Agricultural and Forest Meteorology 232 (2017) 359–366

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Effects of warming and increased precipitation on net ecosystem productivity: A long-term manipulative experiment in a semiarid grassland

Guoyong Li[a], Hongyan Han[a], Yue Du[b], Dafeng Hui[c], Jianyang Xia[d], Shuli Niu[e], Xiaona Li[a], Shiqiang Wan[a,*]

[a] International Joint Research Laboratory for Global Change Ecology, College of Life Sciences, Henan University, Kaifeng, Henan 475004, China
[b] College of Life Sciences, University of Chinese Academy of Sciences, Beijing 100049, China
[c] Department of Biological Sciences, Tennessee State University, Nashville, TN 37209, USA
[d] Tiantong National Forest Ecosystem Observation and Research Station, School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200062, China
[e] Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China

ARTICLE INFO

Article history:
Received 12 August 2015
Received in revised form 31 August 2016
Accepted 12 September 2016
Available online 15 September 2016

Keywords:
Carbon cycle
Temperate grassland
Global warming
Precipitation regime
Gross primary productivity
Ecosystem respiration

ABSTRACT

The balance between ecosystem carbon dioxide (CO_2) uptake and release determines the level of carbon (C) sequestration in terrestrial ecosystems and its potential impact on CO_2 concentration in the atmosphere. However, how changes in temperature and precipitation will affect the relationships of net ecosystem productivity (NEP) with gross primary productivity (GPP) and ecosystem respiration (ER) remains unclear. In this study, a nine-year field manipulative experiment was conducted with elevated temperature and increased precipitation in a semiarid steppe of Inner Mongolia, China. Experimental warming reduced GPP and ER by almost the same amount, leading to a slight change in NEP ($-0.16\ \mu mol\ m^{-2}\ s^{-1}$), whereas increased precipitation stimulated GPP more than ER during the growing seasons, resulting in an enhanced NEP ($+0.63\ \mu mol\ m^{-2}\ s^{-1}$). In addition, seasonal patterns of ecosystem C fluxes and the NEP-GPP or NEP-ER relationships were not altered by experimental warming. However, increased precipitation delayed the peak of GPP during the growing seasons and enhanced the correlation between NEP and GPP in the steppe ecosystem. The enhanced control of GPP over NEP under the increased precipitation suggests that ecosystem C sequestration is attributed more to C uptake than C release when water availability is improved in the semiarid grassland. Our findings provide an insight into the response mechanism of ecosystem C flux to warming and precipitation change in semiarid grasslands, and facilitate the projection of terrestrial ecosystem C dynamics and climate feedbacks in the future.

1. Introduction

Terrestrial ecosystems absorb carbon (C) from the atmosphere through photosynthesis (i.e. gross primary productivity, GPP) and release C into the atmosphere via ecosystem respiration (ER) (Chen et al., 2015; Lasslop et al., 2010; Law et al., 2002; Valentini et al., 2000; van Dijk and Dolman, 2004; Yu et al., 2013). As the net balance of these two processes, net ecosystem productivity (NEP) is an indicator of the C sink or source in terrestrial ecosystems. Therefore, quantifying the NEP-GPP and NEP-ER relationships and their responses to climate warming and changing precipitation regime is critical for projections of net C balance and global C cycling in the future.

The NEP-GPP and NEP-ER relationships generally vary with climate zones and biomes. Global assessments in forest, grassland, cropland, and wetland ecosystems have demonstrated that NEP change is more closely related to variation in GPP than in ER (Law et al., 2002; Niu et al., 2012; van Dijk and Dolman, 2004; Wohlfahrt et al., 2008). Inter-annual fluctuation in NEP is more similar to that in GPP than that in ER, implying that NEP is more strongly controlled by GPP (Beringer et al., 2007; Saigusa et al., 2005; Urbanski et al., 2007). By contrast, a study across 15 European forests revealed that spatial variability of NEP is influenced more by ER change because ER increases with latitudes, but GPP remains relatively constant (Valentini et al., 2000). The closer relationship between NEP and ER is also supported by several previous studies in tropical forests

* Corresponding author.
E-mail addresses: swan@henu.edu.cn, swan@ibcas.ac.cn (S. Wan).

http://dx.doi.org/10.1016/j.agrformet.2016.09.004
0168-1923/

(Saleska et al., 2003; Yan et al., 2013; Zhang et al., 2010). The conflicting results on the NEP-GPP and NEP-ER relationships may be attributable to the differences in vegetation types, soil nutrients, precipitation, temperature, and solar radiation at different sites (Goulden et al., 1996; van Dijk et al., 2005; Wilson and Baldocchi, 2001). Understanding of the NEP-GPP and NEP-ER relationships in different ecosystems is necessary to resolve the disputes.

Moreover, the current knowledge on the NEP-GPP and NEP-ER relationships is primarily obtained by using the eddy covariance technique under natural climate conditions, with the potential impacts of changes in temperature and precipitation on the relationships largely being neglected. Concurrent climate warming and changes in global and regional precipitation regimes (IPCC, 2013) will have profound impacts on temperature- and water-associated biological processes, with subsequent influences on terrestrial C balance (Hui et al., 2003; Liu et al., 2009; Niu et al., 2008; Scanlon and Albertson, 2004; Wan et al., 2009; Wu et al., 2011; Xia et al., 2014). It has been well illustrated that GPP and ER have differential responses and sensitivities to changes in temperature and water availabilities (Luo, 2007; Ma et al., 2007; Niu et al., 2012; Urbanski et al., 2007; Yan et al., 2013), suggesting shifts in contributions of GPP and ER to NEP in response to climate warming and changing precipitation regimes.

Grassland in arid and semiarid regions is one of the major terrestrial biomes and plays an important role in driving dynamic of global land C sink (Poulter et al., 2014). A field manipulative experiment was established in April 2005 in a semiarid temperate steppe in the Mongolian Plateau to examine the potential impact of warming and increased precipitation on ecosystem C cycling. Ecosystem C fluxes were measured using the chamber-based technique during the growing seasons from 2005 to 2013. The specific objectives of this study were: (1) to examine long-term effect of warming and increased precipitation on ecosystem C fluxes, and (2) to investigate the possible impacts of warming and increased precipitation on the NEP-GPP and NEP-ER relationships in the semiarid grassland.

