



Differential responses of soil organic carbon fractions to warming: Results from an analysis with data assimilation



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ABSTRACT

This study was aimed to assess the decomposition temperature sensitivity (Q_{10}) of C fractions cycling from yearly through decades' and up to centennial timescales using a data assimilation approach. A three-pool C-cycling model was optimally fitted with previously-published data from a 588-day long soil incubation experiment conducted at two temperatures (25 and 35 °C) for 12 soils collected from six sites arrayed across a mean annual temperature gradient from 2.0 to 25.6 °C. Three sets of key parameters of the model, which are initial C pool fractions, decomposition rates and Q_{10} of individual pools, were estimated with a Markov chain, Monte Carlo technique. Initial C pool fractions were well constrained with pool 1 (the most labile pool), pool 2 (more recalcitrant pool) and pool 3 (the most recalcitrant pool) accounting for $4.7\% \pm 2.6\%$ (mean \pm SD), $22.4\% \pm 16.1\%$ and $72.9\% \pm 17.6\%$, respectively, of the total initial C pools. Mean residence time (MRT) was 0.19 ± 0.17 , 2.71 ± 2.34 and 80.15 ± 61.14 years for pool 1, pool 2 and pool 3, respectively. Q_{10} values increased from pool 1 to pool 3 for individual soils or across all the soils. When Q_{10} values were plotted against MRT after the data were log-transformed, Q_{10} for the three pools formed three clusters and increased with MRT. Higher Q_{10} for decades-old C fractions implies that a major portion of soil C may become a source of atmospheric CO_2 under global warming in the 21st century.

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1. Introduction

Soil represents one of the largest reservoirs of carbon (C) globally, with a soil organic C (SOC) pool about four times as much as the biotic C pool or three times as much as the atmospheric C pool (Lal, 2004). The acceleration of SOC decomposition with global warming has become one of the major concerns in predicting future climate change, but the predictions are highly uncertain in terms of how rapidly the large amounts of C stored as SOC will respond to warming (Trumbore, 2009), partly due to the uncertainty regarding the temperature sensitivity of decomposition

(expressed as Q_{10} , which means change in decomposition rate for a 10 °C difference in temperature) of different SOC fractions. If only young and more labile SOC reacts sensitively to warming, any feedback between climate change and soil C would be minor and short-lived because the largest fraction of SOC is old and stable (von Lützow and Kögel-Knabner, 2009). To predict changes of atmospheric CO_2 concentration or climate change over the 21st century, it is critical to better understand how sensitive the decades old C fractions are to warming (Conant et al., 2011; Hopkins et al., 2012; Karhu et al., 2010; Trumbore, 2009), since older fractions will not have much effect on feedbacks in the 21st century due to too slow decomposition rates (Sierra, 2012).

Our knowledge on decomposition temperature sensitivity of decades old SOC fractions is limited since the temperature sensitivity of different SOC fractions has proven difficult to investigate (Conant et al., 2008; Davidson and Janssens, 2006). The existing approaches have been comprehensively reviewed recently (Conant

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et al., 2011; Conen et al., 2006; von Lützow and Kögel-Knabner, 2009). According to these reviews, appropriate field experiments are difficult to implement and interpret while gradient studies are constrained by our limited ability to control for factors other than temperature, therefore most of the recent work investigating the relationship between temperature sensitivity of decomposition and SOC age has been based on laboratory incubations (Conant et al., 2011). The majority of laboratory incubations can roughly fall into three approaches: (i) to incubate soils at different temperatures and arbitrarily assume that Q_{10} at the beginning and end of the incubation is attributable to new or labile and older or more resistant C fractions, respectively; (ii) to study temperature sensitivity by comparing soil C of different qualities by means of physical-chemical fractionation and to investigate them separately; and (iii) to make use of progressive enrichment of soil $\delta^{13}\text{C}$ and ^{14}C to track changes in the response of decomposition rate to temperature over time, and loss of newly derived soil C identified using changes in $\delta^{13}\text{C}$ associated with C_3/C_4 plant shifts. Each approach has shortcomings. For approach (i), SOC age was usually not quantified during the incubation period. Furthermore, due to differential depletion of labile versus more resistant SOC fractions under different temperature, this approach inherently reduces the apparent temperature sensitivity of labile soil C fraction while increasing the apparent temperature sensitivity of more resistant soil C fraction when Q_{10} values are calculated using total heterotrophic respiration (Conant et al., 2010). With regard to approach (ii), the destructive nature (particularly refer to disturbance during fractionation, especially the chemical interference) of this approach hampers the transferability of its results to natural conditions, and there is no unequivocal assignment of the evolved CO_2 to young vs. old organic matter (Conen et al., 2006). As for approach (iii), it has not been clear whether these results were caused by shifts in substrate utilization patterns or by differences in the temperature responses of young versus old SOC decomposition (Hartley and Ineson, 2008). In addition, differences in the intrinsic stability of material derived from the different plants types may limit the utility of $\text{C}_3\text{--}\text{C}_4$ plant shifts (Wynn and Bird, 2007). Since approach (iii) also incubates soils at different temperatures and calculates Q_{10} values using total heterotrophic respiration, the shortcomings for approach (i) also applies to this approach (Conant et al., 2010). Due to the limitations involved in the existing approaches, it is undoubtedly needed to explore new approaches. A potential way is to use the modeling approach to analyze data from bulk soil incubation in order to separate total soil C pool into theoretical C fractions according to their mean residence time (MRT. The inverse of decomposition rate, represents the average time required to completely renew the C of a pool at steady state) and relate MRT with Q_{10} of individual C fractions.

