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Modeled ecosystem responses to intra-annual redistribution and levels of precipitation in a prairie grassland

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ABSTRACT

Global models projected that, precipitation in Great Plains of the United States will decrease in summer and increase in spring and winter. However, few studies had carefully examined ecosystem responses to this intra-annual redistribution of precipitation. Here we used a process-based model, Terrestrial ECOsystem (TECO) Model, to evaluate responses of ecosystem carbon processes (including net primary production (NPP), heterotrophic respiration (R_h), and net ecosystem production (NEP)) and hydrological cycles (including evapotranspiration, and runoff) to precipitation redistribution at three levels (−50%, ambient, and +50% precipitation) in five soil textures (sand, sandy loam, loam, silt loam, and clay loam). Redistribution was designed by subtracting 40% summer precipitation and adding to spring and fall. Results showed that precipitation redistribution decreased NPP, R_h, and NEP at all three precipitation levels. Responses of NPP, R_h, and NEP differed in five soil textures. Redistribution slightly increased runoff and decreased evapotranspiration. Runoff was higher in coarse textured soils and lower in fine textured soils. Responses of evapotranspiration were contrary to runoff. Precipitation levels and redistribution had little effect on mean annual soil water content (SWC), especially in coarse textured soils. Our results indicated that, besides amount and timing of precipitation, the intra-annual redistribution could also affect ecosystem carbon and water processes. Moreover, the extent to which the ecosystem responses to redistribution of precipitation is largely controlled by soil texture.

1. Introduction

Ongoing global warming may alter regional precipitation regime (Harper et al., 2005). Global mean precipitation may not change significantly, but regional and temporal patterns have changed (IPCC, 2013). Magnitude of precipitation directly affects ecosystem productivity. For example, aboveground net primary productivity (ANPP) increases 0.64% when precipitation increases by 1% (Hsu et al., 2012). Precipitation is the most limiting factor for belowground net primary productivity and its fraction to total net primary productivity (NPP) in tallgrass prairie (Xu et al., 2012). Increased precipitation stimulates plant growth and ecosystem C fluxes, whereas decreased precipitation had the opposite effects (Wu et al., 2011). Meanwhile, timing of precipitation is crucial to ANPP across a broad range of ecosystems and plant types (Robinson et al., 2013). A 27 years observation in tallgrass prairie of Kansas also suggests that the timing of precipitation is as important as the precipitation amount for plant productivity (Craine, 2013; Craine et al., 2012). Changing in timing of precipitation will change intervals between rainfall events (Fay et al., 2000), which affects the seasonal availability of soil water.

Climate change projections suggest there will be a slight increase in annual precipitation, while a slight decrease in summer precipitation in the western and central United States (IPCC, 2007; Parton et al., 2012). In southern part of the Great Plains, spring will be wetter, and summer will be drier in mid twenty-first century (Patricola and Cook, 2013). In the southern USA, precipitation will not have a discernible upward or downward trend in the twenty-first century, but fall and winter will become wetter than the late twentieth century (Liu et al., 2012). The precipitation in Kansas is also likely to slightly increase in winter, but decrease in summer and fall in the twenty-first century (Brunsell et al., 2010). Therefore, the Great Plains is likely to have a drier summer, but wetter spring and winter. Intra- and inter- annual variability of precipitation is likely to increase (Hsu et al., 2012; Knapp et al., 2002), while annual precipitation amount has little change.

The tallgrass prairie of the Great Plains stores huge amount of carbon (An et al., 2013). This ecosystem is primarily driven by

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rainfall patterns (Knapp et al., 2006). Precipitation significantly alters ecosystem processes, which affects carbon dynamics (An et al., 2013; Knapp et al., 2002). Meanwhile, soil texture highly affects ecosystem productivity (Epstein et al., 1997). Precipitation events will be translated to potential biological activity by soils (Huxman et al., 2004). The ability of soil to store water, which could be quantified by the available water capacity (Weng and Luo 2008), is crucial for ecosystem carbon processes and hydrologic cycles.

Effects of amount and timing of precipitation to ecosystem carbon cycle had been well documented (Austin et al., 2004; Chou et al., 2008; Harper et al., 2005; Heisler-White et al., 2008; Jongen et al., 2011; Knapp et al., 2002; Parton et al., 2012; Takemi, 2010). However, most of these studies were experimental research. Few modeling studies concerned about this issue. Besides, the effects of intra-annual rainfall redistribution without altering timing and amount of precipitation were rarely reported. In this study, we used a process-based ecological model to estimate ecosystem responses to precipitation patterns. In this paper, we hypothesized that carbon processes (NPP, heterotrophic respiration (R_h), and net ecosystem production (NEP)) and hydrological cycles (evapotranspiration and runoff) will be affected by precipitation redistribution, and the responses of these processes was different in diverse soil textures. Thus, our objectives are to evaluate the effect of precipitation redistribution to ecosystem carbon processes and hydrological cycles at three precipitation levels (−50%, ambient, and +50%), and to evaluate different responses under these precipitation levels in diverse textured soils.

2. Materials and methods

2.1. Model description

In this research, we used a process-based model: Terrestrial ECOsystem (TECO) Model (Weng and Luo, 2008). The TECO model had four components: canopy photosynthesis submodel, soil water dynamic submodel, plant growth submodel, and soil carbon transfer submodel. The canopy photosynthesis and soil water dynamic submodels ran at hourly steps, while the plant growth and soil carbon transfer submodels ran at daily steps. The TECO model was described in detail by Weng and Luo (2008). Here we provide a brief overview.

The canopy submodel photosynthesis referred from a two-leaf model developed by Wang and Leuning (1998). Two-leaf meant sunlit and shaded leaves. This submodel simulated canopy conductance, photosynthesis, and partitioning of available energy. For leaf photosynthesis, the model combined Farquhar model (Farquhar et al., 1980) and a stomatal conductance model developed by Harley et al. (1992). In the soil water dynamic submodel, soil was divided into 10 layers. The surface layer was 10 cm deep and the other 9 layers were 20 cm deep. Soil water content (SWC) of these layers was determined by the mass balance between water influx (from the precipitation in the surface layer and percolation in deeper layers) and efflux (by adding evapotranspiration and runoff). In this model, runoff include both surface runoff and the water flow out from the bottom (190 cm). The plant growth submodel could simulate the carbon allocation and phenology. Allocation of the carbon among different plant components, such as leaves, stems and roots, depended on growth rates of these components, and varied with phenology. And the phenology dynamics was represented by the variation of leaf area index. Leaf onset was triggered by the growing degree days, while leaf senescence was determined by low temperature and soil moisture. The end of the growing season was recognized when leaf area index was less than 0.1. The carbon transfer submodel estimated carbon transferring from plant to litter and soil. The soil profile was divided into three layers, carbon moved from upper to deeper layers. Soil carbon influx from root growth and dead root residues were partitioned into these three layers.

