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RESPONSES OF COMMUNITY STRUCTURE AND ECOSYSTEM FUNCTIONING TO CLIMATE CHANGE – META-ANALYSIS, MODELING, EXPERIMENTAL STUDY AND DATA-MODEL FUSION

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RESPONSES OF COMMUNITY STRUCTURE AND ECOSYSTEM FUNCTIONING TO CLIMATE CHANGE – META-ANALYSIS, MODELING, EXPERIMENTAL STUDY AND DATA-MODEL FUSION

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DEPARTMENT OF MICROBIOLOGY AND PLANT BIOLOGY

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Abstract

Observations, experimental studies and modeling endeavors all show that global climate change, mainly increased surface air temperature and associated change in precipitation regime, has caused impacts on plant community structure and terrestrial ecosystem functioning. The direction, rate and magnitude of ecosystem responses to climate change vary across time and space. Mechanisms and feedbacks responsible for the ecosystem responses are complex, from physiological and phonological to community-shift driven. Therefore, to advance our understanding, it is of great importance to recognize general patterns in the ecosystem responses and identify probably underlying mechanisms. In this dissertation, I attempted to generalize central patterns of effects of warming and altered precipitation on plant community and ecosystem carbon (C) dynamics and identify mechanisms using multiple approaches including meta-analysis, manipulative experiment, ecosystem C modeling and model-data fusion.

In the first study, I conducted a modeling analysis of the effects of extreme drought on two key ecosystem processes, production and respiration, and to provide broader context I complemented this with a synthesis of published results across multiple ecosystems. The synthesis indicated that across a broad range of biomes gross primary production (GPP) generally was more sensitive to extreme drought than was ecosystem respiration (ER). Furthermore, this differential sensitivity between production and respiration increased as drought severity increased and occurred only in grassland ecosystems but not in evergreen needle-leaf and broad-leaf forests or woody savannahs. The modeling analysis was designed to better understand the mechanisms underlying this pattern and focused on four grassland sites arrayed across the Great Plains, USA. Model results consistently showed that net primary productivity (NPP) was reduced more than heterotrophic respiration (Rh) by extreme drought (i.e., 67% reduction in annual ambient rainfall) at all four study sites. The sensitivity of NPP to drought was directly attributable to rainfall amount, whereas sensitivity of Rh to drought was driven by soil drying, reduced carbon (C) input and a drought-induced reduction in soil C content, a much slower process. However, differences in reductions in NPP and Rh diminished as extreme drought continued due to a gradual decline in the soil C pool leading to further reductions in Rh. The findings suggest that responses of production and respiration differ in magnitude, occur on different timescales and are affected by different mechanisms under extreme, prolonged drought.

In the second study, I used a meta-analysis approach to quantify the responses of community productivity and structure to both increased and decreased precipitation by synthesizing 44 experimental studies in grassland ecosystem. The results showed that decreased precipitation suppress aboveground net primary productivity (ANPP) by 16.7% and belowground net primary productivity (BNPP) by 5.4%; increased precipitation enhanced ANPP by 25.7% but had no impact on BNPP; community structure showed little responses to precipitation change, except species richness responding negatively to decreased precipitation by 8%. Response of ANPP to altered precipitation was significantly greater than that of BNPP and response of ANPP to increased precipitation was stronger than that to decreased precipitation. In general, ANPP of different PFTs, except C_4 showed positive and negative responses to decreased and increased precipitation, respectively, but we did not detect any difference in responses among the PFTs. The response ratios of dominant PFTs to altered precipitation positively correlated with that of the whole plant community, with the slope less than 1. Productivity sensitivity to both precipitation change declined exponentially with mean annual precipitation. Our analyses provide a complementary perspective to long-term observational productivity-precipitation relationship, suggest that changes in ecosystem functioning driven by community shift under precipitation change was uncommon and indicate that future greater precipitation variability could overall favor plant growth. Our findings have implications for both modeling community and experimental studies.

In the third study, I explored the long-term responses of a prairie plant community to 14-year (2000-2013) manipulations of climate warming and clipping in Oklahoma, USA. Community composition was resistant to experimental warming in the first seven years, but started to show responses since the eighth year; clipping consistently affected community composition over the years. Compositional change under long-term warming was mainly contributed by one invasive species and three dominant species. The negative correlations in relative abundance between the invasive species and the dominant species suggest inter-specific competition. Community structure (i.e., richness, evenness and diversity) had no overall response to experimental warming. However, in 2007, the extreme wet year, warming reduced species richness by 30%. Clipping promoted species richness by 10% on average over the 14 years but decreased community evenness. Warming did not interact with clipping in influencing the plant community variables. Our study provides experimental evidence for long-term

shifts in plant community composition due to climate warming and revealed novel mechanisms (i.e., species invasion and associated biotic interactions) underlying the long-term shift. The results also suggest that climate extremes may elicit or advance community responses to climate warming. The findings have implications for terrestrial carbon modeling with dynamic global vegetation.

In the fourth study, measurements from a nine-year warming experimental site in a tallgrass prairie were assimilated into a terrestrial ecosystem C cycle model to assess warming effect on key model parameters and to quantify uncertainties of long-term C projection. Warming decreased allocation of gross primary production (GPP) to shoot, and turnover rate of the live C pools (i.e., shoot and root C), but increased the turnover rates of litter and fast soil C pools. Consequently, warming increased live C pools, but decreased litter and soil C pools, and overall decreased total ecosystem C in a 90-year model projection. Information content gained from assimilated datasets was much greater for plant, litter and fast soil C pools than for slow and passive soil C pools. Sensitivity analysis revealed that fast turnover C pools were most sensitive to their turnover rates and modest to C-input related parameters on both short-term and long-term time scales. However, slow turnover C pools were sensitive to turnover rate and C input in long-term prediction, not in short-term prediction. As a result , total soil and ecosystem C pools were generally insensitive to any parameter in short term, but determined by turnover rates of the fast, slow and passive soil C and transfer coefficients from upstream C to slow and passive C pools. Our findings suggest that data assimilation is an effective tool to explore the effect of warming on C dynamics; the nine-year field data contribute more information for the fast C processes

than for the slow C processes ; and C cycle model parameters change with warming, and models need to account for that phenomenon not to produce bias in C projections. However, warming-induced changes in parameter values also suggest that some important ecosystem processes may be missing or not adequately represented in the ecosystem C models.

These studies demonstrated that the patterns in responses of community structure and ecosystem functioning to climate change could be generalized and showed the complexity of potential mechanisms and feedbacks underlying the ecological responses. Future research is still needed in synthesizing existing observations and experiments, unifying them through statistical and process-based modeling and data assimilation and developing theories in this research area.

Keywords: global change, terrestrial ecosystems, carbon cycle, TECO model, , data assimilation, information theory, meta-analysis, state shift, warming, altered precipitation

Chapter 1 Introduction

1.1 Introduction

Global change drivers (GCDs) affect terrestrial ecosystem structure and functioning. For example, CO_2 enrichment increased net primary production in a sweetgum forest stand in Tennessee (Norby et al., 2010) and in a shortgrass steppe in Wyoming (Morgan et al., 2001). Furthermore, elevated CO_2 favored C3 grasses over C4 grasses (Morgan et al., 2011). Warming enhanced tree growth, soil respiration and nitrogen mineralization in a deciduous forest in New England (Melillo et al., 2011) and increased cover of deciduous shrubs and graminoids in tundra ecosystems (Walker et al., 2006). In addition, warming favored C4 grasses over C3 grasses in a mixed-grass prairie (Morgan et al., 2011) and decreased species diversity and evenness across tundra biome (Walker et al., 2006). Increased precipitation favored grassland production in a tallgrass prairie (Xu et al., 2013) and hasten soil carbon decomposition (Thomey et al., 2011), whereas reduced precipitation adversely impact plant carbon and water functioning and decomposition (Fay et al., 2008). Increased precipitation was also found to increase grassland biodiversity in a Mediterranean annual grassland (Zavaleta et al., 2003), whereas decreased precipitation reduced species diversity in a semiarid grassland (Miranda et al., 2009).

Manipulative experiments on whole ecosystem or ecosystem components are powerful tool to study the GCDs effect (Rustad, 2006 and 2008, Luo et al., 2011). Hundreds of global change experiments have been conducted over a wide range of ecosystems/biomes (Rustad, 2008). Due to the heterogeneity of ecosystems, idiosyncratic findings across ecosystems require overall synthesis of the manipulative experiments to explore central tendency of the GCDs effect on various ecosystem processes (Rustad et al., 2001, Luo et al., 2006, Walker et al., 2006, Wu et al., 2011, Lu et al., 2013). Through compiling the GCDs manipulative experiments (also called meta-analysis), Luo et al., (2006) showed that elevated CO_2 concentration increased both C and N in plant and soil pools; Lu et al. (2013) found that warming stimulated ecosystem photosynthesis by 16%, net primary production by 4%, soil respiration by 9%, but had no impact on soil carbon content; Wu et al. (2011) reported that increased/decreased precipitation favored/suppressed plant growth; Bai et al. (2013) found that net N mineralization and nitrification rate were enhanced accompanying with increase in N pools.

The two largest ecosystem carbon (C) fluxes, photosynthetic uptake of CO2 from atmosphere and ecosystem respiration (i.e., release of CO2 to atmosphere), are likely to be affected differently by the GCDs (Mission et al., 2010, Schwalm et al., 2010) due to different mechanisms involved. Responses of the two ecosystem C fluxes to the GCDs are critical given that any net change of ecosystem C balance acts as a feedback to climate change. Drought as one aspect of global climate change, has been predicted to increase in the frequency and magnitude in the future (Dai, 2011). Although there are now many studies that have reported responses of the two fluxes to both natural and experimentally imposed droughts in a variety of biomes (e.g., Reichstein et al., 2002, Ciais et al., 2005, Schwalm et al., 2012, Potts et al., 2012), these have not been synthesized to determine if there are any general patterns of production and respiration responses to extreme drought across terrestrial biomes (but see Schwalm et al., 2010a). Therefore, scientific questions need to be addressed, such as if general patterns of drought effects on production and respiration exist across multiple biomes and what are the mechanisms possibly underlying differential sensitivity of production and respiration.

Community composition change is both a consequence of the GCDs effect (Gornish et al., 2013) and a critical mechanism regulating responses of ecosystem C processes to the GCDs (Metcalfe et al., 2011). It can be more important than physiological responses in influencing long-term ecosystem dynamics (Smith et al., 2009). For example, in a wetland dominated by both C3 and C4 grasses, ecosystem production responded positively to elevated CO_2 concentration in the first year of the experiment. However, the positive response diminished in four experiment years due to plant community shift. So far no comprehensive analysis has been conducted to synthesize the effects of GCDs on community composition, but a few qualitative assessments (e.g., Gornish et al., 2013, Porter et al., 2013). GCDs have the potential to favor dominant species or plant function types (PFTs), further strengthen their competitive advantage and likely reduce species richness and biodiversity. On the other hand, GCDs could stimulate the growth of sub-dominant and even sub-ordinate species or PFTs and therefore increase biodiversity (Zavaleta et al., 2003). The questions rise whether there are central tendency of responses of dominant or sub-dominant species or PFTs to the GCDs, what the consequences of the responses are to species richness and biodiversity, and whether there are interactions among the GCDs.

Long-term global change experiments are invaluable because some of the ecological processes are changing at slow rates (Luo et al., 2011) and long-term experiments are needed to reveal these processes and associated mechanisms. For example, Wu et al., (2012) showed that response of plant growth to warming gradually decreased over a decade due to slowly reduced species richness and increased N loss in four grassland ecosystems. A gradually decreased effect of CO_2 enrichments on tree growth (i.e., NPP) was observed due to progressive N limitation over 11 years in a sweetgum forest ecosystem (Norby et al., 2010). Therefore, long-term experiments can provide a relatively complete overview on the GCDs effects and reveal key mechanisms critical for long-term model prediction. In a tallgrass prairie, a warming experiment was set up in 1999 and lasts until present. The information in long-term responses of its community composition to warming could be an asset to global change experiments and model parameterization. The collected data will be analyzed to address following question: are there directional changes in community composition over the long-term warming and what are the underlying mechanisms?

The ultimate goal of global change ecology is for prediction. To be useful for predictive ecology, we need both process-based ecological models, to represent key processes that determine the dynamic behavior of an ecological system, and also data, to identify those key processes and constrain model parameters and state variables via data assimilation (also called data-model fusion). Data assimilation (DA) treats the model structure and ranges of parameter values as prior information in a Bayesian frame work to represent the current state of knowledge. It uses global optimization techniques to update parameters and state variables of a model based on information contained in multiple, heterogeneous data sets that describe the past and current states of an ecosystem. The posterior distributions of estimated parameters through DA usually include the maximum likelihood estimates and are used for forward modeling towards prediction. It is therefore an effective research tool in climate change ecology.

1.2 Literature review

1.2.1 Effects of drought on ecosystem production and respiration

Responses of ecosystem processes to drought, especially carbon (C) fluxes, are critical given that any net change of ecosystem C balance acts as a feedback to climate change. Many studies have reported ecosystem responses to climate extremes. For example, Ciais et al. (2005) reported that heat and severe drought caused an unprecedented continental scale reduction in primary productivity with ecosystem respiration decreasing concurrently. In contrast, by analyzing observational data from a global network of eddy flux towers, Schwalm et al. (2010a) found that global mean gross primary production (GPP) was more sensitive to a drought event than respiration. In a long-term field experiment, Jentsch et al. (2011) imposed an extreme drought in a constructed grassland and reported the opposite - that drought decreased soil respiration without reducing net primary production (NPP). Finally, by decreasing throughfall in a Mediterranean evergreen forest, Mission et al. (2010) reported a greater reduction in GPP than that in ecosystem respiration (ER), especially soil respiration. Such divergent responses of ecosystem productivity and respiration to extreme drought suggests that greater mechanistic understanding is needed with regard to how these two key C cycling processes are likely to respond to climate extremes.

Drought can affect production and respiration through both common and unique mechanisms. Drought lowers plant C uptake by reducing stomatal conductance and leaf area, and by increasing soil water deficit (Bréda et al., 2006), whereas soil water deficits and reduced substrate availability can reduce ecosystem respiration (Luo and Zhou, 2006). Although there are now many studies that have reported C cycling responses to both natural and experimentally imposed droughts in a variety of biomes (e.g., Reichstein et al., 2002, Ciais et al., 2005, Schwalm et al., 2012), these have not been synthesized to determine if there are any general patterns of production and respiration responses to extreme drought across terrestrial biomes (but see Schwalm et al., 2010a). Identifying such patterns is key for determining if general mechanisms underlie production and respiration responses.

1.2. 2 Grassland community dynamics under global change

Given the importance of community composition in regulating ecosystem C cycling responses to the GCDs, many global change experiments measured community composition changes both as responses to the GCDs and mechanisms to explain altered responses of C cycles to the GCDs (e.g., Morgan et al., 2001 and 2011, Zavaleta et al., 2003, Kardol et al., 2010, Souza et al., 2010, Yang et al., 2011, Collins et al., 2013).

Diverse findings of plant community responses to the GCDs have been reported. In a mesic old-field community, Kardol et al. (2010) found that elevated CO2 increased the whole community productivity, but did not have significant effect on any individual species and thus community evenness. A cool temperate grassland did not show response to increased CO2 in terms of community productivity and species diversity (Bloor et al., 2010). In contrast, Zaveleta et al., (2003) reported a CO2-induced decrease in species richness in a Mediterranean annual grassland and Morgan et al., (2007) showed serious encroachment of shrubs into a shortgrass steppe under elevated CO2 concentration.

Different responses were also found in warming and precipitation experiments. Warming decreased species richness in a desert steppe (Hou et al., 2013), whereas did not have impact on both community productivity and species richness in a temperate old field (Hoeppner and Dukes, 2012). Yang et al., (2011) found that increased precipitation increased both dominant plant functional coverage and species richness in an arid steppe. Kardol et al., (2010) also found significant increase in dominant species productivity and thus reduced community evenness under wet condition in a mesic old field. Baez et al., (2013) reported limited responses of dominant C4 grass and C3 shrub to increased precipitation in terms of productivity and species richness in a mixed-grass dominated vegetation. Reduced precipitation or drought often decreases community or dominant species productivity and species richness (Evans et al., 2011, Miranda et al., 2009, Kardol et al., 2010), whereas Hoeppner and Dukes (2012) did not found any significant impact of reduced precipitation on production and species richness.

Both additive and interactive effects among multiple GCDs have been reported. For example, Zaveleta et al., (2003) showed an additive effect of warming, elevated CO2 and precipitation on species richness in an annual grassland and Kardol et al., (2010) found an additive effect of warming, elevated CO2 and precipitation on community productivity. However, warming and precipitation treatments often have interactive effect. Hoeppner and Dukes (2012) reported that warming only coupled with drought decreased species richness. Increased precipitation amplified warming effect on dominant C4 grasses productivity in a desert steppe (Hou et al., 2013). Elevated CO2 can also interact with other GCDs. For example, in a mixed semi-arid grassland, Morgan et al., (2011) found that elevated CO2 favored C4 grasses only in warmed plots.

Making useful inference from these diverse responses is critical but challenging. There are still traces from theory or universal mechanisms we can follow to possibly put the idiosyncratic outcomes in line. For example, in ecosystems with moderate-to-high productivity, the GCDs are likely to alleviate constraints on production and generally reduce diversity due to competitive exclusion of rare species. This hypothesis can be tested against data synthesized from global change experiments. Dominant species in arid or semi-arid community have likely adapted to drought and could be resistant to it (Evans et al., 2013). Therefore, decreased precipitation may have little impact on them, but greatly suppress subordinate species and thus reduce species richness and biodiversity. On the other hand, increased precipitation may just enhance non-dominant species or even rare species and thus increase species richness and biodiversity. According to the characteristics of the two different photosynthetic pathways (i.e., C3 and C4), warming is expected to favor C4 plants and elevated CO2 favors C3 plants. Such conclusions were drawn mostly at individual plant level. Can they be extrapolated to field conditions given the complex abiotic and biotic interactions and feedbacks such as water condition and biotic competition? The question could also be addressed against synthesized experimental data.

1.2.3 Long-term responses of community composition to climate warming

Significant change in community composition such as species reordering, species gain and loss can be a slow process (Smith et al., 2009, Luo et al., 2011). There are only a few studies which have reported long-term dynamics of community composition in responses to the GCDs. Wu et al., (2012) showed declined species richness under long-term warming in four grassland ecosystem, whereas Grime et al., (2008) found that an infertile grassland was quite insensitive to simulated warming and Collins et al., (2012) also found that a tallgrass prairie was relatively stable to increased precipitation. Evans et al., (2011) reported reduction in dominant species to long-term drought in a semi-arid grassland.

Long-term responses could be different from short-term in many ways. At long term, the GCDs are more likely to interact with abnormal weather conditions such as extreme drought and heat wave and cause dramatic change in community composition. Also at long term, some other biogeochemical feedbacks might start to play a major role. For example, with long-term warming, possibly warming-induced increased N content in the soil can alter species composition. Moreover, the GCDs would need longer time for them to take effect. For example, reduced precipitation can favor drought-tolerant plant species. However, the recruitment processes for such species in order for the species composition to significantly change could take more time (Smith et al., 2009).

1.2.4 Data assimilation in global change ecology

Data assimilation is a statistical method that allows incorporating multi-sourced convoluted measurements into ecological models, constraining model parameters, and evaluating model structures. For example, Braswell et al., (2005) used eddy flux data and C stock data from Harvard forest to evaluate an ecosystem carbon flux model

(SIPNET) to evaluate rate of carbon sequestration. By assimilating soil respiration and biometric carbon data from Duke Forest, Xu et al., (2006) applied probabilistic inversion to quantify uncertainties of model parameters and predicted carbon pool dynamics. Wang et al., (2007) estimated parameters in a land surface model using eight eddy flux data and concluded that model with optimizing photosynthetic parameters improved model performance in predicting carbon and water fluxes. Keenan et al., (2013) evaluated information content in different types of datasets and found that C fluxes in combination with stocks provide more information. Weng et al., (2011) quantified relative information content contributed by model only and both model and data together to short- and long-term prediction and concluded that relative information contributions of model and data varied with forecasting time and C pools. Lastly, instead of using batch data assimilation approaches, Gao et al., (2011) applied ensemble Kalman filter to assimilate carbon flux and biometric carbon data and found that after data assimilation the model forecasted long-term dynamics with greater confidence. Overall, previous research showed that data assimilation was an effective tool to estimate parameter values and uncertainties.

1.3 Studies conducted in this dissertation

Four studies were conducted in this dissertation to explore the responses of community structure and ecosystem functioning to climate change, warming and altered precipitation in particular. In chapter 2, I first determined if general patterns of drought effects on production and respiration exist across multiple biomes based on published papers of both observational and experimental studies. Second, I used an ecosystem model to examine mechanisms possibly underlying differential sensitivity of production and respiration in four different grassland types over a rainfall gradient in Central US Great Plains. In the modeling analysis, I assessed responses of NPP and heterotrophic respiration (Rh) to a long-term severe drought imposed by either reducing the size or the number of individual rainfall events. In addition to assessing responses over longer time scales and mechanistically, I also compared responses in these sites to identical treatments, thus overcoming a weakness of syntheses of published studies that each impose drought in different ways and of different magnitudes and measure responses uniquely.

In chapter 3, I synthesized 42 studies manipulating precipitation deduction and 44 studies with increasing precipitation manipulation to address the following questions and hypotheses: I hypothesized that (1) both aboveground net primary production (ANPP) and belowground net primary production (BNPP) would show negative responses to decreased precipitation and positive responses to increased precipitation; the response of ANPP to altered precipitation would be greater than that of BNPP; (2) climate, vegetation and edaphic conditions would together determine the sensitivity of ANPP and BNPP to altered precipitation; (3) the response of dominant species and PFTs to precipitation change reflects the whole plant community sensitivity; (4) C3 and grass PFTs show greater responses to altered precipitation than C4 and forbs; (5) community structure would be altered by precipitation changes.

In chapter 4, by analyzing a 14-year manipulative experiment in a tallgrass prairie, I first hypothesized that experimental warming would have minimal impacts on plant community structure and composition in short term, whereas clipping could have significant effects on plant community due to its direct removal of plant species. Furthermore, based on general theory of chronic resource alterations under climate change (Smith, Knapp & Collins 2009) and given that our study site experienced extraordinarily wet and dry years, we predicted that warming would alter plant community structure and composition over the long term through species reordering and/or species invasion. In addition, we hypothesized that clipping would interact with warming in influencing community structure and composition.

In chapter 5, I integrated 9-year experimental data (soil carbon fluxes and stocks) in control and warming treatments into an ecosystem carbon model to explore whether warming could affect model parameters and the consequence of the changes in parameter values on long-term carbon dynamics. Specifically, I explored how warming changed the mechanisms of C cycling by testing whether warming had an effect on key model parameters such as turnover rate and transfer coefficients, and investigated warming effect on long-term projections for C pools. Lastly, I examined the sensitivities of both short-term and long-term projections to model parameters.

It should be noted that Chapters 2-5 are developed for peer-review publication.

Chapter 2 Differential Effects of Extreme Drought on Production and Respiration: Synthesis and Modeling Analysis [1]

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Abstract:

Extremes in climate may severely impact ecosystem structure and function, with both the magnitude and rate of response differing among ecosystem types and processes. We conducted a modeling analysis of the effects of extreme drought on two key ecosystem processes, production and respiration, and to provide broader context we complemented this with a synthesis of published results across multiple ecosystems. The synthesis indicated that across a broad range of biomes gross primary production (GPP) generally was more sensitive to extreme drought (defined as proportional reduction relative to average rainfall periods) than was ecosystem respiration (ER). Furthermore, this differential sensitivity between production and respiration increased as drought severity increased and occurred only in grassland ecosystems but not in evergreen needle-leaf and broad-leaf forests or woody savannahs. The modeling analysis was designed to better understand the mechanisms underlying this pattern and focused on four grassland sites arrayed across the Great Plains, USA. Model results consistently showed that net primary productivity (NPP) was reduced more than heterotrophic respiration (Rh) by extreme drought (i.e., 67% reduction in annual ambient rainfall) at all four study sites. The sensitivity of NPP to drought was directly attributable to rainfall amount, whereas sensitivity of Rh to drought was driven by soil drying, reduced carbon (C) input and a drought-induced reduction in soil C content, a much slower process. However, differences in reductions in NPP and Rh diminished as extreme drought continued due to a gradual decline in the soil C pool leading to further reductions in Rh. We also varied the way in which drought was imposed in the modeling analysis, either as reductions in rainfall event size (ESR) or by reducing

rainfall event number (REN). Modeled NPP and Rh decreased more by ESR than REN at the two relatively mesic sites but less so at the two xeric sites. Our findings suggest that responses of production and respiration differ in magnitude, occur on different timescales and are affected by different mechanisms under extreme, prolonged drought.

2.1 Introduction

The hydrological cycle is forecast to be intensified by climate warming, leading to increased drought frequency and severity, especially in water-limited ecosystems (IPCC, 2007). Responses of ecosystem processes to drought, especially carbon (C) fluxes, are critical given that any net change of ecosystem C balance acts as a feedback to climate change. Many studies have reported ecosystem responses to climate extremes. For example, Ciais et al. (2005) reported that heat and severe drought caused an unprecedented continental scale reduction in primary productivity with ecosystem respiration decreasing concurrently. In contrast, by analyzing observational data from a global network of eddy flux towers, Schwarm et al. (2010a) found that global mean gross primary production (GPP) was more sensitive to a drought event than respiration. In a long-term field experiment, Jentsch et al. (2011) imposed an extreme drought in a constructed grassland and reported the opposite - that drought decreased soil respiration without reducing net primary production (NPP). Finally, by decreasing throughfall in a Mediterranean evergreen forest, Mission et al. (2010) reported a greater reduction in GPP than that in ecosystem respiration (ER), especially soil respiration. Such divergent responses of ecosystem productivity and respiration to extreme drought suggests that greater mechanistic understanding is needed with regard to how these two key C cycling processes are likely to respond to climate extremes.

Drought can affect production and respiration through both common and unique mechanisms. Drought lowers plant C uptake by reducing stomatal conductance and leaf area, and by increasing soil water deficit (Bréda et al., 2006), whereas soil water deficits and reduced substrate availability can reduce ecosystem respiration (Luo and Zhou, 2006). Although there are now many studies that have reported C cycling responses to both natural and experimentally imposed droughts in a variety of biomes (e.g., Reichstein et al., 2002, Ciais et al., 2005, Schwalm et al., 2012), these have not been synthesized to determine if there are any general patterns of production and respiration responses to extreme drought across terrestrial biomes (but see Schwalm et al., 2010a). Identifying such patterns is key for determining if general mechanisms underlie production and respiration responses.

One critical limitation to both observational and experimental studies is that they are all conducted at short time scales - from seasonal to annual in length - whereas ecological responses to drought over the longer term are likely to be more complex (Anderson et al., 2011). This is especially true for heterotrophic respiration, which is affected by drought induced reductions in the soil C pool as a function of lower GPP (Mission et al., 2010). Knowing how ecosystems respond to long-term, extreme drought is important given that climate models predict an increase in the frequency and magnitude of these events in the future (Dai, 2011). It has been hypothesized that although the sensitivity of production and respiration to drought may differ initially, they will eventually become equivalent as carbon cycle processes equilibrate over time

(Luo and Weng, 2011). Such long-term response patterns of ecosystems to drought are difficult to reveal in experiments or observational studies but can be explored by ecosystem modeling (Luo et al., 2011).

Drought has often been imposed in global change experiments by reducing each rainfall event amount (Yahdjian and Sala, 2006, Mission et al., 2010, Cherwin and Knapp, 2012). However, as climate models have predicted decreases in rainfall frequency in the future, drought could also occur due to declines in rainfall event number (e.g., Báez et al. 2013). These two different types of drought may affect ecosystem functions differently. For example, Harper et al. (2005) observed more drought-induced reduction on aboveground NPP (ANPP) and soil CO_2 flux under natural drought caused by reducing rainfall event number and size than simply altering the size of each rainfall event. This drought-event size interaction has also been observed in shortgrass steppe where experimental droughts only reduced ANPP when rainfall events were frequent and small rather than few but large (Cherwin and Knapp, 2012).

Our objectives were 2-fold. First, we determined if general patterns of drought effects on production and respiration exist across multiple biomes based on published papers of both observational and experimental studies. Second, we used an ecosystem model to examine mechanisms possibly underlying differential sensitivity of production and respiration in four different grassland types over a rainfall gradient in Central US Great Plains. In the modeling analysis, we assessed responses of NPP and heterotrophic respiration (Rh) to a long-term severe drought imposed by either reducing the size or the number of individual rainfall events. In addition to assessing responses over longer time scales and mechanistically, we also compared responses in these sites to identical treatments, thus overcoming a weakness of syntheses of published studies that each impose drought in different ways and of different magnitudes and measure responses uniquely (Luo et al. 2011).

2.2 Material and method:

2.2.1 Synthesis methods and data analysis

We searched ISI's Web of Science using these search strings: '(drought OR severe drought OR extreme drought) AND (ecosystem fluxes OR ecosystem carbon balance)', 'drought AND NEE AND eddy covariance', '(precipitation OR drought OR rainfall) AND net ecosystem exchange AND manipulation' and 'drought AND NPP AND respiration' to identify both observational and manipulative studies of drought effects on ecosystem C fluxes over global terrestrial biomes. We also used 'rain forest AND eddy flux AND drought' to search for studies focused more appropriately on seasonal droughts in rain forest dry seasons. We reviewed the most relevant studies in which GPP and ER were reported in both drought and normal years or dry and wet seasons for rain forest (Table 3 and Table S1).

Drought was categorized as extreme drought when ecosystems experienced more than a 40% decrease in annual precipitation relative to the long term average, as moderate drought with less than a 40% but more than a 25% rainfall decrease, and minor drought with less than 25% precipitation reduction. The drought sensitivity of production as estimated by GPP and respiration estimated by ER for each study site was calculated as the drought induced absolute reduction relative to the normal year divided by GPP or ER in the normal years (i.e. ΔGPP% = (GPP_{normal} – $GPP_{drought}$)/GPP_{normal} or ΔER% = (ER_{normal} - $ER_{drought}$)/ER_{normal}). The differential sensitivities were also assessed based on ecosystem types. The ecosystems were divided into grassland, evergreen needle-leaf forest (ENF), broad-leaf forest (BF) and woody savannahs (WS). One open shrubland, one oak woodland and one pine woodland were not included into the data analysis due to limited sample size. The significance between ΔGPP% and ΔER% was tested using paired-sample T test. Seasonal drought effects on ΔGPP% and ΔER% in rainforest were not included in this analysis because of different responses and underlying mechanisms. Thus, seasonal drought effects in rainforest are discussed separately in this study.

2.2.2 Modeling analyses

2.2.2.1 Model description

The terrestrial ecosystem model (TECO) is a process-based ecosystem model and was designed to examine ecosystem responses to climatic perturbations including elevated CO_2, warming and altered precipitation (Luo et al., 2008, Weng and Luo, 2008). The algorithms applied in TECO are described in detail by Weng and Luo (2008). Here we provide a brief description, focusing on mechanisms related to drought.

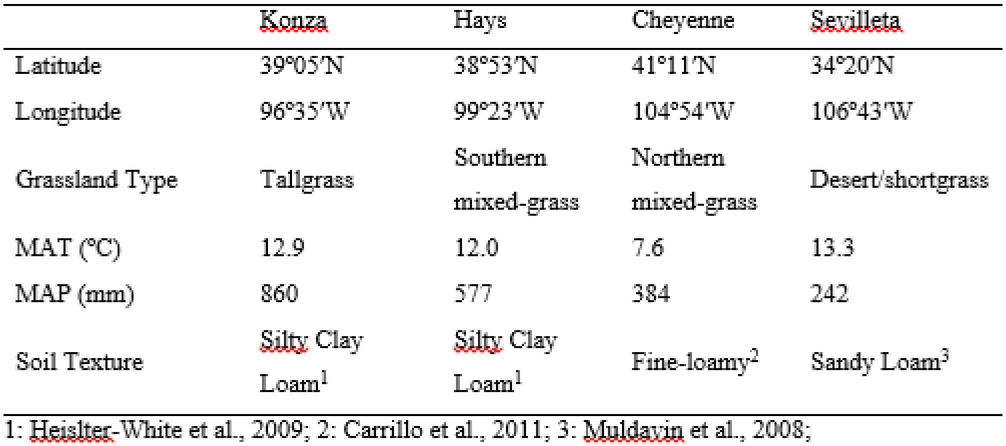
TECO is composed of four major sub-models that represent canopy processes, plant growth, C transfer, and soil water dynamics. The canopy photosynthesis-transpiration submodel is a two-leaf model with multiple canopy layers, derived primarily from Wang and Leuning (1998), to simulate canopy energy balance, canopy photosynthesis and conductance. For each layer, foliage is divided into sunlit and shaded leaves. Leaf photosynthesis and transpiration are estimated by coupling the Farquhar photosynthesis (Farquhar et al., 1980) and Ball-Berry stomata-conductance model (Ball et al., 1987). In the plant growth submodel, allocation of photosynthetic assimilates depends on growth rate of leaves, stems and roots following ALPHAPHA model (Denison and Loomis, 1989), and varies with phenology following CTEM (Arora and Boer, 2005). Phenology is represented by seasonal variation in leaf area index (LAI). Leaf onset is determined by growing degree days and leaf senescence is induced by low temperature and low soil water content. The C transfer submodel simulates movement of C from plant to soil C pools in three layers through litterfall and the decomposition of litter and soil organic C. Carbon fluxes from litter and soil carbon pools are based on residence time of each C pool and C pool sizes (Luo and Reynolds, 1999).

