

## Experimental warming altered rates of carbon processes, allocation, and carbon storage in a tallgrass prairie

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

**Key words:** Bayes' theorem; carbon cycle; global climate change; model-data fusion; sensitivity analysis.

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## INTRODUCTION

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

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

Data assimilation is a statistical method that allows incorporating multi-sourced convoluted measurements into ecological models, constraining model parameters, and quantifying uncertainties of model parameters and predictions. For

example, Braswell et al. (2005) used daily and seasonal eddy flux data from Harvard forest to estimate parameters in an ecosystem C flux model (SIPNET). The better fitting between model output and observations demonstrated the effectiveness of the model-data integration. By assimilating soil respiration and biometric C data from Duke Forest, Xu et al. (2006) applied probabilistic inversion to quantify uncertainties of model parameters and predicted carbon pool dynamics in ambient and elevated CO<sub>2</sub> treatments. They found significant difference in extracted parameter values under the two treatments and large uncertainties associated with residence time of the passive C pool. Wang et al. (2007) estimated parameters in a land surface model using multiple eddy flux datasets and found good agreement between constrained parameter values and independent estimates. Weng and Luo (2011) quantified uncertainties contributed by model only and model and data together to short- and long-term predictions and concluded that uncertainties introduced by model and data varied with forecasting time and C pools. Keenan et al. (2013) evaluated information content from 17 datasets and found that many datasets were redundant in terms of providing information content. Overall, previous research showed that data assimilation was an effective tool to estimate parameter values and uncertainties.

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

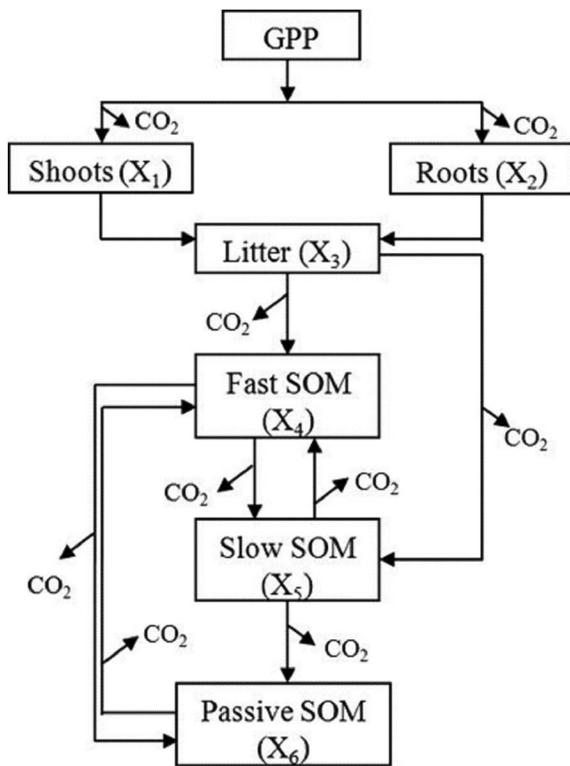


Fig. 1. Model structure with carbon pools ( $X_1$ – $X_6$ ) and fluxes in a grassland ecosystem. SOM stands for soil organic matter; GPP stands for gross primary productivity. Arrows show directions of carbon transfer.

## MATERIALS AND METHODS

### The TECO model

The Terrestrial ECOSystem (TECO) model is a CENTURY-type C pool and flux model that is used to simulate ecosystem C dynamics under various climatic conditions (Luo et al. 2008, Weng and Luo 2008, De Kauwe et al. 2013). TECO has been used to assimilate observations from forest ecosystems (Xu et al. 2006, Weng and Luo 2011). Here, we modified TECO model to represent grassland ecosystems by partitioning newly fixed C between plant shoots and roots and combining metabolic and structural litter pools into a one litter pool (Fig. 1). Soil C pool in the TECO model consists of fast, slow and passive pools and was left unchanged. Carbon dynamics in the TECO model can be

described by the following first-order differential equation:

$$\frac{dX(t)}{dt} = \xi(t)ACX(t) + BU(t) \quad (1)$$

$$X(0) = X_0$$

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

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

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

$$C = \begin{pmatrix} C_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & C_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & C_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & C_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & C_5 & 0 \\ 0 & 0 & 0 & 0 & 0 & C_6 \end{pmatrix} \quad (3)$$

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

$$\xi(t) = F_T(t)F_W(t) \quad (4)$$

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

### Data sources

We assimilated six data sets collected from a

Table 1. Abbreviations, descriptions and units of model parameters.

Parameter	Description	Units
$b_1$	allocation of GPP to shoot	...
$b_2$	allocation of GPP to root	...
$c_1$	turnover rate of C from shoot pool	$\text{g C g C}^{-1} \text{d}^{-1}$
$c_2$	turnover rate of C from root pool	$\text{g C g C}^{-1} \text{d}^{-1}$
$c_3$	turnover rate of C from litter pool	$\text{g C g C}^{-1} \text{d}^{-1}$
$c_4$	turnover rate of C from fast SOM	$\text{g C g C}^{-1} \text{d}^{-1}$
$c_5$	turnover rate of C from slow SOM	$\text{g C g C}^{-1} \text{d}^{-1}$
$c_6$	turnover rate of C from passive SOM	$\text{g C g C}^{-1} \text{d}^{-1}$
$f_{43}$	fraction of C in litter pool transferring to fast SOM	...
$f_{53}$	fraction of C in litter pool transferring to slow SOM	...
$f_{54}$	fraction of C in fast SOM transferring to slow SOM	...
$f_{64}$	fraction of C in fast SOM transferring to passive SOM	...
$f_{45}$	fraction of C in slow SOM transferring to fast SOM	...
$f_{65}$	fraction of C in slow SOM transferring to passive SOM	...
$f_{46}$	fraction of C in passive SOM transferring to fast SOM	...
$R_{10}$	temperature relative effects when temperature is at 10°C	...
$Q_{10}$	temperature sensitivity of decomposition	...

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

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

We used air temperature, soil moisture, and GPP for the period of 2000–2008 as input data to drive the TECO model. Air temperature and soil water content were observed in the experimental plots, and daily values of GPP were derived from TECO photosynthesis sub-model (Appendix: Fig. A1). Long-term (i.e., 90 years) projection and associated uncertainties were generated by cycling through 2000–2008 forcing data (air temperature, soil moisture and GPP) using 10000 sets of accepted parameters.

#### Data assimilation

We estimated a total of 17 model parameters: two allocation coefficients ( $b_i$ ), six turnover rates

( $c_i$ ) the inverses of which were residence or turnover times, seven transfer coefficients ( $f_{ij}$ ) and two parameters for environmental scalar ( $R_{10}$  and  $Q_{10}$ ). Prior ranges of the 17 parameters (Tables 1 and 2) were set based on published papers. The prior ranges of  $b_i$ s were based on Hui and Jackson (2006), prior ranges of  $c_i$ s and  $f_{ij}$ s were based on Weng and Luo (2011) and Zhou et al. (2010). We assumed that the parameters were distributed uniformly within their prior ranges.

