

Water response of ecosystem respiration regulates future projection of net ecosystem productivity in a semiarid grassland

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ABSTRACT

Recent evidences show that terrestrial biogeochemical models have large uncertainty in estimating climate-change effect on grassland net ecosystem productivity (NEP), which is defined as the difference between gross ecosystem photosynthesis (GEP) and respiration (ER). It remains unclear that whether GEP or ER limits the model capability to simulate NEP responses to climate change in semiarid grasslands. Given the surrogate CENTURY-type model is widely used for Earth system modeling, we investigated two of them (i.e., DAYCENT and TECO models) and examined which processes dominate their ability to capture the responses of NEP to experimental climate changes in a temperate steppe of northern China. During the simulation from 2006 to 2008, the two models captured the observed mean annual NEP in the control plots when they were validated by the observations from an adjacent eddy-flux tower. However, they failed to capture the treatment effects of experimental warming and increased precipitation on NEP because of the poor estimations of ER responses. DAYCENT model simulated a higher precipitation effect on ER (37.83%) and TECO model overestimated the warming effect on ER by 8.18%. The simulation of treatment effects on ER and therefore NEP can be improved by an optimized parameterization of the water-related decay functions for soil organic carbon (C). The simulated cumulative loss of total ecosystem C stock during 2010–2100 were decreased when the TECO model used experiment-fitted parameters (0.72 kg C m^{-2}) instead of using the initial validation with eddy-flux data (0.96 kg C m^{-2}). The ecosystem shifted from C sink to source at threshold of 435 mm of annual total precipitation. Our findings indicate that future projection of C cycle in semiarid grasslands could be improved by better understanding of water response of ecosystem respiratory processes.

1. Introduction

Convincing projections of terrestrial carbon (C) feedback to climate change need better understanding of the response of net ecosystem productivity (NEP) to climate change. NEP represents the balance between gross ecosystem photosynthesis (GEP) and ecosystem respiration (ER) (Oberbauer et al., 2007; Niu et al., 2008). Despite their importance, large projection uncertainties of those ecosystem CO_2 fluxes

and their sensitivities to climate change still remain in current Earth system models (Arora et al., 2013; Friedlingstein et al., 2006, 2014; Jones et al., 2013). Semi-arid grassland is one large contributor to the trend and inter-annual variability of global land CO_2 sink (Ahlström et al., 2015). Thus, an improved simulation of grassland NEP and its two components is particularly important for accurately predicting global land C dynamics under future climate change.

The responses of terrestrial NEP to climate change have been

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studied by many field manipulative experiments (Wu et al., 2011; Lu et al., 2013), so results from these studies have been increasingly used to evaluate model performance on terrestrial C cycle. Some studies evaluate the model performance indirectly using the meta-analysis results of multiple experiments. For example, Piao et al. (2013) used the weighted response of multiple global-change experiments from a meta-analysis to assess the modeled response of GEP to climate change. In that study, the averaged response ratios among experiments were used to evaluate the regression coefficients derived from the time-series analysis of GEP against climate factors. This approach is useful to explore the systematic bias of the models, but is hard to tell which processes or parameters of the models could be improved. Also, the application of this approach is strongly challenged by the large difference in the spatial scale between field experiments (10^1 – 10^2 m²) and global land models (0.5° – 1° of latitude-longitude degree). Some recent studies have tried to use field experiments to improve model performance at the site level. One excellent example is the FACE Model-Data Synthesis (FACE-MDS) project (e.g., De Kauwe et al., 2013; Medlyn et al., 2016), which runs multiple models at different FACE experimental sites to explore the research needs for current terrestrial ecosystem models. For example, they found the models were unable to replicate the observed aboveground net primary productivity from both ambient and treatment plots in the Prairie Heating and CO₂ Enrichment (PHACE) experiment in the semiarid grassland in Wyoming, USA (De Kauwe et al., 2017). As suggested by that study, using multi-model comparisons in advance of ecosystem-scale experiments need to become normal practice in grassland. However, the ecosystem-level CO₂ fluxes (i.e., GEP and ER) are difficult to measure directly, thus it remains unclear that how their observations could improve the model performance in the semiarid grassland.

The temperate steppe in arid and semiarid regions of northern China is one of dominant grassland types on the Eurasian continent (Li et al., 2003; Niu et al., 2011). With the large diurnal temperature difference and uneven distribution of precipitation, ecosystem C cycle in this area is sensitive to climate warming and changing precipitation regimes (Christensen et al., 2004; Xia et al., 2009; Niu et al., 2011). Many ecosystem manipulative experiments have been done to investigate the response of CO₂ exchange to warming and increased precipitation in this grassland (Niu et al., 2008; Xia et al., 2009; Zhao et al., 2016). Most of them have demonstrated that soil water availability plays a predominant role in mediating ecosystem CO₂ response to climate change (Song et al., 2012; Xia and Wan, 2012; Liu et al., 2016). For example, water availability regulates the responses of ecosystem C uptake (Niu et al., 2008, 2011) and soil respiration (Liu et al., 2009) to experimental warming. In addition, previous analysis has already shown that precipitation non-linearly regulates C cycle in semiarid grassland of Inner Mongolia (Peng et al., 2013). Thus, it is important to examine which model processes can be improved and thus better predict C feedback to climate changes in this area.

In this study, we used data from a field manipulative experiment with warming and increased precipitation to evaluate the performance of two ecosystem models. The field experiment has been run since 2005 in the Mongolian Plateau and has four treatments, including control, warming, increased precipitation, and warming plus increased precipitation. DAYCENT and TECO models as the representative of CENTURY-type model have been used to simulate response of C cycle to climate change in grassland (Shi et al., 2014; Ryals et al., 2015). We force the two models with the climate conditions from different treatments, and then evaluate (1) how the models perform in simulating the observed NEP response to climate change in the experiment, and (2) whether the photosynthetic or respiratory processes limit the model estimates of NEP responses to future climate change in this region.

2. Materials and methods

2.1. Experimental description

The experiment was conducted in Duolun County, Inner Mongolia, China ($42^\circ 02' \text{ N}$, $116^\circ 17' \text{ E}$, 1324 m). The mean annual temperature is 2.1° C , with monthly average temperature ranging from -17.5° C in January to 18.9° C in July. The mean annual precipitation is 385.5 mm, with approximately 90% occurring from May to October. The soil type is classified as Haplic Calcisols according to the FAO classification, with $62.75 \pm 0.04\%$ sand, $20.30 \pm 0.01\%$ silt, and $16.95 \pm 0.01\%$ clay. This typical temperate steppe is dominated by *Stipa krylovii*, *Artemisia frigida*, *Potentilla acaulis*, *Cleistogenes squarrosa*, *Allium bidentatum*, and *Agropyron cristatum*.

The field experiment used a nested design with increased precipitation as the main factor, and warming as subplot level. Thus, four treatments in the experiment were control, warming, increased precipitation, and warming plus increased precipitation with six replicates. The warming subplots were heated by infrared radiators (Kalglo Electronics Inc., Bethlehem, PA, USA). In the increased precipitation plots, 15 mm of water was supplied weekly in July and August by sprinklers. Therefore, totally 120 mm precipitation was added in each year, which was equivalent to about 30% of mean annual precipitation at the study site. The detailed experimental design has been provided by Liu et al. (2009).

ER and NEP were measured using a transparent chamber ($0.5 \text{ m} \times 0.5 \text{ m} \times 0.5 \text{ m}$) attached to an infrared gas analyzer (IRGA; LI-6400, LiCor, Lincoln, NE, USA). The chamber was placed on the permanent square aluminum frame in each plot during measurement (Steduto et al., 2002; Huxman et al., 2004c; Niu et al., 2011; Ganjurjav et al., 2016). GEP was calculated as the sum of ER and NEP. All measurements were taken during 9:00–12:00 in the sunny morning during the growing season (from May to October). The details of the measuring method have been described in Niu et al. (2008, 2011) and Xia et al. (2009). The daily estimate of the CO₂ fluxes were derived from their relationships between hourly observations and daily averages in an adjacent experiment (Xia et al., 2009; Wan et al., 2009; Fig. A1). In this paper, NEP represented the net CO₂ exchange between ecosystem and atmosphere. The CO₂ flux from atmosphere to biosphere was defined as a positive value and from biosphere to atmosphere was defined as a negative value.

2.2. DAYCENT model

The DAYCENT model is the version of the CENTURY model with daily time step, which has been widely used for simulating ecosystem processes in grasslands and croplands (Abdalla et al., 2010; Lee et al., 2012; Chang et al., 2013; Lugato et al., 2014). The input parameters include daily climate data (e.g., precipitation, the maximum and minimum air temperature, relative humidity, solar radiation, and wind speed), site latitude and longitude, soil properties, and plant growth characteristics (Table A1). Net primary productivity (NPP) (Fig. 1a) is calculated by a function of plant potential growth rate, which is limited by solar radiation, temperature, soil water, and vegetation type. C flow is affected by many factors, such as C sources, temperature, soil water content, and soil physical properties. Decomposition rate (k) of litters or soil organic C (SOC) is calculated by a nonlinear function, which is expressed as:

$$k = d \xi_C \xi_T \xi_W \quad (1)$$

where d is intrinsic decomposition rate of surface or soil. ξ_C , ξ_T , and ξ_W are soil texture or litter, temperature, and water response function, respectively. ξ_T and ξ_W are calculated by:

$$\xi_T = 0.65 + 0.5 \operatorname{atan}(0.097 (T_s - 21.5)) \quad (2)$$

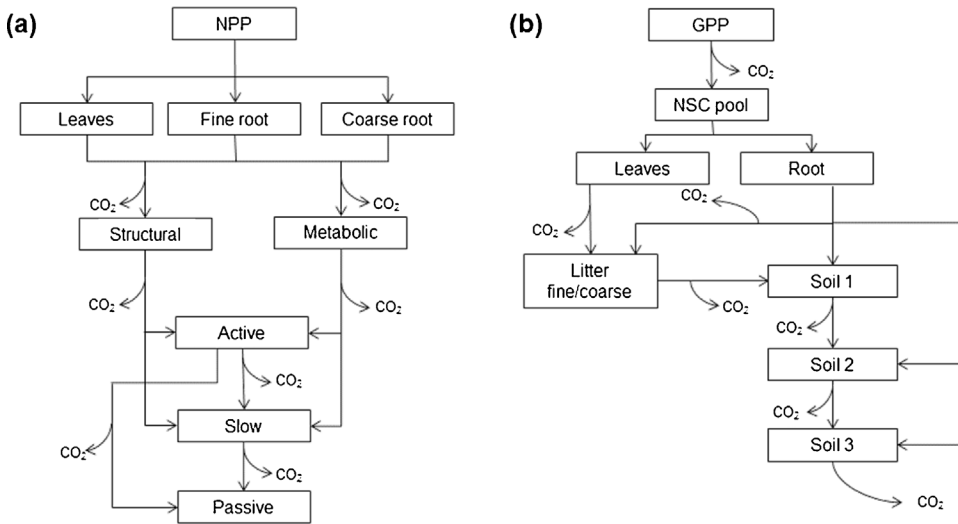


Fig. 1. Schematic presentation of C cycle in (a) DAYCENT model and (b) TECO model.

$$\xi_w = 1 / (1 + 30 e^{-8.5\chi}) \quad (3)$$

T_s is soil temperature, and χ represents the ratio of precipitation to potential evapotranspiration. The land surface submodel is modified by the water flow submodel and soil temperature submodel (Parton et al., 1998). The daily water flow from plant canopy to soil is calculated by the water flow submodel. The soil temperature submodel simulates thermal diffusivity and daily maximum soil temperature.

2.3. TECO model

The TECO model is a process-based ecosystem model, which is used to simulate ecosystem responses to climatic perturbations (Weng and Luo, 2008). TECO has been widely used to model C and hydrological cycle in grassland and forest ecosystems (Zhou et al., 2008; Bell et al., 2010; Shi et al., 2014; Xu et al., 2015). The TECO model includes four submodels, which are canopy photosynthesis, plant growth, soil C transfer (Fig. 1b), and soil water dynamic. The canopy photosynthesis and soil water dynamics submodels run at hourly time step, and the plant growth and soil C transfer submodels are simulated at daily time step. The canopy photosynthesis submodel, which is a two-leaf photosynthesis model, is used to simulate canopy energy balance, canopy photosynthesis, and conductance (Wang and Leuning, 1998). Leaf photosynthesis is calculated by coupling the Farquhar photosynthesis model (Farquhar et al., 1980) with the Ball-Berry stomatal conductance model (Ball et al., 1987). The plant growth submodel simulates C allocation of leaves, stems, and roots following the ALFALFA model (Luo et al., 1995). Phenology is represented through changes in LAI. Autotrophic respiration (R_a) is controlled by air temperature (T_a) and tissue biomass (B), which is expressed as:

$$R_a = B e^{n T_a} \xi_f \quad (4)$$

n is a constant. ξ_f is the response function of photosynthesis. The C transfer submodel simulates the process of C flow from plant tissues to atmosphere. Heterotrophic respiration (R_h) is calculated by following equation:

$$R_h = q k f \quad (5)$$

where q and k are the size and turnover rate (day^{-1}) of the C-pool, respectively. f is the ratio of CO_2 flux released to the atmosphere from the C-pool. Turnover rate (k) is calculated by independent turnover time (τ), temperature response function (ξ_T), and water response function (ξ_w):

$$k = \frac{(\xi_T + 1) \xi_w}{\tau} \quad (6)$$

$$\xi_T = \frac{e^{0.18 T_s}}{19} \quad (7)$$

$$\xi_w = 0.5 + 0.5 \frac{W_C - W_{\min}}{W_{\max} - W_{\min}} \quad (8)$$

where W_C is soil water content. $W_{\max}$ is the field capacity. $W_{\min}$ is the wilting point. In soil water dynamic submodel, the soil is divided into ten layers. Dynamics of soil water content is determined by precipitation, transpiration, evaporation, and runoff.