The soil water dynamics submodel has ten soil layers and simulates the dynamics of soil water content based on precipitation, evaporation, transpiration and runoff. Evaporation is determined by water content of the first soil layer and evaporative demand of the atmosphere. Transpiration is regulated by stomatal conductance and soil water content of layers where roots are present. When precipitation exceeds water recharge to soil water holding capacity, runoff occurs. In this study, a soil moisture scalar, ω, is the most important parameter because the reduction in precipitation directly affects soil water content and thus the soil moisture scalar. In TECO, relative soil water content is defined as $\omega = (W_{soil}-W_{min})/ (W_{max}-W_{min})$ where W_{max} is soil water holding capacity, W_{min} is the permanent wilting point and W_{soil} is soil water content. Photosynthesis and plant growth rate are reduced whenever ω is less than 0.3.

2.2.2.2 Study sites

The sites selected for the modeling analysis are the Konza Prairie Biological Station (Konza), the Hays Agricultural Research Center (Hays), the High Plains Grasslands Research Center (Cheyenne), and the Sevilleta National Wildlife Refuge (Sevilleta). The four grasslands are distributed along mean annual temperature (MAT) and mean annual precipitation (MAP) gradients (Table 2.1). Cheyenne has the lowest mean annual temperature among the four sites (Table 2.1). Sevilleta has much coarser soil texture than the other three grasslands.

Table 2.1 Key climate, plant, and soil characteristics of four grassland ecosystem types located within the US America Great Plains



	Konza	Hays	Cheyenne	Sevilleta
Latitude	39°05′N	38°53′N	41°11′N	34°20′N
Longitude	96°35′W	99°23′W	104°54′W	106°43′W
Grassland Type	Tallgrass	Southern mixed-grass	Northern mixed-grass	Desert/shortgrass
MAT (°C)	12.9	12.0	7.6	13.3
MAP (mm)	860	577	384	242
Soil Texture	Silty Clay Loam[1]	Silty Clay Loam[1]	Fine-loamy[2]	Sandy Loam[3]

1: Heislter-White et al., 2009; 2: Carrillo et al., 2011; 3: Muldavin et al., 2008;

2.2.2.3 Modeling scenarios

The objective of this experimental simulation was to use the long-term records of rainfall to model extreme drought effects on ecosystem C dynamics. Therefore, the long-term records of daily rainfall data were collected from weather stations closest to each grassland. The periods of rainfall data were 1982-2010 for Konza, 1949-2010 for Hays and Sevilleta and 1949-2011 for Cheyenne. The four meteorological variables (solar radiation, air temperature, soil temperature, and relative humidity) used to drive the model were from year 2007 for Konza, Cheyenne, and Sevilleta, and from year 2006 for Hays, repeated for each rainfall year. In order to simulate the effects of extreme drought, the annual rainfall amount was reduced to 33% of ambient rainfall by two approaches. One was to reduce each rainfall event size (ESR) by 67% of ambient rainfall (AMB), and the other was to reduce rainfall event number (REN) to achieve the same 67% reduction in annual rainfall as ESR. The REN treatment resulted in intermittent periods with no rain events and thus increased precipitation variability compared with ESR treatment. These two treatments allowed us to explore the differential effects of drought and increased rainfall variability on ecosystem C dynamics in different grassland ecosystems along the MAT and MAP gradients. The selection of 67% rainfall reduction in the model was based on analysis of long-term rainfall records in central US grasslands. Multi-year drought similar to 67% rainfall reduction occurred but only for 4-6 times in a 70-year record for semi-arid Colorado and 108-year record for mesic Kansas (data not shown).

2.2.2.4 Statistical analysis

The linear regressions were conducted in SigmaPlot version 12. A student's t-test for the slope difference between ambient condition and rainfall reduction treatments was conducted in SAS software (SAS Institute Inc., Cary, NC, USA). A multiple regression between relative reduction in Rh (dependent variable) and relative reduction in soil water content (SWC), NPP and soil C content (independent variables) was performed to assess the relative contribution to drought-induced reduction in Rh from each of the three factors. The regression model is $\Delta Rh = a*\Delta SWC + b*\Delta NPP + c*\Delta Soil\ C + \varepsilon$. The relative contributions are calculated as $a*\Delta SWC/\ \Delta Rh*100\%$, $b*\Delta NPP/\ \Delta Rh*100\%$ and $c*\Delta Soil\ C/\ \Delta Rh*100\%$.

2.3 Results

2.3.1 Model validation

The TECO model was driven by meteorological data from eddy flux towers for Konza tallgrass prairie and Sevilleta desert grassland and from meteorological stations for the Hays and Cheyenne mixed-grass prairie sites. Meteorological data include hourly solar radiation, air temperature, soil temperature, precipitation and relative humidity from 2007 - 2010. For Hays, meteorological data in 2006 were used, instead of 2007 due to its incomplete record. The model was validated against daily net ecosystem CO_2 exchange (NEE) from eddy flux towers during 2007 -2010 at Konza and Sevilleta (Fig. 2.1), along with biometric data including ANPP and soil respiration measured at these grasslands (Table 2.2). For all the variables, the modeled results were in good agreement with observational data (Fig. 2.1 and Table 2.2).

Table 2.2 Comparisons between modeled and measured aboveground net primary production (ANPP) and soil respiration (Rs).

	ANPP(g m^{-2})		Monsoon Rs* (g C m^{-2})	
	Observed	Modeled	Observed	Modeled
Konza	461 (134)^a	488 (38)	-	-
Hays	300(-)^b	342 (46)	-	-
Cheyenne	130 (25)^c	163 (15)	-	-
Sevilleta	140 (3)^d	165 (2)	63 (3)^e	81 (8)

a: mean ANPP from 1984-1998 (Knapp et al., 2006); b: Long term mean ANPP (Heisler-White et al., 2009); c: PHACE measurement (Personal communication); d: average in 2007 and 2008 (Thomey et al., 2011); e: average in 2007 and 2008 (Vargas et al., 2012). Values in the parentheses are standard errors across years. '-' mean that values were not available. '*' monsoon Rs is cumulative soil respiration during monsoon season from July through September in Sevilleta desert grassland.

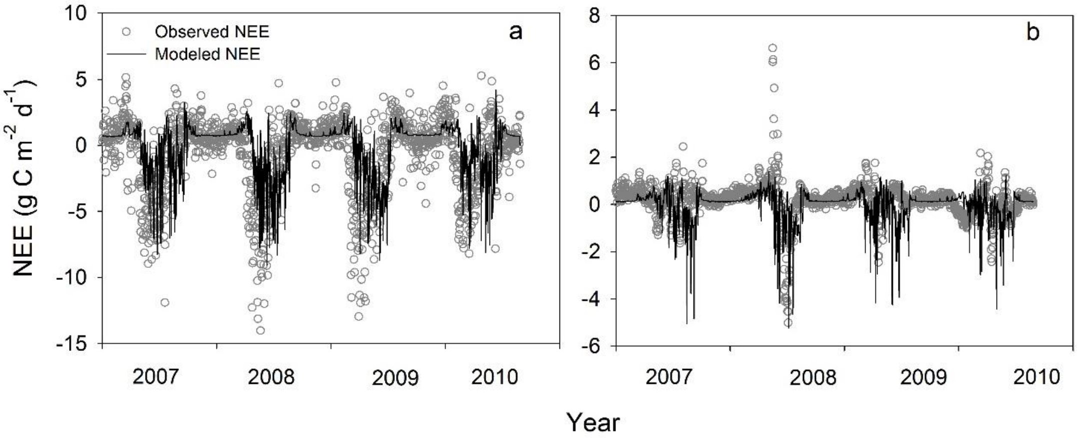


Figure 2.1 Comparisons between observed daily net ecosystem CO$_2$ exchange (NEE) from eddy flux data and modeled daily NEE in Konza tallgrass prairie and Sevilleta

desert grassland from 2007 to 2010. Open black circles represent observed daily NEE. Black solid lines represent modeled daily NEE.

2.3.2 Differential drought effects on production and respiration and mechanisms: Literature synthesis

We synthesized results from 39 studies that included grasslands, deciduous broad-leaf forests, evergreen needle-leaf forests, woody savanna and shrubland (Table S2.1). Eleven out of the 39 study sites experienced extreme drought (i.e., >40% below long-term average rainfall), 10 sites experienced moderate drought and 18 sites were subject to minor drought. GPP was more sensitive to drought than ER under extreme and moderate drought (Fig. 2.2a). Minor drought had no differential impacts on GPP or ER. Drought had greater impact on GPP than ER in grassland ecosystems, whereas in forest and woody savannah ecosystem drought did not have differential impact (Fig. 2.2b).

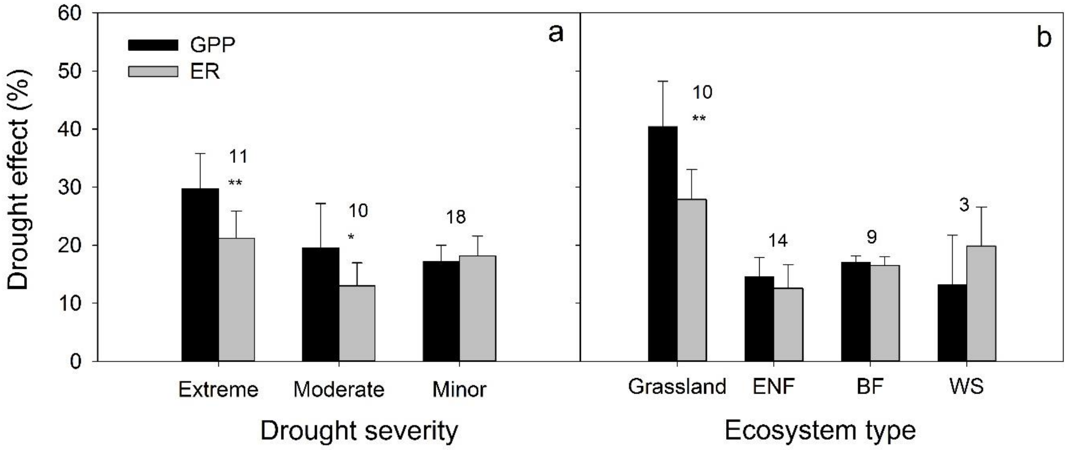


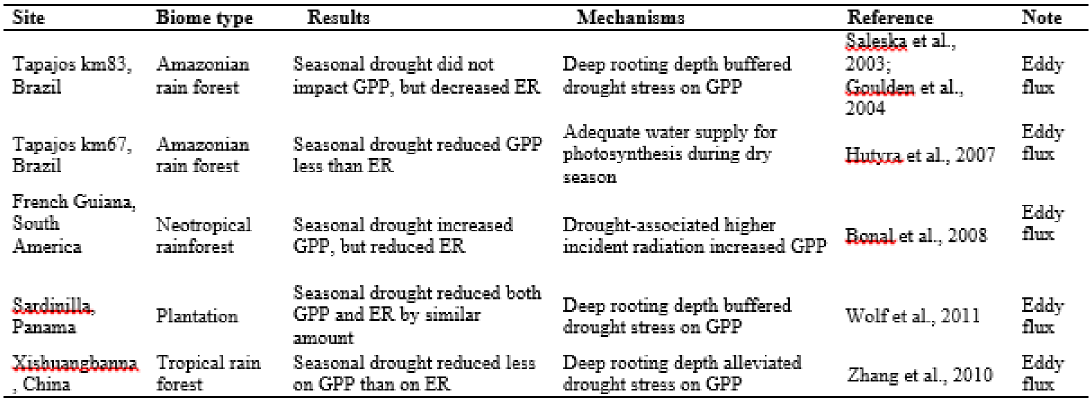
Figure 2.2 Synthesized published observational and experimental results on sensitivity of gross primary production (GPP) and ecosystem respiration (ER) to drought severity (a) and to drought in different ecosystem types (b). The ecosystems were divided into grassland, evergreen needle-leaf forest (ENF), broad-leaf forest (BF) and woody savannahs (WS). One open shrubland, one oak woodland and one pine woodland were not included into the data analysis due to limited sample size. Numbers represent the number of studies included, ** represents significant ($P < 0.05$) difference and * represents marginally significant difference ($P< 0.1$).

For the five study sites with data available, seasonal drought in rainforest had only a limited impact on GPP (Table 2.3) likely because the tree root systems had access to an adequate water supply in deep soil layers. Respiration, especially heterotrophic respiration was reduced due to drying of the surface soil. As a consequence, ecosystem carbon uptake actually increased under seasonal drought in tropical rainforests.

2.3.3 Modeled drought effect on ecosystem C variables

Both extreme drought treatments decreased annual NPP, heterotrophic respiration (Rh), NEE and soil C content with similar patterns over modeled years in each of the four grasslands (Fig. 2.3 and Fig. S2.1). The relative reduction in NPP was consistently greater than in Rh in all the grassland sites, but the difference diminished over time due to continued decreases in Rh with drought (Fig. 2.3a-h). Annual GPP and ER showed similar drought responses to annual NPP and Rh, respectively (Fig. S2.2). However, in order to reveal directional change in Rh, we used annual NPP and Rh in the model analysis. The differential responses of NPP and Rh to drought caused NEE to increase (more ecosystem CO_2 release), but the drought-induced change in NEE decreased over time (Fig. 2.3i-l). Drought-induced reduction in soil C content also increased over time, the same as Rh in all the study sites (Fig. 2.3m-p).

Table 2.3 Synthesis of published studies in differential responses of GPP and ER to extreme seasonal drought in tropical rainforest



Site	Biome type	Results	Mechanisms	Reference	Note
Tapajos km83, Brazil	Amazonian rain forest	Seasonal drought did not impact GPP, but decreased ER	Deep rooting depth buffered drought stress on GPP	Saleska et al., 2003; Goulden et al., 2004	Eddy flux
Tapajos km67, Brazil	Amazonian rain forest	Seasonal drought reduced GPP less than ER	Adequate water supply for photosynthesis during dry season	Hutyra et al., 2007	Eddy flux
French Guiana, South America	Neotropical rainforest	Seasonal drought increased GPP, but reduced ER	Drought-associated higher incident radiation increased GPP	Bonal et al., 2008	Eddy flux
Sardinilla, Panama	Plantation	Seasonal drought reduced both GPP and ER by similar amount	Deep rooting depth buffered drought stress on GPP	Wolf et al., 2011	Eddy flux
Xishuangbanna, China	Tropical rain forest	Seasonal drought reduced less on GPP than on ER	Deep rooting depth alleviated drought stress on GPP	Zhang et al., 2010	Eddy flux

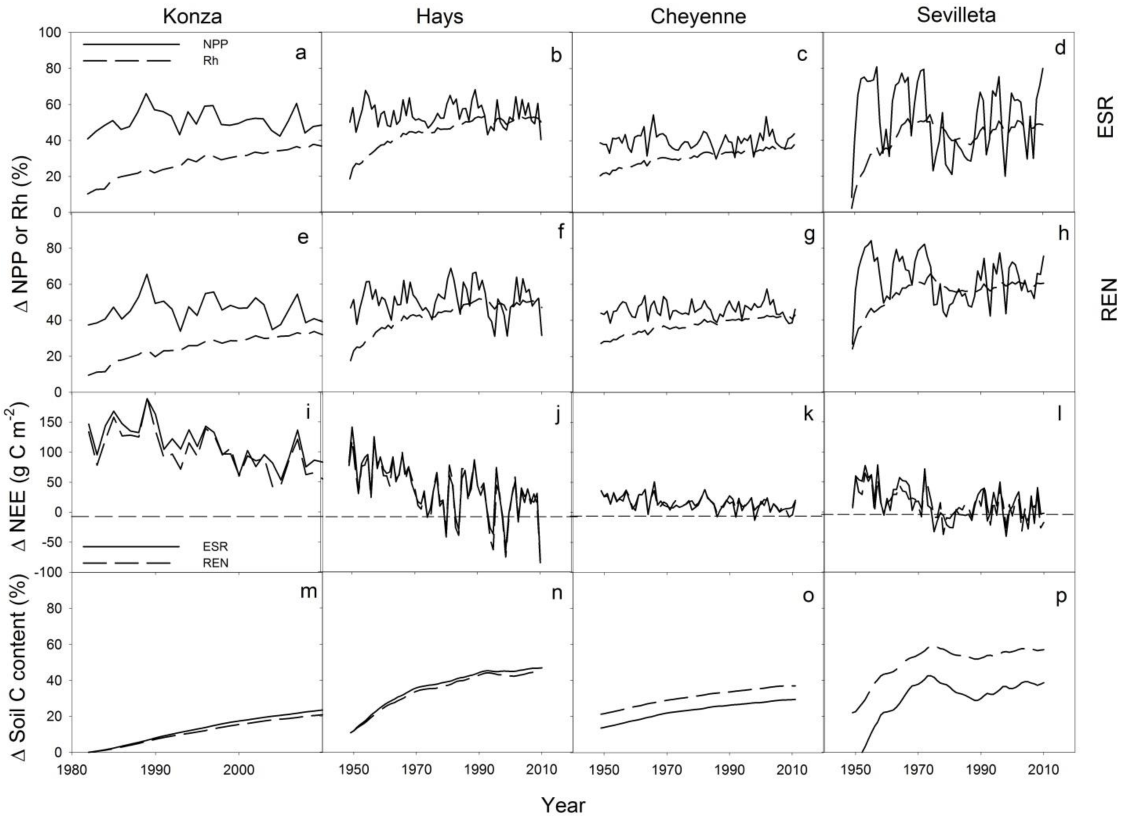


Figure 2.3 Drought-induced reductions in modeled annual NPP, Rh, NEE and soil C content over time in four North American grasslands (Konza: a, e, i and m; Hays: b, f, j and n; Cheyenne: c, g, k and o; Sevilleta: d, h, l and p). Absolute reduction in NEE was calculated as the difference in NEE between drought treatments and ambient condition. Relative reduction in NPP, Rh and soil C content were presented and calculated as absolute reduction divided by ambient condition. Differential effects of long-term droughts diminish over time as soil C content decreases.

Annual NPP, Rh, NEE and soil C content responded differently to the two different drought types (Fig. S2.1, Fig. 2.3 and Table S2.2). In the tallgrass prairie and the Hays mixed-grass prairie, annual NPP, Rh, and soil C content decreased more under ESR than under REN, whereas annual NPP, Rh, and soil C content decreased less under ESR than under REN in the Cheyenne mixed-grass prairie and the desert grassland

(Sevilleta). Differential responses of NEE to the two drought types were contingent upon year. Overall, Sevilleta had the greatest inter-annual variability (23%, 19%, and 29% average coefficient of variation over the two rainfall treatments) whereas the mixed grass site near Cheyenne had the lowest inter-annual variability (10%, 12%, and 17% average coefficient of variation over the two rainfall treatments) for relative reductions in NPP, Rh, and soil C, respectively with drought.

2.3.4 Controls on annual C fluxes and the long-term impacts of drought

Annual NPP increased with increasing rainfall amounts for all the grasslands under each of the three rainfall scenarios (ambient, ESR and REN) (Fig. 2.4a-d). The slopes of change in NPP were greater under the drought scenarios than that under ambient conditions (Table S2.3). Annual NEE decreased with rainfall (Fig. 2.4i-l). The slopes were negative and smaller under drought treatments than under ambient condition (Table S2.3). Annual Rh was not related to rainfall under drought scenarios, but a positive linear relationship with rainfall was noted under ambient conditions for all grasslands (Fig. 2.4e-h). The interannual variation in the relative reduction in NPP negatively correlated with annual rainfall amount in all grassland sites except for Cheyenne (Fig. 2.5) and the relative reduction in Rh was positively correlated with drought-induced relative reductions in soil C content (Fig. 2.6).

Contribution from reduced soil C to drought sensitivity of Rh increased over time and contributions from both reduced NPP and soil water content decreased over time (Fig. 2.7). In general, reductions in NPP and soil water content contributed more than reduction in soil C in the early years, whereas their relative importance switched later on (Fig. 2.7) due to gradually increased reduction in soil C content.

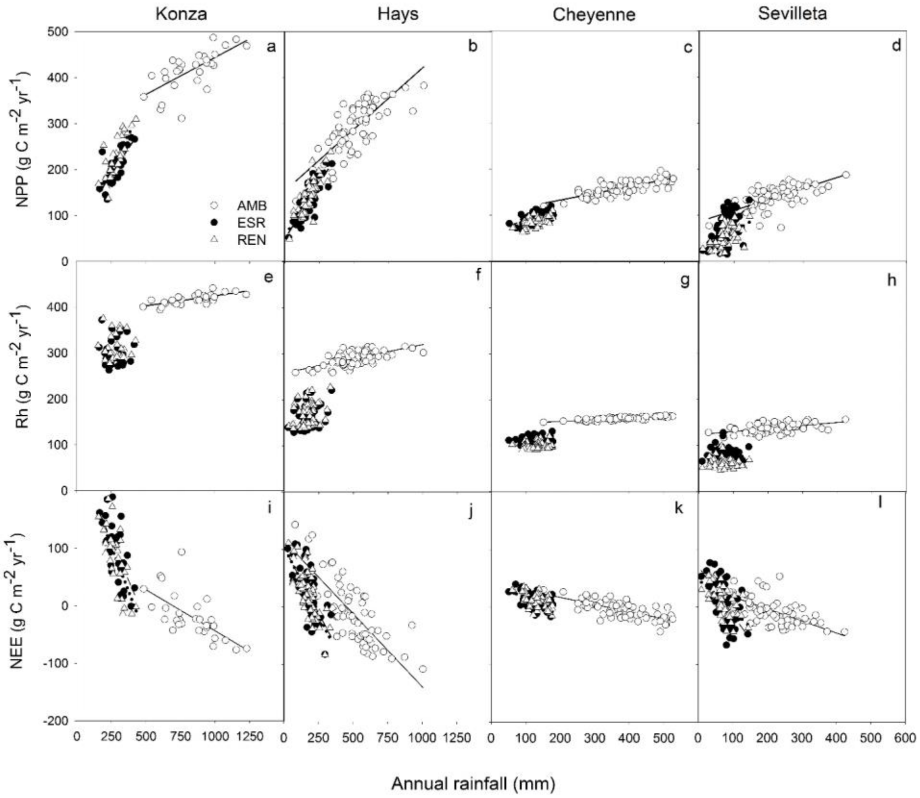


Figure 2.4 Relationships between annual rainfall and annual C fluxes under the three rainfall scenarios (AMB: ambient rainfall; ESR: rainfall event size reduction; REN: reduced event number) in four North American grasslands (Konza: a, e and i; Hays: b, f and j; Cheyenne: c, g and k; Sevilleta: d, h and l). Annual rainfall determined grassland ecosystem carbon fluxes.

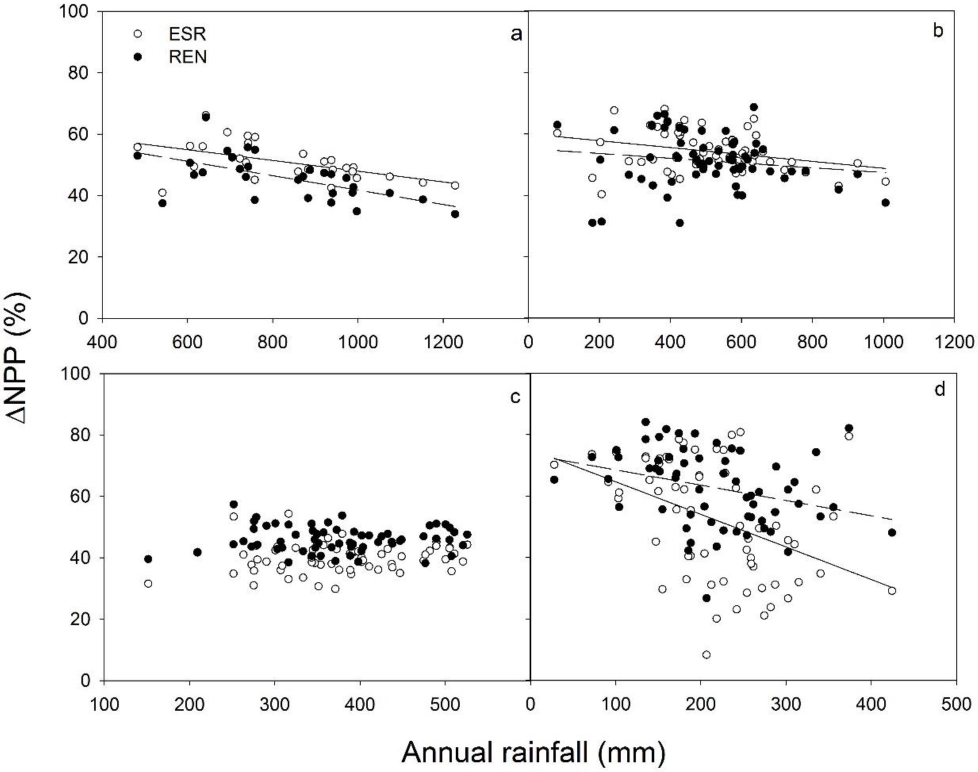


Figure 2.5 Relationships between annual rainfall and drought-induced relative reduction in NPP in four North American grasslands (Konza: a; Hays: b; Cheyenne: c; Sevilleta: d). Open circles represent ESR treatment. Solid circles represent REN treatment. Variation in drought-induced relative reduction in NPP was significantly related to annual precipitation for all but the northern mixed grass site (Cheyenne).

2.4 Discussion

Our synthesis and modeling analysis both revealed that production (GPP and NPP) was more sensitive to moderate to severe drought than respiration (ER and Rh). Furthermore, this differential sensitivity between production and respiration increased as drought severity increased and occurred only in grassland ecosystems but not in evergreen needle-leaf and broad-leaf forests or woody savannahs. In the modeling analysis, NPP was reduced more than Rh by extreme drought. However, the difference between NPP and Rh (i.e., NEE) diminished over time with drought over multiple years. Our findings suggest that responses of production and respiration to drought differ in magnitude, occur on different timescales and are affected by different mechanisms under extreme, prolonged drought. Additionally, the finding of different responses to drought types indicates the diverse interactive effects on ecosystem functions between rainfall variability and rainfall amount.

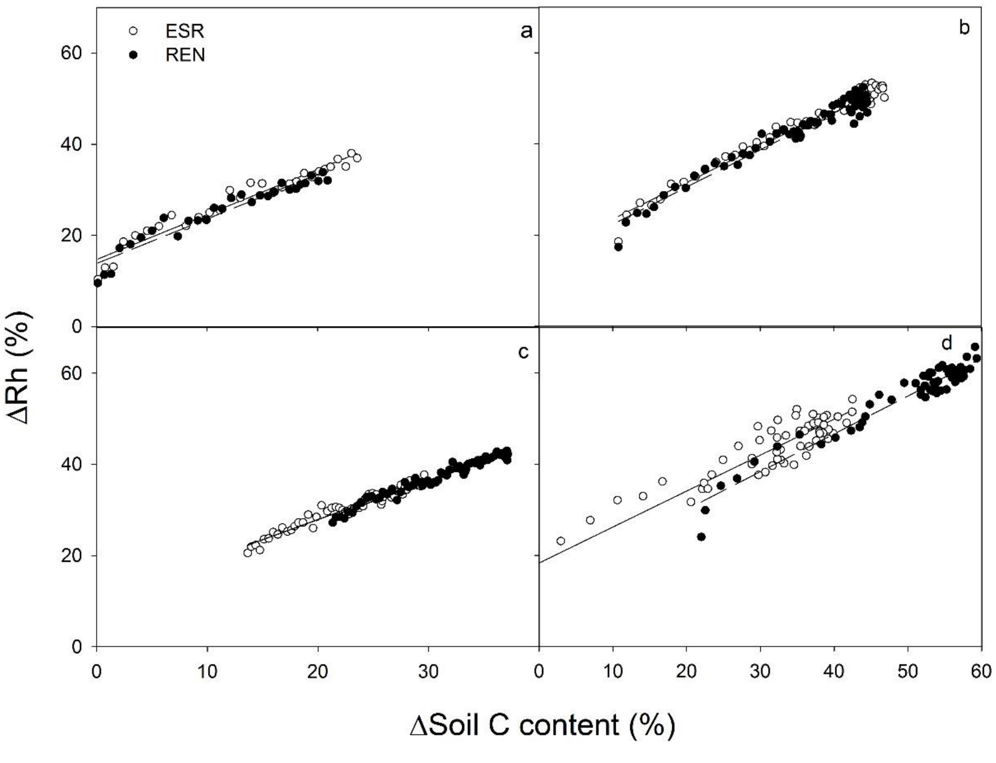


Figure 2.6 Relationships between drought-induced relative reduction in soil C content and relative reduction in Rh in four North American grasslands (Konza: a; Hays: b; Cheyenne: c; Sevilleta: d). Open circles represent ESR treatment. Solid circles represent

REN treatment. Drought-induced reductions in soil C were significantly and positively related to Rh reduction.

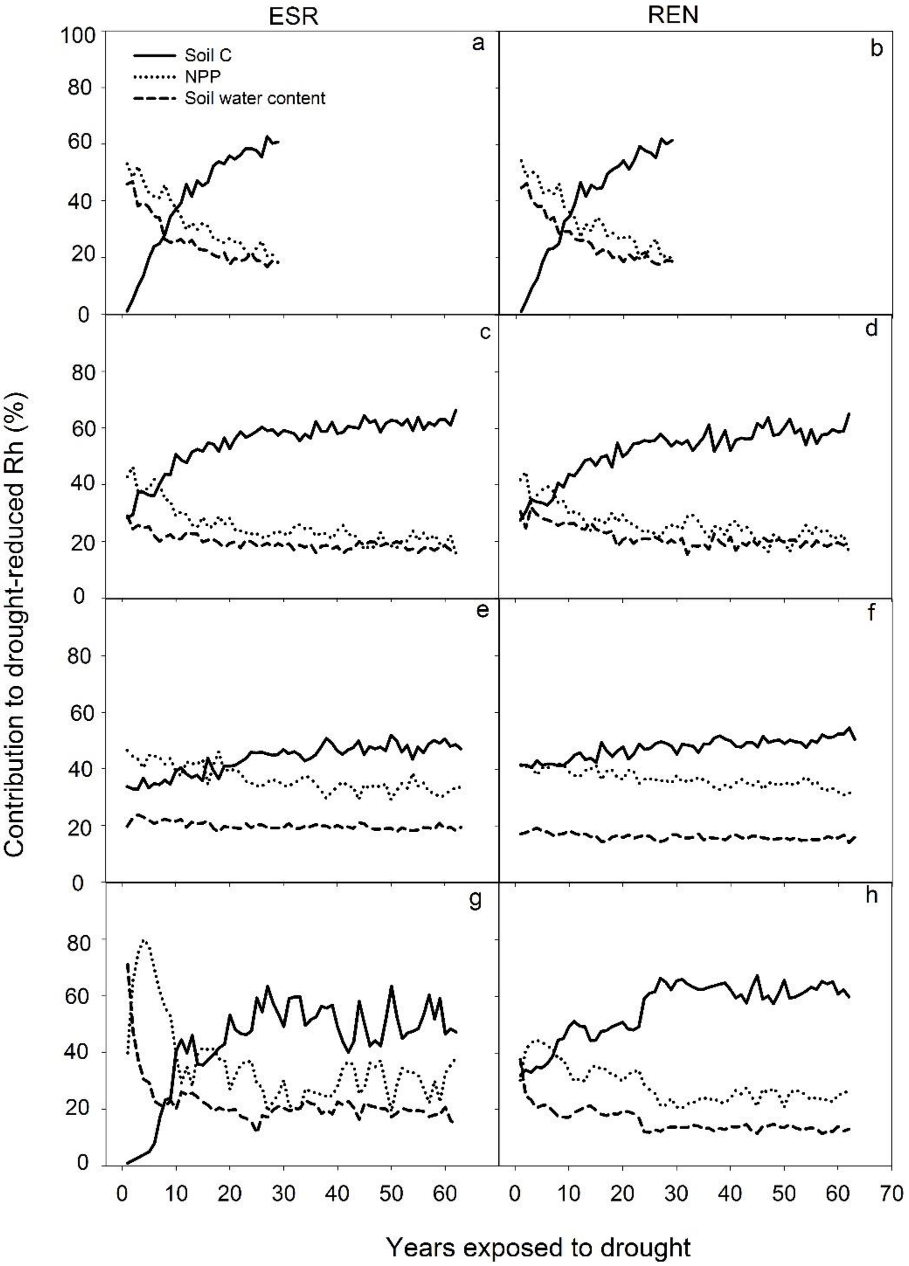


Fig. 7 Relative contributions to drought sensitivity of Rh from reductions in soil C content, NPP and soil water content under both rainfall reduction treatments in four North American grasslands (Konza: a and b; Hays: c and d; Cheyenne: e and f; Sevilleta: g and h). Solid line represents contribution from reduction in soil C, dotted

line represents contribution from reduction in NPP and dashed line represents contribution from reduction in soil water content.

