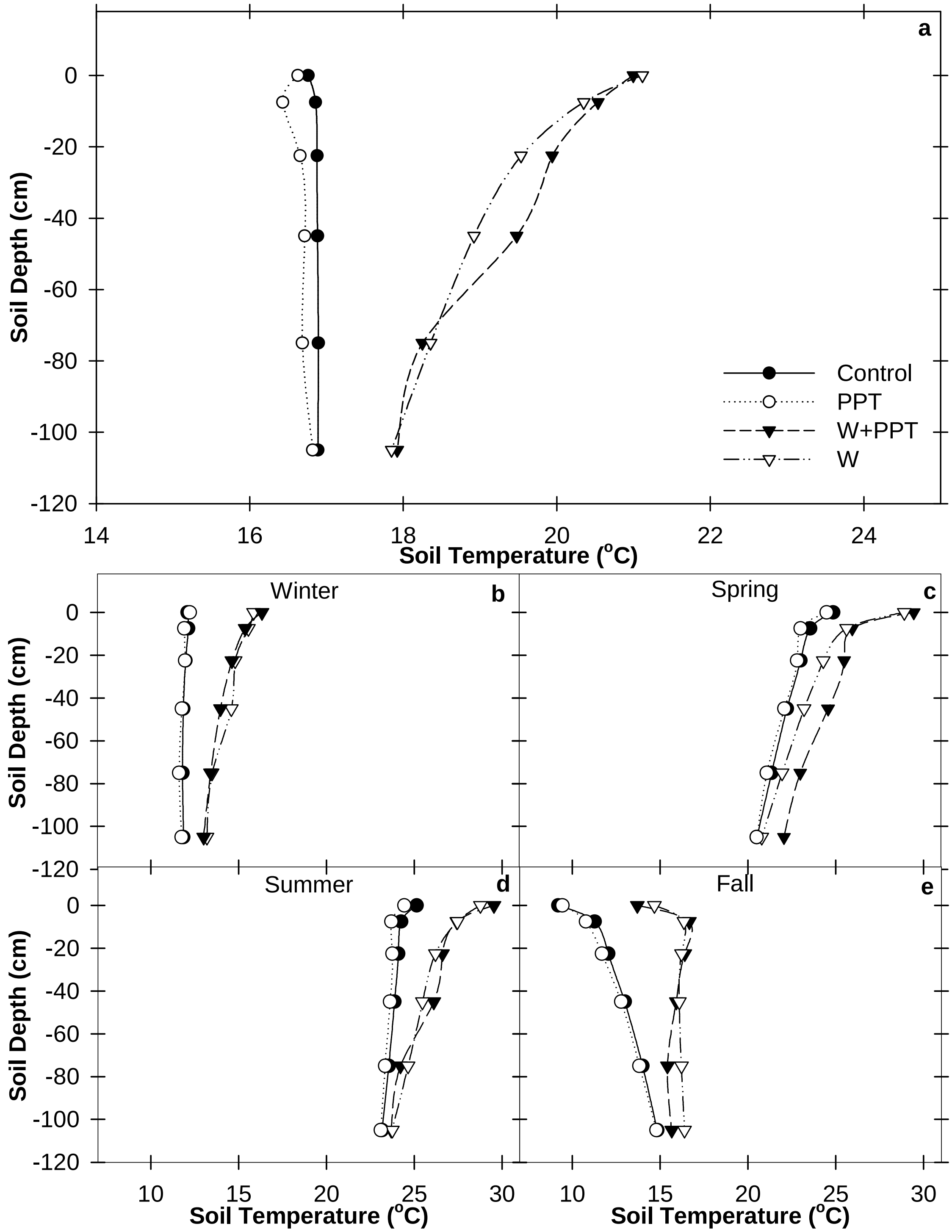


Figure 6. Average soil temperature at multiple depths; (a) yearly average, (b) winter, (c) spring, (d) summer, and (e) fall divided among different treatments.

Our results also indicated that this experimental system was affective in influencing climatic change among all treatment types. Similar results were obtained in a congruent experiment using similar methods (Wan et al., 2002). In addition, our results further explain how experimental warming, from infrared heaters, alters temperature along a soil profile. Other infrared warming studies have identified changes in soil temperature and moisture (Harte et al., 1995; Bridgham et al., 1999; Wan et al., 2002); whereas, our study identifies that there are significant changes in temperature and moisture at multiple depths.

Change in probability distribution and the environment

Changes that occur in soil moisture frequency distribution also affect the overall climate-vegetation-soil interaction. Our study used frequency distributions to understand potential climate change impacts on soil moisture dynamics; these results could be helpful for future probabilistic modeling studies (Porporato et al., 2004). Both W and W+PPT plots had changes in frequency distributions to lower soil moisture conditions. These results indicate that there is a higher likelihood of changes in other ecosystem processes due to lower soil moisture availability.

Soil moisture dynamics are directly linked to both the carbon and nitrogen cycle (Porporato et al. 2003); hence, the change in soil moisture frequency will likely alter other nutrient cycles. Furthermore, earlier articles have highlighted that our experiment should expect a decrease in litter quality and lower rates of organic matter decomposition in W and W+PPT plots (Rodriguez-Iturbe et al., 2001; Porporato et al. 2003). Thus, there would be less microbial activity and enzymatic oxidation of organic matter to produce soil respiration (Howard and Howard, 1979; Davidson et al., 1998). However, Zhou et al. (2006) showed the opposite results with an increase in soil CO_2 efflux with experimental warming; additionally, increases in soil moisture content caused greater soil CO_2 efflux, but the change was smaller than increased temperature. This suggests that increases in temperature will have a larger impact on microbial activity than moisture availability. Furthermore, the changes in the carbon cycle should cause an associated change in the nitrogen cycle (i.e. ammonification and nitrification).

Additionally, drier soil moisture frequency distributions, in the W and W+PPT plots, could also cause plant water stress. Change in water stress has been shown to cause an associated change in the ecosystem vegetative community composition. For example, Porporato et al., (2003) showed how varying amounts of water stress across a precipitation gradient in the Kalahari affected both the plant community type and ecohydrological processes. Other experiments also showed similar results (Rodriguez-Iturbe et al., 1999; Laio et al., 2001). Plant water stress, caused by changes in the soil moisture dynamics, can in turn cause varying transpiration rates in plant, thus impacting the total amount of evapotranspiration (Rodriguez-Iturbe 2000). These responses will then cause overall changes in ecohydrological processes.

Other changes in the grassland ecosystem could occur with effects that are consistent with our study but occur on a much larger scale. For example, a change in the frequency distribution of soil moisture could impact the amount of plant biomass (Sherry et al. 2008); hence, having a direct affect on the nitrogen and carbon cycle (Rodriguez-Iturbe et al. 2001). Our results hopefully demonstrate the important effects of climate change on soil moisture dynamics, and the possible implications on biogeochemical cycling. In addition, we observed that warming, even combined with increased precipitation, had a drying effect on the soil moisture frequency. This suggests that warming may have a greater impact on soil moisture conditions than increased precipitation.

Changes in E_w and E_{max}

To understand the full impact of the four climate change scenarios on ecohydrological processes we analyzed the changes in wilting point (E_w) to the maximum evaporation rate (E_{max}). These results showed the conditions between E_w and E_{max} changed with each climate change scenario. We were able to make some predictions on how belowground processes of water uptake were changing with different climate conditions.

W+PPT treatment showed a slight change in E_w to E_{max} to wetter soil moisture conditions than the control; additionally, there was a shift to drier soil moisture conditions in the warming plots and little change in the PPT plots. Shifts in the W plots E_w to E_{max} are likely a plant level response to environmental stress. Less soil moisture would cause the plants to increase belowground activity and root growth in search of water (Turner and Kramer, 1980). This increased belowground activity would allow for more soil water to be available for plant use and the plants would be able to withstand lower soil moisture percentages, causing shifts in E_w and E_{max} to drier soil moisture conditions.

Plant level stress response would also be an explanation of why both C and PPT showed similar E_w to E_{max}. Hence, the availability of water will cause no stress to the plant. However, this could also be the reason W+PPT has an E_w to E_{max} shift to wetter soil moisture conditions. W+PPT could have lower stress due to higher temperature with the addition of doubled precipitation. Hence, there would be more photosynthesis and increased available water to meet the plant's demand. Thus, W+PPT would show a slight shift in E_w to E_{max} to higher soil moisture conditions, than those of C.

