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Concurrent and lagged impacts of an anomalously warm year on autotrophic and heterotrophic components of soil respiration: a deconvolution analysis

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Summary

• Partitioning soil respiration into autotrophic (R_A) and heterotrophic (R_H) components is critical for understanding their differential responses to climate warming.

• Here, we used a deconvolution analysis to partition soil respiration in a pulse warming experiment. We first conducted a sensitivity analysis to determine which parameters can be identified by soil respiration data. A Markov chain Monte Carlo technique was then used to optimize those identifiable parameters in a terrestrial ecosystem model. Finally, the optimized parameters were employed to quantify R_A and R_H in a forward analysis.

• Our results displayed that more than one-half of parameters were constrained by daily soil respiration data. The optimized model simulation showed that warming stimulated R_H and had little effect on R_A in the first 2 months, but decreased both R_H and R_A during the remainder of the treatment and post-treatment years. Clipping of above-ground biomass stimulated the warming effect on R_H but not on R_A. Overall, warming decreased R_A and R_H significantly, by 28.9% and 24.9%, respectively, during the treatment year and by 27.3% and 33.3%, respectively, during the post-treatment year, largely as a result of decreased canopy greenness and biomass.

• Lagged effects of climate anomalies on soil respiration and its components are important in assessing terrestrial carbon cycle feedbacks to climate warming.

Introduction

Global warming induced by rising atmospheric greenhouse gases has increased the Earth's surface temperature by 0.76°C since 1850, and the temperature is expected to increase by another 1.1–6.4°C by the end of this century (IPCC, 2007). This projected warming has the potential to alter ecosystem carbon (C) cycling and probably turn terrestrial ecosystems (TECOs) from C sinks to sources (Cox *et al.*, 2000; Friedlingstein *et al.*, 2006). On a global scale, climate warming by 1°C could result in an extra 11–34 Pg C yr^{-1} release to the atmosphere as a result of enhanced decomposition (Jenkinson *et al.*, 1991; Schimel *et al.*, 1994). Soil respiration (R_S) is the largest terrestrial flux of CO_2 to the atmosphere in the global C cycle (Raich & Schlesinger, 1992; Raich *et al.*, 2002), and therefore is an important regulator of global change. This flux comprises autotrophic respiration (R_A) from roots and their symbionts and a heterotrophic component (R_H) during litter and soil organic matter (SOM) decomposition (Hanson *et al.*, 2000; Kuzyakov, 2006; Subke *et al.*, 2006).

Although the partitioning of R_S into R_A and R_H has received considerable attention, reliable and reproducible quantification of these two processes remains one of the major challenges facing global change research (Baggs, 2006). It is important to resolve this issue, as R_A and R_H have been shown to respond differently to temperature (Boone *et al.*, 1998; Lavigne *et al.*, 2003; Niinistö *et al.*,

2004; Zhou *et al.*, 2007). Understanding the differential controls of R_A and R_H would provide us with greater insight into feedbacks between terrestrial C cycling and climate warming (Cox *et al.*, 2000; Friedlingstein *et al.*, 2006). However, current results from modeling, mesocosm and field experiments, and transect studies are highly contradictory (Lin *et al.*, 1999, 2001; Lavigne *et al.*, 2003; Eliasson *et al.*, 2005; Zhou *et al.*, 2007). For example, Lin *et al.* (1999, 2001) observed that R_H was more sensitive than R_A to warming in experimental forest mesocosms. A transect study by Lavigne *et al.* (2003), however, indicated that the response of R_S to temperature was controlled more by R_A than R_H in balsam fir ecosystems. In girdling and trenching experiments, the temperature sensitivity of R_A, indicated by Q_{10} (a relative increase in respiration for every 10°C rise in temperature), was higher than that of R_H, indicating that R_A was more sensitive than R_H to temperature change (Högberg *et al.*, 2001; Zhou *et al.*, 2007). The potential change in R_S associated with climate warming will largely depend on the relative contribution of autotrophic and heterotrophic components (Buchmann, 2000; Zhou *et al.*, 2007). Therefore, an understanding of the controls on the partitioning of R_S is critical to elucidate the nature and extent of feedbacks between climate change and soil processes and to predict ecosystem responses to environmental change (Melillo *et al.*, 2002; Luo, 2007).

Recent climate change trends and modeling studies have indicated an increase in the frequency and intensity of extreme weather events, such as extreme heat waves, droughts and floods (Diffenbaugh *et al.*, 2005; Jentsch *et al.*, 2007). These anomalous events may have effects on ecosystems that could carry over into following years – a lag effect (Arnone *et al.*, 2008; Sherry *et al.*, 2008). Lagged effects of an anomalous year might play an important role in R_S and its components in the following years, probably resulting in persistent responses to the anomaly and subsequent positive or negative feedback between the atmosphere and climate change (Cox *et al.*, 2000). In the past, most of the research related to lag responses has focused on the effects of precipitation on plant biomass production with a lag time from one to several years (Andersen *et al.*, 1997; Potter *et al.*, 1999; Wiegand *et al.*, 2004; Sherry *et al.*, 2008). To the best of our knowledge, no studies have examined lagged effects of warming on R_S and its components (R_A and R_H). An understanding of the lagged effects of climate warming is urgently needed to improve the prediction of ecosystem C cycling and to appreciate feedbacks between climate change and the atmosphere after an anomalously warm year (Reichstein *et al.*, 2007).

The relative contribution of R_A or R_H to R_S varies greatly from as little as 10% to as much as 90% for both forest and nonforest ecosystems (Hanson *et al.*, 2000; Bond-Lamberty *et al.*, 2004; Subke *et al.*, 2006). Much of this variability has been attributed to differences in measurement techniques and partitioning methods (Hanson *et al.*, 2000; Bond-Lamberty *et al.*, 2004; Subke *et al.*, 2006). Common experimental approaches for the separation of R_H from R_A include both intrusive methods (e.g. trenching and root exclusions) and nonintrusive methods using isotopic techniques (Luo & Zhou, 2006). Each method has a unique set of limitations and merits (Rochette *et al.*, 1999; Jassal & Black, 2006). For example, intrusive methods disturb soil and sever the intimately linked processes of C flow from fine roots to mycorrhizal symbionts and the wider soil community. Isotopic methods require distinguishable signature sources, which are often not available in many ecosystems (Hanson *et al.*, 2000; Luo & Zhou, 2006).

Deconvolution analysis was first introduced by Luo *et al.* (2001b) to partition components of R_S on the basis of distinctive response times of various C processes to a perturbation. The approach has the potential to untangle soil biocomplexity. This kinetics-based approach focuses on system-level performance and underlying processes with data–model integration (Luo *et al.*, 2001b). When a measurable quantity represents a convolved product of several processes with distinguishable characteristics, deconvolution analysis can differentiate these complex processes according to their distinctive response times and estimate C transfer coefficients between C pools. Soil respiration is the product of multiple rhizosphere processes, including root exudation, root respiration, and litter and SOM decomposition. Different processes have different response times (or residence times) – the time of C remaining in an ecosystem from entrance via photosynthesis to exit via respiration – to perturbation. Therefore, observed R_S responses to a perturbation can be separated so as to probe the underlying processes in a manner that the observations alone cannot achieve.