The model was driven by climate data, which included air and soil temperature, vapor-pressure deficit, relative humidity, incident photosynthetically active radiation, and precipitation at hourly steps. Climate data was collected from the Washington MESONET site, Oklahoma from 1998 to 2012. The simulated results were recorded after the model was run 1200 years and reached the equilibrium state. After precipitation was redistributed, all following years' results exhibited the same pattern. We used the first year's results to illustrate the impact of precipitation redistribution on grassland.

2.2. Model validation

The TECO model was validated by observation data from a long-term warming experiment at the Kessler's Farm Field Laboratory in McClain County, Oklahoma, USA (34°59′N, 97°31′W). The validating dataset included soil respiration, above and below ground biomass, net ecosystem exchange (NEE), and soil moisture. Soil respiration and soil moisture were measured approximately once a month from 2000 to 2005. Soil respiration showed no significant difference between simulated and observed (P = 0.21). And simulated soil moisture was slightly higher than the measured values when soil was very dry. Aboveground biomass were measured once a year in these 6 years, and belowground biomass were measured in 2002 and 2004. the simulated results are in good agreement with observational data. Full description and graphical representation of the validation could be found in Weng and Luo (2008) and Zhou et al. (2008). The modeled outputs matched well with observed data.

2.3. Simulation scenarios

In order to test ecosystem responses, we defined 30 simulation scenarios from combinations of five soil textures and six precipitation patterns. Soil textures were classified according to their field capacities and wilting points. Five soil textures named sand, sandy loam, loam, silt loam, and clay loam (Table 1) (Weng and Luo, 2008). In order to simplify the interpretation of modeling results, we assumed all soil layers have the same field capacity and wilting point.

Six precipitation patterns were denoted as 1.0P, 1.5P, 0.5P, 1.0PR, 1.5PR, and 0.5PR. 1.0P stood for ambient scenario. 1.5P and 0.5P were defined by increasing and decreasing 50% precipitation for each rainfall event of 1.0P. 1.0PR represented the scenario in which precipitation of each rainfall event was subtracted by 40% in summer (May–September) and evenly added to rainfall events in spring (March and April) and fall (October and November). 1.5PR and 0.5PR followed previous redistribution method at +50% and −50% precipitation levels. Each rain day was treated as a rainfall event in this study. This redistribution method could well represent the intensified summer drought and seasonal rainfall alternation (Volder et al., 2013). Fig. 1 represented monthly precipitation of 6 precipitation patterns. We also defined three precipitation levels: increased, ambient, and decreased as P+, C, and P− levels to facilitate analyzing.

Table 1
Field capacities and wilting points of the five soil texture types.

Soil texture	Sand	Sandy loam	Loam	Silt loam	Clay loam
Field capacity(%)*	10.0	15.0	25.0	35.0	45.0
Wilting point(%)*	5.0	7.5	10.0	12.0	15.0

* The parameters was cited from Weng and Luo (2008).

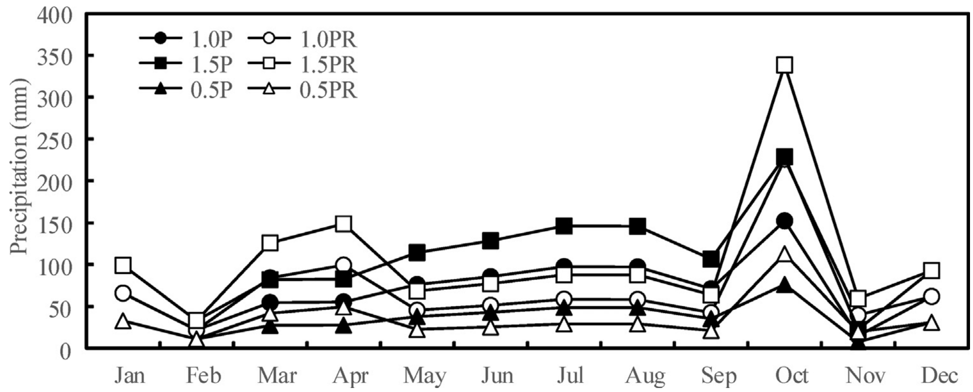

Fig. 1. Monthly precipitation of 6 precipitation patterns.

We analyzed the daily climate data of Kessler's Farm Field Laboratory during 1998–2012 to define the ambient precipitation scenario. Mean annual precipitation was 849.63 mm, and mean rainfall events were 90.29 days per year. From May to September, mean precipitation was 450.43 mm and rainfall events was 65.21 days. In March, April, October, and November, average precipitation was 277.78 mm and rainfall events were 31.5 days. Above parameters in 2002 were the closest to the averages during 1998–2012. In 2002, total precipitation was 854.90 mm, and rainfall events were 89 days. From May to September, precipitation was 427.23 mm, and rainfall events were 64 days. In March, April, October, and November, precipitation was 256.29 mm and rainfall events were 34 days. Therefore, we define the year of 2002 as the ambient scenario (1.0P). Other precipitation scenarios were developed based on 1.0P.

3. Results

3.1. Responses of NPP

NPP was the highest at 1.5P and the lowest at 0.5PR in all five soil textures, which were 452.12 $g\,C\,m^{-2}\,yr^{-1}$ and 116.44 $g\,C\,m^{-2}\,yr^{-1}$, respectively (Fig. 2a). Comparing with 1.0P, NPP increased at 1.5P, and decreased at 0.5PR, 1.0PR and 0.5P. At 1.5PR, NPP