2.4.1 General patterns of drought effects on production and respiration

In the literature synthesis, GPP and ER responded differently to extreme and moderate drought, but not to minor drought, which suggests that moderate to extreme drought may override other confounding factors, for example site characteristics, climate conditions, and dominant plant species. However, during minor drought, evidence indicates that the responses of GPP and ER were largely regulated by topographic position and soil texture (Kljun et al., 2006), drought-associated high summer radiation (Granier et al., 2007) and high summer temperature (Welp et al., 2007), along with a lagged effect from previous soil water condition (Welp et al., 2007). A broad range of ecosystems were included in the synthesis (Table S1), for example grasslands, deciduous broad-leaf forests, evergreen needle-leaf forests, woody savanna and shrubland. Thus, the general pattern of such differential responses is representative and robust across biomes. When synthesized data were analyzed based on ecosystem types, differential responses of production and respiration were not found in forest ecosystems. There are two possibly main reasons. The rooting systems of forests could partially relieve drought stress on production by tapping deep soil water (Kerhoulas et al., 2013) and secondly, most of the forest ecosystems only experienced moderate or minor drought in the synthesized studies. On the other hand, most of the grassland ecosystems went through extreme drought and do not have deep rooting systems, together resulting in the differential responses.

In contrast to the general pattern, however, in rainforest ecosystems where dry seasons occur annually, seasonal drought had limited effects on GPP due to adequate water supply from deep soil layers and hydraulic redistribution by deep roots. Therefore, rainforest GPP is generally controlled more by factors such as solar radiation (Bonal et al., 2008) rather than precipitation. Indeed, previous modeling studies that included deep water supply and hydraulic redistribution closely captured the seasonal drought effects in rain forest (Baker et al., 2008). Even though trees in other ecosystems were also able to tap deep soil water (e.g., Kerhoulas et al., 2013), GPP was still reduced due to drought-increased vapor pressure deficit which causes leaf stomata to partially close (Kolb et al., 2013).

2.4.2 Mechanisms underlying differential response of production and respiration to drought

In agreement with the synthesis results, the modeling analysis revealed the general pattern that production (GPP and NPP) was more drought sensitive than respiration (ER and Rh). The underlying mechanisms were explored in the model analysis of four grasslands over a rainfall gradient ranging from 240 to 860 mm. The greater sensitivity of modeled NPP to extreme drought that we observed (Fig. 3) at all four sites was due to different controls of the two ecosystem C variables. In grassland ecosystems, production generally increases linearly or asymptotically with rainfall amount (e.g., Fig. 4; Sala et al., 1988; Huxman et al., 2004). Therefore, in the extreme drought treatments NPP declined almost linearly with precipitation amount. However, heterotrophic respiration, which is the mineralization of litter and soil C, is a C pool-controlled ecological process that is often regulated by soil temperature over the long term in addition to soil water content and substrate availability in the short term (Luo and Zhou, 2006, Vargas et al., 2010). Therefore, drought-induced reductions in NPP, soil water content and soil C content all contributed to the reduction in Rh. Responses of NPP and soil water content were prompt and contributed significantly to reduced Rh in the early years, especially in the most mesic site. However, their contributions generally decreased over time due to increased relative importance of reduction in soil C content. As a consequence, Rh was less impacted than NPP in the short-term and the difference gradually disappears over time. Even though reduction in soil C content is relative smaller to short-term drought than NPP and soil water content, its smaller reduction played more important role than NPP and soil water content due to its high correlation with Rh, especially in the arid sites.

The model analysis also showed that the reduction in Rh increased during long-term drought due to diminishment of soil C pool size. The decrease in the soil C pool could be caused by drought-reduced NPP, the primary source of soil C. To our knowledge, we are not aware of any empirical studies that reported long-term effects of drought on soil C and Rh. However, space-for-time studies provide indirect evidence regarding ecosystem C dynamics under long-term climatic changes (Luo et al., 2011). For example, soil C declined linearly with decreasing precipitation in observations along precipitation gradients (Anderson et al., 2011; Talmon et al., 2011), which indirectly supports model results indicating a long-term drought-induced decrease in soil C content. This long-term decline in soil C content could cause the difference between the drought sensitivities of production and respiration to diminish gradually over time. Due to these differential responses over longer timescales, our modeling results showed that grassland ecosystems all released CO_2 to the atmosphere during drought, but the amount of released CO_2 decreased over time as soil C pools declined. The model results, however, would benefit from long-term field experiments to provide direct support for these results. This exploration of ecosystem sensitivity dynamics over the long term is critical for global change studies because many ecological responses are strongly regulated by slow processes (Luo et al., 2011).

Our model results also showed that Sevilleta and Cheyenne had the largest and least inter-annual variation, respectively, in the relative reduction of NPP and Rh. Soil texture has long been known to affect plant productivity through the inverse soil texture effect (Noy-Meir, 1973) and has the potential to interact with rainfall regimes to mediate the impacts of drought (Weng and Luo, 2008). The much larger inter-annual variability in relative reduction in NPP and Rh in Sevilleta could be explained by coarse-textured soils because lower average water availability can amplify drought effects (Paruelo et al., 1999). The low variability and lack of correlation between rainfall and relative reduction in NPP at Cheyenne may have occurred because the lower average temperatures for this site relative to the other three (Table 1) resulted in less evaporation, and thus increased available water for plants and constrained the inter-annual variation in sensitivity to drought. These results emphasize the need for multi-site long-term drought experiments, because inter-annual variation in precipitation as well as lagged effects from soil water storage likely play important roles in regulating ecosystem responses to climate extremes (Granier et al., 2007).

The mechanisms associated with drought responses in forest ecosystems are likely to be similar to those in grasslands. The primary responses of forests to drought are to reduce productivity and respiration due to water deficit (Dale et al., 2001) and the responses of production and respiration could be different. However, it is also likely that the mechanisms could be more complicated in forest ecosystems than in grasslands and consequently have different long-term effects. For example, deep rooting systems in forest ecosystems could buffer drought effect on production in forest ecosystems; drought associated increase in solar radiation might increase production as we found in rainforest; hydraulic lifting by tree roots could also alleviate drought effect on C processes. As we found out in our synthesis, drought had similar effects on both production and respiration in forest ecosystems (Fig. 2b). As a consequence, the long-term response pattern may be different from that in the grassland ecosystems. Therefore, it is critical to include above possible mechanisms when simulating long term drought effect in forest ecosystem.

2.4.3 Drought attributes and differential responses of production and respiration

In our modeling analyses, total annual rainfall in the two reduced rainfall treatments was the same. Drought imposed by reducing every event (ESR treatment) was characterized by lower rainfall event size (1/3 of ambient rainfall), but ambient rainfall frequency. In comparison, the REN treatment was characterized by ambient rainfall event size but lower frequency, and longer dry intervals between rain events. Responses of NPP and Rh to these treatments were contingent on grassland type, with greater reductions in NPP and Rh when drought was caused by every rain event becoming smaller (ESR scenario) at the two most mesic and productive grasslands (Konza and Hays) However, REN also caused in reduction in both NPP and Rh.

Knapp et al. (2002) also observed that lower frequency in rainfall events without changing total rainfall in a mesic tallgrass prairie resulted in less production than ambient rainfall frequency. However, if annual precipitation amount was low (1/3 of ambient rainfall in our study), the larger rainfall event size under REN relative to ESR could lead to higher soil water content and consequently higher production (Fig. S1a and b) in mesic grasslands. More water was stored in deep soil layers under ambient rainfall event size compared to lower rainfall event size in ESR, which decreased evaporative loss to the atmosphere and increased water availability to plants. Lower rainfall frequency (i.e. REN treatment), however, led to lower NPP in xeric grasslands (Fig. S1c and d). Frequent small rainfall events (the ESR treatment) can potentially alleviate chronic water stress, whereas the longer dry period under REN could affect early leaf and root growth due to constantly under the threshold of certain soil water content level. The under-developed leaf and root can have legacy effect on photosynthesis and water uptake later on and therefore decreased production more. In addition, different levels of rainfall frequency could affect its effect size (Heisler-White et al., 2009). Responses of Rh to the two drought types are consistent with those of NPP, indicating NPP controls the responses of Rh to different drought types.

2.4.4 Implications for future experimental studies

Our findings have several important implications for field experiments. First, reported observations and manipulative climate change studies are often short term. The snapshot of observed responses, therefore, may not be representative of long-term response, especially when slow ecological processes are involved. Second, many manipulated drought experiments only decrease event sizes. Our results showed that reduced rainfall event number had differential effects on ecological processes than simply decreasing the size of each rain event. Future experiments should impose drought through different patterns of rainfall size, different levels of frequency and intensity. Third, other components of ecosystem C processes should be assessed in global change experiments in addition to production. Different ecosystem C variables are likely to have different response patterns to imposed perturbation. In order to provide information on positive or negative feedbacks of terrestrial biomes to climate change, measurements of both production and respiration are needed.

2.4.5 Model limitations

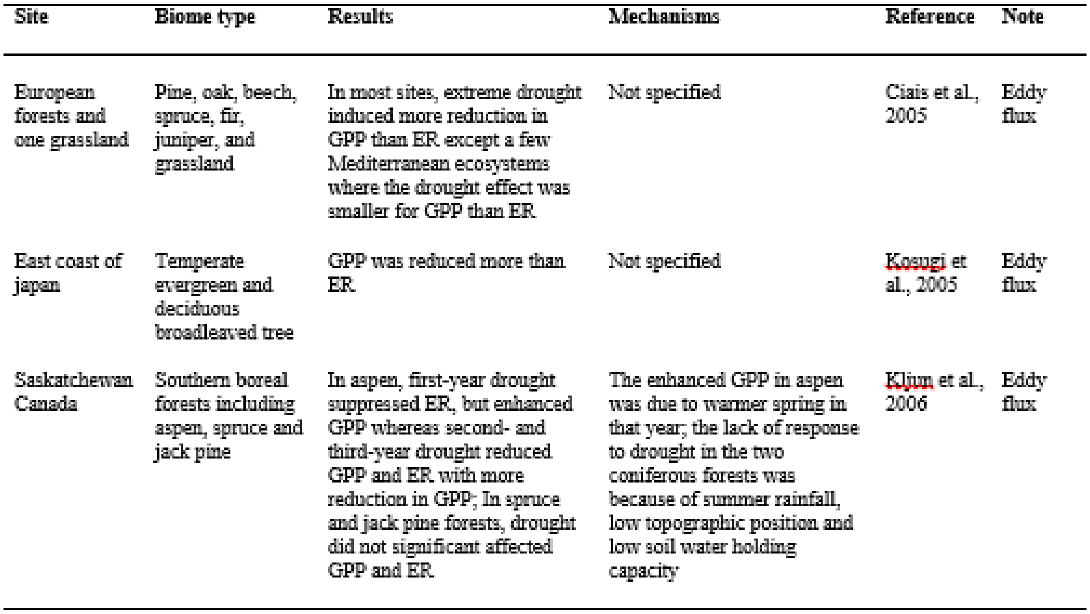
Ecosystem carbon models have often been used as a tool to investigate effects of global changing on ecosystem carbon cycling (Norby and Luo, 2004; Parton et al., 2007; Luo et al., 2008; Schwalm et al., 2010b; Grant et al., 2011). At present, most of the models, however, do not represent photosynthetic and respiratory acclimation (Smith and Dukes, 2013), mortality (McDowell et al., 2013), and species shift (Sebastia et al., 2008) well yet due to limited understanding. As a consequence, their regulations may not be well captured in the modeling results when models are used to simulate long-term effects of climate changing factors on ecosystems. In this study, we used data from space-for-time studies to support our model results. For example, soil C declined linearly with decreasing precipitation in observations along precipitation gradients (Anderson et al., 2011; Talmon et al., 2011), which is consistent with our modeling results indicating a long-term drought-induced decrease in soil C content. This consistency between model and empirical studies suggest that the responses of ecosystem variables to extreme climatic changes are unlikely to be overridden by biotic adaptation (Anderson et al. 2011). Rather, the extent of the responses might be attenuated or exacerbated (Smith 2011, Reichstein et al., 2013). Nonetheless, further research is needed to incorporate acclimation, adaptation and vegetation change into ecosystem models to improve ecological forecasting.

Vegetation mortality due to carbon starvation or hydraulic failure or both (McDowell et al., 2008) is likely to occur if the drought is severe enough and can therefore have legacy effect on most aspects of ecosystem carbon cycling (Liu et al., 2011). It is difficult for ecosystem models to accurately capture plant mortality due to the lack of thorough understanding on the mechanisms (Xu et al., 2013, McDowell et al., 2013, Reichstein et al., 2013). Mortality in grasslands differs from that in forest ecosystems. In a forest ecosystem, when large area of mortality occurs, the whole ecosystem would have to start over from secondary succession. However, grasslands are characterized by the high recovery potential of plant growth and they would recover to their original states in a very short time and had less impact on carbon cycling than forest ecosystems (Reichstein et al., 2013).

Another limitation in our study is possible model bias due to only one ecosystem model was used. A multiple-model inter-comparisons (MI) would be nice to test the robustness of our main conclusion that extreme drought had differential effect on production and respiration in grassland ecosystems. However, it is not our focus of this study. Nonetheless, findings from previous multiple model analysis can provide evidence for the robustness of our conclusion. For example, using four ecosystem C models, Luo et al. (2008) explored potential individual and interactive effects of climate warming, altered precipitation amount and elevated CO_2 concentration across a broad range of biomes. They found that half precipitation reduced net primary production more than heterotrophic respiration, and as a result decreased net ecosystem production.

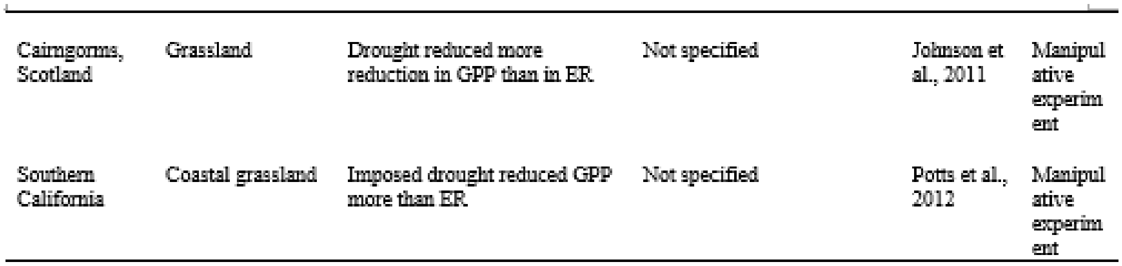
Supplementary materials

Table S2.1 Literature review of differential responses of production and respiration to drought in field observations and manipulative experiments across different biomes



Site	**Biome type**	**Results**	**Mechanisms**	**Reference**	**Note**
European forests and one grassland	Pine, oak, beech, spruce, fir, juniper, and grassland	In most sites, extreme drought induced more reduction in GPP than ER except a few Mediterranean ecosystems where the drought effect was smaller for GPP than ER	Not specified	Ciais et al., 2005	Eddy flux
East coast of japan	Temperate evergreen and deciduous broadleaved tree	GPP was reduced more than ER	Not specified	Kosugi et al., 2005	Eddy flux
Saskatchewan Canada	Southern boreal forests including aspen, spruce and jack pine	In aspen, first-year drought suppressed ER, but enhanced GPP whereas second- and third-year drought reduced GPP and ER with more reduction in GPP; In spruce and jack pine forests, drought did not significant affected GPP and ER	The enhanced GPP in aspen was due to warmer spring in that year; the lack of response to drought in the two coniferous forests was because of summer rainfall, low topographic position and low soil water holding capacity	Kljun et al., 2006	Eddy flux

European forests	Beech, Douglas-fir, Scots pine, Spruce, mixed coniferous	Drought inhibited GPP greater than ER	Not specified	Granier et al., 2007	Eddy flux
Hungaria	Semi-arid sandy grassland	Drought is more effective in reducing plant CO2 uptake than in reducing ER	Uncoupled heterotrophic respiration to photosynthesis is more resistant to drought	Nagy et al., 2007	Eddy flux
Southern Portugal	Evergreen oak woodland, grassland, and eucalyptus plantation	Severe drought affected more GPP than ER	Not specified	Pereira et al., 2007	Eddy flux
Interior Alaska, USA	Black spruce and aspen	GPP was reduced in the two forests, but ER increased	Drought-associated temperature increase might cause ER to rise	Welp et al., 2007	Eddy flux
Northwest Ohio, USA	Oak and red maple	Greater suppression of GPP than of ER by drought	Drought caused lower leaf area, lower apparent quantum yield and lower canopy conductance	Noormets et al., 2008	Eddy flux
Global network of eddy flux towers	Grassland, forest, shrubland, wetland, savannas	Overall, production is 50% more sensitive than respiration to drought, with a few exceptions	Not specified	Schwalm et al., 2010a	Eddy flux
Kendall grassland, USA	Semi-desert grassland	Drought reduced more gpp than ER	Not specified	Scott et al., 2010	Eddy flux
Southern Portugal	semi-natural Mediterranean grassland	Drought reduced GPP more than ER	Not specified	Jongen et al., 2011	Eddy flux
Western North America	Grassland, evergreen needle forest (ENF), woody savannas	GPP of grassland and ENF were more sensitive to drought, whereas in woody savannas GPP was less sensitive	Not specified	Schwalm et al., 2012	Eddy flux
Inner-Mongolia, China	Arid grassland	GPP was more sensitive to seasonal drought than ER	None but suggested drought might have lasted longer for assimilation than respiration in this ecosystem	Yang and Zhou, 2013	Eddy flux
Southwestern US	Ponderosa pine and grassland	GPP was more sensitive to summer drought than ER in the forest, but less sensitive in the grassland/shrubland	Not specified	Kolb et al., 2013	Eddy flux
France	Mediterranean evergreen oak forest	Drought inhibited GPP greater than ER	Shallow soil water content was not strongly affected by drought and thus soil respiration was less affected than GPP	Misson et al., 2010	Manipulative experiment
Wyoming, USA	High Plains Grassland	GPP was more sensitive to reduced rainfall than ER	Not specified	Chimner et al., 2010	Manipulative experiments
Northern Arizona	Desert grassland, pinyon-juniper, ponderosa pine forest, mixed conifer forest	Precipitation reduction did not impact both GPP and ER	Not specified	Wu et al., 2011	Manipulative experiments

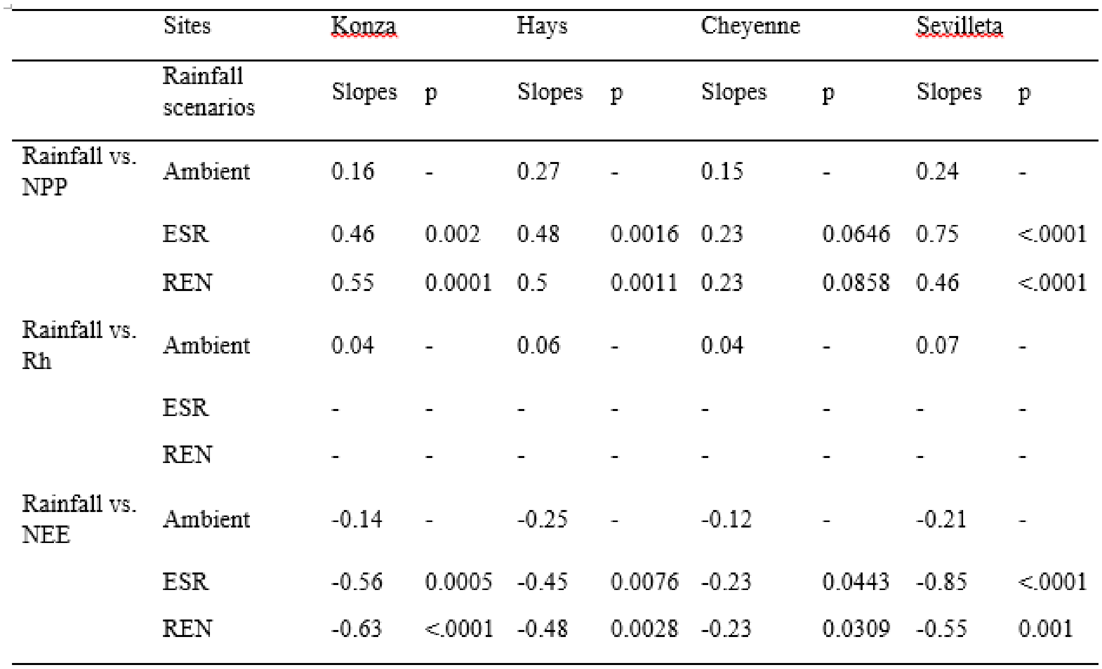


Cairngorms, Scotland	Grassland	Drought reduced more reduction in GPP than in ER	Not specified	Johnson et al., 2011	Manipulative experiment
Southern California	Coastal grassland	Imposed drought reduced GPP more than ER	Not specified	Potts et al., 2012	Manipulative experiment

Table S2.2 Results (p values) of paired-sample T test in reduction of C variable (ΔNPP, ΔRh, ΔNEE, ΔSoil C) between the two drought types (even size reduction and reduced event number) in the four grassland sites

Sites	Konza	Hays	Cheyenne	Sevilleta
NPP	0	0	0	0
Rh	0	0	0	0
NEE	0	0.044	0.098	0.412
Soil C	0	0	0	0

Table S2.3 Slopes of the linear regression between rainfall and C variables (NPP, Rh, and NEE) in each of three rainfall scenarios, and the significance (p) in slope difference between ambient and rainfall treatments. "-" means not applicable.



	Sites	Konza		Hays		Cheyenne		Sevilleta	
	Rainfall scenarios	Slopes	p	Slopes	p	Slopes	p	Slopes	p
Rainfall vs. NPP	Ambient	0.16	-	0.27	-	0.15	-	0.24	-
	ESR	0.46	0.002	0.48	0.0016	0.23	0.0646	0.75	<.0001
	REN	0.55	0.0001	0.5	0.0011	0.23	0.0858	0.46	<.0001
Rainfall vs. Rh	Ambient	0.04	-	0.06	-	0.04	-	0.07	-
	ESR	-	-	-	-	-	-	-	-
	REN	-	-	-	-	-	-	-	-
Rainfall vs. NEE	Ambient	-0.14	-	-0.25	-	-0.12	-	-0.21	-
	ESR	-0.56	0.0005	-0.45	0.0076	-0.23	0.0443	-0.85	<.0001
	REN	-0.63	<.0001	-0.48	0.0028	-0.23	0.0309	-0.55	0.001

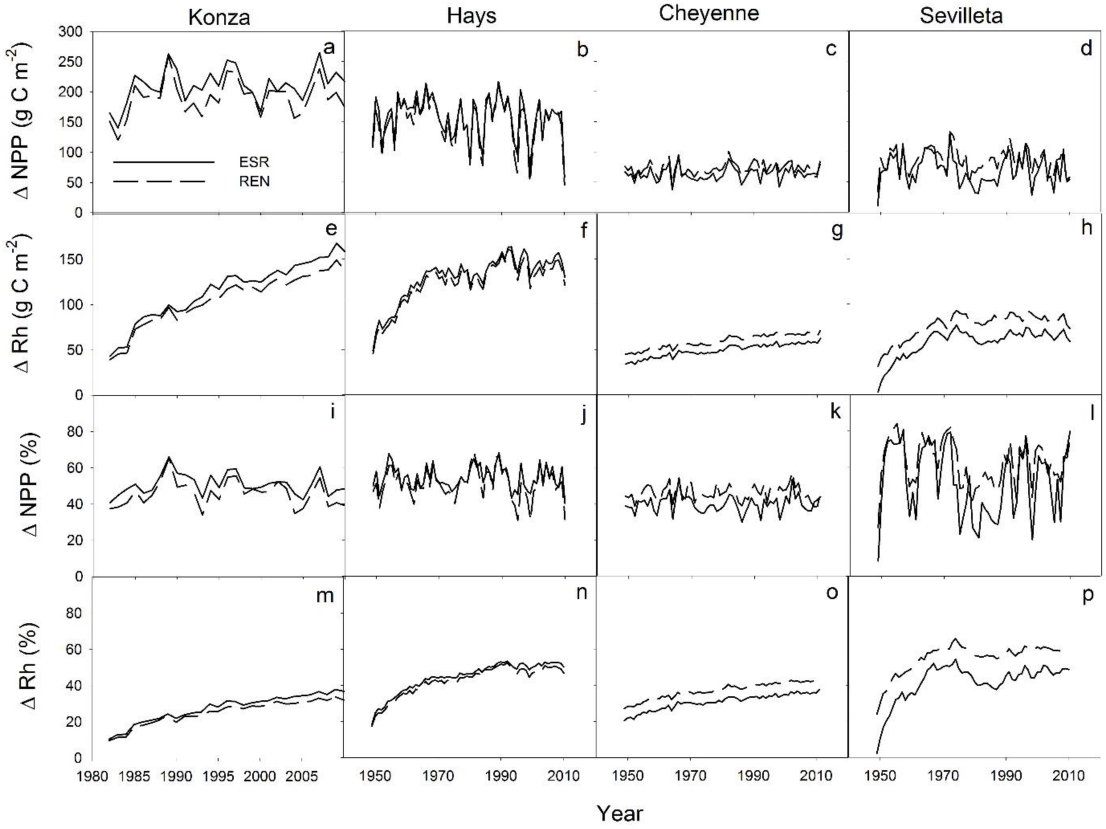


Figure S2.1 Drought-induced reductions in NPP and Rh along modeled years in four North American grasslands (Konza: a, e, i and m; Hays: b, f, j and n; Cheyenne: c, g, k and o; Sevilleta: d, h, l and p). ESR is rainfall event size reduction and REN is reduced rainfall event number. Solid line represents ESR treatment and dash line represents REN treatment.

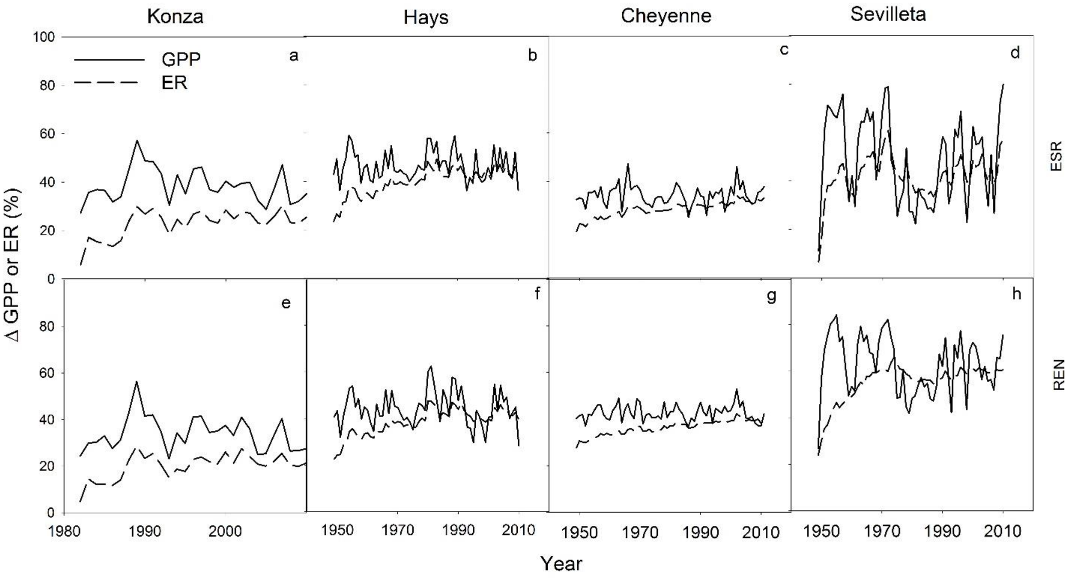


Figure S2.2 Drought-induced reductions in GPP and ER along modeled years in four North American grasslands (Konza: a and e; Hays: b and f; Cheyenne: c and g; Sevilleta: d and h). ESR is rainfall event size reduction and REN is reduced rainfall event number. Solid line represents GPP and dash line represents ER.

Chapter 3 Responses of plant community structure and productivity to altered precipitation: a meta-analysis of grassland ecosystems

Abstract

Global climate change has intensified the hydrological processes, leading to great variability in precipitation. However, how plant community structure and ecosystem functioning respond to altered precipitation remains unclear. In this study, we used a meta-analysis approach to quantify the response ratios of community productivity and structure to both increased and decreased precipitation. Our results showed that decreased precipitation suppress aboveground net primary productivity (ANPP) by 16.7% and belowground net primary productivity (BNPP) by 5.4%; increased precipitation enhanced ANPP by 25.7% but had no impact on BNPP; community structure showed little responses to precipitation change, except species richness responding negatively to decreased precipitation by 8%. Response of ANPP to altered precipitation was significantly greater than that of BNPP and response of ANPP to increased precipitation was stronger than that to decreased precipitation. In general, ANPP of different PFTs, except C_4 showed positive and negative responses to decreased and increased precipitation, respectively, but we did not detect any difference in responses among the PFTs. The response ratios of dominant PFTs to altered precipitation positively correlated with that of the whole plant community, with the slope less than 1. Productivity sensitivity to both precipitation change declined exponentially with mean annual precipitation. Our analyses provide a complementary perspective to long-term observational productivity-precipitation relationship, suggest that changes in ecosystem functioning driven by community shift under precipitation change was uncommon and indicate that future greater precipitation variability could

overall favor plant growth. Our findings have implications for both modeling community and experimental studies.

3.1 Introduction

Global climate change has intensified the hydrological processes (Huntington, 2006). The general circulation models predicted diverse responses of water cycle to climate change, with altered precipitation in particular (IPCC, 2013). To understand ecosystem responses to precipitation change, a number of field experiments have been conducted, mostly in grassland ecosystems (e.g., Knapp et al., 2001; Dukes et al., 2005; Yang et al., 2011; Collins et al., 2012). The responses of plant community to altered precipitation vary among sites and years. For example, greater responses of productivity to experimentally increased precipitation were observed in two C_4 grassland ecosystems, whereas the response was minimal in a C_3 mixed prairie (Wilcox et al., 2014); plant community composition in a semi-arid mixed prairie only showed significant response to water addition in dry years (Zelikova et al., 2014). It is therefore necessary to synthesize these studies to reveal general patterns and to determine the controls in ecological responses to altered precipitation.

Productivity, one of most important ecosystem functioning, is comprised of aboveground net primary productivity (ANPP) and belowground net primary productivity (BNPP). The ANPP and BNPP often show differential, sometimes opposite responses to altered precipitation (Xu et al., 2012; Byrne et al., 2013; Wilcox et al., 2014). Theoretically, when plant community encounters wet years, it has the tendency to allocate more photosynthetic assimilates to the aboveground compartments to strengthen its competitiveness for resources; on the other hand, in dry years, plants incline to channel more carbohydrates to roots and less to aboveground parts in order to alleviate the water stress (Hui & Jackson, 2005; Lambers et al., 2008). We therefore predicted that ANPP would be more sensitive to precipitation change than BNPP.

Both short- and long-term observations in ANPP across regional scales have demonstrated greater sensitivity in drier sites (Huxman et al., 2004; Knapp et al., 2015). However, inconsistent findings showed that the sensitivity increased with mean annual precipitation in Euroasian temperate grassland within a narrower precipitation range (Guo et al., 2012). Furthermore, the sensitivity could be mediated by soil property and plant community traits as both are often covariate with climate. Therefore, synthesis of manipulative experiments could potentially add another perspective from a different angle and reveal the controls of ecological responses to altered precipitation.

Global land models use plant functional types (PFTs) to represent vegetation in grid points (Bonan et al., 2002). However, it still remains untested whether the response of dominant PFTs could reflect that of the total plant community to altered precipitation. The PFTs that differ in photosynthetic pathway and structural traits often have contrasting responses to altered precipitation. For example, at individual level, C_3 plants often show greater variability to precipitation change than C_4 plants due to its lower water use efficiency; grass species may be more sensitive to altered precipitation than forb species due to the difference in root architecture (Nippert & Knapp, 2007). Furthermore, competition among PFTs at community level may obscure the predictions by plant physiology at individual level. In this meta-analysis, we directly addressed these open questions.

Plant community structure (i.e., species richness, evenness and diversity) and composition within ecosystems often regulate ecological responses to resource change (Smith et al., 2009). For example, high diversity usually associates with high productivity and greater stability to perturbation (Tilman, 1999; Loreau et al., 2001). Altered precipitation has the potential to affect the plant community structure by favoring certain species or PFTs and consequently change the competition among them, which may lead to species reordering and turnover. The changes in community structure could eventually have large impacts on ecosystem functioning (Hooper & Vitousek, 1997; Smith et al., 2009; Wardle et al., 2011; Hooper et al., 2012). One of the goals in this meta-analysis was to examine whether community structure changes with precipitation manipulation.

