Contents lists available at SciVerse ScienceDirect

Agricultural and Forest Meteorology





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

Precipitation amount, seasonality and frequency regulate carbon cycling of a semi-arid grassland ecosystem in Inner Mongolia, China: A modeling analysis



Shushi Peng^a, Shilong Piao^{a,b,*}, Zehao Shen^a, Philippe Ciais^c, Zhenzhong Sun^a, Shiping Chen^d, Cédric Bacour^c, Philippe Peylin^c, Anping Chen^e

^a Department of Ecology, College of Urban and Environmental Sciences, Peking University, Beijing 100871, China

^b Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100085, China

^c Laboratoire des Sciences du Climat et de l'Environnement, CEA CNRS UVSQ, 91191 Gif-sur-Yvette, France

^d Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China

^e Department of Ecology, Princeton University, Princeton, NJ 08544, USA

ARTICLE INFO

Article history: Received 16 August 2012 Received in revised form 30 January 2013 Accepted 4 February 2013

Keywords:

Precipitation amount Precipitation seasonality Precipitation frequency Grassland Net primary production Net ecosystem production Heterotrophic respiration

ABSTRACT

Over the last century, precipitation has shown significant changes, reflecting both natural variability and radiative forcing changes from greenhouse gases and aerosols. Arid and semi-arid ecosystems are particularly sensitive to changes in precipitation regimes. In this study, we investigate how variation in annual total, seasonal distribution and frequency of precipitation affect CO₂ fluxes of semi-arid grassland in Inner Mongolia. To this aim, we combine eddy-covariance measurements with a process-based model (ORCHIDEE). First, the ORCHIDEE parameters were optimized using half-hourly CO₂ flux data and actual precipitation forcing. Second, the response of CO₂ fluxes to altered precipitation scenarios is computed using the model with optimized parameters. Our results show that modeled net primary production (NPP) responds non-linearly to increased vs. decreased rainfall. Re-allocating precipitation from other seasons to spring enhances annual NPP and net ecosystem production (NEP). By contrast, re-allocating more precipitation to autumn was found to decrease annual NPP and NEP. Increasing the frequency of heavy rainfall days (PF_{10mm}, days with precipitation more than 10mm) induces a positive response of simulated NPP during the growing season. However, the increase of the frequency of moderately rainy days (PF_{5-10mm}, days with precipitation between 5 mm and 10 mm) rather increases soil heterotrophic respiration. Taken together, our modeling results are consistent with that of grassland field manipulation experiments. This study highlights the importance of changes in precipitation seasonality and frequency for semi-arid grassland. Further investigations should focus on testing the ability of models to reproduced manipulation experiment data, and on evaluating the performances of climate models to reproduce rainfall intensity/frequency in semi-arid areas.

© 2013 Elsevier B.V. All rights reserved.

1. Introduction

An amplification of the hydrological cycle has been observed along with increasing temperature during the past several decades (IPCC, 2007). This human induced alteration of the hydrological cycle superimposed on a large natural variability may result in altered regional precipitation amount, frequency, intensity, duration and extremes (Easterling et al., 2000; Trenberth et al., 2003; IPCC, 2007). Over the 20th century, possible change in annual precipitation amount and an intensification of inter- and intra-annual

* Corresponding author at: Peking University, Beijing 100871, China.

Tel.: +86 10 6276 5578; fax: +86 10 6275 6560.

E-mail addresses: slpiao@pku.edu.cn, ShiLong.Piao@lsce.ipsl.fr (S. Piao).

variability of precipitation were reported (Easterling et al., 2000; IPCC, 2007). Precipitation appears to shift toward fewer and larger rainfall events (Tank and Konnen, 2003; Trenberth et al., 2003). For example, East Asia has experienced a significant decrease of precipitation frequency, and a significant change of precipitation seasonality. Autumn precipitation decreased while winter precipitation increased, from 1960 to 2006 (Ding et al., 2007; Piao et al., 2010). The change in soil moisture induced by these precipitation regime changes in water-limited ecosystems impact carbon cycling processes such as net primary production (NPP), heterotrophic respiration (Rh) and the sum of both, net ecosystem production (NEP) (Knapp and Smith, 2001; Knapp et al., 2002; Gerten et al., 2008; Luo et al., 2008; Robertson et al., 2009; Fay, 2009; Ross et al., 2012). Climate models projections predict significant changes in precipitation amount, timing and frequency for the next 50 years (IPCC,

^{0168-1923/\$ –} see front matter © 2013 Elsevier B.V. All rights reserved. http://dx.doi.org/10.1016/j.agrformet.2013.02.002

2007; Wentz et al., 2007; Gao et al., 2008), which will continue to influence productivity and carbon sequestration of terrestrial ecosystems (Luo et al., 2008; Knapp et al., 2008). Therefore, it is essential to understand how changes in precipitation regimes impacts carbon cycling processes in terrestrial ecosystems using observations and ecosystem models, especially for water-limited ecosystems that directly and strongly respond to precipitation changes.

In water-limited ecosystems, many studies found a significant and positive correlation between inter-annual variation of precipitation amount and NPP from site level studies (e.g. Churkina et al., 1999; Knapp and Smith, 2001; Huxman et al., 2004). However, variability in the seasonality and frequency of precipitation events, as well as co-variability of other climate drivers with precipitation, could lead to confounding effects when investigating the response of ecosystem processes to annual precipitation changes using real-world conditions (Huxman et al., 2004; Fay, 2009; Wu et al., 2011). On the other hand, ecosystem manipulation experiments (under controlled climate conditions) and ecosystem model simulations of precipitation addition and reduction have shown that higher precipitation amount leads to larger NPP, when keeping other confounding variables (e.g. precipitation seasonality, precipitation frequency and temperature) constant (Zavaleta et al., 2003; Dukes et al., 2005; Chou et al., 2008; Gerten et al., 2008; Luo et al., 2008). Hence, the first goal of this study is to investigate, using a process-based ecosystem model prescribed with high frequency climate forcing data, how changes in precipitation amount change the carbon fluxes of a semi-arid grassland ecosystem while keeping precipitation timing and other confounding variables constant.

The impacts of precipitation on NPP are different between the growing season and the non-growing season, in particular for grassland ecosystems (Robertson et al., 2009). Precipitation during the growing season directly and positively impact vegetation NPP in semi-arid grasslands, whereas precipitation outside the growing season only have an indirect lagged effect through soil moisture (Muldavin et al., 2008; Robertson et al., 2009). Thus, the second goal of this study is to investigate how changes in the seasonal distribution of precipitation influence carbon fluxes in a semi-arid grassland ecosystem.