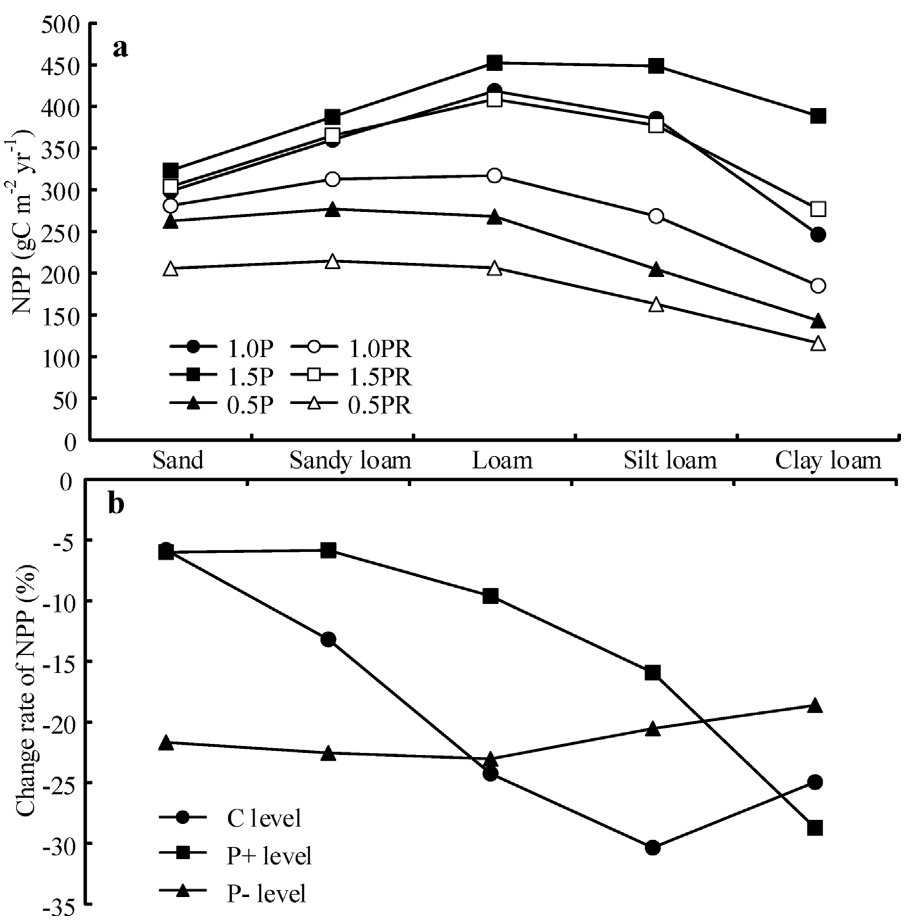

Fig. 2. Net primary productivity (NPP) responses to different precipitation scenarios in five soil types. (a) NPP in different combination of soils and precipitation regimes; (b) effect of redistribution to NPP represented by relative changing rate at three precipitation levels. The relative changing rates were calculated from following formula: C level = $(NPP_{1.0PR} - NPP_{1.0P})/NPP_{1.0P}$; P+ level = $(NPP_{1.5PR} - NPP_{1.5P})/NPP_{1.5P}$; P− level = $(NPP_{0.5PR} - NPP_{0.5P})/NPP_{0.5P}$.

increased by 5.29 g C m^{-2} yr^{-1}, 5.03 g C m^{-2} yr^{-1}, and 30.66 g C m^{-2} yr^{-1} in sand, sandy loam, and clay loam respectively, and decreased by 9.68 g C m^{-2} yr^{-1} and 8.11 g C m^{-2} yr^{-1} in loam and silt loam in comparison to 1.0P.

Responses of NPP to soil textures differed in three precipitation levels. At P+ and C levels, NPP reached the maximum in loam. In both coarse textured sand soil and fine textured clay loam, NPP was relatively low. Meanwhile, at P− level, NPP was higher in coarse textured soils (sand and sandy loam). Responses of NPP to precipitation redistributions and levels were slighter in coarse textured soils than in fine textured soils.

Redistribution of precipitation decreased NPP in spite of precipitation levels (Fig. 2b). At P− level, NPP were greater in coarse textured soils (sand and sandy loam) than in fine textured soils (silt loam and clay loam). Contrarily, at P+ level, the effect of redistribution was greater in fine textured soils than in coarse textured soils. On average, NPP decreased more at P− level (21.27%) than other at P+ (13.21%) and C levels (19.70%). However, the greatest NPP reducing rate, 30.35%, occurred at ambient precipitation level in silt loam.

3.2. Responses of R_h

Response pattern of R_h (Fig. 3) was similar to that of NPP (Fig. 2). R_h was also the highest at 1.5P (428.57 g cm^{-2} yr^{-1}), and the lowest at 0.5PR (225.51 g cm^{-2} yr^{-1}). Comparing with NPP, response of R_h were slighter, especially in sand. R_h was the highest in medium textured soils (loam) in all precipitation scenarios (Fig. 3a). Generally, precipitation redistribution decreased R_h, except slightly increased in sand at P+ level (0.04%) (Fig. 3b). In P− level, responses of R_h to redistribution were greater in coarse textures (such as sand and sandy loam). Rather, in P+ level, responses of R_h were greater in fine textured soils.

3.3. Responses of NEP

NEP was the highest at 1.5P among 6 precipitation scenarios. At 1.5P, NEP was nearly equal in sand, sandy loam, and loam. At 1.5PR, NEP was 4.77 g cm^{-2} yr^{-1}, 3.15 g cm^{-2} $yr^{-1}$and 24.24 g cm^{-2} yr^{-1} in sand, sandy loam, and clay loam, respectively, while it was negative in loam (−9.52 g cm^{-2} yr^{-1}) and silt loam (−8.00 g cm^{-2} yr^{-1}). NEP was zero at 1.0P in all soil types. Response patterns of NEP in 1.0PR, 0.5P, and 0.5PR were similar, in which NEP was higher in both coarse and fine textured soils, and lower in medium textured soils (Fig. 4a).

Precipitation redistribution reduced NEP in all three precipitation levels (Fig. 4b). NEP decreased by −45.54 g cm^{-2} yr^{-1}, by −60.40 g cm^{-2} yr^{-1}, and −44.28 g cm^{-2} yr^{-1} at P+, C, and P− levels, respectively. At P+ level, NEP decreased more in fine textured soils than in coarse textured soils (Fig. 4b). The opposite trend was observed at P− level. In C level, redistribution reduced more NEP in medium textured soils than in other soils.

The NEP responses illustrated that at P+ level, the carbon uptake would be totally or partly offset by redistribution. And at C level, redistribution would probably destroy the equilibrium state, and turn the ecosystem into carbon source. Moreover, at P− level, the carbon release would be enhanced by redistribution.