2.4. Model simulations

All the four experimental treatments were mimicked by the two ecosystem models. Hourly data of air and soil temperature were record by CR1000 datalogger (Campbell Scientific, Logan, UT, USA) in each experimental plot (Niu et al., 2008). Since DAYCENT model simulates with a daily time step, we calculated daily climate data by averaging hourly records. Hourly precipitation data were derived from an adjacent eddy-flux tower (about 200 m). Under the treatments of increased precipitation, we added the same amount of precipitation (15 mm) in the same day as experimental treatment from 2006 to 2008.

2.5. Analyses of warming and increased precipitation effects

We calculated treatment effects of warming and increased precipitation as suggested by Sahai and Ojeda (2004) and Luo et al. (2008), which used the percent changes of variables between control and treatments as:

$$\text{Treatment effect (\%)} = \frac{\text{Treatment} - \text{Control}}{\text{Control}} \times 100 \quad (9)$$

2.6. Analyses of model performance

The goodness of fit between simulated C fluxes from two models and observations were quantified by root mean square error (RMSE) and Nash–Sutcliffe model efficiency coefficient (ME). The RMSE and ME were calculated by following equations (Janssen and Heuberger, 1995):

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^N (S_i - O_i)^2}{N}} \quad (10)$$

where S and O were simulated and observed C fluxes, respectively. N is the number of data from 2006 to 2008.

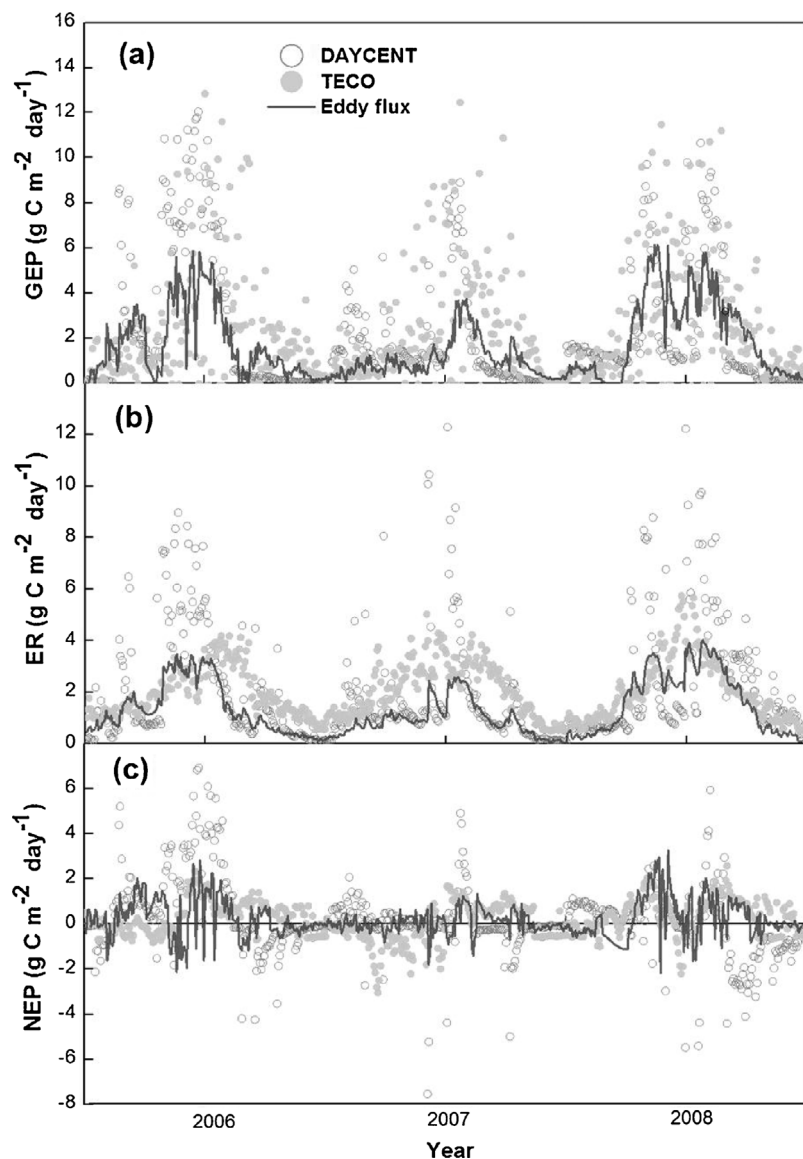


Fig. 2. Observed and simulated daily (a) GEP, (b) ER, and (c) NEP in Inner Mongolia grassland from May to October in 2006–2008. Eddy flux data (Eddy flux) are compared with the DAYCENT model (DAYCENT) and the TECO model (TECO). GEP: gross ecosystem photosynthesis, ER: ecosystem respiration, NEP: net ecosystem productivity.

$$ME = \frac{\sum_{i=1}^N (O_i - \bar{O})^2 - \sum_{i=1}^N (S_i - O_i)^2}{\sum_{i=1}^N (O_i - \bar{O})^2} \quad (11)$$

where $\bar{O}$ was the mean of observed C flux. Simulations perfectly capture observations when the RMSE is 0 and ME is 1.

3. Results

3.1. Model validation

The measurements from an eddy flux tower were used to validate the simulated results. The eddy flux data included daily GEP, ER, and NEP from May to October in 2006–2008. The simulated C fluxes matched well with observations (Figs. 2 and A2). The RMSE of GEP were 2.27 g C m⁻² day⁻¹ for DAYCENT and 2.51 g C m⁻² day⁻¹ for TECO. The RMSE of ER were 1.80 and 1.14 g C m⁻² day⁻¹ for DAYCENT and TECO, respectively. The RMSE of NEE were 1.67 g C m⁻² day⁻¹ for DAYCENT and 1.02 g C m⁻² day⁻¹ for TECO.

The monthly mean GEP and ER during the growing seasons (May–October) simulated by DAYCENT and TECO agreed well with the measured data in the experimental control plots in 2006, 2007, and 2008 (Fig. 3a and b). Over the three years, the simulated mean annual GEP were 2.40 g C m⁻² day⁻¹ by DAYCENT and 2.31 g C m⁻² day⁻¹ by

TECO, both of which captured the observed GEP (2.43 ± 0.30 g C m⁻² day⁻¹). The simulated mean annual ER by DAYCENT (2.22 g C m⁻² day⁻¹) and TECO (2.04 g C m⁻² day⁻¹) matched well with the observed ER (2.28 ± 0.26 g C m⁻² day⁻¹). In general, the simulated mean annual GEP and ER were both within the variation ranges of observed data under the control treatment.

3.2. Comparisons between modeled and observed CO₂ fluxes

We compared the simulated mean annual NEP with the experimental data to evaluate the performance of DAYCENT and TECO model under the four treatments from May to October in 2006–2008. Over the three years, the simulated mean annual NEP by DAYCENT (0.19 g C m⁻² day⁻¹) and TECO (0.19 g C m⁻² day⁻¹) satisfactorily represented the observed mean annual NEP (0.16 ± 0.05 g C m⁻² day⁻¹) under the control treatment (Fig. 4a). Under the climate-change treatments, however, the two models performed differently. DAYCENT overestimated the strength of net CO₂ uptake under the warming treatment (0.07 ± 0.07 vs. 0.26 g C m⁻² day⁻¹), but simulated a net CO₂ loss under the increased precipitation and warming plus increased precipitation treatments (Fig. 4a). TECO model well captured mean annual NEP under all the warming (0.05 g C m⁻² day⁻¹), increased precipitation

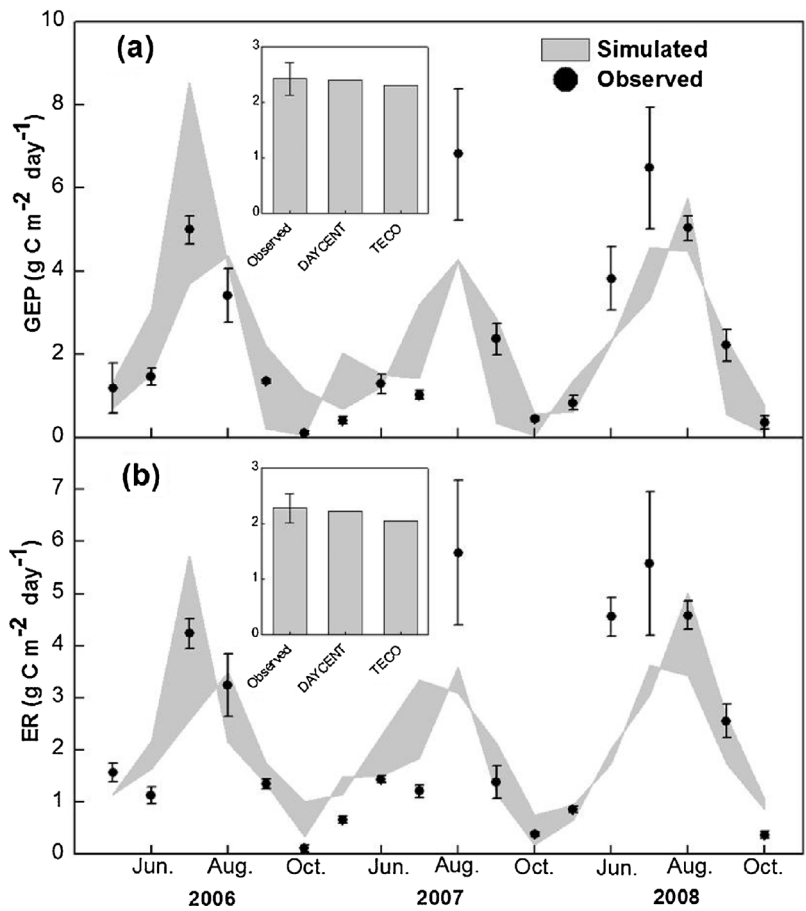


Fig. 3. Monthly dynamics of observed (means $\pm$ SD) and simulated (a) GEP and (b) ER in 2006, 2007, and 2008. The gray shaded areas show the ranges of the simulated values by DAYCENT and TECO. Inset figures show mean annual of observed (means $\pm$ SD) and simulated values over three years. See Fig. 2 for abbreviations.

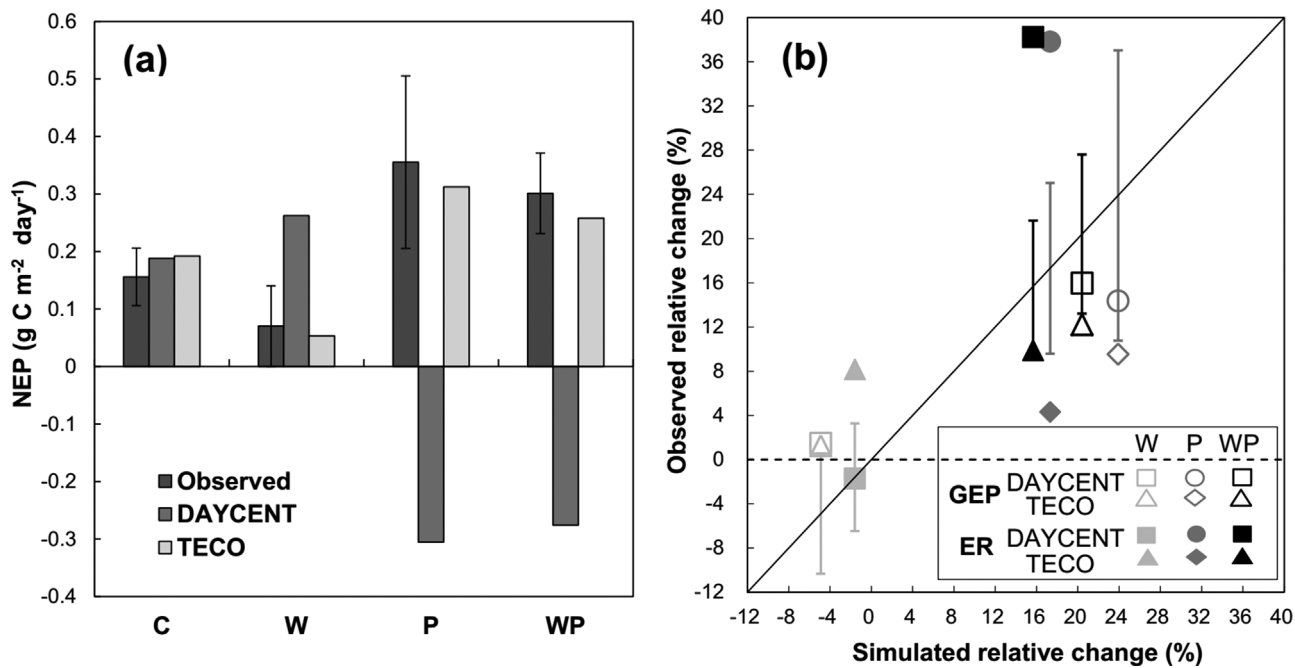


Fig. 4. Observed (means $\pm$ SD) and simulated (a) mean annual NEP, and (b) the responses of GEP and ER to warming, increased precipitation, and warming plus increased precipitation from May to October in 2006–2008. C: control treatment, W: warming treatment, P: increased precipitation treatment, WP: warming plus increased precipitation treatment. See Fig. 2 for abbreviations.