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

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

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

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

where,  $Z(t)$  is observation and  $i$  represents  $i$ th data set,  $X(t)$  are the six carbon pools at time  $t$ , and  $\emptyset$  is the mapping vector that maps the simulated carbon pools to observations. For aboveground biomass  $\emptyset_1 = (1 \ 0 \ 0 \ 0 \ 0 \ 0)$ ; for root biomass:  $\emptyset_2 = (0 \ 1 \ 0 \ 0 \ 0 \ 0)$ , for heterotrophic

Table 2. Model parameters and default values in TECO, prior ranges, maximum likelihood estimates (MLE) and Gelman-Rubin (G-R) statistics

Parameter	Default	LL	UL	MLE <sub>control</sub>	MLE <sub>warming</sub>	G-R statistics
$b_1$	0.17	0.1	0.45	0.27	0.24	1.0
$b_2$	0.36	0.1	0.45	0.31	0.31	1.0
$c_1$	$9 \times 10^{-3}$	$1 \times 10^{-4}$	$1 \times 10^{-2}$	$6.64 \times 10^{-3}$	$5.06 \times 10^{-3}$	1.0
$c_2$	$9 \times 10^{-3}$	$1 \times 10^{-4}$	$1 \times 10^{-2}$	$4.24 \times 10^{-3}$	$2.86 \times 10^{-3}$	1.0
$c_3$	$9 \times 10^{-3}$	$1 \times 10^{-4}$	$2 \times 10^{-2}$	$6.66 \times 10^{-3}$	$9.72 \times 10^{-3}$	1.0
$c_4$	0.015	$1 \times 10^{-4}$	$5 \times 10^{-2}$	$1.69 \times 10^{-2}$	$1.85 \times 10^{-2}$	1.0
$c_5$	$6 \times 10^{-4}$	$1 \times 10^{-5}$	$2 \times 10^{-3}$	$7.43 \times 10^{-4}$	$7.45 \times 10^{-4}$	1.0
$c_6$	$2 \times 10^{-5}$	$1 \times 10^{-8}$	$3 \times 10^{-5}$	$1.55 \times 10^{-5}$	$1.47 \times 10^{-5}\dagger$	1.0
$f_{43}$	0.5	0.3	0.7	0.53	0.41	1.0
$f_{53}$	0.12	0.05	0.15	0.10a	0.10a	1.0
$f_{54}$	0.6	0.2	0.7	0.54	0.54	1.0
$f_{64}$	0.005	0.0	0.008	0.0038a	0.0041a	1.0
$f_{45}$	0.5	0.1	0.6	0.47	0.51	1.0
$f_{65}$	0.01	0.0	0.02	0.01a	0.01a	1.0
$f_{46}$	0.5	0.3	0.7	0.50a	0.51a	1.0
$R_{10}$	0.8	0.5	1.0	0.58	0.57	1.0
$Q_{10}$	2.6	1.0	5.0	2.09	2.06	1.0

† Mean value.

respiration  $\mathcal{O}_3 = (0 \ 0 \ 1-f_{43}-f_{53} \ 1-f_{64}-f_{54} \ 1-f_{45}-f_{65} \ 1-f_{46})$ ; the component of autotrophic respiration:  $R_a = 0.25 \cdot (1-b_1-b_2) \cdot \text{GPP}(t)$ , and total soil respiration is the sum of  $R_a$  and  $R_h$ ; labile carbon was mapped as  $\mathcal{O}_4 = (0 \ 0 \ 0 \ 1 \ 0 \ 0)$ , and total soil carbon was mapped as  $\mathcal{O}_5 = (0 \ 0 \ 0 \ 1 \ 1 \ 1)$ .  $p(\theta)$  was a set of uniform distributions over the ranges specified in Table 2, and  $p(Z)$  was the probability distribution function of observations.

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

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

where  $\theta_{\text{max}}$  and  $\theta_{\text{min}}$  are the maximum and minimum values of parameters,  $r$  is a random variable between  $-0.5$  and  $0.5$ , and  $D$  is used to control the proposing step size and was set to 5 as is Xu et al. (2006). In each moving step,  $\theta^{\text{new}}$  was tested against the Metropolis criterion to examine if the new parameter set should be accepted or rejected. The first 2500 accepted samples were discarded (burn-in period) and the

rest were used to generate posterior parameter distributions. To test for convergence of posterior parameter estimates, we ran the M-H algorithm four times, generating four chains with 100,000 parameter samples and tested the chains with Gelman-Rubin diagnostics (Gelman and Rubin 1992).

#### Data analysis

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

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

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

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

Data collected in the field are often not sufficient to constrain some of the counteracting processes in a C cycle model (Ricciuto et al. 2011). As a consequence, model parameters which

control the counteracting processes are likely to correlate with each other. Therefore, in addition to analyzing the information content in the observations, we analyzed the correlations between posterior parameter estimates.

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

## RESULTS

### *Parameter constraint and variability with warming*

After assimilating the experimental data, uncertainties in many TECO model parameters were significantly reduced, with the exceptions of turnover rate of passive C ( $c_6$ ) and most of the transfer coefficients (e.g.,  $f_{53}$ ,  $f_{64}$ ,  $f_{65}$  and  $f_{46}$ ; Fig. 2). A maximum likelihood estimate (MLE) was calculated for each of the well constrained parameters, while a mean value was calculated for the poorly constrained parameter (Table 2). MLEs for C allocation to leaves ( $b_1$ ), turnover rates of leaves and roots ( $c_1$  and  $c_2$ ), and partitioning from roots to litter pool ( $f_{43}$ ) were greater in the warming treatment than in the control condition; whereas the MLEs for the turnover rates of litter and labile C ( $c_3$  and  $c_4$ ) was greater in the warming treatment; MLEs for the other parameters were similar between the two conditions (Fig. 2 and Table 2).

### *Parameter correlations*

Correlations among model parameters differed little between control and warming conditions (Table 3; Appendix: Table A1), therefore we presented only the results for control treatment in the main text (Table 3). Three levels of correlation were defined: high ( $|r| > 0.5$ ), modest ( $0.3 < |r| < 0.5$ ) and low ( $0.1 < |r| < 0.3$ ). Predictably, the parameters with the highest correlations were those associated with counteracting processes, e.g., C allocation to leaves and

leaf turnover rate ( $b_1$  and  $c_1$ ); C allocation to roots and root turnover rate ( $b_2$  and  $c_2$ ); transfer coefficient from litter to labile C and the turnover rate of the latter ( $c_4$  and  $f_{43}$ ); and transfer coefficient from labile to slow C pool and the slow C turnover rate ( $c_5$  and  $f_{54}$ ). Some parameter pairs showed unexpectedly high degree of association, e.g., C allocation to shoots and roots ( $b_1$  and  $b_2$ ), C allocation to leaves and root turnover rate ( $b_1$  and  $c_2$ ), root and labile C turnover rates ( $c_2$  and  $c_4$ ); and labile and slow C turnover rates ( $c_4$  and  $c_5$ ). Passive C turnover rate ( $c_6$ ) had weak correlation with other parameters, and transfer coefficients had fairly low correlation among one another as well as with the other parameters.