Variations in precipitation intensity and frequency are receiving more and more attention for their effect in controlling semi-arid grassland ecosystem processes (Knapp et al., 2002, 2008; Robertson et al., 2009; Fay, 2009). A different precipitation frequency is likely to modify soil moisture, which will in turn influence NPP, respiration and the net carbon balance of the ecosystem (Knapp et al., 2002, 2008). A decrease in precipitation frequency accompanied by an increase in precipitation intensity per rainfall event, as projected from climate models, could amplify the magnitude of the soil moisture fluctuations, and lengthen the period of water stress inbetween two consecutive rainfall events (Knapp et al., 2002, 2008). On the other hand, larger (more extreme) rainfall events could also more efficiently replenish deep soil moisture in xeric ecosystems (Knapp et al., 2008) and cause an increase in NPP. Thus, research results on the impacts of intra-annual variations of precipitation distribution on ecosystem processes are still inconclusive (Knapp et al., 2008; Fay, 2009; Ross et al., 2012). Until now, only a few studies including ecosystem manipulation experiments, remote sensing and model simulations explored the effects of altered precipitation frequency on ecosystem processes (e.g. Fang et al., 2005; Luo et al., 2008; Wu et al., 2011). Thus, the third aim of this study is to simulate with a process-based ecosystem model how variation of number of daily precipitation events influences carbon cycling processes of a semi-arid grassland ecosystem in China while maintaining annual total precipitation amount constant.

We constructed different altered precipitation input data for the model, in order to separate the influence of changes in precipitation annual amount, seasonal distribution, and daily frequency on carbon fluxes at the Chinese semi-arid grassland ecosystem site investigated. Before applying this altered precipitation forcing to the model, we optimized its parameters against one year carbon flux measurements, in order to ensure that the observed response of carbon fluxes to real-world precipitation is correctly reproduced. We address the following three questions for a semi-arid grassland ecosystem site, representative of Inner Asia semi-arid grasslands.

- (1) How does a change in annual precipitation modify ecosystem carbon fluxes when keeping precipitation timing and frequency constant?
- (2) How does a change in precipitation seasonality modify ecosystem carbon fluxes when keeping total precipitation amount and frequency constant?
- (3) How does an altered precipitation frequency modify ecosystem carbon fluxes when keeping total precipitation amount constant?

2. Materials and methods

2.1. Study site

Simulation experiments with altered precipitation were conducted at a grassland site (N43°33'16", E116°40'17") equipped with an eddy flux tower (CN-Xi2) in Xilinhot, Inner Mongolia, China. This site, 1250 m above sea level, has a temperate continental climate with mean annual precipitation of 342 mm (average during the period of 1980-2009). Driven by Asian monsoon, a large portion of annual precipitation (87%) occurs from May to September. Mean annual temperature is 1.2 °C (long term), while monthly mean temperature is 19.0 °C in July and -19.2 °C in January (Fig. 1). Soils in this site are Chestnut series (Yuan et al., 2005). Soil texture is comprised by \sim 58% sand, \sim 27% silt and \sim 15% clay, respectively. Vegetation basal cover ranges from 30% to 45% and is mainly comprised of C₃ species with dominant species of Stipa grandis and Artemisia frigida, and the biomass of Stipa grandis is about 70–90% (Li et al., 2008). Half-hour eddy flux data in the year 2006 is from the global fluxnet (http://www.fluxdata.org/), and detailed gap-filling and uncertainty of flux data in this site are given in Zhang et al. (2011). The chosen site for this study is a typical semi-arid grassland ecosystem and could represent the large area of semi-arid grassland in Inner Asia (Zhang et al., 2011).

2.2. ORCHIDEE model

In this study we used ORCHIDEE, a process-based land-surface model (Krinner et al., 2005), to simulate how carbon fluxes respond



Fig. 1. Seasonal cycle of average monthly temperature and precipitation during the period 1950–2000 for the CN-Xi2 site.

Table	1

ORCHIDEE	parameters that are o	ptimized in this stud	v and their	prior and	posterior v	values for the	Plant Function	Type of C3	grassland
	paranecers chat are s		y and cherry	or tor and	,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	and contraction the	· · · · · · · · · · · · · · · · · · ·	.,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	gi abbiance

Parameter	Description	Prior value	Prior range	Units	Posterior value	Posterior uncertainty
Vcmax	Photosynthesis maximum carboxylation capacity	70	42-98	μ mol m $^{-2}$ s $^{-1}$	61.3	11.4
LAImax	Phenology maximum obtainable LAI	2.5	1.5-3.5	$m^2 m^{-2}$	2.6	0.7
SLA	Specific leaf area	0.026	0.013-0.05	$m^2 g^{-1}$	0.025	0.010
Q10	Temperature dependence of heterotrophic respiration	1.99	1-2.5	_	2.5	0.4
MR_c	Offset of the relationship between temperature and maintenance respiration	1	0.1-2	-	1.1	0.7
MR_slope_c	Offset of the temperature quadratic function that determines the slope of the function between temperature and maintenance respiration	0.16	0.08-0.24	-	0.17	0.06
GR_fraction	Fraction of biomass allocated to growth respiration	0.28	0.2-0.36	-	0.29	0.06
Ksoilc	Multiplicative factor that adjust the initial (soil) carbon stocks from spin-up	1	0.25-4	-	0.25	0.52
fstress	Parameter that determines threshold of soil water content. Under this threshold stomata start to close.	6	0.8-10	-	5.6	3.4
Dpu_cste	Total depth of soil reservoir	2	0.1-6	m	2.4	0.2

to precipitation changes. ORCHIDEE simulates fluxes of CO₂, water and energy exchanged with the atmosphere at a 1/2-hourly time step, and ecosystem carbon and water dynamics at a daily time step. The model used in this study is structured into two submodules (Krinner et al., 2005). The first module SECHIBA (de Ducoudre et al., 1993; de Rosnay and Polcher, 1998) calculates the exchange of water and energy in the soil–plant–atmosphere continuum with a half-hourly time step. The second module STOMATE simulates the terrestrial carbon cycle including photosynthesis, respiration, carbon allocation, litter decomposition, soil carbon dynamics, phenology and mortality with a daily time step. Within ORCHIDEE, the global vegetation is described using 12 plant functional types (PFTs) and bare soil (Krinner et al., 2005). In this study, we prescribed the PFT composition at this site with 40% C₃ grassland and 60% bare ground, according to local data.