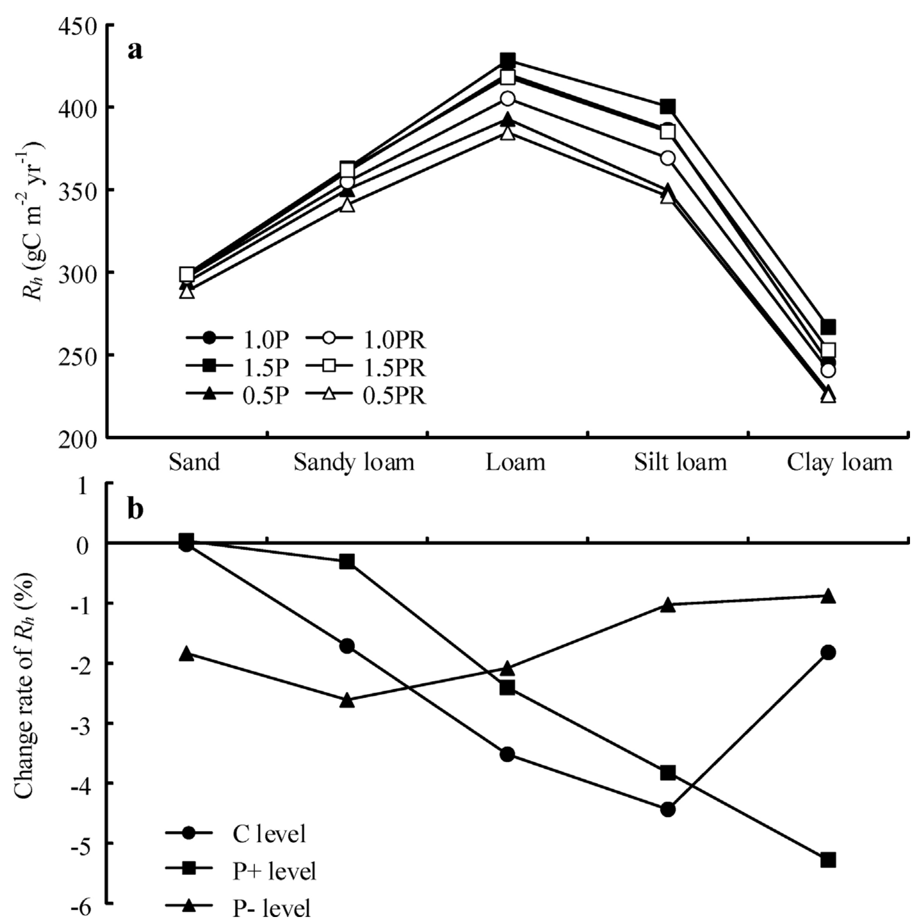

Fig. 3. Heterotrophic respiration (R_h) responses to different precipitation scenarios in five soil types. (a) R_h in different combination of soils and precipitation regimes; (b) impact of redistributed precipitation to R_h represented by relative changing rate at three precipitation levels. The relative changing rates were calculated from following formula: C level = $(R_{h\,1.0PR} - R_{h\,1.0P})/R_{h\,1.0P}$; P+ level = $(R_{h\,1.5PR} - R_{h\,1.5P})/R_{h\,1.5P}$; P− level = $(R_{h\,0.5PR} - R_{h\,0.5P})/R_{h\,0.5P}$.

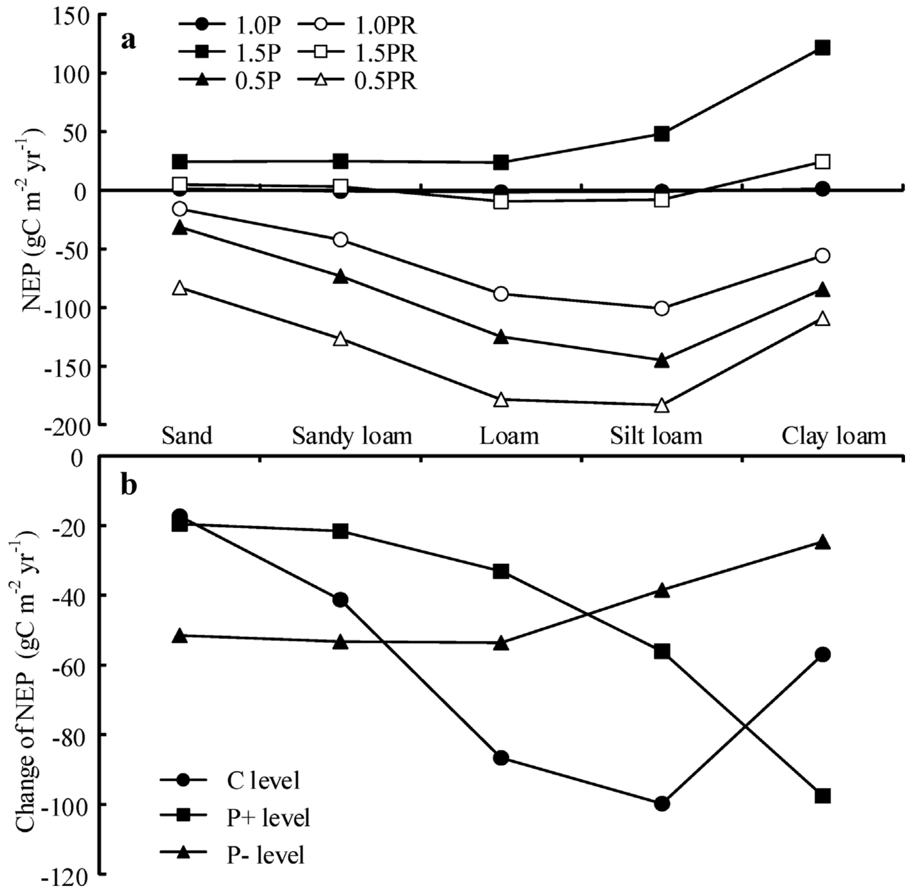

Fig. 4. Net ecosystem productivity (NEP) responses to different precipitation scenarios in five soil types. (a) NEP in different combination of soils and precipitation regimes; (b) relative change of NEP in responses to precipitation redistribution. The relative changes were calculated from following formula: C level = $NEP_{1.0PR} - NEP_{1.0P}$; P+ level = $NEP_{1.5PR} - NEP_{1.5P}$; P- level = $NEP_{0.5PR} - NEP_{0.5P}$.

3.4. Runoff and evapotranspiration

Runoff increased with precipitation (Fig. 5a). It was higher in coarse textured soils and lower in fine textured soils. Redistribution increased runoff by 42.25 mm, 39.72 mm, and 33.80 mm averagely at P+, C, and P− levels respectively. Responses of runoff were slighter in fine textured soils than in coarse textured soils.

Evapotranspiration exhibited an inverse pattern to runoff (Fig. 5b). Evapotranspiration was higher in fine textured soils and lower in coarse textured soils regardless precipitation levels. On average of five textured soils, redistribution decreased evapotranspiration by −42.35 mm, −43.94 mm and −46.23 mm at P+, C, and P− levels respectively. Meanwhile, responses of evapotranspiration in coarse textured soils were slighter than in fine textured soils.

3.5. Soil water content (0–10 cm)

Precipitation redistribution significantly affected surface SWC, which increased with precipitation in March, April, October, and November. From May to September, precipitation was reduced, surface SWC decreased correspondingly (Fig. 6). Surface SWC showed similar trend in three precipitation levels.

Responses of SWC varied with soil textures. SWC at 1.5P and 1.5PR increased more in fine textured clay loam soil than in other soils. Surface SWC at 0.5P and 0.5PR decreased more in clay loam soil than other soils except in sand (Fig. 6). Responses of SWC was slighter in coarse textured soils. In sandy loam and sand, surface SWC changed little with precipitation patterns in January, February, March, April, and December (Fig. 6d and e).

Precipitation redistribution slightly affected mean annual SWC (Fig. 6f). At ambient precipitation level, redistribution reduced SWC in all textured soils, from 10.81% in clay loam to 0.96% in sandy loam. At +50% precipitation level, redistribution decreased SWC in clay loam and silt loam, and increased SWC in loam, sandy loam, and sand. SWC at −50% precipitation level decreased in loam and silt loam. In both fine textured soils and coarse textured soils, surface SWC increased.

4. Discussion

4.1. NPP responses to precipitation redistribution

Generally, NPP was promoted by high precipitation and reduced by low precipitation. Previous studies indicated annual NPP was closely related to precipitation (Hsu et al., 2012; Sala et al., 1988). Increased precipitation could stimulate photosynthesis and increase productivity, while decreased precipitation could suppress photosynthesis and reduce NPP (Wu et al., 2011). At P− level (0.5P and 0.5PR), NPP was higher in coarse textured soils and lower in fine texture soils (Fig. 2a). The pattern agreed with the “inverse texture effect”, which suggested NPP was relatively high in coarse textured sand and sandy loam in arid and semi-arid areas, because coarse textured soils usually support taller and denser perennial vegetation than fine textured soils in these areas (Noy-Meir, 1973).