In the present study, we developed an alternative approach to assess the decomposition temperature sensitivity of SOC fractions using an incubation dataset, which has been used to detect the role of soil characteristics in temperature sensitivity of SOC decomposition in a previous paper (Haddix et al., 2011). We developed a data assimilation approach by assimilating the information from the incubation experiment to assess the decomposition temperature sensitivity of C fractions cycling from yearly through decades' and up to centennial timescales. Data assimilation is an approach to estimate initial conditions, constrain parameters, evaluate alternative response functions and assess model uncertainties (Luo et al., 2011). Recently, data assimilation has been used to estimate or constrain processes or parameters of terrestrial C cycling, including C pool sizes, residence times, allocation coefficients, transfer coefficients, temperature sensitivity of soil heterotrophic respiration and deconvolution of soil respiration into autotrophic and heterotrophic components (Schädel et al., 2013; Weng and Luo,

2011; Xu et al., 2006; Zhou and Luo, 2008; Zhou et al., 2009, 2010). In the current study, the total soil C pool was partitioned into three theoretical C fractions with different MRTs. Our approach can be alternatively used to separate soil C pool into different fractions but the interference during fractionation is avoided. Q_{10} values and decomposition rates or MRTs were estimated for different C fractions. Therefore, Q_{10} values could be directly related to SOC age.

2. Materials and methods

2.1. Dataset used for data assimilation

The dataset used for data assimilation in the current study includes 12 soils from six sites along a mean annual temperature (MAT) gradient from 2.0 to 25.6 °C. Each of the temperate sites had native grassland and cultivated land use (SK, ND, CO and TX), and the tropical sites had a native forest and pasture land use (CR and BR). Samples were collected from three locations separated by several meters each (field replicate $n = 3$) within each land use. Surface litter and aboveground vegetation were cleared away before sampling. Small pits were dug to a depth of 20 cm, and samples were collected from 0 to 20 cm. Soils were packaged and transported to the laboratory, where rocks, surface litter, and root materials were removed. The soil was homogenized by gently breaking large soil clods by hand and passing the soil through a 2-mm sieve. Information regarding sampling sites and soil characteristics was presented in Table S1 and Table S2 (Detailed information in Haddix et al., 2011). Briefly, four replicates of composite soil samples for each soil were incubated at 15, 25 and 35 °C for 588 days, respectively. The CO_2 measurements were taken daily during the first 2 weeks of the incubation, weekly for the next 2 weeks and then every 4 weeks thereafter, generating a total of 36 sampling times over the course of 588 days. However, only the data from incubation at 25 and 35 °C were used in this study, because our purpose was to capture the signal of decomposition of C fractions cycling from yearly through decades and up to centennial timescales in order to assess the relationship between temperature sensitivity and SOC age. The older C fractions had the lowest decomposition rates at the lowest temperature so that the signal from decomposition was the lowest and not strong enough to constrain the parameters related to decomposition of decades old fraction. However, there may be bias in the temperature response of SOC decomposition when the soils were not incubated in the native temperature range (Ågren and Bosatta, 2002).

2.2. Model description

The Q_{10} model was developed with a 3-pool structure (Fig. 1). The decomposition of each pool follows a first-order exponential decay (Eqn (1)). This is widely adopted in other models including the RothC Model (Setia et al., 2011).

$$C_{\text{emit}} = \sum_{i=1}^n f_i C_0 (1 - e^{-k_i t}) \quad (1)$$

where C_{emit} (mg C g^{-1} soil) represents the total CO_2 emission due to decomposition; n denotes C pools ($n = 3$ in this study); C_0 is the initial size of total C pool before decomposition; f_i is the initial fraction of the i th pool in C_0 ($0 \leq f_i \leq 1$ and $\sum_{i=1}^n f_i = 1$); k_i represents the decomposition rate constant of the i th pool; t represents day of decomposition.

The three pools are called pool 1, pool 2 and pool 3 (Fig. 1). For convenience purposes, 35 °C was used as the reference temperature (T_{ref}). To do the data assimilation, prior parameter ranges

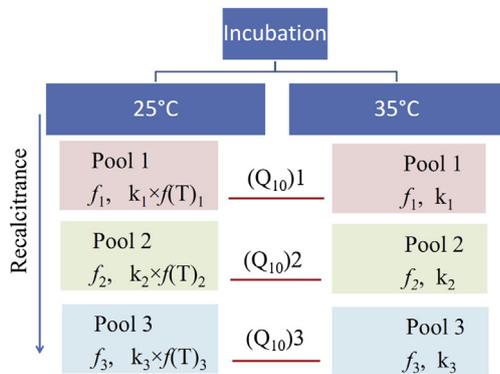


Fig. 1. A schematic diagram of the structure of the 3-pool model. Since 35 °C was used as the reference temperature in this study, the decomposition rates at 25 °C were obtained by multiplying the corresponding decomposition rates at 35 °C by temperature scale functions ($f(T)_i$, i denotes the i th pool). $f_3 = 1 - (f_1 + f_2)$.

are needed and were estimated based on literature (Table 1). Since the decomposition rate constants k_i are temperature dependent, temperature scale functions (Eqn (2)) were used to connect decomposition rates between temperatures (Fig. 1). In the current study, the following temperature scale function was adopted (Rey and Jarvis, 2006):

$$f(T)_i = (Q_{10})_i^{(T-T_{ref})/10} \quad (2)$$

where T is the temperature other than reference temperature, T_{ref} is the reference temperature (here 35 °C), and $(Q_{10})_i$ represents the temperature sensitivity of C decomposition for i th C pool.