Table 1

Water and temperature response functions on soil decomposition from four different terrestrial biosphere models. W_C : soil water content, T_s : soil temperature, T_o : optimal soil temperature.

Provenance	Water response function	Temperature response function
IBIS	$e^{\frac{-(W_C - 0.6)^2}{0.08}}$	$e^{308.56 \left(\frac{-1}{81.02} \cdot \frac{1}{T_s + 46.02} \right)}$
LPJ-DGVM	$0.25 + 0.75 W_C$	
ORCHIDEE	$-1.1 W_C^2 + 2.4 W_C - 0.29$	$2^{\frac{T_s - T_o}{10}}$
CABLE	$\left(\frac{1.7 - W_C}{1.15} \right)^{6.6481} \left(\frac{W_C + 0.007}{0.557} \right)^{3.22}$	

($0.31 \text{ g C m}^{-2} \text{ day}^{-1}$), and warming plus increased precipitation ($0.26 \text{ g C m}^{-2} \text{ day}^{-1}$) treatments.

The ER mismatches between the observed and simulated treatment responses were larger than those of GEP. The observed ER responses were $-1.60 \pm 4.88\%$, $17.32 \pm 7.74\%$, and $15.67 \pm 5.96\%$ to warming, increased precipitation, and warming plus increased precipitation, respectively (Fig. 4b). TECO overestimated the warming effect on ER (8.18%), but underestimated ER response to increased precipitation (4.31%). DAYCENT produced higher ER responses in the plots with both increased precipitation (37.83%) and warming plus increased precipitation (38.25%).

3.3. Water response functions of SOC decomposition in the models

The experimental observations showed that warming increased mean annual air and soil temperature (Fig. A3a), but reduced mean annual soil water content (Fig. A3b) over the three years. Increased precipitation significantly enhanced mean annual soil water content (Fig. A3b). In TECO model, warming not only directly affected R_h by elevating soil temperature, but also indirectly affected R_h by altering soil water content (Eqs. (5–8)), and R_a was only directly influenced by warming through changing air temperature (Eq. (4)) (Weng and Luo, 2008). Warming effect on R_h was larger than that on R_a (Fig. A3c), thus

the discrepancy of simulated and observed climate-change effect on ER might largely come from the different responses of R_h response functions to climate change (Fig. A3d).

We incorporated five water response functions of SOC decomposition from DAYCENT and four terrestrial biogeochemical models (IBIS, LPJ-DGVM, ORCHIDEE, and CABLE) (Table 1) into the TECO model and examined whether they can capture the observed ER responses in Fig. 4b. The six water response functions varied with soil water content differently (Fig. 5a). The results showed that all the water response functions produced lower precipitation impact on ER (Fig. 5b), which was consistent with results using the original water response function in TECO (Fig. 4b). Simulated response of ER to increased precipitation by DAYCENT (8.51%) and ORCHIDEE (8.34%) water response functions were more close to observations ($17.32 \pm 7.74\%$) than that using water response function in TECO (4.31%).

3.4. Parameters evaluated by experimental observations

Water response functions in TECO model (Eq. (8)) were calculated by parameters of field capacity (W_{max}) and wilting point (W_{min}), which determined the model performance of simulated climate-change effects. Through random selecting parameters for 1200 times, W_{max} and W_{min} were estimated using the observed CO_2 flux data under the warming, increased precipitation, and warming plus increased precipitation treatments, respectively. The distribution ranges of W_{max} and W_{min} showed substantial differences under the three climate-change treatments (Fig. 6a). Performance of the TECO model was improved by optimized parameterization in water response function of soil decomposition. With the optimized W_{max} and W_{min} (Fig. A4), TECO performed well in capturing the response of ER to climate change under the warming, increased precipitation, and warming plus increased precipitation treatments (Fig. 6b). Simulated climate-change effect on ER were 1.80%, 20.93%, and 17.76% under the warming, increased precipitation, and warming plus increased precipitation treatments, respectively, which were all within the range of observations. ME of monthly ER was increased by 17% with the optimized

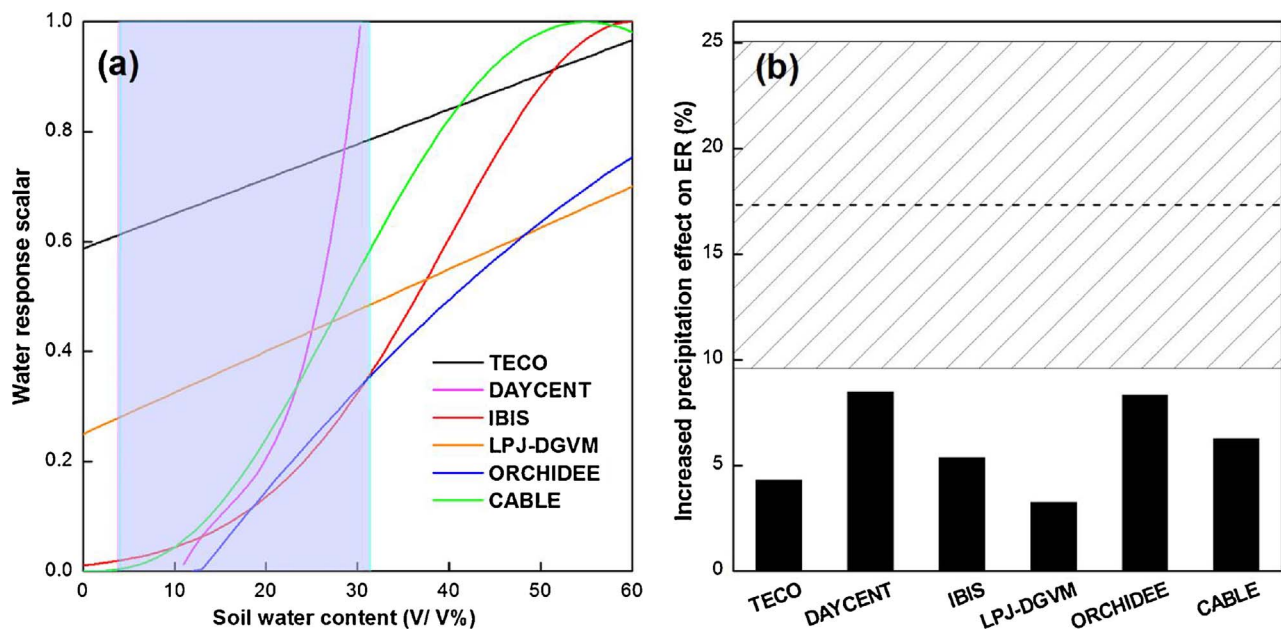


Fig. 5. (a) Relationships of water response scalars from six terrestrial biogeochemical models with soil water content. The ranges of soil water content varied from 3.8 to 30.5 V/V% in 2006–2008 under the control treatment (the pink shaded area). Increased precipitation enhanced soil water content, which ranged from 4.1 to 31.3 V/V% (the blue shaded area). The relationship in DAYCENT was cubic polynomial fitted by water response scalar with simulated soil water content. (b) Simulated increased precipitation effect on ecosystem respiration (ER) by different water response functions. Dash line and oblique line area show the observed means and range (means $\pm$ SD) of increased precipitation effect on ER, respectively.

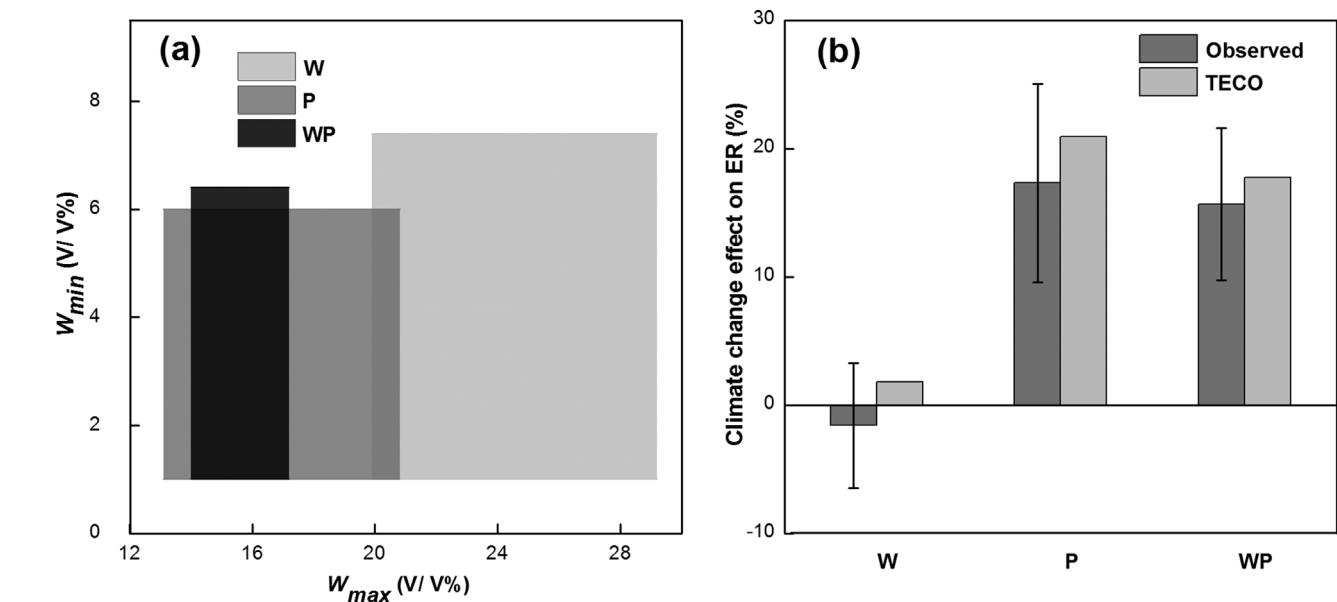


Fig. 6. (a) The distribution ranges of field capacity (W_{max}) and wilting point (W_{min}) under warming, increased precipitation, and warming plus increased precipitation treatments. (b) Observed (mean $\pm$ SD) and simulated (TECO) climate-change effect on ER over three years from 2006 to 2008. See Fig. 2 and Fig. 4 for abbreviations.

Table 2
The root mean square error (RMSE) and Nash–Sutcliffe model efficiency coefficient (ME) of monthly ecosystem respiration ($\text{g C m}^{-2} \text{ day}^{-1}$) by eddy-flux validated parameters (validated) and optimized parameters (optimized), respectively. See Fig. 4 for abbreviations.

Treatment	RMSE		ME	
	Validated	Optimized	Validated	Optimized
W	1.3	1.26	0.48	0.51
P	1.61	1.48	0.48	0.56
WP	1.51	1.48	0.51	0.53

parameters under the increased precipitation treatment (Table 2).

3.5. The difference of simulated cumulative change in ecosystem C pool

We performed the forward simulations from 2010 to 2100 to estimate the cumulative changes in ecosystem C pool. The climate forcing data were provided by the HadGEM2-ES model (<https://esg.pik-potsdam.de/search/isimip2/>) for the Representative Concentration Pathway 4.5 (RCP 4.5). Based on the modified water response functions from DAYCENT, IBIS, LPJ-DGVM, ORCHIDEE, and CABLE, the cumulative changes in ecosystem C pool ranged from a C sink of 0.8 kg C m^{-2} to a C source of 2.2 kg C m^{-2} in 2100 (Fig. 7). Over the whole time period, the grassland ecosystem released 0.3 kg C m^{-2} using TECO

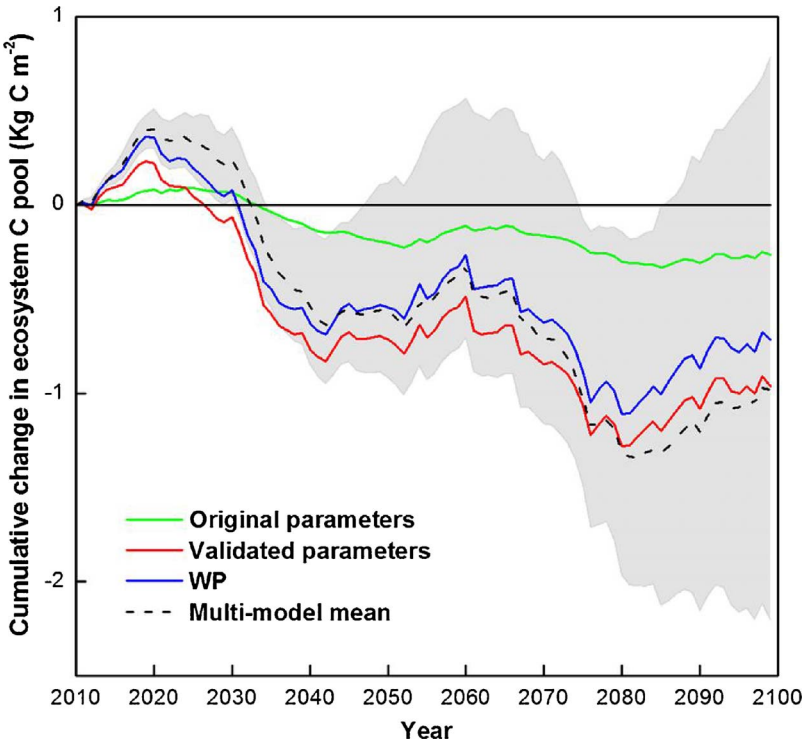


Fig. 7. Simulated cumulative changes in ecosystem C pool from 2010 to 2100. Dash line and gray shaded area represent means and ranges of simulated cumulative change in ecosystem C pool by modifying water response function from DAYCENT, IBIS, LPJ-DGVM, ORCHIDEE, and CABLE, respectively. Green, red, and blue lines represent the cumulative changes in ecosystem C pool simulated by TECO original parameters, validated parameters using eddy flux data, and optimum parameters under warming plus increased precipitation treatment (WP), respectively.

original parameters. The cumulative ecosystem C loss was increased with the parameters validated by eddy-flux measurements ($-0.96 \text{ kg C m}^{-2}$), and with the optimized $W_{\max}$ ($15.6 \text{ V/V\%}$) and $W_{\min}$ ($4 \text{ V/V\%}$) under the warming plus increased precipitation treatment ($-0.72 \text{ kg C m}^{-2}$).