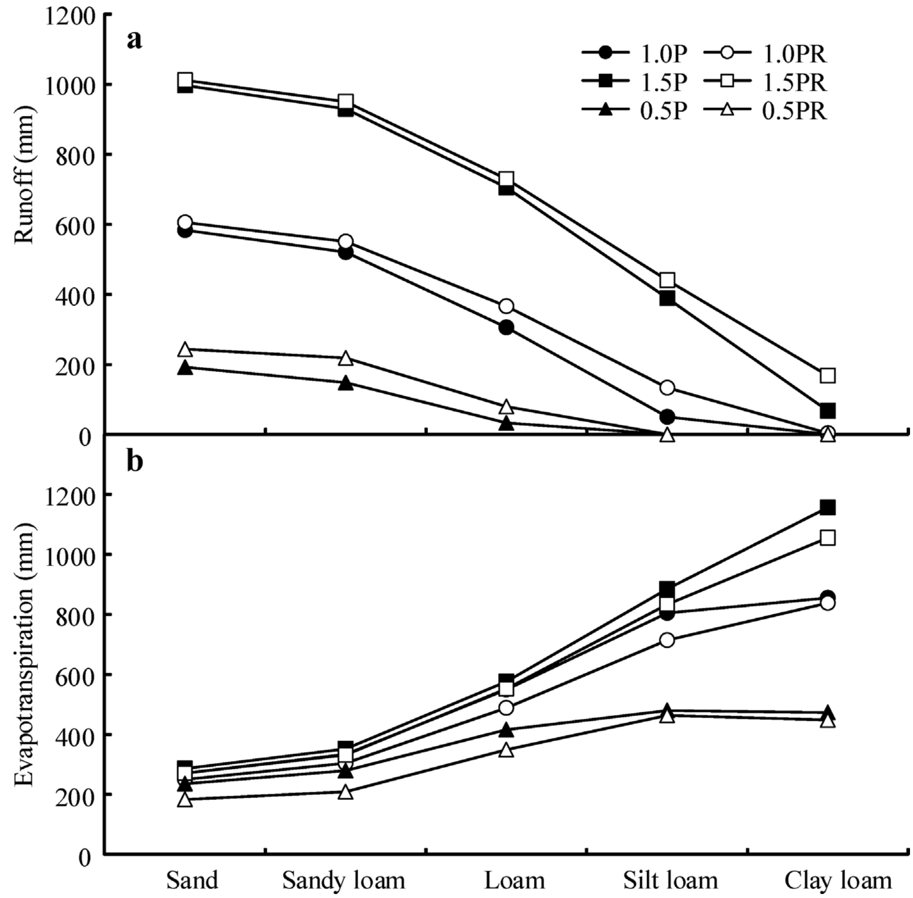

Fig. 5. Runoff and evapotranspiration responses to different precipitation scenarios in five soil types. (a) runoff; (b) evapotranspiration.

Evapotranspiration was positively related to NPP (Rosenzweig, 1968). Different runoff and evapotranspiration amounts caused the NPP variations in different soils (Barth et al., 2007; Heisler-White et al., 2008). The ratio of transpiration to evapotranspiration controlled the amount of transpiration and evaporation. Some research revealed that the ratio of transpiration to evapotranspiration was high in coarse textured soils and low in fine textured soils (Lauenroth and Bradford, 2006). Therefore, coarse textured soils with low evapotranspiration amount (Fig. 5b) but high transpiration: evapotranspiration ratio, and fine textured soils with high evapotranspiration amount (Fig. 5b) but low transpiration: evapotranspiration ratio had lower transpiration than medium textured soils. Vandegriend and Owe (1994) suggested that more water held in surface soil layer favored water evaporation. Fine textured soils with higher field capacities could store more water in the surface layer. That caused higher evaporation in fine textured soils. Although evapotranspiration amount was high in fine textured soils (Fig. 5b), more water was evaporated, thus transpiration was low. Evaporation rate might be relatively high in coarse textured soils, however, low total evapotranspiration amount of coarse textured soils limit transpiration amount. Low transpiration indicated plants had diminished the stomatal openings, which decreased productivities (Claesson and Nycander, 2013; Karim et al., 2008). Consequently, NPP was lower in both fine and coarse textured soils than in medium textured soils.

Soil moisture in surface layer was of great importance to the evaporation regulation (Chanzy and Bruckler, 1993). Coarse textured soils with low surface soil water content (SWC) constrained evaporation (Fig. 6f). Consequently, in fine textured soils, which has high evaporation but low runoff, and coarse textured soils, which has high runoff but low evaporation, transpiration was relatively low.

Moreover, in fine textured soils, relatively small pores among soil particles prevented water from reaching deep soil layers (Rodriguez-Alleres et al., 2007). This also limited the root growth, and caused low NPP. In coarse texture soils, although more water can penetrate into deep soil layers, the low field capacity still limited water availability, which regulated root growth as well.

Soil texture not only controlled the soil water availability which directly constrained NPP, but also was a primary factor of regulating nutrient availability (Lane et al., 1998). Generally, soil organic matter and nutrient availability were higher in fine textured soils than in coarse textured soils (Austin et al., 2004; Lane et al., 1998). Productivity of tallgrass prairie was correlated with nitrogen and water availability (Schimel et al., 1991). Thus in coarse textured soils, even when the precipitation was enhanced, the low nutrient level limited net productivity. Responses of NPP to precipitation redistribution in this kind of soil were relatively slight. Meanwhile, in fine textured soils, the ecosystem productivity was more likely to be limited by water which was mainly drove by precipitation in natural ecosystems. Thus, in fine textured soils, NPP was sensitive to different precipitation patterns.

Redistributed precipitation decreased NPP at all three precipitation levels (Fig. 2a). The reduction rate was lower in increased precipitation levels than in decreased precipitation levels (Fig. 2b). Reduced rainfall amount from May to September caused the transpiration diminished in this period. On the other hand, increased precipitation in spring and fall did not enhance transpiration accordingly, because less plants biomass in these periods transpired less water. This caused a low transpiration in redistribution scenarios (Fig. 5c). As analyzed before, low