2.3. Data assimilation

We used the probabilistic inversion approach as used by Xu et al. (2006) to assimilate the dataset from Haddix et al. (2011) (including CO₂ emissions, initial total C concentration (mg C g⁻¹ soil), incubation temperatures (25 and 35 °C)). The probabilistic inversion is based on Bayes' theorem (Eqn (3)):

$$P(\theta|Z) \propto P(Z|\theta)P(\theta) \quad (3)$$

where the posterior probability distribution of parameters (θ), $P(\theta|Z)$, is obtained from *prior* knowledge represented by a *prior* probability distribution $P(\theta)$ and information in the data sets represented by a likelihood function $P(Z|\theta)$. The *prior* probability distribution function of the estimated parameters $P(\theta)$ was specified as the uniform distributions over a set of specific intervals (Table 1). The likelihood function $P(Z|\theta)$ was calculated with the assumption

Table 1
Parameters and Q_{10} s involved in the 3-pool model (Fig. 1).

Parameter	Description	Lower limit	Upper limit	Unit
f_1	Initial fraction of pool 1	0.1	30.0	%
f_2	Initial fraction of pool 2	5.0	80.0	%
k_1	Decomposition rate of pool 1 at 35 °C	1.0×10^{-3}	5.0×10^{-2}	mg C mg ⁻¹ C d ⁻¹
k_2	Decomposition rate of pool 2 at 35 °C	1.0×10^{-4}	3.0×10^{-3}	mg C mg ⁻¹ C d ⁻¹
k_3	Decomposition rate of pool 3 at 35 °C	1.0×10^{-7}	2.0×10^{-4}	mg C mg ⁻¹ C d ⁻¹
$(Q_{10})_1$	Q_{10} for pool 1	0.5	10.0	—
$(Q_{10})_2$	Q_{10} for pool 2	0.5	10.0	—
$(Q_{10})_3$	Q_{10} for pool 3	0.5	10.0	—

that each component is Gaussian and independently distributed according to the following equation (Eqn (4)):

$$P(Z|\theta) \propto \exp \left\{ -\frac{1}{2\sigma^2} \sum_{t \in \text{obs}(Z_i)} [Z_i(t) - X_i(t)]^2 \right\} \quad (4)$$

where, $Z(t)$ is data obtained from measurement, $X(t)$ is simulated value and σ is the observed standard deviation of measurements.

The probabilistic inversion was performed using a Metropolis-Hastings algorithm (M–H algorithm, thereafter) to construct posterior probability density functions of parameters. The detailed description of the M–H algorithm was provided by Xu et al. (2006) with a brief summary here. The M–H algorithm samples random variables in high-dimensional probability density functions in the parameter space via a sampling procedure based on Markov chain Monte Carlo (MCMC) theorems (Gelfand and Smith, 1990; Hastings, 1970; Metropolis et al., 1953). In brief, the M–H algorithm was run by repeating two steps: a proposing step and a moving step. In each proposing step, the algorithm generated a new point θ^{new} for a parameter vector θ based on the previously accepted point θ^{old} with a proposal distribution $P(\theta^{\text{new}}|\theta^{\text{old}})$ (Eqn (5)).

$$\theta^{\text{new}} = \theta^{\text{old}} + r(\theta_{\text{max}} - \theta_{\text{min}})/D \quad (5)$$

where, θ_{max} and θ_{min} are the maximum and minimum values in the *prior* range of the given parameter. In this study, prior ranges of the parameters (Table 1) were obtained from literature (Haddix et al., 2011; Paul et al., 2006; Rey and Jarvis, 2006). r is a random variable between -0.5 and 0.5 with a uniform distribution. D controls the proposing step size. In each moving step, point θ^{new} was tested against the Metropolis criterion (Xu et al., 2006) to examine if it should be accepted or rejected. The accepted parameters were used to simulate cumulative CO₂ evolution during the same incubation period. The M–H algorithm then repeated the proposing and moving steps until approximately 40,000 sets of parameter values were accepted. All the accepted parameter values were used to construct posterior PDFs (Fig. 2, and Fig. S1).

3. Results

Among the eight target parameters, the initial C fractions were all well constrained (Fig. 2 and Fig. S1). Decomposition rates and Q_{10} s for pool 1 and pool 2 were mostly constrained, but those for pool 3 were mostly not well constrained. Overall most of the target parameters were constrained.

The total CO₂ emissions were partitioned into pool-specific emissions (Fig. 3a, b). Accordingly dynamics of individual C pools at each time point over the incubation period were estimated (Fig. 3c, d). The strong relationship ($R^2 > 0.99$, $P < 0.0001$) between observed and modeled CO₂ emissions showed that the model performed quite well (Fig. 3). Over the 588 days of incubation period, pool 1 was almost completely (98.3% on average) decomposed for most sites at the two temperatures. On average 28.8% of pool 2 and 1.5% of pool 3 were decomposed at 25 °C, while 55.0% of pool 2 and 4.2% of pool 3 were decomposed at 35 °C (Table 2).