4. Discussions

4.1. Role of water responses in model performance on ecosystem C cycle in grassland

Although two models can well capture the major ecosystem CO_2 fluxes (i.e., GEP and ER) and their balance (i.e., NEP) under the control treatment, they failed to predict the treatment effects of climate-change on NEP. The results indicate that models calibrated with current observations, e.g., eddy-flux measurements, may not be able to successfully predict ecosystem C cycle associated with climate change in the future (Hararuk et al., 2014; Shi et al., 2015). Our findings highlight that model evaluations need to focus on not only the direct comparisons against observations, but also the assumptions revealed by manipulative experiments (Medlyn et al., 2015; Medlyn et al., 2015, 2016).

Improving the water response function in grassland model performance is an important research agenda during the past decades. In water-limited regions, biogeochemical models would be meaningless without well simulating the hydrological processes and their impacts on C processes (Noy-Meir, 1973; Rodriguez-Iturbe et al., 2001; Huxman et al., 2004a; Knapp et al., 2017). In this study, the models perform better in simulating the response of GEP than ER to precipitation change (Fig. 4b). This might mainly due to that the ecosystem CO_2 uptake usually responds to precipitation change in a linear manner at a given location (Huxman et al., 2004a; Luo et al., 2017). However, Knapp et al. (2017) has recently hypothesized a double asymmetric model which suggests nonlinear response of aboveground net primary productivity to precipitation changes associated with more extremely dry and wet years. This hypothesis indicates a more complexity of simulating ecosystem CO_2 uptake under future climate scenarios. Nonlinear response of soil respiration to precipitation change has been widely confirmed by both field experiments (Liu et al., 2002; Huxman et al., 2004b; Yan et al., 2010) and modeling studies (Zhou et al., 2008). Many previous studies have already indicated that models have difficulty in capturing climate-change effect on ecosystem respiration (Vicca et al., 2014; Tang and Riley, 2015), especially in the water-limited ecosystems (Reichstein et al., 2003). We detected that the poor simulation of respiratory responses at ecosystem scale is also largely accounted for the unrealistic relationship between R_h and soil water availability in this study (Fig. 5). By replacing the water response functions of R_h in TECO with those in other models, we found a large inter-model variation of simulated precipitation effect on ER (Fig. 5b). Among the six models, the water-response function of DAYCENT (8.51%) and ORCHIDEE (8.34%) produced closer ER response to increased precipitation than the original functions in TECO (4.31%) to the measurements ($17.32 \pm 7.74\%$). It means that the water-response function in the current version of TECO model needs improvement when it is used for predicting ecosystem C cycle in the Eurasian grassland.

The large impact of the water-response function on simulated ER response in current ecosystem models (Fig. 5b) indicates that it could be one large source for the uncertain grassland C feedback to climate change (Weltzin et al., 2003; Kucharik and Twine, 2007; Hoover and Rogers, 2016). Diagnostic studies on current global land models, e.g., Exbrayat et al. (2013), also have shown that the water-response functions for decomposition of SOC are highly uncertain. In fact, the

response of ecosystem C cycle to precipitation change is a complex and changeable process in the arid and semiarid regions (Knapp et al., 2002; Thomey et al., 2011; Shen et al., 2015). Many manipulative experiments have illustrated that available water can directly and indirectly limit primary production (Knapp et al., 2002; Huxman et al., 2004a; Fay et al., 2008; Robertson et al., 2009) and the different components of ecosystem respiration (Wan et al., 2007; Ross et al., 2012; Suseela et al., 2012). A meta-analysis has demonstrated that ER responds more strongly to increased precipitation than decreased precipitation (Wu et al., 2011). In addition, the nonlinear responses of ecosystem C processes to precipitation change have been widely reported in modeling studies (Cowling and Shin, 2006; Zhou et al., 2008). Thus, such complicated responses of ecosystem CO_2 fluxes to precipitation are difficult to precisely describe in the model. Given the important role of precipitation in regulating plant growth and productivity, reasonable evaluating precipitation effect on ecosystem C fluxes is beneficial to accurately simulate future ecosystem processes.

4.2. Varied parameters of C cycle with changing climate

This study found that models using the parameters under current climate conditions had difficulty in predicting future ecosystem progresses (Fig. 4). In this study, the difference between the simulations and observations mainly results from the fixed values of parameters. These fixed parameters would lead to substantial errors in model projections for future ecosystem C cycle (Wythers et al., 2005; Shi et al., 2015; Tang and Riley, 2015). When the water-related parameters are constrained by the experimental observations, they showed large variability under different climate-change treatments (Figs. 6a and A3). $W_{\max}$ and $W_{\min}$ in the water response function of soil decomposition are important in representing soil texture in the TECO model (Xu et al., 2015). Climate change would influence $W_{\max}$ more than $W_{\min}$ because $W_{\max}$ is positively regulated by the total porosity (Xu et al., 1997), which could be increased by warming but be reduced by increased precipitation (Chen et al., 2013). These variations of $W_{\max}$ under different climate-change treatments were also found in an unpublished experiment in this area. These results suggest the models to switch the water-related parameters from constants to variables. Thus, more research efforts on the covariations between those water-related parameters and environmental factors are needed to improve the simulation accuracy of biogeochemical model under climate-change scenarios. The varied parameters improve model performance on reproducing the observed responses of ER to climate change (Fig. 6b) because the changed parameters can reflect the altered temperature and moisture sensitivity under climate change. Temperature acclimation of C fluxes has been demonstrated as a fundamental characteristic of terrestrial ecosystem processes (Smith et al., 2016). With long-term warming, the temperature sensitivity of decomposition rate and ecosystem respiration are reduced (Giardina and Ryan, 2000; Luo et al., 2001; Knorr et al., 2005; Atkin et al., 2008; Reich et al., 2016) or enhanced (Karhu et al., 2014) by temperature acclimation. The mechanism of altered moisture sensitivity is still unclear (Jiang et al., 2013), but it has been demonstrated that increased precipitation has significant impact on soil microbial respiration (Liu et al., 2009), root production (Bai et al., 2010), water-use efficiency (Niu et al., 2011), SOC fractions (Song et al., 2012), and soil microbial community composition (Zhao et al., 2016) in this grassland. Altered moisture sensitivity can be partly explained by the differential relationships of biotic and abiotic factors with changing precipitation regime. Omitting the changes of temperature and moisture sensitivity may cause biased projections of future C cycle (Jiang et al., 2013; Smith et al., 2016).

The changes of key C-cycle parameters with climate change have

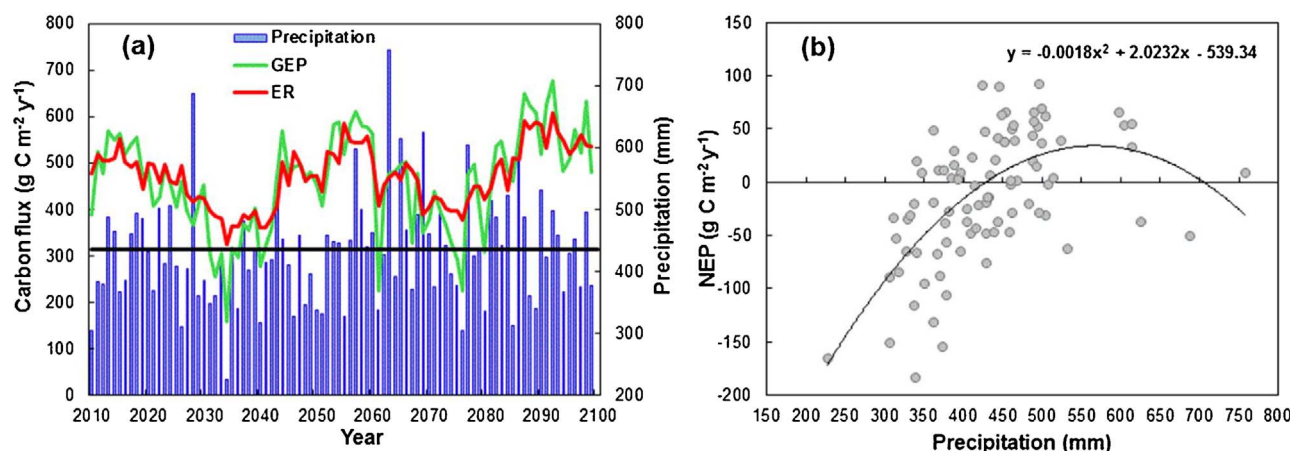


Fig. 8. (a) The annual dynamic of gross ecosystem photosynthesis (GEP), ecosystem respiration (ER), and precipitation amount from 2010 to 2100. The black line represents the threshold of annual total precipitation (≈ 435 mm). (b) Relationships of annual mean net ecosystem productivity (NEP) with precipitation amount from 2010 to 2100.

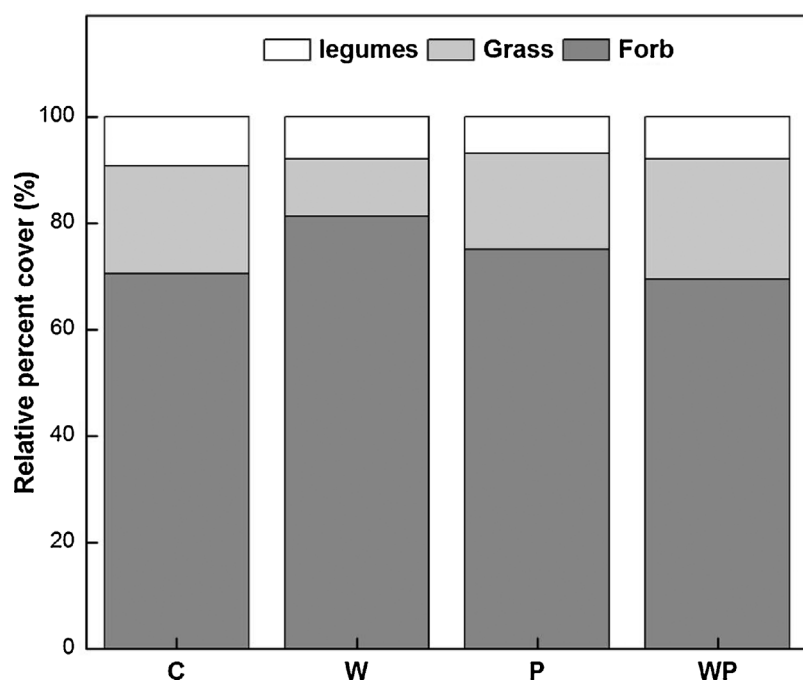


Fig. 9. Observed mean annual relative percent cover under the four treatments from May to October in 2006–2008. See Fig. 4 for abbreviations.

been reported by many studies. For example, model parameters of carboxylation capacity and electron transport capacity can vary with leaf temperature (Kattge and Knorr, 2007). Using data assimilation to assess model parameters also indicates that the parameters of C allocation have large difference under different treatments (Xu et al., 2006; Shi et al., 2015). Thus, models used for projections of future climate change and ecosystem states should consider the flexibility of those key parameters related to temperature and moisture in grasslands.

4.3. Field manipulative experiment as a platform for evaluating ecosystem models

This study has revealed that the diverse response functions among different models can generate huge uncertainty in projection of terrestrial C cycle in the future (Fig. 7). Due to GEP was more sensitive to

decreased precipitation than ER (Shi et al., 2014), dramatic reductions in GEP rather than ER was simulated in extremely dry years (Fig. 8a). There is a threshold of annual total precipitation (≈ 435 mm), below which the ecosystem shifted from C sink to source. The switch of NEP (Fig. 8b) is attributed to the rapid response of ecosystem function (e.g. leaf area index and leaf-level stomatal opening) to drying-rewetting periods in grassland (Scott et al., 2015). However, the decreased degrees of cumulative changes in ecosystem C pool in 2100 were inconsistent under different functions and parameters (Fig. 7). To diagnose and reduce such uncertainty, previous efforts usually examine the model performances against a suite of observational data, such as the benchmarking analysis (Luo et al., 2012). This approach is useful to diagnose whether the model performances are good or bad in the areas or periods that covered by the data, but is difficult to benefit model projections of future ecosystem dynamics. In this study, the TECO

model predicts losses of 0.3, 0.96, and 0.72 kg C m⁻² in 2100 with the original parameters, tuned parameters with eddy-flux measurements and optimized parameters with experimental observations, respectively (Fig. 7). Although it is worthy of discussion that whether the experiment-based prediction is more accurate than the simulation benchmarked by eddy-flux data, the findings in this study suggest that manipulative experiments provide, to some extent, a good platform for assessing ecosystem models in specific ecosystem or region. In fact, manipulative experiments have revealed diverse response patterns of ecosystem processes to different drivers of climate change (Wu et al., 2011; Lu et al., 2013). Thus, harmonizing the observed responses in experiments and models are critical for improving model performance in predicting future C cycle.