In this study, we synthesized 44 experimental studies with precipitation manipulation (increasing or decreasing precipitation amount) in grassland ecosystem to address the following hypotheses: (1) both ANPP and BNPP would show negative responses to decreased precipitation and positive responses to increased precipitation; the response of ANPP to altered precipitation would be greater than that of BNPP; (2) climate, vegetation and edaphic conditions would together determine the sensitivity of ANPP and BNPP to altered precipitation; (3) the response of dominant PFTs to precipitation change reflects that of whole plant community; (4) PFTs of C_3 and grass show greater responses to altered precipitation than C_4 and forbs, respectively; (5) community structure would be altered by precipitation change.

3.2 Methods

3.2.1 Data compilation

Publications that studied productivity and community structure responses to experimental precipitation manipulations (including both increased and decreased precipitation) were collected by searching Web of Science. The compiled database contained 9 variables, including ANPP, ANPP of different PFTs (i.e., grass, forbs, C_3 and C_4), BNPP, richness, community evenness and diversity. Since studies showed that productivity and community structure often respond differently in years with different precipitation amount and rarely with directional changes, we therefore included all-year data into our analyses to avoid bias. Climatic factors (i.e., mean annual temperature and mean annual precipitation), edaphic properties (i.e., sand, silt and clay content) and functional composition (i.e., C_3, C_4, forb and grass proportions) were recorded for each study site. The means, standard deviations (or standard errors), and sample sizes of the chosen variables were directly provided or could be calculated from the studies. Most of the 44 studies were conducted in North America and Europe. Measurements under different magnitudes of precipitation changes in one study site were considered as independent observations. In addition, the compiled studies were all from natural grassland ecosystem under field condition only.

3.2.2 Analyses

In this study, we employed a meta-analysis approach and calculated the response ratio (RR) to reflect the effects of altered precipitation on community productivity and structure (Gurevitch and Hedges 1999). RR is defined as the ratio of the mean value of a given variable in the treatment group (Xt) to that in the control group (Xc), and was used as the measure of the treatment effect on that corresponding variable (Eq. 1).

$$RR = \ln\left(\frac{\overline{X_t}}{\overline{X_c}}\right) = \ln\left(\overline{X_t}\right) - \ln\left(\overline{X_c}\right) \qquad \text{Eq.1}$$

Thus, RR is an effective index of effect size for many manipulative experiments, and the logarithm of RR is a suitable measure for meta-analyses as its bias is small and its sampling distribution is approximately normal (Hedges et al. 1999). More specifically, the mean and standard deviation (S) with sample size of each treatment were extracted to calculate the logarithm of RR (LnRR), variance (v), weighting factor (wij), the weighted response ratio (RR_{++}), and the 95 % confidence interval (CI) of RR_{++} for the purpose of statistical tests (Gurevitch and Hedges 1999, Hedges et al. 1999, Luoet al. 2006).

The variance (*v*) for each RR was calculated by:

$$v = \frac{s_t^2}{n_t \overline{X}_t^2} + \frac{s_c^2}{n_c \overline{X}_c^2} \qquad \text{Eq. 2}$$

here n_t and n_c are the replicate numbers, S_t and S_c are standard deviation for treatment group and control group, respectively. Reciprocal of variance ($w = \frac{1}{v}$) was considered as the weight of each RR. The overall mean response ratio RR_{++} was computed from individual RR between treatment group and control group as below:

$$RR_{++} = \frac{\sum_{j=1}^{k} w_j RR_j}{\sum_{j=1}^{k} w_j} \qquad \text{Eq. 3}$$

where k was the number of comparisons. The SE of RR_{++} was estimated by:

$$\mathrm{SE}(RR_{++}) = \sqrt{\frac{1}{\sum_{j=1}^{k} w_j}} \qquad \text{Eq. 4}$$

We calculated a weighted response ratio (RR_{++}) from individual RR_j by giving greater weight to the studies whose estimates have greater precision (smaller v) so that the precision of the combined estimate and the power of the tests can be improved (Gurevitch and Hedges 1999). We calculated 95% confidence interval (CI) directly by $95\%\ \mathrm{CI} = RR_{++} \pm 1.96 \times \mathrm{SE}(RR_{++})$. If the 95 % CI value of RR_{++} for a variable does not cover zero, the response of the variable to precipitation change is considered significantly different between the two treatments. Otherwise, the response is considered not to differ significantly. The percentage change of a variable was obtained by the formula: $[\exp(RR_{++}) - 1] \times 100\%$.

We used the homogeneity test to determine whether different groups of independent variables resulted in different responses. In meta-analysis, the total heterogeneity (Q_T) can be portioned into within-group heterogeneity (Q_W) and between group heterogeneity (Q_B). The Q statistic approximately has a chi-square distribution (Curtis and Wang 1998), which allows a significance test of the null hypothesis that all response ratios are equal. A Q_B larger than a critical value indicated that there was significant difference between categories.

3.2.3 Statistical analysis

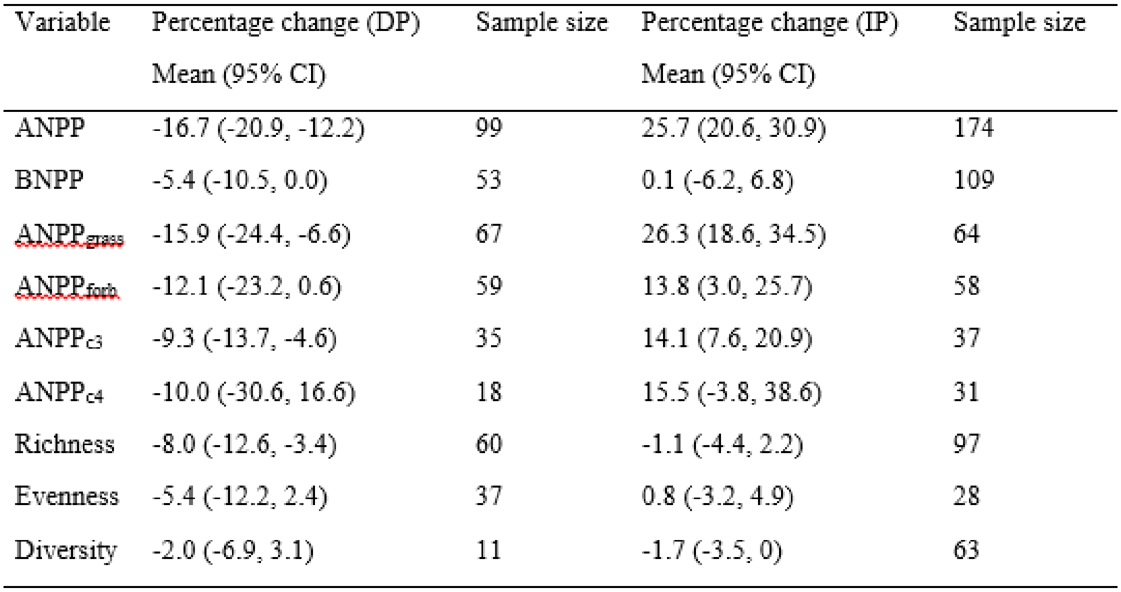
The productivity sensitivity to altered precipitation was calculated as a ratio between absolute changes in ANPP or BNPP and changes in precipitation amount. We used linear and nonlinear regression to investigate the relationships between productivity sensitivity and climate, vegetation and soil factors. The relationship between LnRR and precipitation change was also tested using linear regression.

3.3 Results

Decreased precipitation significantly reduced ANPP and BNPP by 16.7% and 5.4%, respectively; increased precipitation significantly enhanced ANPP by 25.7% but did not affect BNPP (Table 3.1; Fig. 3.1). The responses of ANPP to altered precipitation were always greater than that of BNPP. ANPP showed greater responses to increased precipitation than to decreased precipitation (Table 3.1; Fig. 3.1).

Decreased precipitation suppressed ANPP of grass, forb, and C_3 by 15.9%, 12.1%, and 9.3%, respectively, but did not significantly affect ANPP of C_4 (Table 3.1; Fig. 3.1). Increased precipitation promoted ANPP of grass, forb, and C_3 by 26.3%, 13.8%, and 14.1% respectively, and tend to increase ANPP of C_4 by 15.5% with 95% confidence interval slightly overlapping with 0. The response of ANPP of each PFT to decreased precipitation did not differ from that to increased precipitation (Table 3.1; Fig. 3.1).

Table 3.1 Percentage changes of 9 variables related to community productivity and structure in response to manipulated precipitation change.



Variable	Percentage change (DP) Mean (95% CI)	Sample size	Percentage change (IP) Mean (95% CI)	Sample size
ANPP	-16.7 (-20.9, -12.2)	99	25.7 (20.6, 30.9)	174
BNPP	-5.4 (-10.5, 0.0)	53	0.1 (-6.2, 6.8)	109
ANPP$_{grass}$	-15.9 (-24.4, -6.6)	67	26.3 (18.6, 34.5)	64
ANPP$_{forb}$	-12.1 (-23.2, 0.6)	59	13.8 (3.0, 25.7)	58
ANPP$_{c3}$	-9.3 (-13.7, -4.6)	35	14.1 (7.6, 20.9)	37
ANPP$_{c4}$	-10.0 (-30.6, 16.6)	18	15.5 (-3.8, 38.6)	31
Richness	-8.0 (-12.6, -3.4)	60	-1.1 (-4.4, 2.2)	97
Evenness	-5.4 (-12.2, 2.4)	37	0.8 (-3.2, 4.9)	28
Diversity	-2.0 (-6.9, 3.1)	11	-1.7 (-3.5, 0)	63

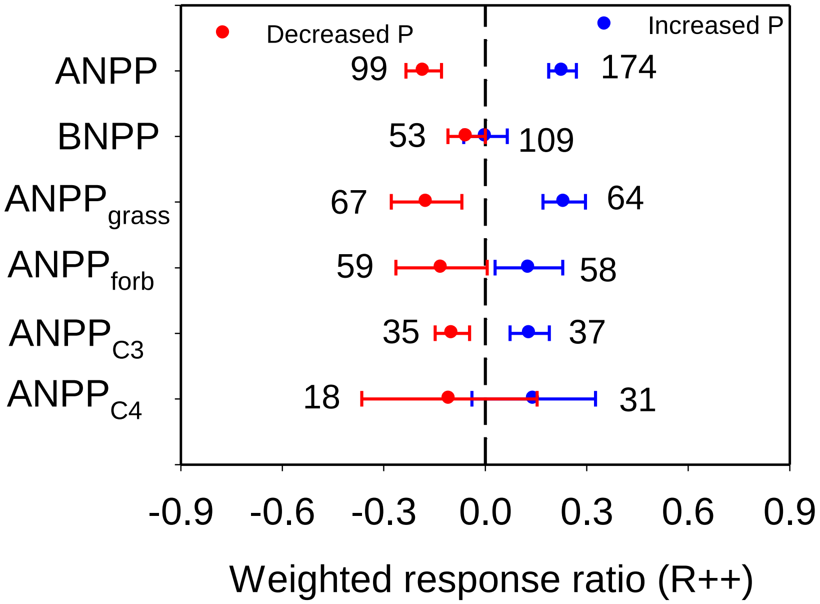


Figure 3.1 The weighted response ratio for the responses to decreased and increased precipitation of ANPP, BNPP and ANPP of plant functional types (i.e., grass, forb, C$_3$

and C_4). Mean ± 95% confidence intervals. The number of observations used in the analysis is shown near the bar.

To test whether the response of dominant PFTs to precipitation changes could reflect that of whole plant community, we correlated response ratio of the dominant PFTs with that of total ANPP. We found significantly positive, linear relationships between the two in both increased and decreased precipitation scenarios (Fig. 3.2). Furthermore, the slopes were significantly lower than 1 (Fig. 3.2).

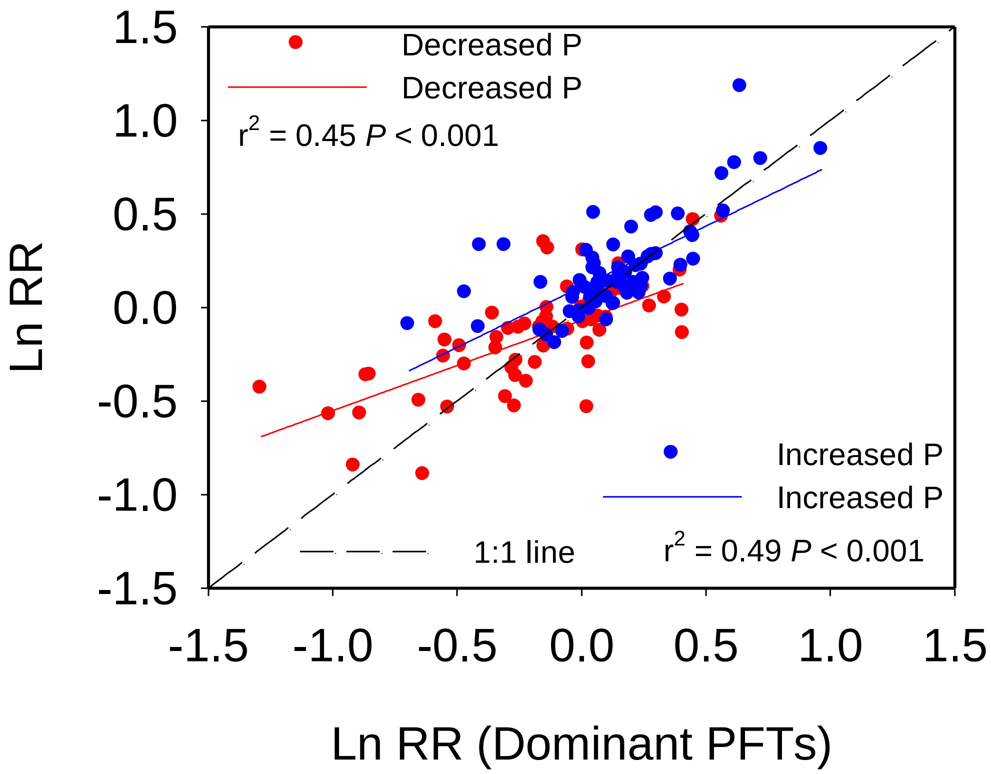


Figure 3.2 The correlation analyses between logarithm response ratio (LnRR) of ANPP of dominant PFTs and LnRR of total community ANPP to altered precipitation

Changes in productivity especially ANPP, induced by altered precipitation showed large variability among studies. We therefore conducted regressions between the productivity sensitivity and climatic, edaphic and plant functional traits. We found that both sensitivity of ANPP and BNPP to altered precipitation decreased exponentially with mean annual precipitation (Fig. 3.3). However, no other significant relationships were detected between sensitivity and other factors (Table S3.1). We also tested whether the response ratio had significant relationship with precipitation change and found that the response ratio of ANPP increased with precipitation change (Fig. 3.4a). No significant relationships were found between response ratio of BNPP and altered precipitation (Fig. 3.4b)

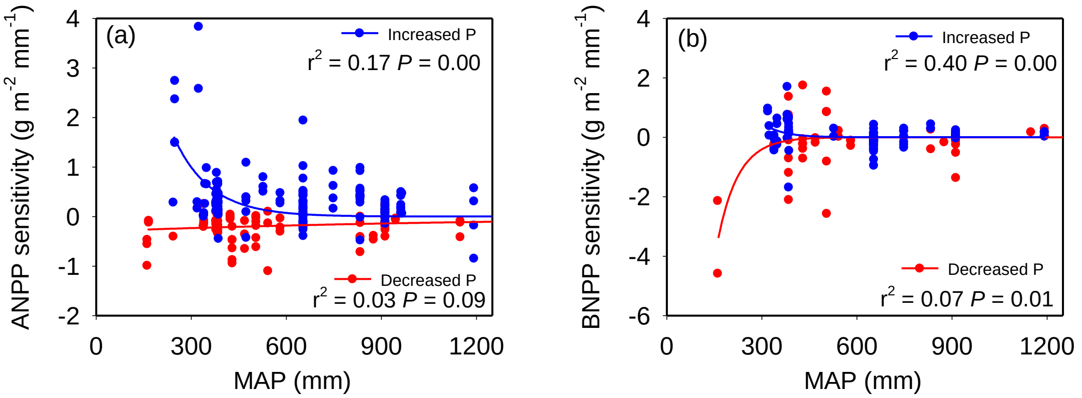


Figure 3.3 Relationships between productivity sensitivity to precipitation change and mean annual precipitation (MAP). The sensitivity of ANPP (a) and BNPP (b) to altered precipitation decreased exponentially with MAP.

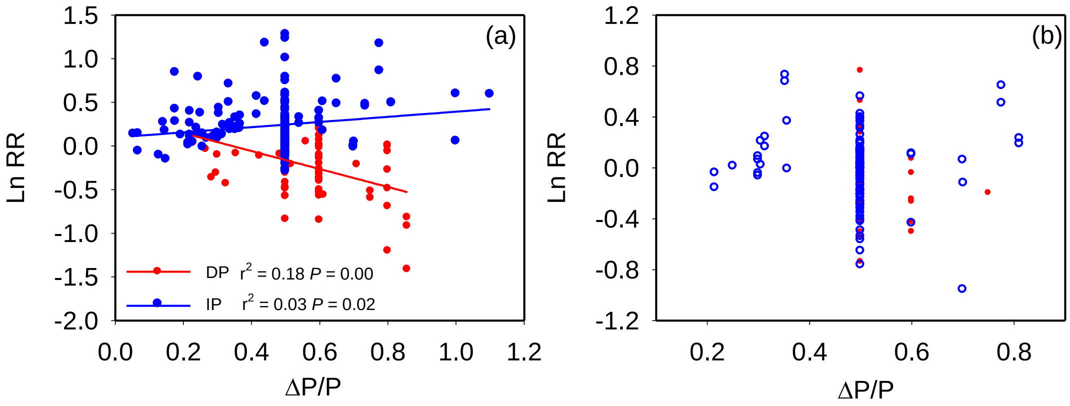


Figure 3.4 Relationships between logarithm response ratios (LnRR) of ANPP (a) and BNPP (b) and precipitation change (ΔP/P). The responses of ANPP became stronger with larger precipitation change, whereas the responses of BNPP did not have significant linear relationships with precipitation change.

The great responses of productivity, especially ANPP to altered precipitation could cause changes in community structure. Our synthesis showed that species richness was reduced by 8% by decreased precipitation and showed no response to increased precipitation (Table 3.1; Fig. 3.5). Community evenness and diversity were not changed by altered precipitation (Table 3.1; Fig. 3.5).

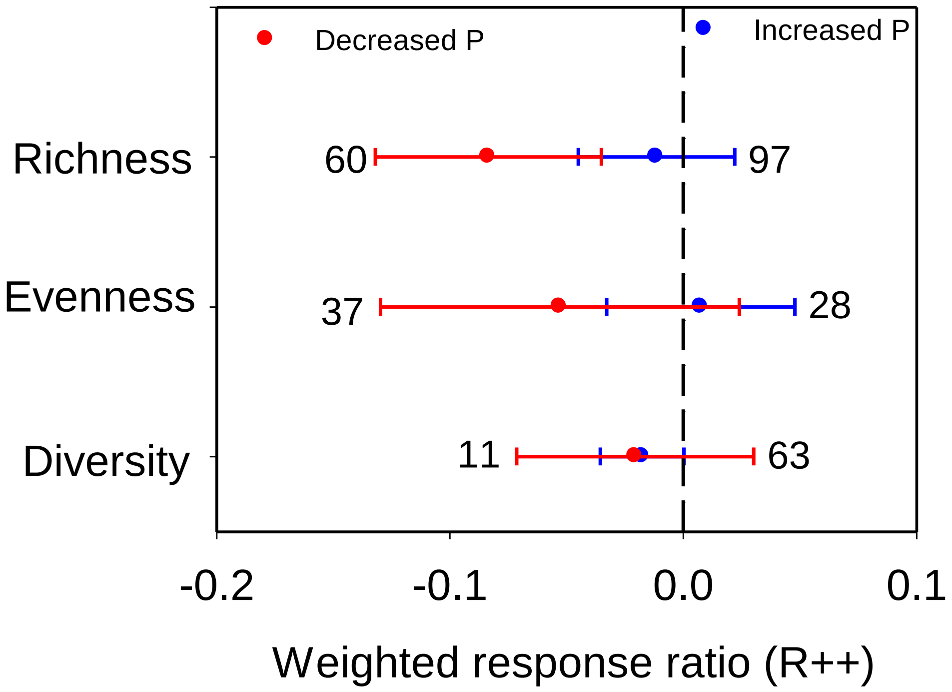


Figure 3.5 The weighted response ratio for the responses to decreased and increased precipitation of richness, evenness and diversity. Mean ±95% confidence intervals. The number of observations used in the analysis is shown near the bar.

3.4 Discussion

The first hypothesis was generally supported by our findings. Both ANPP and BNPP showed negative responses to decreased precipitation, ANPP responded positively whereas BNPP showed neutral response to increased precipitation and the responses of ANPP to altered precipitation were greater than that of BNPP. The findings were consistent with plant resource acquisition strategy (Grime, 2006). Decreased precipitation suppresses plant growth, both aboveground and belowground. However, in shortage of precipitation, plants tend to allocate more photosynthates to roots to intercept more soil water in order to cope with water deficit (Lambers et al.,

2008) and consequently compensate for the decreased root growth under drought. Increased precipitation favors plant growth and plants invest more carbohydrate aboveground to achieve optimal growth and less carbon for root growth. As a result, this carbon allocation strategy offsets some of the enhanced root growth by increased precipitation. Our results demonstrate that root growth is more plastic to altered precipitation than aboveground growth. Greater response ratio of ANPP to increased precipitation than that to decreased precipitation was consistent with a long-term precipitation-productivity analysis. In that analysis, Knapp et al., (2001) found ANPP responded more strongly to wet than to dry years. Therefore, the differential responses of ANPP to altered precipitation suggest that predicted increase in precipitation variability may overall favor plant growth.

The exponential decay of productivity sensitivity to altered precipitation with mean annual precipitation is in line with previous findings (Huxman et al., 2004; Knapp et al., 2015). However, the variation explained by MAP was low, especially for productivity sensitivity to decreased precipitation, which indicates involvement of other factors in account for the unexplained variation. Unfortunately, we failed to detect any significant relationships between mean annual temperature, functional composition and soil texture and the productivity sensitivity. The non-significant relationships between all the factors and the productivity sensitivity indicate that some other factors such species richness or functional richness (Heisler-White et al., 2009) contributing to the variability were not accounted; and/or the sensitivity obtained in short experimental duration (most studies were less than three years) were not likely to represent mean sensitivity of the ecosystem.

Our findings did not support the third hypothesis that ANPP of grass and C_3 plants would show greater sensitivity to altered precipitation than forb and C_4 PFTs, respectively. Due to the physiological and structural characteristics of forb (e.g., taproots) and C_4 (e.g., high water use efficiency) plants, we expected buffer effect of them to altered precipitation. However, our analysis showed no significant difference in responses to altered precipitation among the four PFTs. A couple of reasons could contribute to such non-significance. First of all, at community level there are more influencing factors than physiology in determining the response to altered precipitation such as inter-specific competition and plant phenology (Walther et al., 2002; Cleland et al., 2012). Low sample size, especially for C_4 PFT, could cause statistical bias in our results. The findings suggest that caution should be paid when upscaling responses from PFT level to ecosystem level.

The responses of dominant species or PFTs are often considered to determine the sensitivity of whole plant community (Grime 1970; Smith et al., 2009). The findings of significant correlation between responses of dominant PFTs to altered precipitation and those of the whole plant community provide direct evidence that the response of dominant PFTs to precipitation change reflects the whole plant community sensitivity. However, the slopes were significantly less than 1, indicating that using responses of dominant PFTs to altered precipitation to represent that of whole plant community may overestimate the sensitivity. The greater negative responses of the dominant PFTs in decreased precipitation scenario could alleviate competition against non-dominant PFTs, whereas the higher positive responses of the dominant PFTs in increased precipitation could aggravate the competition and therefore suppress the growth of non-dominant PFTs (Fowler, 1986). As a result, the response of the whole plant community to altered precipitation is lower than that of the dominant PFTs. Our findings indicate the importance of considering biotic competition among PFTs in the global land models.

Species-specific responses to climate changes are often observed in experimental studies. For example, Kardol et al., (2010) reported the greatest response of a dominant species to altered precipitation and therefore led to changes in community diversity. We therefore expected changes in community structure in response to altered precipitation. However, our analysis showed that the community structure (i.e., species richness, community evenness and diversity) had neutral responses to both decreased and increased precipitation, except loss of species richness under drought. The results indicate that generally grassland plant community is resistant to changes in precipitation (Grime et al., 2008; White et al., 2014). The species-specific responses are possibly not large enough or universal enough to cause significant divergence in community structure. Additionally, we expected the variations in the response ratio could be at least partly explained by background climate. For example, the magnitude of specific-response to increased precipitation may be much larger in dry systems than that in mesic systems (citation). However, due to limited sample size, we could not test any relationships between climatic factors (i.e., MAT and MAP) and community structure.

There are uncertainties in our meta-analysis due to the inherent limitations of the methodologies. By lumping all manipulative experiments, we introduced large biases from different magnitude and methods of rainfall manipulations, different study length and different methods of measuring relevant variables. Moreover, most of the synthesized study sites locate in North America and Western Europe, whereas very few study sites are from other areas of the world. Therefore, spatially coordinated comparative experiments are in urgent need (Rustad et al., 2008; Luo et al., 2011; Fraser et al., 2012) in the future to avoid aforementioned shortcomings of meta-analysis, and more experiments should be especially carried out in currently under-represented areas such Africa and South America. Additionally, since most of the studies were in grassland, the scientific community should consider setting up precipitation-manipulated experiments in forest ecosystem which has distinct climate, soil and vegetation characteristics from grassland ecosystem.

To sum up, our meta-analysis demonstrated that ANPP and BNPP showed negative responses to decreased precipitation, but ANPP responded more than two times greater than BNPP. ANPP showed positive response to increased precipitation whereas BNPP had no response. Generally ANPP of different PFTs, except C_4 showed positive and negative responses to decreased and increased precipitation, respectively, but we did not detect any difference in responses among the PFTs. The responses of dominant PFTs reflect that of the whole plant community with overestimation; community structure showed little responses to precipitation change and productivity sensitivity declined exponentially with mean annual precipitation. Our analyses have great implications for both modeling community and experimental studies.

Supplementary materials

Table S3.1 P values of correlation analysis between climate, soil texture and plant functional composition and productivity sensitivity to decreased precipitation (DP) and increased precipitation (IP)

	MAT (^{o}C)	Sand (%)	Silt (%)	Clay (%)	Grass (%)	Forb (%)	C3 (%)	C4 (%)
S_{ANPP} (DP)	0.12	0.46	0.17	0.94	0.45	0.32	0.49	0.35
S_{ANPP} (IP)	0.49	0.77	0.86	0.43	0.24	0.40	0.67	0.63
S_{BNPP} (DP)	0.42	0.69	0.74	0.67	0.48	0.50	0.54	0.66
S_{BNPP} (IP)	0.50	0.18	0.09	0.57	0.08	0.09	0.36	0.32

Chapter 4 Evidence for long-term shift in plant community composition under decadal experimental warming

Abstract

Long-term, slow ecological processes such as changes in plant community structure and composition strongly regulate ecosystem responses to climate change. Shifts in plant community are expected in chronically altered environments under warming. However, experimental evidence for long-term shifts and the associated mechanisms is still scarce in temperate grasslands. Here, we explore the long-term responses of a prairie plant community to 14-year (2000-2013) manipulations of climate warming and clipping in Oklahoma, USA. Community composition was resistant to experimental warming in the first seven years, but started to show responses since the eighth year; clipping consistently affected community composition over the years. Compositional change under long-term warming was mainly contributed by one invasive species and three dominant species. The negative correlations in relative abundance between the invasive species and the dominant species suggest inter-specific competition. Community structure (i.e., richness, evenness and diversity) had no overall response to experimental warming. However, in 2007, the extreme wet year, warming reduced species richness by 30%. Clipping promoted species richness by 10% on average over the 14 years but decreased community evenness. Warming did not interact with clipping in influencing the plant community variables. Our study provides experimental evidence for long-term shifts in plant community composition due to climate warming and revealed novel mechanisms (i.e., species invasion and associated biotic interactions) underlying the long-term shift. The results also suggest that climate extremes may elicit or advance community responses to climate warming. The findings have implications for terrestrial carbon modeling with dynamic global vegetation.

4.1 Introduction

Global mean temperature has increased by 0.85 ^{o}C since 1880s and is predicted to continue rising over the 21st Century (IPCC 2013). Field experiments showed prompt ecosystem responses to climate warming (Rustad *et al*. 2001; Wu *et al*. 2011; Lu *et al*. 2013), which were due mainly to short-term, physiological mechanisms. However, ecosystem responses to warming are strongly regulated by long-term, slow processes (Rastetter 1996; Luo *et al*. 2011) such as shifts in plant community structure and composition (Chapin *et al*. 1995; Saleska *et al*. 2002; Field *et al*. 2007; Luo 2007; Smith, Knapp & Collins 2009). Climate warming has the potential to alter plant community through shifting species dominance (Klanderud & Todland 2005; Prieto *et al.* 2009; Dieleman *et al.* 2015), facilitating species invasion (Dukes & Mooney 1999; Walther *et al.* 2009) and triggering species loss (Klein, Harte & Zhao 2004; Gedan & Bertness, 2009). Therefore, shifts in community structure and composition are expected in chronically altered environment under long-term warming (Smith, Knapp & Collins 2009). However, experimental evidence for long-term shifts in community structure and composition to climate warming in temperate grasslands is still scarce.

Although plant communities in many temperate grassland ecosystems have shown no responses to experimental warming (Zaveleta *et al*. 2003; Dukes *et al*. 2005; Kardol *et al*. 2010; Hoeppner & Dukes 2012; Hoover, Knapp & Smith 2014) based on relatively short-term experiments (but see Grime *et al*. 2008), plant communities can see major shifts in structure and composition with longer-term change in temperature. Significant changes in community structure and composition such as species reordering and species gain and loss are likely to be slow processes, as they are often affected by chronically altered resource availability in a long timescale (Smith, Knapp & Collins 2009). For example, in a moist tussock tundra, a pronounced response in the plant community was not revealed until the ninth year due to warming-induced slow accumulation of nutrient availability (Chapin *et al*. 1995). Additionally, chronically altered resource availability under warming can also change inter-specific competition (Shaver *et al*. 2000) and may cause community compositional change. Therefore, long-term experiments are necessary to provide relatively complete understanding of climate change impacts on plant community and reveal key mechanisms critical for long-term predictions of ecosystem responses (Rastetter 1996).

Natural disturbances such as extreme precipitation events are expected to interact with climate warming to elicit or accelerate shifts in plant community structure and composition (Jentsch, Kreyling & Beierkuhnlein 2007; Smith, Knapp & Collins 2009). In other words, natural disturbances can reduce inertia of a system to climate change (Jentsch & Beierkuhnlein 2003). For example, extreme drought can reduce the competitive strength of the resident vegetation and create available niche for possible species invasion (Davis *et al*. 2000); extreme wet condition can also increase the invisibility of plant community either due to a direct effect of water supply or through enhanced nutrient availability (Dukes & Mooney 1999; Davis *et al*. 2000). Warming may interact with both extreme scenarios by further limiting water availability to plants (Lu *et al*. 2013) in dry years and by increasing more nutrient availability due to the elevated mineralization (Bai *et al*. 2013) in wet years. Therefore, warming may interplay with natural disturbances to cause permanent shifts in community structure and composition.

The responses of plant community to climate warming may vary strongly with land management practices (Harmens *et al*. 2004; Chapin *et al*. 2008; White *et al*. 2012). Land management practices in grassland ecosystems significantly affect plant community structure and composition (Collins *et al*. 1998; Koerner *et al*. 2014; Borer *et al*. 2014). For example, mowing or grazing often increases species richness by increasing light availability (Collins *et al.* 1998; Yang *et al.* 2012; Borer *et al*. 2014) and grazing suppresses growth of dominant species, increasing species richness (Koerner *et al.* 2014). Hay harvest in the southern Great Plains, where this study was conducted, is a common land management practice. Harvesting plants without returning any material back likely influences soil microclimate, light availability and nutrient dynamics and eventually alters community responses to climate warming. In our study, annual clipping was to mimic hay harvest.

An ongoing warming and clipping experiment was set up in a tallgrass prairie in central Oklahoma in November of 1999 (Luo *et al*. 2001). Besides monitoring C fluxes (Wan *et al.* 2005; Zhou, Wan & Luo 2007; Niu *et al.* 2013) and stocks (Luo *et al.* 2009; Niu *et al.* 2010; Xu *et al.* 2012a, b), plant community surveys including species richness and abundance have been conducted every year. Low warming effects on soil microclimate (Wan, Luo & Wallace 2002), soil nutrient dynamics (Wan *et al.* 2005) and ecosystem functioning (Zhou, Wan & Luo 2007; Luo *et al.* 2009) were found in previous studies, most of which reported experimental data from before 2008. Therefore, we first hypothesized that experimental warming would have minimal impacts on plant community structure and composition in short term, whereas clipping could have significant effects on plant community due to its direct removal of plant species. Furthermore, based on general theory of chronic resource alterations under climate change (Smith, Knapp & Collins 2009) and given that our study site experienced extraordinarily wet and dry years, we predicted that warming would alter plant community structure and composition over the long term through species reordering and/or species invasion. In addition, we hypothesized that clipping would interact with warming in influencing community structure and composition.