In this study, we employed a deconvolution approach to an analysis of R_S observed in the EcoCELL facility at the Desert Research Institute, Nevada, USA, to examine the impacts of a warming treatment and their lagged effects on components of R_S (Verburg *et al.*, 2005; Arnone *et al.*, 2008). Deconvolution analysis first differentiates C flux pathways in ecosystems and then quantifies autotrophic and heterotrophic fluxes in response to a 1-yr warming treatment and lagged effects in the following year. Thus, this method allows us to evaluate the relative responses of the constituent processes to climate change. Specifically, we first conducted a sensitivity analysis with all parameters to determine which parameters can be identified by observations of soil respiration. A Markov chain Monte Carlo (MCMC) technique was then applied to a TECO model to optimize the identifiable parameters (i.e. C transfer coefficients and parameters of temperature and moisture effects) and analyze their uncertainties. The model was validated against measured R_S under control and warming treatments, and was subsequently used to deconvolve the effects of warming

and post-treatment on R_A and R_H using a forward analysis. Uncertainties of modeled soil respiration and its components were assessed from samples of a Metropolis–Hastings simulation. In the EcoCELL facility at the Desert Research Institute, Nevada, warming largely decreased R_S, canopy greenness and net primary productivity (NPP) in an anomalously warm year (Verburg *et al.*, 2005; Arnone *et al.*, 2008), which was consistent with other experimental studies showing that warming reduced soil respiration (Saleska *et al.*, 1999; Wan *et al.*, 2007; Lellei-Kovacs *et al.*, 2008) and plant productivity (Tingey *et al.*, 1996; De Boeck *et al.*, 2007; Klein *et al.*, 2007) in a variety of ecosystems. Based on higher Q_{10} for R_A than R_H, as already mentioned, and experimental results in the literature and EcoCELLs (Boone *et al.*, 1998; Högberg *et al.*, 2001; Rey *et al.*, 2002; Lavigne *et al.*, 2003; Verburg *et al.*, 2005; Arnone *et al.*, 2008; Lellei-Kovacs *et al.*, 2008), we hypothesized that warming would decrease R_A more than R_H in an anomalously warm year. We also hypothesized that the lagged effect would occur on both R_A and R_H with a time scale of at least 1 yr.

Materials and Methods

Model description and data sources

The model used in the deconvolution study is a TECO model developed by Luo & Reynolds (1999). By adding and subtracting transfer pathways, we evaluated the likelihood of the individual processes involved in C transfer in the rhizosphere. The TECO model used in the deconvolution analysis has a 10-pool compartmental structure (Fig. 1). Carbon enters the ecosystem via canopy photosynthesis and is partitioned into shoots and roots. Dead shoot and root materials are transferred to metabolic and structural litter compartments, and are decomposed by microbes (including fungi and soil fauna). Part of the litter C is respired and the remainder is converted into slow and passive SOM pools. C transfer coefficients are rate constants that determine the amounts of C per unit mass leaving each of the pools per day (Table 1). The inverse of each transfer coefficient represents the mean C residence time, which is the key parameter determining the C sequestration capacity of the ecosystem when combined with primary production (Barrett, 2002; Luo *et al.*, 2003). Mathematically, the model

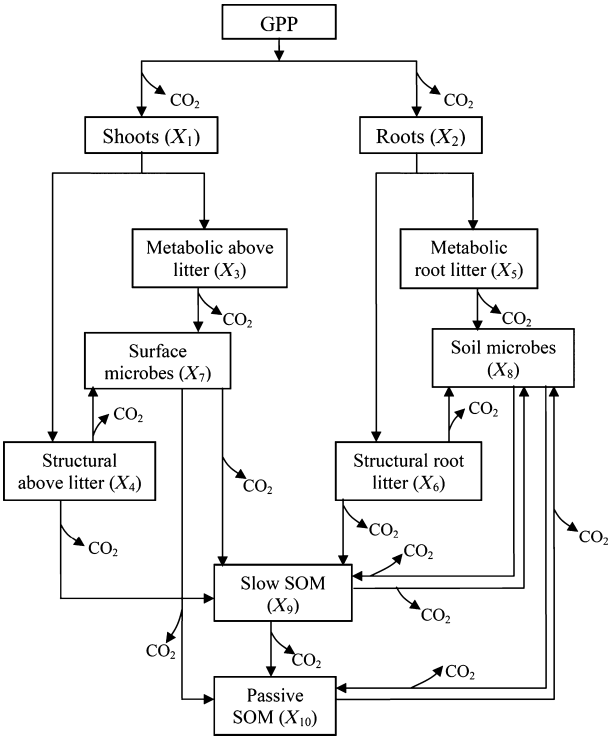

Fig. 1 Carbon (C) pools and pathways of C flux in the terrestrial ecosystem (TECO) model. GPP, gross primary productivity; SOM, soil organic matter.

Table 1 Description of carbon (C) transfer coefficients among C pools shown in Fig. 1 and parameters of temperature and moisture effects

Parameters	Intervals	Description
c_1	0.1–1.0	From pool 'shoots' (X_1) to pools 'metabolic shoot litter' (X_4) and 'structure shoot litter' (X_5)
c_2	0. 2–2.0	From pool 'roots' (X_2) to pools 'metabolic root litter' (X_6) and 'structure root litter' (X_7)
c_3	0.1–2.0	From pool 'metabolic shoot litter' (X_3) to pool 'surface microbes' (X_7)
c_4	0.1–1.0	From pool 'structure shoot litter' (X_4) to pools 'surface microbes' (X_7) and 'slow SOM' (X_9)
c_5	0.2–40	From pool 'metabolic root litter' (X_5) to pool 'soil microbes' (X_8)
c_6	0.2–10	From pool 'structure root litter' (X_6) to pools 'soil microbes' (X_8) and 'slow SOM' (X_9)
c_7	0.03–30	From pool 'surface microbes' (X_7) to pools 'slow SOM' (X_9) and 'passive SOM' (X_{10})
c_8	0.2–10	From pool 'soil microbes' (X_8) to pools 'slow SOM' (X_9) and 'passive SOM' (X_{10})
c_9	0.002–1.0	From pool 'slow SOM' (X_9) to pools 'soil microbes' (X_8) and 'passive SOM' (X_{10})
c_{10}	0.0002–0.03	From pool 'passive SOM' (X_{10}) to pool 'soil microbes' (X_8)
R_{10}	0.4–0.9	Temperature relative effects when temperature is at 10°C
Q_{10}	1.0–4.0	Temperature sensitivity of respiration
m	0.1–0.4	Moisture index of respiration

SOM, soil organic matter. Unit for c_i is mg g^{-1} d^{-1}. Unit for R_{10} is g C m^{-2} d^{-1}. Dimensionless for Q_{10} and m.

is represented by the following first-order ordinary differential equation:

$$\frac{dX(t)}{dt} = \xi(t)ACX(t) + bU(t)$$
$$X(0) = X_0 \qquad \text{Eqn 1}$$

where $X(t) = (X_1(t), X_2(t), \ldots, X_{10}(t))^T$ is a 10×1 vector describing C pool sizes, and A and C are 10×10 matrices given below. Parameters $a_1, a_2, \ldots, a_{15}$ describe C partitioning to different pools.

$$A = \begin{Bmatrix} -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ a_1 & 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1-a_1 & 0 & 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & a_2 & 0 & 0 & -1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1-a_2 & 0 & 0 & 0 & -1 & 0 & 0 & 0 & 0 \\ 0 & 0 & a_3 & a_4 & 0 & 0 & -1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & a_6 & a_7 & 0 & -1 & a_{13} & a_{15} \\ 0 & 0 & 0 & a_5 & 0 & a_8 & a_9 & a_{11} & -1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & a_{10} & a_{12} & a_{14} & -1 \end{Bmatrix}$$
$$C = \mathrm{diag}(c) \qquad \text{Eqn 2}$$

where diag(c) denotes a 10×10 diagonal matrix with diagonal entries given by vector $c = (c_1, c_2, \ldots, c_{10})^T$. Components c_i ($i = 1, 2, \ldots, 10$) represent C transfer coefficients associated with pool X_i ($i = 1, 2, \ldots, 10$) (Table 1).

$$B = (0.25 \quad 0.30 \quad 0 \quad 0 \quad 0 \quad 0 \quad 0 \quad 0 \quad 0 \quad 0)^T$$

is a vector that partitions the photosynthetically fixed C to shoots and roots. $U(\cdot)$ is the system input of photosynthetically fixed C given by a canopy photosynthetic model.