The modeled initial fractions of pool 1 varied from 0.5% to 8.2% with an average of $4.7\% \pm 2.6\%$ (mean \pm standard deviation) of the total C pools (Table 3). The initial fractions of pool 2 and pool 3 on average accounted for $22.4\% \pm 16.1\%$ and $72.9\% \pm 17.6\%$, respectively, of the total initial C pools.

Since the decomposition rates of the three pools varied greatly among sites and land use types, there were substantial variations of MRTs (Table 3). MRTs varied between 0.05 and 0.60 years (with a mean of 0.19 ± 0.17 years) for pool 1, 0.49–8.16 years (2.71 ± 2.34

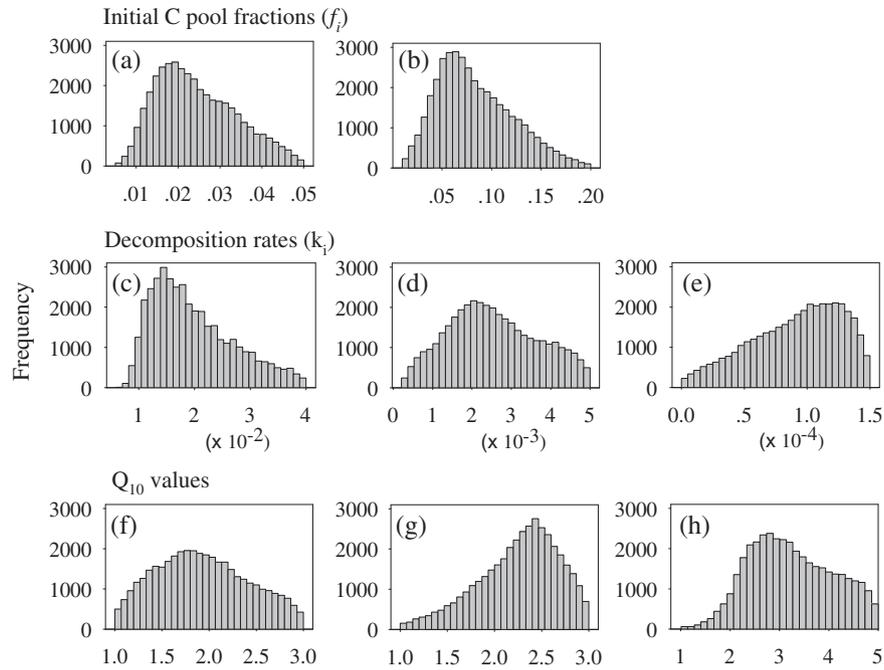


Fig. 2. Typical schematic of the posterior distributions of the free parameters and Q_{10} values. (a) and (b) denote f_1 and f_2 ; (c), (d) and (e) represent the decomposition rates of pool 1, pool 2 and pool 3, respectively; (f), (g) and (h) are Q_{10} values for pool 1, pool 2 and pool 3, respectively. Only the data from SK-C was presented as an example. The same below.

years) for pool 2, and 16.50–209.71 years (80.15 ± 61.14 years) for pool 3.

Q_{10} values varied substantially among soils, but generally increased from pool 1 to pool 3 for individual soils (Table 4). When

the data were pooled together, Q_{10} values ranged from 1.2 to 2.8 (1.9 ± 0.6 on average) for pool 1, 1.9 to 4.8 (2.8 ± 0.8 on average) for pool 2, and 2.4 to 7.5 (3.9 ± 1.4 on average) for pool 3. When Q_{10} values were plotted against MRT after the data were log-transformed (Fig. 4), Q_{10} for the three pools formed three clusters and increased linearly with MRT ($R^2 = 0.45$, $P < 0.0001$, $n = 36$). However, within each pool, there was no significant relationship between Q_{10} and MRT (Fig. 4).

4. Discussion

4.1. Model performance

Our approach directly constrained the initial fractions of pool 1 (f_1) and pool 2 (f_2), while the initial fraction of pool 3 (f_3) was estimated as the difference between total initial SOC fraction (=1) and the total initial fractions of pool 1 and pool 2. Therefore, whether the initial fraction of pool 3 could be well estimated or not depended on if pool 1 and pool 2 were constrained well. Since both f_1 and f_2 were well constrained, the initial fraction of pool 3 (f_3) could have been constrained as well.

The data assimilation approach used in the current study can also be called deconvolution analysis (Luo et al., 2001; Zhou et al., 2010). 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 (Luo et al., 2001; Zhou et al., 2010). In the current study, soil respiration during SOM decomposition is the decomposition product of different C fractions, which have distinctive response times (or residence times). However among the total soil respiration, only a very small portion was from the decomposition of pool 3 since on average only 1.5% (at 25 °C) and 4.2% (at 35 °C) of pool 3 were decomposed over the 588-day incubation period. Therefore, the signal which can be used to constrain the parameters related to the decomposition of pool 3 was relatively weak. For this reason, Q_{10} and decomposition rates