The ORCHIDEE model has been tested for simulation of carbon and water fluxes both at site level and at continental scale (Ciais et al., 2005; Piao et al., 2007; Tan et al., 2010; Schwalm et al., 2010). Moreover, the model has been evaluated for simulating soil moisture and applied for drought events of different spatio-temporal scales (e.g. Gerten et al., 2008; Luo et al., 2008; Schwalm et al., 2010; Rebel et al., 2012). For this study, we run ORCHIDEE at local scale for one full year with site measured and gap-filled half-hour meteorological forcing data: air temperature, rainfall, short-wave radiation, long-wave radiation, air humidity, atmospheric pressure, and wind speed in 2006 (Wang et al., 2012). In addition to meteorological inputs, we used growing season half-hour gap-filled time series of gross primary production (GPP) and net ecosystem exchange (NEE) data from the eddy covariance flux tower (CN-Xi2) to optimize the model parameters because winter NEE and GPP are missing in this site

The model parameters optimization is performed with a Bayesian inversion called ORCHIS which minimizes a quadratic cost function, sum of two terms, one with the parameters a priori values and their uncertainty, and the other with the flux observations and their uncertainties, all uncertainties being assumed Gaussian (Santaren et al., 2007; Verbeeck et al., 2011; Kuppel et al., 2012). ORCHIS determines optimal parameter values that define a compromise between their assigned priori values and the best fit to the observations (here eddy covariance CO₂ fluxes) within their uncertainties. The posterior uncertainty on optimized parameters is calculated from the second derivative of model around optimal values, given the post variance matrix on the observations and on the parameters (Verbeeck et al., 2011; Kuppel et al., 2012). The choice of parameters to be optimized is left to the discretion of the modeler. These parameters should be chosen (e.g. from expert knowledge) for their controlling effects on the model output variables. Because NEE is observed while GPP is calculated from the measured temperature and NEE, we set a lower weight for GPP (25%) than for NEE (75%) in the cost function to optimize the ORCHIDEE parameters (Eq. (1) in Kuppel et al., 2012). The prior uncertainty is set as RMSE between fluxes from the eddy covariance flux tower and prior model simulation. At the end of the parameters optimization, the values of cost function for NEE and GPP are of 50 and 4, respectively. The optimized parameters for the Xilinhot location are listed in Table 1. The model with optimized parameters can better capture the variations of measured GPP and NEE at the site compared to the simulation with prior parameter values (Fig. 2). The root-mean-square error (RMSE) between observed and modeled NEE is improved from 0.7 g C m⁻² day⁻¹ with default



Fig. 2. Measured and modeled seasonal patterns of daily (a) gross primary production (GPP) and (b) net ecosystem exchange (NEE) of the CN-Xi2 site. Eddy covariance measurements (Obs, black line) are compared with the prior model (prior, blue line) and the optimized model (optimized, red line). The gray shaded area shows the prior uncertainty of observed and modeled fluxes.

parameters to $0.4 \text{ g C m}^{-2} \text{ day}^{-1}$ with optimized parameters, and RMSE of GPP is also improved (from $1.4 \text{ g C m}^{-2} \text{ day}^{-1}$ with default parameters to $0.5 \text{ g C m}^{-2} \text{ day}^{-1}$ with optimized parameters). We then conducted each simulation experiment using optimal parameters, and analyzed ORCHIDEE outputs for carbon and water fluxes.

2.3. Simulation scenarios with altered precipitation

We used the half-hour meteorological data of year 2006 for the CN-Xi2 site as input forcing data for ORCHIDEE. For each precipitation treatment scenario, we keep other climate variables unchanged except for precipitation. First, to test the effects of altered precipitation amount on grassland ecosystem processes; we changed evenly the precipitation amount of each precipitation event and kept the precipitation timing unchanged. We define 7 levels: ambient, precipitation annual amount decreases by 30% (P – 30%), 20% (P – 20%) and 10% (P – 10%), precipitation amount increases by 10% (P+10%), 20% (P+20%) and 30% (P+30%), respectively.

Fig. 2 shows the seasonality of simulated GPP for CN-Xi2 site. We divided the growing season into three sub-periods: May and June (MJ), July and August (JA) and September and October (SO), which correspond with the start (spring), peak (summer) and decline (autumn) of vegetation growth. The non-growing season (NGS) covers the period from November to April in the next year.

For the precipitation *seasonality treatment* during the growing season, we added (removed) 10-30% of the precipitation during one sub-period and removed (added) the same amount evenly during the other two sub-periods in order to conserve the growing season precipitation amount. We designed factorial simulations: in addition to one control simulation (ambient), for each of the 3 sub-periods, we ran ORCHIDEE with 6 different scenarios of *seasonality treatment*: 30% (that is 30% added to this sub-period and removed from the two others), 20% and 10% as well as -10%, -20% and -30%. In total, $7 \times 3 = 21$ different factorial simulations are performed for the seasonal treatment.

For the precipitation *frequency treatment*, we kept the timing of each precipitation and the total growing season precipitation amount constant, but randomly changed the precipitation amount for each precipitation event in the growing season (sub-periods: spring, summer and autumn). After generating 1000 growing season precipitation distributions randomly, we ranked these 1000 distributions by precipitation frequency (i.e. the number of days on which precipitation exceeds 10 mm (PF_{10 mm}), the number of days on which precipitation exceeds 5 mm but less than 10 mm (PF_{5-10 mm}), and the number of days on which precipitation exceeds 1 mm but less than 5 mm (PF_{1-5 mm}).

3. Results

3.1. Impacts of altered precipitation amount

Generally, during the growing season, an increase in precipitation amount was found to augment NPP of the CN-Xi2 semi-arid grassland ecosystem, while a decrease in precipitation amount reduced NPP. The sensitivity of NPP to precipitation amount is non-symmetric, being larger for a decrease than for an increase in precipitation amount, especially in autumn (Figs. 3a and 4). Rh is less sensitive than NPP to increased or decreased growing season precipitation amount (Fig. 3b). Therefore, increased precipitation amount is modeled to enhance NEP (larger sink) while decreased precipitation amount is modeled to diminish NEP (Fig. 3c). The response of NPP to a prescribed change in precipitation amount is non-linear in the ORCHIDEE simulations with optimized parameters (Fig. 4). When precipitation increases by 10%, 20% and 30%,



Fig. 3. Modeled changes in (a) net primary production (Δ NPP), (b) heterotrophic respiration (Δ Rh), (c) net ecosystem production (Δ NEP) and (d) soil moisture (Δ SM) of the six scenarios of precipitation amount change compared to the control model experiment during the growing season for the CN-Xi2 site. (e) Growing season precipitation events (gray black bars) and daily soil moisture (gray dash line) from the control model experiment for the CN-Xi2 site.



Fig. 4. Modeled relative percentage changes in net primary production (Δ NPP) in the six precipitation amount scenarios (P – 10%, P – 20%, P – 30%, P + 10%, P + 20% and P + 30%) compared to the control model simulation for the CN-Xi2 site.

Table 2	
Chamman im	

Changes in seasonal	precipitation in	each precipitation	seasonality scenario.