A growing body of research has been done to improve terrestrial ecosystem models with experimental studies (Dukes et al., 2014). For example, the ‘assumption-centred’ approach used in free-air CO₂ enrichment (FACE) model-data synthesis (FACE-MDS) project provides us an effective way for integrating FACE experiments with terrestrial ecosystem and biosphere models (Walker et al., 2014; Medlyn et al., 2015; Norby et al., 2016). This approach allows models to test ecological hypotheses revealed by field experiments, and linking these observations with models can explain how and why differences appear in predictions of ecosystem responses (Medlyn et al., 2015; Norby et al., 2016). In the temperate steppe of northern China, the experimental studies have hypothesized that ecosystem C responses to climate change are mainly regulated by water availability in the soil (Niu et al., 2008; Liu et al., 2009; Xia et al., 2009). Based on such assumption, this study shows that the projection of C cycle in this area could be more accurate with a better parameterization of the water-related processes in the models. However, in comparison with the large amount of field studies at the global scale (Norby and Luo, 2004; Wu et al., 2011; Zeppel et al., 2014), the attempt of using experimental data to evaluate and improve models is still at an early stage. Therefore, more research efforts are needed to incorporate field experimental studies into the evaluation of terrestrial ecosystem models.

4.4. Challenges for integrating grassland experiments and terrestrial ecosystem models

Manipulative experiments provide direct responses of ecosystem processes to climate change for improving model structures and parameters. Though model performance is improved by evaluating parameters using experimental data, there are still some limitations in our research. First, initial conditions can affect the measured impacts of climate change on ecosystem CO₂ fluxes (Shaver et al., 2000), but they are not examined in this and most previous modeling studies. We suggest future field experiments could be designed to measure more initial conditions of vegetation, soil nutrients, and microclimate in both control and treatment plots. Second, given the scale limitation, it might be biased to directly using plot-scale experimental observations to evaluate regional-scale models (Dukes et al., 2014; Norby et al., 2016). Due to the complexity of ecosystem processes, models may not be able to capture plot-scale experimental observations at each site (Bonan, 2014). To overcome this limitation, the observed relationships should be proved in different ecosystems and time scales before integrating into the models (Schwalm et al., 2010; Piao et al., 2013; Bonan, 2014). Third, plant functional groups have been altered under the warming and/or increased precipitation treatments in this grassland (Yang et al., 2011), but both models use constant vegetation types. From 2006 to 2008, relative percent cover of legumes and grass were decreased,

while forb was enhanced under both the warming and increased precipitation treatments (Fig. 9). Warming and increased precipitation directly influenced relative percent cover via altering temperature and soil water content (Fig. A3a and b; Yang et al., 2011). With intrinsic difference in optimum temperature and water use efficiency, the dominant species would shift under climate change (Way et al., 2014; Shi et al., 2016). Many previous studies have demonstrated that warming and increased precipitation have profound influence on plant functional group (Shi et al., 2016), species richness, and diversity (Walker et al., 2006; Hou et al., 2013), and consequently affect ecosystem functions (Chisholm et al., 2013; Shi et al., 2016; Yang et al., 2016). Fourth, explicit soil microbial processes were omitted in this study. Soil decomposition processes were calculated by empirical functions in most CENTURY-type models (Parton et al., 1987). Many previous studies have indicated soil microbial respiration reacts rapidly to change of soil water availability in this area (Liu et al., 2009; Zhao et al., 2016). Modeling studies also showed that model performance was improved by incorporating microbial processes (Wieder et al., 2013, 2015; Hararuk et al., 2015). Thus, we recommend the biogeochemical models to explicitly simulate the drying-rewetting cycles in the grassland ecosystems. Finally, the two models used in this study are typical CENTURY-type models which are broadly used for Earth system modeling. The soil C module in both of the CENTURY and TECO models is composed by three SOC pools, including fast, slow and passive pool of soil organic matter (Parton et al., 1987; Weng and Luo, 2008). However, this CENTURY-type soil C module is not used in some other ecosystem models. For example, the soil module in the JULES model is developed from the RothC model, which consists of decomposable plant material (DPM), recalcitrant plant material (RPM), microbial biomass (BIO separated into slow and fast), humus (HUM) and biologically stable or inert organic matter (IOM) (Coleman and Jenkinson, 1996). Thus, when more models are used for predicting the regional C cycle, uncertainty could be a new issue (Xia et al., 2013; Luo et al., 2016). As shown in this study (Fig. 5), the water response equations in current models need further validation and diagnose before they are used for regional grassland C projections.

5. Conclusions

This study demonstrated that, although the two models captured the values of CO₂ fluxes under the control treatment, they poorly reproduced the responses of NEP to experimental climate change. The poor simulation of NEP response can be largely improved by a better parameterization of the water-response functions of respiratory processes. Models validated by observations of current ecosystem state, such as the eddy-flux measurements in this study, cannot guarantee the accurate projection of future net C accumulation in the grassland in northern China. Thus, more research efforts incorporating field experimental data into benefit model evaluation and development are urgently needed for a convincing projection of future terrestrial C cycle.

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Appendix A

See Table A1.

Table A1

The symbols, definitions, units, and values of main parameters effect on plant growth and soil decomposition in DAYCENT and TECO. PET represents potential evapotranspiration.

Parameter	Definition	Units	Values
<i>DAYCENT</i>			
dec1(1)	Maximum surface structural decomposition rate	year ⁻¹	9
dec1(2)	Maximum soil structural decomposition rate	year ⁻¹	2.5
dec2(1)	Maximum surface metabolic decomposition rate	year ⁻¹	4.2
dec2(2)	Maximum soil metabolic decomposition rate	year ⁻¹	1
dec3(1)	Maximum decay rate of surface organic matter with active turnover	year ⁻¹	7.9
dec3(2)	Maximum decay rate of soil organic matter with active turnover	year ⁻¹	1
dec4	Maximum decay rate of soil organic matter with slow turnover	year ⁻¹	0.001774
PPDF	Poisson Density Function curve to simulate temperature effect on growth:		
	Optimum temperature for production	°C	18
	Maximum temperature for production	°C	36.5
	Left curve shape		1.2
	Right curve shape		3.8
PPRPTS	Water restriction on production:		
	The minimum ratio of available water to PET		0.01
	The effect of water content on the intercept		0.4
	The lowest ratio of available water to PET		0.7
PRDX	Coefficient for calculating potential aboveground monthly		0.8
TEFF	Determining the temperature component of temperature scalar:		
	"x" location of inflection point		19
	"y" location of inflection point		11.75
	Step size		29.7
	Slope of line at inflection point		0.031
<i>TECO</i>			
LAI _{max}	Maximum leaf area index		3
LAI _{min}	Minimum leaf area index		0.1
SLA	Specific leaf area	m ² g ⁻¹	0.035
tau_F	Residence time of fine litter carbon pool	year	3.1
tau_S ₁	Residence time of the first soil layer	year	15
tau_S ₂	Residence time of the second soil layer	year	110
tau_S ₃	Residence time of the third soil layer	year	200
T _{max}	High temperature intercept of temperature function	°C	25
T _{min}	Low temperature intercept of temperature function	°C	-5
T _{opt}	Optimum temperature for photosynthesis	°C	18
W _{max}	Maximum soil water content	V/ V%	21
W _{min}	Minimum soil water content	V/ V%	2
V _{cmx0}	Maximum carboxylation rate	μmol m ⁻² s ⁻¹	0.0001

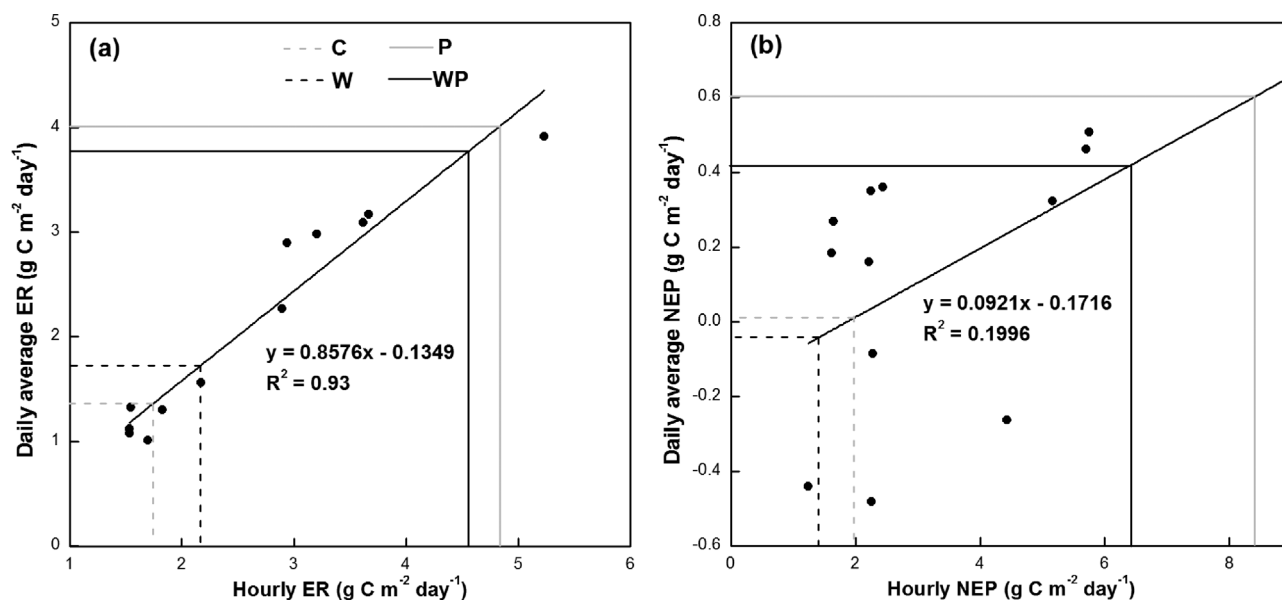


Fig. A1. The linear relationships were fitted by observed (a) daily mean ecosystem respiration (ER) with hourly ER at 9:00, and (b) daily mean net ecosystem productivity (NEP) with hourly NEP at 9:00 on Aug. 21st, 2006 in an adjacent experiment. The diurnal dynamics of ER and NEP were measured once or twice a month under the control treatment from May to October in 2006–2008. Observed ER and NEP at 9:00 on Aug. 24th, 2006 (x-axis) in this study were modified by the linear relation to estimate daily average observations (y-axis), respectively. Colors show observed hourly and estimated daily data under four treatments.

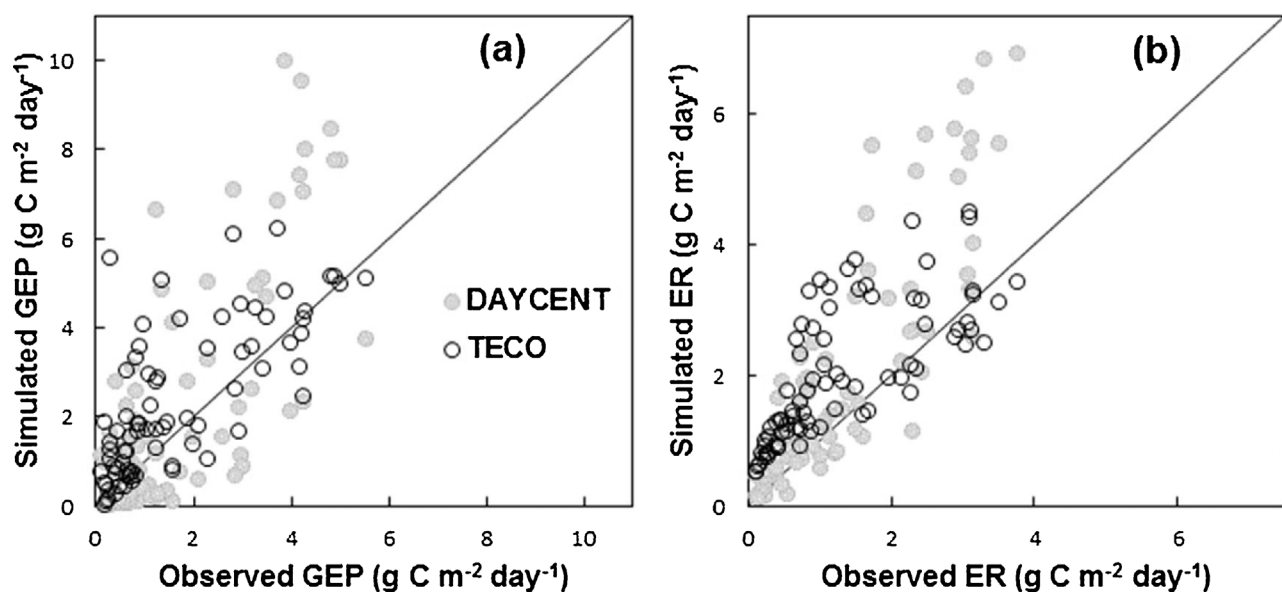


Fig. A2. Observed and simulated weekly (a) gross ecosystem photosynthesis (GEP), and (b) ecosystem respiration (ER) in Inner Mongolia grassland from May to October in 2006–2008. ME of GEP were -0.7 for DAYCENT and 0.2 for TECO. ME of ER were -0.7 for DAYCENT and -0.07 for TECO.