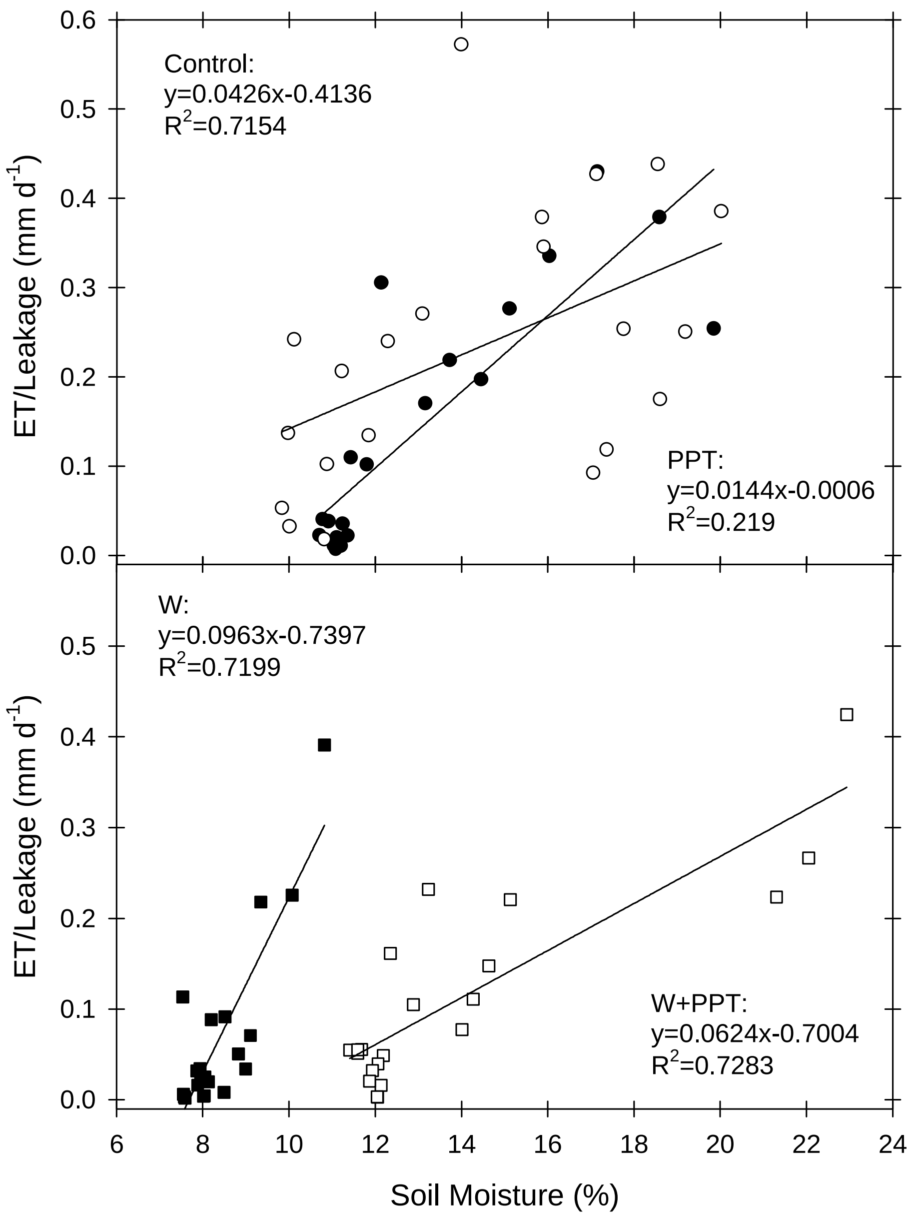


Figure 7. Ew and Emax were calculated to see changes in different treatments types. C (dark circles) is for experimental control ($p < 0.001$), W (dark squares) is for increased warming ($p < 0.001$), PPT (open cicles) is for increased precipitation ($p < 0.023$), W+PPT (open squares) is for increase warming and precipitation ($p < 0.001$).

These results suggest that different climate change conditions will possibly shift an ecosystem's ability to use and acquire water, which is critical in understanding the soil-plant-climate interface (Rodriguez-Iturbe 2000). Additionally, it should be noted, that the warming experiment is not increasing overall atmospheric water demand and that this might change with future climate change (Huntington 2006); hence, there could be even greater evapotranspiration in actual future scenarios.

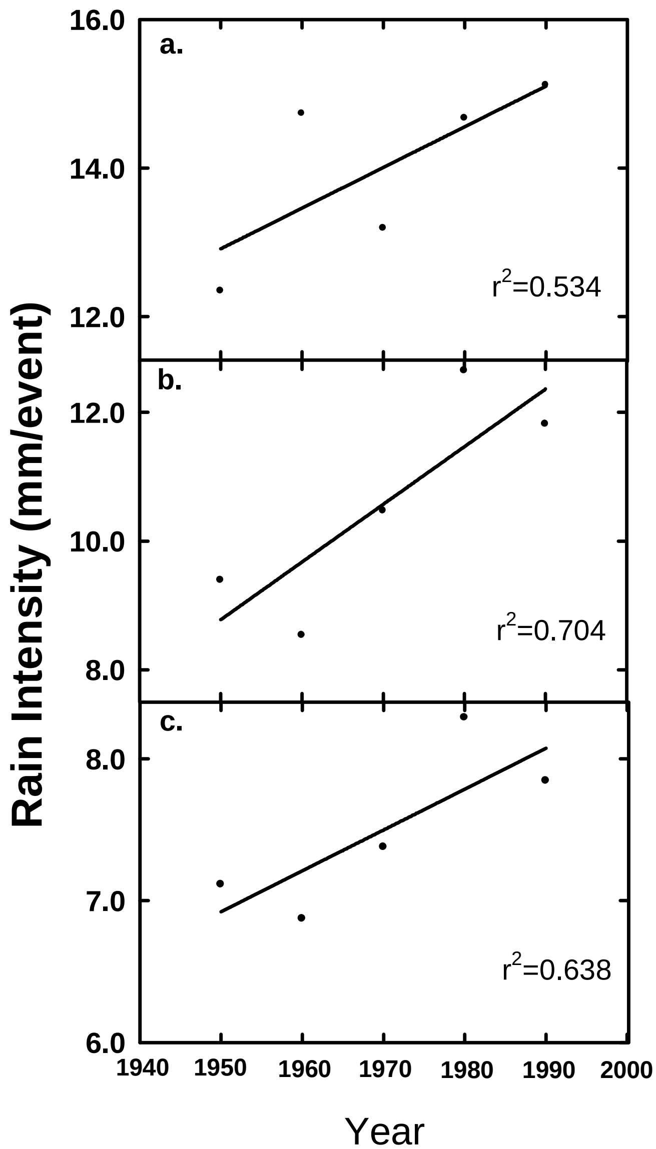
3.5 Conclusions

A complete understanding of the effects of climate change on soil moisture dynamics is increasingly important. Particular focus needs to be made on recognizing how changes in available moisture will affect the entire ecosystem. Multifactor experiments must be performed to fully understand the climate-vegetation-soil interaction under different climate change scenarios (Shaw et al., 2002; Norby and Luo, 2004). Experiments similar to this one will help explain changes in nutrient cycles, vegetation and biomass, and numerous other ecosystem components that are influenced by soil moisture changes. This will then enable better predictions of the future alterations to the environment and ecohydrology of natural systems.

3.6 Acknowledgments

The authors would like to thank Dr. Edwin Kessler for donating his farm to the University of Oklahoma for scientific research, Nancy Zehrbach for organization of data and maintaining the experiment and Tao Zhou for statistical assistance. We would also like to thank J. Janecka, X. Zhou, and E. J. Bradford for editorial comments. This research was financially supported by the U.S. National Science Foundation (NSF) under DEB 0078325 and by the Office of Science (BER), Department of Energy, Grant No. DE-FG03-99ER62800.

Appendix A. Demonstrates that precipitation intensity has increased over the last 50 years in Oklahoma. a-c Ten year averages of rainfall intensity from 1950-2000 across a precipitation gradient encompassing much of the state of Oklahoma (USA) a) Southeastern Oklahoma where the average yearly rainfall was 270 mm. b) Central Oklahoma where the average yearly rainfall was 970 mm. c) Western panhandle of Oklahoma where the average yearly rainfall was 480mm.



Chapter 4

Changes in rain use efficiency across multiple biomes with increased temperature: a meta-analysis approach

Abstract

Terrestrial ecosystem processes (e.g. biogeochemical cycling) are limited by the availability of water. Recently, a maximum rain-use efficiency (RUE = ANPP/precipitation) across multiple biomes was established for years with low average precipitation (Huxman et al. 2004). However, little is known about the impact of temperature on the limitation of water to ecosystem processes. Here we show that RUE varies across different biomes with different mean annual precipitation and analyzed the impact of temperature change on RUE within biomes. Our results show that increases in temperature cause an increase in RUE. Additionally, we show that experimental warming had the largest impact on shrubland and tundra sites. Grassland, receiving the highest amount of precipitation and lowest experimental temperatures, had the second lowest response to experimental warming. Wetland biomes had the lowest response to experimental warming. Increase in temperature allows for ecosystems to reach a RUE_{max} despite variations in area specific sensitivities to physical and biological differences. This research demonstrates that there are temperature limitations on ecosystem processes. These results should be considered for future large-scale modeling projects.

Keywords: rain-use efficiency, warming, carbon, water, global climate change

4.1 Introduction

Anthropogenic climate change, over the 21st century, is predicted to increase global atmospheric temperatures from 1.1–6.4 °C (IPCC 2007). Temperature is known to be a factor in regulating ecosystem processes and biogeochemical cycles. For example, atmospheric warming has been shown to be responsible for regulating most terrestrial plant processes; including aboveground net primary productivity (ANPP) (Rustad et al. 2001), plant productivity (Warren-Wilson 1957), photosynthesis (Coughenour and Chen 1997), root dynamics (Boone et al. 1998; Pregitzer et al. 2000; Gill and Jackson 2000), and plant nutrient uptake (BassiriRad et al. 2000; Rustad et al. 2001). Furthermore, water is the primary resource that can limit these various biological activities; this is especially true in arid and semi-arid areas (Knapp et al. 2008). Despite the connection of temperature and water on ecosystem processes, there has been little research conducted on the impact of higher atmospheric temperature on carbon – water coupling at the ecosystem level.