$$X_0 = [84 \quad 144 \quad 47.5 \quad 141 \quad 67 \quad 158 \quad 105 \quad 83 \quad 1586 \quad 905]$$

represents an initial condition, estimated by the method used in Luo *et al.* (2001b) based on an initial steady-state C balance in the TECO model and experimental data at the start of this study. $\xi(\cdot)$ is a scaling function accounting for temperature and moisture effects on C decomposition: $\xi(\cdot) = F_T F_W$. F_T describes temperature effects on plant respiration and decomposition of litter and SOM as $F_T = R_{10} Q_{10}^{(T-10)/10}$, and F_W represents the effects of soil water content (W) as follows:

$$F_W = \begin{cases} 1.0 - (1/m)(m - W), & W < m \\ 1, & W \geq m \end{cases} \qquad \text{Eqn 3}$$

Thus, CO_2 release resulting from litter and SOM decomposition (R_H) is calculated by

$$R_H = \sum_{i=3}^{10} \left[\left(1 - \sum_{j=8}^{10} a_{j,i} \right) c_{i,i} X_i \right], \quad i = 3, 4, \dot{s}, 10 \qquad \text{Eqn 4}$$

The modeled R_S is calculated by

$$R_S = R_A + R_H \qquad \text{Eqn 5}$$

where R_A is the respiratory CO_2 release by roots, which includes growth respiration directly proportional to photosynthetic C input and maintenance respiration from root biomass. Growth respiration is generally considered to be independent of temperature and is proportional to gross primary productivity (GPP) (Ryan, 1991; Chen *et al.*, 1999). Based on experimental results (ratio of R_A to GPP = 10.0–26.4%; Ledig *et al.*, 1976; Reich *et al.*, 1998; Högberg *et al.*, 2002; Tang *et al.*, 2005; Atkin *et al.*, 2007) and the use of the proportion of GPP in other models such as TEM (Raich *et al.*, 1991; McGuire *et al.*, 2001), LoTEC Carbon Model (Post *et al.*, 1997) and modified BIOME-BGC (Chen *et al.*, 1999), we chose 20% of GPP for root growth respiration in our deconvolution analysis. A value of 0.025 for the maintenance respiration coefficient was used to calculate root maintenance respiration from root biomass according to the respiration model of Thornley & Cannell (2000). That is to say, $R_A = 0.20 \times GPP + 0.025X_2$. Eqn 5 is called a mapping function to match the modeling estimates with measurements of R_S.

The datasets used in this deconvolution analysis are the R_S and net ecosystem exchange (NEE) data from August 2002 to February 2005 as measured in the EcoCELL facility. A detailed description of the EcoCELL facility, experimental design and measurement methods of R_S and NEE can be found in Arnone *et al.* (2008) and Supporting Information Methods S1. As the TECO model used GPP as C input, we estimated GPP based on NEE and R_S as follows: by calculating the ratio of night NEE (i.e. ecosystem respiration: R_{ECO}) to night soil respiration; by using this ratio to calculate daily R_{ECO} from daily R_S; and by daily GPP = daily R_{ECO} + daily NEE.

Parameter sensitivity analysis

Parameter identifiability is a critical issue in data assimilation (Luo *et al.*, 2009). When observations are used to constrain parameters in data assimilation, the sensitivity of the observational variables to the variation in parameter values may be different (Roulier & Jarvis, 2003). To determine which parameters are identifiable by observations of soil respiration in this study, we conducted a sensitivity analysis using the first-order approximation method (Saltelli, 2004). For observation variables Z, we first quantified an unconditional variance $V(Z)$ from model output when all

parameters in matrices A and C, and temperature and moisture effects, p_i, freely vary over their entire initial ranges. Then we fixed p_i (i = 1, 2, …, k; k = 28 in this study) at one of the r (= 100) evenly distributed values, p_i^*, within its *Prior* range. For each fixed value p_i^*, we randomly sampled M (= 1000) times of the other parameters, p_1, …, p_{i-1}, p_{i+1}, …, p_{28} within their *prior* ranges using a Monte Carlo method. From the M samples, we estimated a conditional expectation m $E(Z|p_i = p_i^*)$, r of which were used to estimate variance $V(E(Z|p_i))$. This procedure was repeated for each of p_i. A sensitivity index S_i was calculated for each parameter p_i (i = 1, 2, …, 28):

$$S_i = \frac{V(E(Z|p_i))}{V(Z)} \qquad \text{Eqn 6}$$

To compare S_i for all the parameters, we normalized S_i by:

$$I_i = \frac{S_i}{\sqrt{\sum_{i=1}^{r} S_i^2}} \qquad \text{Eqn 7}$$

where I_i is the normalized sensitivity index. The higher the value of I_i, the more sensitive the observational variable to the parameter. In this study, parameters were considered to be sensitive to soil respiration if $I_i > 0.01$.

Deconvolution analysis

In the deconvolution study, a Bayesian probabilistic inversion approach was employed to optimize the selected parameters identified from the sensitivity analysis. Our inversion analyses were performed for each EcoCELL under control (Eco 2 and 4), warming (Eco 1 and 3) and post-treatment (Eco 1 and 3) conditions. In this study, the selected parameters included C transfer coefficients (c_i, i = 1, 2, …, 10) and parameters of temperature and moisture effects (R_{10}, Q_{10} and m). The off-diagonal elements in matrix A in Eqn 2, a_1, a_2, …, a_{15}, were fixed, as well as c_3 and c_4 (see Methods S1 for fixed values), as these parameters were not identifiable by soil respiration as determined from the sensitivity analysis. A detailed description of the Bayes' theorem has been given by McCarthy (2007) and Xu *et al.* (2006). Here, we only provide a brief overview.

The Bayes' theorem states that the posterior probability density function (PPDF) $p(c|Z)$ of model parameters $\boldsymbol{c}$ can be obtained from a prior knowledge of parameters $\boldsymbol{c}$, represented by a prior probability density function (PDF) $p(c)$, and information contained in soil respiration, represented by a likelihood function $p(Z|c)$. To apply Bayes' theorem, we first specified the prior PDF $p(c)$ by giving a set of limiting intervals for parameters $\boldsymbol{c}$ with uniform distribution (Table 1), and then constructed the likelihood function $p(Z|c)$ on the basis of the assumption that errors in the observed data followed Gaussian distributions. The likelihood function $p(Z|c)$ was specified according to distributions of observation errors ($e(t)$).

$$p(Z|c) \propto \exp\left\{\frac{1}{2\sigma^2}\sum_{t\in obs(Z_i)}[Z_i(t) - \varphi_i X(t)]^2\right\} \qquad \text{Eqn 8}$$

where constant σ^2 is the error variance of soil respiration, $Z(t)$ is the observed soil respiration at time t and $\varphi X(t)$ is the modeled value, which is a product of $X(t)$ from Eqn 1 and $\boldsymbol{c}$ from Eqn 2. Then, with Bayes' theorem, the PPDF of parameters $\boldsymbol{c}$ is given by

$$p(c|Z) \propto p(Z|c)p(c) \qquad \text{Eqn 9}$$

To draw samples from $p(c|Z)$, a Metropolis–Hastings (M–H) algorithm, which is a MCMC technique revealing high-dimensional probability PPDFs of random variables via a sampling procedure (Metropolis *et al.*, 1953; Hastings, 1970; Gelfand & Smith, 1990), was employed to construct PPDFs of model parameters on the basis of their prior information, model structure and datasets. (See Methods S1 for a detailed description of the M–H algorithm, as well as an estimate of maximum likelihood estimators (MLEs) and means and cross-correlations between parameters.)