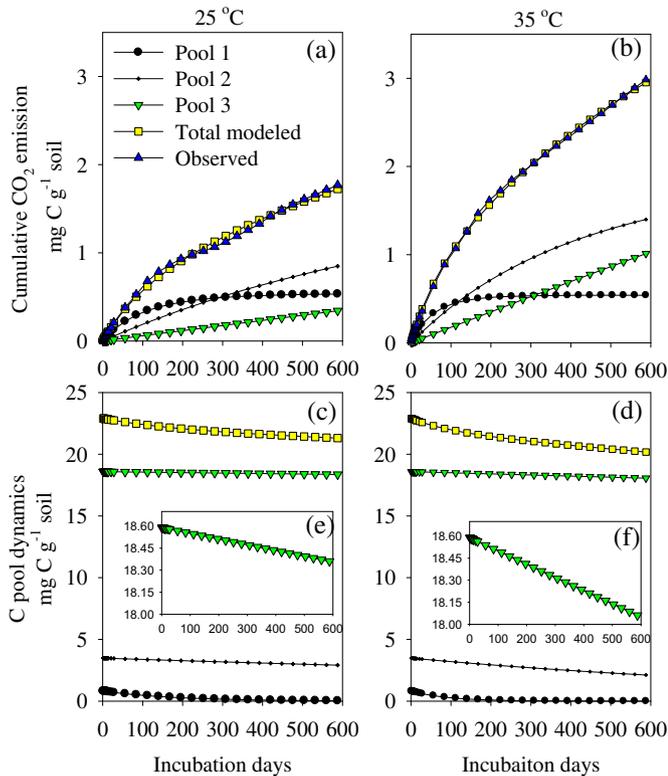


Fig. 3. Observed CO_2 emissions and modeled CO_2 emissions ((a) for 25 °C ($R^2 = 0.9976$, $P < 0.0001$); (b) for 35 °C ($R^2 = 0.9996$, $P < 0.0001$)), and dynamics of total C pool and individual C pools with time ((a) for 25 °C; (b) for 35 °C). R^2 and P values are for the relationship between modeled and observed total emissions. The inserted panels (e) and (f) show the dynamics of pool 3 with time.

Table 2

The fractions of C decomposed (%) during the incubation period for individual C pools modeled by the 3-pool model with fixed f_i . The fraction of C decomposed for each pool was calculated as the percentage of the difference between initial pool size and end pool size divided by the initial pool size.

	25 °C			35 °C		
	Pool 1	Pool 2	Pool 3	Pool 1	Pool 2	Pool 3
BR-NF	100.0	48.8	3.8	100	78.3	8.4
BR-P	100	25.2	0.4	100	52.5	1.8
CO-C	95.9	8.2	5.2	100	33.5	7.9
CO-NG	100	58.8	2.1	100	90.1	8.3
CR-NF	100	25.6	0.1	100	66.8	1.2
CR-P	100	50.2	0.1	100	95.4	1.1
ND-C	89.9	8.9	0.5	94	20.0	1.2
ND-NG	100	26.7	3.5	100	56.4	10.7
SK-C	96.0	16.4	1.2	99.8	39.2	2.8
SK-NG	99.4	4.3	0.1	99.8	11.0	0.4
TX-C	100	58.9	0.8	100	83.2	5.3
TX-NG	99.4	13.6	0.4	100	33.4	0.8

SK, Saskatchewan; ND, North Dakota; CO, Colorado; TX, Texas; CR, Costa Rica; BR, Brazil. NF, NG, P and C represent native forest, native grassland, pasture and cultivated land, respectively.

for pool 3 were mostly not well constrained. This is also consistent with other studies which showed that the decomposition rate of the most recalcitrant pool could not be well constrained (Weng and Luo, 2011).

From the range of MRTs, it was evident that only the parameters were constrained in associate with the “active pool” (with MRT < 5 years) and “intermediate pool” (with MRT from less than 10 to more than 100 years) as presented in the CENTURY model (Parton et al., 1987). In spite of the limitation that parameters related to the very old C fractions could not be constrained, our study provided an alternative to estimate the MRTs for SOC fractions cycling from yearly through decades and up to centennial timescales. Radiocarbon (^{14}C) has been widely used and proven useful to estimate MRT of soil C fractions; however, limitations are also involved in using this method. For example, the radiocarbon age of soil C is not necessarily indicative of biochemical stability (Rethemeyer et al., 2004), since plant residues arrive in the soil with different ages (years for leaves, centuries for tree stems) so that the radiocarbon age of SOC is not merely a measure of the time period organic matter spends in soils, which may bias interpretations of its stability (Trumbore, 2009).

4.2. Temperature sensitivity of SOC decomposition

On the basis of fundamental principles of enzyme kinetics associated with the Arrhenius equation (Bosatta and Ågren, 1999),

Table 4

Maximum likelihood estimates (MLEs, or means when unconstrained) of Q_{10} values. Values are presented as MLEs or mean \pm standard deviation (SD).

Site	Pool 1	Pool 2	Pool 3
BR-NF	2.7 \pm 0.3	1.9 \pm 0.2	3.5 \pm 0.8
BR-P	2.8 \pm 0.6	3.1 \pm 0.2	3.5 \pm 0.8
CO-C	2.8 \pm 0.7	2.9 \pm 0.6	4.2 \pm 1.7
CO-NG	1.9 \pm 0.6	2.8 \pm 0.6	3.0 \pm 1.3
CR-NF	1.4 \pm 0.4	4.1 \pm 0.3	5.4 \pm 2.5
CR-P	1.4 \pm 0.3	4.8 \pm 0.2	7.5 \pm 1.5
ND-C	1.2 \pm 0.1	2.2 \pm 0.2	2.4 \pm 0.3
ND-NG	2.0 \pm 0.5	2.3 \pm 0.5	3.4 \pm 0.7
SK-C	1.9 \pm 0.5	2.3 \pm 0.4	3.1 \pm 0.9
SK-NG	1.3 \pm 0.2	2.1 \pm 0.2	2.9 \pm 1.1
TX-C	1.5 \pm 0.3	2.4 \pm 0.3	4.6 \pm 2.7
TX-NG	1.7 \pm 0.2	2.9 \pm 0.3	3.3 \pm 1.4

the C-quality temperature (CQT) hypothesis predicts that the temperature sensitivity of microbial decomposition should increase with increasing activation energy (E_a) of a reaction; and hence the enzymatic decomposition of biochemically recalcitrant substrates, which require high activation energy to degrade, generally should be more sensitive to changes in temperature than the decomposition of more labile substrates (Craine et al., 2010). The pattern observed in our study, i.e., Q_{10} increased with MRT, consistent with the CQT hypothesis.