4.2 Materials and Methods

4.2.1 Study site

The experiment was conducted in a tallgrass prairie on the Kessler Farm Field Laboratory in Oklahoma, USA (34°59'N, 97°31'W). The study site was neither cultivated nor grazed by large herbivores for the past 40 years prior to the start of the experiment. The grassland was dominated by the C_4 perennial grasses *Schizachyrium scoparium* (*S. scoparium*) and *Sorghastrum nutans* (*S. nutans*) and the C_3 perennial forbs *Ambrosia psilostachya* (*A. psilostachya*), *Solidago nemoralis* (*S. nemoralis*) and *Solidago rigida* (*S. rigida*) with few annual grasses (*Aristida oligantha*) and forbs (e.g., *Croton glandulosus*). There are also a few subordinate legume species, such as *Dalea candida* (*D. candida*), *Dalea purpurea* (*D. purpurea*) and *Desmanthus illinoensis* (*D. illinoensis*). Mean annual temperature was 16.3°C with a monthly mean temperature of 4.4°C in January and 27.7°C in July. Mean annual precipitation at the site is 914 mm (Oklahoma Climatological Survey, Norman, OK, USA). The soil was part of the Nash-Lucien complex with neutral pH, high available water holding capacity (around 37%), and a moderately penetrable root zone (US Department of Agriculture 1979).

4.2.2 Experimental design

The experiment used a paired factorial split-plot design. Warming was the main factor and clipping was nested within warming (Luo *et al.* 2001). Within each of six pairs of 2 m × 2 m plots, one plot was subjected to continuous warming from an infrared heater (100 W m^{-2}, Kalglo Electronics Inc, Bethlehem, PA, USA) hung 1.5m above the ground since November 1999, while the other plot, equipped with a ‘dummy’ heater, served as a control. The distance between warmed and control plots was approximately 5 m. Each plot was divided into four 1m × 1 m subplots. Plants in two diagonal subplots were clipped at a height of 10 cm above the ground annually to mimic hay harvest every year at peak biomass. Clipped materials including aboveground leaf, stem, inflorescence, and fruit production were all taken away and not returned to the plots. The other two subplots were left unclipped. Thus there were totally four treatments: unclipped and control (ambient) temperature (UC), unclipped and warmed (UW), clipped and control temperature (CC), and clipped plus warmed (CW).

4.2.3 Soil temperature, soil water content and precipitation measurements

Soil temperature was measured by thermocouples at a depth of 2.5 cm in the center of one clipped and one unclipped subplot in each plot. The thermocouples were connected to a datalogger (Campbell Scientific Inc., Logan, UT, USA) and recorded soil temperature every 10 minutes. Volumetric soil water content (v/v %) was measured twice a month using portable Time Domain Reflectometry equipment (Soil Moisture

Equipment Corp., Santa Barbara, CA, USA) at a depth of 1-15cm. Precipitation data were obtained from an Oklahoma Mesonet Station (Washington Station) located approximately 200 m away from our experimental site.

4.2.4 Vegetation sampling and community structure calculation

Species abundance was estimated at peak biomass in August from 2000 to 2013. We measured species abundance using the point-quadrat method. From 2000 to 2004, a grid frame (1m × 0.5m) with 36 points was placed once in the center of each subplot. The plant species touched by a pin placed at each point on the grid was recorded as one hit. Beginning in 2005, community assessment was combined with the pin-contact method. Ten pins, 5 cm apart between any adjacent two pins, were held at a 60^{o} angle in a frame placed in each subplot four times (once in each of the four cardinal directions) and pins could be raised within the frame to count hits up to 1 m high. One hit was recorded for each species if they touched any part of the pins and species having no contact with any of the pins was recorded as one hit.

The number of hits in the two subplots under each treatment was summed together before any calculation or statistical analysis. To calculate relative abundance of each species, the number of hits for each species was divided by the total number of hits for all species in the two subplots under each treatment. Species richness (S) was calculated as the total number of plant species in the two subplots. We calculated the Shannon-Weiner diversity index (H') as $H' = -\Sigma p_i * \ln(p_i)$ where p_i is the relative abundance of species i; and evenness (E) as $E = H'/\ln(S)$.

4.2.5 Statistical analysis

We used repeated-measures ANOVA to examine main and interactive effects on soil temperature, soil water content, species richness, diversity, and evenness, with warming and clipping as main effects, year as the repeated factor, and plot pair as a random effect. Linear regressions were performed to explore the relationships between community structure (i.e., species richness, diversity and evenness) and abiotic variables (i.e., soil temperature and soil water content) over time in each treatment and all treatments together. All statistical analyses were conducted using SAS V.8.1 (SAS Institute Inc., Cary, NC, USA).

To examine the effects of the treatments over time on plant community composition, we used a two-way permutational analysis of variance (PERMANOVA) on the Bray Curtis similarity index of species relative abundance, with year, warming and clipping as fixed effects in the model and plot pair as a random effect. The main effects were tested for three time periods: 2000-2013, 2000-2006 and 2007-2013. The same main effects were also tested within each year. A SIMPER (Similarity Percentage) analysis was performed to quantify the contribution of individual species to compositional divergence among the treatments. Principle Coordinates Analysis (PCO) ordination was performed to visualize whole plot composition in a two-dimensional space. Because the first two axes explained the majority of the variation in plot location in multivariate space, we used PCO axis 1 and 2 scores as an index of community composition. The multivariate community analyses PERMANOVA, SIMPER and PCO were performed using PRIMER (version 1.0.3; Plymouth Marine Laboratory, UK).

4.3 Results

4.3.1 Precipitation and soil microclimate

Annual precipitation varied from 515 mm in 2005 which was the driest year in the last 54 years, to 1307 mm in 2007 which was the wettest year in the last 54 years with a mean of 874 mm during the 54 years (Fig. S4.1). There was strong interannual variability in soil temperature and water content (Fig. 4.1; Table 4.1). Experimental warming elevated soil temperature by 1.3 ℃ on average in the unclipped plots and 2.2 ℃ on average in the clipped plots (Fig. 1a, b). Clipping increased soil temperature by 0.5 ℃ and 1.3 ℃ in unwarmed and warmed plots, respectively. Warming decreased soil water content by 1.5% on average across the 14 years, and clipping decreased soil water content by 0.6% on average (Fig. 4.1c, d). Warming did not interact with clipping to impact soil water content (Table 4.1).

Table 4.1 Results of repeated-measures ANOVA (*F* and *P* values) for responses of soil temperature (T_{soil}), soil water content (W_{soil}), species richness (S), Shannon-Weiner diversity index (H’), evenness (E), grass species richness (GR S), forb species richness (Forb S) and legume species richness (LE S) to warming (W), clipping (C), year (Y), and their interactions. Significant results ($P < 0.05$) are bolded.

	df	T_{soil}		W_{soil}		S		H'		E		GR S		Forb S		LE S	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
W	1, 5	132.5	**<0.0001**	42.0	**0.001**	0.9	0.39	0.3	0.60	0.4	0.56	8.8	**0.03**	0.4	0.54	1.0	0.35
C	1, 270	108.1	**<0.0001**	56.7	**<0.0001**	14.2	**0.0002**	1.6	0.21	17.1	**<0.0001**	3.6	0.06	17.3	**<0.0001**	3.4	0.07
W × C	1, 270	7.4	**0.0068**	0.07	0.80	0.2	0.67	1.4	0.24	1.55	0.21	2.6	0.11	0.08	0.78	0.02	0.89
Y	13, 270	2217	**<0.0001**	35.2	**<0.0001**	34.2	**<0.0001**	10.4	**<0.0001**	17.3	**<0.0001**	16.1	**<0.0001**	45.7	**<0.0001**	4.5	**<0.0001**
W × Y	13, 270	1.2	0.28	0.79	0.66	1.77	**0.05**	0.3	1	0.46	0.94	1.2	0.29	1.6	0.09	1.7	0.07
C × Y	13, 270	4.7	**<0.0001**	0.2	1	0.71	0.75	1.9	**0.03**	2.17	**0.01**	0.8	0.69	1.13	0.33	0.7	0.80
W × C × Y	13, 270	2.1	**0.016**	0.08	1	0.14	1.00	1.5	0.11	0.72	0.74	0.4	0.98	0.24	1	1	0.49

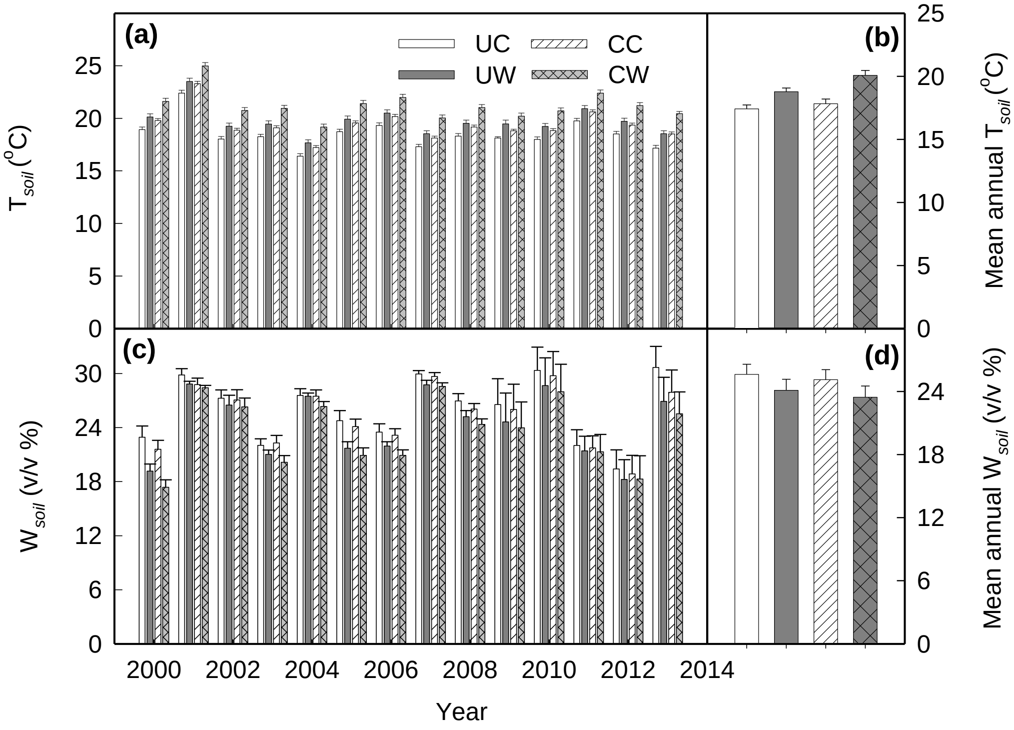


Figure 4.1 Soil temperature at 2.5 cm depth (a, b), and soil water content at ~ 15cm depth (c, d) under the four treatments from 2000 to 2013 (Mean ± 1SE). UC, unclipped

with control (ambient) temperature; UW, unclipped and warmed; CC, clipped with control temperature; CW, clipped and warmed; T_{soil}, soil temperatue; W_{soil}, soil water content.

4.3.2 Species richness, diversity and evenness

The number of species was ca. 10% greater in the clipped plots than in the unclipped plots, whereas no significant difference was found between the warmed and unwarmed plots in most years (Fig. 4.2a, b; Table 4.1). However, in 2007, the wettest year, species richness was 30% more in the unwarmed plots than in the warmed plots. Community diversity and evenness did not respond to warming (Fig. 4.2c-f), whereas clipping tended to decrease evenness (Fig. 4.2e-f). Interactive effects of clipping and year on diversity and evenness were significant. There was strong interannual variability in species richness, diversity and evenness (Fig. 4.2).

Grass, forb, and legume richness differed in their responses to warming and clipping treatments. Grass species richness was 13% higher on average in the unwarmed plots than in the warmed plots, whereas clipping did not yield a significant response (Fig. 4.3a, b; Table 4.1). Forb species richness was 19% greater on average in the clipped plots than in the unclipped ones, whereas warming had no impact (Fig. 4.3c, d). Clipping increased legume richness with marginal significance ($P = 0.07$), whereas warming did not affect legume richness (Fig. 4.3e, f). Warming did not interact with clipping in influencing species richness of any functional group (Table 4.1).

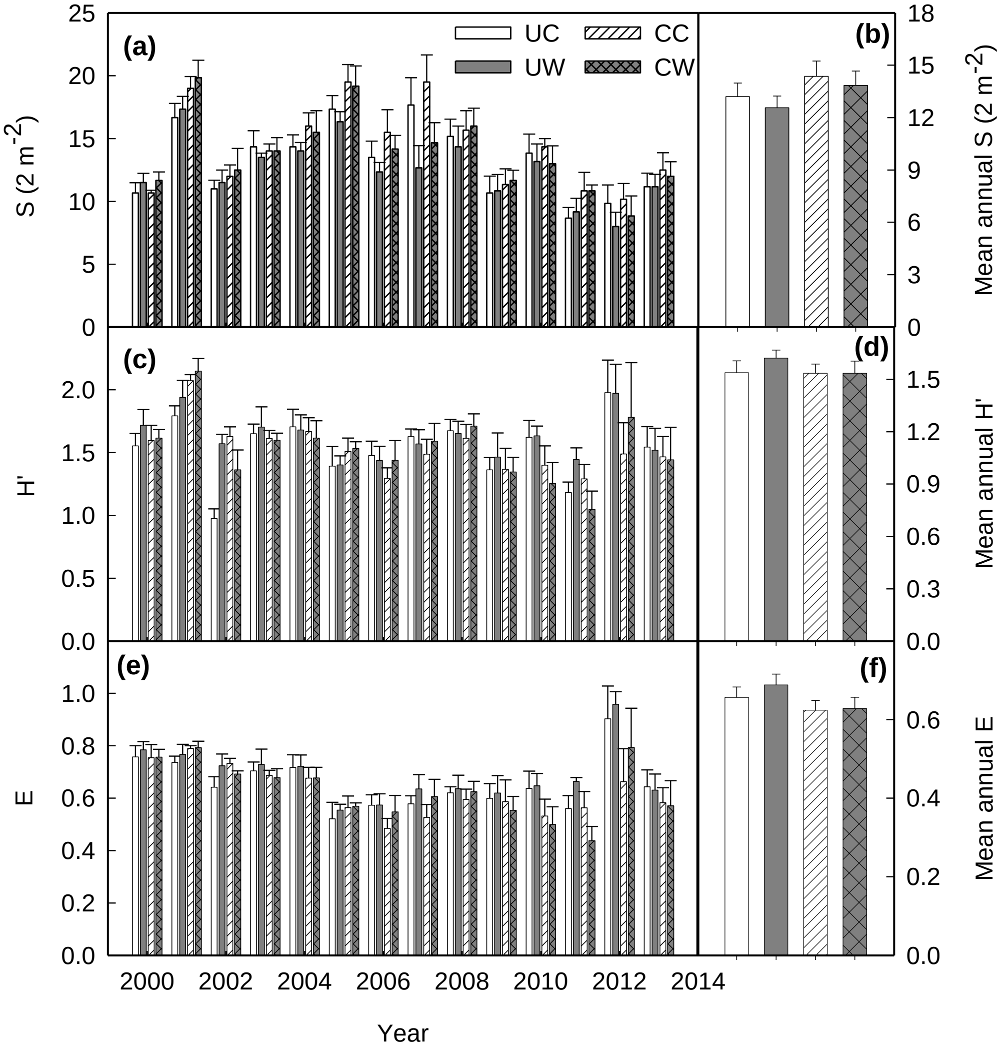


Figure 4.2 Effects of warming and clipping on species richness, S (a, b), Shannon–Wiener diversity index, H’ (c, d) and Pielou’s evenness index, E (e, f) from

2000 to 2013 (Mean ± 1SE). See Figure 1 for treatments abbreviations.

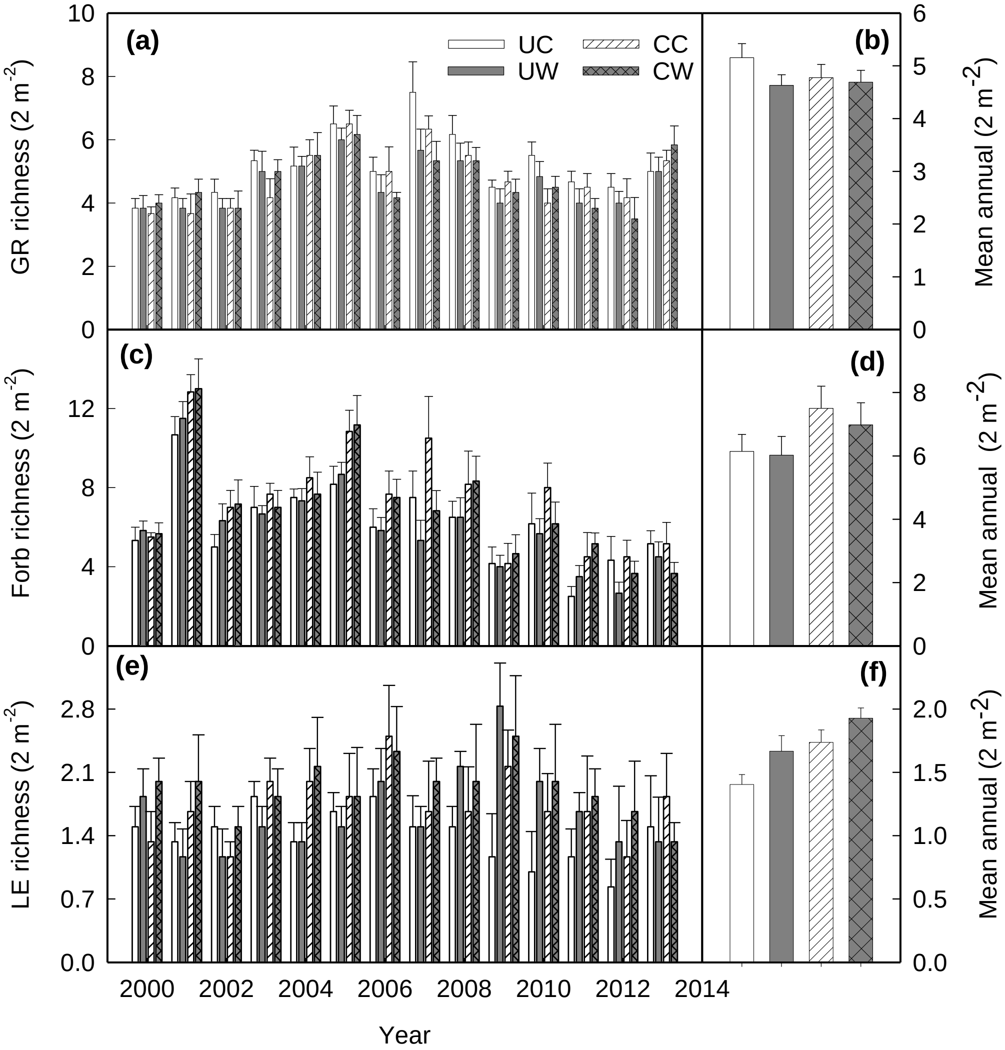


Figure 4.3 Effects of warming and clipping on GR richness (a, b), Forb richness (c, d) and LE richness (e, f) from 2000 to 2013 (Mean ± 1SE). GR, grass; LE, legume. See Figure 1 for treatments abbreviations.

4.3.3 Relationships of interannual variations in community structure with soil microclimate

Soil temperature and soil water content significantly accounted for the interannual variation in species richness across all treatments and years (Fig. 4.4). However, none of the relationships was significant for any individual treatment (Fig. S4.2). Multiple linear regression showed that soil water content was the dominant climatic factor in controlling interannual variation in species richness ($r^2 = 0.18$, $P < 0.01$). Community diversity and evenness did not significantly correlate with soil temperature or soil water content (Fig. S4.3).

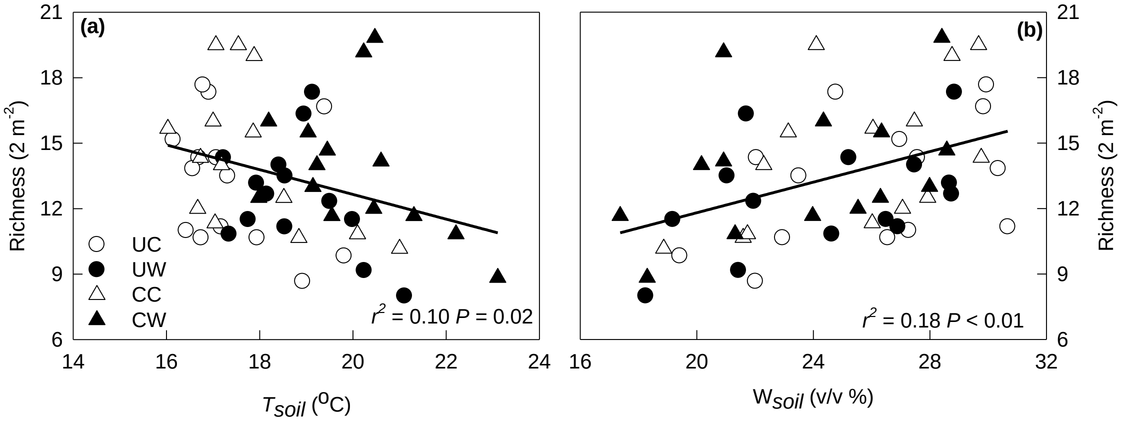


Figure 4.4 Relationships of species richness with soil temperature (a) and soil water content (b) across all treatments from 2000 to 2013. Each point represents mean value in each year under each treatment. See Figure 1 for treatments abbreviations.

4.3.4 Warming and clipping effects on community composition

Warming interacted with year in influencing community composition (Table 4.2) starting in 2007, with marginal significance in 2007 and 2008 (Fig. S4.4). We therefore performed separate analyses for the two study periods, 2000-2006 and 2007-2013. Warming had significant effect on community composition in 2007-2013, but had no impact in 2000-2006 (Fig. 4.5). Clipping and year consistently had significant individual and interactive impacts on community composition (Fig. 4.5). The interactive effect of warming and clipping on composition was significant only in 2011 (Fig. S4.4).

Table 4.2 Results from two-way permutational ANOVA analyses (*F* and *P* values) of the effects of warming (W), clipping (C), year (Y) and their interactions on Bray-Curtis plant community composition within 2000-2013, 2000-2006 and 2007-2013. Significant results ($P < 0.05$) are bolded.

	2000-2013			2000-2006			2007-2013		
	df	Pseudo-*F*	$P_{(perm)}$	df	Pseudo-*F*	$P_{(perm)}$	df	Pseudo-*F*	$P_{(perm)}$
W	1	2.49	0.08	1	0.89	0.52	1	5.44	**0.01**
C	1	6.72	**0.008**	1	3.24	**0.04**	1	6.18	**0.015**
Y	13	9.05	**0.001**	6	7.58	**0.001**	6	6.11	**0.001**
W x C	1	1.04	0.41	1	0.64	0.60	1	2.16	0.14
W x Y	13	3.52	**0.001**	6	0.71	0.87	6	4.81	**0.001**
C x Y	13	2.29	**0.001**	6	2.30	**0.002**	6	2.65	**0.001**
W x C x Y	13	1.22	0.15	6	0.68	0.87	6	1.85	**0.025**

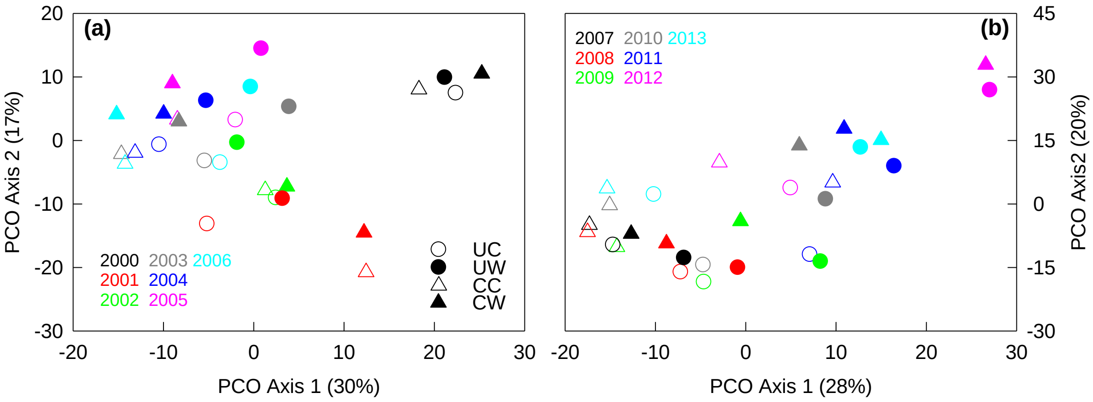
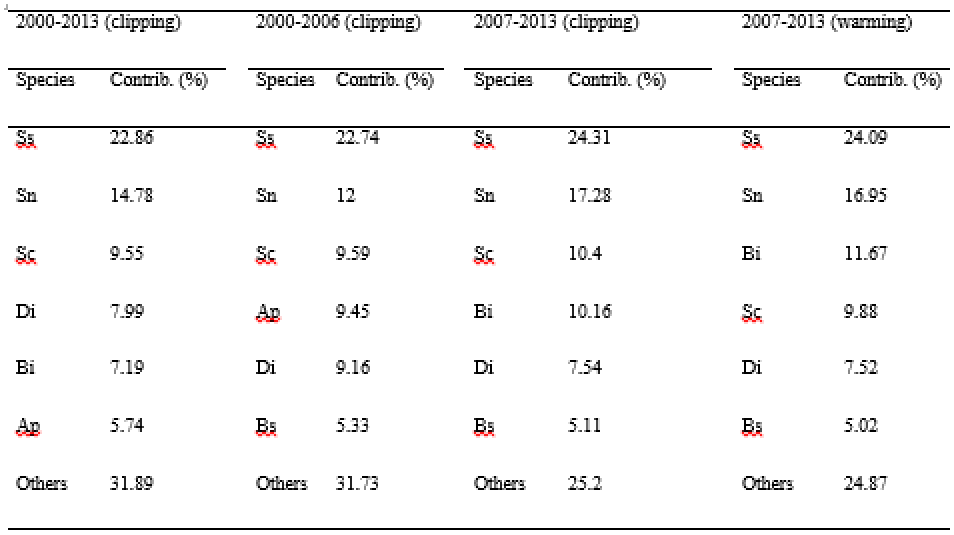


Figure 4.5 Species PCO ordination plots for period 2000-2006 (a) and 2007-2013 (b), with axis 1 and 2 scores. Each point represents mean coordinates under each treatment in each year. Different colors stand for different years. Solid symbols are warmed treatments and empty symbols are unwarmed treatments. Circles are unclipped and triangles are clipped treatments. Error bars are omitted for clarity only. See Fig. S4.6 for PCO ordination plots with error bars.

Seven species contributed 68-75% to the compositional changes under warming or clipping (Table 4.3). The three dominant species, *S. scoparium* (Ss, 40% relative abundance under control, Table S1), *S. nutans* (Sn, 12% relative abundance under control) and *S. compositus* (Sc, 11% relative abundance under control) together with the invasive species, *Bothriochloa ischaemum* (*B. ischaemum*, Bi), contributed more than 60% of the compositional change under warming treatment in 2007-2013 (Table 4.3; Fig. S4.5). The species Ss, Sn and *Sporobolus compositus* together accounted for more than 45% of the compositional change under clipping treatment in 2000-2013, 2000-2006 and 2007-2013 (Table 4.3; Fig. S4.5). Each of the other species (*A.*

psilostachya, Ap; *Bothriochloa saccharoides*, Bs; *Desmanthus illinoensis*, Di) also contributed more than 5% to the community divergence (Table 4.3; Fig. S4.5).

Table 4.3 Percentage contribution (Contrib. %) of different plant species to community divergence between control and treatments (i.e., warming and clipping) based on SIMPER analysis (shown here are species contributing > 5% to divergence). Ap: *Ambrosia psilostachya*; Bi: *Bothriochloa ischaemum*; Bs: *Bothriochloa saccharoides*; Di: *Desmanthus illinoensis*; Ss: *Schizachyrium scoparium*; Sn: *Sorghastrum nutans*; Sc: *Sporobolus compositus*. Note: warming or clipping in the parentheses means community divergence under warming or clipping, respectively.



2000-2013 (clipping)		2000-2006 (clipping)		2007-2013 (clipping)		2007-2013 (warming)	
Species	Contrib. (%)	Species	Contrib. (%)	Species	Contrib. (%)	Species	Contrib. (%)
Ss	22.86	Ss	22.74	Ss	24.31	Ss	24.09
Sn	14.78	Sn	12	Sn	17.28	Sn	16.95
Sc	9.55	Sc	9.59	Sc	10.4	Bi	11.67
Di	7.99	Ap	9.45	Bi	10.16	Sc	9.88
Bi	7.19	Di	9.16	Di	7.54	Di	7.52
Ap	5.74	Bs	5.33	Bs	5.11	Bs	5.02
Others	31.89	Others	31.73	Others	25.2	Others	24.87

Relative abundance of the invasive species (Bi) negatively correlated with the relative abundance of the two dominant species (Ss and Sc) from 2007 to 2013(Fig. 4.6).

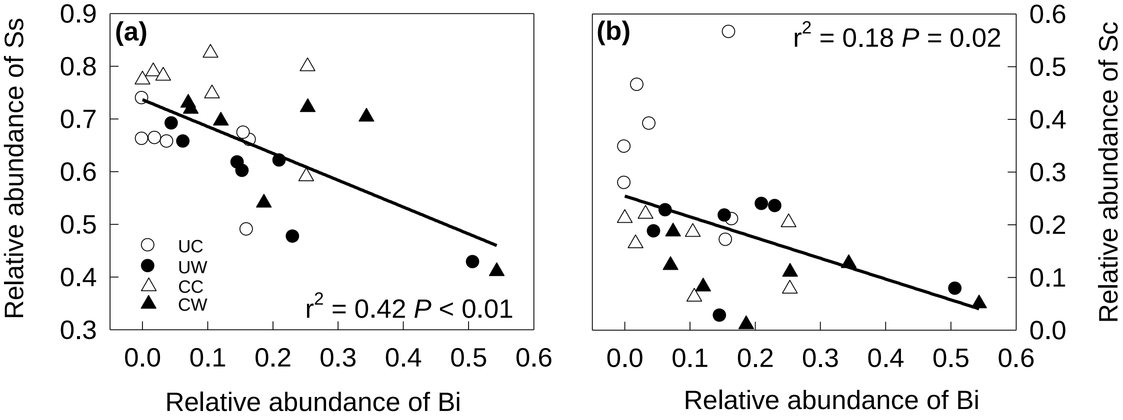


Figure 4.6 The relationships between relative abundance of the invasive species (Bi: *Bothriochloa ischaemum*) and Ss (*Schizachyrium scoparium*) (a) and Sc (*Sporobolus compositus*) (b) from 2007 to 2013. Each point represents mean value in each year under each treatment. See Figure 1 for treatments abbreviations.

4.4 Discussion

4.4.1 Sensitivity of community structure and composition to climate warming

A growing body of literature has demonstrated that climate warming alters plant community structure and composition in cold regions. Elevated temperature increased the cover of deciduous shrubs and graminoids in the Arctic tundra ecosystems (Arft *et al*. 1999; Walker *et al*. 2006) and caused loss of plant species in some critical ecosystems such as alpine meadow and wetlands (Klein, Harte & Zhao 2004; Gedan & Bertness 2009). In temperate grasslands, however, plant communities are rather resistant to increased temperature alone (Zaveleta *et al*. 2003; Harmens *et al.* 2004;

Dukes *et al*. 2005; Grime *et al*. 2008; Kardol *et al*. 2010; Arnone *et al*. 2011; Hoeppner & Dukes 2012; Hoover, Knapp & Smith 2014; White, Bork & Cahill 2014). Most of the experiments were relative short-term, less than five years (but see Grime *et al.* 2008). Resistance of community structure and composition to experimental warming in the first seven years of our study is consistent with previous findings in temperate grasslands.

Background climate variability, dominant species traits, biodiversity and biogeochemistry are often proposed as key factors to define sensitivity of an ecosystem to disturbances (Grime *et al.* 2000; Smith, Knapp & Collins 2009). Tallgrass prairies are exposed to naturally high inter-annual climate variability, but plant species composition remains relatively constant (Knapp *et al.* 1998). C_4 grasses dominated our studied system and are considered well-adapted to heat and drought conditions (Christie & Delting 1982; Seastedt *et al.* 1994). Slow rates of biogeochemical cycling (Wan *et al.* 2005; Zhou, Wan & Luo 2007), low nitrogen content (Niu *et al.* 2010) and relative low productivity in our study site (Luo *et al.* 2009) might also constrain the response of the ecosystem to climatic perturbations. Indeed, previous studies in our site reported low warming effects on soil microclimate (Wan, Luo & Wallace 2002), soil nutrient dynamics (Wan *et al.* 2005) and ecosystem functioning (Zhou, Wan & Luo 2007; Luo *et al.* 2009). The aforementioned factors might together determine the resistance of the plant community in our study site to climate warming within 2000-2006.