Recently, Huxman et al. (2004) established a relationship between ANPP, precipitation, and rain-use efficiency (RUE) among different biomes. Additionally, they found that there was a common RUE with the driest years in each biome (RUE_{max}). Furthermore, there was evidence that increases in resource availability would shift an ecosystem's rain-use efficiency closer to a RUE_{max}. For example, the addition of resources (nitrogen and carbon dioxide) to a grassland in Jasper Ridge, California, caused RUE to increase near a predicted RUE_{max}. These results demonstrate that there are common constraints on ANPP across a large geographical scale, and changes in resource availability in varying geographic sites will allow for the maximization of carbon uptake. However, the Huxman et al., (2004) study did not investigate how increases in temperature would alter rain-use efficiency.

Over the last 10-15 years, multiple active research projects have addressed ecosystem responses to changing temperature in the form of temperature-manipulation experiments (Rustad et al. 2001). These experiments have shown a wide array of ecosystem responses (e.g. plant productivity, soil respiration, N mineralization and soil moisture) to warmer temperatures; including many different trends in ecosystem responses with each individual site (Arft et al. 1999; Rustad et al. 2001). However, no study has tried to evaluate how rain-use efficiency changes in different ecosystem types with experimental warming. This leads to the question, "How is experimental warming altering rain-use efficiency across different ecosystems?"

In this paper, we use meta-analysis to analyze different ecosystem's rain-use efficiency in four ecosystem types and 48 site years of data. There were four broadly categorized ecosystem types, including tundra, grassland, shrubland, and wetland. Additionally, a variety of warming apparatuses were used in the analysis (infrared lamp, greenhouses, cables, etc.). Meta-analysis allows us to synthesize rain-use efficiency data from multiple sites and make comparisons based on changes in different geographic locations. Due to the lack of continuous measurements and site locations, there were some limitations to the analytical abilities of the meta-analysis.

We hypothesized that rain-use efficiency will increase with experimental warming in all sites. We also hypothesized that tundra would receive the largest amount of change in RUE with higher temperature because tundra is more limited by temperature than other systems. Grassland sites were hypothesized to have the second largest change in rain-use efficiency with increased temperatures because these systems regularly experience large fluctuations in temperature and the known ability of this biome to physically adapt to climate change (Knapp et al. 2002; Fay et al. 2003; Porporato et al. 2004; Sherry et al. 2008). Meanwhile, shrublands and wetlands would be less apt to change because of slow growth and being controlled by water availability, respectively. For example, the shrubland systems will have slower growth because the primary vegetation component was woody biomass and should take longer to growth. Wetland sites should have more limitations based on nutrient availability and water availability instead of temperature.

4.2 Material and Methods

Experimental sites

The data for this study came from 48 years of experimental ecosystem warming across various biomes in the Northern Hemisphere. Mean annual precipitation for all of the experimental warming sites ranged from 301 to 1741 mm. Increased experimental warming at the individual experiments varied from 1.5 to 5 ^{o}C. Individual characteristics of each site are given in Appendix 1. A variety of heating apparatuses were used in the various experiments, including ground cables, greenhouses, infrared lamps, and night time warming. Most sites were selected from a thorough literature review and additional data were obtained from access to local experimental sites. All data from published papers were extracted from figures and tables. A complete list of experimental sites and citations can be found in Appendix 1.

Each site year was characterized into tundra (n=7), shrubland (n=11), grassland (n=16), or wetland (n=4) based on the dominant vegetation types. In our study, unlike Rustad et al (2001), bogs were incorporated into the wetland sites because they also have the ability of accessing non-precipitation water for growth. All sites were selected on the condition that ANPP (or peak biomass) along with measurements of mean annual precipitation were available in the study. No forested sites were included in our analysis because of a lack of ANPP or peak biomass data from warming studies.

Meta-analysis

Rain-use efficiency was calculated using the ANPP and the mean annual precipitation for each site (RUE = ANPP/Precipitation). For each experimental year we retrieved the mean, sample size, and the standard error, in order to calculate the standard deviation. In cases where no standard errors or standard deviations are reported, a standard deviation was assigned by using 10% of the mean.

The means in the treatment group and control group were then used to calculate the response ratio. A weighted response ratio was calculated from individual response ratios to give greater statistical weight to sites with higher precision and low variance. The 95% confidence interval is derived from the log response ratio. If the confidence limits do not overlap zero, the response ratio is significantly different.

Additionally, a frequency distribution was used to show the variability of the response ratio in the experimental warming studies. Frequency distribution was derived using SPSS software. Luo et al. (2006) provides a full description of the meta-analysis procedure followed in this study. Meta-analyses were run with MetaWin 2.0 (Rosenberg et al. 1997).

4.3 Results

Temperature and Precipitation

The mean temperature increase for all experimental warming sites was 2.92 ^{o}C, with shrublands having the highest average temperature increase of 3.76 ^{o}C, tundra having an average increase of 3.57 ^{o}C, wetlands having an average increase of 2.85 ^{o}C, and grasslands having an average increase of 1.50 ^{o}C (Figure 1A).

Average yearly precipitation across all sites was 582.70mm. The highest average yearly precipitation was found at all grassland biome sites (777.67mm), followed by all wetland sites (634mm), then by shrubland sites (560.86mm), and then by tundra sites (358.26mm) with the lowest average precipitation among the biomes (Figure 1B).

Rain-use efficiency

Rain-use efficiency response to warming at individual experimental sites was slightly variable. There was an increase in RUE with experimental warming in most of the site years; however, some sites experienced negative to no change in RUE with warming. Experimental warming increased RUE at 37 of the 48 sites years, and decreased RUE at 11 of the 48 sites, for which data were available. Histogram was constructed to demonstrate the variation in RUE among individual sites (Figure 2). Additionally, there was an increase in the total mean value of experimental warming RUE (0.475, ±SE = 0.044) from control RUE (0.424, ±SE = 0.045).

Meta-analysis was preformed to compare RUE responses to warming across all biomes and within individual biomes (Table 1). Mean *RR++* for RUE in all of the experimental site years, across all biomes, significantly increased under additional warming (RR++ = 0.1489, with a 95% confidence interval of 0.1648 – 0.1329). Individual biomes had diverse variations in RUE due to experimental warming; however, all biomes (wetland, shrubland, grassland, and tundra) had a positive increase in RUE in response to

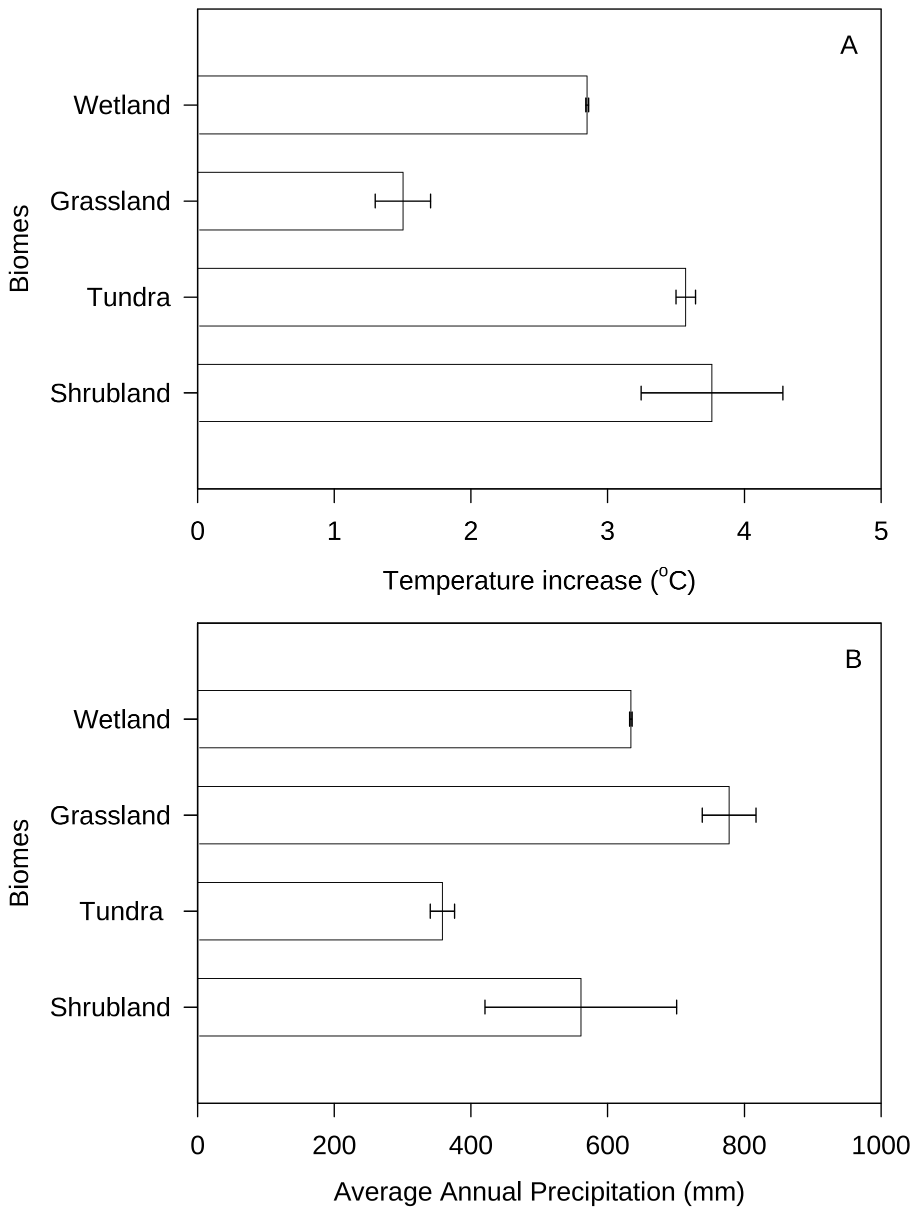


Figure 1. Experimental warming site conditions for each biome (Shrubland, Grassland, Tundra and Wetland). A, Average experimental temperature increases at the different biome types. B, Average annual precipitation amongst different sites used for the meta-analysis.

experimental warming (Figure 3). Wetland biomes had the lowest significant response to warming with a RR++ of 0.1089 (95% confidence interval of 0.1963 – 0.0214); whereas, shrubland biomes had the greatest significant response to experimental warming (with a RR++ of 0.1840 and a 95% confidence interval of 0.2240 – 0.1440). Tundra biomes also experienced a large change in RUE with experimental warming (RR++ of 0.1446, 95% confidence interval = 0.1988 – 0.0903). As for the grassland biome, there was a significant increase in RUE with warming of 0.1278 RR++ (95% confidence interval of 0.1460 – 0.1096).