The inverse analysis described above was used to evaluate parameter values by deconvolving the observed responses of R_S to warming, and the forward analysis was designed to generate R_S and its components from a given model structure and set of parameter values (Luo *et al.*, 2001b). Given the model structure and MLEs or means of the parameters from the inverse analysis, we simulated the quantity of C released from each of the 10 pools for each EcoCELL under control and warming conditions. We estimated R_S and its components (i.e. R_A and R_H) according to Eqns 3 and 4. R_S is experimentally measurable, whereas R_A and R_H are difficult to measure in the field but represent the processes we aimed to quantify. The model was employed to estimate parameters and simulate R_S for the control EcoCELLs during the 3-yr study period, consisting of the pretreatment period, one warming year and one post-treatment year, as well as the pretreatment period in to-be-warmed EcoCELLs. During the pretreatment period (August 2002 to February 2003), we used the estimated parameters from the control to simulate R_S. Uncertainties of modeled soil respiration and its components were evaluated from all samples of the M–H simulation.

Statistical analysis

As we estimated the parameters and modeled R_S, R_A and R_H for each EcoCELL, statistical analysis was performed to determine the treatment effects of measured R_S and modeled R_S, R_A and R_H using a mixed model approach with

treatment and time as fixed factors. In 2003, we also performed a similar analysis for measured R_S and modeled R_S, R_A and R_H in the first 2 months and the rest of the treatment, respectively. We used paired Student's *t*-tests to compare observed with modeled values of R_S. The significance of the effects of warming and post-treatment on C transfer coefficients ($\boldsymbol{c}_i$, i = 1, 2, 5, …, 10) and parameters of temperature and moisture effects (R_{10}, Q_{10} and m) was examined by a *t*-test method as described by Zhou *et al.* (2006).

Results

The sensitivity analysis showed that soil respiration is very sensitive to C transfer parameters $\boldsymbol{c}_9$ (slow SOM) and temperature sensitivity Q_{10}, with normalized sensitivity indices (I_i) of nearly 1.0, and to parameters $\boldsymbol{c}_1$ (shoot) and $\boldsymbol{c}_2$ (root), with I_i of greater than 0.2 (Table 2). Normalized sensitivity indices of $\boldsymbol{c}_5$ (metabolic root litter), $\boldsymbol{c}_6$ (structural root litter), $\boldsymbol{c}_7$ (surface microbes), $\boldsymbol{c}_8$ (soil microbes), R_{10} (basal respiration at 10°C) and m (moisture index) were between 0.01 and 0.05. However, soil respiration had no sensitivity to C transfer coefficients $\boldsymbol{c}_3$ and $\boldsymbol{c}_4$ (metabolic and structural above litter), and all C partitioning parameters in matrix A (a_1, a_2, …, a_{15}). Our analysis suggested that parameters a_1, a_2, …, a_{15}, c_3 and c_4 were not identifiable by soil respiration and we therefore used fixed values for the rest of this study. Consequently, the eight transfer coefficients and three parameters of temperature and moisture effects were estimated in this study.

Parameters $\boldsymbol{c}_2$, c_5, c_6, c_7, c_9, R_{10}, Q_{10} and m were constrained to different degrees within their prespecified ranges under control and warming conditions, and parameters c_1 and c_{10} were poorly constrained (Fig. S2). Under post-treatment conditions, only parameters c_2, c_9, R_{10} and Q_{10} were constrained to some degree. Comparison of parameter distributions showed that parameters c_5, c_6, c_7, c_8 and R_{10} were significantly higher under warming than control, whereas warming lowered parameters c_2 and c_9 (Fig. 2). The post-treatment year following 1 yr of warming did not affect significantly the estimated parameters (Fig. 2).

For these constrained parameters, MLEs were identified by observing the parameter values corresponding to the peaks of their marginal distributions (Figs S2 and 2). For those unconstrained parameters for which we could not calculate MLEs, we calculated the sample means to determine the mean estimates. The standard deviations (SDs) of all parameters were estimated from the PPDFs of 80 000 samples (Fig. S2) to quantify parameter uncertainty (Fig. 2). Among the parameters, the poorly constrained parameters $\boldsymbol{c}_1$ and $\boldsymbol{c}_{10}$ had the largest variability relative to their range (Fig. 2). The cross-correlation analysis showed that the 11 parameters were not significantly correlated, except for the pairs $\boldsymbol{c}_7$–$\boldsymbol{c}_9$ and $\boldsymbol{c}_8$–$\boldsymbol{c}_9$ with correlation coefficients of 0.30 and 0.28, respectively (data not shown).

Using these MLEs and means in combination with the forward analysis, the model can adequately reproduce the seasonal variation in measured R_S under both control and warming conditions (Fig. 3). It is important to note that we

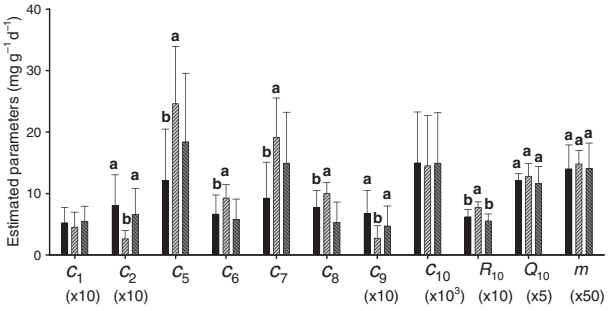

Fig. 2 Maximum likelihood estimators (MLEs) (or means for unconstrained parameters) of transfer coefficients and parameters of temperature and moisture effects with 80 000 samples from Metropolis–Hastings simulation. Error bars represent standard deviations (SDs) of parameters. Letters a, b and c above the bars indicate statistical significance. See Table 1 for parameter abbreviations. Note that only constrained parameters were shown for statistical significance ($P < 0.05$).

Table 2 Normalized sensitivity indices of parameters to soil respiration data

Parameters (p_i)	Soil respiration	Parameters (p_i)	Soil respiration	Parameters (p_i)	Soil respiration
c_1	***0.198529***	a_1	0.004165	a_{11}	0.000754
c_2	**0.412155**	a_2	0.000878	a_{12}	0.000958
c_3	0.000755	a_3	0.000185	a_{13}	0.000974
c_4	0.003819	a_4	0.002039	a_{14}	0.001732
c_5	***0.028017***	a_5	0.004197	a_{15}	2.46E-05
c_6	***0.015286***	a_6	0.000369	R_{10}	***0.033969***
c_7	***0.045488***	a_7	0.002509	Q_{10}	**0.997603**
c_8	***0.021541***	a_8	0.005459	m	***0.012427***
c_9	**0.859526**	a_9	0.000464		
c_{10}	***0.014066***	a_{10}	0.000697		

Bolds with underline indicate normalized sensitivity indices >0.2. Bold italic indicates normalized sensitivity indices larger than 0.01 and <0.20.

used parameters from the control treatment for the pretreatment period of the warming treatment. Plotting modeled (y) against measured (x) R_S results in regression lines $y = 0.920x + 0.233$ with a determinant coefficient $R^2 = 0.91$ for the control, and $y = 0.883x + 0.259$ with $R^2 = 0.92$ for warming (inserted figures). The warming treatment showed larger uncertainty in 2004 than the control because soil respiration measurements showed a large difference between the two warmed EcoCELLs during this period (Figs 3, S1).