### *Model performance and information gain under both treatments*

After data assimilation, TECO model generated similar mean values and patterns of respiration, plant and soil C content to the observations under control and warming conditions (Fig. 3). However, the model failed to fully capture effects of drought on respiration and biomass in 2006 under both treatments (Fig. 3A–H). Dynamics of soil C was not fully captured by the model possibly due to the large errors associated with the observations and our model structure, but the temporal trend in soil C change was generally captured (Fig. 3I–L). In order to test the effectiveness of the optimization, we also did another set of optimization by assimilating first six-year data (2000–2005) and then compared the observations with simulations. The results were quite similar to those we obtained by assimilating all the data (Appendix: Fig. A2). However, simulated root carbon was not well agreed with observations, because only one data point was measured in the first six years. Besides the poor simulation of root carbon within 2006–2008, soil labile carbon was consistently overestimated from 2006–2008 with only assimilation of data with 2000–2005. The other modeled variables were reasonably well simulated within 2006–2008. Meanwhile, we also ran the simulation using default parameter values (values before data assimilation) and compared the model results with both observations and simulations with parameter values after data assimilation (Fig. 4). We found that for most of the variables

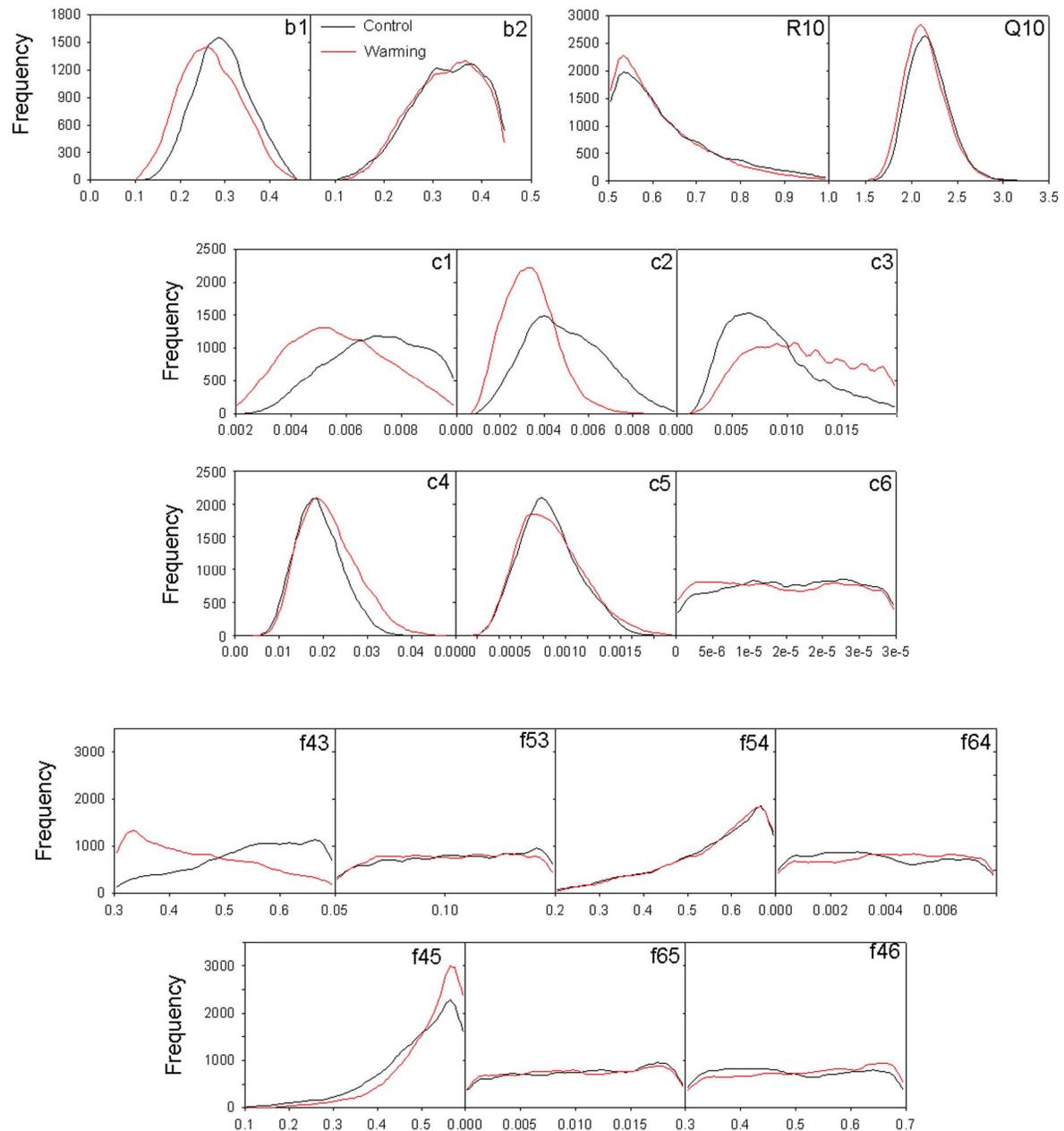


Fig. 2. Posterior distribution of the 17 model parameters under control and warming treatments. The *bs* are allocation coefficients, *cs* refer to turnover rates and *fs* are transfer coefficients. See Table 1 for parameter abbreviations.

RMSEs were consistently greater for simulation with default values than that with parameters after data assimilation (Appendix: Table A2). Higher RMSEs suggest poor model performance. However, heterotrophic respiration was an exception. The RMSEs were slightly smaller for

default simulation.

Assimilated observations contributed most information to the labile C pool (Fig. 5), increasing the information content in the labile C pool by 290% (control) and 310% (warming) compared to model with original parameters.

Table 3. Correlation coefficients among parameters in control treatments (superscript 1:  $|r| > 0.5$ ; 2:  $0.5 > |r| > 0.3$ ; 3:  $0.3 > |r| > 0.1$ ; +: positive correlation; -: negative correlation). Similar correlation coefficients in warming treatment.