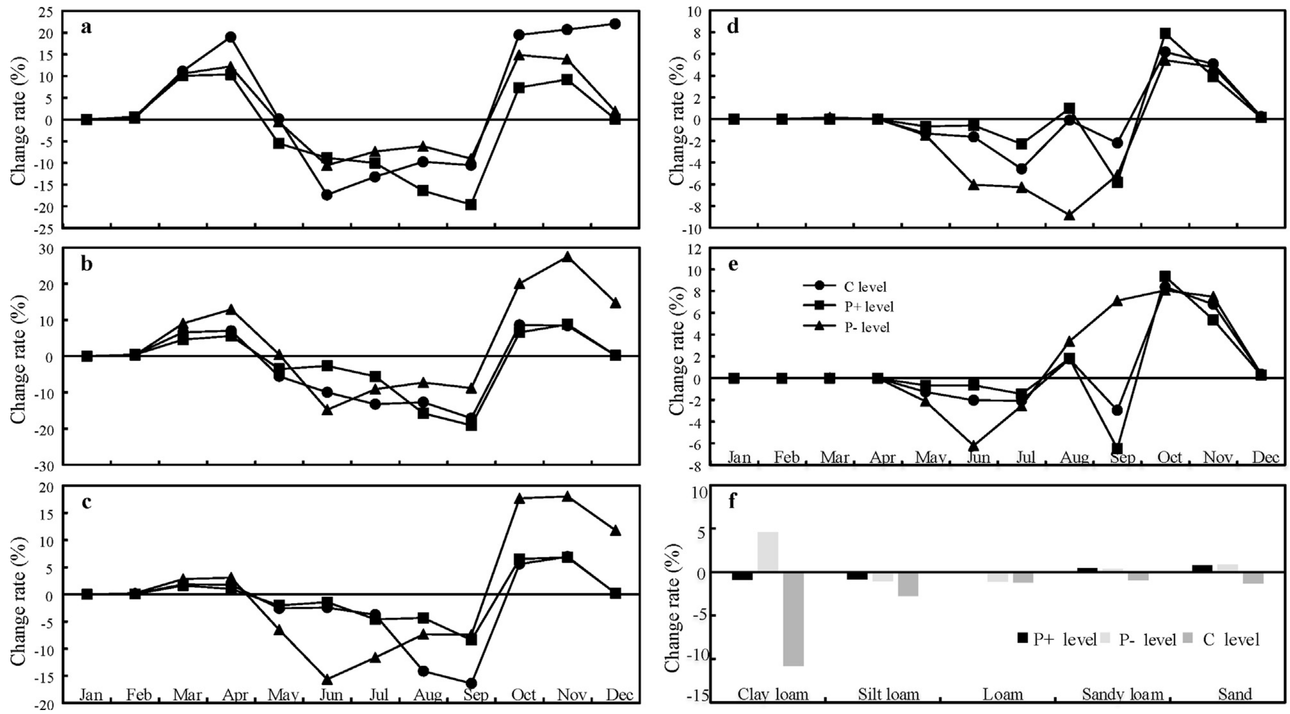

Fig. 6. Relative change rates of surface soil water content (SWC) at different precipitation scenarios. (a) (b) (c) (d) (e) represent the monthly variations of clay loam, silt loam, loam, sandy loam, and sand respectively. And (f) shows the annual mean. The relative change rates were calculated from following formula: C level = $SWC_{1.0PR} - SWC_{1.0P}/SWC_{1.0P}$; P+ level = $SWC_{1.5PR} - SWC_{1.5P}/SWC_{1.5P}$; P− level = $SWC_{0.5PR} - SWC_{0.5P}/SWC_{0.5P}$.

transpiration indicated low productivity. From May to September, tallgrass was undergoing the greatest leaf net photosynthetic rate across the whole year (Zhou et al., 2007). Reduced precipitation decreased water availability for photosynthesis. Moreover, in spring and fall, less intensive photosynthetic rate caused smaller productivity in spite of enhanced precipitation. Comprehensively, annual NPP decreased with precipitation redistribution. In a warm-temperate savanna in Texas, a manipulated experiment also revealed that the redistributed precipitation reduced relative growth rate of plants (Volder et al., 2013).

4.2. R_h responses to precipitation redistribution

R_h was generated from microbial decomposition of root exudates in rhizosphere, aboveground and belowground litter, and soil organic matter (Luo and Zhou, 2006). The main controlling factors of R_h were carbon substrate, temperature, and water availability (Wan et al., 2007). Response patterns of R_h to different precipitation scenarios were similar to those of NPP: enhanced/reduced precipitation increased/decreased R_h, and redistributed rainfall also decreased R_h at all three precipitation levels (Fig. 3a). However, the responses of R_h were much slighter than NPP. This was mainly because SWC, rather than precipitation, directly affected R_h by changing substrate availability and altering the composition and activity of decomposer microbes (Suseela et al., 2012; Williams, 2007). And SWC, especially the surface SWC, was the major driver of soil respiration (Jin et al., 2010). Less variational SWC caused a relatively smaller change in R_h. Similarly, slightly decreased R_h by redistribution at all three precipitation levels could also be attributed to the small decrease of SWC caused by redistribution.

According to our modeling results, R_h was the high in medium textured soils, and low in both fine textured and coarse textured soils. This pattern was similar to NPP. Although carbon substrate might be sufficient, the fine textured soils regulated water from permeating to deep soil layers (Rodriguez-Alleres et al., 2007). Lack of water in deeper soil layers limited root and soil microbial activities and respiration (Wan et al., 2007). And in coarse textured soils, low SWC due to its small field capacity and soil organic matter also constrained the root growth and activity of soil microbes. Many other studies also illustrated that both high and low SWC constrained respiration (Balogh et al., 2011; Byrne et al., 2005; Wan et al., 2007).

Responses of coarse textured soils to precipitation scenarios seemed less dramatic. Coarse textured soils could easily reach its wilting point, but could not store much water due to its low field capacity. In other words, SWC was less sensitive to precipitation alternation in this kind of soil (Fig. 6). In fine textured soils, however, SWC was more easily to be influenced by precipitation amount (Fig. 6) since field capacity was no longer the limiting factor. Surface SWC was the major driver of soil respiration (Jin et al., 2010), thus R_h variation was larger in fine textured soils.

4.3. NEP responses to precipitation redistribution

Due to a highly variational NPP and less changeable R_h under different precipitation scenarios, NEP exhibited a different pattern from both NPP and R_h (Fig. 4). Increased precipitation potentially stimulated net carbon uptake, and the uptake amount was greater in fine textured soils than in other soils. For ambient precipitation level, NEP was zero, because the ecosystem had reached the equilibrium state. For 1.0PR, 0.5P and 0.5PR, NEP decreased in all soil types. In these three scenarios, both coarse and fine textured soils seemed to be resistant to carbon emission. The results of NEP increasing/decreasing with enhanced/reduced precipitation agreed with the key finding of a meta-analysis of 85 experimental manipulations (Wu et al., 2011). Jongen et al. (2011) also observed a negative correlation between annually integrated NEE and annual precipitation, which indicate NEP had a positive correlation with precipitation.

As reported by Parton et al. (2012), more than 95% of the net carbon uptake occurring during May and June. Low precipitation during this period greatly reduced net carbon uptake. Moreover, Jongen et al. (2011) suggested that low precipitation at the peak of the growing season, as in the spring, decreased carbon sequestration. In our study, precipitation from May to September had been subtracted by 40%, so NEP had been reduced correspondingly.