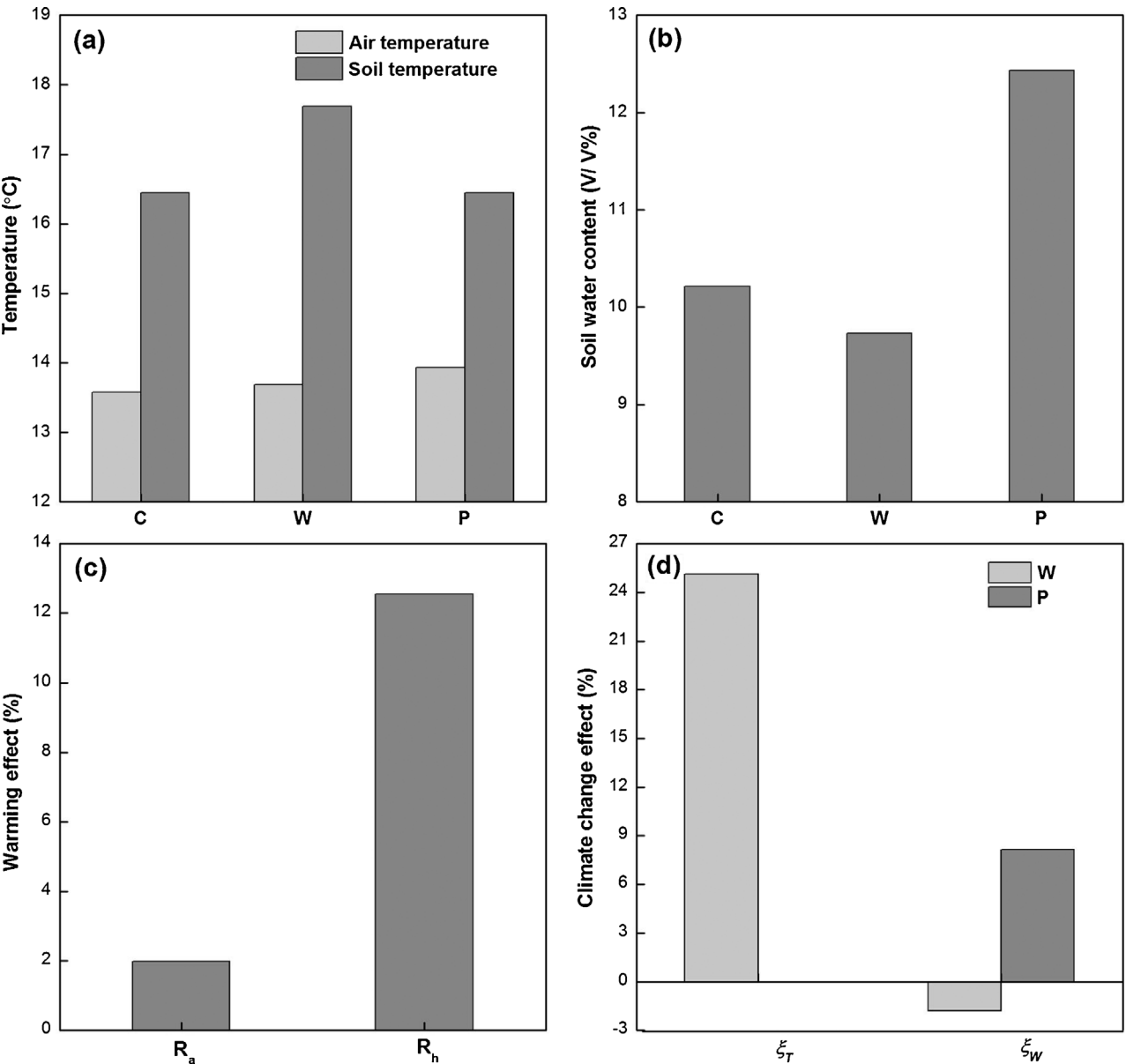


Fig. A3. The observed mean annual (a) air and soil temperature, and (b) soil water content under the control (C), warming(W), and increased precipitation (P) treatments from May to October over the three years, respectively. (c) Warming effect on autotrophic respiration (R_a) and heterotrophic respiration (R_h) in TECO model. (d) Warming (W) and increased precipitation (P) effect on temperature (ξ_T) and water (ξ_W) response functions of R_h in TECO model, respectively.

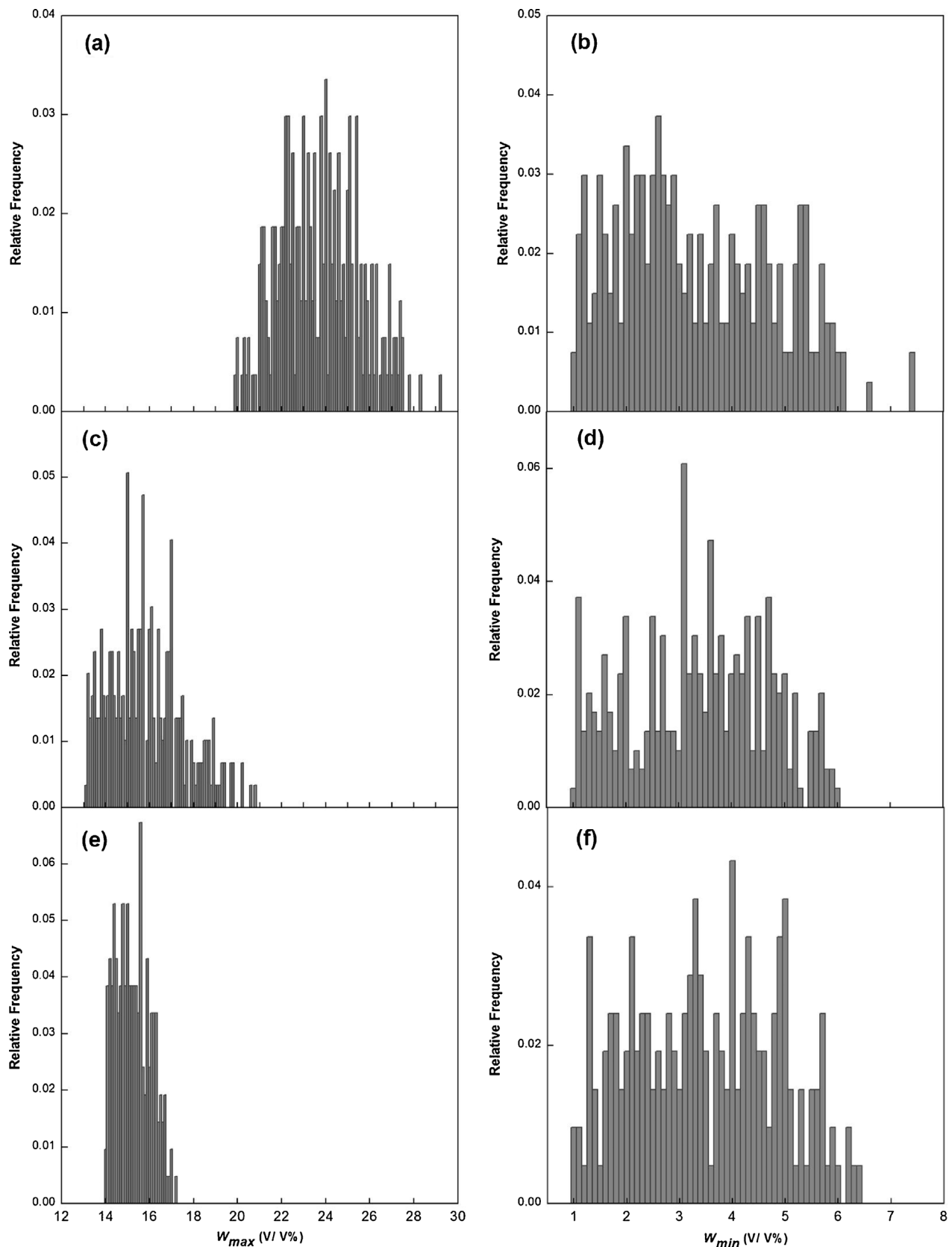


Fig. A4. The relative frequency distributions of field capacity (W_{max}) and wilting point (W_{min}) under (a and b) warming, (c and d) increased precipitation, and (e and f) warming plus increased precipitation treatments, respectively.