Treatment season	Scenario	Changes in seasonal precipitation (mm)				
		MJ	JA	SO	NGS	
May and June (MJ)	$P_{MJ} - 30\%$	-34.1	14.7	13.4	6.0	
	$P_{MJ} - 20\%$	-22.7	9.8	9.0	4.0	
	$P_{MJ} - 10\%$	-11.4	4.9	4.5	2.0	
	P _{MJ} + 10%	11.4	-4.9	-4.5	-2.0	
	P _{MJ} + 20%	22.7	-9.8	-9.0	-4.0	
	P _{MJ} + 30%	34.1	-14.7	-13.4	-6.0	
July and August (JA)	$P_{JA}-30\%$	13.1	-26.6	9.3	4.2	
	$P_{JA} - 20\%$	8.7	-17.7	6.2	2.8	
	$P_{JA} - 10\%$	4.4	-8.9	3.1	1.4	
	P _{JA} + 10%	-4.4	8.9	-3.1	-1.4	
	P _{JA} + 20%	-8.7	17.7	-6.2	-2.8	
	P _{JA} + 30%	-13.1	26.6	-9.3	-4.2	
September and October (SO)	$P_{SO}-30\%$	11.6	9.0	-24.3	3.7	
	$P_{SO}-20\%$	7.7	6.0	-16.2	2.5	
	$P_{SO}-10\%$	3.9	3.0	-8.1	1.2	
	P _{SO} + 10%	-3.9	-3.0	8.1	-1.2	
	P _{SO} + 20%	-7.7	-6.0	16.2	-2.5	
	P _{SO} + 30%	-11.6	-9.0	24.3	-3.7	

annual modeled NPP increases by 23%, 31% and 42%, respectively. But when precipitation decreases by 10%, 20% and 30%, annual modeled NPP decreases by 27%, 42% and 54%, respectively.

3.2. Impacts of altered precipitation seasonality

The precipitation seasonality treatment is symmetrical (Fig. 5a, e and i), but the response of annual man NPP, Rh and NEP to this treatment is modeled to be asymmetrical (Fig. 5). When we shift 10% (11 mm), 20% (23 mm) and 30% (34 mm) of precipitation from MJ to the other sub-periods (scenarios $P_{\text{MJ}}-10\%,\,P_{\text{MJ}}-20\%$ and P_{MI} – 30%; Fig. 5a; Table 2), annual NPP decreases by 13 (9%), 23 (16%) and 28 g C m⁻² yr⁻¹ (19%), respectively (Fig. 5b). By contrast, when we add 10% (11 mm), 20% (23 mm) and 30% (34 mm) of precipitation in MJ and reduce precipitation by the same amount evenly during the other two sub-periods of the year (scenarios P_{MI} + 10%, P_{MI} + 20% and P_{MI} + 30%), the annual NPP increases by 15 (10%), 27 (18%) and 31 g Cm^{-2} yr⁻¹ (21%), respectively (Fig. 5b). Unlike NPP, modeled Rh is not sensitive to changes in precipitation seasonality (Fig. 5c). The total annual Rh changes are very small compared to the one of NPP in response to modified precipitation seasonality (Fig. 5b and c). Therefore, the response of NEP to the precipitation seasonality treatment is similar to the one of NPP (Fig. 5d). Annual NEP decreases by 14, 25 and $28 \text{ gCm}^{-2} \text{ yr}^{-1}$ in the P_{MJ} – 10%, P_{MJ} – 20% and P_{MJ} – 30% treatment respectively, but increases by 15, 27 and 32 g C m⁻² yr⁻¹ in the P_{MJ} + 10%, P_{MJ} + 20% and P_{MI}+30% treatment respectively (Fig. 5d). Thus, reduced MJ precipitation results into a smaller effect on the absolute value of NEP and NPP changes than does increased MJ precipitation.

Interestingly, for the three sub-periods of the growing season (MJ, JA and SO) annual NPP always decreases when MJ rainfall is decreased, even though this spring decrease is compensated by increased JA and SO precipitation (Fig. 5b) in scenarios $P_{MJ} - 10\%$, $P_{MJ} - 20\%$ and $P_{MJ} - 30\%$. At face value, NPP increases in MJ, JA and SO in all the scenarios when spring is wetter, i.e. $P_{MJ} + 10\%$, $P_{MJ} + 20\%$ and $P_{MJ} + 30\%$, even though precipitation was lower during the growing season in JA and SO (Fig. 5b). There is almost no response of Rh to changes in spring (MJ) precipitation. The response of Rh to altered JA and SO precipitation was also much smaller than the response of NPP (Fig. 5c) for the same scenario. An increase in MJ precipitation compensated by a consecutive decrease in JA, SO and NGS precipitation enhanced NEP (more sink) in MJ and JA, and resulted into no effects on NEP during SO and NGS (Fig. 5d). The

results of these simulations thus show that altered precipitation in spring largely determines the response of NEP an NPP during the rest of the growing season.

In the six scenarios of *seasonality treatment* during July and August ($P_{JA} - 10\%$, $P_{JA} - 20\%$, $P_{JA} - 30\%$, $P_{JA} + 10\%$, $P_{JA} + 20\%$ and $P_{JA} + 30\%$), even though JA precipitation changed from -27 mm to 27 mm (Table 2), there was no significant response of NPP, Rh and NEP (Fig. 5e–h). Changes of annual NPP ranged between $-4 \text{ g C m}^{-2} \text{ yr}^{-1}$ (-2%) in the scenario $P_{JA} - 20\%$, and $4 \text{ g C m}^{-2} \text{ yr}^{-1}$ (2%) in $P_{JA} + 30\%$. The annual Rh did not change significantly either ($-0-1 \text{ g C m}^{-2} \text{ yr}^{-1}$) for these six scenarios. Annual NEP only changed from $-4 \text{ g C m}^{-2} \text{ yr}^{-1}$ in $P_{JA} - 20\%$ to $4 \text{ g C m}^{-2} \text{ yr}^{-1}$ in $P_{JA} + 30\%$, thus a small change only.

The results of the six seasonality treatment scenarios for September and October ($P_{SO} - 10\%$, $P_{SO} - 20\%$, $P_{SO} - 30\%$, $P_{SO} + 10\%$, P_{SO} + 20% and P_{SO} + 30%) are shown in Fig. 5i–l. A shift of precipitation from SO to the other three sub-periods of the year enhanced annual NPP by 5 ($P_{SO} - 10\%$ scenario) to 18 g C m⁻² yr⁻¹ ($P_{SO} - 30\%$ scenario). This means that a combination of dryer SO (autumn) and wetter other periods is beneficial to NPP, just opposite to the effect of dryer MJ (spring). In contrast, a shift of precipitation from other seasons to SO reduced annual NPP by 9 (P_{SO} + 10% scenario) to $25 \text{ g C m}^{-2} \text{ yr}^{-1}$ (P_{SO} + 30% scenario). Annual Rh slightly increased (0–1 g C m⁻² yr⁻¹) in P_{SO} – 10%, P_{SO} – 20% and P_{SO} – 30% scenarios, and slightly decreased $(-1-0 \text{ g C m}^{-2} \text{ yr}^{-1})$ in P_{SO} + 10%, P_{SO} + 20% and P_{SO} + 30% scenarios (Fig. 5k). Hence, dryer autumns increased annual NEP (larger sink), the converse being true for wetter autumns (see Fig. 51). The impacts of shift of precipitation between SO and other seasons on NPP or NEP is explained by changes in those fluxes during JA (Figs. 5 and 6).