2. Materials and methods

2.1. Experimental site

The experimental field site was located in a temperate steppe in Duolun County (42°02′N, 116°17′E, 1324 m a.s.l), Inner Mongolia, China. Mean annual temperature (1960–2013) was 2.4 °C with a monthly mean temperature ranging from −17.6 °C in January to 19.2 °C in July. Mean annual precipitation (1960–2013) was 374.5 mm, fluctuating greatly between years, and approximately 90% of precipitation occurred during the growing season (from May to October). The plant community was dominated by grasses (*Stipa krylovii*, *Cleistogenes squarrosa*, *Agropyron cristatum*) and forbs (*Artemisia frigida*, *Potentilla acaulis*, *Allium bidentatum*). Plant community cover was estimated using a canopy interception technique based on a $1 \times 1\,m^2$ frame with 100 equally distributed grids ($10 \times 10\,cm^2$) at the middle of the growing season for each year from 2005 to 2013. Plant community cover was calculated as the percentage of grids occupied by plant canopy, which ranged from 20 to 70%. The aboveground primary productivity of grassland at the study site was approximately 100–200 $g\,m^{-2}\,yr^{-1}$ (Niu et al., 2008). The soil at the site was classified as chestnut according to the Chinese soil classification system and pH value was 6.84 ± 0.07.

2.2. Experimental design

A split-plot design was employed in the current study with precipitation as the primary factor and temperature as the secondary factor. In April 2005, three pairs of $10 \times 15\,m^2$ plots were selected in the fenced study area and the distance between the two plots of each pair was 1 m. One plot in each pair was assigned to the increased precipitation treatment and another to the ambient precipitation treatment. In each of the increased or ambient precipitation plots, four $3 \times 4\,m^2$ subplots were chosen and randomly treated as warmed or unwarmed subplots. Therefore, there were 4 treatments including control, warming, increased precipitation, and warming plus increased precipitation. For each treatment, there were 6 replicates.

The increased precipitation treatments were performed using 6 sprinklers during the growing seasons from 2005 to 2013. In July and August of each year, a total amount of 120 mm water was evenly added ($15\,mm\,wk^{-1} \times 8\,wk$) to the increased precipitation plots. The warming treatments were conducted with 165-cm (Length) × 15-cm (Width) MSR-2420 infrared radiators (Kalglo Eletronics, Bethlehem, PA, USA) fixed 2.5 m above the ground. The warmed subplots were heated continuously from March 15 to November 15 each year. To simulate the shading effects of the infrared radiator on the warmed subplot, a “dummy” heater with the same shape and size as the heat equipment was suspended 2.5 m high in the unwarmed subplots. More details of the experimental design were described in Niu et al. (2008), Liu et al. (2009), and Yang et al. (2011).

2.3. Measurements of environmental variables

Soil temperature at 5 cm depth was measured with thermocouples and recorded in a CR1000 datalogger (Campbell Scientific, Logan, UT, USA) every hour from June 2005 to October 2013. Volumetric soil water content (0–10 cm) was measured with a portable device (Diviner 2000, Sentek Pty Ltd, Balmain, Australia) 2–6 times per month throughout the 9 growing seasons from 2005 to 2013.

2.4. Measurements of ecosystem C fluxes

Ecosystem C fluxes were measured using a transparent sampling chamber (50 cm length × 50 cm width × 50 cm height) attached to the LI-6400 Portable Photosynthesis System (Li-Cor, Lincoln, NE, USA) for all the subplots. In each subplot, two aluminum (stainless steel later) frames ($50 \times 50\,cm^2$ for each) were installed into soil to a depth of 2–3 cm at two opposite corners in April 2005. The fixed frames acted as a linkage between the sampling chamber and the soil surface.

The measured C fluxes included the fluxes of net ecosystem CO_2 exchange (NEE, NEP = −NEE) between ecosystem and atmosphere and ER. During each measurement of NEE, the sampling chamber was placed on the frame surface and two small fans fixed at two opposite top corners of chamber ran continuously to mix the air inside the sampling chamber. The concentration of CO_2 in the chamber was analyzed by the infrared gas analyzer every 10 s and recorded in the flash card of LI-6400 Portable Photosynthesis System during a 90-s period. NEP was calculated from changes in CO_2 concentration during the measuring period. Following the measurements of NEE, the chamber was opened for over 30 s, replaced on the frame again, and then covered with an opaque cloth for ER measurement. NEE and ER were measured between 9:00 a.m. and 12:00 p.m. (local time) on the measuring days during each month. Ecosystem CO_2 fluxes were usually measured twice per month in the first six years (2005–2010) and three times per month in the last three years (2011–2013).

2.5. Statistical analyses

Positive and negative NEP values represented CO_2 uptake by and release from the ecosystem, respectively. Ecosystem respiration and NEP were averaged for the 2 frames in each subplot repre-

Table 1
Results (*P* values) of two-way repeated measurement ANOVAs on the impacts of warming (W), increased precipitation (P), and their interaction on net ecosystem productivity (NEP), gross primary productivity (GPP), ecosystem respiration (ER), soil temperature (ST), and soil moisture (SM). The total sampling size was 2760.

Factors	df	NEP	GPP	ER	ST	SM
P	1	0.012	0.015	0.017	<0.001	0.024
W	1	0.096	0.027	0.030	<0.001	0.003
P × W	1	0.859	0.792	0.792	0.514	0.289

senting the measured CO_2 fluxes of the subplot. GPP was estimated as the sum of NEP and ER.

Split-design repeated-measurement ANOVAs were used to examine the effects of warming, increased precipitation, and their interaction on CO_2 fluxes, as well as soil moisture and temperature, across the 9 growing seasons. Regression analyses were used to examine the NEP-GPP and NEP-ER relationships observed during the growing seasons from 2005 to 2013. The seasonal-average values of NEP, GPP, and ER for each plot were used in the regression analyses. The heterogeneity of regression slopes was tested and the common slope was calculated when homogeneity of slopes occurred (Hui et al., 2003; Warton and Weber, 2002). The calculations and tests of common slope were conducted using Standardized Major Axis Tests & Routines (SMATR) Version 2.0 (Falster et al., 2006; http://www.bio.mq.edu.au/ecology/SMATR/) between temperature or precipitation treatments.

To assess the direct and indirect impacts of microclimate (soil temperature and moisture) on GPP and ER, as well as the control of GPP over ER, path analysis was conducted using R statistical software (lavaan package, R 3.0.3).

3. Results

3.1. Soil microclimate

Across the 9 growing seasons, soil temperature at 5 cm depth was elevated, on average, by 0.4 °C by warming ($P<0.001$), but decreased by 0.5 °C by increased precipitation ($P<0.001$). Mean soil water content was reduced by 1.0% (absolute change) under experimental warming ($P=0.003$, Table 1), whereas enhanced by 1.6% (absolute change) under increased precipitation ($P=0.024$, Table 1). No interactive effect was found between warming and increased precipitation on either soil water availability or temperature (both $P>0.05$, Table 1).

3.2. Seasonal patterns of CO_2 fluxes under experimental warming and increased precipitation

During the growing seasons, NEP and GPP reached their peaks in August (Fig. 1a and b), whereas maximum ER occurred in July without and with warming (Fig. 1c). The seasonal patterns of NEP and ER did not change under the ambient and increased precipitation treatments (Fig. 2a,c). However, the maximum GPP under the increased precipitation treatments occurred in August (Fig. 2b).