Overall, experimental warming was found to increase the amount of carbon uptake per unit of rainfall received in all biomes and under varied experimental warming techniques. An analysis of RUE_{max} was not preformed due to a lack of sufficient data. In order to do an analysis of RUE_{max}, multiple years of ANPP data must be present at each site to locate the minimum annual yearly precipitation. However, an estimate of RUE_{max} was obtained from Huxman et al. (2004). The estimated RUE_{max} was not stated in these results, but is used in the discussion section of this paper for a comparison to our observed RUE_{max}. Estimated RUE_{max} can be obtained from Huxman et al. (2004).

Biome	*RR++*	*SE(RR++)*	*n*
Tundra	14.46	0.0277	7
Grassland	12.78	0.0093	16
Shrubland	18.4	0.0204	11
Wetland	10.89	0.0446	4

Table 1. Response ratios (x100) of the rain-use efficiency and standard error for warming treatments in the four biome types.

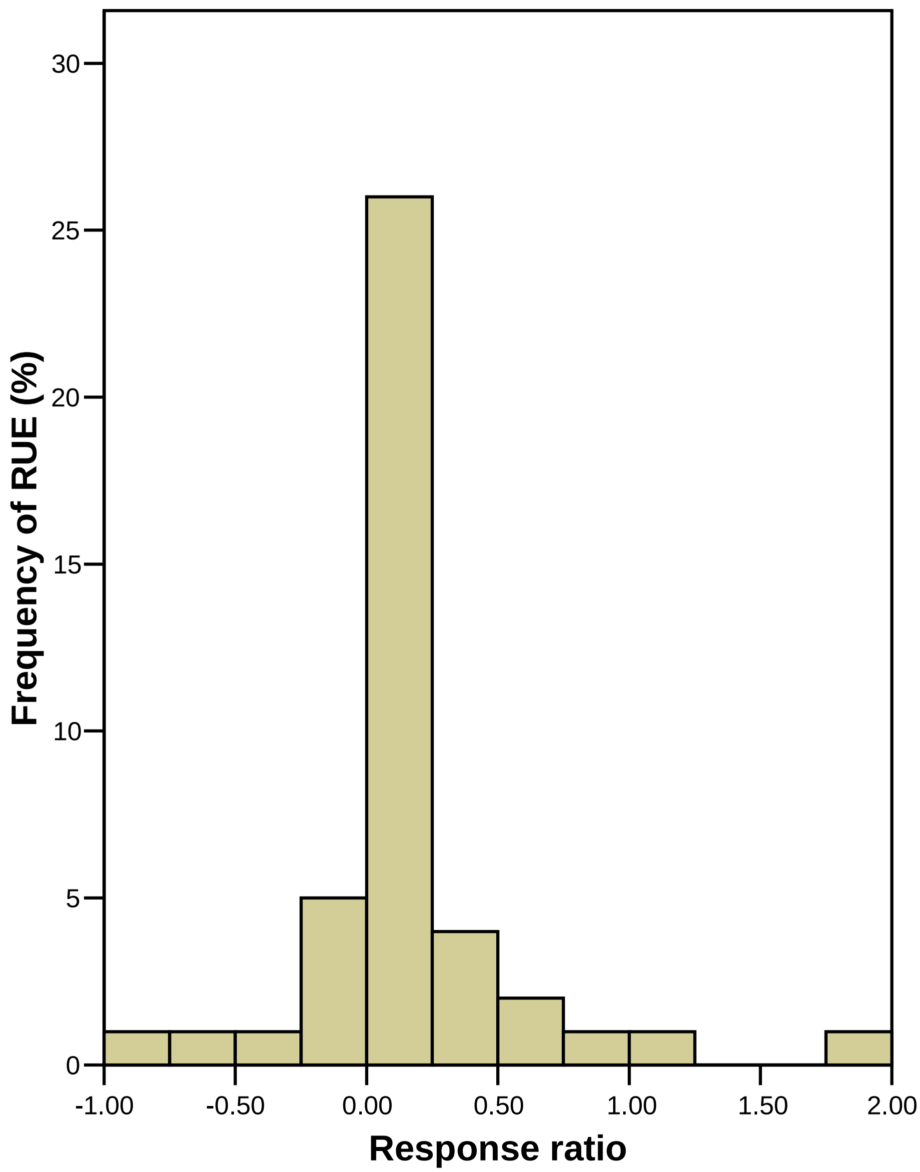


Figure 2. Frequency distributions of the response ratios (RR) of rain-use efficiency amongst all experimental site years. Mean = 0.1567, STDEV = 0.40719, N = 48.

4.4 Discussion

Experimental warming of ecosystems significantly increased rain-use efficiency across all treatment sites for which data were available (Figure 3). Generally, the response was greater in the ecosystems that were in colder environments and had lower annual precipitation with the strongest responses found in the shrubland and tundra sites. The increase in rain-use efficiency may be an effect of either higher rates of photosynthesis due to higher atmospheric temperatures (Coughenour & Chen 1997), or sufficiently longer growing seasons (Sherry et al. 2007). Changes in soil water availability, resulting from increased rates of root production and root growth (Boone et al. 1998; Pregitzer et al. 2000; Gill and Jackson 2000), is also a potential explanation. These effects of experimental warming could be particularly important in colder ecosystems and in water-limited ecosystems because both tend to be limited by temperature and resources (Arft et al. 1999).

Experimental warming has been shown to increase plant productivity in multiple reports from individual subarctic tundra sites (Chapin et al. 1995; Jonasson et al. 1996; Press et al. 1998; Hartley et al. 1999, Rustad et al. 2001). Increased levels of plant production would result in a greater uptake of CO_2 and increase the available carbon in roots and leaves for transfer into soils. However, our study is the first to address changes in carbon uptake per unit of precipitation from experimental warming.

Huxman et al. (2004) reported changes in rain-use efficiency with the addition and subtraction of resources, but no significant research has focused on large scale changes in RUE with changes in resources. Additionally, Huxman et al. (2004)

performed an analysis of different temporal and precipitation trends across different biome types. This study tried to replicate their results and focus on the variation in RUE_{max} across different biomes. A lack of sufficient long term data made the analysis incomplete, and we were not able to determine a RUE_{max} for the experimental study sites. However, based on the increase in RUE at each site, it can be determined that RUE individual sites will approach RUE_{max} with higher temperatures. This is illustrated in Huxman et al. (2004), where an addition of resources (carbon dioxide and nitrogen) caused RUE to increase near RUE_{max}. Additionally, our meta-analysis concluded that all biomes will increase RUE with increases in temperature, demonstrating that RUE is increasing to a RUEmax. Under these conditions there is a greater utilization of water resources for ecosystem processes with a moderate increase in temperature. Our study is not able to precisely estimate how close RUE is to RUE_{max} or what the response of RUE will be with temperature increases that surpass RUE_{max}. There is modeling evidence that RUE in a tallgrass prairie will decrease with temperatures past a 4 °C increase (Bell et al. *in review*).