Previous studies have reported that the more resistant or older SOC fractions were more, less or equally sensitive relative to those of more labile or young SOC pools (Conant et al., 2011, 2008; von Lützow and Kögel-Knabner, 2009). This apparent discrepancy may have been caused by inappropriate approaches adopted or data interpretation (Hopkins et al., 2012; Karhu et al., 2010). The differential depletion of labile versus more resistant SOC fractions under different temperature inherently reduces the apparent temperature sensitivity of labile soil C fraction while increasing the apparent temperature sensitivity of more resistant soil C fraction when Q_{10} values are calculated using total heterotrophic soil respiration for incubation experiments (Conant et al., 2010). Similar temperature sensitivity for young and old SOC fractions was reported in an incubation study of six months based on total heterotrophic soil respiration analysis (Fang et al., 2005). A recent study indicated that despite relatively similar Q_{10} values for total heterotrophic soil respiration, different SOC fractions may still have remarkably different Q_{10} values (Karhu et al., 2010). For some studies that used C-isotope labels in soil to infer temperature sensitivities of different ages of SOC fractions, the data interpretation is crucial. For example, Li et al. (2012) found that higher temperature sensitivity for C fraction of six decades old relative to very

Table 3

Maximum likelihood estimates (MLEs) of parameters (or means for unconstrained parameters) for the 3-pool model and the corresponding mean residence time (MRT). Values are presented as MLEs or mean \pm standard deviation (SD).

Sites	Initial pool fractions (%)		Decomposition rate (mg C mg ⁻¹ C d ⁻¹)			MRT (years)		
	f_1	f_2	$k_1 \times 10^{-2}$	$k_2 \times 10^{-3}$	$k_3 \times 10^{-5}$	Pool 1	Pool 2	Pool 3
BR-NF	7.3 \pm 3.7	44.7 \pm 18.6	0.6 \pm 0.3	0.5 \pm 0.2	2.6 \pm 1.4	0.46 \pm 0.24	5.51 \pm 2.41	104.81 \pm 54.15
BR-P	4.3 \pm 0.4	49.0 \pm 10.4	4.4 \pm 0.8	0.7 \pm 0.2	2.9 \pm 1.4	0.06 \pm 0.01	4.04 \pm 1.20	95.38 \pm 45.14
CO-C	6.1 \pm 1.6	20.5 \pm 8.3	1.7 \pm 0.5	1.6 \pm 0.8	12.7 \pm 5.1	0.16 \pm 0.05	1.71 \pm 0.86	21.57 \pm 8.72
CO-NG	6.1 \pm 1.6	23.6 \pm 6.7	1.9 \pm 0.5	2.7 \pm 1.0	14.5 \pm 6.5	0.14 \pm 0.04	1.03 \pm 0.37	18.95 \pm 8.57
CR-NF	1.0 \pm 0.2	11.9 \pm 1.6	4.1 \pm 0.7	2.0 \pm 0.4	1.3 \pm 0.7	0.07 \pm 0.01	1.38 \pm 0.25	209.71 \pm 110.71
CR-P	0.5 \pm 0.1	4.1 \pm 0.3	6.0 \pm 1.1	5.6 \pm 0.4	1.9 \pm 0.5	0.05 \pm 0.01	0.49 \pm 0.03	144.65 \pm 40.99
ND-C	7.7 \pm 0.9	8.8 \pm 3.6	0.5 \pm 0.1	0.6 \pm 0.5	2.1 \pm 1.8	0.60 \pm 0.07	4.33 \pm 3.20	129.41 \pm 107.55
ND-NG	2.8 \pm 0.6	7.5 \pm 4.6	2.2 \pm 0.7	1.8 \pm 1.1	16.6 \pm 4.9	0.12 \pm 0.04	1.57 \pm 1.02	16.5 \pm 4.87
SK-C	2.2 \pm 0.9	8.0 \pm 3.9	1.9 \pm 0.7	2.4 \pm 1.1	9.1 \pm 3.7	0.14 \pm 0.06	1.12 \pm 0.51	30.21 \pm 12.16
SK-NG	5.7 \pm 0.4	44.9 \pm 12.2	1.2 \pm 0.1	0.3 \pm 0.1	2.7 \pm 1.4	0.23 \pm 0.03	8.16 \pm 2.02	101.46 \pm 51.17
TX-C	4.7 \pm 0.7	16.6 \pm 2.7	3.0 \pm 0.7	3.6 \pm 0.8	7.9 \pm 3.7	0.09 \pm 0.02	0.76 \pm 0.18	34.84 \pm 16.40
TX-NG	8.1 \pm 1.0	29.2 \pm 8.1	1.6 \pm 0.2	1.2 \pm 0.4	5.1 \pm 2.4	0.18 \pm 0.02	2.38 \pm 0.80	54.25 \pm 26.25