Seasonal mean NEP, GPP and ER were substantially increased by 29.3% (0.63 μmol m^{-2} s^{-1}, absolute value), 31.5% (1.56 μmol m^{-2} s^{-1}), and 33.2% (0.93 μmol m^{-2} s^{-1}), respectively, under the increased precipitation across the 9 growing seasons (*P* values: 0.012, 0.015, and 0.017 for NEP, GPP, and ER, respectively; Table 1). Mean GPP and ER were significantly decreased by 5.9% (0.35 μmol m^{-2} s^{-1}, absolute value) and 5.5% (0.18 μmol m^{-2} s^{-1}), respectively (*P* values: 0.027 and 0.030 for GPP and ER, respectively; Table 1), by warming. However, mean NEP decreased slightly under the warming treatments (−6.4%, 0.16 μmol m^{-2} s^{-1}; $P=0.096$; Table 1). No interactions of warming and increased precipitation on CO_2 fluxes were found (all $P>0.05$; Table 1).

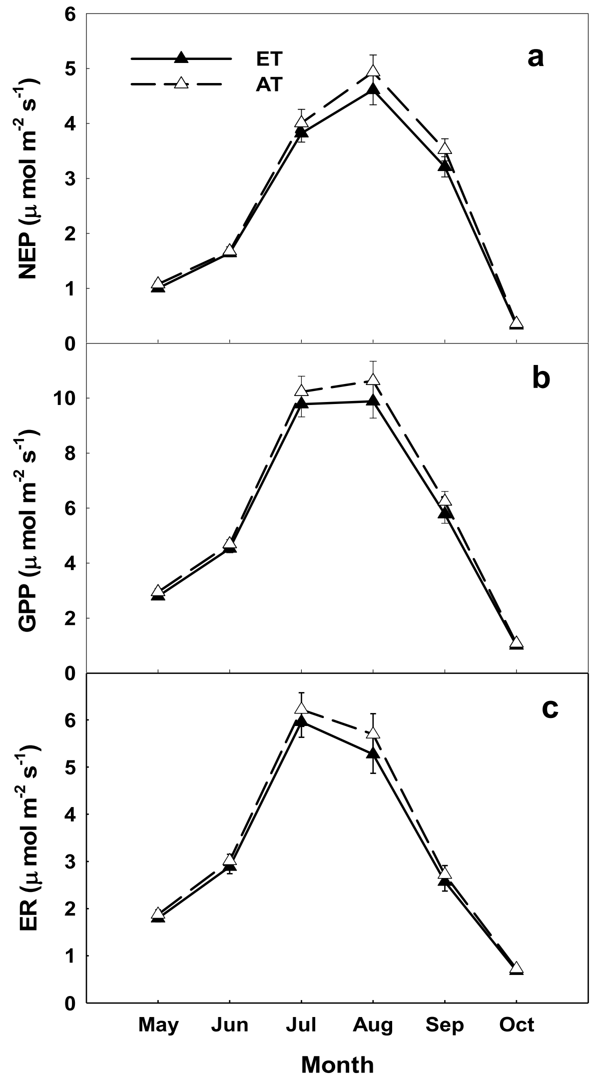

Fig. 1. Carbon fluxes, including net ecosystem productivity (NEP; a), gross primary productivity (GPP; b), and ecosystem respiration (ER; c), in the unwarmed (open triangles) and warmed (filled triangles) plots during the growing season (May–October) across 9 years (from 2005 to 2013) in a semiarid steppe. AT: ambient temperature treatments (control and increased precipitation), ET: elevated temperature treatments (warming and warming plus increased precipitation). Each data point represents the monthly mean value of CO_2 flux across 9 years under the two temperature treatments.

3.3. Contributions of GPP and ER to NEP under different experimental treatments

Annual mean NEP linearly increased with GPP and ER under the ambient ($R^2=081$, $P<0.001$ for NEP vs. GPP; $R^2=0.58$, $P=0.004$; Fig. 3a and b) and warming treatments ($R^2=0.62$, $P=0.003$ for NEP vs. GPP; $R^2=0.32$, $P=0.056$ for NEP vs. ER; Fig. 3a and b) over the 9 growing seasons. A common slope between NEP-GPP relationships (common slope = 0.381, $P=0.759$), as well as that between NEP-ER relationships (common slope = 0.541, $P=0.563$), was found in the unwarmed and warmed plots. Both slopes had no shift in elevation or along the common slope between the two temperature treatments (all $P>0.05$; Fig. 3). In addition, NEP increased with GPP ($R^2=0.51$, $P=0.009$) in the increased precipitation plots, but not in the ambient precipitation plots (Fig. 4a), suggesting the enhanced correlation between changes in NEP and GPP under

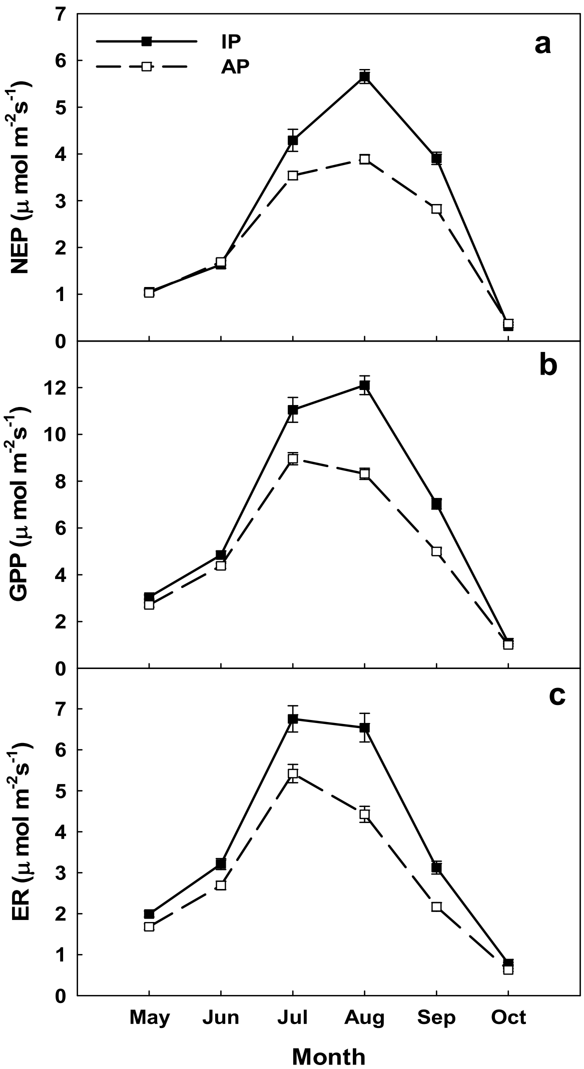

Fig. 2. Carbon (C) fluxes, including net ecosystem productivity (NEP; a), gross primary productivity (GPP; b), and ecosystem respiration (ER; c), under ambient (open squares) and increased precipitation (solid squares) during the growing season (May-October) across 9 years (from 2005 to 2013) in a semiarid steppe. AP: ambient precipitation treatments (control and warming), IP: increased precipitation treatments (increased precipitation only and warming plus increased precipitation). Each data point represents the monthly mean value of CO_2 flux across 9 years under the two precipitation treatments.

increased precipitation. No correlation of NEP change with variation in ER was found under any of the precipitation scenarios (both $P > 0.05$; Fig. 4b).