There was some inconsistency with our original hypotheses on the patterns of RUE in different biome types. Foremost, we predicted that shrubland systems would have the lowest amount of change with experimental warming based on the fact that shrubland sites are composed of woody vegetation and should have a less dramatic response to short-term warming experiments. Rustad et al (2001) found that woody vegetation sites had no significant difference in plant production with

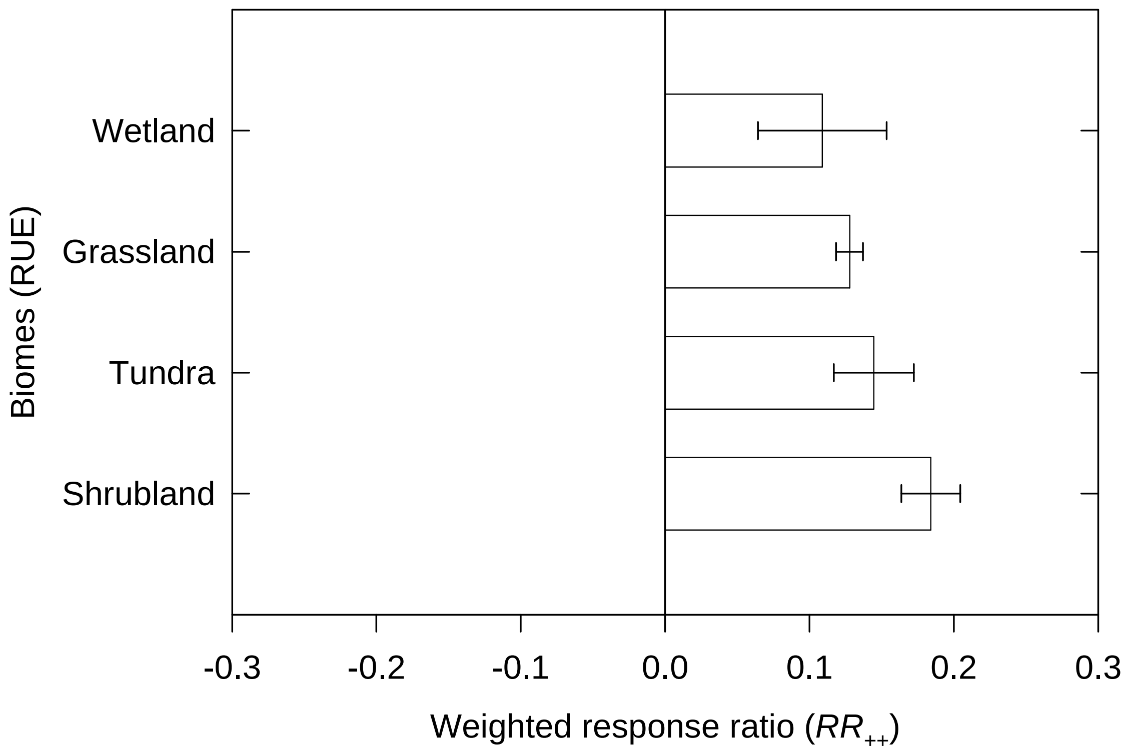


Figure 3. Response ratios (RR, mean ± SE for each biome) of rain-use efficiency under experimental warming.

experimental warming. However, our analysis found that shrubland biomes had the largest change in RUE. Some factors can contribute to large increases in RUE at shrubland sites. First, data for our study were predominantly available for shrubland ecosystems in colder, higher latitude areas. Secondly, shrubland sites had the highest average experimental warming among all sites. Combined, these factors could allow for higher rates of photosynthesis and greater increases in rain-use efficiency (Arft et al. 1999).

Furthermore, our results differed from our original hypothesis that grassland systems would have larger variations due to increased temperatures. This was due to most of the grassland sites being located in temperate areas which are exposed to dramatic fluctuations in temperature. These areas seasonally experience fluctuations in climate and are less likely to respond to slight temperature increases. In addition, the grassland sites had the lowest average temperature increases of all the sites and the highest average yearly precipitation. Our analysis suggests that more temperate ecosystems may not be as limited by temperature, in regard to carbon uptake per unit of rainfall, when compared to colder regions.

Overall, our analysis suggests that temperature can act as a limitation on rain-use efficiency across a variety of biomes and that an increase in temperature will allow for ecosystems to near a RUE_{max}. These trends are evident despite variations that occur among biomes based on soil properties, plant species composition and climate differences. In addition, no information has been acquired on how these biomes will respond to additional increases in temperature and how RUE will respond to temperature increases past the point of RUE_{max}. Further warming experiments must address the possibility of ecosystem “tipping points” (Knapp et al. 2008). Lastly, the responses of ecosystems to changes in temperature could result in additional ecological constraints and should be incorporated into ecosystem modeling for future predictions on the global carbon balance.

5.5 Acknowledgements

We would like to thank Elizabeth J. Bradford for her helpful editorial comments. This research was supported by the National Science Foundation, under DEB 0078325 and DEB 0444518, and additional funding was by the Terrestrial Carbon Program at the Office of Science, United States Department of Energy, from Grant No. DE-FG03-99ER62800 and DE-FG02-006ER64317.

Appendix 1. List of all the sites and manuscripts used for the analysis of RUE.

Site	Location	Year	Biome	Citation
Toolik Lake (tussock)	Alaska, USA	1997	Tundra	Grogan & Chapin, 2000
Toolik Lake (inter-tussock)	Alaska, USA	1997	Tundra	Grogan & Chapin, 2000
Alaska (LTER-Brook Range)	Alaska, USA	1983	Tundra	Chapin et al. 1996
Alaska (LTER-Brook Range)	Alaska, USA	1989	Tundra	Chapin et al. 1996
Alaska (LTER-Brook Range)	Alaska, USA	2000	Tundra	Gough & Hobbie, 2003
Toolik Lake	Alaska, USA	1983	Tundra	Chapin, 1995
Toolik Lake	Alaska, USA	1989	Tundra	Chapin, 1995
Taisetsu Mountains	Japan	1995-1999	Shrubland	Kudo & Suzuki, 2003
Abisko Scientific Research Station	Sweden	1993	Shrubland	Hartley et al. 1999
Abisko Scientific Research Station	Sweden	1994	Shrubland	Hartley et al. 2000
Abisko Scientific Research Station	Sweden	1995	Shrubland	Hartley et al. 2001
Abisko Scientific Research Station	Sweden	1994	Shrubland	Hartley et al. 2002
Abisko Scientific Research Station	Sweden	1995	Shrubland	Hartley et al. 2003
Abisko Scientific Research Station	Sweden	1997	Shrubland	Hartley et al. 2004
Abisko Scientific Research Station	Sweden	1998	Shrubland	Press et al. 1998
Ericacea Site	UK	2000	Shrubland	Penuelas et al. 2004
Ericacea Site	Netherlands	2000	Shrubland	Penuelas et al. 2004
Ericacea Site	Spain	2000	Shrubland	Penuelas et al. 2004
Toivola and Alborn	USA	1994-1997	Wetland	Weltzin et al. 2000
Toivola and Alborn	USA	1994-1997	Wetland	Weltzin et al. 2000
Toivola and Alborn	USA	1994-1997	Wetland	Weltzin et al. 2000
Toivola and Alborn	USA	1994-1997	Wetland	Weltzin et al. 2000
Jasper Ridge Bio Station	USA	1999	Grassland	Zaveleta et al. 2003
Jasper Ridge Bio Station	USA	2000	Grassland	Zaveleta et al. 2003
Jasper Ridge Bio Station	USA	2001	Grassland	Zaveleta et al. 2003
Jasper Ridge Bio Station	USA	2001	Grassland	Zaveleta et al. 2003
Rocky Mountain Biological Lab	USA	1996	Grassland	Valpine & Harte, 2001
Rocky Mountain Biological Lab	USA	1997	Grassland	Valpine & Harte, 2002
Buxton Site	UK	1994-1998	Grassland	Grime et al. 2000
Wytham Site	UK	1994-1998	Grassland	Grime et al. 2000
Gunnison Site	USA	1992	Grassland	Harte et al. 1995
Gunnison Site	USA	1992	Grassland	Harte et al. 1995
One-year Warming Site Oklahoma	USA	2003	Grassland	Not cited
Multi-year Warming Site Oklahoma	USA	2000-2006	Grassland	Not cited

Chapter 5

Conclusions

5.1. Conclusions

The analysis presented in this thesis proposes several important conclusions regarding the response of ecosystems to climate change. As illustrated in Chapter 1, there is a relatively large amount of data on how global climate change impacts on ecosystem processes. However, there is little known about ecosystem would respond to different combinations of climate change scenarios with carbon-water coupling associated with future changes. Understanding these responses is exceedingly important for developing a conceptual framework of possible future environmental change.

In this thesis, a direct investigation of multifactor (both with modeling and field experiments) climate change was done on understanding the response of ecosystem processes (i.e. carbon and water cycles). Additionally, an evaluation of climate change's impact on carbon-water coupling was done. Some of the major findings are below:

The terrestrial ecosystem modeling showed that ecohydrological processes varied in a tallgrass prairie with different combinations of altered yearly precipitation, CO_2, and temperature. Temperature and precipitation had the greatest impact on most components of the hydrological cycle; however, CO_2 had a greater impact on rain use efficiency and water use efficiency. Three-factor combinations of CO_2, temperature, and precipitation produce slight variations from two-factor responses. The modeling results show that rain use efficiency increases with temperature to around 4°C, but any additional temperature increase past 4-5°C causes a decrease in RUE. This pattern with RUE peaking at 4-5°C is more prominent with combinations of precipitation and CO_2. Furthermore, there was no similar pattern of peaking with water use efficiency. It should also be noted that runoff had a considerable decrease with temperature.

The experimental warming and doubled precipitation experiment gave multiple insights on changes to soil moisture dynamics under different climate change scenarios. Warming caused a significant decrease in soil moisture at multiple soil depths and precipitation caused a significant increase in soil moisture at lower depths. Under the combination of warming and doubled precipitation, the soil moisture content was significantly decreased from control. This suggests that warming has a larger impact on soil moisture dynamics than increased precipitation. Furthermore, the probabilistic analysis of soil moisture dynamics under different climate conditions is very important for modeling.

Based on the analysis of evapotranspiration vs. soil moisture, there was an overall change in the ecosystem's ability to use water. The estimated wilting point shifted to drier soil moisture conditions with higher atmospheric temperature, along with the maximum evapotranspiration point. Other shifts in wilting point and maximum evapotranspiration were found in the other treatment types, suggesting that internal ecosystem mechanisms can change with different climate change conditions and cause changes to the hydrological cycle.