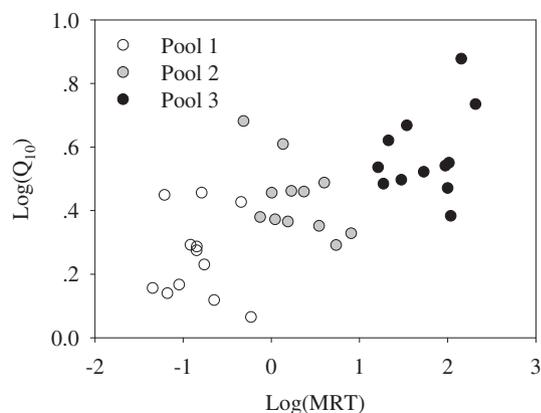


Fig. 4. Relationship between temperature sensitivities of SOC fractions and their corresponding MRTs. Both Q_{10} and MRT were log-transformed.

young C fraction. However, Conen et al. (2006) reported similar Q_{10} values for young and old SOC fractions by using the change in stable isotope composition in transitional systems from C_3 to C_4 vegetation. A possibility is that the C fraction with higher temperature sensitivity was categorized as younger C, so its response cannot be resolved from the temperature response of the majority of respiratory C substrate, resulting in equal apparent temperature sensitivity of the two age classes (Hopkins et al., 2012). This kind of issue was avoided by using distinctive age of SOC fractions and corresponding Q_{10} values in the present study.

The finding that the older C fractions were more temperature sensitive had significant implications for both climate-C cycle feedback and model development. Since the decades old C fraction accounted for a major portion of total soil C pool (Conant et al., 2011; Hopkins et al., 2012), higher temperature sensitivity of this C fraction implies that a major portion of soil C may become a source of atmospheric CO_2 under global warming in the 21st century. Currently, most models assume an acceleration of decay with temperature, however, these models adopted a constant Q_{10} of 2 or lower for all soil fractions, and some models even used higher Q_{10} for the fast turnover soil C fraction (Friedlingstein et al., 2006). Based on our study, the Q_{10} would be greater for the older C fractions.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.soilbio.2013.07.008>.

References

- Ågren, G.I., Bosatta, E., 2002. Reconciling differences in predictions of temperature response of soil organic matter. *Soil Biology & Biochemistry* 34, 129–132.
- Bosatta, E., Ågren, G.I., 1999. Soil organic matter quality interpreted thermodynamically. *Soil Biology & Biochemistry* 31, 1889–1891.
- Conant, R.T., Haddix, M., Paustian, K., 2010. Partitioning soil carbon responses to warming: model-derived guidance for data interpretation. *Soil Biology & Biochemistry* 42, 2034–2036.
- Conant, R.T., Ryan, M.G., Ågren, G.I., Birge, H.E., Davidson, E.A., Eliasson, P.E., Evans, S.E., Frey, S.D., Giardina, C.P., Hopkins, F.M., Hyvönen, R., Kirschbaum, M.U.F., Lavallee, J.M., Leifeld, J., Parton, W.J., Steinweg, J.M., Wallenstein, M.D., Wetterstedt, J.A.M., Bradford, M.A., 2011. Temperature and

soil organic matter decomposition rates – synthesis of current knowledge and a way forward. *Global Change Biology* 17, 3392–3404.