4.4. Evapotranspiration and runoff response to precipitation redistribution

Runoff was generated after soil being saturated. Field capacity of soil, which was the difference of field capacity and wilting point, measured the capacity of soil to hold water (Weng and Luo, 2008). Under increased precipitation scenarios, the soil water capacity could be easy to reach. Thus runoff would increase. Similarly, more precipitation could be used by plants, and evapotranspiration was likely to increase. On the contrary, under decreased precipitation level, less water caused lower runoff and evapotranspiration.

Fine textured soils had higher field capacity (Table 1), and could store more water than coarse textured soils. Therefore in each rainfall event, more water were stored in fine textured soils, this induced lower runoff amount (Fig. 5a). Descroix et al. (2001) also concluded the similar trend. Contrarily, in coarse textured soils, soil could not store much water because of its lower field capacity. The exceeded water was lost through runoff. Thus runoff was higher in coarse textured soils such (Fig. 5a). Other research also found that runoff amount was greater in coarse textured soils (Descroix et al., 2001; Kemper and Noonan, 1970). Large runoff in coarse textured sand soil indicated small evapotranspiration, while small runoff meant large evapotranspiration in fine textured soil. Therefore, responses of different soils to six precipitation patterns were opposite to those of runoff. Moreover, the higher field capacity of fine textured clay loam soil could keep it more resistant for precipitation alternation, thus this soil was less sensitive. Lower field capacity of coarse textured soil could be more easily affected by precipitation. Thus runoff in coarse textured soils are more sensitive.

The plants needed more water because of intensive activities in summer. Less precipitation during summer caused a decreased evapotranspiration. In spring and fall, although the precipitation was more, less plants activities generated lower evapotranspiration. Consequently, redistributed precipitation decreased evapotranspiration in all three precipitation levels. Decreased evapotranspiration also inferred the increased runoff by redistributed precipitation.

4.5. Surface soil water content responses to precipitation redistribution

SWC will stop increasing when soil reached its field capacity (Novak and Havrila, 2006). In the months with higher precipitation, SWC will increase because of higher water availability. Also, it will decrease in those decreased precipitation months. This pattern was consistent in all soil textures (Fig. 6a–e).

However, responses of SWC in diverse soil textures were different. Fine textured soils needed more precipitation to reach its maximum SWC. Thus surface SWC changed more in clay loam than other soil types. Contrarily, even small amount of rainfall could saturate coarse textured soils with lower field capacity. Therefore sand soils changed less with precipitation scenarios.

The mean annual surface SWC changed little with precipitation, especially in coarse textured soils (Fig. 6f). Fay et al. (2000) and Flanagan et al. (2013) also observed SWC changed little with precipitation change. Additionally, Fay et al. (2000) argued that SWC was significantly affected by precipitation amount under increased precipitation interval, while altered precipitation amount had little effect on SWC under nature interval. Surface SWC was directly affected by precipitation intervals. Our study did not change the timing and interval of rainfall events, thus SWC changed little with different precipitation scenarios.

5. Conclusions

Our modeling study showed that redistribution of precipitation was likely to decrease NPP, R_h and NEP at P+, C, and P− levels. Soil texture was a crucial regulator for ecosystem carbon and water processes. Through impacting soil water cycles, the intra-annual redistribution of precipitation from summer to spring and fall will promote carbon release, regardless of precipitation levels. Additionally, the extent to which the ecosystem responses to redistribution of precipitation is largely controlled by soil texture.

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References

An, N., Price, K.P., Blair, J.M., 2013. Estimating above-ground net primary productivity of the tallgrass prairie ecosystem of the Central Great Plains using AVHRR NDVI. Int. J. Remote Sens. 34, 3717–3735.

Austin, A.T., Yahdjian, L., Stark, J.M., Belnap, J., Porporato, A., Norton, U., Ravetta, D.A., Schaeffer, S.M., 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141, 221–235.

Balogh, J., Pinter, K., Foti, S., Cserhalmi, D., Papp, M., Nagy, Z., 2011. Dependence of soil respiration on soil moisture, clay content, soil organic matter, and CO_2 uptake in dry grasslands. Soil Biol. Biochem. 43, 1006–1013.

Barth, J.A.C., Freitag, H., Fowler, H.J., Smith, A., Ingle, C., Karim, A., 2007. Water fluxes and their control on the terrestrial carbon balance: results from a stable isotope study on the Clyde Watershed (Scotland). Appl. Geochem. 22, 2684–2694.

Brunsell, N.A., Jones, A.R., Jackson, T.L., Feddema, J.J., 2010. Seasonal trends in air temperature and precipitation in IPCC AR4 GCM output for Kansas, USA: evaluation and implications. Int. J. Climatol. 30, 1178–1193.

Byrne, K.A., Kiely, G., Leahy, P., 2005. CO_2 fluxes in adjacent new and permanent temperate grasslands. Agr. For. Meteorol. 135, 82–92.

Chanzy, A., Bruckler, L., 1993. Significance of soil surface moisture with respect to daily bare soil evaporation. Water Resour. Res. 29, 1113–1125.

Chou, W.W., Silver, W.L., Jackson, R.D., Thompson, A.W., Allen-Diaz, B., 2008. The sensitivity of annual grassland carbon cycling to the quantity and timing of rainfall. Global Change Biol. 14, 1382–1394.

Claesson, J., Nycander, J., 2013. Combined effect of global warming and increased CO_2-concentration on vegetation growth in water-limited conditions. Ecol. Model 256, 23–30.

Craine, J.M., 2013. The importance of precipitation timing for grassland productivity. Plant Ecol. 214, 1085–1089.

Craine, J.M., Nippert, J.B., Elmore, A.J., Skibbe, A.M., Hutchinson, S.L., Brunsell, N.A., 2012. Timing of climate variability and grassland productivity. Proc. Nat. Acad. Sci. U.S.A. 109, 3401–3405.

Descroix, L., Viramontes, D., Vauclin, M., Barrios, J.L.G., Esteves, M., 2001. Influence of soil surface features and vegetation on runoff and erosion in the Western Sierra Madre (Durango, Northwest Mexico). Catena 43, 115–135.

Epstein, H.E., Lauenroth, W.K., Burke, I.C., 1997. Effects of temperature and soil texture on ANPP in the US great plains. Ecology 78, 2628–2631.

Farquhar, G.D., Caemmerer, S.V., Berry, J.A., 1980. A biochemical-model of photosynthetic CO_2 Assimilation in Leaves of C-3 Species. Planta 149, 78–90.

Fay, P.A., Carlisle, J.D., Knapp, A.K., Blair, J.M., Collins, S.L., 2000. Altering rainfall timing and quantity in a mesic grassland ecosystem: design and performance of rainfall manipulation shelters. Ecosystems 3, 308–319.

Flanagan, L.B., Sharp, E.J., Letts, M.G., 2013. Response of plant biomass and soil respiration to experimental warming and precipitation manipulation in a Northern Great Plains grassland. Agr. For. Meteorol. 173, 40–52.