3.3. Impacts of altered precipitation frequency

Fig. 7 shows the impacts of the precipitation frequency treatment (PF) on growing season carbon fluxes and soil moisture when keeping the growing season precipitation amount constant. During the growing season, an increase in the number of heavy rain days exceeding 10 mm ($PF_{10 mm}$) significantly enhanced NPP (P < 0.001), and slightly inhibited Rh (Fig. 7a and d). This resulted into substantially higher NEP (larger sink) during the growing season (Fig. 7g). Oppositely, an increase in the number of moderate rain days for which precipitation is in-between 5 mm and 10 mm (PF_{5-10 mm}) was found to reduce NPP (P<0.001) and to increase Rh (P<0.001), thus resulting in a net loss of carbon (larger negative NEP values) (Fig. 7b, e and h). The frequency of small rainfall days for which precipitation is comprised between 1 and $5 \text{ mm} (PF_{1-5 \text{ mm}})$ was found to have little impacts on ecosystem carbon fluxes (Fig. 7c, f and i). The modeled growing season soil moisture significantly increased with increased $PF_{10\,mm}$ and decreased with increased PF_{5-10 mm} (Fig. 7j and k), but showed no significant relationship with increased $PF_{1-5 \text{ mm}}$ (Fig. 71).

4. Discussion

4.1. Semi-arid Inner Asian grassland ecosystem responses to changes in precipitation amount

There is evidence that NPP positively correlates with annual precipitation amount across different sites or different years in water-limited grassland ecosystems (e.g. Churkina et al., 1999; Knapp and Smith, 2001; Huxman et al., 2004). The response of NPP to precipitation across sites and seasons is generally found to be explained by water limitation (Dukes et al., 2005; Gerten et al., 2008; Luo et al., 2008). This is in line with our simulation results. During dry periods (between two large precipitation events



Fig. 5. Changes in seasonal (May and June (MJ), July and August (JA), September and October (SO), non-growing season (NGS)) and annual (ANN) precipitation (ΔP) and carbon fluxes for the six precipitation seasonality scenarios (-10%, -20%, -30%, +10%, +20% and +30%) for MJ, JA and SO in Table 2 compared with the control simulation, respectively. Left, middle and right columns indicate precipitation seasonality treatment scenarios for MJ, JA and SO, respectively. (a), (e) and (i) changes in precipitation (ΔP); (b), (f) and (j) changes in net primary production (ΔNPP); (c), (g) and (k) changes in heterotrophic respiration (ΔRh); (d), (h) and (l) changes in net ecosystem production (ΔNPP) of the precipitation seasonality treatment compared with the control scenario over the CN-Xi2 site.

during the growing season), under any precipitation decrease scenarios, we found a decrease of NPP governed by soil moisture depletion (Fig. 3a). NPP is more directly responsive to soil moisture availability than to precipitation amount (Ogle and Reynolds, 2004; Robertson et al., 2009). Therefore, during low ambient soil moisture conditions during the growing season, addition or removal of rainfall could have larger impacts on NPP than that during high ambient soil moisture conditions (Fig. 3a; Gerten et al., 2008).

Our results in Figs. 3 and 4 show that the response of NPP of the semi-arid grassland ecosystem studied to precipitation amount is asymmetrical. The increase of NPP in response to more precipitation is smaller in absolute value than the decrease of NPP from less precipitation (Figs. 3 and 4). The modeled NPP response (-53% to +42%) to annual precipitation changes going from -30%

to +30% is non-linear (Fig. 4), a result similar to Gerten et al. (2008).

There is less studies focusing on the effects of precipitation amount on Rh than on NPP (e.g. Chou et al., 2008). In our simulation results, precipitation addition or removal has no significant effects on Rh. The reason for this is that Rh mainly depends on temperature under non water-limited situations in ORCHIDEE (Chou et al., 2008). Therefore, the effects of altered precipitation amount on NEP are comparable in sign and magnitude to those on NPP. A future increase in annual precipitation amount, such as projected by climate models over north western China (Piao et al., 2010) could be expected to increase carbon storage in the studied grassland ecosystem (see also Parton et al., 2012), while a decrease in annual precipitation should have an effect of opposite sign and larger absolute magnitude.



Fig. 6. Changes in seasonal (May and June (MJ), July and August (JA), September and October (SO), non-growing season (NGS)) and annual (ANN) soil moisture (Δ SM) for the six precipitation seasonality scenarios (-10%, -20%, -30%, +10%, +20% and +30%) for (a) MJ, (b) JA and (c) SO in Table 2 compared with the control simulation, respectively.



Fig. 7. Box and whisker plots of growing season net primary production (NPP), ecosystem heterotrophic respiration (Rh), net ecosystem production (NEP) and soil moisture (SM) response to changes in precipitation frequency (PF) when keeping total precipitation amount constant during the growing season. PF_{10mm} is the number of days on which precipitation exceeds 5 mm but less than 10 mm; and PF_{1-5 mm} is the number of days on which precipitation exceeds 1 mm but less than 5 mm. Growing season NPP responses to (a) PF_{10mm}, (b) PF_{5-10 mm} and (c) PF_{1-5 mm}; growing season Rh responses to changes in (d) PF_{10mm}, (e) PF_{5-10 mm} and (f) PF_{1-5 mm}; growing season SM responses to changes in (g) PF_{10 mm}, (h) PF_{5-10 mm} and (i) PF_{1-5 mm}; and growing season SM responses to changes in (j) PF_{10 mm}, (k) PF_{5-10 mm} and (l) PF_{1-5 mm} over the CN-Xi2 site.

4.2. Semi-arid grassland ecosystem responses to changes in precipitation seasonality

In several grass species of the Patagonian steppe, ANPP was observed to be weakly correlated with annual precipitation and strongly correlated with seasonal precipitation and temperature (Jobbagy and Sala, 2000). This result suggests that grass ANPP can be more responsive to the seasonal availability of precipitation than to the amount of annual precipitation (Jobbagy and Sala, 2000; Robertson et al., 2009). Precipitation seasonality has large impacts on grassland ecosystems NPP (Robertson et al., 2009; Peng et al., 2011; Parton et al., 2012). Moreover, soil moisture has a time lag from precipitation, which regulates carbon cycling processes in semi-arid grasslands (Knapp et al., 2008). In our simulation results, more spring precipitation induces an increase of spring soil moisture that is carried over summer, and offsets a summer precipitation decrease (Figs. 5a and 6a). This legacy of spring precipitation on summer soil moisture leads to increased summer and even annual NPP and NEP (Fig. 5b and d), even when associated with a summer precipitation decrease. In contrast, less spring

precipitation associated with more summer precipitation leads to decreased spring and summer soil moisture and thus reduces NPP and NEP (Fig. 5b and d). This suggests that any change in spring precipitation has larger controlling effects on summer soil moisture than changes in summer precipitation. An additional reason explaining why higher spring precipitation increases annual NPP and NEP is that abundant spring soil moisture may ensure root growth and enhance soil water acquisition in the subsequent summer (e.g. Bates et al., 2006), although this mechanism is not fully included in ORCHIDEE and could not explain the results in this study.