Both R_A and R_H showed distinct seasonal patterns in the control and warmed treatments, but the maximum values of R_A came earlier than those of R_H (Fig. 4a,b) because R_A is tightly coupled with photosynthetic C input, whereas R_H follows the pattern of daily soil temperature (Fig. 4c). Warming stimulated R_H significantly ($P < 0.001$, df = 1, $n = 106$), but had little effect on R_A ($P > 0.05$, df = 1, $n = 106$) in the first 2 months, whereas both decreased during the active growing season (Figs 4, 5b). Clipping, however, stimulated responses of R_A to warming at first, followed by a gradual decrease over time, but absolute values were relatively low at this period. Clipping did not affect responses of R_H to warming. During the post-warming period, R_A and R_H persistently decreased as a result of the lagged effects of warming (Fig. 5b). Overall, warming decreased R_A and R_H significantly, by 28.9% and 24.9%, respectively, during the warming period, and by 27.3% and 33.3%, respectively, during the 1-yr post-warming period (Fig. 5c and Table 3). Coefficients of variance (CVs) of modeled R_S and R_H, representing their uncertainty, were relatively low with a range of 3–6% (Fig. 6). The CV of modeled R_A was even lower than those of R_S and R_H, because R_A mainly represented growth respiration from photosynthesis with a low percentage from maintenance respiration of biomass (data not shown). To examine the latent effects of the unselected parameters (a_1, a_2, …, a_{15}, c_3 and c_4) on the partitioning of soil respiration, we used an ensemble of experiments with random selection for the parameters of matrix A to assess the contribution of parameter uncertainty when the C transfer coefficients (c_1, c_2, c_5, …, c_{10}) and parameters of temperature and moisture effects (R_{10}, Q_{10} and m) were fixed. We did not find significant effects of latent variables on the partitioning of soil respiration (R_A and R_H) (data not shown).

Discussion

Soil respiration (R_S) is a composite of multiple processes that have usually been partitioned by intrusive methods into R_A and R_H (Luo & Zhou, 2006). In past decades, isotopic methods have also been used to separate R_S (Lin *et al.*, 1999; Rochette *et al.*, 1999; Trumbore, 2000). This study used deconvolution analysis with probabilistic inversion to untangle complex soil processes by examining distinctive

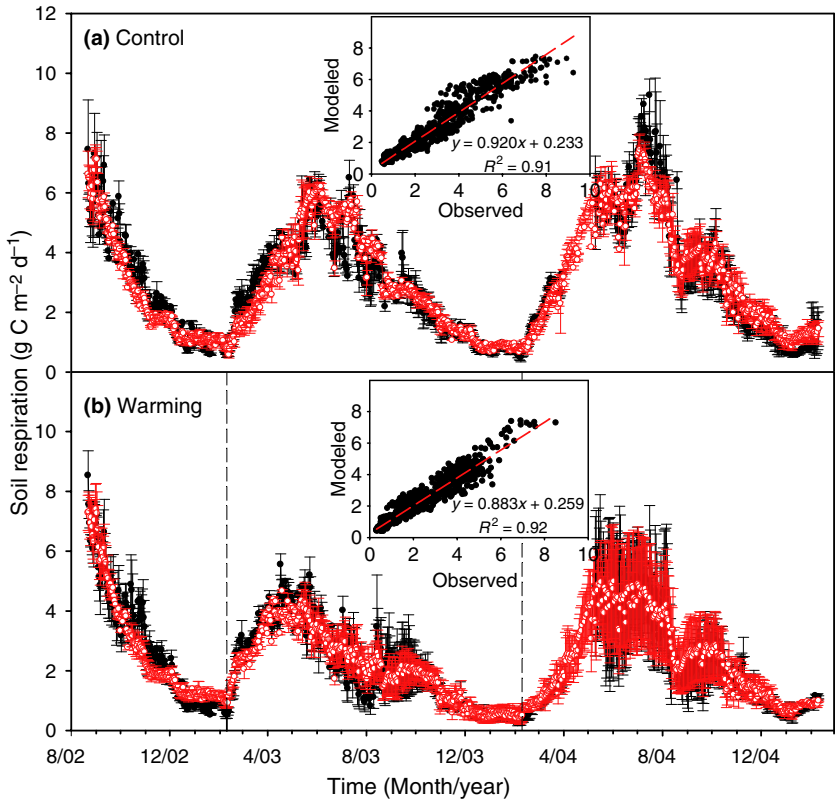

Fig. 3 Modeled (open circles) vs measured (closed circles) daily soil respiration (R_S) values under control (a) and warming (b) conditions. Insets show the correlation between the modeled and measured soil respiration values under control and warming conditions, respectively. Error bars represent standard error (±SE).

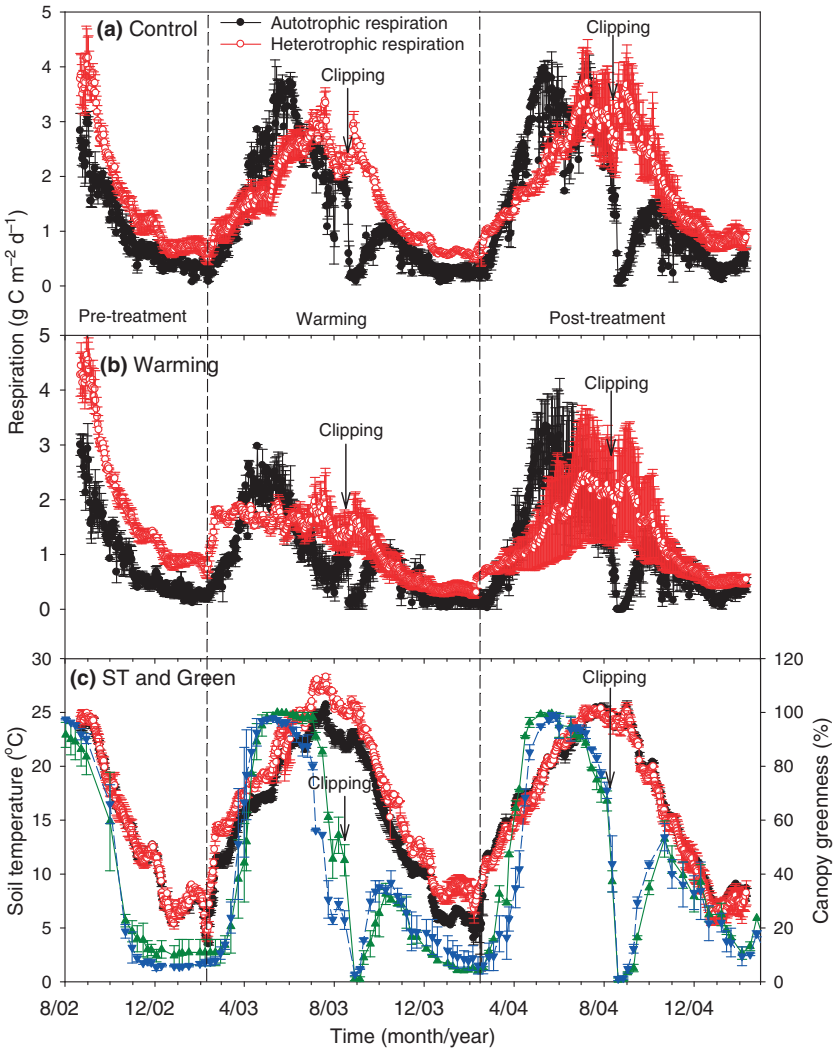

Fig. 4 Modeled autotrophic (closed circles) and heterotrophic (open circles) respiration values under control (a) and warming (b) treatments from August 2002 to February 2005. (c) The soil temperature (ST) and canopy greenness (Green) under control and warming treatments for the same period. Error bars represent standard error (±SE).

response times of various C processes to warming as well as post-warming conditions. Our analysis suggests that: warming decreased significantly both R_A and R_H as a result of decreases in canopy greenness and NPP, but clipping stimulated the responses of R_A to warming in experimental grassland ecosystems in the EcoCELL facility; lagged effects of warming were important for R_S and its components; and kinetics-based deconvolution analysis is a useful technique to examine the responses of components of observed R_S to climate change.