Path analysis demonstrated that GPP increased with soil moisture (SM; correlation coefficients $r = 0.37–0.42$) and soil temperature (ST; $r = 0.40–0.52$), whereas ER change was positively dependent on GPP change ($r = 0.81–0.85$) and ST ($r = 0.15–0.19$; Fig. 5). A significant correlation between SM and ST was found under the different experimental treatments ($r = 0.14–0.25$; Fig. 5). In addition, little change in all the correlation coefficients among GPP, ER, SM, and ST was found under warming. However, increased precipitation enhanced the correlation coefficient between SM and ST, as well as between GPP and ST, compared with those under the ambient precipitation.

4. Discussion

The primary control of NEP by GPP instead of ER over the 9 years observed in this semiarid grassland ecosystem is consistent with the conclusions in several previous studies (Niu et al., 2012; van Dijk and Dolman, 2004; Wohlfahrt et al., 2008). The stronger correlation between NEP and GPP could have been attributable to the response magnitude of GPP to climate fluctuations, which is larger than that of ER. In the current study, the slope (0.67) of ER vs. GPP demonstrated that ER increased by 0.67 $\mu mol\, m^{-2}\, s^{-1}$ with 1 $\mu mol\, m^{-2}\, s^{-1}$ increment in GPP on average. Therefore, GPP increased more than ER under improved precipitation/water availability, leading to the enhanced NEP across the 9 years. As a substrate-constrained process, ER is mainly controlled by the recent photosynthate (Chen et al., 2015; Janssens et al., 2001; Ma et al., 2007), and thus shows less change than GPP in response to warming and increased precipitation in the semiarid grassland ecosystem.

The controls of GPP and ER on NEP are determined by the kinetic sensitivities of GPP and ER to environmental change at temporal and spatial scales (Luo, 2007). The kinetic sensitivities of ER and GPP to environmental change revealed in the temperate steppe as well as in the aforementioned terrestrial ecosystems could be ascribed to two possible factors. First, climate factors (e.g., temperature and precipitation) may concurrently affect GPP and ER, but the direction and magnitude of GPP and ER changes may vary with ecosystem types. Their effects on GPP and ER may result in different outcomes. Indeed, warming decreased GPP and ER in the temperate grassland (e.g., this study), but stimulated them at high latitudes and altitudes (Boelman et al., 2003; Welker et al., 2004; Wu et al., 2011). Enhancement of soil moisture under increased precipitation stimulated GPP more than ER (Niu et al., 2008). Second, GPP is only related to plants whereas ER (including autotrophic and heterotrophic respiration) is also affected by soil microbes and fauna.

No interactive effect of warming and increased precipitation on soil moisture or temperature found in the current study suggests that soil moisture and temperature are influenced by temperature and precipitation treatments independently in the steppe ecosystem. Soil temperature is increased through external heat energy under the warming treatments, but decreased by enhanced plant community cover (data not shown) under the increased precipitation treatments. The decreased soil moisture may be induced by the stimulated evapotranspiration under the warming treatments. Although increased precipitation can facilitate plant growth (the enhanced plant community cover) and reduce soil moisture, the declination of soil moisture is offset by the amount of increased precipitation. Soil moisture is enhanced by increased precipitation in the semiarid steppe. Therefore, warming and increased precipitation independently affect soil moisture and temperature, and, consequently, ecosystem C fluxes in the current study.

Warming can increase photosynthesis and respiration of terrestrial ecosystems by facilitating plant growth and microbe activities, especially in temperature-limited ecosystems (Liang et al., 2013; Lin et al., 2010; Rustad et al., 2001; Wan et al., 2005; Welker et al., 2004; Zhou et al., 2007). On the other hand, warming can also reduce C uptake and release in some terrestrial ecosystems when plant physiological activities and soil respiration (an important part of ER) are suppressed by warming-exacerbated atmospheric and soil water deficits (Liu et al., 2009; Niu et al., 2008; Rustad et al., 2001; Saleska et al., 1999; Shaver et al., 2000; Wan et al., 2007). In this study, GPP and ER decreased in the warmed subplots over the 9 growing seasons, resulting in a neutral change in NEP. This result is inconsistent with the conclusion from the first two-year study of this project, which showed that GPP and NEP were reduced by warming, but no change in ER was found under the warming treatment (Niu et al., 2008). The negative warming effect on GPP may be caused by the higher evaporative demands (vapor pressure deficits, VPD) and lower soil water content, and consequently lower leaf stomatal conductance and photosynthesis in the warmed plots (Niu

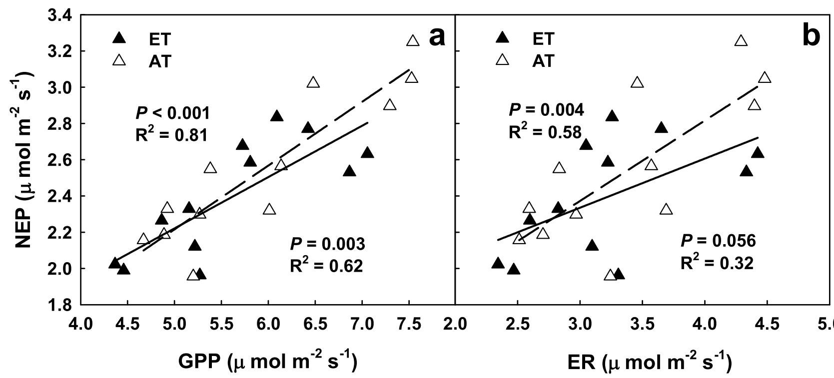

Fig. 3. Relationships between net ecosystem productivity (NEP) and its two components (gross primary productivity, GPP, a and ecosystem respiration, ER, b) in the unwarmed (open triangles and dashed lines) and warmed (filled triangles and solid lines) plots across 9 years (2005–2013) in a semiarid steppe. AT: ambient temperature treatments (control and increased precipitation), ET: elevated temperature treatments (warming and warming plus increased precipitation). Each data point represents growing-season average of each plot over 9 years under the two temperature treatments.