Compared to the effect of spring precipitation, a shift of summer precipitation to (from) other seasons did not remarkably change modeled annual NPP, Rh and NEP values in the semi-arid grassland ecosystem investigated in this study (Fig. 5f–h). Even if spring precipitation is moved to the summer period, we found no significant changes in summer soil moisture, as well as in summer and annual NPP, Rh and NEP (Figs. 5f–h and 6b). This supports a key controlling role of spring precipitation on annual and particularly summer NPP in the ORCHDEE model (Fig. 5). Spring precipitation seems to have a higher efficiency of transformation to soil moisture than summer precipitation, likely because a larger proportion of precipitation is lost in evaporation under higher temperature in summer. On the other hand, if extra spring precipitation exceeds the soil water storage capacity, it is going to be lost in runoff. In addition, the time lag effect of soil moisture from precipitation is determined by the soil water storage capacity. At the CN-Xi2 semi-arid grassland, prescribing a shift of summer precipitation to spring in the ORCHIDEE model increases annual NPP and NEP (Fig. 5d), while a shift of summer precipitation to autumn or non-growing season decreases annual NPP (Fig. 5l).

Shift of precipitation from other seasons to spring increases annual NPP and NEP, whereas shift of precipitation from other seasons to autumn has the opposite effect (Fig. 5). Autumn precipitation is not as effective as spring or summer precipitation for vegetation NPP and NEP at the studied site. Because solar radiation and temperature in autumn are not as favorable as during spring and summer (Niu et al., 2011; Peng et al., 2011), even if autumn soil moisture is sufficient, grassland NPP in autumn is limited by other factors. Decreased autumn precipitation with increased Rh in autumn because soil labile carbon pools increase from previous seasons (MJ and JA) (increased MJ and JA NPP in Fig. 5). Taken together, a shift of autumn precipitation to spring and summer is expected to increase NPP and NEP at the site studied. One uncertainty of our analysis is the controlling effect of nutrients on NPP and TER which are mineralized more effectively under wet and warm soil conditions, and are likely to cause carry over effects from one season to another. We speculate that these effects are likely to be additive to the carry over effects of spring precipitation anomalies, with wetter anomalies in spring causing higher nitrogen availability during the follow-up summer and possibly autumn as well. Conversely, wetter conditions in autumn could induce higher growth during the next year, a process not investigated in this study. Using a version of the ORCHIDEE model enhanced for nitrogen cycling (Zaehle et al., 2010) is recommended for future work to investigate the ecosystem response to seasonal rainfall shifts, and even more to inter-annual rainfall variability changes (see for instance Haddad et al., 2002).

4.3. Responses to changes in precipitation daily frequency

Precipitation frequency directly affects the intra-annual variation or allocation of soil moisture between shallow and deep soil layers (e.g. Knapp et al., 2008; Robertson et al., 2009; Piao et al., 2009; Parton et al., 2012). In our study, even though ORCHIDEE uses a soil moisture model with only two soil layers, and hence may not describe realistically the infiltration of individual precipitation events, we found that the number of heavy rainfall days is positively and significantly correlated with annual NPP. Further, the number of intermediate precipitation (PF_{5-10 mm}) is positively and significantly correlated with Rh (Fig. 7). This simulation result is in accordance with the experimental results of a 3-year manipulative experiment on a shortgrass steppe in northeastern Colorado, USA (Parton et al., 2012). That study showed that a shift toward more large precipitation events (>10 mm) increased carbon uptake, while more small precipitation events (<10 mm) increased heterotrophic respiration (Parton et al., 2012). In our simulation results, NPP increases with increased PF_{10 mm} because soil moisture increase with PF_{10 mm} (Fig. 7j). Rh increases with increased PF5-10 mm because of the increased soil labile carbon pools with increased PF_{5-10 mm} in ORCHIDEE. But note that the Rh response is smaller to NPP response (Fig. 7), which reflects Rh is not as sensitive as NPP to soil moisture in ORCHIDEE model. At larger scales, using vegetation index from remote sensing to indicate vegetation production, Fang et al. (2005) showed that inter-annual variations of grassland production positively correlates with not only annual precipitation amount but also precipitation frequency.

Large rainfall event recharge the soil water more effectively than small rainfall events. This is particularly true when temperature is high, with a competition between soil moisture removal by evapotranspiration and infiltration of rain to deeper soil. Semi-arid grassland ecosystems may thus experience less seasonal water stress with more large rainfall events (Knapp et al., 2008). Moreover, large rainfall event infiltrate to deeper soil lavers, whereas small rainfall event could only wet the shallow soil or the surface soil (e.g. Knapp et al., 2008; Parton et al., 2012), which may be not included in 2-layers bucket ORCHIDEE. The soil water stored in the shallow soil layers could be evaporated much faster than that in the deep soil layers under the high solar radiation and high temperature circumstance during the growing season. Water from small rainfall event is more easily depleted by evaporation than used for photosynthesis, i.e. plant water use efficiency from small rainfall events could be lower than that from large rainfall events. This process will depend on the vertical distribution of active plant roots. Shallow-rooted plants may take better advantage of small rainfall events, and deep-rooted plants of larger rainfall events (Robertson et al., 2009). The magnitude of the effect calculated in this study with the ORCHIDEE model depends however on the structure of the model, even though its parameters were optimized against CO₂ flux observations. The soil model of ORCHIDEE is a 2-layers bucket. This structure overestimates the residence time of water in the soil after each rainfall (too high auto-correlation function of soil moisture high frequency variation compared with measurements) as shown by Rebel et al. (2012). It is thus possible that our simulation results over-estimate the resilience of soil moisture after large rainfall events, and its beneficial effects on NPP, NEP in this study. Using a soil model with multiple layers is recommended for future studies.

5. Conclusions

Based on scenarios simulations, results from this study show the impact of changes in precipitation amount, seasonality and frequency on soil moisture and subsequently on NPP, Rh and NEP in a semi-arid grassland ecosystem in Inner Mongolia. Increase in annual precipitation amount by 10%, 20% and 30% result into higher annual NPP by 23%, 31% and 42%, respectively. Conversely, decrease in precipitation amount by 10%, 20% and 30% reduce annual NPP by 27%, 42% and 54%, respectively. The NPP response to annual precipitation amount is found to be non-linear. Keeping the annual precipitation amount constant, a shift in the seasonal distribution of precipitation toward spring increases spring and summer soil moisture, and thus enhances spring, but also summer and total annual NPP and NEP. On the other hand, increased autumn precipitation associated with decreased spring and summer precipitation decreases annual NPP and NEP. More frequent large rainfall events (>10 mm) during growing seasons could enhance growing season NPP and NEP, while more small rainfall events (>5 mm and <10 mm) could increase heterotrophic respiration and cause a net carbon loss.