Control	$b_1$	$b_2$	$c_1$	$c_2$	$c_3$	$c_4$	$c_5$	$c_6$	$R_{10}$	$Q_{10}$	$f_{43}$	$f_{53}$	$f_{54}$	$f_{64}$	$f_{45}$	$f_{65}$	$f_{46}$
$b_1$	1	- <sup>1</sup>	+ <sup>1</sup>	- <sup>1</sup>		- <sup>3</sup>			+ <sup>3</sup>								
$b_2$		1	- <sup>2</sup>	+ <sup>1</sup>	- <sup>3</sup>	+ <sup>3</sup>	+ <sup>3</sup>			- <sup>2</sup>							
$c_1$			1			+ <sup>2</sup>	+ <sup>2</sup>		- <sup>3</sup>	- <sup>3</sup>							
$c_2$				1		+ <sup>1</sup>	+ <sup>2</sup>		- <sup>2</sup>	- <sup>2</sup>				+ <sup>3</sup>			
$c_3$					1				- <sup>3</sup>		+ <sup>3</sup>			- <sup>3</sup>			
$c_4$						1	+ <sup>1</sup>		- <sup>2</sup>	- <sup>2</sup>	+ <sup>1</sup>		+ <sup>3</sup>	+ <sup>3</sup>		+ <sup>2</sup>	
$c_5$							1		-	- <sup>2</sup>	+ <sup>2</sup>		+ <sup>1</sup>	+ <sup>3</sup>		+ <sup>2</sup>	
$c_6$								1									
$R_{10}$									1	- <sup>3</sup>			+ <sup>3</sup>	- <sup>3</sup>			
$Q_{10}$										1			- <sup>3</sup>	- <sup>3</sup>			
$f_{43}$											1						
$f_{53}$												1					
$f_{54}$													1				
$f_{64}$														1			
$f_{45}$															1		
$f_{65}$																1	
$f_{46}$																	1

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

#### Effect of warming on projected C pools

Warming had different effects on C pools in a 90-year model prediction (Fig. 6): it increased live C pools ( $X_1$  and  $X_2$ ), decreased dead C pools ( $X_3$ ,  $X_4$  and  $X_5$ ), and had little effect on passive soil C pool ( $X_6$ ). Overall, warming decreased total soil C content and ecosystem C content. Due to low information gain from the observations, we observed substantial inflation of uncertainty for passive C pool ( $X_6$ ) after 90 years of simulation, whereas for other C pools uncertainty stabilized after 1–9 years of simulation. Because of inflating uncertainties in the soil C pool, uncertainties in the ecosystem C pool also increase with time under both warming and control treatments.

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

Sensitivities of projected C pools to parameters were similar under control and warming treatments (Fig. 7; Appendix: Fig. A3), therefore we presented the results for the control condition only (Fig. 7). Sensitivities of the four fast turnover C pools (i.e., pool 1–4) to parameters were similar between short-term and long-term projections: C pools were most sensitive to their respective turnover rates and modest to allocation coefficients or transfer coefficients which represent C input.

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

The sensitivities of soil and ecosystem C pools to parameters also differed between short-term and long-term projections. In short term, ecosystem C was sensitive solely to  $c_3$ , and soil C was generally insensitive to any one model parameter (Fig. 7A). In long term, however, the two pools were rather sensitive to turnover rates of the litter C and three soil C pools and the transfer

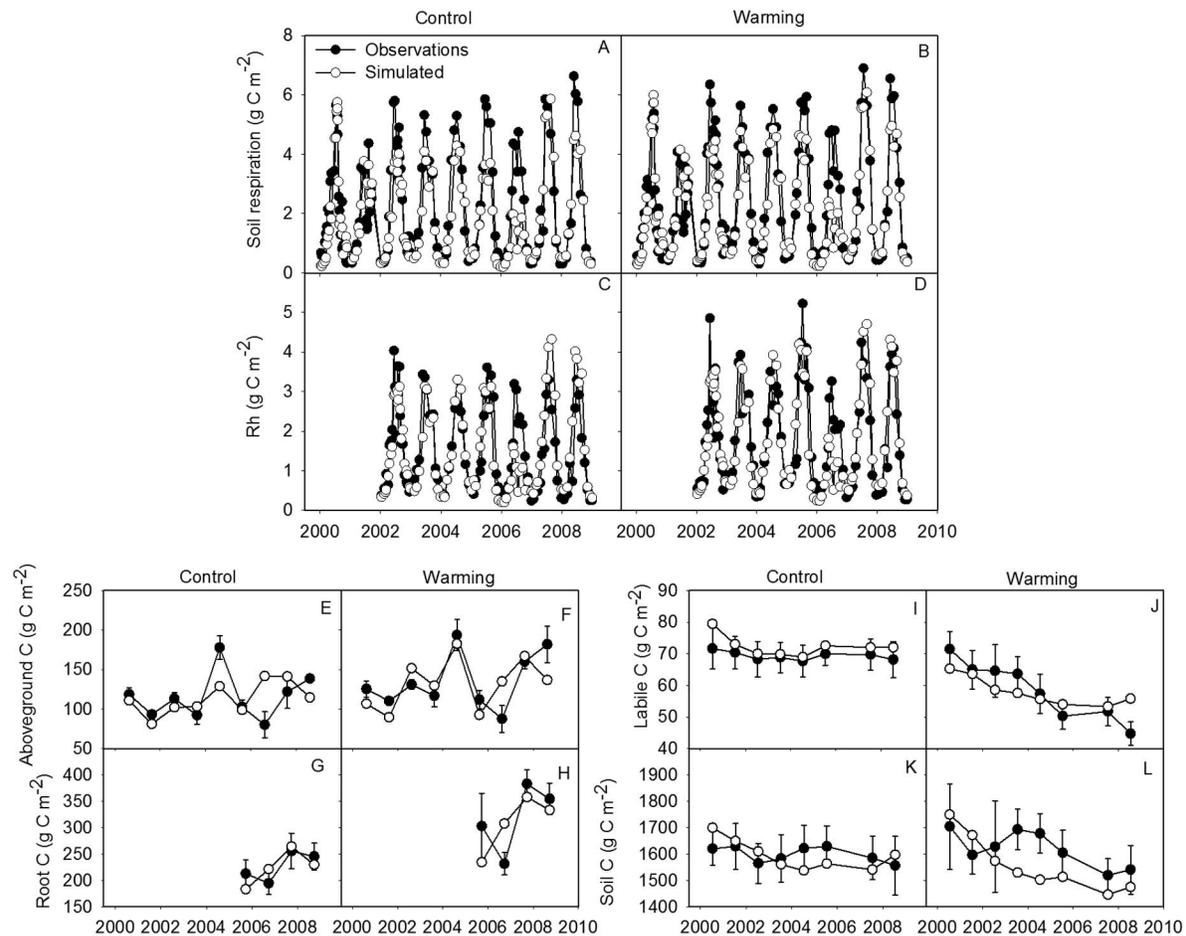


Fig. 3. Comparison of the observations and the mean values of the simulated observational variables with the parameters accepted under control and warming treatments. Panels (A–B): soil respiration under control and warming; (C–D): heterotrophic respiration (Rh); (E–F): aboveground biomass carbon; (G–H): root biomass carbon; (I–J): labile soil organic carbon; (K–L): soil organic carbon. Note: observations are mean with standard error except for soil respiration and Rh for clarity.

coefficients from upstream C pools to slow and passive C pools (Fig. 7B).