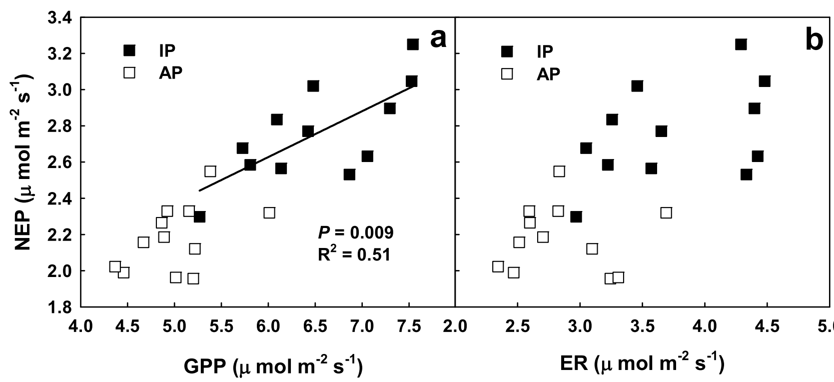

Fig. 4. Relationships between net ecosystem productivity (NEP) and its two components (gross primary productivity, GPP, a and ecosystem respiration, ER, b) under ambient (open squares) and increased precipitation (filled squares and solid line) across 9 years (from 2005 to 2013) in a semiarid steppe. AP: ambient precipitation treatments (control and warming), IP: increased precipitation treatments (increased precipitation only and warming plus increased precipitation). Each data point represents growing-season average of each plot over 9 years under the two precipitation treatments.

et al., 2008). However, the decrease in ER under the warming treatment over the 9 growing seasons in the steppe may be attributed to the reduction of GPP, because GPP is the key factor regulating ER variations and the correlation coefficient remains constant under warming.

Ecosystems CO_2 fluxes (NEP, ER and GPP) in the semiarid grassland are water-limited and sensitive to precipitation change. As expected, all components of ecosystem C exchange were stimulated by the increased precipitation treatment in summer from 2005 to 2013. The stimulation of ecosystem C flux caused by increased precipitation is also found in other grasslands (Flanagan et al., 2002; Harper et al., 2005; Hastings et al., 2005; Huxman et al., 2004; Patrick et al., 2007). Higher GPP under increased precipitation could have resulted from higher soil moisture and larger positive correlation between GPP and soil temperature when soil water availability is improved. The greater GPP could supply more substrate for root growth, microbial activities, and soil respiration, contributing to greater ER. However, the precipitation-induced increase in GPP is greater than that in ER, leading to an enhanced C sink in the temperate steppe, which is consistent with the early observation in the same experiment (Niu et al., 2008). No interactions of warming and increased precipitation on ecosystem C fluxes in either short-term (Liu et al., 2009; Niu et al., 2008) or long-term observations (this study) in this experiment indicate additive effects of climate warming and precipitation change on ecosystem C cycling in the semiarid grassland.

The NEP-GPP and NEP-ER relationships show common slopes with no shifts under the two temperature scenarios, suggesting that the positive NEP-GPP and NEP-ER relationships are not altered by warming in this study. The common slope of the NEP-GPP relationship implies that the NEP increment per unit increase in GPP (dNEP/dGPP; Ma et al., 2007; Verón et al., 2005) remains constant in response to climate warming, suggesting a strong capacity of the semiarid grassland ecosystem to maintain C balance under climate warming. However, dNEP/dGPP is different from the ratio of NEP to GPP (Carbon sequestration efficiency, CSE; Goulden et al., 2011) which is defined as the amount of NEP produced per unit GPP (Verón et al., 2005). In the current study, no difference was found in the values of CSE among the 4 treatments across the 9 years in the steppe irrespective of the substantially interannual variability in CSE (data not shown).

In this study, NEP change was significantly correlated with variation in GPP under increased precipitation, but not under the ambient precipitation, implying that the correlation between C balance and C uptake was strengthened by increased precipitation in the semiarid steppe. Two mechanisms may contribute to the enhanced control of GPP on NEP. First, the seasonal pattern of NEP is more similar to the changed seasonal pattern of GPP mainly driven by soil moisture, which contributes to the strengthened correlation between changes in NEP and GPP. Second, the sensitivity of GPP to temperature change increases during the growing season when soil water availability is improved, which is supported by a previous study (Ma et al., 2007). Therefore, the shifted NEP-GPP relationship under changing precipitation should be taken into consideration in the model projections of atmospheric CO_2 concentration in the future.

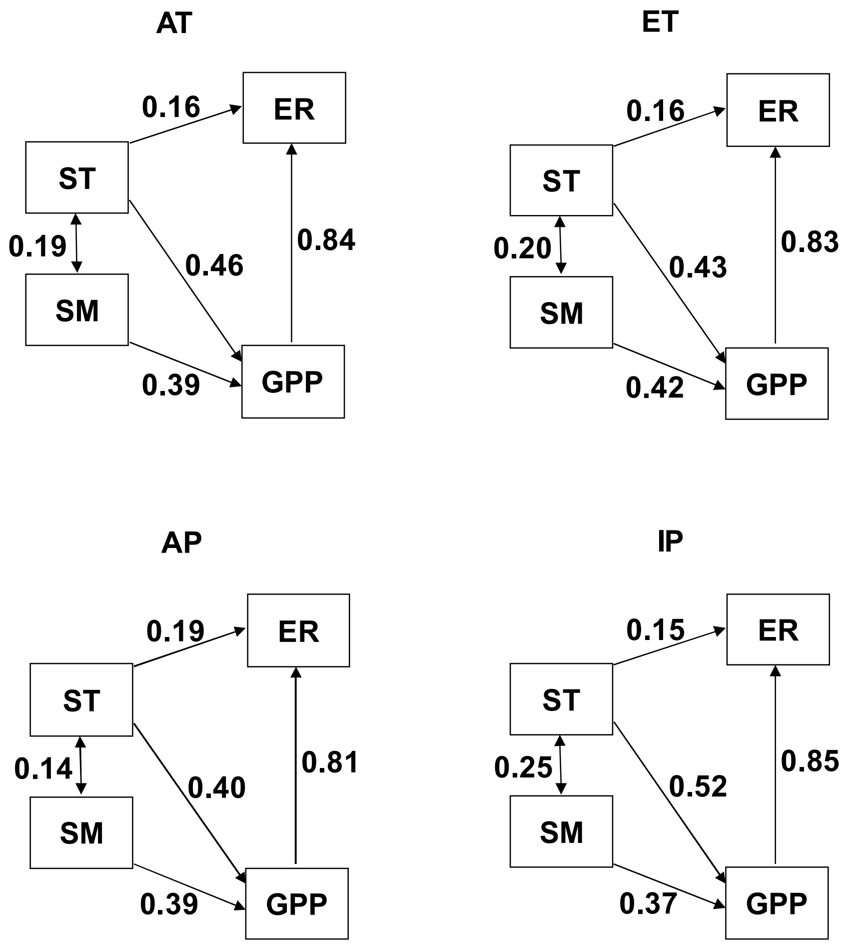

Fig. 5. Path diagrams showing the effects of ST and GPP on ER, the impacts of ST and SM on GPP, and the interaction between SM and ST under the warming and increased precipitation during the growing season from 2005 to 2013 in the temperate steppe. The value beside each arrow represents the standardized path coefficient. ST: soil temperature, SM: soil moisture, GPP: gross primary productivity, ER: ecosystem respiration, AT: ambient temperature treatments (control and increased precipitation), ET: elevated temperature treatments (warming and warming plus increased precipitation), AP: ambient precipitation treatments (control and warming), IP: increased precipitation treatments (increased precipitation only and warming plus increased precipitation).