The grassland production and carbon balance are quite sensitive to changes in precipitation amount, seasonality and frequency. During the past five decades, annual precipitation was relatively constant in northern China while winter precipitation increased and spring, summer and autumn precipitation decreased significantly (Piao et al., 2010). It has been suggested that changes in precipitation seasonality and frequency in the past decades were not beneficial for vegetation growth and carbon sequestration in the semi-arid regions in northern China (Fang et al., 2005). In the future, it is projected that winter and summer precipitation amount is likely to increase in most regions of Asia, and intense precipitation events frequency is likely to increase in the 21st century, although the projections of precipitation still have large uncertainties (IPCC, 2007). Therefore, the increase in winter and summer precipitation and large rainfall events frequency could enhance grassland NPP and NEP over semi-arid regions in the 21st century without considering the changes in temperature.

Acknowledgments

We thank T. Wang and B. Zhu for the constructive comments. This study was supported by the National Natural Science Foundation of China (41125004), National Basic Research Program of China (2013CB956303), Foundation for Sino-EU research cooperation of Ministry of Science and Technology of China (1003), and the European Commission's Seventh Framework Programme ([FP7/2007–2013]) under grant agreement No. 242316.

References

- Bates, J.D., Svejcar, T., Miller, R.F., Angell, R.A., 2006. The effects of precipitation timing on sagebrush steppe vegetation. J. Arid Environ. 64, 670–697.
- 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. Glob. Change Biol. 14, 1382–1394.
- Churkina, G., Running, S.W., Schloss, A.L., Intercomparison, T.P.O.F.T.P.N.M., 1999. Comparing global models of terrestrial net primary productivity (NPP): the importance of water availability. Glob. Change Biol. 5, 46–55.
- Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend, A.D., Friedlingstein, P., Grunwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J.M., Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J.F., Sanz, M.J., Schulze, E.D., Vesala, T., Valentini, R., 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437, 529–533.
- de Ducoudre, N.I., Laval, K., Perrier, A., 1993. SECHIBA, a new set of parameterizations of the hydrologic exchanges at the land atmosphere interface within the lmd atmospheric general-circulation model. J. Clim. 6, 248–273.
- de Rosnay, P., Polcher, J., 1998. Modelling root water uptake in a complex land surface scheme coupled to a GCM. Hydrol. Earth Syst. Sci. 2, 239–255.
- Ding, Y.H., Ren, G.Y., Zhao, Z.C., Xu, Y., Luo, Y., Li, Q.P., Zhang, J., 2007. Detection, causes and projection of climate change over China: an overview of recent progress. Adv. Atmos. Sci. 24, 954–971.
- Dukes, J.S., Chiariello, N.R., Cleland, E.E., Moore, L.A., Shaw, M.R., Thayer, S., Tobeck, T., Mooney, H.A., Field, C.B., 2005. Responses of grassland production to single and multiple global environmental changes. Plos Biol. 3, 1829–1837.
- Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R., Mearns, L.O., 2000. Climate extremes: observations, modeling, and impacts. Science 289, 2068–2074.
- Fang, J.Y., Piao, S.L., Zhou, L.M., He, J.S., Wei, F.Y., Myneni, R.B., Tucker, C.J., Tan, K., 2005. Precipitation patterns alter growth of temperate vegetation. Geophys. Res. Lett. 32, L21411.
- Fay, P.A., 2009. Precipitation variability and primary productivity in water-limited ecosystems: how plants 'leverage' precipitation to 'finance' growth. New Phytol. 181, 5–8.
- Gao, X., Shi, Y., Song, R., Giorgi, F., Wang, Y., Zhang, D., 2008. Reduction of future monsoon precipitation over China: comparison between a high resolution RCM simulation and the driving GCM. Meteorol. Atmos. Phys. 100, 73–86.
- Gerten, D., Luo, Y., Le Maire, G., Parton, W.J., Keough, C., Weng, E., Beier, C., Ciais, P., Cramer, W., Dukes, J.S., Hanson, P.J., Knapp, A.A.K., Linder, S., Nepstad, D., Rustad, L., Sowerby, A., 2008. Modelled effects of precipitation on ecosystem carbon and water dynamics in different climatic zones. Glob. Change Biol. 14, 2365–2379.
- Haddad, N.M., Tilman, D., Knops, J.M.H., 2002. Long-term oscillations in grassland productivity induced by drought. Ecol. Lett. 5, 110–120.
- Huxman, T.E., Smith, M.D., Fay, P.A., Knapp, A.K., Shaw, M.R., Loik, M.E., Smith, S.D., Tissue, D.T., Zak, J.C., Weltzin, J.F., Pockman, W.T., Sala, O.E., Haddad, B.M., Harte, J., Koch, G.W., Schwinning, S., Small, E.E., Williams, D.G., 2004. Convergence across biomes to a common rain-use efficiency. Nature 429, 651–654.
- IPCC Climate Change, 2007. The Physical Science Basis. Cambridge Univ. Press, Cambridge, UK.
- Jobbagy, E.G., Sala, O.E., 2000. Controls of grass and shrub aboveground production in the Patagonian steppe. Ecol. Appl. 10, 541–549.
- Knapp, A.K., Beier, C., Briske, D.D., Classen, A.T., Luo, Y., Reichstein, M., Smith, M.D., Smith, S.D., Bell, J.E., Fay, P.A., Heisler, J.L., Leavitt, S.W., Sherry, R., Smith, B., Weng, E., 2008. Consequences of more extreme precipitation regimes for terrestrial ecosystems. Bioscience 58, 811–821.
- 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.