## DISCUSSION

### *Constraints of parameters and parameter correlations*

Recently, alternative model structures or additional components have been incorporated into global land models to better represent C cycling or fit empirical observations (e.g., Thornton et al. 2009, Wang et al. 2010, Wieder et al. 2013, Xu et al. 2014). As a result, the models have become more and more complex, but less tractable (Xia et

al. 2013). Improving the parameterization of an existing model structure through data assimilation has been largely ignored, yet has been proved an effective method to increase model fit to observations (Hararuk et al. 2014). The difference in parameter values between control and warming treatments in our study further evidenced that scenario-invariant parameterization in global land models could contribute significant uncertainty to model predictions. Therefore, the disparity between model results and empirical findings in climate-C cycle feedback could be resolved to some extent if parameter values are allowed to vary with

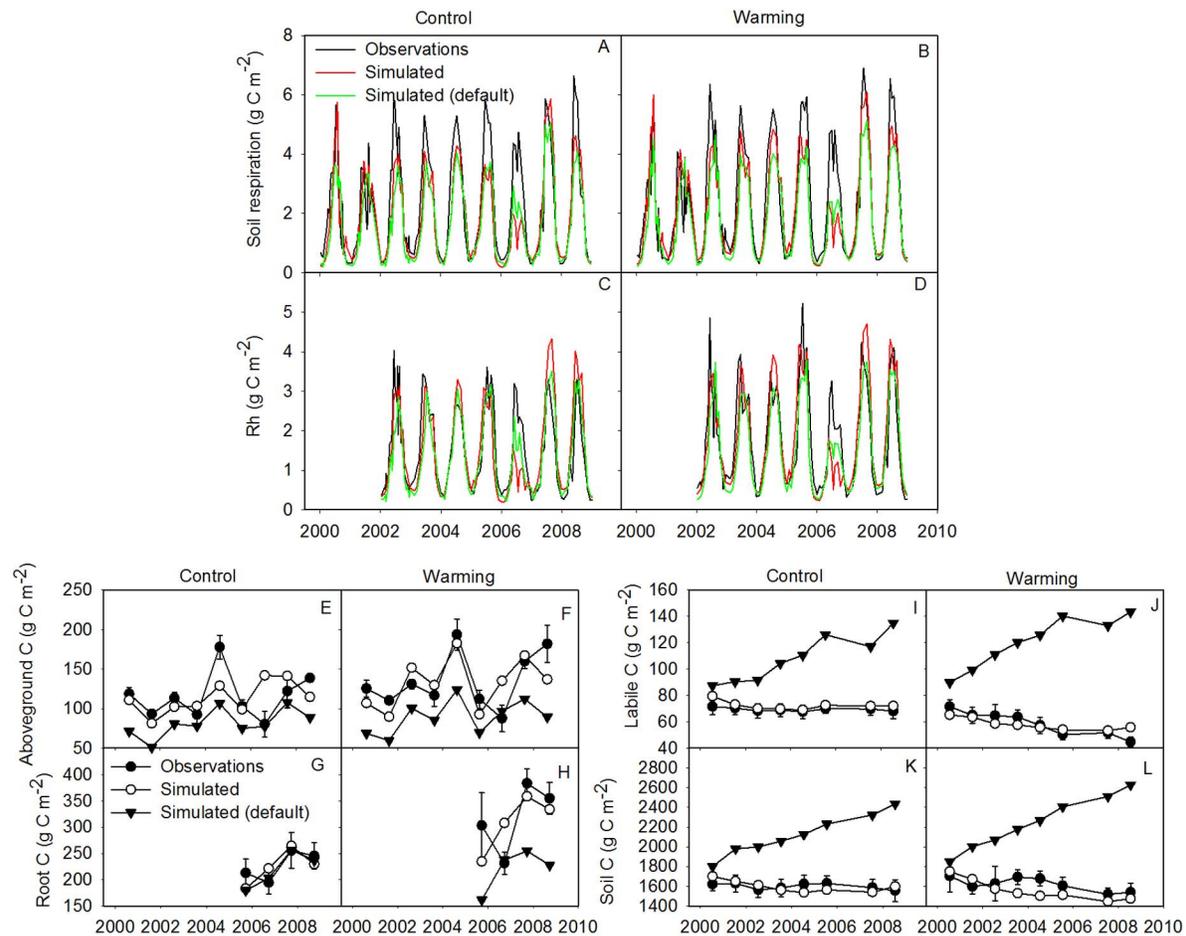


Fig. 4. Comparison of the observations and the values of the simulated observational variables with the default model parameters and parameters accepted under control and warming treatments. Panels (A–B): soil respiration under control and warming; (C–D): heterotrophic respiration (Rh); (E–F): aboveground biomass carbon; (G–H): root biomass carbon; (I–J): labile soil organic carbon; (K–L): soil organic carbon. Note: observations are mean with standard error except for soil respiration and Rh for clarity.

different climatic scenarios. On the other hand, warming-induced changes in parameter values also suggest that some important mechanisms are missing or not adequately represented in the land models. For example, warming-enhanced turnover rates of litter and labile C pools could be due to changes of plant community; however it also indicates possible inadequately representation of model processes such as temperature or soil moisture response functions.

The six data sets used in our study contained information for allocation coefficients of GPP to shoots and roots ( $b_1$  and  $b_2$ ), temperature sensitivity of turnover rates ( $Q_{10}$ ) and all turn-

over rates except for passive soil C under both treatments. The poorly constrained transfer coefficients ( $f_s$ ) implied that the six data sets did not contain much information about carbon partition among litter pool and soil organic matter pools (Weng and Luo 2011). In addition, the measurements duration (2000–2008) is relatively short in comparison to residence time of passive C pool (inverse of  $c_6$ ), which may have been the reason why data sets contributed little information to passive C pool. Passive C pool as one form of recalcitrant C, is critical for long-term carbon projections of the states of terrestrial ecosystems, as models are often used to evaluate

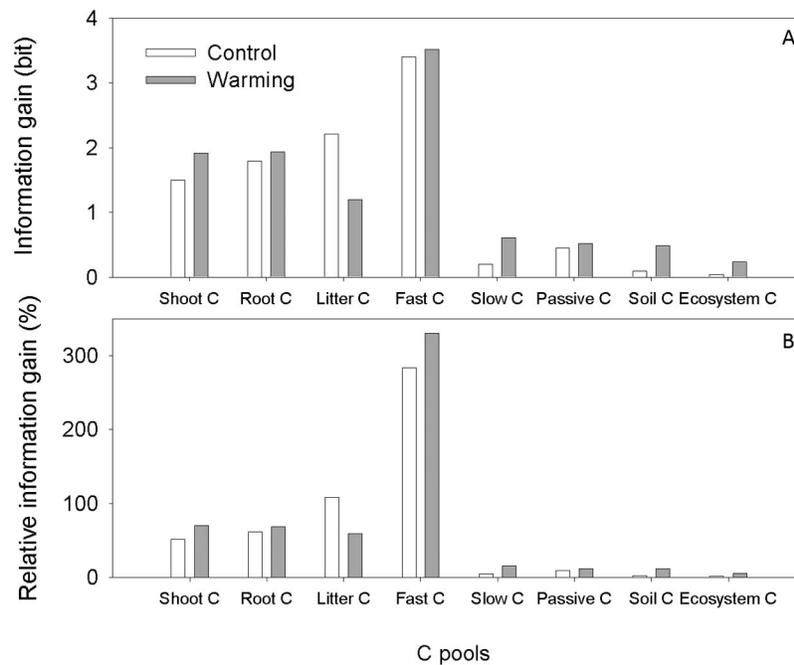


Fig. 5. Information gain (A) and relative information gain (B) of long-term C prediction derived from the distributions of carbon content simulated by the model with prior and posterior parameters.

ecosystem responses to climate changes at decadal and century time scales. Therefore, collecting information relevant to the transfer coefficients and the passive C pool dynamics would help constrain the parameters and increase the accuracy of model projections.