The shift from resistance to responsiveness of community composition to warming since 2007 was intriguing. A hierarchical-response framework predicts that chronically altered environment under long-term climate change can induce nonlinear changes in community structure and composition through species reordering and/or species invasion (Smith, Knapp & Collins 2009). In our study, the three dominant C_4 species (*S. scoparium*, *S. nutans* and *S. compositus*) and one invasive species (*B. ischaemum*) contributed the most to the warming-induced changes in community composition since 2007. *S. scoparium* and *S. compositus* showed negative responses to warming. *S. nutans* was generally more abundant in the warmed plots. *B. ischaemum* co-dominated with the other three species in the warmed plots. *B. ischaemum*, a warm-season C_4 grass, is known as an invasive species to the Great Plains prairies (Schmidt *et al.* 2008; Wilson, Hickman & Williamson 2012). Because habitats with highly fluctuating resource availability are susceptible to invasion (Davis *et al.* 2000), the extreme wet year in 2007 likely facilitated the invasion of *B.ischaemum* in the chronically altered environment by warming. The negative responses of *S. scoparium* and *S. compositus* to warming may partly be caused by the inter-specific competition with the invasive species, which is suggested by the negative correlations in the relative abundance between *B. ischaemum* and *S. scoparium* and *S. compositus*.

Multiple linear regression showed that soil moisture was the controlling factor for interannual variation in species richness across all treatments in our study site. Therefore, we expected that warming would decrease species richness due to its negative effect on soil water content. Surprisingly, warming did not cause any loss in total species richness in most years due possibly to the limited reduction (ca. 2%) in soil water content by warming. However, significant reduction (ca. 30%) in species richness occurred in the warmed plots relative to the unwarmed plots in 2007, the extreme wet year, suggesting interaction between long-term warming and natural disturbances.

Reduction in species richness in 2007 likely came from increased competition due to increased biomass and decreased light, which were probably triggered by increased available nitrogen in the extreme wet year, not by decreased soil water content.

4.4.2 Sensitivity of community structure and composition to clipping

In our study, clipping had significant effects on community composition in most years. We expected clipping to have greater impact on community structure and composition with time. Because removing all clipped plant materials including inflorescence could have cumulative effects on soil fertility and plant reproduction, long-term clipping might have pronounced effects with time. In contrast to our expectation, the responses of plant community composition to clipping differed little between the short term and the long term. Three dominant species (*S. scoparium*, *S. nutans* and *S. compositus*) consistently contributed the most to the compositional change under clipping over time. Clipping generally favored the most dominant species (*S. scoparium*) and suppressed the two subdominant species (*S. nutans* and *S. compositus*). The long-term aboveground biomass data can indirectly support that clipping did not have cumulative effects on soil fertility as aboveground biomass did not decrease with time in the clipped plots (Luo *et al.* 2009; Niu *et al.* 2010).

Our finding that clipping increased species richness has been widely recognized (Foster & Gross 1998; Collins *et al.* 1998; Klein, Harte & Zhao 2004; Yang *et al.* 2012). Increase in species richness by clipping is often attributed to alleviated interspecific competition (Koerner *et al.* 2014) and decreased litter accumulation, which increases ground-level light availability in a variety of grassland ecosystems (Borer *et* *al.* 2014). In our study site, harvesting the plants without returning significantly reduced litter accumulation (Cheng *et al.* 2010). Additionally, clipping-stimulated species richness in our study was by enhancing number of forb species, also consistent with previous findings (Harmens *et al.* 2004; Yang *et al.* 2012).

4.2.3 Sensitivity of community structure and composition to warming and clipping interaction

We expected significant interactive effects between warming and clipping on community structure and composition for at least two reasons. Firstly, warming and clipping interacted to influence soil temperature. The interactive effect on soil microclimate could propagate into plant community. Secondly, clipping was expected to have cumulative effect on soil fertility, which could alter community responses to warming. However, our analysis showed that the interaction between warming and clipping on composition was significant only in 2011, suggesting for the majority of the study, their effects were additive rather than interactive. We have argued that clipping did not have cumulative effect on soil fertility. The interactive effect of warming and clipping on soil temperature was likely too small to affect the plant community. A synthesis of global change experiments also showed that there were usually few interactions between global changing factors and land management in temperate grassland communities (White, Bork & Cahill 2012).

In summary, the study provides direct experimental evidence for long-term shifts in prairie community composition under warming and reveals the underlying mechanisms (i.e., species invasion and associated biotic interactions). The findings also suggest that possible interactions of long-term warming and natural disturbances likely elicit or accelerate community responses. As extreme precipitation events have been predicted to occur more often (IPCC, 2013), the interactions could pose a great threat to plant communities in grassland ecosystems. Our analyses showed that the community structure (i.e., species richness, diversity and evenness) of a tallgrass prairie was resistant to long-term warming. However, warming significantly decreased species richness in an extremely wet year, which indicates possible interactions between warming and extreme events. Community structure and composition showed significant responses to clipping, but the responses differed little between short term and long term. Altogether, our findings support that plant community in temperate grassland is rather resistant to climate warming, but further reveal that grasslands can become susceptible to species invasion under long-term climate change.

Supplementary materials

Table S4.1 List of common species (occurred in at least six times among the plot-years) in the experimental site across the 14 years

Functional groups	Species	Abbreviation	LHT	PP	Relative abundance (%)
Forb	*Ambrosia psilostachya*	Ap	P	C3	3
	Amphiachyris dracunculoides	Ad	A	C3	-
	Asclepias arenaria	Aa	P	C3	-
	Buchnera americana	Ba	P	C3	-
	Calyophus serrulatus	Cs	P	C3	-
	Croton glandulosus	Cg	A	C3	-

	Diodia teres	Dt	A	C3	-
	Erigeron strigosus	Es	B	C3	-
	Euphorbia dentata	Ed	A	C3	-
	Gaillardia aestivalis	Ga	A	C3	-
	Hedeoma hispida	Hh	A	C3	-
	Hedyotis nigricans	Hn	P	C3	-
	Liatris squarrosa	Ls	P	C3	-
	Ratibida columnifera	Rc	P	C3	-
	Ruellia humilis	Rh	P	C3	-
	Solidago ludoviciana	Sl	P	C3	-
	Solidago nemoralis	Sne	P	C3	-
	Solidago rigida	Sr	P	C3	-
	Stenosiphon linifolius	Sli	P	C3	-
	Symphyotrichum ericoides	Se	P	C3	-
	Tragia betonicifolia	Tb	P	C3	-
Grass	*Aristida oligantha*	Ao	A	C4	-
	Bothriochloa ischaemum	Bi	P	C4	1
	Bothriochloa saccharoides	Bs	P	C4	2
	Dichanthelium oligosanthes	Do	P	C3	-
	Elymus canadensis	Ec	P	C3	-
	Eragrostis trichodes	Et	P	C4	-
	Panicum capillare	Pc	P	C4	-
	Panicum virgatum	Pv	P	C4	-
	Schizachyrium scoparium	Ss	P	C4	40
	Scleria ciliata	Sci	P	C4	-
	Sorghastrum nutans	Sn	P	C4	12
	Sporobolus compositus	Sc	P	C4	11
Legume	*Chamaecrista fasciculata*	Cf	A	C3	-
	Dalea candida	Dc	P	C3	-
	Dalea purpurea	Dp	P	C3	-
	Desmanthus illinoensis	Di	P	C3	7
	Melilotus alba	Ma	A	C3	-
	Mimosa nuttallii	Mn	P	C3	-
	Psoralidium tenuiflorum	Pt	P	C3	-

LHT: life history; PP: photosynthetic pathway; A: annual; B: biennial; P: perennial. “-” means the relative abundance less than 1%.

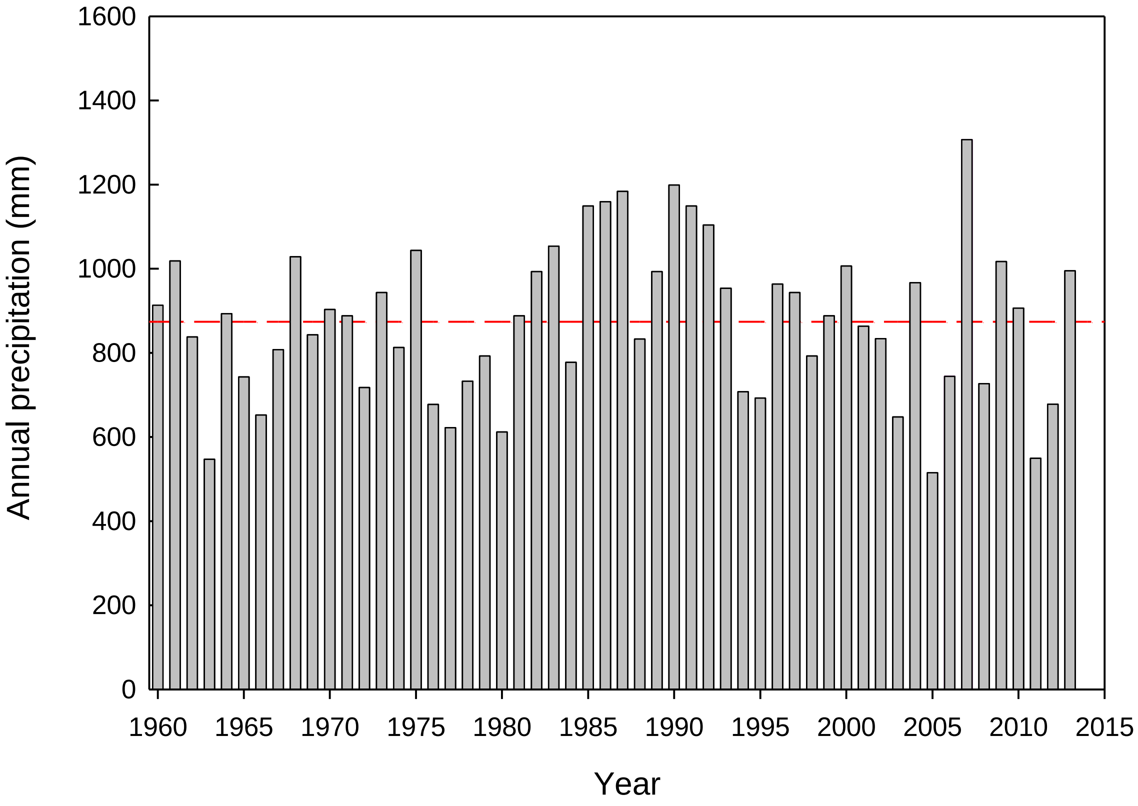


Figure S4.1 Annual precipitation from 1960 to 2014. The red dashed line represents the mean annual precipitation (874 mm) of the 54 years. The 54 years of precipitation data was obtained from the Oklahoma Climate Survey (http://climate.ok.gov/cgi-bin/public/climate.timeseries.one.cgi) from 1960 to 1993 and an Oklahoma Mesonet Station (Washington Station, 200 m away from the study site) from 1994 to 2013.

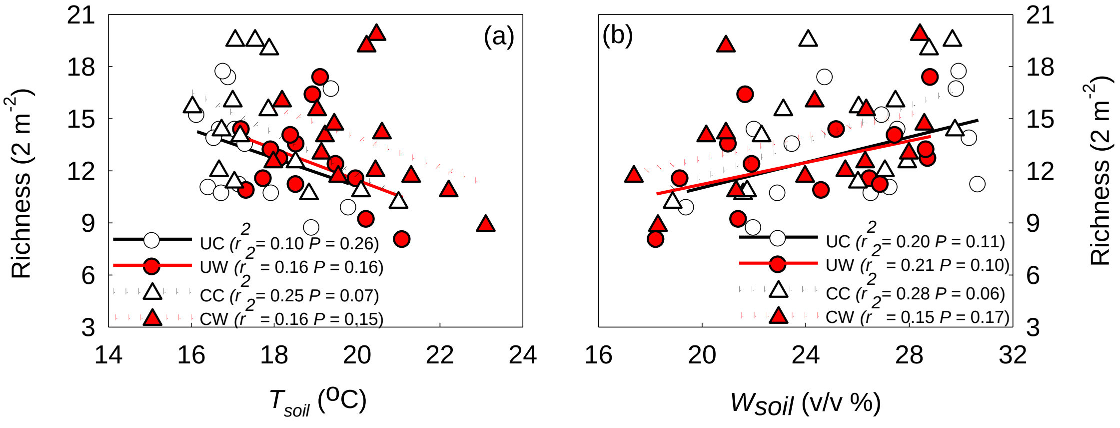


Figure S4.2 Relationships of species richness with soil temperature (a) and soil water content (b) under each treatment from 2000 to 2013. Each point represents mean value in each year under each treatment. T_{soil}, soil temperatue; W_{soil}, soil water content.

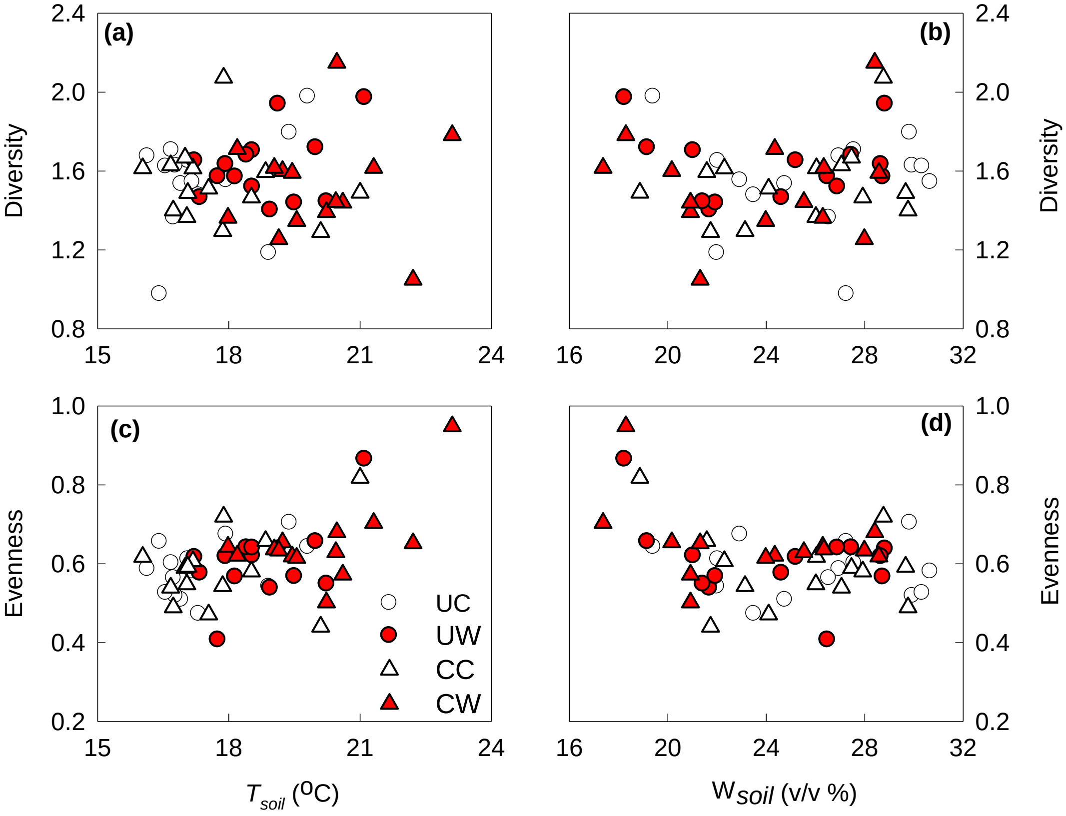


Figure S4.3 Relationships of community diversity and evenness with soil temperature (a, c) and soil water content (b, d) under each treatment from 2000 to 2013. Each point represents mean value in each year under each treatment. T_{soil}, soil temperatue; W_{soil}, soil water content.

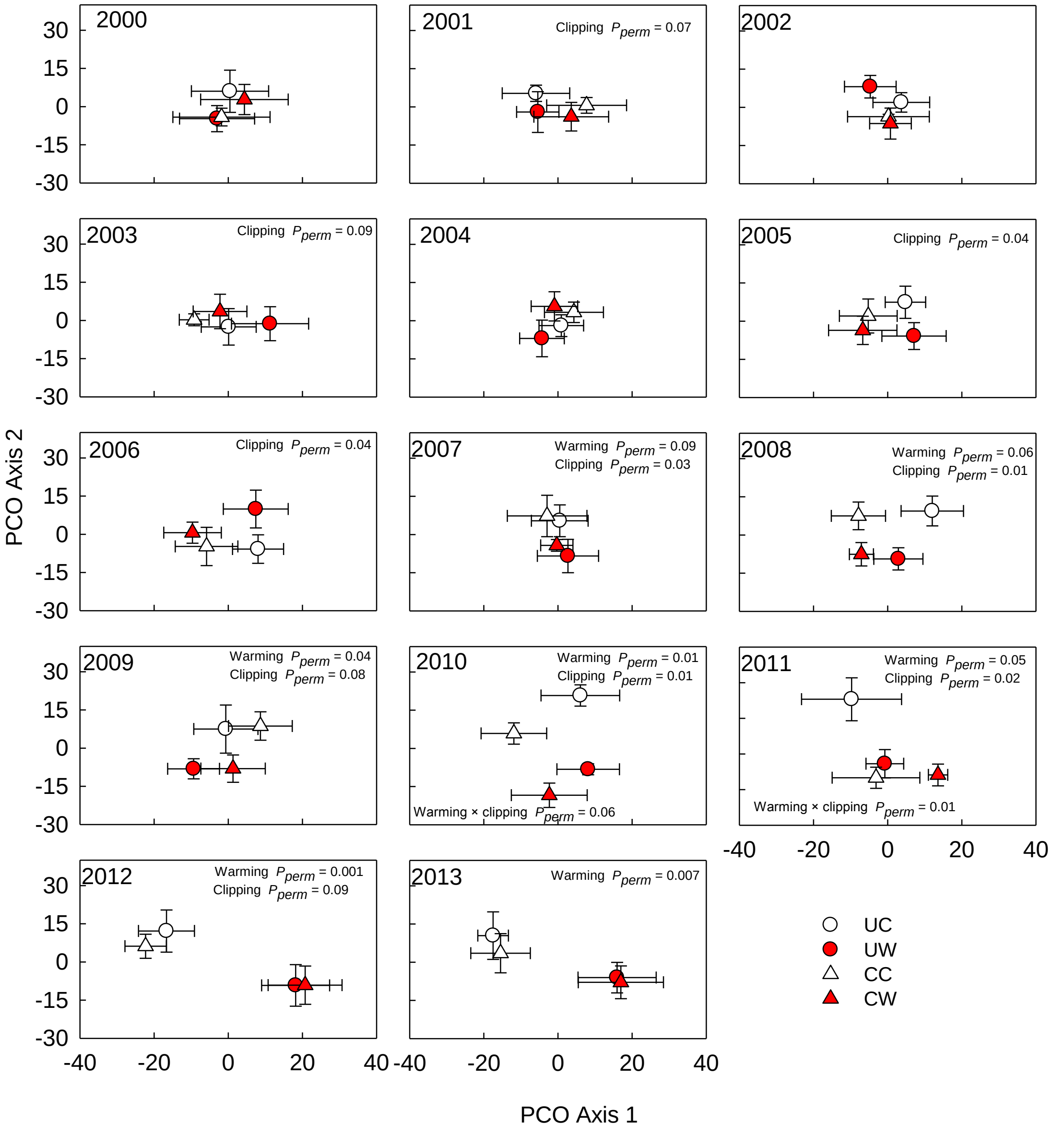


Figure S4.4 Species PCO ordination plots within each year from 2000 to 2013, with axis 1 and 2 scores. Individual and interactive effects of the treatments are noted, where significance level less than 0.1 in the PERMANOVA.

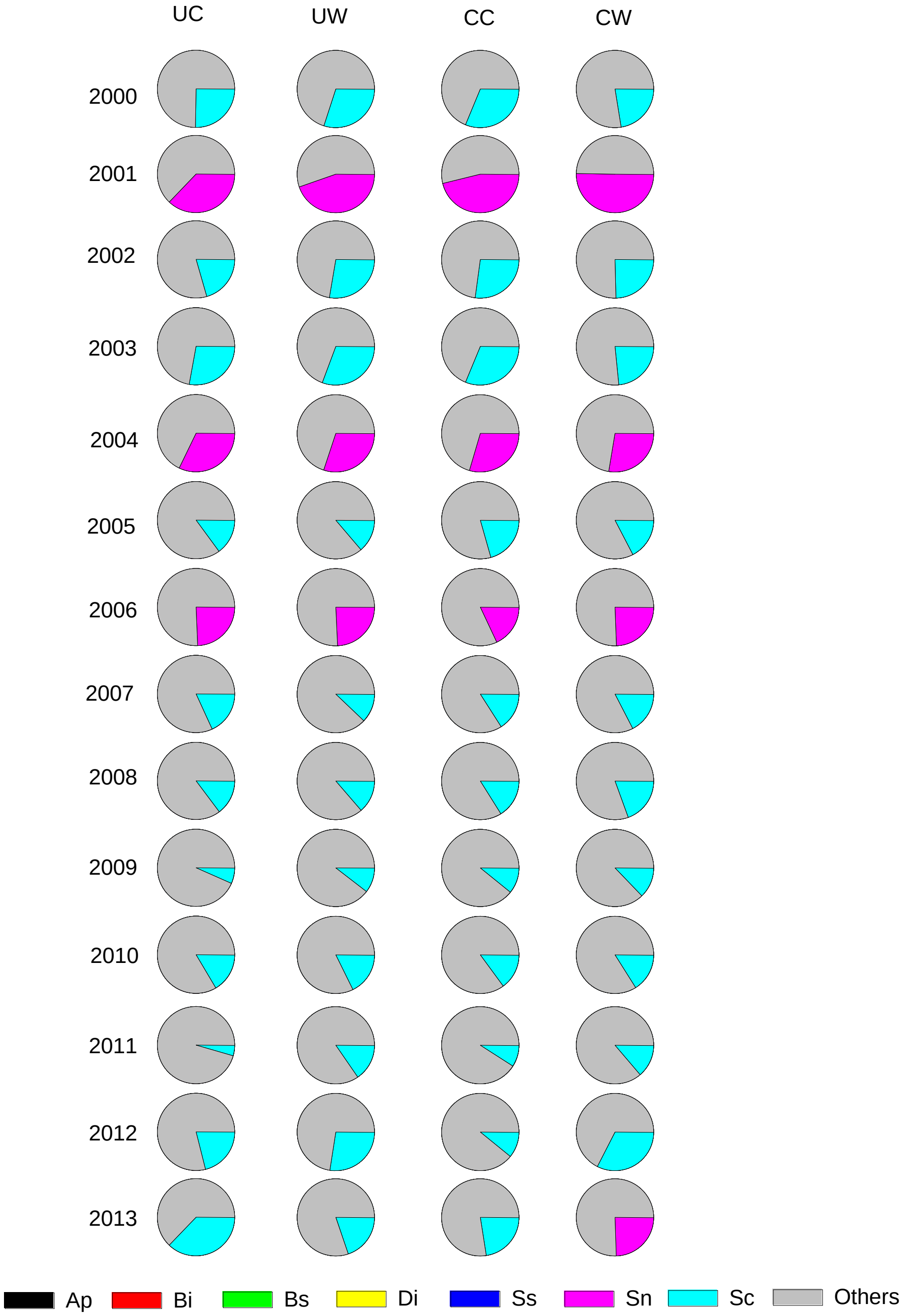


Figure S4.5 Temporal dynamics in species composition from 2000 to 2013 under each treatment. Ap: *Ambrosia psilostachya*; Bi: *Bothriochloa ischaemum*; Bs: *Bothriochloa saccharoides*; Di: *Desmanthus illinoensis*; Ss: *Schizachyrium scoparium*; Sn: *Sorghastrum nutans*; Sc: *Sporobolus compositus*.

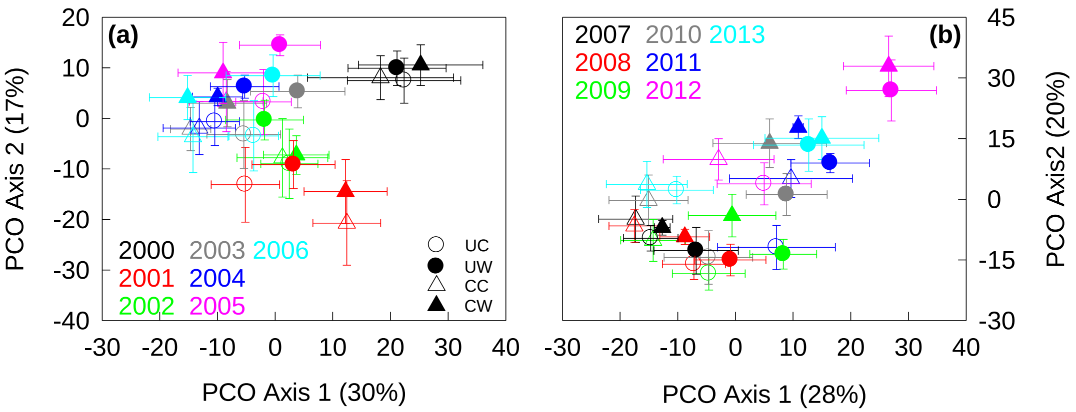


Figure S4.6 Species PCO ordination plots for period 2000-2006 (a) and 2007-2013 (b), with axis 1 and 2 scores. Each point represents mean coordinates ±SE under each treatment in each year. Different colors stand for different years. Solid symbols are warmed treatments and empty symbols are unwarmed treatments. Circles are unclipped and triangles are clipped treatments.

Chapter 5 Experimental warming altered rates of carbon processes, allocation, and carbon storage in a tallgrass prairie: A data assimilation approach [2]

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[2] This part has been accepted by Ecosphere.

Abstract

Climate warming affects ecosystem functioning by altering the rates of carbon (C) fixation and release. Modeling warming effect on terrestrial C cycling is critical given the feedbacks between climate and C cycling. However, the effect of warming on key model parameters and the resulting long-term C dynamics has not been carefully examined. In this study, measurements from a nine-year warming experimental site in a tallgrass prairie were assimilated into a terrestrial ecosystem C cycle model to assess warming effect on key model parameters and to quantify uncertainties of long-term C projection. Warming decreased allocation of gross primary production (GPP) to shoot, and turnover rate of the live C pools (i.e., shoot and root C), but increased the turnover rates of litter and fast soil C pools. Consequently, warming increased live C pools, but decreased litter and soil C pools, and overall decreased total ecosystem C in a 90-year model projection. Information content gained from assimilated datasets was much greater for plant, litter and fast soil C pools than for slow and passive soil C pools. Sensitivity analysis revealed that fast turnover C pools were most sensitive to their turnover rates and modest to C-input related parameters on both short-term and long-term time scales. However, slow turnover C pools were sensitive to turnover rate and C input in long-term prediction, not in short-term prediction. As a result , total soil and ecosystem C pools were generally insensitive to any parameter in short term, but determined by turnover rates of the fast, slow and passive soil C and transfer coefficients from upstream C to slow and passive C pools. Our findings suggest that data assimilation is an effective tool to explore the effect of warming on C dynamics; the nine-year field data contribute more information for the fast C processes than for the

slow C processes ; and C cycle model parameters change with warming, and models need to account for that phenomenon not to produce bias in C projections. However, warming-induced changes in parameter values also suggest that some important ecosystem processes may be missing or not adequately represented in the ecosystem C models.

5.1 Introduction

Global mean temperature has increased by 0.85 ^{o}C since 1880s and is predicted to continue rising over the 21st Century (IPCC, 2013). Numerous field experiments showed prompt ecosystem responses to climate warming (e.g., Harte and Shaw 1995, Hobbie and Chapin, 1998, Luo et al. 2001b, Mellilo et al. 2002, Dukes et al. 2005, Grime et al. 2008, Niu et al. 2013). Warming often enhance both ecosystem C influx and effluxes, such as plant growth and soil respiration (Rustad et al., 2001; Wu et al., 2011; Lu et al., 2013). Many ecosystem C cycle models were designed to predict warming effect on ecosystem C uptake through photosynthesis and release via plant and soil respiration (Parton et al. 2007, Luo et al. 2008). However, there is often great divergence in predictions among models (Norby and Luo 2004, De Kauwe et al. 2013). To simulate future states of ecosystems and climate realistically, it is essential to carefully examine how climate warming affects the mechanisms of C cycling.

Global C cycle models predict positive feedback to climate warming (Cox et al. 2000, Cramer et al. 2001). However, field experiments and observations suggest negative or neutral feedback (Welker et al., 2004, Giardina et al. 2014). In addition, most recent meta-analyses by Wu et al. (2011) and Lu et al. (2013) showed neutral feedback of terrestrial ecosystems to increased temperature due to the compensation of warming-enhanced C uptake with warming-induced increases in C effluxes. The disparity between model results and empirical studies could partly stem from inadequate model parameterization, because the models assume that parameter values are scenario-invariant constants. Additionally, assessing uncertainties associated with model parameters and predictions is critical for accurate projections (Braswell et al., 2005; Xiao et al., 2011; Xiao et al., 2014). Therefore, it is necessary to calibrate model parameters against observations to improve model performance and gain insights into changes in mechanisms of C cycling.

Data assimilation is a statistical method that allows incorporating multi-sourced convoluted measurements into ecological models, constraining model parameters, and quantifying uncertainties of model parameters and predictions. For example, Braswell et al., (2005) used daily and seasonal eddy flux data from Harvard forest to estimate parameters in an ecosystem C flux model (SIPNET). The better fitting between model output and observations demonstrated the effectiveness of the model-data integration. By assimilating soil respiration and biometric C data from Duke Forest, Xu et al., (2006) applied probabilistic inversion to quantify uncertainties of model parameters and predicted carbon pool dynamics in ambient and elevated CO_2 treatments. They found significant difference in extracted parameter values under the two treatments and large uncertainties associated with residence time of the passive C pool. Wang et al., (2007) estimated parameters in a land surface model using multiple eddy flux datasets and found good agreement between constrained parameter values and independent estimates. Weng et al., (2011) quantified uncertainties contributed by model only and model and data together to short- and long-term predictions and concluded that uncertainties introduced by model and data varied with forecasting time and C pools. Keenan et al., (2013) evaluated information content from 17 datasets and found that many datasets were redundant in terms of providing information content. Overall, previous research showed that data assimilation was an effective tool to estimate parameter values and uncertainties.

Long-term warming experiment in a tallgrass prairie in central Oklahoma, USA, has been conducted since 1999 (Luo et al. 2001b, Niu et al. 2010). In this study, C stocks and fluxes collected from 2000 to 2008 under ambient and warming conditions were assimilated into an ecosystem C model (Weng and Luo 2008) to constrain its parameters and make model projection of the long-term carbon dynamics. Specifically, we explored how warming changed the mechanisms of C cycling by testing whether warming had an effect on key model parameters such as turnover rate and transfer coefficients, and investigated warming effect on long-term projections for C pools. Lastly, we examined the sensitivities of both short-term and long-term projections to model parameters.

5.2 Methods

5.2.1 The TECO model

The Terrestrial ECOsystem (TECO) model is a CENTURY-type C pool and flux model that is used to simulate ecosystem C dynamics under various climatic conditions (Weng and Luo 2008, Luo et al. 2008, De Kauwe et al. 2013). TECO has been used to assimilate observations from forest ecosystems (Xu et al. 2006, Weng and Luo 2011). Here, we modified TECO model to represent grassland ecosystems by partitioning newly fixed C between plant shoots and roots and combining metabolic and structural litter pools into a one litter pool (Fig. 5.1). Soil C pool in the TECO model consists of fast, slow and passive pools and was left unchanged. Carbon dynamics in the TECO model can be described by the following first-order differential equation:

$$\begin{aligned} \frac{dX(t)}{dt} &= \xi(t)ACX(t) + BU(t) \\ X(0) &= X_0 \end{aligned} \tag{1}$$

where A is a 6×6 matrix describing carbon transfers among the pools as illustrated by arrows in Fig. 1.

$$A = \begin{pmatrix} -1 & 0 & 0 & 0 & 0 & 0 \\ 0 & -1 & 0 & 0 & 0 & 0 \\ 1 & 1 & -1 & 0 & 0 & 0 \\ 0 & 0 & f_{43} & -1 & f_{45} & f_{46} \\ 0 & 0 & f_{53} & f_{54} & -1 & 0 \\ 0 & 0 & 0 & f_{64} & f_{65} & -1 \end{pmatrix} \tag{2}$$

The f_{ij}'s in matrix A (eq. 2) represent the fractions of carbon entering i^{th} pool from j^{th} pool, termed transfer coefficients. C is a 6×6 diagonal matrix, with its elements representing fractions of pools that leave the pools in a day, termed turnover rate:

$$C = \begin{pmatrix} c_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & c_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & c_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & c_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & c_5 & 0 \\ 0 & 0 & 0 & 0 & 0 & c_6 \end{pmatrix} \qquad (3)$$

$X(t) = (X_1(t) \quad X_2(t) \quad X_3(t) \quad X_4(t) \quad X_5(t) \quad X_6(t))^T$ is a 6×1 vector representing the carbon content of six carbon pools at time t. X_0 is the initial values for X(t) at time 0. $X_0 = (0\ 150\ 200\ 100\ 1350\ 300)^T$ estimated from experimental data when the experiment was set up. B is a vector of allocation coefficients partitioning newly fixed C among the two live pools (shoots and roots). U(t) is the carbon input (i.e., GPP) at time t. $\xi(t)$ is is an environmental scalar, depending on air temperature (T) and soil moisture (W):

$$\xi(t) = F_T(t) \bullet F_W(t) \qquad (4)$$

$F_T(t)$ represents temperature effects calculated as $F_T(t) = R_{10}\, Q_{10}^{(T(t)-10)/10}$ and $F_W(t)$ represents the effects of soil water content calculated as $F_W(t) = 5W(t)$ when $W(t) < 0.2$ or $F_W(t) = 1$ when $W(t) \geq 0.2$.