Warming effects on R_A and R_H

Partitioning R_S into R_A and R_H remains one of the major challenges facing global change ecosystem research with either experimental or modeling methods. Few studies have examined the effects of warming on these two fluxes (Lin *et al.*, 1999; Rochette *et al.*, 1999; Trumbore, 2000; Melillo *et al.*, 2002; Eliasson *et al.*, 2005; Zhou *et al.*, 2007), but numerous studies have investigated the responses of total R_S to warming (Peterjohn *et al.*, 1994; Rustad *et al.*, 2001; Melillo *et al.*, 2002; Niinistö *et al.*, 2004; Zhou *et al.*, 2006). Our deconvolution analysis found that warming stimulated R_H significantly in the first 2 months (Figs 4, 5). However, R_A was not affected significantly by warming during this period ($P > 0.05$, df = 1, $n = 106$; Figs 2, 6). The warming-induced transient stimulation in R_H probably resulted from enhanced oxidation of soil C compounds, especially labile C (e.g. faster turnover), followed by lowered substrate availability under warming conditions, referred to as substrate depletion (Lin *et al.*, 2001; Melillo *et al.*, 2002; Eliasson *et al.*, 2005; Zhou *et al.*, 2007). In addition, changes in microbial community may contribute to warming-induced stimulation in R_H in the first 2 months (Fig. 6a; Bradford *et al.*, 2008). R_H overestimation in the first 2 months may have exacerbated the responses to warming (Figs 4, 5). However, the responses of plants to warming may be slower than those of soil microbes, causing insignificant effects on R_A (Jonasson *et al.*, 1999; Shaver *et al.*, 2000).

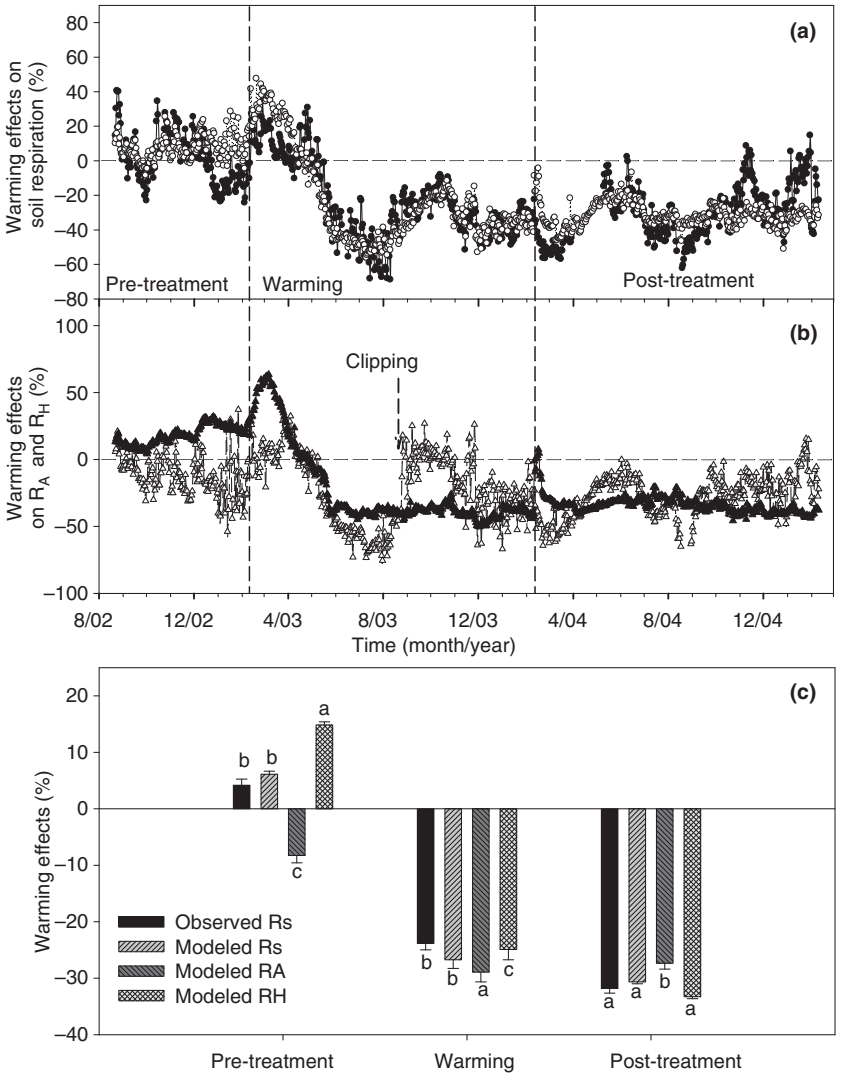

Fig. 5 Modeled (open circles) and measured (closed circles) warming effects (i.e. percentage changes under warming compared with that in the control) on soil respiration (R_S) (a), modelled warming effects on autotrophic (R_A; open triangles) and heterotrophic (R_H; closed triangles) respiration (b), and overall warming effects in R_S and its components during the study period of pre-treatment, warming and post-treatment (c). Error bars represent standard error (±SD). Letters a, b and c above the bars indicate statistical significance ($P < 0.05$).

After 2 months, warming substantially decreased both R_A and R_H (Figs 5, 6 and Table 3) and canopy greenness (Fig. 4c; Verburg *et al.*, 2005). Significant linear relationships between weekly R_S and NPP-weighted canopy greenness were found that were similar for both control and warmed treatments (Fig. 7; Verburg *et al.*, 2005). The decline in canopy greenness or NEE might result largely from a warming-induced increase in mean daytime vapor pressure deficit (VPD; Arnone *et al.*, 2008). Verburg *et al.* (2005) speculated that a decrease in R_S under warming conditions was dominated by a decrease in R_A. Our results from deconvolution analysis found that warming decreased both R_A (28.9%) and R_H (24.9%), indicating that decreases in canopy greenness and biomass not only reduced R_A, but also R_H indirectly through a decrease in the supply of current photosynthate from the canopy to heterotrophic organisms (Högberg *et al.*, 2001; Bhupinderpal-Singh *et al.*, 2003). The strong evidence of the importance of C supply by vegetation on R_H in grasslands was presented by Verburg *et al.* (2004). Under constant temperature and moisture conditions, R_H showed strong seasonal patterns because of the seasonality in C supply and C use that were not related to direct effects of temperature and moisture on microbial activity. Meanwhile, depletion of fast-cycling labile C pools and thermal acclimation and/or adaptation of microbial respiration could also have contributed to decreased R_H under warming (Luo *et al.*, 2001a; Bradford *et al.*, 2008). The former may be caused by the warming-induced stimulation in R_H in the first 2 months, as has been found in many studies (Lin *et al.*, 2001; Melillo *et al.*, 2002; Eliasson *et al.*, 2005). The latter probably results from temperature-induced changes in microbial community and subsequent decreases in mass-specific respiration rates under experimental warming (Bradford *et al.*, 2008). In addition, decreased soil moisture in the warmed EcoCELLs from June to August 2003 amplified the responses of R_H to