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

#### Warming effect on model parameters and projected carbon pools

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

Warming affected short-term and long-term C pool sizes through regulating photosynthetic input (GPP), allocation coefficients, turnover rates, environmental factors ( $R_{10}$  and  $Q_{10}$ ), and transfer coefficients individually or together. Warming-induced changes in C pool sizes were net results of different effects of warming on the

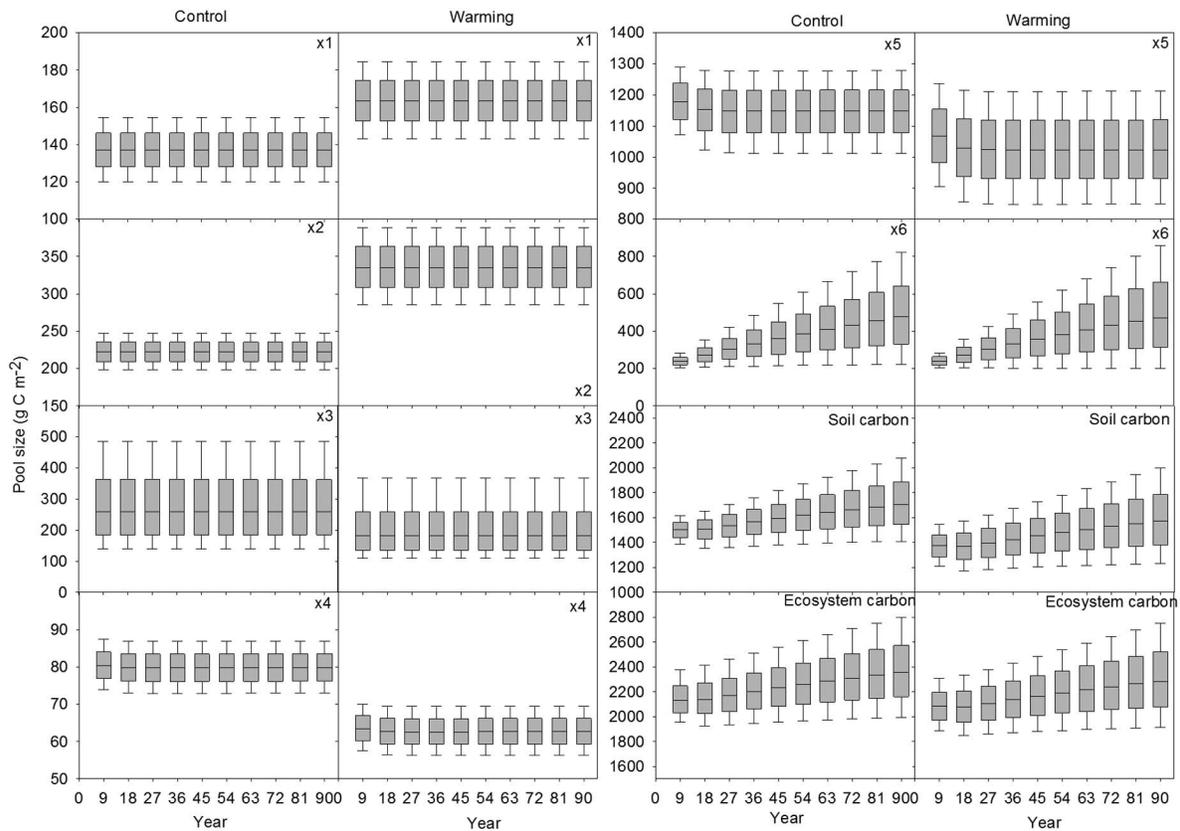


Fig. 6. Long-term (90 years) projections based on accepted parameters for each of the carbon pools, soil organic carbon and ecosystem carbon under control and warming treatments. Box plots show visual summaries of carbon content distributions in the 5% (bottom bar), 25% (bottom hinge of the box), 50% (line across the box), 75% (upper hinge of the box), and 95% (upper bar) intervals. Note that  $x_1$  represents the peak aboveground biomass carbon.

key parameters, which were not always unidirectional in their changes. For instance,  $b_1$  was reduced by warming, but plant biomass still increased as a result of warming-enhanced GPP combined with decreased turnover rates of shoots and roots. For the fast and slow soil C pools, warming-induced increase in the turnover rates resulted in diminishment of the pool size. Warming had little effect on passive soil C pool due to little warming effects on relevant parameters such as  $c_6$  and  $f_{64}$ . As a result, warming slightly decreased both total soil C and ecosystem C content.

The processes that are not calibrated in our study may also affect long-term C cycle projection. For example, our results are subject to uncertainties caused by modeled GPP as model input (Xu et al. 2006, Zhang et al. 2010, Weng and

Luo 2011) and TECO model structure. Ideally, one would calibrate an integrated canopy photosynthesis model and ecosystem C cycling model simultaneously. However, many parameters in photosynthesis model cause equifinality. Therefore, it is still a challenge to calibrate them against data at the same time (Zhang et al. 2010, Weng and Luo 2011). TECO model structure may also contribute to uncertainties. For instance, the largest difference between observed and modeled respiration and biomass occurred in the driest year, which implied model inadequacy in capturing severe drought effect. The little change in temperature sensitivity under warming also indicates the possible uncertainties contributed by model structure. The lack of parameterization of microbial activity and nitrogen dynamics in TEOC could also contribute to the uncertainties.