It is worth noting that GPP was not measured directly in the present study. It was estimated from the NEP and ER, following the similar approach of previous studies (e.g., Valentini et al., 2000; van Dijk and Dolman, 2004; Chen et al., 2015). Certain degrees of self-correlation between NEP and GPP might be introduced when the correlation between NEP and GPP is examined. The potential bias induced by the self-correlation was tested using the equation proposed by Brett (2004). The result showed that the self-correlations were 4–10% in the relationship of NEP with GPP for different treatments (Table 2). The results of the correlation between NEP and GPP did not change after excluding the self-correlation between the two fluxes.

The lesser responses of NEP, GPP, and ER to warming than to increased precipitation, in combination with the altered NEP-GPP relationship under increased precipitation, indicate that precipitation/water availability plays a predominant role in regulating ecosystem C fluxes in the semiarid grassland. The conclusion from the long-term observations in this study confirms those of short-term studies in this system (Bai et al., 2010; Liu et al., 2009; Niu et al., 2008). However, the response of ER to experimental warming detected with the long-term observations is different from that in a short-term study in the same project, implying the importance of long-term observations. The shifted correlation between ecosystem C sequestration potential and C uptake observed in this study indicates that changing precipitation regimes has the potential to influence the C exchange between the terrestrial biosphere and the atmosphere.

Table 2
The coefficients of determination (R^2 values) for the self-correlation ($R_s{}^2$), the observed correlation ($R_o{}^2$), and the adjusted correlation ($R_{o\text{-}s}{}^2$) between NEP and GPP.

Treatments	CV_{NEP}	CV_{ER}	$R_s{}^2$	$R_o{}^2$	$R_{o\text{-}s}{}^2$
AP	0.03	0.16	0.04	0.17	0.13
IP	0.07	0.34	0.04	0.51	0.47
AT	0.17	0.50	0.10	0.81	0.71
ET	0.10	0.44	0.05	0.62	0.56
All	0.14	0.46	0.08	0.74	0.66

Note: $R_s = \frac{1}{\left(1+\left(CV_{ER}/CV_{NEP}\right)^2\right)^{1/2}}$.
$R_{o\text{-}s}{}^2 = R_o{}^2 - R_s{}^2$.
CV_{NEP} and CV_{ER} are the coefficient of variance of net ecosystem productivity (NEP) and ecosystem respiration (ER), respectively. AT: ambient temperature treatments (control and increased precipitation), ET: elevated temperature treatments (warming and warming plus increased precipitation), AP: ambient precipitation treatments (control and warming), IP: increased precipitation treatments (increased precipitation only and warming plus increased precipitation), All: all of the treatments. All $R_o{}^2$ values are significant at the 0.05 level except the one in the IP treatment.

The negative warming responses and positive precipitation responses of ecosystem C fluxes were observed in the short- (Liu et al., 2009; Niu et al., 2008) and long-term (this study) observations in the field manipulative experiment performed in the semi-arid grassland of Inner Mongolia, Northern China. The positive NEP-GPP and NEP-ER relationships were not altered by experimental warming over the 9 growing seasons, suggesting the strong ability of this semiarid ecosystem to maintain C balance under climate warming. However, increased precipitation strengthened the C uptake control on ecosystem C sequestration. The finding of the shifted relationship between ecosystem C sequestration and C uptake under increased precipitation in the temperate steppe can facilitate model parameterization and projection of terrestrial C dynamics and climate feedbacks.

Our findings from this manipulative experiment may be site-specific to the semiarid grassland. This is because ecosystem C cycling is a complex process, and C uptake and release have different responses and sensitivities to environmental factors. As NEP is the difference between GPP and ER, change in NEP could result from many different combinations of changes in GPP and ER. Our study in the semiarid steppe revealed one of the possibilities (GPP and ER increased under increased precipitation). Other possibilities could be possible in different grassland ecosystems. For instance, more combinations of changes in GPP and ER induced by experimental warming were found in three tundra ecosystems (Welker et al., 2004). Therefore, more manipulative experiments should be conducted to examine the NEP-GPP and NEP-ER relationships in various terrestrial ecosystems, and combined with eddy covariance measurements to reveal the response mechanisms of net C balance to warming and changing precipitation.

5. Conclusions

Consistent with the short-term observation, ecosystem CO_2 fluxes were suppressed by experimental warming, but stimulated by increased precipitation across the 9 growing seasons in the semi-arid steppe of Inner Mongolia, China. Experimental warming did not affect the seasonal dynamics of ecosystem C fluxes and the NEP-GPP and NEP-ER relationships during the growing seasons, whereas increased precipitation delayed the peak of GPP and enhanced the control of GPP on NEP in the steppe ecosystem. Our results improve the understanding of ecosystem C cycling in response to warming and precipitation amount change in semiarid grasslands. However, the findings in this study may be ecosystem-specific and are difficult to extrapolate to other terrestrial ecosystems. More manipulative experiments should be performed in various terrestrial ecosystems, and combined with eddy covariance measurements to provide insights of ecosystem C sequestration in response to warming and changing precipitation.

Acknowledgements

We thank Yinzhan Liu, Qian Zhang, Jingjing Gao, Yuan Miao, Pengshuai Shao, Fanglong Su, Fan Yang, Bin Liu, Gaigai Ma, and Jian Song for help in field measurements, Zhongling Yang and Deliang Kong for their valuable advice on the manuscript, and Brett Seybert for his editing of the manuscript. This study was financially supported by the Ministry of Science and Technology of China (2013CB956301) and the National Natural Science Foundation of China (41030104, 31270564).

References

Bai, W.M., Wan, S.Q., Niu, S.L., Liu, W.X., Chen, Q.S., Wang, Q.B., Zhang, W.H., Han, X.G., Li, L.H., 2010. Increased temperature and precipitation interact to affect root production mortality, and turnover in a temperate steppe: implications for ecosystem C cycling. Global Change Biol. 16, 1306–1316.

Beringer, J., Hutley, L.B., Tapper, N.J., Cernusak, L.A., 2007. Savanna fires and their impact on net ecosystem productivity in North Austria. Global Change Biol. 13, 990–1004.