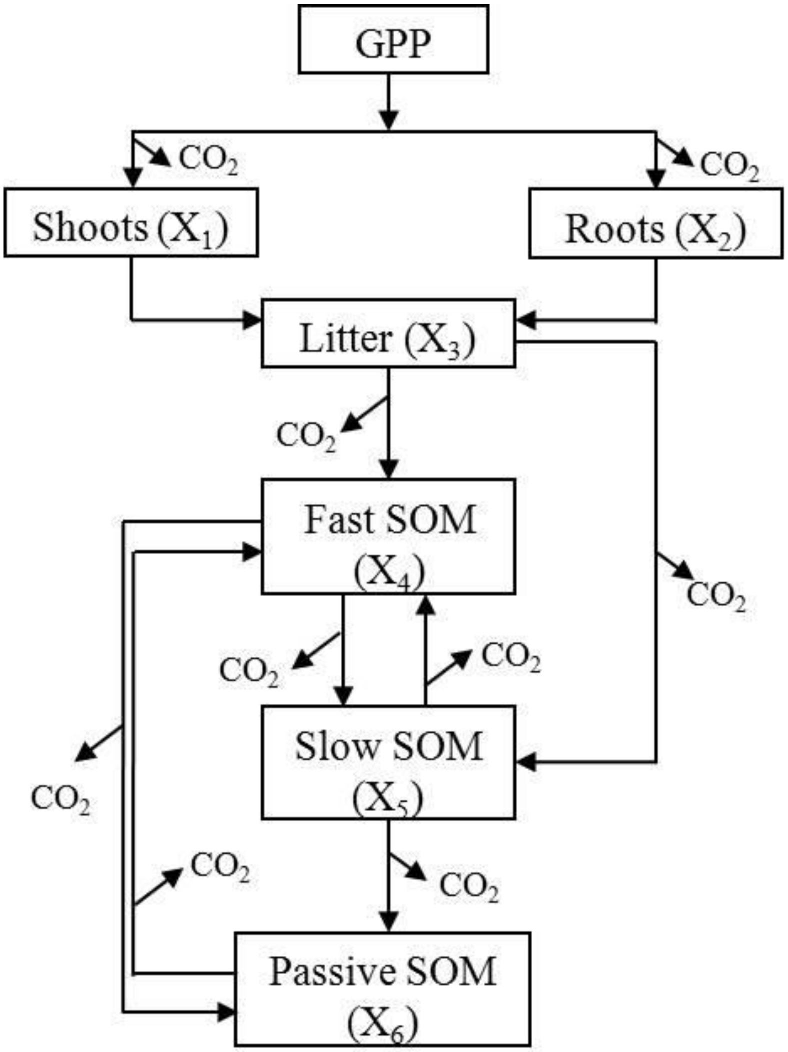


Figure 5.1 Model structure with carbon pools (X_1-X_6) and fluxes in a grassland ecosystem. SOM stands for soil organic matter; GPP stands for gross primary productivity. Arrows show directions of carbon transfer.

5.2.2 Data sources

We assimilated six data sets collected from a tallgrass prairie in central Oklahoma (34°59’N, 97°31’W) into the TECO model, including soil respiration, heterotrophic respiration, aboveground biomass, root biomass, labile soil carbon and total soil carbon. We used the data collected from both control and warming conditions from 2000 to 2008. We also manipulated hay harvest in the studied system. However, we did not use any data from the clipped plots.

Data on soil respiration have been collected once or twice a month since 2000 and on heterotrophic respiration since October 2001 (Zhou et al. 2007). Aboveground biomass and belowground net primary productivity (BNPP) were collected once a year from 2000 to 2008 (Niu et al., 2010). Root biomass was calculated from BNPP and a root turnover rate (Luo et al. 2009b). Labile and soil carbon were collected yearly from 2000 to 2008 (Xu et al. 2012).

We used air temperature, soil moisture, and GPP for the period of 2000–2008 as input data to drive the TECO model. Air temperature and soil water content were observed in the experimental plots, and daily values of GPP were derived from TECO photosynthesis sub-model (Fig. S1). Long-term (i.e., 90 years) projection and associated uncertainties were generated by cycling through 2000-2008 forcing data (air temperature, soil moisture and GPP) using 10000 sets of accepted parameters.

5.2.3 Data assimilation

We estimated a total of 17 model parameters: two allocation coefficients (b_i), six turnover rates (C_i) the inverses of which were residence or turnover times, seven transfer coefficients ($f_{i,j}$) and two parameters for environmental scalar (R_{10} and Q_{10}). Prior ranges of the 17 parameters (Table 1) were set based on published papers. The prior ranges of b_i’s were based on Hui and Robertson (2006), prior ranges of c_i’s and

f_{ij}'s were based on Weng and Luo (2011) and Zhou et al. (2010). We assumed that the parameters were distributed uniformly within their prior ranges.

We applied Bayes' theorem (equation 5) to estimate parameter values and associated uncertainties (Xu et al. 2006, Weng and Luo 2011).

$$p(\theta|Z) = \frac{p(Z|\theta)p(\theta)}{p(Z)} \qquad (5)$$

where, $p(\theta|Z)$ is the posterior distribution of the parameters θ given the observations Z. $p(Z|\theta)$ is a likelihood function calculated with the assumption that each component is independent from all other components and has Gaussian distribution with a zero mean:

$$P(Z|\theta) \propto exp\left\{-\sum_{i=1}^{6}\sum_{t\in obs(Z_i)}\frac{[Z_i(t)-\emptyset_i X(t)]^2}{2\sigma_i^2(t)}\right\} \qquad (6)$$

where, Z(t) is observation and i represents ith data set, X(t) are the six carbon pools at time t, and $\emptyset$ is the mapping vector that maps the simulated carbon pools to observations. For aboveground biomass $\emptyset_1$ = (1 0 0 0 0 0); for root biomass: $\emptyset_2$ = (0 1 0 0 0 0), for heterotrophic respiration $\emptyset_3$ = (0 0 1-f_{43}-f_{53} 1-f_{64}-f_{54} 1-f_{45}-f_{65} 1-f_{46}); the component of autotrophic respiration: Ra = 0.25 ·(1-b_1-b_2) ·GPP(t), and total soil respiration is the sum of Ra and Rh; labile carbon was mapped as $\emptyset_4$ = (0 0 0 1 0 0), and total soil carbon was mapped as $\emptyset_5$ = (0 0 0 1 1 1).

$p(\theta)$ was a set of uniform distributions over the ranges specified in Table 1, and $p(Z)$ was the probability distribution function of observations.

Posterior probability distributions of parameters were obtained using a Metropolis-Hastings (M-H) algorithm, a Markov Chain Monte Carlo (MCMC) technique (Metropolis et al. 1953, Hastings 1970). The detailed description of M-H algorithm can be found in Xu et al. (2006). In brief, the M-H algorithm repeated two steps: a proposing step and a moving step. In the proposing step, a new parameter set θ^{new} was generated based on the previously accepted parameter set θ^{old} and a proposal distribution, which was uniform in our study:

$$\theta^{new} = \theta^{old} + r(\theta_{max} - \theta_{min})/D \qquad (7)$$

where θ_{max} and θ_{min} are the maximum and minimum values of parameters, r is a random variable between -0.5 and 0.5, and D is used to control the proposing step size and was set to 5 as is Xu et al. (2006). In each moving step, θ^{new} was tested against the Metropolis criterion to examine if the new parameter set should be accepted or rejected. The first 2500 accepted samples were discarded (burn-in period) and the rest were used to generate posterior parameter distributions. To test for convergence of posterior parameter estimates, we ran the M-H algorithm four times, generating four chains with 100,000 parameter samples and tested the chains with Gelman-Rubin diagnostics (Gelman and Rubin 1992).

5.2.4 Data analysis

Maximum likelihood estimates (MLEs) were calculated when parameters were well constrained. The mean values were calculated when parameters were not constrained. MLEs were estimated by observing the value with greatest frequency.

We used Shannon information index (Shannon 1948) to quantify information content contributed by observations for each projected C pool:

$$H(X) = -\sum p(x_i) \log_b p(x_i) \qquad (8)$$

where $p(x_i)$ is the probability of a pool size x_i. Parameter b equals 2, and units of information content were bits. Information gain was calculated as the difference in information content of each C pool before and after data assimilation. The relative information gain was the relative difference in information content before and after assimilation of the observations.

Data collected in the field are often not sufficient to constrain some of the counteracting processes in a C cycle model (Ricciuto et al. 2011). As a consequence, model parameters which control the counteracting processes are likely to correlate with each other. Therefore, in addition to analyzing the information content in the observations, we analyzed the correlations between posterior parameter estimates.

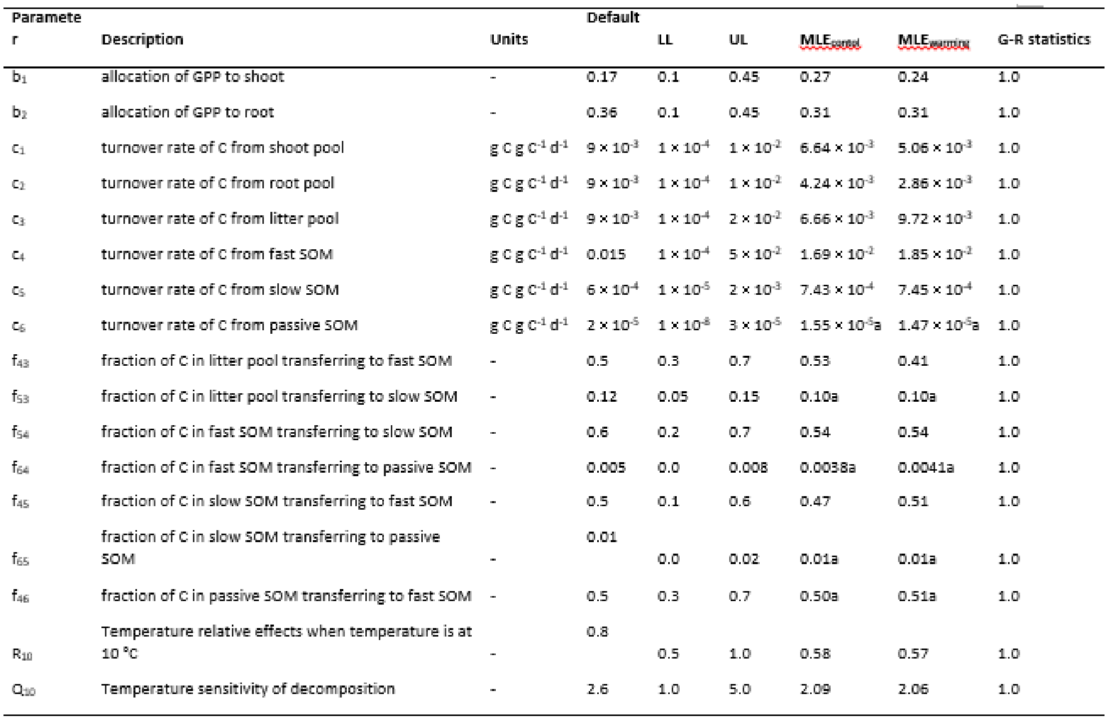
To characterize the sensitivity of C pools to model parameters we calculated the coefficients of determination (R^2) between the projected C pool sizes and the model parameters and used them as a measure of sensitivity of C pools to the parameters (Weng and Luo 2011). C pool sizes at different projected timescales might be sensitive to different model parameters (Weng and Luo 2011). Thus, we analyzed the sensitivity of each projected C pool at the end of ninth year (i.e., short term) and 90th year (i.e., long term) to each of the 17 parameters.

5.3 Results

5.3.1 Parameter constraint and variability with warming

After assimilating the experimental data, uncertainties in many TECO model parameters were significantly reduced, with the exceptions of turnover rate of passive C (c_6) and most of the transfer coefficients (e.g., f53, f64, f65 and f46, Fig. 5.2). A maximum likelihood estimate (MLE) was calculated for each of the well constrained parameters, while a mean value was calculated for the poorly constrained parameter (Table 5.1). MLEs for C allocation to leaves (b_1), turnover rates of leaves and roots, (c_1 and c_2) and partitioning from roots to litter pool (f_{43}) were greater in the warming treatment than in the control condition; whereas the MLEs for the turnover rates of litter and labile C (c_3 and c_4) was greater in the warming treatment; MLEs for the other parameters were similar between the two conditions (Fig. 5.2 and Table 5.1).

Table 5.1 Model parameters and default values in TECO, prior ranges, maximum likelihood estimates (MLE) and Gelman-Rubin (G-R) statistics



Parameter	Description	Units	Default	LL	UL	$MLE_{control}$	$MLE_{warming}$	G-R statistics
b_1	allocation of GPP to shoot	-	0.17	0.1	0.45	0.27	0.24	1.0
b_2	allocation of GPP to root	-	0.36	0.1	0.45	0.31	0.31	1.0
c_1	turnover rate of C from shoot pool	$g\ C\ g\ C^{-1}\ d^{-1}$	9×10^{-3}	1×10^{-4}	1×10^{-2}	6.64×10^{-3}	5.06×10^{-3}	1.0
c_2	turnover rate of C from root pool	$g\ C\ g\ C^{-1}\ d^{-1}$	9×10^{-3}	1×10^{-4}	1×10^{-2}	4.24×10^{-3}	2.86×10^{-3}	1.0
c_3	turnover rate of C from litter pool	$g\ C\ g\ C^{-1}\ d^{-1}$	9×10^{-3}	1×10^{-4}	2×10^{-2}	6.66×10^{-3}	9.72×10^{-3}	1.0
c_4	turnover rate of C from fast SOM	$g\ C\ g\ C^{-1}\ d^{-1}$	0.015	1×10^{-4}	5×10^{-2}	1.69×10^{-2}	1.85×10^{-2}	1.0
c_5	turnover rate of C from slow SOM	$g\ C\ g\ C^{-1}\ d^{-1}$	6×10^{-4}	1×10^{-5}	2×10^{-3}	7.43×10^{-4}	7.45×10^{-4}	1.0
c_6	turnover rate of C from passive SOM	$g\ C\ g\ C^{-1}\ d^{-1}$	2×10^{-5}	1×10^{-8}	3×10^{-5}	1.55×10^{-5}a	1.47×10^{-5}a	1.0
f_{43}	fraction of C in litter pool transferring to fast SOM	-	0.5	0.3	0.7	0.53	0.41	1.0
f_{53}	fraction of C in litter pool transferring to slow SOM	-	0.12	0.05	0.15	0.10a	0.10a	1.0
f_{54}	fraction of C in fast SOM transferring to slow SOM	-	0.6	0.2	0.7	0.54	0.54	1.0
f_{64}	fraction of C in fast SOM transferring to passive SOM	-	0.005	0.0	0.008	0.0038a	0.0041a	1.0
f_{45}	fraction of C in slow SOM transferring to fast SOM	-	0.5	0.1	0.6	0.47	0.51	1.0
f_{65}	fraction of C in slow SOM transferring to passive SOM	-	0.01	0.0	0.02	0.01a	0.01a	1.0
f_{46}	fraction of C in passive SOM transferring to fast SOM	-	0.5	0.3	0.7	0.50a	0.51a	1.0
R_{10}	Temperature relative effects when temperature is at 10 °C	-	0.8	0.5	1.0	0.58	0.57	1.0
Q_{10}	Temperature sensitivity of decomposition	-	2.6	1.0	5.0	2.09	2.06	1.0

a: mean value

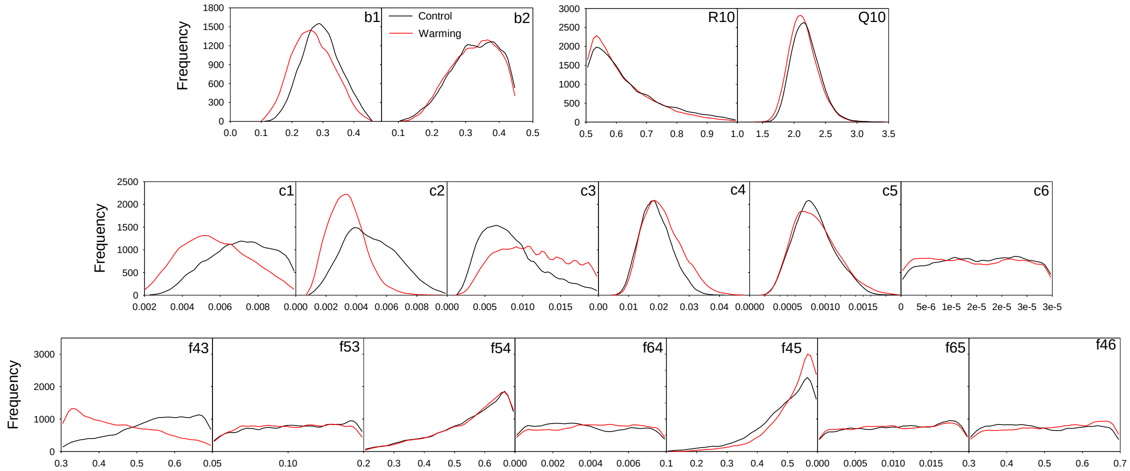
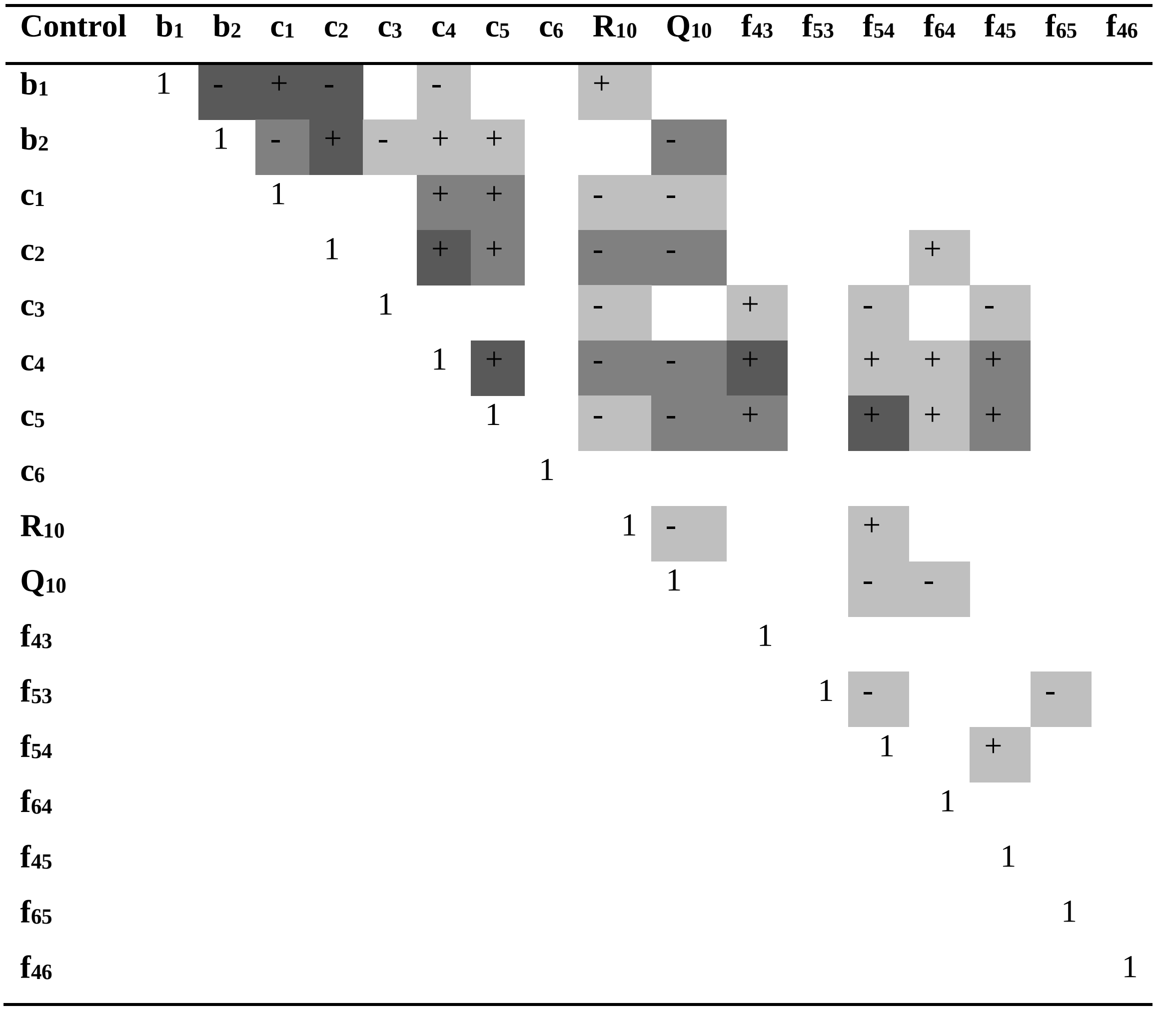


Figure 5.2 Posterior distribution of the 17 model parameters under control and warming treatments. The b's are allocation coefficients, c's refer to turnover rates and f's are transfer coefficients. See Table 1 for parameter abbreviations.

5.3.2 Parameter correlations

Correlations among model parameters differed little between control and warming conditions (Table 5.2 and Table S5.1), therefore we presented only the results for control treatment in the main text (Table 2). Three levels of correlation were defined: high ($|r| > 0.5$), modest ($0.3 < |r| < 0.5$) and low ($0.1 < |r| < 0.3$). Predictably, the parameters with the highest correlations were those associated with counteracting processes, e.g. C allocation to leaves and leaf turnover rate (b_1 and c_1); C allocation to roots and root turnover rate (b_2 and c_2); transfer coefficient from litter to labile C and the turnover rate of the latter (c_4 and f_{43}); and transfer coefficient from labile to slow C pool and the slow C turnover rate (c_5 and f_{54}). Some parameter pairs showed unexpectedly high degree of association, e.g. C allocation to shoots and roots (b_1 and b_2), C allocation to leaves and root turnover rate (b_1 and c_2), root and labile C turnover rates (c_2 and c_4); and labile and slow C turnover rates (c_4 and c_5). Passive C turnover rate (c_6) had weak correlation with other parameters, and transfer coefficients had fairly low correlation among one another as well as with the other parameters.

Table 5.2 Correlation coefficients among parameters in control treatments (dark grey: |r| > 0.5; moderate grey: 0.5>|r| >0.3; light grey: 0.3> |r| > 0.1; white: |r|<0.1; +: positive correlation; -: negative correlation). Similar correlation coefficients in warming treatment.



Control	**b_1**	**b_2**	**c_1**	**c_2**	**c_3**	**c_4**	**c_5**	**c_6**	**R_{10}**	**Q_{10}**	**f_{43}**	**f_{53}**	**f_{54}**	**f_{64}**	**f_{45}**	**f_{65}**	**f_{46}**
b_1	1	-	+	-		-			+								
b_2		1	-	+	-	+	+			-							
c_1			1			+	+		-	-							
c_2				1		+	+		-	-				+			
c_3					1				-		+		-		-		
c_4						1	+		-	-	+		+	+	+		
c_5							1		-	-	+		+	+	+		
c_6								1									
R_{10}									1	-			+				
Q_{10}										1			-	-			
f_{43}											1						
f_{53}												1	-			-	
f_{54}													1		+		
f_{64}														1			
f_{45}															1		
f_{65}																1	
f_{46}																	1

5.3.3 Model performance and information gain under both treatments

After data assimilation, TECO model generated similar mean values and patterns of respiration, plant and soil C content to the observations under control and warming conditions (Fig. 5.3). However, the model failed to fully capture effects of drought on respiration and biomass in 2006 under both treatments (Fig. 5.3 a-h). Dynamics of soil C was not fully captured by the model possibly due to the large errors associated with the observations and our model structure, but the temporal trend in soil C change was generally captured (Fig. 5.3 i-l). In order to test the effectiveness of the optimization, we also did another set of optimization by assimilating first six-year data (2000-2005) and then compared the observations with simulations. The results were quite similar to those we obtained by assimilating all the data (Fig. S5.2). However, simulated root carbon was not well agreed with observations, because only one data point was measured in the first six years. Besides the poor simulation of root carbon within 2006-2008, soil labile carbon was consistently overestimated from 2006-2008 with only assimilation of data with 2000-2005. The other modeled variables were reasonably well simulated within 2006-2008. Meanwhile, we also ran the simulation using default parameter values (values before data assimilation) and compared the model results with both observations and simulations with parameter values after data assimilation (Fig. 5.4). We found that for most of the variables RMSEs were consistently greater for simulation with default values than that with parameters after data assimilation (Table S5.2). Higher RMSEs suggest poor model performance. However, heterotrophic respiration was an exception. The RMSEs were slightly smaller for default simulation.

Assimilated observations contributed most information to the labile C pool (Fig. 5.5), increasing the information content in the labile C pool by 290% (control) and 310% (warming) compared to model with original parameters. Observations also increased the information content in the modeled live and litter C pools, increasing it by up to 100% compared to the original model prediction. Observations contributed the least amount of information to the slow and passive C pools (5-10%). Interestingly, the information content contributed by observations from the warming plots differed from information contributed by data from the control plots: warming increased information contribution of the observations for all pools except for the litter C pool.

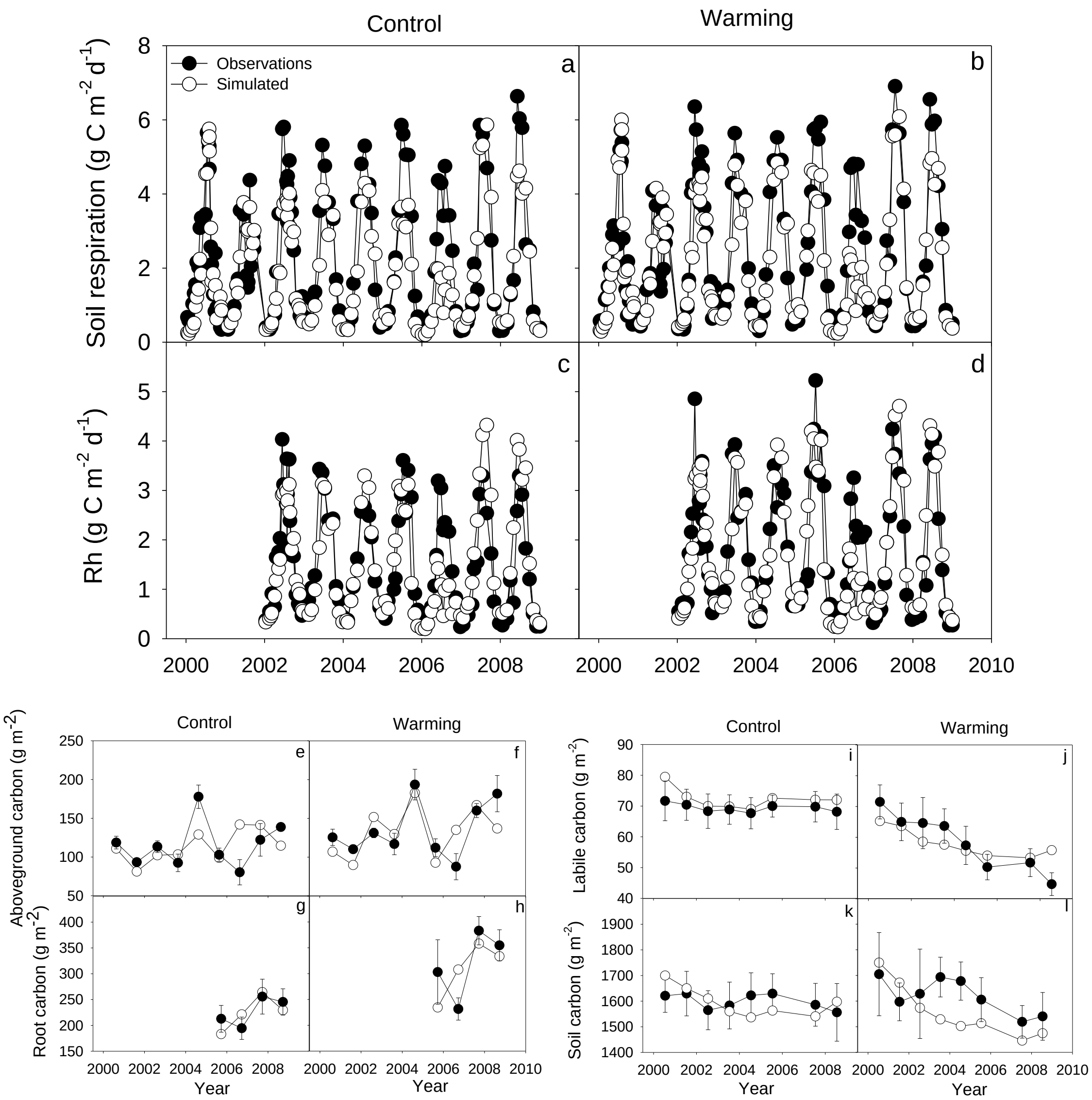


Figure 5.3 Comparison of the observations and the mean values of the simulated observational variables with the parameters accepted under control and warming treatments. a-b: soil respiration under control and warming; c-d: heterotrophic respiration (Rh); e-f: aboveground biomass carbon; g-h: root biomass carbon; i-j: labile soil organic carbon; k-l: soil organic carbon. Note: observations are mean with standard error except for soil respiration and Rh for clarity.

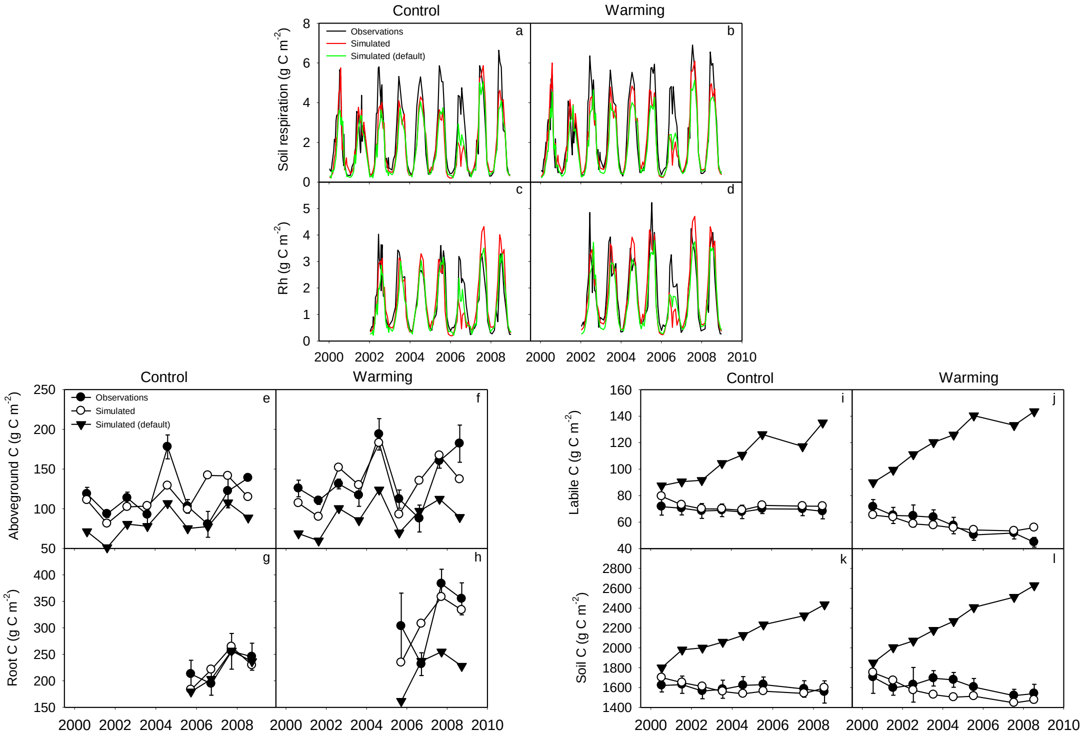


Figure 5.4 Comparison of the observations and the values of the simulated observational variables with the default model parameters and parameters accepted under control and warming treatments. a-b: soil respiration under control and warming; c-d: heterotrophic respiration (Rh); e-f: aboveground biomass carbon; g-h: root biomass carbon; i-j: labile soil organic carbon; k-l: soil organic carbon. Note: observations are mean with standard error except for soil respiration and Rh for clarity.