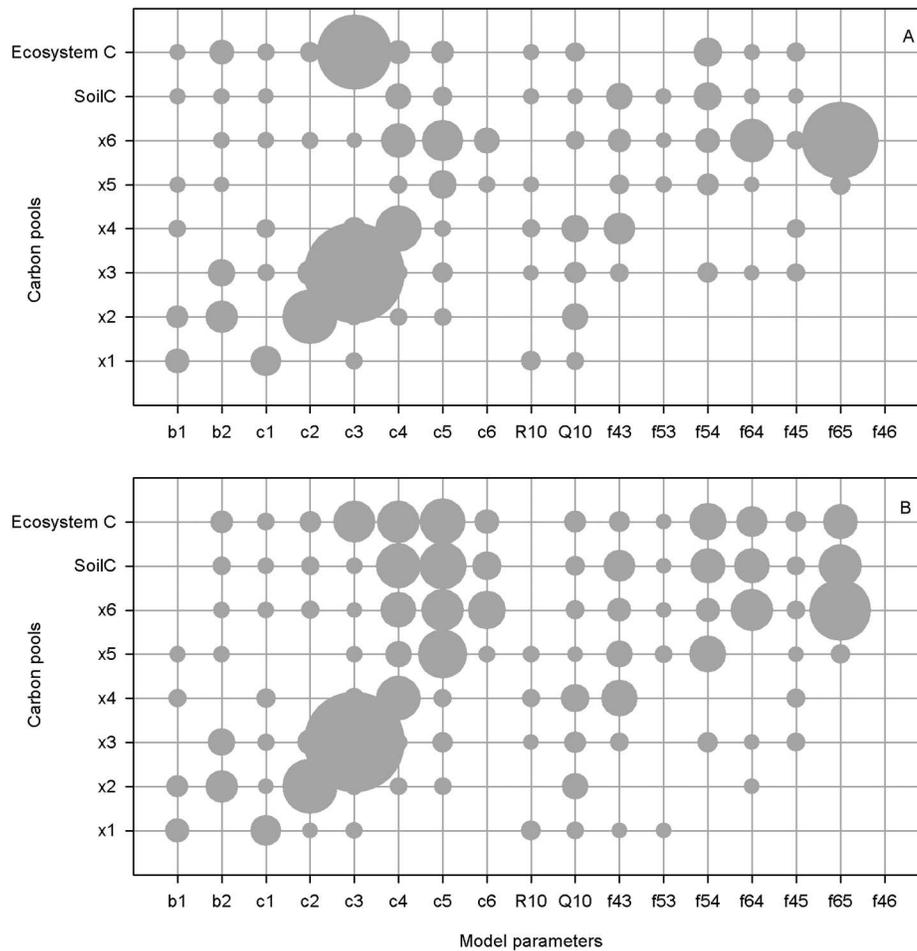


Fig. 7. The sensitivity of the carbon pools in short term (nine-year simulation; (A)) and long term (90-year simulation; (B)) to the 17 parameters in control treatment.  $x_1$ – $x_6$  are the six carbon pools as shown in Fig. 1;  $c_1$ – $c_6$  are turnover rates of the carbon pools;  $b_1$ – $b_2$  are the allocation coefficients of GPP to shoot and root, respectively;  $f_{ij}$  values are the carbon transfer coefficients from pool  $j$  to pool  $i$ . The area of the circle represents the value of the coefficient of determination.

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

Pool sizes at equilibrium state are determined by C input and turnover rate (Luo et al. 2001a, Weng and Luo 2011). The fast turnover pools (i.e., pool 1–4) all reached steady states in short-term prediction. Therefore, as expected, the turnover rates and allocation or transfer coefficients controlled the C pool sizes in both short and long terms in our study. However, the turnover rates played greater role in determining pool sizes than the C inputs represented by allocation or transfer coefficients. The underestimation of aboveground and root C and the

overestimation of labile and soil C before data assimilation were likely caused by these sensitive parameters. Specifically, the aboveground C simulation was sensitive to  $b_1$  and  $c_1$  (Fig. 7A). The improvement was likely caused by the two parameters after data assimilation. The root C simulation was sensitive to  $b_2$  and  $c_2$  (Fig. 7A), which improved the simulation after data assimilation. Labile C was sensitive to  $c_4$  and  $f_{43}$  and soil C was sensitive to  $c_4$ ,  $f_{43}$  and  $f_{54}$ , which were all well-estimated after data assimilation.

The two slow turnover pools were sensitive to different parameters between short- and long-term predictions. The  $X_5$  did not reach equilib-

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

## CONCLUSIONS

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

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## LITERATURE CITED

- Braswell, B. H., W. J. Sacks, E. Linder, and D. S. Schimel. 2005. Estimating diurnal to annual ecosystem parameters by synthesis of a carbon flux model with eddy covariance net ecosystem exchange observations. *Global Change Biology* 11:335–355.
- Cox, P. M., R. A. Betts, C. D. Jones, S. A. Spall, and I. J. Totterdell. 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* 408:184–187.
- Cramer, W., et al. 2001. Global response of terrestrial ecosystem structure and function to CO<sub>2</sub> and climate change: results from six dynamic global vegetation models. *Global Change Biology* 7:357–373.
- De Kauwe, M. G., et al. 2013. Forest water use and water use efficiency at elevated CO<sub>2</sub>: a model-data intercomparison at two contrasting temperate forest FACE sites. *Global Change Biology* 19:1759–1779.
- Dukes, J. S., N. R. Chiariello, E. E. Cleland, L. A. Moore, M. R. Shaw, S. Thayer, T. Tobeck, H. A. Mooney, and C. B. Field. 2005. Responses of grassland production to single and multiple global environmental changes. *PLoS Biology* 3:1829–1837.
- Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 7:457–511.
- Giardina, C. P., C. M. Litton, S. E. Crow, and G. P. Asner. 2014. Warming-related increases in soil CO<sub>2</sub> efflux are explained by increased below-ground carbon flux. *Nature Climate Change* 4:822–827.
- Grime, J. P., J. D. Fridley, A. P. Askew, K. Thompson, J. G. Hodgson, and C. R. Bennett. 2008. Long-term resistance to simulated climate change in an infertile grassland. *Proceedings of the National Academy of Sciences USA* 105:10028–10032.
- Hararuk, O., J. Xia, and Y. Luo. 2014. Evaluation and improvement of a global land model against soil carbon data using a Bayesian Markov chain Monte Carlo method. *Journal of Geophysical Research: Biogeosciences* 119:403–417.
- Harte, J., and R. Shaw. 1995. Shifting dominance within a montane vegetation community: results of a climate-warming experiment. *Science* 267:876–880.
- Hastings, W. K. 1970. Monte Carlo sampling methods using Markov chain and their applications. *Biometrika* 57:97–109.
- Hobbie, S. E., and F. S. Chapin. 1998. The response of tundra plant biomass, aboveground production,