Boelman, N.T., Stieglitz, M., Rueth, H.M., Sommerkorn, M., Griffin, K.L., Shaver, G.R., Gamon, J.A., 2003. Response of NDVI, biomass, and ecosystem gas exchange to long-term warming and fertilization in wet sedge tundra. Oecologia 135, 414–421.

Brett, M.T., 2004. When is a correlation between non-independent variables spurious? Oikos 105, 647–656.

Chen, Z., Yu, G.R., Zhu, X.J., Wang, Q.F., Niu, S.L., Hu, Z.M., 2015. Covariation between gross primary production and ecosystem respiration across space and the underlying mechanisms: a global synthesis. Agric. For. Meteorol. 203, 180–190.

Falster, D.S., Warton, D.I., Wright, I.J., 2006. User's guide to SMATR: Standardized Major Axis Tests & Routines Version 2.0, Copyright 2006, Homepage: http://www.bio.mq.edu.au/ecology/SMATR/.

Flanagan, L.B., Wever, L.A., Carlson, P.J., 2002. Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. Global Change Biol. 8, 599–615.

Goulden, M.L., Munger, J.W., Fan, S.M., Daube, B.C., Wofsy, S.C., 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. Science 271, 1576–1578.

Goulden, M.L., McMillan, A.M., Winston, G.C., Rocha, A.V., Manies, K.L., Harden, J.W., Bond-Lamberty, B.P., 2011. Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. Global Change Biol. 17, 855–871.

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.

Hastings, S.J., Oechel, W.C., Muhlia-Melo, A., 2005. Diurnal, seasonal and annual variation in the net ecosystem CO_2 exchange of a desert shrub community (*Sarcocaulescent*) in Baja California, Mexico. Global Change Biol. 11, 927–939.

Hui, D., Luo, Y., Katul, G., 2003. Partitioning interannual variability in net ecosystem exchange into climatic variability and functional change. Tree Physiol. 23, 433–442.

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 semiarid grassland: the role of native versus non-native grasses and soil texture. Oecologia 141, 295–305.

IPCC, et al., 2013. Summary for policy makers. In: Stocker, T.F., Qin, D., Plattner, G.K. (Eds.), 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, pp. 20–23.

Janssens, I.A., Lankreijer, H., Matteucci, G., Kowalski, A.S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grünwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E.J., Grelle, A., Rannik, Ü., Morgenstern, K., Oltchev, S., Clement, R., Gudmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N.O., Vesala, T., Granier, A., Schulze, E.D., Lindroth, A., Dolman, A.J., Jarvis, P.G., Ceulemans, R., Valentini, R., 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. Global Change Biol. 7, 269–278.

Lasslop, G., Reichstein, M., Papale, D., Richardson, A.D., Arneth, A., Barr, A., Stoy, P., Wohlfahrt, G., 2010. Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: critical issues and global evaluation. Global Change Biol. 16, 187–208.

Law, B.E., Falge, E., Gu, L., Baldocchi, D.D., Bakwin, P., Berbigier, P., Davis, K., Dolman, A.J., Falk, M., Fuentes, J.D., Goldstein, A., Granier, A., Grelle, A., Hollinger, D., Janssens, I.A., Jarvis, P., Jensen, N.O., Katul, G., Mahli, Y., Matteucci, G., Meyers, T., Monson, R., Munger, W., Oechel, W., Olson, R., Pilegaard, K., Paw, U.K.T., Thorgeirsson, H., Valentini, R., Verma, S., Vesala, T., Wilson, K., Wofsy, S., 2002. Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. Agric. For. Meteorol. 113, 97–120.

Liang, J.Y., Xia, J.Y., Liu, L.L., Wan, S.Q., 2013. Global patterns of the responses of leaf-level photosynthesis and respiration in terrestrial plants to experimental warming. J. Plant Ecol. 6, 437–447.

Lin, D.L., Xia, J.Y., Wan, S.Q., 2010. Climate warming and biomass accumulation of terrestrial plants: a meta-analysis. New Phytol. 188, 187–198.

Liu, W.X., Zhang, Z., Wan, S.Q., 2009. Predominant role of water in regulating soil and microbial respiration and their responses to climate change in a semiarid grassland. Global Change Biol. 15, 184–195.

Luo, Y.Q., 2007. Terrestrial carbon-cycle feedback to climate warming. Annu. Rev. Ecol. Evol. Syst. 38, 683–712.

Ma, S.Y., Baldocchi, D.D., Xu, L.K., Hehn, T., 2007. Inter-annual variability in carbon dioxide exchange of an oak/grass savanna and open grassland in California. Agric. For. Meteorol. 147, 157–171.

Niu, S.L., Wu, M.Y., Han, Y., Xia, J.Y., Li, L.H., Wan, S.Q., 2008. Water-mediated responses of ecosystem carbon fluxes to climate change in a temperate steppe. New Phytol. 177, 209–219.

Niu, S.L., Luo, Y.Q., Fei, S.F., Yuan, W.P., Schimel, D., Law, B.E., Ammann, C., Arain, M.A., Arneth, A., Aubinet, M., Barr, A., Beringer, J., Bernhofer, C., Black, T.A., Buchmann, N., Cescatti, A., Chen, J.Q., Davis, K.J., Dellwik, E., Desai, A.R., Etzold, S., Francois, L., Gianelle, D., Gielen, B., Goldstein, A., Groenendijk, M., Gu, L.H., Hanan, N., Helfter, C., Hirano, T., Hollinger, D.Y., Jones, M.B., Kiely, G., Kolb, T.E., Kutsch, W.L., Lafleur, P., Lawrence, D.M., Li, L.H., Lindroth, A., Litvak, M., Loustau, D., Lund, M., Marek, M., Martin, T.A., Matteucci, G., Migliavacca, M., Montagnani, L., Moors, E., Munger, J.W., Noormets, A., Oechel, W., Olejnik, J., Paw, U.K.T., Pilegaard, K., Rambal, S., Raschi, A., Scott, R.L., Seufert, G., Spano, D., Stoy, P., Sutton, M.A., Varlagin, A., Vesala, T., Weng, E.S., Wohlfahrt, G., Yang, B., Zhang, Z.D., Zhou, X.H., 2012. Thermal optimality of net ecosystem exchange of carbon dioxide and underlying mechanisms. New Phytol. 194, 775–783.

Patrick, L., Cable, J., Potts, D., 2007. Effects of an increase in summer precipitation on leaf, soil, and ecosystem fluxes of CO_2 and H_2O in a sotol grassland in Big Bend National Park, Texas. Oecologia 151, 704–718.