- Conant, R.T., Steinweg, J.M., Haddix, M.L., Paul, E.A., Plante, A.F., Six, J., 2008. Experimental warming shows that decomposition temperature sensitivity increases with soil organic matter recalcitrance. *Ecology* 89, 2384–2391.
- Conen, F., Leifeld, J., Seth, B., Alewell, C., 2006. Warming mineralises young and old soil carbon equally. *Biogeochemistry* 3, 515–519.
- Craine, J.M., Fierer, N., McLauchlan, K.K., 2010. Widespread coupling between the rate and temperature sensitivity of organic matter decay. *Nature Geoscience* 3, 854–857.
- Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440, 165–173.
- Fang, C., Smith, P., Moncrieff, J.B., Smith, J.U., 2005. Similar response of labile and resistant soil organic matter pools to changes in temperature. *Nature* 433, 57–59.
- Friedlingstein, P., Cox, P., Betts, R., Bopp, L., Von Bloh, W., Brovkin, V., Cadule, P., Doney, S., Eby, M., Fung, I., Bala, G., John, J., Jones, C., Joos, F., Kato, T., Kawamiya, M., Knorr, W., Lindsay, K., Matthews, H.D., Raddatz, T., Rayner, P., Reick, C., Roeckner, E., Schnitzler, K.G., Schnur, R., Strassmann, K., Weaver, A.J., Yoshikawa, C., Zeng, N., 2006. Climate-carbon cycle feedback analysis: results from the (CMIP)-M-4 model intercomparison. *Journal of Climate* 19, 3337–3353.
- Gelfand, A.E., Smith, A.F.M., 1990. Sampling-based approaches to calculating marginal densities. *Journal of the American Statistical Association* 85, 398–409.
- Haddix, M.L., Plante, A.F., Conant, R.T., Six, J., Steinweg, J.M., Magrini-Bair, K., Drijber, R.A., Morris, S.J., Paul, E.A., 2011. The role of soil characteristics on temperature sensitivity of soil organic matter. *Soil Science Society of America Journal* 75, 56–68.
- Hartley, I.P., Ineson, P., 2008. Substrate quality and the temperature sensitivity of soil organic matter decomposition. *Soil Biology & Biochemistry* 40, 1567–1574.
- Hastings, W.K., 1970. Monte Carlo sampling methods using Markov chain and their applications. *Biometrika* 57, 97–109.
- Hopkins, F.M., Torn, M.S., Trumbore, S.E., 2012. Warming accelerates decomposition of decades-old carbon in forest soils. *Proceedings of the National Academy of Sciences of the United States of America* 109, E1753–E1761.
- Karhu, K., Fritze, H., Hamalainen, K., Vanhala, P., Jungner, H., Oinonen, M., Sonninen, E., Tuomi, M., Spetz, P., Kitunen, V., Liski, J., 2010. Temperature sensitivity of soil carbon fractions in boreal forest soil. *Ecology* 91, 370–376.
- Lal, R., 2004. Soil carbon sequestration to mitigate climate change. *Geoderma* 123, 1–22.
- Li, J., Ziegler, S., Lane, C.S., Billings, S.A., 2012. Warming-enhanced preferential microbial mineralization of humified boreal forest soil organic matter: interpretation of soil profiles along a climate transect using laboratory incubations. *Journal of Geophysical Research* 117, G02008.
- Luo, Y., Ogle, K., Tucker, C., Fei, S., Gao, C., LaDeau, S., Clark, J.S., Schimel, D.S., 2011. Ecological forecasting and data assimilation in a data-rich era. *Ecological Applications* 21, 1429–1442.
- Luo, Y.Q., Wu, L.H., Andrews, J.A., White, L., Matamala, R., Schäfer, K.V.R., Schlesinger, W.H., 2001. Elevated CO_2 differentiates ecosystem carbon processes: deconvolution analysis of Duke Forest FACE data. *Ecological Monographs* 71, 357–376.
- Metropolis, N., Rosenbluth, A.W., Rosenbluth, M.N., Teller, A.H., Teller, E., 1953. Equation of state calculation by fast computer machines. *Journal of Chemical Physics* 21, 1087–1092.
- Parton, W.J., Schimel, D.S., Cole, C.V., Ojima, D.S., 1987. Analysis of factors controlling soil organic-matter levels in great-plains grasslands. *Soil Science Society of America Journal* 51, 1173–1179.
- Paul, E.A., Morris, S.J., Conant, R.T., Plante, A.F., 2006. Does the acid hydrolysis-incubation method measure meaningful soil organic carbon pools? *Soil Science Society of America Journal* 70, 1023–1035.
- Rethemeyer, J., Kramer, C., Gleixner, G., Wiesenberg, G.L.B., Schwark, L., Andersen, N., Nadeau, M.J., Grootes, P.M., 2004. Complexity of soil organic matter: AMS C-14 analysis of soil lipid fractions and individual compounds. *Radiocarbon* 46, 465–473.
- Rey, A., Jarvis, P., 2006. Modelling the effect of temperature on carbon mineralization rates across a network of European forest sites (FORCAST). *Global Change Biology* 12, 1894–1908.
- Schädel, C., Luo, Y., Evans, R.D., Fei, S., Schaeffer, S.M., 2013. Separating soil CO_2 efflux into C-pool-specific decay rates via inverse analysis of soil incubation data. *Oecologia* 171, 721–732.
- Setia, R., Smith, P., Marschner, P., Baldock, J., Chittleborough, D., Smith, J., 2011. Introducing a decomposition rate modifier in the Rothamsted carbon model to predict soil organic carbon stocks in saline soils. *Environmental Science & Technology* 45, 6396–6403.
- Sierra, C., 2012. Temperature sensitivity of organic matter decomposition in the Arrhenius equation: some theoretical considerations. *Biogeochemistry* 18, 1–15.
- Trumbore, S., 2009. Radiocarbon and soil carbon dynamics. *Annual Review of Earth and Planetary Sciences*, 47–66.
- von Lützw, M., Kögel-Knabner, I., 2009. Temperature sensitivity of soil organic matter decomposition—what do we know? *Biology and Fertility of Soils* 46, 1–15.
- Weng, E., Luo, Y., 2011. Relative information contributions of model vs. data to short- and long-term forecasts of forest carbon dynamics. *Ecological Applications* 21, 1490–1505.
- Wynn, J.C., Bird, M.I., 2007. C_4 -derived soil organic carbon decomposes faster than its C_3 counterpart in mixed C_3/C_4 soils. *Global Change Biology* 13, 2206–2217.

- Xu, T., White, L., Hui, D.F., Luo, Y.Q., 2006. Probabilistic inversion of a terrestrial ecosystem model: analysis of uncertainty in parameter estimation and model prediction. *Global Biogeochemical Cycles* 20, GB2007. <http://dx.doi.org/10.1029/2005gb002468>.
- Zhou, T., Luo, Y., 2008. Spatial patterns of ecosystem carbon residence time and NPP-driven carbon uptake in the conterminous United States. *Global Biogeochemical Cycles* 22, Gb3032. <http://dx.doi.org/10.1029/2007gb002939>.
- Zhou, T., Shi, P., Hui, D., Luo, Y., 2009. Global pattern of temperature sensitivity of soil heterotrophic respiration (Q_{10}) and its implications for carbon-climate feedback. *Journal of Geophysical Research* 114, G02016. <http://dx.doi.org/10.1029/2008jg000850>.
- Zhou, X., Luo, Y., Gao, C., Verburg, P.S.J., Arnone III, J.A., Darrrouzet-Nardi, A., Schimel, D.S., 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.