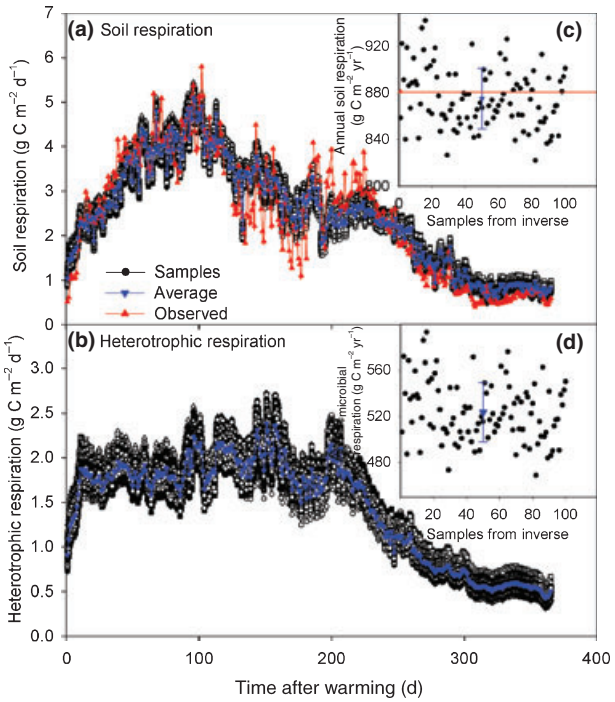

Fig. 6 Uncertainty of predicted soil respiration (a) and heterotrophic respiration (b) with 100 randomly selected samples from 40 000 samples of Metropolis–Hastings simulation in the warming treatment year. Insets show the annual soil (c) and heterotrophic (d) respiration, respectively. The red line (a) and red triangles (c) are the daily and annual observed soil respiration, respectively, in the warming treatment year. The blue lines (a, b) and blue triangles (c, d) are the average modeled soil and heterotrophic respiration, respectively, from 40 000 samples. Note that autotrophic respiration is mainly from photosynthesis with low uncertainty and is not shown.

warming (decrease; Fig. 4). This anomalously warm year not only led to decreases in soil respiration and its components, but also a decrease in NEE or C sequestration of a grassland ecosystem (Fig. S1; Arnone *et al.*, 2008). In addition, R_H reached a maximum value before the maximum photosynthesis and soil temperature under warming compared with control conditions, probably resulting from a lower substrate availability in the warmed EcoCELLs, suppressing the responses of R_H to soil temperature.

After clipping the above-ground biomass on 21 August, 2003, warming effects on R_A (i.e. percentage changes under warming compared with control conditions) increased significantly, although the absolute warming-induced change was very low (Fig. 5b). Clipping resulted in a strong positive effect of warming on R_A compared with the control. Our results are consistent with Grogan & Chapin's (2000) findings, who observed that below-ground CO_2 release was enhanced significantly 36 h after clipping in warmed inter-tussock areas in Alaska (USA). During the first several days following clipping, a wound or disturbance response to shoot removal might contribute considerably to the higher autotrophic fluxes (Grogan & Chapin, 2000). Higher temperature under warming may be important in stimulating vegetative development from plant stubble after clipping above 10 cm in the field and EcoCELLs, resulting in the large increase in R_A. Similar results were found in the field using a deep-collar insertion method to determine R_A (Zhou *et al.*, 2007). This warming response of R_A to clipping decreased over time (Fig. 5b) as a result of decreased plant growth in late fall and winter.

Our deconvolution analysis showed that warming decreased R_S, R_A and R_H by 26.7%, 28.9% and 24.9%, respectively, which did not follow the general trend (i.e. a 20% increase) inferred from a meta-analysis of 17 ecosystem warming experiments by Rustad *et al.* (2001). Currently, most studies have observed that warming stimulates R_S as well as R_A and R_H (Peterjohn *et al.*, 1994; McHale *et al.*, 1998; Lin *et al.*, 1999; 2007; Rustad *et al.*, 2001; Melillo *et al.*, 2002; Niinistö *et al.*, 2004; Zhou *et al.*, 2006). The different responses of R_S and its components to warming may be different in (semi-)arid than humid ecosystems (Verburg *et al.*, 2005). In the meta-analysis by Rustad *et al.* (2001), most of the studies

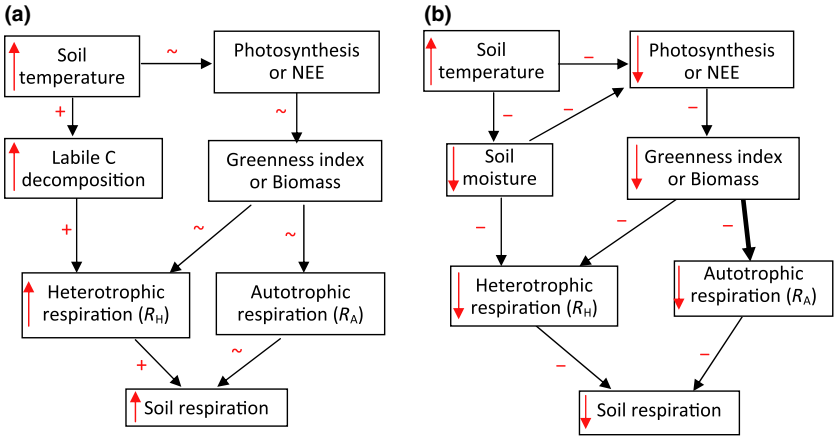

Fig. 7 A diagram of the mechanisms and processes that regulate autotrophic (R_A), heterotrophic (R_H) and soil (R_S) respiration during a pulse warming experiment. In the first 2 months, warming stimulated R_H significantly as a result of enhanced labile carbon (C) decomposition compared with the control (a). In this period, warming did not affect soil moisture significantly. After 2 months, warming decreased R_A, R_H and R_S significantly as a result of decreased soil moisture, photosynthesis and greenness index or biomass (b). +, – and ~ represent positive, negative and neutral effects. NEE, net ecosystem exchange.

Table 3 Results of ANOVA using a mixed model with treatment and time as fixed factors to show the *P* values, degrees of freedom (df) and sample size (*n*) and levels of significance for effects of pretreatment (2002), warming (2003) and post-treatment (2004) on observed soil respiration (R_S), and modeled R_S, autotrophic respiration (R_A) and heterotrophic respiration (R_H)

	Pretreatment (2002)			Warming (2003)			Post-treatment (2004)		
	P	df	*n*	*P*	df	*n*	*P*	df	*n*
Observed R_S	0.347	1	692	< 0.001	1	1460	< 0.001	1	1464
Modeled R_S	0.125	1	692	< 0.001	1	1460	< 0.001	1	1464
Modeled R_A	0.195	1	692	< 0.001	1	1460	< 0.001	1	1464
Modeled R_H	0.089	1	692	< 0.001	1	1460	< 0.001	1	1464
Comparison between observed and modeled R_S		–	–	0.589	1	1460	0.909	1	1464

We also show the statistical results of paired Student's *t*-test for comparison between observed and modeled R_S (*P* value). Time effects are statistically significant ($P < 0.0001$) and time × treatment effects are not significant ($P = 1.0$) for all analyses, which are shown in the table.

were located in humid areas, compared with our study which took place in a semi-arid ecosystem. Moreover, our results supported Saleska *et al.*'s (1999) findings, who also observed the negative responses of R_S and its components to warming. They speculated that decreases in R_A and R_H resulted from a decrease in photosynthetic activity caused by decreased soil moisture, and thus resulted in decreased R_S.