- Knapp, A.K., Smith, M.D., 2001. Variation among biomes in temporal dynamics of aboveground primary production. Science 291, 481–484.
- Krinner, G., Viovy, N., de Noblet-Ducoudré, N., Ogée, J., Polcher, J., Friedlingstein, P., Ciais, P., Sitch, S., Prentice, I.C., 2005. A dynamic global vegetation model for studies of the coupled atmosphere–biosphere system. Global Biogeochem. Cycles 19, GB1015.
- Kuppel, S., Peylin, P., Chevallier, F., Bacour, C., Maignan, F., Richardson, A.D., 2012. Constraining a global ecosystem model with multi-site eddy-covariance data. Biogeosciences 9, 3757–3776.
- Li, Z.H., Bao, Y.J., Wang, H.M., Xu, T., Cheng, Y., Gao, J.X., 2008. The analysis on degeneration status and the driving force of Xilinguole Steppe. Ecology Environ. 17, 2312–2318 (in Chinese).
- Luo, Y., Gerten, D., Le Maire, G., Parton, W.J., Weng, E., Zhou, X., Keough, C., Beier, C., Ciais, P., Cramer, W., Dukes, J.S., Emmett, B., Hanson, P.J., Knapp, A., Linder, S., Nepstad, D., Rustad, L., 2008. Modeled interactive effects of precipitation, temperature, and CO(2) on ecosystem carbon and water dynamics in different climatic zones. Glob. Change Biol. 14, 1986–1999.
- Muldavin, E.H., Moore, D.I., Collins, S.L., Wetherill, K.R., Lightfoot, D.C., 2008. Aboveground net primary production dynamics in a northern Chihuahuan Desert ecosystem. Oecologia 155, 123–132.
- Niu, S., Luo, Y., Fei, S., Montagnan, L., Bohrer, G.I.L., Janssens, I.A., Gielen, B., Rambal, S., Moors, E., Matteucci, G., 2011. Seasonal hysteresis of net ecosystem exchange in response to temperature change: patterns and causes. Glob. Change Biol. 17, 3102–3114.
- Ogle, K., Reynolds, J.F., 2004. Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays. Oecologia 141, 282–294.
- 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. Glob. Change Biol. 18, 915–927.
- Peng, S., Chen, A., Xu, L., Cao, C., Fang, J., Myneni, R.B., Pinzon, J.E., Tucker, C.J., Piao, S., 2011. Recent change of vegetation growth trend in China. Environ. Res. Lett. 6, 044027.
- Piao, S., Friedlingstein, P., Ciais, P., de Noblet-Ducoudre, N., Labat, D., Zaehle, S., 2007. Changes in climate and land use have a larger direct impact than rising CO₂ on global river runoff trends. Proc. Natl. Acad. Sci. U.S.A 104, 15242–15247.
- Piao, S., Yin, L., Wang, X., Ciais, P., Peng, S., Shen, Z., Seneviratne, S.I., 2009. Summer soil moisture regulated by precipitation frequency in China. Environ. Res. Lett. 4, 044012.
- Piao, S.L., Ciais, P., Huang, Y., Shen, Z.H., Peng, S.S., Li, J.S., Zhou, L.P., Liu, H.Y., Ma, Y.C., Ding, Y.H., Friedlingstein, P., Liu, C.Z., Tan, K., Yu, Y.Q., Zhang, T.Y., Fang, J.Y., 2010. The impacts of climate change on water resources and agriculture in China. Nature 467, 43–51.
- Rebel, K.T., de Jeu, R.A.M., Ciais, P., Viovy, N., Piao, S.L., Kiely, G., Dolman, A.J., 2012. A global analysis of soil moisture derived from satellite observations and a land surface model. Hydrol. Earth Syst. Sci. 6, 833–847.
- Robertson, T.R., Bell, C.W., Zak, J.C., Tissue, D.T., 2009. Precipitation timing and magnitude differentially affect aboveground annual net primary productivity in three perennial species in a Chihuahuan Desert grassland. New Phytol. 181, 230–242.
- Ross, I., Misson, L., Rambal, S., Arneth, A., Scott, R.L., Carrara, A., Cescatti, A., Genesio, L., 2012. How do variations in the temporal distribution of rainfall events affect ecosystem fluxes in seasonally water-limited Northern Hemisphere shrublands and forests? Biogeosciences 9, 1007–1024.
- Santaren, D., Peylin, P., Viovy, N., Ciais, P., 2007. Optimizing a process-based ecosystem model with eddy-covariance flux measurements: a pine forest in southern France. Global Biogeochem. Cycles 21, GB2013.
- Schwalm, C.R., Williams, C.A., Schaefer, K., Anderson, R., Arain, M.A., Baker, I., Barr, A., Black, T.A., Chen, G., Chen, J.M., Ciais, P., Davis, K.J., Desai, A., Dietze, M., Dragoni, D., Fischer, M.L., Flanagan, L.B., Grant, R., Gu, L., Hollinger, D., Izaurralde, R.C., Kucharik, C., Lafleur, P., Law, B.E., Li, L., Li, Z., Liu, S., Lokupitiya, E., Luo, Y., Ma, S., Margolis, H., Matamala, R., McCaughey, H., Monson, R.K., Oechel, W.C., Peng, C., Poulter, B., Price, D.T., Riciutto, D.M., Riley, W., Sahoo, A.K., Sprintsin, M., Sun, J., Tian, H., Tonitto, C., Verbeeck, H., Verma, S.B., 2010. A model-data intercomparison of CO₂ exchange across North America: results from the North American carbon program site synthesis. J. Geophys. Res. 115, G00H05.
- Tan, K., Ciais, P., Piao, S., Wu, X., Tang, Y., Vuichard, N., Liang, S., Fang, J., 2010. Application of the ORCHIDEE global vegetation model to evaluate biomass and soil carbon stocks of Qinghai-Tibetan grasslands. Global Biogeochem. Cycles 24, GB1013.
- Tank, A., Konnen, G.P., 2003. Trends in indices of daily temperature and precipitation extremes in Europe, 1946–99. J. Clim. 16, 3665–3680.
- Trenberth, K.E., Dai, A., Rasmussen, R.M., Parsons, D.B., 2003. The changing character of precipitation. Bull. Amer. Meteor. Soc. 84, 1205–1217.
- Verbeeck, H., Peylin, P., Bacour, C., Bonal, D., Steppe, K., Ciais, P., 2011. Seasonal patterns of CO(2) fluxes in Amazon forests: fusion of eddy covariance data and the ORCHIDEE model. J. Geophys. Res. 116, G02018.
- Wang, T., Brender, P., Ciais, P., Piao, S.L., Mahecha, M.D., Chevallier, F., Reichstein, M., Ottle, C., Maignan, F., Arain, A., Bohrer, G., Cescatti, A., Kiely, G., Law, B.E., Lutz, M., Montagnani, L., Moors, E., Osborne, B., Panferov, O., Papale, D., Vaccari, F.P., 2012. State-dependent errors in a land surface model across biomes inferred from eddy covariance observations on multiple timescales. Ecol. Model 246, 11–25.
- Wentz, F.J., Ricciardulli, L., Hilburn, K., Mears, C., 2007. How much more rain will global warming bring? Science 317, 233–235.

- Wu, Z., 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. Glob. Change Biol. 17, 927–942.
- Yuan, Z.Y., Li, L.H., Han, X.G., Huang, J.H., Jiang, G.M., Wan, S.Q., 2005. Soil characteristics and nitrogen resorption in *Stipa krylovii* native to northern China. Plant Soil 273, 257–268.
- Zaehle, S., Friedlingstein, P., Friend, A.D., 2010. Terrestrial nitrogen feedbacks may accelerate future climate change. Geophys. Res. Lett. 37, L01401.
- Zavaleta, E.S., Shaw, M.R., Chiariello, N.R., Thomas, B.D., Cleland, E.E., Field, C.B., Mooney, H.A., 2003. Grassland responses to three years of elevated temperature, CO(2), precipitation, and N deposition. Ecol. Monogr. 73, 585–604.
- Zhang, P., Chen, S., Zhang, W., Miao, H., Chen, J., Han, X., Lin, G., 2011. Biophysical regulations of NEE light response in a steppe and a cropland in Inner Mongolia. J. Plant Ecol. 5, 238–248.