Harley, P.C., Thomas, R.B., Reynolds, J.F., Strain, B.R., 1992. Modeling photosynthesis of cotton grown in elevated CO_2. Plant Cell Environ. 15, 271–282.

Harper, C.W., Blair, J.M., Fay, P.A., Knapp, A.K., Carlisle, J.D., 2005. Increased rainfall variability and reduced rainfall amount decreases soil CO_2 flux in a grassland ecosystem. Global Change Biol. 11, 322–334.

Heisler-White, J.L., Knapp, A.K., Kelly, E.F., 2008. Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland. Oecologia 158, 129–140.

Hsu, J.S., Powell, J., Adler, P.B., 2012. Sensitivity of mean annual primary production to precipitation. Global Change Biol. 18, 2246–2255.

Huxman, T.E., Cable, J.M., Ignace, D.D., Eilts, J.A., English, N.B., Weltzin, J., Williams, D.G., 2004. Response of net ecosystem gas exchange to a simulated precipitation pulse in a semi-arid grassland: the role of native versus non-native grasses and soil texture. Oecologia 141, 295–305.

IPCC, 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

IPCC, 2013. Summary for Policymakers. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Jin, Z., Dong, Y.S., Qi, Y.C., An, Z.S., 2010. Soil respiration and net primary productivity in perennial grass and desert shrub ecosystems at the Ordos Plateau of Inner Mongolia, China. J. Arid. Environ. 74, 1248–1256.

Jongen, M., Pereira, J.S., Aires, L.M.I., Pio, C.A., 2011. The effects of drought and timing of precipitation on the inter-annual variation in ecosystem–atmosphere exchange in a Mediterranean grassland. Agr. Forest Meteorol. 151, 595–606.

Karim, A., Veizer, J., Barth, J., 2008. Net ecosystem production in the great lakes basin and its implications for the North American missing carbon sink: a hydrologic and stable isotope approach. Global Planet. Change 61, 15–27.

Kemper, W.D., Noonan, L., 1970. Runoff as affected by salt treatments and soil texture. Soil Sci. Soc. Am. Proc. 34, 126–130.

Knapp, A.K., Burns, C.E., Fynn, R.W.S., Kirkman, K.P., Morris, C.D., Smith, M.D., 2006. Convergence and contingency in production–precipitation relationships in North American and South African C-4 grasslands. Oecologia 149, 456–464.

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

Lane, D.R., Coffin, D.P., Lauenroth, W.K., 1998. Effects of soil texture and precipitation on above-ground net primary productivity and vegetation structure across the Central Grassland region of the United States. J. Veg. Sci. 9, 239–250.

Lauenroth, W.K., Bradford, J.B., 2006. Ecohydrology and the partitioning AET between transpiration and evaporation in a semiarid steppe. Ecosystems 9, 756–767.

Liu, L., Hong, Y., Hocker, J.E., Shafer, M.A., Carter, L.M., Gourley, J.J., Bednarczyk, C.N., Yong, B., Adhikari, P., 2012. Analyzing projected changes and trends of temperature and precipitation in the southern USA from 16 downscaled global climate models. Theor. Appl. Climatol. 109, 345–360.

Luo, Y., Zhou, X., 2006. Soil respiration and the environment. Elsevier Academic Press, Amsterdam; Boston xi, pp. 316.

Novak, V., Havrila, J., 2006. Method to estimate the critical soil water content of limited availability for plants. Biologia 61, S289–S293.

Noy-Meir, I., 1973. Desert ecosystems: environment and producers. Annu. Rev. Ecol. Syst. 4, 25–51.

Parton, W., Morgan, J., Smith, D., Del Grosso, S., Prihodko, L., Lecain, D., Kelly, R., Lutz, S., 2012. Impact of precipitation dynamics on net ecosystem productivity. Global Change Biol. 18, 915–927.

Patricola, C.M., Cook, K.H., 2013. Mid-twenty-first century warm season climate change in the Central United States. Part I: regional and global model predictions. Clim. Dyn. 40, 551–568.

Robinson, T.M.P., La Pierre, K.J., Vadeboncoeur, M.A., Byrne, K.M., Thomey, M.L., Colby, S.E., 2013. Seasonal, not annual precipitation drives community productivity across ecosystems. Oikos 122, 727–738.

Rodriguez-Alleres, M., de Blas, E., Benito, E., 2007. Estimation of soil water repellency of different particle size fractions in relation with carbon content by different methods. Sci. Total Environ. 378, 147–150.

Rosenzweig, M.L., 1968. Net primary productivity of terrestrial communities: prediction from climatological data. Am. Nat. 102, 67–74.

Sala, O.E., Parton, W.J., Joyce, L.A., Lauenroth, W.K., 1988. Primary production of the Central Grassland Region of the United States. Ecology 69, 40–45.

Schimel, D.S., Kittel, T.G.F., Knapp, A.K., Seastedt, T.R., Parton, W.J., Brown, V.B., 1991. Physiological interactions along resource gradients in a tallgrass prairie. Ecology 72, 672–684.

Suseela, V., Conant, R.T., Wallenstein, M.D., Dukes, J.S., 2012. Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. Global Change Biol. 18, 336–348.

Takemi, T., 2010. Dependence of the precipitation intensity in mesoscale convective systems to temperature lapse rate. Atmos. Res. 96, 273–285.

Vandegriend, A.A., Owe, M., 1994. Bare soil surface-resistance to evaporation by vapor diffusion under semiarid conditions. Water Resour. Res. 30, 181–188.

Volder, A., Briske, D.D., Tjoelker, M.G., 2013. Climate warming and precipitation redistribution modify tree-grass interactions and tree species establishment in a warm-temperate savanna. Global Change Biol. 19, 843–857.

Wan, S., Norby, R.J., Ledford, J., Weltzin, J.F., 2007. Responses of soil respiration to elevated CO_2, air warming, and changing soil water availability in a model old-field grassland. Global Change Biol. 13, 2411–2424.

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

Weng, E.S., Luo, Y.Q., 2008. Soil hydrological properties regulate grassland ecosystem responses to multifactor global change: a modeling analysis. J. Geophys. Res. Biogeo. 113.

Williams, M.A., 2007. Response of microbial communities to water stress in irrigated and drought-prone tallgrass prairie soils. Soil Biol. Biochem. 39, 2750–2757.

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

Xu, X., Niu, S.L., Sherry, R.A., Zhou, X.H., Zhou, J.Z., Luo, Y.Q., 2012. Interannual variability in responses of belowground net primary productivity (NPP) and NPP partitioning to long-term warming and clipping in a tallgrass prairie. Global Change Biol. 18, 1648–1656.

Zhou, X.H., Liu, X.Z., Wallace, L.L., Luo, Y.Q., 2007. Photosynthetic and respiratory acclimation to experimental warming for four species in a tallgrass prairie ecosystem. J. Integr. Plant Biol. 49, 270–281.

Zhou, X.H., Weng, E.S., Luo, Y.Q., 2008. Modeling patterns of nonlinearity in ecosystem responses to temperature, CO_2, and precipitation changes. Ecol. Appl. 18, 453–466.