References

- Abdalla, M., Jones, M., Yeluripati, J., Smith, P., Burke, J., Williams, M., 2010. Testing DAYCENT and DNDC model simulations of N₂O fluxes and assessing the impacts of climate change on the gas flux and biomass production from a humid pasture. *Atmos. Environ.* 44, 2961–2970.
- Ahlström, A., Raupach, M.R., Schurgers, G., Smith, B., Arneth, A., Jung, M., Reichstein, M., Canadell, J.G., Friedlingstein, P., Jain, A.K., Kato, E., Poulter, B., Sitch, S., Stocker, B.D., Viovy, N., Wang, Y.-P., Wiltshire, A., Zaehle, S., Zeng, N., 2015. The dominant role of semi-arid ecosystems in the trend and variability of the land CO₂ sink. *Science* 348, 895–899.
- Arora, V.K., Boer, G.J., Friedlingstein, P., Eby, M., Jones, C.D., Christian, J.R., Bonan, G., Bopp, L., Brovkin, V., Cadule, P., Hajima, T., Ilyina, T., Lindsay, K., Tjiputra, J.F., Wu, T., 2013. Carbon-concentration and carbon-climate feedbacks in CMIP5 Earth system models. *J. Clim.* 26, 5289–5314.
- Atkin, O.K., Atkinson, L.J., Fisher, R.A., Campbell, C.D., Zaragoza-Castells, J., Pitchford, J.W., Woodward, F.I., Hurry, V., 2008. Using temperature-dependent changes in leaf scaling relationships to quantitatively account for thermal acclimation of respiration in a coupled global climate vegetation model. *Global Change Biol.* 14, 2709–2726.
- Bai, W., Wan, S., Niu, S., Liu, W., Chen, Q., Wang, Q., Zhang, W., Han, X., Li, L., 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.
- Ball, J.T., Woodrow, I.E., Berry, J.A., 1987. A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: Biggens, J., Nijhoff, Martinus (Eds.), *Progress in Photosynthesis Research*, pp. 221–224. Zoetermeer, Netherlands.
- Bell, J.E., Weng, E., Luo, Y., 2010. Ecohydrological responses to multifactor global change in a tallgrass prairie: a modeling analysis. *J. Geophys. Res.* 115. <http://dx.doi.org/10.1029/2009JG001120>.
- Bonan, G.B., 2014. Connecting mathematical ecosystems, real-world ecosystems, and climate science. *New Phytol.* 202, 731–733.
- Chang, K.-H., Warland, J., Voroney, P., Bartlett, P., Wagner-Riddle, C., 2013. Using DAYCENT to simulate carbon dynamics in conventional and no-till agriculture. *Soil Sci. Soc. Am. J.* 77, 941–950.
- Chen, S., Lin, J., Sun, Y., Lammers, P.S., 2013. Predicting topsoil porosity using soil surface roughness under rainfall influence. *J. Beijing For. Univ.* 35, 69–74.
- Chisholm, R.A., Muller-Landau, H.C., Rahman, K.A., 2013. Scale-dependent relationships between tree species richness and ecosystem function in forests. *J. Ecol.* 101, 1214–1224.
- Christensen, L., Coughenour, M.B., Ellis, J.E., Chen, Z.Z., 2004. Vulnerability of the Asian typical steppe to grazing and climate change. *Clim. Change* 63, 351–368.
- Coleman, K., Jenkinson, D.S., 1996. RothC-26.3 - a model for the turnover of carbon in soil. *Eval. Soil Org. Matter Models* 38, 237–246.
- Cowling, S.A., Shin, Y., 2006. Simulated ecosystem threshold responses to co-varying temperature, precipitation and atmospheric CO₂ within a region of Amazonia. *Global Ecol. Biogeogr.* 15, 553–566.
- De Kauwe, M.G., Medlyn, B.E., Walker, A.P., Zaehle, S., Asao, S., Guenet, B., Harper, A.B., Hickler, T., Jain, A.K., Luo, Y., Lu, X., Luus, K., Parton, W.J., Shu, S., Wang, Y., Werner, C., Xia, J., Pendall, E., Morgan, J.A., Ryan, E.M., Carrillo, Y., Dijkstra, F.A., Zelikova, T.J., Norby, R.J., 2017. Challenging terrestrial biosphere models with data from the long-term multifactor prairie heating and CO₂ enrichment experiment. *Global Change Biol.* 23, 3623–3645.
- De Kauwe, M.G., Medlyn, B.E., Zaehle, S., Walker, A.P., Dietze, M.C., Hickler, T., Jain, A.K., Luo, Y., Parton, W.J., Prentice, I.C., Smith, B., Thornton, P.E., Wang, S., Wang, Y.P., Wärlind, D., Weng, E., Crous, K.Y., Ellsworth, D.S., Hanson, P.J., Kim, H., Warren, J.M., Oren, R., Norby, R.J., 2013. Forest water use and water use efficiency at elevated CO₂: a model-data intercomparison at two contrasting temperate forest FACE sites. *Global Change Biol.* 19, 1759–1779.
- Dukes, J.S., Classen, A.T., Wan, S., Langley, J.A., 2014. Using results from global change experiments to inform land model development and calibration. *New Phytol.* 204, 744–746.
- Exbrayat, J.-F., Pitman, A.J., Zhang, Q., Abramowitz, G., Wang, Y.-P., 2013. Examining soil carbon uncertainty in a global model: response of microbial decomposition to temperature, moisture and nutrient limitation. *Biogeosciences* 10, 7095–7108.
- Farquhar, G.D., von Caemmerer, S., Berry, J.A., 1980. A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta* 149, 78–90.
- Fay, P.A., Kaufman, D.M., Nippert, J.B., Carlisle, J.D., Harper, C.W., 2008. Changes in grassland ecosystem function due to extreme rainfall events: implications for responses to climate change. *Global Change Biol.* 14, 1600–1608.
- Friedlingstein, P., Cox, P., Betts, R., Bopp, L., von Bloh, W., Brovkin, V., Cadule, P., Doney, S., Eby, M., Fung, I., Bala, G., John, J., Jones, C., Joos, F., Kato, T., Kawamiya, M., Knorr, W., Lindsay, K., Matthews, H.D., Raddatz, T., Rayner, P., Reick, C., Roeckner, E., Schnitzler, K.-G., Schnur, R., Strassmann, K., Weaver, A.J., Yoshikawa, C., Zeng, N., 2006. Climate-carbon cycle feedback analysis: results from the C4MIP model intercomparison. *J. Clim.* 19, 3337–3353.
- Friedlingstein, P., Meinshausen, M., Arora, V.K., Jones, C.D., Anav, A., Liddicoat, S.K., Knutti, R., 2014. Uncertainties in CMIP5 climate projections due to carbon cycle feedbacks. *J. Clim.* 27, 511–526.
- Ganjurjav, H., Gao, Q., Schwartz, M.W., Zhu, W., Liang, Y., Li, Y., Wan, Y., Cao, X., Williamson, M.A., Jiangcun, W., Guo, H., Lin, E., 2016. Complex responses of spring vegetation growth to climate in a moisture-limited alpine meadow. *Sci. Rep.* 6. <http://dx.doi.org/10.1038/srep23356>.
- Giardina, C.P., Ryan, M.G., 2000. Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature* 404, 858–861.
- Hararuk, O., Smith, M.J., Luo, Y., 2015. Microbial models with data-driven parameters predict stronger soil carbon responses to climate change. *Global Change Biol.* 21, 2439–2453.
- Hararuk, O., Xia, J., Luo, Y., 2014. Evaluation and improvement of a global land model against soil carbon data using a Bayesian Markov chain Monte Carlo method. *J. Geophys. Res. Biogeosci.* 119, 403–417.
- Hoover, D.L., Rogers, B.M., 2016. Not all droughts are created equal: the impacts of interannual drought pattern and magnitude on grassland carbon cycling. *Global Change Biol.* 22, 1809–1820.
- Hou, Y., Zhou, G., Xu, Z., Liu, T., Zhang, X., 2013. Interactive effects of warming and increased precipitation on community structure and composition in an annual forb dominated desert steppe. *PLoS ONE* 8. <http://dx.doi.org/10.1371/journal.pone.0070114>.
- Huxman, T.E., Cable, J.M., Ignace, D.D., Eilts, J.A., English, N.B., Weltzin, J., Williams, D.G., 2004b. Response of net ecosystem gas exchange to a simulated precipitation pulse in a semi-arid grassland: the role of native versus non-native grasses and soil texture. *Oecologia* 141, 295–305.
- 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., Hart, J., Koch, G.W., Schwinning, S., Small, E.E., Williams, D.G., 2004a. Convergence across biomes to a common rain-use efficiency. *Nature* 429, 651–654.
- Huxman, T.E., Snyder, K.A., Tissue, D., Leffler, A.J., Ogle, K., Pockman, W.T., Sandquist, D.R., Potts, D.L., Schwinning, S., 2004c. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia* 141, 254–268.
- Janssen, P.H.M., Heuberger, P.S.C., 1995. Calibration of process-oriented models. *Ecol. Model.* 83, 55–66.
- Jiang, H., Deng, Q., Zhou, G., Hui, D., Zhang, D., Liu, S., Chu, G., Li, J., 2013. Responses of soil respiration and its temperature/moisture sensitivity to precipitation in three subtropical forests in Southern China. *Biogeosciences* 10, 3963–3982.
- Jones, C., Robertson, E., Arora, V., Friedlingstein, P., Sheviakova, E., Bopp, L., Brovkin, V., Hajima, T., Kato, E., Kawamiya, M., Liddicoat, S., Lindsay, K., Reick, C.H., Roelandt, C., Segschneider, J., Tjiputra, J., 2013. Twenty-first-CENTURY compatible CO₂ emissions and airborne fraction simulated by CMIP5 earth system models under four representative concentration pathways. *J. Clim.* 26, 4398–4413.
- Karhu, K., Auffret, M.D., Dungait, J.A.J., Hopkins, D.W., Prosser, J.I., Singh, B.K., Subke, J.-A., Wookey, P.A., Ågren, G.I., Sebastià, M.-T., Gouriveau, F., Bergkvist, G., Meir, P., Nottingham, A.T., Salinas, N., Hartley, I.P., 2014. Temperature sensitivity of soil respiration rates enhanced by microbial community response. *Nature* 513, 81–84.
- Kattge, J., Knorr, W., 2007. Temperature acclimation in a biochemical model of photosynthesis: a reanalysis of data from 36 species. *Plant Cell Environ.* 30, 1176–1190.
- Knapp, A.K., Ciais, P., Smith, M.D., 2017. Reconciling inconsistencies in precipitation–productivity relationships: implications for climate change. *New Phytol.* 214, 41–47.
- 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.
- Knorr, W., Prentice, I.C., House, J.I., Holland, E.A., 2005. Long-term sensitivity of soil carbon turnover to warming. *Nature* 433, 298–301.
- Kucharik, C.J., Twine, T.E., 2007. Residue, respiration, and residuals: evaluation of a dynamic agroecosystem model using eddy flux measurements and biometric data. *Agric. For. Meteorol.* 146, 134–158.
- Lee, J., Pedroso, G., Linquist, B.A., Putnam, D., Kessel, C., Six, J., 2012. Simulating switchgrass biomass production across ecoregions using the DAYCENT model. *GCB Bioenergy* 4, 521–533.
- Li, Z., Liu, Z., Chen, Z., Yang, Z., 2003. The effects of climate change on the productivity in Inner Mongolia steppe of China. *Acta Prataculturae Sin.* 12, 4–10.
- Liu, W., Allison, S.D., Xia, J., Liu, L., Wan, S., 2016. Precipitation regime drives warming responses of microbial biomass and activity in temperate steppe soils. *Biol. Fertil. Soils* 52, 469–477.
- Liu, W., Zhang, Z., Wan, S., 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.
- Liu, X., Wan, S., Su, B., Hui, D., Luo, Y., 2002. Response of soil CO₂ efflux to water manipulation in a tallgrass prairie ecosystem. *Plant Soil* 240, 213–223.
- Lu, M., Zhou, X., Yang, Q., Li, H., Luo, Y., Fang, C., Chen, J., Yang, X., Li, B., 2013. Responses of ecosystem carbon cycle to experimental warming: a meta-analysis. *Ecology* 94, 726–738.
- Lugato, E., Panagos, P., Bampa, F., Jones, A., Montanarella, L., 2014. A new baseline of organic carbon stock in European agricultural soils using a modelling approach. *Global Change Biol.* 20, 313–326.
- Luo, Y., Ahlström, A., Allison, S.D., Batjes, N.H., Brovkin, V., Carvalhais, N., Chappell, A., Ciais, P., Davidson, E.A., Finzi, A., Georgiou, K., Guenet, B., Hararuk, O., Harden, J.W., He, Y., Hopkins, F., Jiang, L., Koven, C., Jackson, R.B., Jones, C.D., Lara, M.J., Liang, J., McGuire, A.D., Parton, W., Peng, C., Randerson, J.T., Salazar, A., Sierra, C.A., Smith, M.J., Tian, H., Todd-Brown, K.E.O., Torn, M., van Groenigen, K.J., Wang, Y.P., West, T.O., Wei, Y., Wieder, W.R., Xia, J., Xu, X., Xu, X., Zhou, T., Tao, 2016. Toward more realistic projections of soil carbon dynamics by Earth system models. *Global Biogeochem. Cycles* 30, 40–56.
- 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.A.N., Rustad, L., 2008. Modeled interactive effects of precipitation, temperature, and [CO₂] on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biol.* 14, 1986–1999.
- Luo, Y., Jiang, L., Niu, S., Zhou, X., 2017. Nonlinear responses of land ecosystems to variation in precipitation. *New Phytol.* 214, 5–7.
- Luo, Y., Meyerhoff, P.A., Loomis, R.S., 1995. Seasonal patterns and vertical distributions