- nitrogen, and CO<sub>2</sub> flux to experimental warming. *Ecology* 79:1526–1544.
- Hui, D. F., and R. B. Jackson. 2006. Geographical and interannual variability in biomass partitioning in grassland ecosystems: a synthesis of field data. *New Phytologist* 169:85–93.
- IPCC [Intergovernmental Panel on Climate Change]. 2013. *Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, London, UK.
- Keenan, T. F., E. A. Davidson, J. W. Munger, and A. D. Richardson. 2013. Rate my data: quantifying the value of ecological data for the development of models of the terrestrial carbon cycle. *Ecological Applications* 23:273–286.
- Lu, M., X. H. Zhou, Q. Yang, H. Li, Y. Q. Luo, C. M. Fang, J. K. Chen, X. Yang, and B. Li. 2013. Responses of ecosystem carbon cycle to experimental warming: a meta-analysis. *Ecology* 94:726–738.
- Luo, Y., E. Weng, X. Wu, C. Gao, X. Zhou, and L. Zhang. 2009a. Parameter identifiability, constraint, and equifinality in data assimilation with ecosystem models. *Ecological Applications* 19:571–574.
- Luo, Y., L. Wu, J. A. Andrews, L. White, R. Matamala, K. V. R. Schäfer, and W. H. Schlesinger. 2001a. Elevated CO<sub>2</sub> differentiates ecosystem carbon processes: deconvolution analysis of Duke Forest face data. *Ecological Monographs* 71:357–376.
- Luo, Y. Q., et al. 2008. Modeled interactive effects of precipitation, temperature, and [CO<sub>2</sub>] on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biology* 14:1986–1999.
- Luo, Y. Q., R. Sherry, X. H. Zhou, and S. Q. Wan. 2009b. Terrestrial carbon-cycle feedback to climate warming: experimental evidence on plant regulation and impacts of biofuel feedstock harvest. *Global Change Biology Bioenergy* 1:62–74.
- Luo, Y. Q., S. Q. Wan, D. F. Hui, and L. L. Wallace. 2001b. Acclimatization of soil respiration to warming in a tall grass prairie. *Nature* 413:622–625.
- Melillo, J. M., P. A. Steudler, J. D. Aber, K. Newkirk, H. Lux, F. P. Bowles, C. Catricala, A. Magill, T. Ahrens, and S. Morribeau. 2002. Soil warming and carbon-cycle feedbacks to the climate system. *Science* 298:2173–2176.
- Metropolis, N., A. W. Rosenbluth, M. N. Rosenbluth, A. H. Teller, and E. Teller. 1953. Equation of state calculation by fast computer machines. *Journal of Chemical Physics* 21:1087–1092.
- Niu, S. L., R. A. Sherry, X. H. Zhou, and Y. Q. Luo. 2013. Ecosystem carbon fluxes in response to warming and clipping in a tallgrass prairie. *Ecosystems* 16:948–961.
- Niu, S. L., R. A. Sherry, X. H. Zhou, S. Q. Wan, and Y. Q. Luo. 2010. Nitrogen regulation of the climate-carbon feedback: evidence from a long-term global change experiment. *Ecology* 91:3261–3273.
- Norby, R. J., and Y. Q. Luo. 2004. Evaluating ecosystem responses to rising atmospheric CO<sub>2</sub> and global warming in a multi-factor world. *New Phytologist* 162:281–293.
- Parton, W. J., J. A. Morgan, G. M. Wang, and S. Del Grosso. 2007. Projected ecosystem impact of the Prairie Heating and CO<sub>2</sub> Enrichment experiment. *New Phytologist* 174:823–834.
- Riccio, D. M., A. W. King, D. Dragoni, and W. M. Post. 2011. Parameter and prediction uncertainty in an optimized terrestrial carbon cycle model: effects of constraining variables and data record length. *Journal of Geophysical Research: Biogeosciences* 116:G01033.
- Rustad, L. E., J. L. Campbell, G. M. Marion, R. J. Norby, M. J. Mitchell, A. E. Hartley, J. H. C. Cornelissen, and J. Gurevitch. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126:543–562.
- Shannon, C. E. 1948. A mathematical theory of communication. *Bell System Technical Journal* 27:379–423.
- Thornton, P. E., S. C. Doney, K. Lindsay, J. K. Moore, N. Mahowald, J. T. Randerson, I. Fung, J. F. Lamarque, J. J. Feddes, and Y. H. Lee. 2009. Carbon-nitrogen interactions regulate climate-carbon cycle feedbacks: results from an atmosphere-ocean general circulation model. *Biogeosciences* 6:2099–2120.
- Wang, Y. P., D. Baldocchi, R. Leuning, E. Falge, and T. Vesala. 2007. Estimating parameters in a land-surface model by applying nonlinear inversion to eddy covariance flux measurements from eight FLUXNET sites. *Global Change Biology* 13:652–670.
- Wang, Y. P., R. M. Law, and B. Pak. 2010. A global model of carbon, nitrogen and phosphorus cycles for the terrestrial biosphere. *Biogeosciences* 7:2261–2282.
- Welker, J. M., J. T. Fahnestock, G. H. R. Henry, K. W. O’Dea, and R. A. Chimner. 2004. CO<sub>2</sub> exchange in three Canadian High Arctic ecosystems: response to long-term experimental warming. *Global Change Biology* 10:1981–1995.
- Weng, E. S., and Y. Q. Luo. 2008. Soil hydrological properties regulate grassland ecosystem responses to multifactor global change: a modeling analysis. *Journal of Geophysical Research-Biogeosciences* 113:G03003.
- Weng, E. S., and Y. Q. Luo. 2011. Relative information contributions of model vs. data to short- and long-term forecasts of forest carbon dynamics. *Ecological Applications* 21:1490–1505.

- Wieder, W. R., G. B. Bonan, and S. D. Allison. 2013. Global soil carbon projections are improved by modelling microbial processes. *Nature Climate Change* 3:909–912.
- Wu, Z. T., P. Dijkstra, G. W. Koch, J. Penuelas, and B. A. Hungate. 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biology* 17:927–942.
- Xia, J., Y. Luo, Y.-P. Wang, and O. Hararuk. 2013. Traceable components of terrestrial carbon storage capacity in biogeochemical models. *Global Change Biology* 19:2104–2116.
- Xiao, J., K. J. Davis, N. M. Urban, and K. Keller. 2014. Uncertainty in model parameters and regional carbon fluxes: a model-data fusion approach. *Agricultural and Forest Meteorology* 189–190:175–186.
- Xiao, J., K. J. Davis, N. M. Urban, K. Keller, and N. Z. Saliendra. 2011. Upscaling carbon fluxes from towers to the regional scale: Influence of parameter variability and land cover representation on regional flux estimates. *Journal of Geophysical Research: Biogeosciences* 116:G00J06.
- Xu, T., L. White, D. F. Hui, and Y. Q. Luo. 2006. Probabilistic inversion of a terrestrial ecosystem model: analysis of uncertainty in parameter estimation and model prediction. *Global Biogeochemical Cycles* 20:GB2007.
- Xu, X., J. P. Schimel, P. E. Thornton, X. Song, F. Yuan, and S. Goswami. 2014. Substrate and environmental controls on microbial assimilation of soil organic carbon: a framework for Earth system models. *Ecology Letters* 17:547–555.
- Xu, X., R. A. Sherry, S. L. Niu, J. Z. Zhou, and Y. Q. Luo. 2012. Long-term experimental warming decreased labile soil organic carbon in a tallgrass prairie. *Plant and Soil* 361:307–315.
- Zhang, L., Y. Luo, G. Yu, and L. Zhang. 2010. Estimated carbon residence times in three forest ecosystems of eastern China: Applications of probabilistic inversion. *Journal of Geophysical Research: Biogeosciences* 115:G01010.
- Zhou, X., S. Q. Wan, and Y. Q. Luo. 2007. Source components and interannual variability of soil CO<sub>2</sub> efflux under experimental warming and clipping in a grassland ecosystem. *Global Change Biology* 13:761–775.
- Zhou, X. H., Y. Q. Luo, C. Gao, P. S. J. Verburg, J. A. Arnone, A. Darrouzet-Nardi, and D. S. Schimel. 2010. Concurrent and lagged impacts of an anomalously warm year on autotrophic and heterotrophic components of soil respiration: a deconvolution analysis. *New Phytologist* 187:184–198.

## SUPPLEMENTAL MATERIAL

### ECOLOGICAL ARCHIVES

The Appendix is available online: <http://dx.doi.org/10.1890/ES14-00335.1.sm>