Poulter, B., Frank, D., Ciais, P., Myneni, R.B., Andela, N., Bi, J., Broquet, G., Canadell, J.G., Chevallier, F., Liu, Y.Y., Running, S.W., Sitch, S., van der Werf, G.R., 2014. Contribution of semiarid ecosystems to interannual variability of the global carbon cycle. Nature 509, 600–603.
Rustad, L., Campbell, J., Marion, G., Norby, R., Mitchell, M., Hartley, A., Cornelissen, J., Gurevitch, J., GCTE-NEWS, 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126, 543–562.
Saigusa, N., Yamamoto, S., Murayama, S., Kondo, H., 2005. Inter-annual variability of carbon budget components in an AsiaFlux forest site estimated by long-term flux measurements. Agric. For. Meteorol. 134, 4–16.
Saleska, S.R., Harte, J., Torn, M.S., 1999. The effect of experimental ecosystem warming on CO_2 fluxes in a montane meadow. Global Change Biol. 5, 125–141.
Saleska, S.R., Miller, S.D., Matross, D.M., Goulden, M.L., Wofsy, S.C., da Rocha, H.R., de Camargo, P.B., Crill, P., Daube, B.C., de Freitas, H.C., Hutyra, L., Keller, M., Kirchhoff, V., Menton, M., Munger, J.W., Pyle, E.H., Rice, A.H., Silva, H., 2003. Carbon in Amazon forests: unexpected seasonal fluxes and disturbance-induced losses. Science 302, 1554–1557.
Scanlon, T.M., Albertson, J.D., 2004. Canopy scale measurements of CO_2 and water vapor exchange along a precipitation gradient in southern Africa. Global Change Biol. 10, 329–341.
Shaver, G.R., Canadell, J., Chapin III, F.S., Gurevitch, J., Harte, J., Henry, G., Ineson, P., Jonasson, S., Melillo, J., Pitelka, L., Rustad, A.L., 2000. Global warming and terrestrial ecosystems: a conceptual framework for analysis. BioScience 50, 871–882.
Urbanski, S., Barford, C., Wofsy, S., Kucharik, C., Pyle, E., Budney, J., McKain, K., Fitzjarrald, D., Czikowsky, M., Munger, J.W., 2007. Factors controlling CO_2 exchange on timescales from hourly to decadal at Harvard Forest. J. Geophys. Res. 112, G02020, http://dx.doi.org/10.1029/2006JG000293.
Valentini, R., Matteucci, G., Dolman, A.J., Schulze, E.D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grünwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, Ü., Berbigier, P., Loustau, D., Guomundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., Jarvis, P.G., 2000. Respiration as the main determinant of carbon balance in European forests. Nature 404, 861–865.
van Dijk, A.J.M., Dolman, A.J., 2004. Estimates of CO_2 uptake and release among European forests based on eddy covariance data. Global Change Biol. 10, 1445–1459.
van Dijk, A., Dolman, A.J., Schulze, E.D., 2005. Radiation, temperature, and leaf area explain ecosystem carbon fluxes in boreal and temperate European forests. Global Biogeochem. Cycles 19, http://dx.doi.org/10.1029/2004gb002417.
Verón, S.R., Oesterheld, M., Paruelo, J.M., 2005. Production as a function of resource availability: slopes and efficiencies are different. J. Veg. Sci. 16, 351–354.
Wan, S.Q., Hui, D.F., Wallace, L.L., Luo, Y.Q., 2005. Direct and indirect warming effects on ecosystem carbon processes in a tallgrass prairie. Global Biogeochem. Cycles 19, http://dx.doi.org/10.1029/2004GB002315, GB2014.
Wan, S.Q., 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.
Wan, S.Q., Xia, J.Y., Liu, W.X., Niu, S.L., 2009. Photosynthetic overcompensation under nocturnal warming enhances grassland carbon sequestration. Ecology 90, 2700–2710.
Warton, D.I., Weber, N.C., 2002. Common slope tests for bivariate errors in-variables models. Biom. J. 44, 161–174.
Welker, J.M., Fahnestock, J.T., Henry, G.H.R., O′Dea, K.W., Chimner, R.A., 2004. CO_2 exchange in three Canadian High Arctic ecosystems: response to long-term experimental warming. Global Change Biol. 10, 1981–1995.
Wilson, K.B., Baldocchi, D.D., 2001. Comparing independent estimates of carbon dioxide exchange over five years at a deciduous forest in the southern United States. J. Geophys. Res. 106, 34167–34178.
Wohlfahrt, G., Hammerle, A., Haslwanter, A., Bahn, M., Tappeiner, U., Cernusca, A., 2008. Seasonal and interannual variability of the net ecosystem CO_2 exchange of a temperate mountain grassland: effects of weather and management. J. Geophys. Res. 113, D08110, http://dx.doi.org/10.1029/2007JD009286.
Wu, Z.T., Koch, G.W., Dijkstra, P., Bowker, M.A., Hungate, B.A., 2011. Responses of ecosystem carbon cycling to climate change treatments along an elevation gradient. Ecosystems 14, 1066–1080.
Xia, J., Chen, J., Piao, S., Ciais, P., Luo, Y., Wan, S., 2014. Terrestrial carbon cycle affected by non-uniform climate warming. Nat. Geosci. 7, 173–180.
Yan, J.H., Zhang, Y.P., Yu, G.R., Zhou, G.Y., Zhang, L.M., Li, K., Tan, Z.H., Sha, L.Q., 2013. Seasonal and interannual variations in net ecosystem exchange of two old-growth forests in southern China. Agric. For. Meteorol. 182/183, 257–265.
Yang, H.J., Wu, M.Y., Liu, W.X., Zhang, Z., Zhang, N.L., Wan, S.Q., 2011. Community structure and composition in response to climate change in a temperate steppe. Global Change Biol. 17, 452–465.
Yu, G.R., Zhu, X.J., Fu, Y.L., He, H.L., Wang, Q.F., Wen, X.F., Li, X.R., Zhang, L.M., Zhang, L., Su, W., Li, S.G., Sun, X.M., Zhang, Y.P., Zhang, J.H., Yan, J.H., Wang, H.M., Zhou, G.S., Jia, B.R., Xiang, W.H., Li, Y.N., Zhao, L., Wang, Y.F., Shi, P.L., Chen, S.P., Xin, X.P., Zhao, F.H., Wang, Y.Y., Tong, C.L., 2013. Spatial patterns and climate drivers of carbon fluxes in terrestrial ecosystems of China. Global Change Biol. 19, 798–810.
Zhang, Y.P., Tan, Z.H., Song, Q.H., Yu, G.R., Sun, X.M., 2010. Respiration controls the unexpected seasonal pattern of carbon flux in an Asian tropical rain forest. Atmos. Environ. 44, 3886–3893.
Zhou, X.H., Wan, S.Q., Luo, Y.Q., 2007. Source components and interannual variability of soil CO2 efflux under experimental warming and clipping in a grassland ecosystem. Global Change Biol. 13, 761–775.