The meta-analysis study examined the patterns of rain use efficiency across multiple biomes (tundra, grassland, shrubland, and wetland) with experimental warming. The results show that warming causes an increase in rain use efficiency for every biome in the analysis. This suggests that warming is increasing rain use efficiency to near maximum rain use efficiency (Huxman et al. 2004). In addition, the ratio of carbon uptake per unit of precipitation increases with an increase in temperature, suggesting that there are large scale ecosystem patterns associated with global climate change.

5.2 Implications for future work

The results from the TECO model demonstrated that runoff changed with varying scenarios of climate change in a grassland ecosystem. It has yet to be examined whether these results are represented in field experiments and consistent across multiple ecosystem types. To clearly understand the response of runoff to climate change, it is imperative to elicit new experiments to determine the rates of runoff change from the actual field, which can examine both single and multifactor experiments. Additionally, new modeling runs should be done on multiple ecosystem types to examine if the pattern holds and what are some of the possible alterations that could cause any incongruity.

The interactive effects of climate change on the hydrological cycle suggest that multifactor experiments are important for understanding the potential responses of ecosystem processes. Few experiments have tried to analyze all hydrological processes with different climate change scenarios. However, this does not suggest that single factor experiments are insubstantial, these studies are actually quite important for isolating ecosystem responses to climate change. Ideally, these results will be important for understanding the availability of water resources and quantifying different plant-atmosphere water "feedbacks" that drive weather and are important for future climate modeling.

The apparent increase in rain use efficiency across multiple biomes with experimental warming suggests that other large-scale ecosystem patterns exist in the presence of climate change. To clearly evaluate the underlying commonalities, it is essential to assemble long-term data and use inventive exploratory processes to elicit patterns. This could include the utilization of other data (e.g. climate) to assess large-scale processes. For example, a great deal of information could be derived by combining precipitation intensity and frequency with ecosystem properties (Figure 1). These results will be important for understanding the response of the biosphere to external drivers and allow for forecasting of anthropogenic and natural climate change.

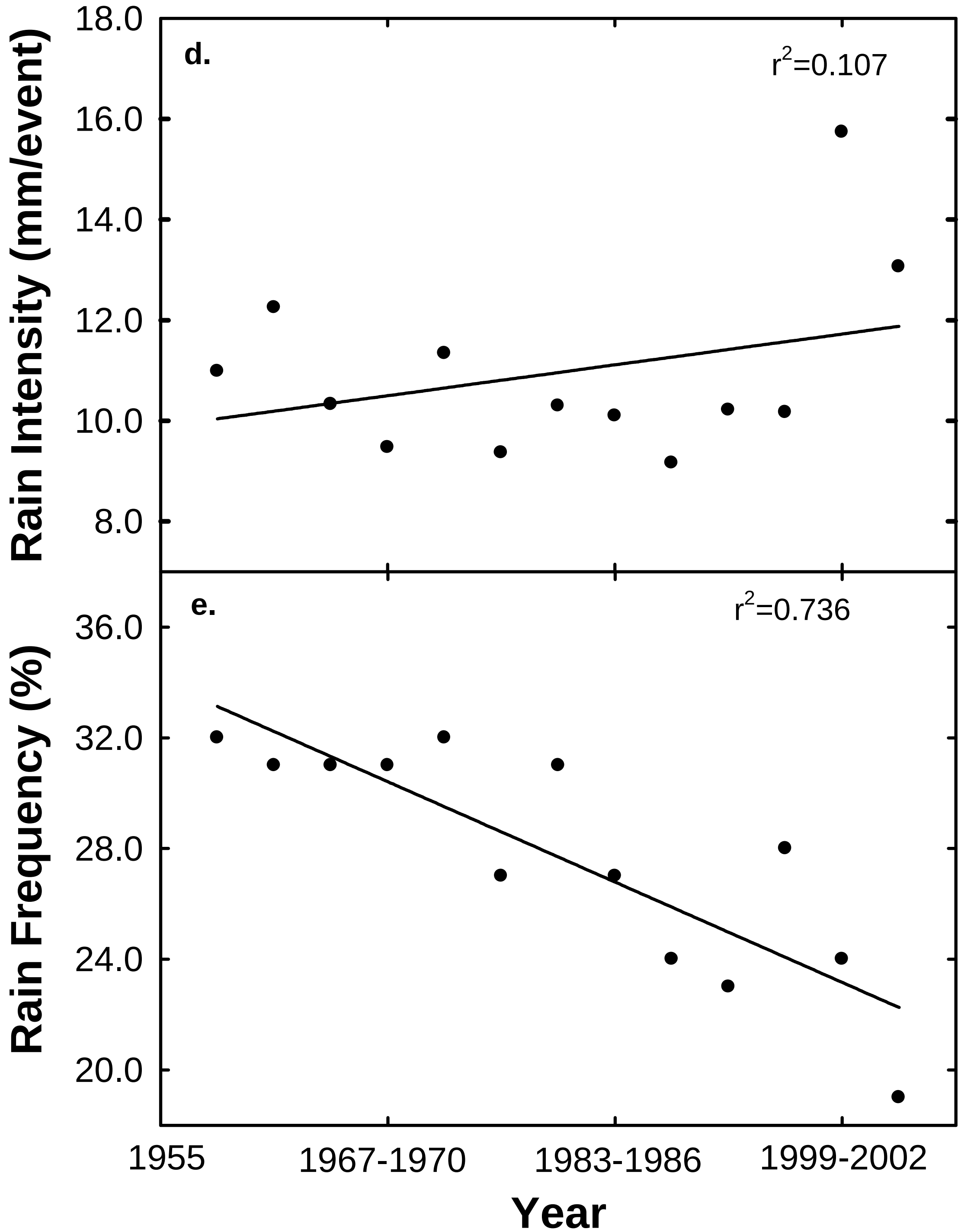


Figure 1. Four year averages from 1955-2006 of (d) rainfall event intensity and (e) frequency of days with rain for Corfu, Greece where the average yearly rainfall was 1100mm (Klein et al., 2002 - Data and metadata available at http://eca.knmi.nl).

Patterns of aboveground net primary production with precipitation were evaluated at local and large-scale patterns. An entire evaluation of total biomass across sites has yet to be performed. Inclusion of root biomass would be important for understanding whole plant response to climate change and give further indication of carbon uptake. Limited information is available on root response to climate change, mostly due to accuracy and difficulty of the measurements.

Global Climate Models are used to predict future climate in response to anthropogenic atmospheric change. Within the GCMs there is a component that includes the land-surface feedbacks (i.e. evapotranspiration and CO_2 efflux). Based on the effective response of the TECO model to climate change, it would prove beneficial to incorporate the TECO model into the GCMs. The mechanistic model will provide for a more realistic terrestrial feedback to the GCMs and allow for more accurate prediction of future climate change.

Many countries and regions have developed a regulatory means of reducing CO_2 emissions to combat anthropogenic climate change. There are, however, no emission control mechanisms in place that will effectively curb the total production of greenhouse gases. Based on the possibility of potential outcomes and the wide range of variance in future climate response, a more scientific approach needs to be implemented on understanding climate change impacts on ecosystem processes. Because of the large number of possible outcomes for future climate, there needs to be more research on various climate scenarios and gradients to determine ecosystem response and potential tipping points. Hence, future climate experiments should include multiple scenarios and give a wider array of possible combinations of climate change. This information will be highly valuable for validating future ecosystem models and making predictions on areas that will be most vulnerable to stress thresholds that cause alteration in ecosystem type.

Science has been closely woven into policy in the United States since before the formation of the National Science Foundation. Based on some of the ecological problems that we face currently and in the coming decades, the science of ecology can be used as an effective way for guiding policy decisions (Clark et al., 2001). Advancements in modeling and analytical techniques along with greater availability of temporal and spatial data, allows for a better ability to predict ecosystem responses in the threat of an ever-changing environment. Connections need to be made between ecology and policy that will allow for a relevant decision-making process. These connections will most likely be formed with the advent of scientists extending their expertise to policy specialists. All fields have some contribution to policy; however, here are a few fields that standout as highly important for future interdisciplinary interaction: global climate change/disturbance, species invasion, disease transmission, and the production of biofuels.

REFERENCE

Allen, M.R., and W.J. Ingram (2002), Constraints on future changes in climate and the hydrologic cycle, *Nature*, 419, 224-232.

Allen Jr., L.H., D. Pan, K.J. Boote, N.B. Pickering, and J.W. Jones (2003), Carbon Dioxide and Temperature Effects on Evapotranspiration and Water Use Efficiency of Soybean, *Agronomy Journal*, 95, 1071-1081.

American Institute of Biological Sciences, Ecological Impacts of Climate Change: Report from a NEON Workshop. 2004.Washington, DC: AIBS.

Arora, V.K., and G.J. Boer (2005), A parameterization of leaf phenology for the terrestrial ecosystem component of climate models, *Global Change Biology*, 11, 39–59.

Ball, J.T., I.E. Woodrow, and J.A. Berry, (1987), *A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions, In Progress in Photosynthesis Research*, edited by J. Biggens, pp. 221–224, Martinus Nijhoff Publishers, The Netherlands.

Betts, R.A., (2006), Forcing and feedbacks by land ecosystem changes on climate change, *Journal De Physique IV*, 139, 119-142.