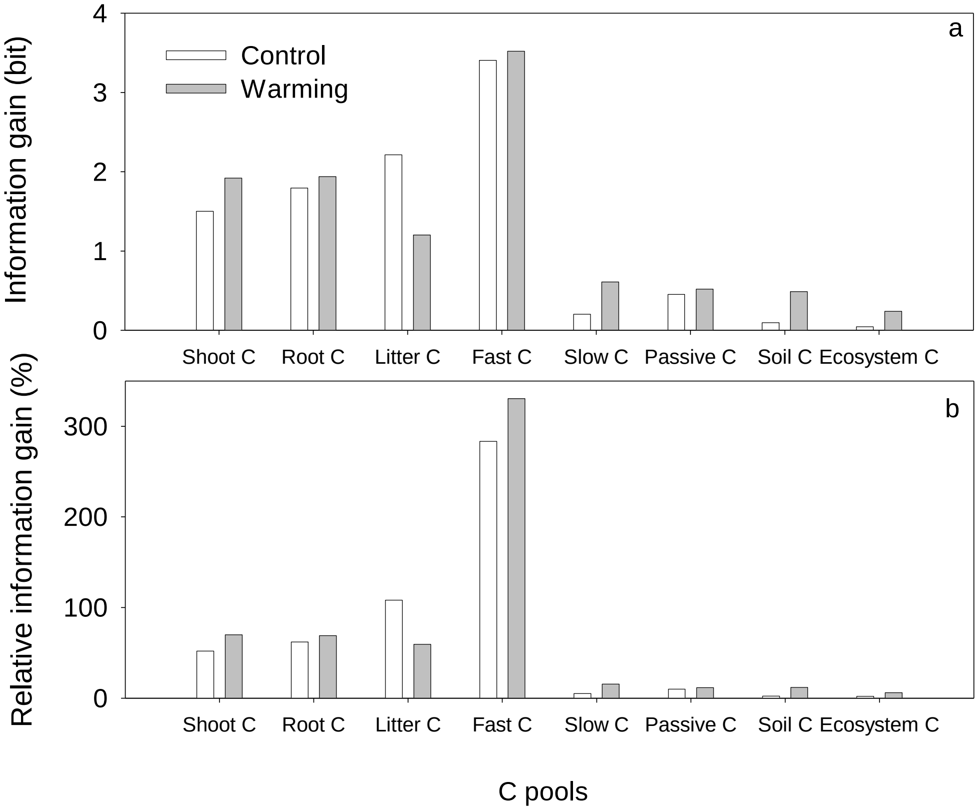


Figure 5.5 Information gain (a) and relative information gain (b) of long-term C prediction derived from the distributions of carbon content simulated by the model with prior and posterior parameters.

5.3.4 Effect of warming on projected C pools

Warming had different effects on C pools in a 90-year model prediction (Fig. 5.6): it increased live C pools (X_1 and X_2), decreased dead C pools (X_3, X_4 and X_5), and had little effect on passive soil C pool (X_6). Overall, warming decreased total soil C content and ecosystem C content. Due to low information gain from the observations, we observed substantial inflation of uncertainty for passive C pool (X_6) after 90 years of simulation, whereas for other C pools uncertainty stabilized after 1-9 years of simulation. Because of inflating uncertainties in the soil C pool, uncertainties in the ecosystem C pool also increase with time under both warming and control treatments.

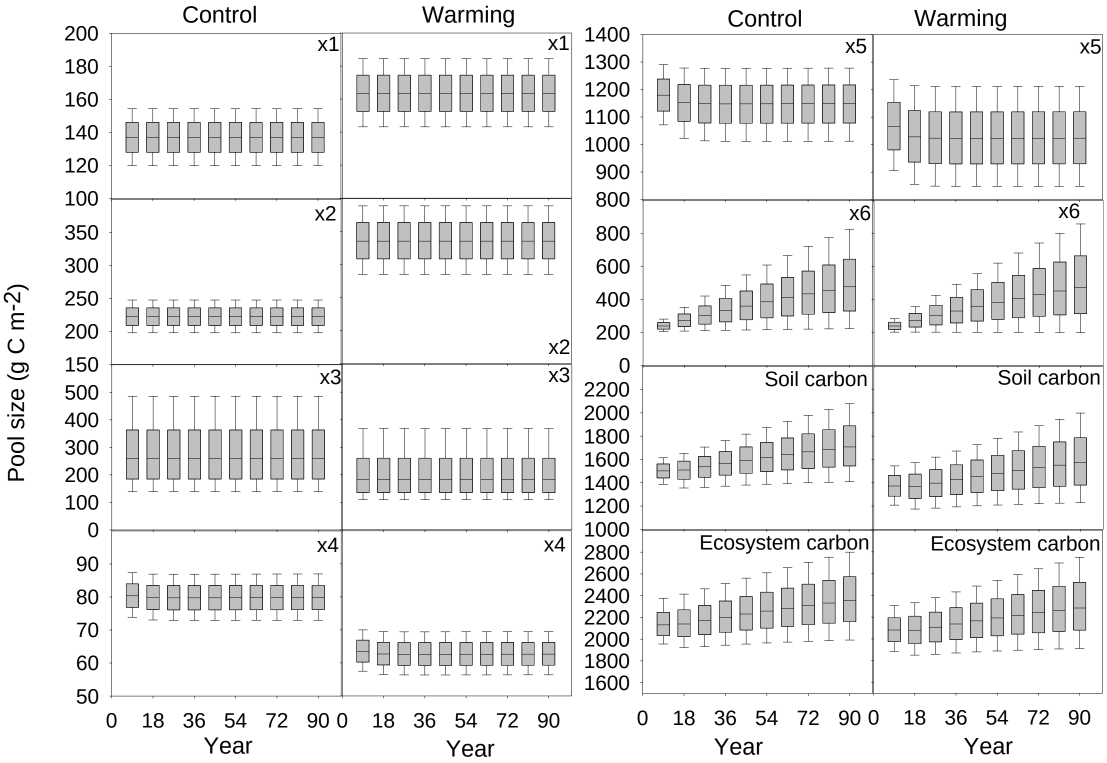


Figure 5.6 Long-term (90 years) projections based on accepted parameters for each of the carbon pools, soil organic carbon and ecosystem carbon under control and warming treatments. Box plots show visual summaries of carbon content distributions in the 5% (bottom bar), 25% (bottom hinge of the box), 50% (line across the box), 75% (upper hinge of the box), and 95% (upper bar) intervals. Note that x_1 represents the peak aboveground biomass carbon.

5.3.5 Sensitivities of short-term and long-term projected C pools to parameters

Sensitivities of projected C pools to parameters were similar under control and warming treatments (Fig. 5.7 and Fig. S5.3), therefore we presented the results for the control condition only (Fig. 5.7). Sensitivities of the four fast turnover C pools (i.e., pool 1-4) to parameters were similar between short-term and long-term projections: C pools were most sensitive to their respective turnover rates and modest to allocation coefficients or transfer coefficients which represent C input.

The two slow turnover C pools (pool 5 and 6) had different sensitivities to parameters between short- and long-term predictions. In short term, X_5 was slightly sensitive to its turnover rate but insensitive to other parameters. In long term, X_5 became more sensitive to c_5 and modest to f_{54}. In short term, X_6 was most sensitive to f_{65}, the transfer coefficient from X_5 to X_6, modest to turnover rates of X_4 and X_5 and f_{64}. In long term, X_6 became more sensitive to turnover rate of itself (c_6).

The sensitivities of soil and ecosystem C pools to parameters also differed between short-term and long-term projections. In short term, ecosystem C was sensitive solely to c_3, and soil C was generally insensitive to any one model parameter (Fig. 5.7a). In long term, however, the two pools were rather sensitive to turnover rates of the litter C and three soil C pools and the transfer coefficients from upstream C pools to slow and passive C pools (Fig. 5.7b).

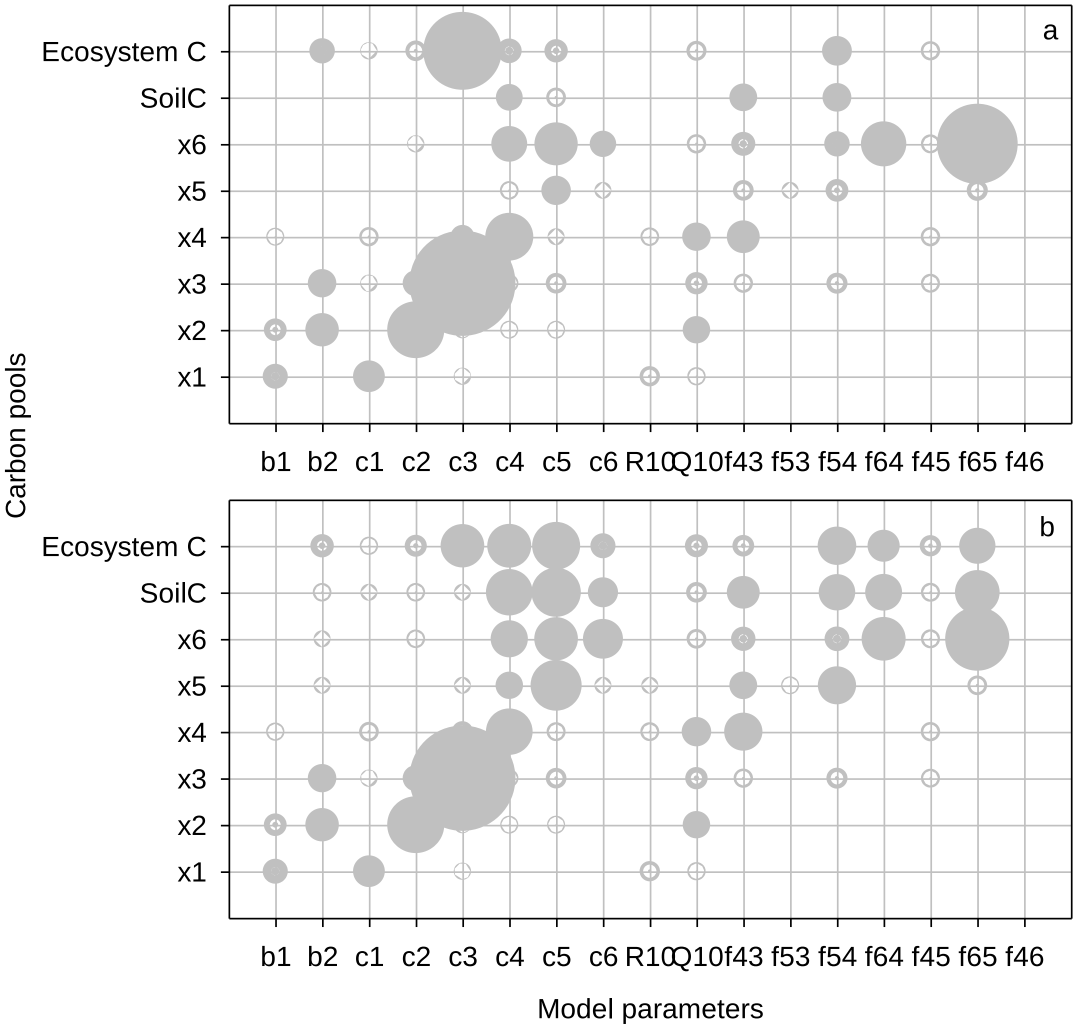


Figure 5.7 The sensitivity of the carbon pools in short term (nine-year simulation; a) and long term (90-year simulation; b) to the 17 parameters in control treatment. x_1–x_6 are the six carbon pools as shown in Fig. 1; c_1–c_6 are turnover rates of the carbon pools; b_1–b_2 are the allocation coefficients of GPP to shoot and root, respectively; $f_{i,\,j}$ values are the carbon transfer coefficients from pool j to pool i. The area of the circle represents the value of the coefficient of determination

5.4 Discussion

5.4.1 Constraints of parameters and parameter correlations

Recently, alternative model structures or additional components have been incorporated into global land models to better represent C cycling or fit empirical observations (e.g., Thornton et al. 2009, Wang et al. 2010, Wieder et al. 2013, Xu et al. 2014). As a result, the models have become more and more complex, but less tractable (Xia et al. 2013). Improving the parameterization of an existing model structure through data assimilation has been largely ignored, yet has been proved an effective method to increase model fit to observations (Hararuk et al. 2014). The difference in parameter values between control and warming treatments in our study further evidenced that scenario-invariant parameterization in global land models could contribute significant uncertainty to model predictions. Therefore, the disparity between model results and empirical findings in climate-C cycle feedback could be resolved to some extent if parameter values are allowed to vary with different climatic scenarios. On the other hand, warming-induced changes in parameter values also suggest that some important mechanisms are missing or not adequately represented in the land models. For example, warming-enhanced turnover rates of litter and labile C pools could be due to changes of plant community; however it also indicates possible inadequately representation of model processes such as temperature or soil moisture response functions.

The six data sets used in our study contained information for allocation coefficients of GPP to shoots and roots (b_1 and b_2), temperature sensitivity of turnover rates (Q_{10}) and all turnover rates except for passive soil C under both treatments. The poorly constrained transfer coefficients (f’s) implied that the six data sets did not contain much information about carbon partition among litter pool and soil organic matter pools (Weng and Luo 2011). In addition, the measurements duration (2000 – 2008) is relatively short in comparison to residence time of passive C pool (inverse of c_6), which may have been the reason why data sets contributed little information to passive C pool. Passive C pool as one form of recalcitrant C, is critical for long-term carbon projections of the states of terrestrial ecosystems, as models are often used to evaluate ecosystem responses to climate changes at decadal and century time scales. Therefore, collecting information relevant to the transfer coefficients and the passive C pool dynamics would help constrain the parameters and increase the accuracy of model projections.

Model complexity often leads to equifinality of model solutions which is indicated by parameter correlations (Luo et al. 2009a). Many close correlations among parameters were identified in our study. The strong parameter correlations indicate that the assimilated data sets are not sufficient to distinguish between counteracting processes in the model (Ricciuto et al. 2011). However, the correlations could also be due to the model structure and could not be reduced by assimilating more data sets (Keenan et al. 2013). Our results indicated that more data are needed to separate the counteracting processes, such as rate of C allocation to leaves and roots, and their respective turnover rates, transfer coefficients from litter to labile C and from labile C to slow C pool, and their respective turnover rates.

5.4.2 Warming effect on model parameters and projected carbon pools

Warming affected C allocation coefficient to shoots (b_1) and most of the turnover rates, but had little impact on temperature sensitivity and transfer coefficients. The negative effect of warming on turnover rates of plant biomass (c_1 and c_2) may have been due to a warming-induced change in the plant community structure (Niu et al. 2010). Positive effects of warming on litter and labile C turnover rates indicate changes in physical and biochemical properties of the two pools. However, warming had little effect on turnover rates of slow and passive soil carbon pools indicating resistance of physical and biochemical properties of these recalcitrant pools to warming or limited information contained in the assimilated observations (e.g. for passive soil C).

Warming affected short-term and long-term C pool sizes through regulating photosynthetic input (GPP), allocation coefficients, turnover rates, environmental factors (R_{10} and Q_{10}), and transfer coefficients individually or together. Warming-induced changes in C pool sizes were net results of different effects of warming on the key parameters, which were not always unidirectional in their changes. For instance, b_1 was reduced by warming, but plant biomass still increased as a result of warming-enhanced GPP combined with decreased turnover rates of shoots and roots. For the fast and slow soil C pools, warming-induced increase in the turnove rates resulted in diminishment of the pool size. Warming had little effect on passive soil C pool due to little warming effects on relevant parameters such as c_6 and f_{64}. As a result, warming slightly decreased both total soil C and ecosystem C content.

The processes that are not calibrated in our study may also affect long-term C cycle projection. For example, our results are subject to uncertainties caused by modeled GPP as model input (Xu et al. 2006, Zhang et al. 2010, Weng and Luo 2011) and TECO model structure. Ideally, one would calibrate an integrated canopy photosynthesis model and ecosystem C cycling model simultaneously. However, many parameters in photosynthesis model cause equifinality. Therefore, it is still a challenge to calibrate them against data at the same time (Zhang et al. 2010, Weng and Luo 2011). TECO model structure may also contribute to uncertainties. For instance, the largest difference between observed and modeled respiration and biomass occurred in the driest year, which implied model inadequacy in capturing severe drought effect. The little change in temperature sensitivity under warming also indicates the possible uncertainties contributed by model structure. The lack of parameterization of microbial activity and nitrogen dynamics in TEOC could also contribute to the uncertainties.

5.4.3 Sensitivities of short- and long-term projected C pools to parameters

Pool sizes at equilibrium state are determined by C input and turnover rate (Luo et al. 2001a, Weng and Luo 2011). The fast turnover pools (i.e., pool 1-4) all reached steady states in short-term prediction. Therefore, as expected, the turnover rates and allocation or transfer coefficients controlled the C pool sizes in both short and long terms in our study. However, the turnover rates played greater role in determining pool sizes than the C inputs represented by allocation or transfer coefficients. The underestimation of aboveground and root C and the overestimation of labile and soil C before data assimilation were likely caused by these sensitive parameters. Specifically, the aboveground C simulation was sensitive to b1 and c1 (Fig. 7a). The improvement was likely caused by the two parameters after data assimilation. The root C simulation was sensitive to b2 and c2 (Fig. 7a), which improved the simulation after data assimilation. Labile C was sensitive to c4 and f43 and soil C was sensitive to c4, f43 and f54, which were all well-estimated after data assimilation.

The two slow turnover pools were sensitive to different parameters between short- and long-term predictions. The X_5 did not reach equilibrium state until 18th year and X_6 was still growing at the end of the long-term prediction. Therefore, the importance of their respective turnover rates and C inputs did not appear in the short term, but increased over time. Different sensitivities of the six individual pools to model parameters determined the sensitivity of soil and ecosystem C between short- and long-term predictions. Such shift in sensitivities between short- and long-term highlights the importance of the soil C dynamics in long-term ecosystem C projections. Since long-term C cycle projection is the primary goal of biogeochemical models, it is critical to accurately estimate parameters related to slow turnover C pools and transfer coefficients.

Conclusions

Assimilation of six observed data sets into the TECO model constrained most of its parameters and facilitated assignment of uncertainties to parameter values. Our results showed that warming affected some of the key model parameters and thus affected C cycle projections, indicating that scenario-invariant parameters in global land models could cause substantial errors in their projections of plant and litter C storage. By comparing information content in the C pools before and after data assimilation, we found that the six data sets contained more information for the pools with fast turnover rates, than the pools with slow turnover rates. The sensitivity analysis revealed that individual C pools were mainly determined by respective turnover rates, regardless of projection period. However, projected soil and ecosystem C pools in short term were generally unresponsive to model parameters, whereas determinants of long-term projected soil and ecosystem C pools were both turnover rates and transfer coefficients. Changes in parameter values under warming suggest that scenario-invariant parameterization could introduce uncertainty in model prediction and also that the ecosystem C model may not well represent some ecosystem processes.

Supplementary materials

Table S5.1 Correlation coefficients among parameters in warming treatments (dark grey: |r| > 0.5; moderate grey: 0.5>|r| >0.3; light grey: 0.3> |r| > 0.1; white: |r|<0.1; +: positive correlation; -: negative correlation).

	b_1	b_2	c_1	c_2	c_3	c_4	c_5	c_6	R_{10}	Q_{10}	f_{43}	f_{53}	f_{54}	f_{64}	f_{45}	f_{65}	f_{46}
b_1	1	-	+	-		-			+								
b_2		1	-	+	-	+	+			-							
c_1			1			+	+		-	-							
c_2				1		+	+		-	-				+			
c_3					1				-		+		-		-		
c_4						1	+		-	-	+		+	+	+		
c_5							1		-	-	+		+	+	+		
c_6								1									
R_{10}									1	-			+				
Q_{10}										1			-	-			
f_{43}											1						
f_{53}												1	-			-	
f_{54}													1		+		
f_{64}														1			
f_{45}															1		
f_{65}																1	
f_{46}																	1

Table S5.2 Root-mean-square error (RMSE) between observations and simulation with default parameters ($RMSE_{obs-default}$), and between observations and simulation with parameters after data assimilation ($RMSE_{obs-simu}$) in both control and warming treatment.

	Control		Warming	
Variable	$RMSE_{obs-default}$	$RMSE_{obs-simu}$	$RMSE_{obs-default}$	$RMSE_{obs-simu}$
Soil respiration ($g\ m^{-2}\ d^{-1}$)	1.11	0.97	1.05	0.93
Rh ($g\ m^{-2}\ d^{-1}$)	0.56	0.66	0.67	0.70
Aboveground carbon ($g\ m^{-2}$)	39.2	29.0	53.0	26.2
Root carbon ($g\ m^{-2}$)	17.9	22.0	114.7	53.9
Labile carbon ($g\ m^{-2}$)	42.1	3.5	67.1	5.7
Soil carbon ($g\ m^{-2}$)	560.1	55.6	687.0	104.1

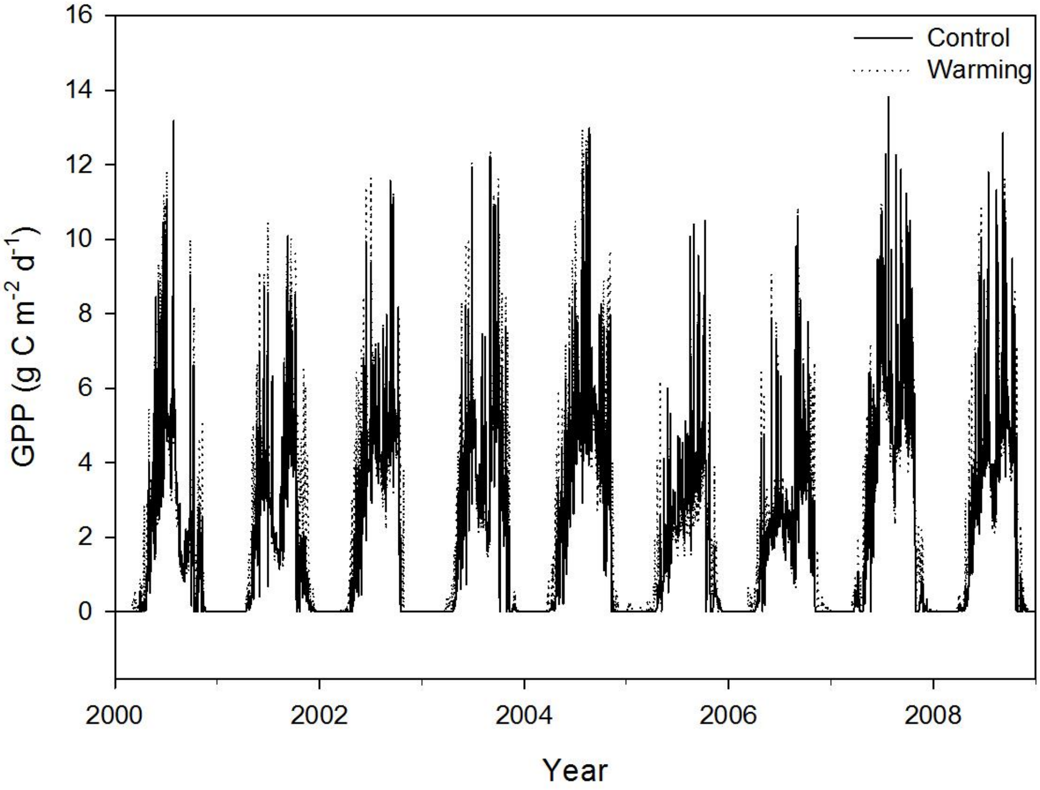


Figure S5.1 Daily values of GPP under control and warming treatments derived from photosynthesis sub-model of TECO model.

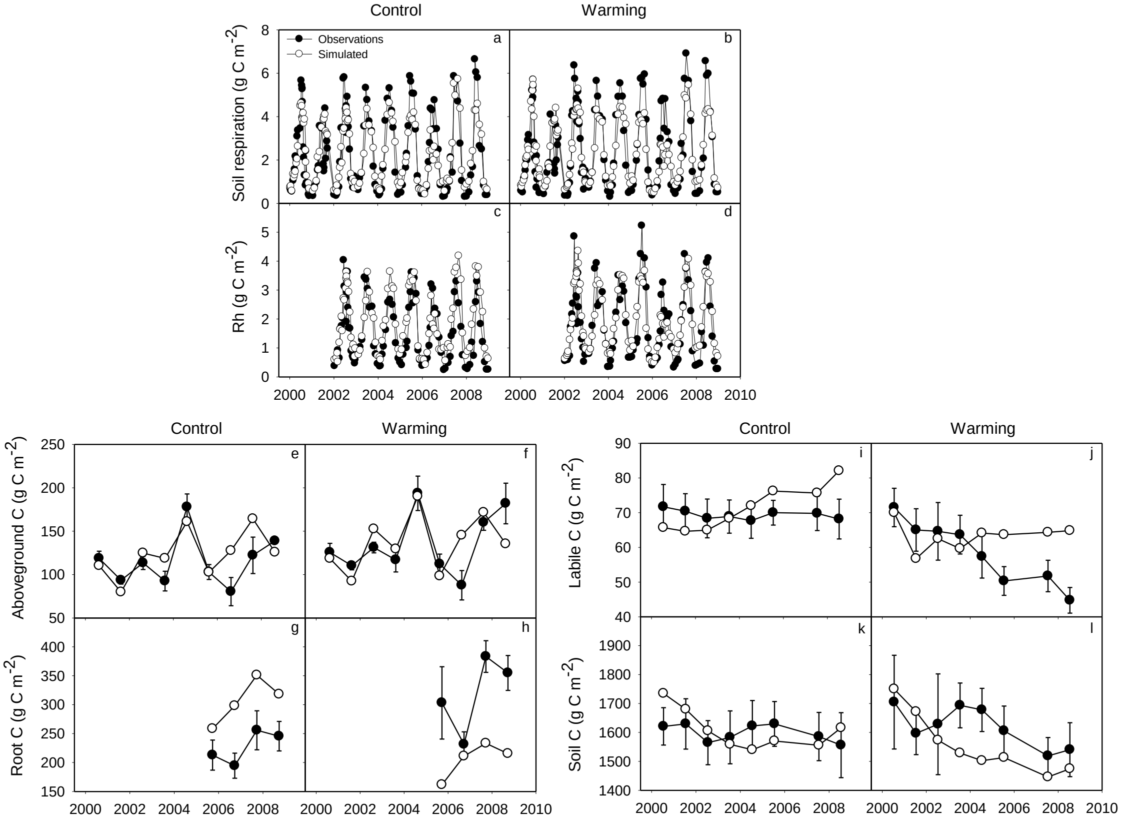


Figure S5.2 Comparison of the observations and the mean values of the simulated observational variables with the parameters accepted under control and warming treatments when first six years data were used to constrain the parameters. a-b: soil respiration under control and warming; c-d: heterotrophic respiration (Rh); e-f: aboveground biomass carbon; g-h: root biomass carbon; i-j: labile soil organic carbon; k-l: soil organic carbon. Note: observations are mean with standard error except for soil respiration and Rh for clarity.

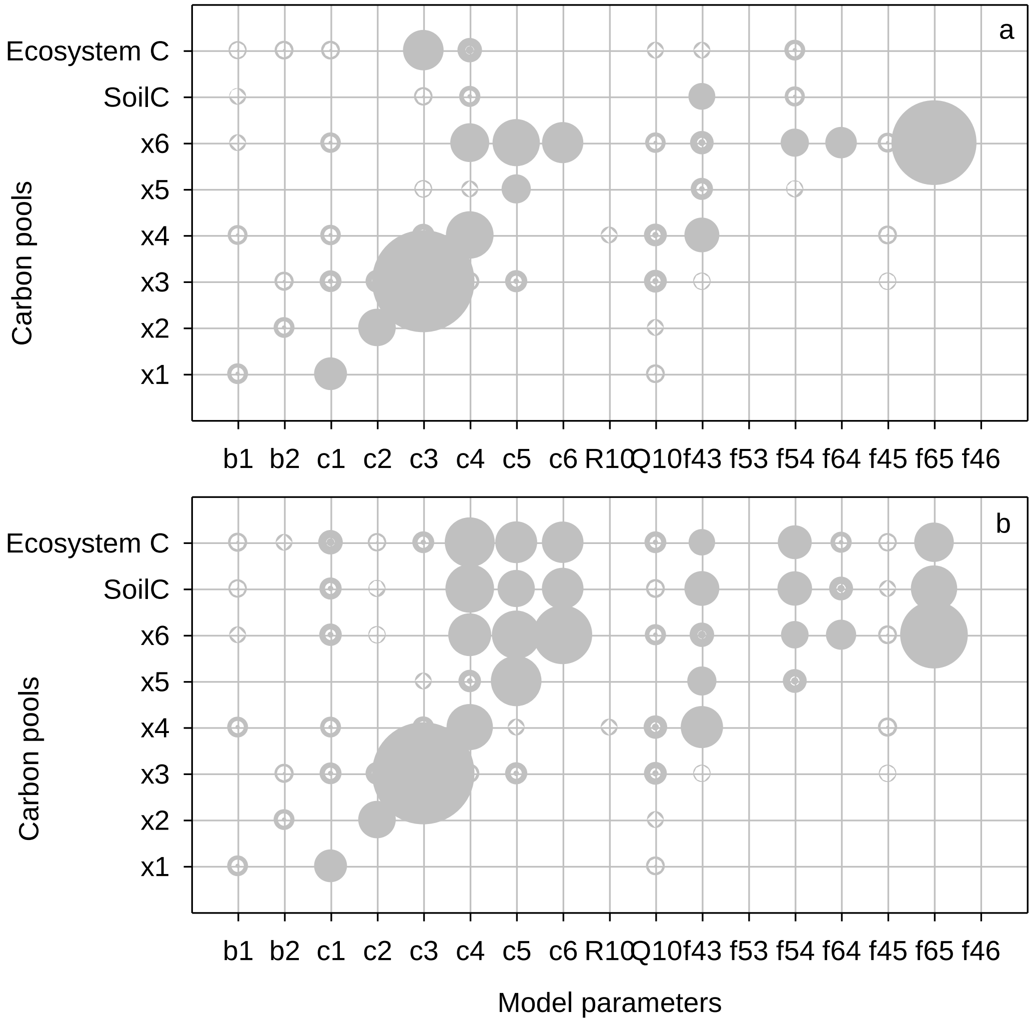


Figure S5.3 The sensitivity of the carbon pools in short term (nine-year simulation; a) and long term (90-year simulation; b) to the 17 parameters in the warming treatments. x1–x6 are the six carbon pools as shown in Fig. 1; c1–c6 are turnover rates of the carbon pools; b1–b2 are the allocation coefficients of GPP to shoot and root, respectively; fi, j values are the carbon transfer coefficients from pool j to pool i. The area of the circle represents the value of the coefficient of determination

Chapter 6 Conclusions and Perspectives

6.1 Conclusions

These studies showed general patterns in responses of community structure and ecosystem functioning to altered precipitation across different biomes (Chapter 2) and different grassland ecosystems (Chapter 3), and probable mechanisms for the patterns, demonstrated the nonlinear response of plant community to long-term field warming (Chapter 4) and identified mechanisms (or processes) accounting for warming-induced changes in ecosystem carbon storage capacity in a tallgrass prairie (Chapter 5).

In specific, extreme drought reduced both productivity and respiration across a broad range of ecosystems including grassland and forest, with stronger reduction in productivity than in respiration (Chapter 2). Modeling analysis suggests that the differential responses of productivity and respiration to drought could be caused by the fast response of plant photosynthesis and slow response of soil carbon mineralization (Chapter 2). Altered precipitation drove changes in productivity across different grassland ecosystems, with suppressed growth under decreased precipitation and enhanced growth under increased precipitation (Chapter 3). The limited responses of community structure to altered precipitation indicate that productivity sensitivity to precipitation changes could be solely physiological (Chapter 3). However, our analysis of a long-term warming experiment in a tallgrass prairie showed that community structure changed at the eighth year of experimental warming (Chapter 4). It indicates that long-term climate change could have stronger effect on ecosystem functioning through altering community structure. The information contained in the carbon-related variables measured in the warming experiment was assessed to reveal warming effects on the carbon processes (Chapter 5). Long-term experimental warming had impacts on key model parameters such as allocation coefficients and residence time (Chapter 5), suggesting that it is more than physiological responses that determined the ecosystem sensitivity to climate warming.

6.2 Perspectives

Research in global change ecology in terrestrial ecosystems started to prosper in 1980s, boomed in 2000s, and has progressed into its fourth decades. Its development trajectory follows typical advancements of any discipline in science. Generally, it went through intensive individual experiments, statistical modeling or syntheses of the individual experimental results, and process-based modeling for prediction. Despite of countless efforts into this area, the prediction of terrestrial C cycling under future environmental and climatic scenarios is still very poor with huge uncertainties. So far, there is no “magic bullet” to significantly reduce the uncertainties. While the whole community is striving to bring down the model uncertainty, two other different perspectives (or questions) are worth considering. Is the C cycle really predictable in a long term for biological (plant) system for its notoriety for predictability and complex external forcing to the system? After all, the main body in the C cycle models is plant. Its metabolism, resource acquisition strategy, allocation scheme and intra- and inter-specific competition are much more complex and delicate than physics. It is a big challenge to simulate them. The other perspective is that the significant advancement of a scientific discipline is often associated with theory development. So far, there is no established theory in this research area to guide the scientific community, which may hinder its development. However, recently there is effort of bringing existing theories into this area, such as metabolic theory and optimization growth hypothesis. Much more effort is still needed in order to fully push this area into a new era.

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