Lagged effects on R_A, R_H and R_S

In the post-treatment period, large lagged effects from the previous year of warming were observed on R_S and its components, which supported our hypothesis. Both R_A and R_H decreased throughout the post-treatment year by 27.3% and 33.3%, respectively, relative to the controls ($P < 0.0001$, df = 1, $n = 640$; Figs 4, 5 and Table 3). As in the warming year, the effects of vegetation on R_A and R_H may also be very important, because both NEE and canopy photosynthetic rates decreased during the 1-yr post-treatment period (Fig. S1b). This might coincide with the persistence of lower soil moisture and a slowing of plant canopy development in warmed EcoCELLs (Fig. S3; Arnone *et al.*, 2008). In addition, after ending the warming treatment, depletion of fast-cycling labile C pools and a change in microbial community may still persist and may take a long time to recover, resulting in lagged effects. The larger lagged effects of warming on R_H (33.3%) than R_A (27.3%) may result from a decrease in dead root input in the previous year (Verburg *et al.*, 2005). Although no studies have been conducted to examine the lagged effects of warming on R_S and its components, significant lagged effects of warming occurred on spring and autumn biomass production and the increased proportion of C_4 species in a field experiment, which was conducted at the location at which intact soil monoliths for the EcoCELL experiment were extracted using the same increase in temperature (4°C; Sherry *et al.*, 2008). In addition, several other studies support the presence of lagged effects under drought, precipitation, ozone and ultraviolet-B radiation (UVBR) exposure (Andersen *et al.*, 1997; Potter *et al.*, 1999; Löf & Welander, 2000; Wiegand *et al.*, 2004). For example, leaf area, shoot length and transpiration were mainly affected by the previous year of drought in *Fagus sylvatica* seedlings (Löf & Welander, 2000). Lagged effects of precipitation on plant production have been demonstrated for a few grasslands and shrublands (Potter *et al.*, 1999; Oesterheld *et al.*, 2001; Wiegand *et al.*, 2004). Decreases in root growth and carbohydrate concentrations by ozone exposure persisted following the removal of ponderosa pine seedlings from ozone (Andersen *et al.*, 1997). The lagged effects of an anomalously warm year on soil respiration, its components and NEE suggest that caution should be taken in assessing terrestrial C cycle feedback to climate warming, as more frequent anomalously warm years may happen in the future.

Deconvolution analysis with probabilistic inversion

Deconvolution analysis is a systems approach to the underlying processes of rhizosphere complexity, which was first introduced by Luo *et al.* (2001b) to data from the Duke Free Air CO_2 Enrichment (FACE) study. Traditionally, intrusive or isotopic methods have been used to partition R_S into R_A and R_H, which are essential to help advance our understanding of these processes (Luo & Zhou, 2006). This study applied deconvolution analysis with a probabilistic inversion technique to partition R_S into R_A and R_H under warming and post-treatment, showing its potential in understanding soil biocomplexity. The deconvoluted results are in good agreement with measured R_S data (Fig. 3; $P = 0.867$). Although there were not many measured data of R_A and R_H to validate our results, at the end of January 2004, R_H contributions to soil respiration in our deconvolution analysis (83.4% vs 88.3% for control and warming, respectively) were similar to those from direct component measurements by digging the soil and separating roots (91.4% for both control and warming) (A. Darrouzet-Nardi & J. A. Arnone, unpublished). We used another experiment with the constructed cheatgrass ecosystem but applied the same deconvolution method and EcoCELL data

to indirectly validate the model results, and found that the modeled R_H fitted the measured R_H from the isotopic method very well (X. Zhou & Y. Luo, unpublished). Another criterion to judge the validity of partitioning with the deconvolution method is the PPDFs of the estimated parameters. When the PPDFs of these parameters converge, the parameters are constrained by data (Fig. S2). Therefore, kinetics-based deconvolution analysis is a useful tool to partition R_S into R_A and R_H and to examine their responses to climate warming. Furthermore, the uncertainties of modeled soil respiration and its components were relatively low, with a CV ranging from 3% to 6% (Fig. 6).

Deconvolution analysis extracts information contained in the observed soil respiration conditioned on the model structure in TECO, and thus is subject to some limitations. The TECO model did not allow Q_{10} to vary with temperature, moisture and/or seasons, although experimental research has shown that Q_{10} values are not always constant (Janssens & Pilegaard, 2003; Davidson *et al.*, 2006). This probably partly causes the differences in deviation between the predicted and observed effects of warming on soil respiration (Fig. 5a). The largest relative difference between the predicted and observed effects of warming on soil respiration occurred during the cooler period of the year (Fig. 5a). In addition, we calculated GPP from the ratio of night-time R_{ECO} and R_S to extrapolate daily values, probably resulting in GPP overestimation, although this is a traditional approach used to estimate GPP in Flux network (Gilmanov *et al.*, 2003). The estimation of R_A is also relatively simple from the constant proportion of GPP and root biomass. Although we did not obtain direct measurements of R_A and R_H to validate our modeled values, the validity of the estimated R_A and R_H values is reflected by their PDFs and by the degree to which the parameters are constrained.

The probabilistic inversion constructs parameter distributions and assesses parameter uncertainties by quantifying MLEs, means and confidence intervals or SD, and offers much richer information contained in data, model structure and prior knowledge on parameters than does deterministic inversion (Raupach *et al.*, 2005; Xu *et al.*, 2006). Daily R_S data contain substantial information to constrain C transfer coefficients (Figs S1, S2). In our study, warming significantly increased the C transfer coefficients c_5 (metabolic root litter), c_6 (structure root litter), c_7 (surface microbes) and c_8 (soil microbes), and decreased the parameters c_2 (root biomass) and c_9 (slow SOM). Increased transfer coefficients c_5, c_6, c_7 and c_8 probably resulted from the stimulated turnover of roots and microbes under warming (especially metabolic root litter), which is supported by manipulative experiments (Forbes *et al.*, 1997; Volder *et al.*, 2007), gradient studies (Fitter *et al.*, 1998) and global dataset analysis for TECOs (Gill & Jackson, 2000). Decreases in photosynthetic rates and NEE impacted directly on the root transfer coefficient c_2 (Figs 4, 5, S1), and subsequent indirect reduction of the transfer coefficient c_9 by reducing the supply of current photosynthates from the canopy (Högberg *et al.*, 2001). The information contained in the daily R_S data is not sufficient to constrain C transfer coefficients of shoot biomass (c_1) and passive SOM (c_{10}; Fig. S2).

The analysis presented in this study was implemented by parameter estimation with a probabilistic inversion technique (MCMC) compared with deconvolution with a deterministic approach (Luo *et al.*, 2001b). The parameter values for the C transfer pathway from the observed data provided probabilities. Certainly, other mathematical techniques can also be used in parameter estimation, such as genetic algorithms, simulated annealing and the Kalman Filter (Raupach *et al.*, 2005). However, successful application of deconvolution depends on the quality of the datasets, which need to be generated from appropriate experimental design and data collection plans with high accuracy of measurements. In addition, partitioned R_A and R_H need to be validated by other methods of separating R_S.

Conclusions

The deconvolution approach uses systems analysis to probe underlying processes with data–model integration according to distinctive response times of various C processes to warming. This approach is relatively new and requires further testing and development. Nevertheless, most of the parameters in the TECO model were constrained by observed R_S, validating this approach. This study showed that warming stimulated R_H and had little effect on R_A in the first 2 months, followed by a significant decrease in R_A and R_H during the remainder of the treatment and post-treatment year. Overall, warming decreased R_A and R_H significantly, by 28.9% and 24.9%, respectively, during the treatment year, and by 27.3% and 33.3%, respectively, during the post-treatment year, largely resulting from decreased canopy greenness and biomass. Depletion of soil C pools and/or thermal adaptation of microbial respiration may also contribute to decreased R_H. Future modeling studies should take into account not only the direct effects of climate anomalies on soil respiration and its components, but also lagged effects, in assessing terrestrial C cycle feedback to climate warming.

Acknowledgements

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experiments comply with the current laws of the USA in which they were performed.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Methods S1 EcoCELL experimental system, measurement methods of soil respiration (R_S) and net ecosystem exchange (NEE), Metropolis–Hastings algorithm and model parameter estimation for maximum likelihood estimators (MLEs), means and cross-correlations.

Fig. S1 Measured daily values of soil respiration and net ecosystem exchange (NEE) at a pulse warming experiment in the EcoCELL facility of Desert Research Institute, Nevada, from August 2002 to February 2005.

Fig. S2 Inversion results showing the histograms of 10 estimated C transfer coefficients and three parameters of temperature and moisture effects with 40 000 samples from Metropolis–Hastings simulation under control, warming and post-treatment for each EcoCELL.

Fig. S3 Measured daily soil moisture at a pulse warming experiment in the EcoCELL facility of Desert Research Institute, Nevada, from August 2002 to February 2005.

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