Betts, R.A., M. O Boucher, P.M. Collins, P.D. Cox, N. Falloon, D.L. Gedney, C. Hemming, C.D. Huntingford, D.M.H Jones, M.J. Sexton, and M.J. Webb (2007), Projected increase in continental runoff due to plant responses to increasing carbon dioxide, *Nature*, 448, 1037-1041.

Bowen G.D. (1991). Soil temperature, root growth, and plant function. In: Plant roots: The hidden half. Y. Waisel, A. Eshel, & U. Kafkaki (eds). Marcel Dekker, New York, pp. 309-330.

Bridgham S.D., J. Pastor, K. Updergraff, T.J. Malterer, K. Johnson, C. Harth, J. Chen. (1999). Ecosystem control over temperature and energy flux in northern peatlands. *Ecological Applications*, 9, 1345-1358.

Coughenour M.B., and D. Chen (1997), Assessment of grassland ecosystem responses to atmospheric change using linked plant-soil process models, *Ecological Applications*, 7, 802-827.

Cramer, W., A. Bondeau, F.I. Woodward, I.C. Prentice, R.A. Betts, V. Brovkin, P.M. Cox, V. Fisher, J.A. Foley, A.D. Friend, C. Kucharik, M.R. Lomas, N. Ramankutty, S. Sitch, B. Smith, A. White, and C. Young-Molling (2001), Global response of terrestrial ecosystem structure and function to CO_2 and climate change: results from six dynamic global vegetation models, *Global Change Biology*, 7, 357–373.

Daly E., A. Porporato, and I. Rodriguez-Iturbe (2004). Coupled dynamics of photosynthesis, transpiration, and soil water balance. Part I: upscaling from hour to daily level. *Journal of Hydrometeorology*. 5, 546-558.

Davidson E.A., E. Belk, and R.D. Boone (1998). Soil water content and temperature as independent or confound factors controlling soil respiration in a temperature mixed hardwood forest. *Global Change Biology*, 4, 217-227.

Day T.A., S.A. Heckathorn, and E.H. Delucia. (1991). Limitations of photosynthesis in Pinus taeda L. (loblolly pine) at low soil temperatures. *Plant Physiology*. 96, 1246-1254.

De Boeck, H.J., C.M.H.M. Lemmens, H. Bossuyt, S. Malchair, M. Carnol, R. Merckx, I. Nijs, and R. Ceulemans (2006), How do climate warming and plant species richness affect water use in a experimental grassland? *Plant and Soil*, 288, 249-261.

Easterling D.R., J.L. Evans, P. Ya, Groisman, T.R. Karl, K.E. Kunkel, and P. Ambenje. (2000) Observed variability and trends in extreme climate events: a brief review. *Bull. Amer. Meteor. Soc*., 81, 417-425.

Farquhar, G.D., S. von Caemmerer, J.A. Berry (1980), A Biochemical Model of Photosynthetic CO_2 Assimilation in Leaves of C_3 species, *Planta*, 149, 78–90.

Farquhar, G.D., and T.D., Sharkey (1982), Stomatal conductance and photosynthesis, *Annual Reviews of Plant Physiology*, 33, 317-345.

Ferretti, D.F., E. Pendall, J.A. Morgan, J.A. Nelson, D. LeCain, and A.R. Mosier (2003), Partitioning evapotranspiration fluxes from a Colorado grassland using stable isotopes: seasonal variations and ecosystem implications of elevated atmospheric CO_2, *Plant and Soil*, 254, 291-303.

Gerten, D., S. Schaphoff, and W. Lucht (2007). Potential future changes in water limitations of the terrestrial biosphere. *Climatic Change*, 80, 277-299.

Gordon, W. and J.S. Famiglietti. (2004). Response of the water balance to climate change in the united states over the 20th and 21st centuries: results from the

VEMAP Phase 2 model intercomparisons. *Global Biogeochemical Cycles*. 181 GB 1030.

Ham, J.M., C.E. Owensby, P.I. Coyne, and D.J. Bremer (1995). Fluxes of CO2 and water vapor from a prairie ecosystem exposed to ambient and elevated atmospheric CO2. *Agricultural and Forest Meteorology*, 77, 73-93.

Harte J., M.S. Torn, F.R. Chang, B. Feifarek., A.P. Kinzig,, R. Shaw, and K. Shen. (1995). Global warming and soil microclimate: Results from a meadow-warming experiment. *Ecological Applications*, 5: 132–150.

Hobbie S.E.and F.S. Chapin III (1998) Response of tundra plant biomass, aboveground production, nitrogen and CO2 flux to experimental warming. *Ecology*, 79, 1526–1544.

Houghton J.T., L.G. Meiro Filho, J. Bruce, B.A. Callender, E. Haites, N. Harries, and K. Maskell. Climate change 1994: Radiative forcing of climate change and an evaluation of the IPCC IS92 emission scenarios. Reports of working group I and III of the Intergovernment Panel on Climate Change. Cambridge University Press, Cambridge, UK. 1995.

Houghton J.T., L.G. Meiro Filho, B.A. Callender, N. Harries, and K. Maskell. Climate change 1995: the science of climate change. Contributions of WGI to the second assessment report of the Intergovernment Panel on Climate Change. Cambridge University Press, Cambridge, UK. 1996.

Howard, P.J.A. and D. M. Howard (1979) Respiration of decomposing litter in relation to temperature and moisture. *Oikos*, 33, 457–465.

Hui, D., Y. Luo, W. Cheng, J.S. Coleman, D.W. Johnson, and D.A. Sims (2001), Canopy radiation- and water-use efficiencies as affected by elevated CO2, *Global Change Biology*, 7, 75 - 91.

Huntington, T.G., 2006, Evidence for intensification of the global water cycle: review and synthesis, *Journal of Hydrology*, 319, 83-95.

Huxman, T.E., M.D. Smith, P.A. Fay, A.K. Knapp, M.R. Shaw, M.E. Loik, S.D. Smith, D.T. Tissue, J.C. Zak, J.F. Weltzin, W.T. Pockman, O.E. Sala, B.M. Haddad, J. Harte, G.W. Koch, S. Schwinning, E.E. Small, and D.G. Williams (2004), Convergence across biomes to a common rain-use efficiency, *Nature*, 429, 651-654.

IPCC. Climate Change 2001: the Scientific Basis- Summary for policymakers. IPCC WGI Third Assessment Report. Shanghai Draft, 21 January 2001.

IPCC, 2007: Summary for Policymakers. In: Climate Change 2007: *The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* [Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., and Miller, H.L., (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Kergoat, L., S. Lafont, H. Douville, B. Berthelot, G. Dedieu, S. Planton, and J. Royer (2002), Impact of doubled CO2 on global-scale leaf area index and evapotranspiration: conflicting stomatal conductance and LAI responses, *Journal of Geophysical Research*, 107(D24), 4808, doi: 10.1029/2001JD001245.

Knapp, A.K., E.K. Hamerlynck, and C.E. Owensby (1993), Photosynthetic and water relations responses to elevated CO_2 in the C4 grass Andropogon Gerardii, *Int. J. Plant Sci.*, 154(4): 459-466.

Knapp, A.K., P.A. Fay, J.M. Blair, S.L. Collins, M.D. Smith, J.D. Carlisle, and C.W. Harper (2002), Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland, *Science*, 298, 2202–2205.

Knapp, A.K., C. Beier, D. Briske, A.T. Classen, Y. Luo, M. Reichstein, M.D. Smith, S.D. Smith, J.E. Bell, P.A. Fay, J.L. Heisler, S.W. Leavitt, R. Sherry, B. Smith, J. Weltzin, E. Weng, and J. Yarie (2008), Consequences of more extreme precipitation regimes for terrestrial ecosystems, *Bioscience*, 58, 811-821.

Laio, F., A. Porporato, C. Fernadez-Illescas, and I. Rodriguez-Iturbe. (2001). Plants in water-controlled ecosystems: active role in hydrological processes and response to water stress. IV. Applications to real cases. *Advances in Water Resources*. 24, 745-762.

Li, X., Y. Feng, & L. Boersma (1994) Partitioning of photosynthates between shoot and root in spring wheat (*Triticum aestivum* L.) as a function of soil water potential and root temperature. *Plant Soil*. 164:43-50.

Lockwood, J.G., (1999), Is Potential Evapotranspiration and Its Relationship with Actual Evapotranspiration Sensitive to Elevated Atmospheric CO2 Levels? *Climatic Change*, 41, 193-212.

Luo, Y., P.A. Meyerhoff, and R.S. Loomis (1995), Seasonal patterns and vertical distributions of fine roots of alfalfa (*Medicago sativa* L.), *Field Crops Res.*, 40, 119–127.

Luo, Y., and J.F. Reynolds (1999), Validity of extrapolating field CO_2 experiments to predict carbon sequestration in natural ecosystems, *Ecology*, 80,1568-1583.

Luo, Y., S. Wan, D. Hui, and L. Wallace (2001), Acclimatization of soil respiration to warming in a tall grass prairie, *Nature*, 413, 622-625.

Luo, Y., L. White, J. Canadell, E. DeLucia, D. Ellsworth, A. Finzi, J. Lichter, and W. Shclesinger (2003), Sustainability of terrestrial carbon sequestration: a case study in Duke Forest with inversion approach, *Global Biogeochemical Cycles*, 17, 1021 [doi:10.1029/2002GB001923].