- of fine roots of alfalfa (*Medicago sativa* L.). *Field Crops Res.* 40, 119–127.
- Luo, Y., Randerson, J.T., Abramowitz, G., Bacour, C., Blyth, E., Carvalhais, N., Ciais, P., Dalmonech, D., Fisher, J.B., Fisher, R., Friedlingstein, P., Hibbard, K., Hoffman, F., Huntzinger, D., Jones, C.D., Koven, C., Lawrence, D., Li, D.J., Mahecha, M., Niu, S., Norby, R., Piao, S., Qi, X., Peylin, P., Prentice, I.C., Riley, W., Reichstein, M., Schwalm, C., Wang, Y.-P., Xia, J., Zaehle, S., Zhou, X., 2012. A framework for benchmarking land models. *Biogeosciences* 9, 3857–3874.
- Luo, Y., Wan, S., Hui, D., Wallace, L.L., 2001. Acclimatization of soil respiration to warming in a tall grass prairie. *Nature* 413, 622–625.
- Medlyn, B.E., De Kauwe, M.G., Zaehle, S., Walker, A.P., Duursma, R.A., Luus, K., Mishurov, M., Pak, B., Smith, B., Wang, Y.-P., Yang, X., Crous, K.Y., Drake, J.E., Gimeno, T.E., Macdonald, C.A., Norby, R.J., Power, S.A., Tjoelker, M.G., Ellsworth, D.S., 2016. Using models to guide field experiments: a priori predictions for the CO₂ response of a nutrient- and water-limited native eucalypt woodland. *Global Change Biol.* 22, 2834–2851.
- Medlyn, B.E., Zaehle, S., De Kauwe, M.G., Walker, A.P., Dietze, M.C., Hanson, P.J., Hickler, T., Jain, A.K., Luo, Y., Parton, W., Prentice, I.C., Thornton, P.E., Wang, S., Wang, Y.-P., Weng, E., Iversen, C.M., McCarthy, H.R., Warren, J.M., Oren, R., Norby, R.J., 2015. Using ecosystem experiments to improve vegetation models. *Nat. Clim. Change* 5, 528–534.
- Niu, S., Wu, M., Han, Y., Xia, J., Li, L., Wan, S., 2008. Water-mediated responses of ecosystem carbon fluxes to climatic change in a temperate steppe. *New Phytol.* 177, 209–219.
- Niu, S., Xing, X., Zhang, Z., Xia, J., Zhou, X., Song, B., Li, L., Wan, S., 2011. Water-use efficiency in response to climate change: from leaf to ecosystem in a temperate steppe. *Global Change Biol.* 17, 1073–1082.
- Norby, R.J., De Kauwe, M.G., Domingues, T.F., Duursma, R.A., Ellsworth, D.S., Goll, D.S., Lapola, D.M., Luus, K.A., Rob MacKenzie, A., Medlyn, B.E., Pavlick, R., Rammig, A., Smith, B., Thomas, R., Thonicke, K., Walker, A.P., Yang, X., Zaehle, S., 2016. Model-data synthesis for the next generation of forest free-air CO₂ enrichment (FACE) experiments. *New Phytol.* 209, 17–28.
- Norby, R.J., Luo, Y., 2004. Evaluating ecosystem responses to rising atmospheric CO₂ and global warming in a multi-factor world. *New Phytol.* 162, 281–293.
- Noy-Meir, I., 1973. Desert ecosystems: environment and producers. *Annual Rev. Ecology Systematics* 4, 25–51.
- Oberbauer, S.F., Tweedie, C.E., Welker, J.M., Fahnestock, J.T., Henry, G.H.R., Webber, P.J., Hollister, R.D., Walker, M.D., Kuchy, A., Elmore, E., Starr, G., 2007. Tundra CO₂ fluxes in response to experimental warming across latitudinal and moisture gradients. *Ecol. Monogr.* 77, 221–238.
- Parton, W.J., Hartman, M., Ojima, D., Schimel, D., 1998. DAYCENT and its land surface submodel: description and testing. *Global Planet. Change* 19, 35–48.
- Parton, W.J., Schimel, D.S., Cole, C.V., Ojima, D.S., 1987. Analysis of factors controlling soil organic matter levels in great plains grassland. *Soil Sci. Soc. Am. J.* 51, 1173–1179.
- Peng, S., Piao, S., Shen, Z., Ciais, P., Sun, Z., Chen, S., Bacour, C., Peylin, P., Chen, A., 2013. Precipitation amount, seasonality and frequency regulate carbon cycling of a semi-arid grassland ecosystem in Inner Mongolia, China: a modeling analysis. *Agric. For. Meteorol.* 178–179, 46–55.
- Piao, S., Sitch, S., Ciais, P., Friedlingstein, P., Peylin, P., Wang, X., Ahlström, A., Anav, A., Canadell, J.G., Cong, N., Huntingford, C., Jung, M., Levis, S., Levy, P.E., Li, J., Lin, X., Lomas, M.R., Lu, M., Luo, Y., Ma, Y., Myrneni, R.B., Poulter, B., Sun, Z., Wang, T., Viovy, N., Zaehle, S., Zeng, N., 2013. Evaluation of terrestrial carbon cycle models for their response to climate variability and to CO₂ trends. *Global Change Biol.* 19, 2117–2132.
- Reich, P.B., Sendall, K.M., Stefanski, A., Wei, X., Rich, R.L., Montgomery, R.A., 2016. Boreal and temperate trees show strong acclimation of respiration to warming. *Nature* 531, 633–636.
- Reichstein, M., Rey, A., Freibauer, A., Tenhunen, J., Valentini, R., Banza, J., Casals, P., Cheng, Y., Grünzweig, J.M., Irvine, J., Joffre, R., Law, B.E., Loustau, D., Miglietta, F., Oechel, W., Ourcival, J.-M., Pereira, J.S., Peressotti, A., Ponti, F., Qi, Y., Rambal, S., Rayment, M., Romanya, J., Rossi, F., Tedeschi, V., Tirone, G., Xu, M., Yakir, D., 2003. Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. *Global Biogeochem. Cycles* 17. <http://dx.doi.org/10.1029/2003GB002035>.
- 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.
- Rodriguez-Iturbe, I., Porporato, A., Laio, F., Ridolfi, L., 2001. Plants in water-controlled ecosystems: active role in hydrologic processes and response to water stress: I. Scope and general outline. *Adv. Water Resour.* 24, 695–705.
- Ross, I., Misson, L., Rambal, S., Arneeth, 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.
- Ryals, R., Hartman, M.D., Parton, W.J., Delong, M.S., Silver, W.L., 2015. Long-term climate change mitigation potential with organic matter management on grasslands. *Ecol. Appl.* 25, 531–545.
- Sahai, H., Ojeda, M.M., 2004. Analysis of variance for random models. *Balanced Data, Theory, Methods, Application, and Data Analysis*, vol. 1 Birkhäuser, Boston.
- Schwalm, C.R., Williams, C.A., Schaefer, K., Arneeth, A., Bonal, D., Buchmann, N., Chen, J., Law, B.E., Lindroth, A., Luyssaert, S., Reichstein, M., Richardson, A.D., 2010. Assimilation exceeds respiration sensitivity to drought: a FLUXNET synthesis. *Global Change Biol.* 16, 657–670.
- Scott, R.L., Biederman, J.A., Hamerlynck, E.P., Barron-Gafford, G.A., 2015. The carbon balance pivot point of southwestern U.S. semiarid ecosystems: insights from the 21st century drought. *J. Geophys. Res. Biogeosci.* 120, 2612–2624.
- Shaver, G.R., Canadell, J., Chapin III, F.S., Gurevitch, J., Harte, J., Henry, G., Ineson, P., Jonasson, S., Melillo, J., Pitelka, L., Rustad, L., 2000. Global warming and terrestrial ecosystems: a conceptual framework for analysis. *BioScience* 50, 871–882.
- Shen, Z.X., Li, Y.L., Fu, G., 2015. Response of soil respiration to short-term experimental warming and precipitation pulses over the growing season in an alpine meadow on the Northern Tibet. *Appl. Soil Ecol.* 90, 35–40.
- Shi, Z., Thomey, M.L., Mowll, W., Litvak, M., Brunsell, N.A., Collins, S.L., Pockman, W.T., Smith, M.D., Knapp, A.K., Luo, Y., 2014. Differential effects of extreme drought on production and respiration: synthesis and modeling analysis. *Biogeosciences* 11, 621–633.
- Shi, Z., Xu, X., Hararuk, O., Jiang, L., Xia, J., Liang, J., Li, D., Luo, Y., 2015. Experimental warming altered rates of carbon processes, allocation, and carbon storage in a tall-grass prairie. *Ecosphere* 6, 1–16.
- Shi, Z., Xu, X., Souza, L., Wilcox, K., Jiang, L., Liang, J., Xia, J., García-Palacios, P., Luo, Y., 2016. Dual mechanisms regulate ecosystem stability under decade-long warming and hay harvest. *Nat. Commun.* 7, 11973.
- Smith, N.G., Malyshev, S.L., Shevliakova, E., Kattge, J., Dukes, J.S., 2016. Foliar temperature acclimation reduces simulated carbon sensitivity to climate. *Nat. Clim. Change* 6, 407–413.
- Song, B., Niu, S., Zhang, Z., Yang, H., Li, L., Wan, S., 2012. Light and heavy fractions of soil organic matter in response to climate warming and increased precipitation in a temperate steppe. *PLoS One* 7, e33217.
- Steduto, P., Çetinköku, Ö., Albrizio, R., Kanber, R., 2002. Automated closed-system canopy-chamber for continuous field-crop monitoring of CO₂ and H₂O fluxes. *Agric. For. Meteorol.* 111, 171–186.
- Suseela, V., Conant, R.T., Wallenstein, M.D., Dukes, J.S., 2012. Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. *Global Change Biol.* 18, 336–348.
- Tang, J., Riley, W.J., 2015. Weaker soil carbon-climate feedbacks resulting from microbial and abiotic interactions. *Nat. Clim. Change* 5, 56–60.
- Thomey, M.L., Collins, S.L., Vargas, R., Johnson, J.E., Brown, R.F., Natvig, D.O., Friggens, M.T., 2011. Effect of precipitation variability on net primary production and soil respiration in a Chihuahuan Desert grassland. *Global Change Biol.* 17, 1505–1515.
- Vicca, S., Bahn, M., Estiarte, M., van Loon, E.E., Vargas, R., Alberti, G., Ambus, P., Arain, M.A., Beier, C., Bentley, L.P., Borken, W., Buchmann, N., Collins, S.L., de Dato, G., Dukes, J.S., Escolar, C., Fay, P., Guidolotti, G., Hanson, P.J., Kahmen, A., Kröel-Dulay, G., Ladreiter-Knauss, T., Larsen, K.S., Lellei-Kovacs, E., Lebrjia-Trejos, E., Maestre, F.T., Marhan, S., Marshall, M., Meir, P., Miao, Y., Muhr, J., Niklaus, P.A., Ogaya, R., Peñuelas, J., Poll, C., Rustad, L.E., Savage, K., Schindlbacher, A., Schmidt, I.K., Smith, A.R., Sotta, E.D., Suseela, V., Tietema, A., van Gestel, N., van Straaten, O., Wan, S., Weber, U., Janssens, I.A., 2014. Can current moisture responses predict soil CO₂ efflux under altered precipitation regimes? A synthesis of manipulation experiments. *Biogeosciences* 11, 2991–3013.
- Walker, A.P., Hanson, P.J., De Kauwe, M.G., Medlyn, B.E., Zaehle, S., Asao, S., Dietze, M., Hickler, T., Huntingford, C., Iversen, C.M., Jain, A., Lomas, M., Luo, Y., McCarthy, H., Parton, W.J., Prentice, I.C., Thornton, P.E., Wang, S., Wang, Y., Warland, D., Weng, E., Warren, J.M., Woodward, F.I., Oren, R., Norby, R.J., 2014. Comprehensive ecosystem model-data synthesis using multiple data sets at two temperate forest free-air CO₂ enrichment experiments: model performance at ambient CO₂ concentration. *J. Geophys. Res. Biogeosci.* 119, 937–964.
- Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H., Ahlquist, L.E., Alatalo, J.M., Bret-Harte, M.S., Calef, M.P., Callaghan, T.V., Carroll, A.B., Epstein, H.E., Jonsdottir, I.S., Klein, J.A., Magnusson, B., Molau, U., Oberbauer, S.F., Rewa, S.P., Robinson, C.H., Shaver, G.R., Suding, K.N., Thompson, C.C., Tolvanen, A., Totland, O., Turner, P.L., Tweedie, C.E., Webber, P.J., Wookey, P.A., 2006. Plant community responses to experimental warming across the tundra biome. *PNAS* 103, 1342–1346.
- Wan, S., Norby, R.J., Ledford, J., Weltzin, J.F., 2007. Responses of soil respiration to elevated CO₂, air warming, and changing soil water availability in a model old-field grassland. *Global Change Biol.* 13, 2411–2424.
- Wan, S., Xia, J., Liu, W., Niu, S., 2009. Photosynthetic overcompensation under nocturnal warming enhances grassland carbon sequestration. *Ecology* 90, 2700–2710.
- Wang, Y.P., Leuning, R., 1998. A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy. I. Model description and comparison with a multi-layered model. *Agric. For. Meteorol.* 91, 89–111.
- Way, D.A., Katul, G.G., Manzoni, S., Vico, G., 2014. Increasing water use efficiency along the C₃ to C₄ evolutionary pathway: a stomatal optimization perspective. *J. Exp. Bot.* 65, 3683–3693.
- Weltzin, J.F., Loik, M.E., Schwinning, S., Williams, D.G., Fay, P.A., Haddad, B.M., Harte, J., Huxman, T.E., Knapp, A.K., Lin, G., Pockman, W.T., Shaw, R.M., Small, E.E., Smith, M.D., Smith, S.D., Tissue, D.T., Zak, J.C., 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. *BioScience* 53, 941–952.
- Weng, E., Luo, Y., 2008. Soil hydrological properties regulate grassland ecosystem responses to multifactor global change: a modeling analysis. *J. Geophys. Res.* 113. <http://dx.doi.org/10.1029/2007JG000539>.
- Wieder, W.R., Allison, S.D., Davidson, E.A., Georgiou, K., Hararuk, O., He, Y., Hopkins, F., Luo, Y., Smith, M., Sulman, B., Todd-Brown, K., Wang, Y.-P., Xia, J., Xu, X., 2015. Explicitly representing soil microbial processes in Earth system models. *Global Biogeochem. Cycles* 10, 1782–1800.
- Wieder, W.R., Bonan, G.B., Allison, S.D., 2013. Global soil carbon projections are improved by modelling microbial processes. *Nat. Clim. Change* 3, 909–912.
- Wu, Z., Dijkstra, P., Koch, G.W., Peñuelas, J., Hungate, B.A., 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biol.* 17, 927–942.
- Wythers, K.R., Reich, P.B., Tjoelker, M.G., Bolstad, P.B., 2005. Foliar respiration acclimation to temperature and temperature variable Q₁₀ alter ecosystem carbon balance. *Global Change Biol.* 11, 435–449.

- Xia, J., Han, Y., Zhang, Z., Zhang, Z., Wan, S., 2009. Effects of diurnal warming on soil respiration are not equal to the summed effects of day and night warming in a temperate steppe. *Biogeosciences* 6, 1361–1370.
- Xia, J., Luo, Y., Wang, Y.P., Hararuk, O., 2013. Traceable components of terrestrial carbon storage capacity in biogeochemical models. *Global Change Biol.* 19, 2104–2116.
- Xia, J., Wan, S., 2012. The effects of warming-shifted plant phenology on ecosystem carbon exchange are regulated by precipitation in a semi-arid grassland. *PLoS One* 7, e32088.
- Xu, G., Shi, L., Lian, H., Zheng, Z., Liu, W., 1997. Path analysis of main factors affecting field moisture capacity. *J. Agric. Sci. Yanbian Univ.* 4, 432–435.
- Xu, T., White, L., Hui, D., Luo, Y., 2006. Probabilistic inversion of a terrestrial ecosystem model: analysis of uncertainty in parameter estimation and model prediction. *Global Biogeochem. Cycles* 20. <http://dx.doi.org/10.1029/2005GB002468>.
- Xu, X., Li, D., Luo, Y., 2015. Modeled ecosystem responses to intra-annual redistribution and levels of precipitation in a prairie grassland. *Ecol. Model.* 297, 33–41.
- Yan, L., Chen, S., Huang, J., Lin, G., 2010. Differential responses of auto- and heterotrophic soil respiration to water and nitrogen addition in a semiarid temperate steppe. *Global Change Biol.* 16, 2345–2357.
- Yang, H., Wu, M., Liu, W., Zhang, Z., Zhang, N., Wan, S., 2011. Community structure and composition in response to climate change in a temperate steppe. *Global Change Biol.* 17, 452–465.
- Yang, Z., Jiang, L., Su, F., Zhang, Q., Xia, J., Wan, S., 2016. Nighttime warming enhances drought of plant communities in a temperate steppe. *Sci. Rep.* 6, 23267.
- Zeppel, M.J.B., Wilks, J.V., Lewis, J.D., 2014. Impacts of extreme precipitation and seasonal changes in precipitation on plants. *Biogeosciences* 11, 3083–3093.
- Zhao, C., Miao, Y., Yu, C., Zhu, L., Wang, F., Jiang, L., Hui, D., Wan, S., 2016. Soil microbial community composition and respiration along an experimental precipitation gradient in a semiarid steppe. *Sci. Rep.* 6, 24317.
- Zhou, X., Weng, E., Luo, Y., 2008. Modeling patterns of nonlinearity in ecosystem responses to temperature, CO₂, and precipitation changes. *Ecol. Appl.* 18, 453–466.