Luo, Y., D. Gerten, G. Le Maire, W.J. Parton, E. Weng, X. Zhou, C. Keough, C. Beier, P. Ciais, W. Cramer, J.S. Dukes, B. Emmett, P.J. Hanson, A. Knapp, S. Linder, D. Nepstad, and L. Rustad (2008), Modeled interactive effects of precipitation, temperature, and [CO_2] on ecosystem carbon and water dynamics in different climatic zones, *Global Change Biology*, 14, 1-14.

Majdi H., J. Ohrvik (2004). Interactive effects of soil warming and fertilization on root production, mortality, and longevity in Norway spruce stand in Northern Sweden. *Global Change Biology* 10: 182-188.

Marion G.M. (1997). Open-top designs for manipulating field temperatures in high-latitude ecosystems. *Global Change Biology* 3 (Supplement1): 20–32.

Melillo J.M., P. A. Steudler, J. D. Aber, K. Newkirk, H. Lux, F. P. Bowles, C. Catricala, A. Magill, T. Ahrens, S. Morrisseau (2002) Soil Warming and carbon-cycle feedbacks to the climate system. *Science*, 298, 2173-2176.

Mellander P.E., K. Bishop, T. Lundmark. (2004). The influence of soil temperature on transpiration: a plot scale manipulation in a young Scots pine stand. *Forest Ecology and Management*. 195, 15-28.

Morgan, J.A., D.E. Pataki, C. Korner, H. Clark, S.J. Del Grosso, J.M. Grunzweig, A.K. Knapp, A.R. Mosier, P.C.D. Newton, P.A. Niklaus, J.B. Nippert, R.S. Nowak, W.J. Parton, H.W. Polley, and M.R. Shaw (2004), Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO2, *Oecologia*, 140, 11-25.

Nijs, I., R. Ferris, H. Blum, G. Hendrey, and I. Impens (1997), Stomatal regulation in a changing climate: a field study using Free Air Temperature Increase (FATI) and Free Air CO2 Enrichment (FACE), *Plant, Cell & Environment*, 20, 1041-1050.

Nilsen, E.T., and D.M. Orcutt (1998), *Physiology of plants under stress: abiotic factors*, Wiley, New York.

Norby, R.J. and Y. Luo. (2004) Evaluating ecosystem responses to rising atmospheric CO2 and global warming in a multi-factor world. New Phytologist 162, 281-293.

Owensby, C.E., P.I. Coyne, J.M. Ham, L.M., Auen, and A.K. Knapp (1993), Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated CO2, *Ecological Applications*, 3, 644-653.

Porporato, A., F. Laio, L. Ridolfi, and I. Rodriguez-Iturbe. (2001) Plants in water-controlled ecosystems: active role in hydrologic processes and response to water stress. III. Vegetation water stress. *Advances in Water Resources*. 24: 725-744.

Porporato, A., F. Laio, L. Ridolfi, K.K. Caylor, and I. Rodriguiz-Iturbe. (2003) Soil moisture and plant stress dynamics along the Kalahari precipitation gradient. *Journal of Geophysical Research*, 108, 4127.

Porporato, A., E. Daly, and I. Rodriguez-Iturbe. (2004) Soil water balance and ecosystem response to climate change. *The American Naturalist*. 164, 625-632.

Porporato, A. P. D'Odorico, F. Laio, and I. Rodriguez-Iturbe. (2004). Hydrolgic controls on carbon and nitrogen cycles. I. modeling scheme. *Advances in Water Resources*, 26, 45-58.

Raddatz, R.L., (2003), Agriculture and tornadoes on the Canadian Prairies: potential impact of increasing atmospheric CO 2 on summer severe weather, *Journal Natural Hazards*, 29**,** 113-122.

Raddatz R.L. and J.D. Cummine (2003). Inter-annual variability of moisture flux from the prairie agro-ecosystem: impact of crop phenology on the seasonal pattern of tornado days. *Boundary-Layer Meteorology*. 106, 283-295.

Robock, A., K. Y. Vinnikov, G. Srinivasan, J. K. Entin, S. E. Hollinger, N. A. Speranskaya, S. Liu, and A. Namkhai, (2000) The Global Soil Moisture Data Bank, *Bull. Am. Meteorol. Soc*., 81, 1281–1299.

Rodriguez-Iturbe, I., P. D'Odorico, A. Porporato, and L. Ridolfi. (1999) Tree-grass coexistence in savannas: the role of spatial dynamics and climate fluctuations. *Geophysical Research Letters*, 26, 247-250.

Rodriguez-Iturbe, I. (2000) Ecohydrology: a hydrologic perspective of climate-soil-vegetation dynamics. *Water Resources Research*, 36, 3-9, 2000.

Rodriguez-Iturbe, I., A. Porporato, F. Laio, and L. Ridolfi. (2001) Plants in water-controlled ecosystems: active role in hydrological processes and response to water stress I. Scope and general outline. *Advances in Water Resources* 24, 695-705, 2001.

Saleska S, J. Harte, M. Torn, (1999). The effect of experimental ecosystem warming on CO2 fluxes in a montane meadow. *Global Change Biology* 5: 125–141.

Sellers, P.J., D.A. Randall, G.J. Collatz, J.A. Berry, C.B. Field, D.A. Dazlich, C. Zhang, G.D. Collelo, and L. Bounoua (1996), A Revised Land Surface Parameterization SiB2) for Atmospheric GCMs. Part I: Model Formulation, *Journal of Climate*, 9, 676–705.

Schafer, K.V.R., R. Oren, C. Lai, and G.C. Kutul (2002), Hydrologic balance in an intact temperate forest ecosystem under ambient and elevated atmospheric CO2 concentration, *Global Change Biology*, 8, 895-911.

Shaw M.R., E.S. Zalvaleta, N.R. Chiariello. (2002) Grassland responses to global environmental changes suppressed by elevated CO2. *Science* 298: 1987-1990.

Sherry, R.A., E.S. Weng, J.A. Arnone III, D. Johnson, D.S. Schimel, P.S. Verburg, L.L. Wallace and Y. Luo. 2008. Lagged effects of experimental warming and doubled precipitation on annual and seasonal aboveground biomass production in a tallgrass prairie. *Global Change Biology* 14: 2923-2936.

Sherry, R.A., X. Zhou, S. Gu, J.A. Arnone III, D.S. Schimel, P.S. Verburg, L.L. Wallace, and Y. Luo (2007), Divergence of reproductive phenology under climate warming, *PNAS*, 104, 198-202.

Stephenson, N. L. (1990). Climatic control of vegetation distribution: the role of the water-balance. *American Naturalist* 135:649–670.

Tarr E., J.G. Botkin, E.L. Rice E. Carpenter, M. Hart. (1980) A broad analysis of fifteen sites in the tall-grass prairie of Oklahoma. *Proceedings of the Oklahoma Academy of Sciences* 60: 39.

Turner N.C., and P.J. Kramer, eds. (1980). Adaptations of plants to water and high temperature stress. Wiley, New York.

USDA . Soil survey of McClain County, Oklahoma. Soil Conservation Service, cooperated with Oklahoma agricultural experiment station, Stillwater, Oklahoma. 1979.

Wan S., Y. Luo and L.L. Wallace. (2002) Changes in microclimate induced by experimental warming and clipping in tallgrass prairie. *Global Change Biology* 8, 754-768,

Wan, S., D. Hui, L.L. Wallace, and Y. Luo (2005), Direct and indirect warming effects on ecosystem carbon processes in a tallgrass prairie, *Global Biogeochemical Cycles,* 19, GB2014, doi: 10.1029/2004GB002315

Wang, Y.P., and R. Leuning (1998), A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy I: Model description and comparison with a multi-layered model, *Agriculture and. Forest Meteorology*, 91, 89–111.

Weng, E., and Y. Luo (2008), Soil water holding capacity regulates ecosystem responses to multifactor global change: a modeling analysis, *Journal of Geophysical Research – Biogeosciences*. doi:10.1029/2007JG000539.

Wetherald, R.T., and S. Manabe (2002), Simulation of hydrologic changes associated with global warming, *Journal of Geophysical Research*, 107, 4379.

Wullschleger, S.D., C.A.Gunderson, P.J. Hanson, K.B. Wilson, and R.J. Norby (2002), Sensitivity of stomatal and canopy conductance to elevated CO2 concentration – interacting variables and perspectives of scale, *New Phytologist*, 153, 485-496.

Yang, Y., M. Watanabe, Z. Wang, Y. Sakura, and C. Tang (2003), Predictions of changes in soil moisture associated with climate changes and their implications for vegetation change: waves model simulation on Taihang Mountain, China, *Climate Change*, 57, 163-183.

Zhou, X., R. Sherry, Y. An, L.L. Wallace, and Y. Luo (2006), Main and interactive effects of warming, clipping, and doubled precipitation on soil CO_2 efflux in a grassland ecosystem, *Global Biogeochemical Cycles*, 20, GB1003, doi:10.1029/2005GB002526.

Zhou, X., E. Weng, and Y. Luo (2008), Ecosystem nonlinear responses to changes in temperature, CO2, and precipitation on carbon and water cycles of a grassland, *Ecological Applications* 18, 453~466.

Xu, T, L. White, D. Hui, and Y. Luo (2006), Probabilistic inversion of a terrestrial ecosystem model: analysis of uncertainty in parameter estimation and model prediction, *Global Biogeochemical Cycles*. doi:10.1029/2005GB002468.