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Temperature sensitivity of soil organic carbon decomposition increased with mean carbon residence time: Field incubation and data assimilation

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Abstract

Temperature sensitivity of soil organic carbon (SOC) decomposition is one of the major uncertainties in predicting climate-carbon (C) cycle feedback. Results from previous studies are highly contradictory with old soil C decomposition being more, similarly, or less sensitive to temperature than decomposition of young fractions. The contradictory results are partly from difficulties in distinguishing old from young SOC and their changes over time in the experiments with or without isotopic techniques. In this study, we have conducted a long-term field incubation experiment with deep soil collars (0–70 cm in depth, 10 cm in diameter of PVC tubes) for excluding root C input to examine apparent temperature sensitivity of SOC decomposition under ambient and warming treatments from 2002 to 2008. The data from the experiment were infused into a multi-pool soil C model to estimate intrinsic temperature sensitivity of SOC decomposition and C residence times of three SOC fractions (i.e., active, slow, and passive) using a data assimilation (DA) technique. As active SOC with the short C residence time was progressively depleted in the deep soil collars under both ambient and warming treatments, the residences times of the whole SOC became longer over time. Concomitantly, the estimated apparent and intrinsic temperature sensitivity of SOC decomposition also became gradually higher over time as more than 50% of active SOC was depleted. Thus, the temperature sensitivity of soil C decomposition in deep soil collars was positively correlated with the mean C residence times. However, the regression slope of the temperature sensitivity against the residence time was lower under the warming treatment than under ambient temperature, indicating that other processes also regulated temperature sensitivity of SOC decomposition. These results indicate that old SOC decomposition is more sensitive to temperature than young components, making the old C more vulnerable to future warmer climate.

KEYWORDS
C turnover time, data assimilation, field incubation, soil organic carbon decomposition, warming

1 | INTRODUCTION

The world's soils hold 2,344 gigatons of carbon (Gt C) at depths of up to 3 m, which is more than plant biomass and the atmosphere combined (Jobbagy & Jackson, 2000). This major pool of organic carbon (C) in soil is very sensitive to climate change (Davidson & Janssens, 2006; Schmidt et al., 2011). Small changes in decomposition rates of soil organic carbon (SOC) could have significant impact on the atmospheric CO_2 concentration (Davidson & Janssens, 2006; Luo & Zhou, 2006), which may significantly exacerbate or ameliorate the consequences of fossil fuel combustion and land use change. A warming climate can substantially impact soil C dynamics (Bond-Lamberty & Thomson, 2010; Luo, Wan, Hui, & Wallace, 2001; Walker et al., 2006), and then influence the stewardship of ecosystem services provided by soil and socioeconomic systems (Su & Fu, 2013; Traill, Lim, Sodhi, & Bradshaw, 2010). The warming-induced changes in soil C storage may lead to a positive or negative feedback to climate warming, which amplify or diminish warming effects (e.g., Arora et al., 2013; Friedlingstein et al., 2006; Heimann & Reichstein, 2008). Understanding the mechanisms governing responses of SOC decomposition (e.g., young and old C pools) to climate warming is crucial for predicting future atmospheric CO_2 concentrations.

The warming-induced effects on SOC decomposition have become one of the major concerns in predicting climate-C cycle feedback. However, the predictions from global coupled climate-C cycle models differ remarkably in the magnitude and even the direction of soil C responses to warming (Arora et al., 2013; Cox, Betts, Jones, Spall, & Totterdell, 2000; Friedlingstein et al., 2006). These differences partly reflect the uncertainties inherent in how models parameterize temperature dependence of soil C decomposition, commonly referred to as Q_{10}, which is a relative increase in soil C decomposition rate for a 10°C increase in temperature. Usually, Earth system models assume that all soil C fractions react similarly to climate warming, independent of SOC stability, which is the persistence in soil due to the recalcitrance of molecular structure, physicochemical and biologic protection, and environmental constraints (Cox et al., 2000; Friedlingstein et al., 2006; Schmidt et al., 2011). Since soil hold large old C pools (50%–90%) with long residence times from decades to centuries (Schmidt et al., 2011; Trumbore, 1997), their temperature sensitivity will largely determine the global pattern and magnitude of the predicted future soil C stock in the long term.

The traditional knowledge from the past decades has shown that the chemical recalcitrance of organic compounds often determined the C residence time of SOM in soil (Bosatta & Ågren, 1999; Davidson & Janssens, 2006) although a more inclusive view has recently attributed it to biotic and abiotic protections (Bradford et al., 2016; Schmidt et al., 2011). However, evidence from soil incubations and warming experiments with or without isotopic techniques as well as near-infrared spectroscopy and modeling approaches has paradoxically concluded that the decomposition of soil old C is more (Cheng et al., 2017; Conant, Drijber, et al., 2008; Hopkins, Torn, & Trumbore, 2012; Knorr, Prentice, House, & Holland, 2005), similarly (Conen, Leifeld, Seth, & Alewell, 2006; Giardina & Ryan, 2000; Hicks Pries, Castanha, Porras, & Torn, 2017), or less (Bradford et al., 2008; Liski, Ilvesniemi, Makela, & Westman, 1999) sensitive to temperature than that of young components with short residence times. The contradictory results are partly due to difficulties in distinguishing old from young SOC. Among the studies, the majority are short-term laboratory incubation with ^{13}C or ^{14}C isotopic techniques from months to a couple of years with disturbed soil by sieving and mixing. The results may not be comparable to soil C decomposition in situ. The incubation experiments may not permit a clear delineation of old from young SOC and quantification of their changes over time (Conant, Steinweg, et al., 2008; Davidson & Janssens, 2006; Giardina & Ryan, 2000; Hopkins et al., 2012; Schmidt et al., 2011). Thus, how soil young and old C decomposition responds to temperature over the long term is largely unknown, especially under the field conditions.

To examine long-term responses of soil young and old C decomposition to temperature, we derived a novel approach, which combined a long-term field incubation experiment with data assimilation (DC) technique under ambient temperature and warming treatments. The long-term field warming experiment has been conducted in a tallgrass prairie in central Oklahoma, USA to examine warming effects on SOC decomposition over time. To quantify relative changes in various SOC fractions with different C residence times (e.g., active, slow, and passive pools) in the deep collars, we also applied the DC analysis with Bayesian probability inversion and a Markov chain Monte Carlo (MCMC) techniques to a terrestrial ecosystem model (TECO), which has been extensively applied to C cycle research through integration of experimental data with models (Luo et al., 2003; Weng & Luo, 2011; Zhou et al., 2010). Based on recent studies, we hypothesized that decomposition of old SOC is more sensitive to temperature than that of young components under both ambient and warming treatments.

2 | MATERIALS AND METHODS

2.1 | Experimental site, design, and warming facility

The study was conducted at the Kessler's Farm Field Laboratory (KFFL) in McClain County, Oklahoma (34°59′N, 97°31′W), approximately 40 km from Norman campus of the University of Oklahoma, USA. The experimental site is an old-field tallgrass prairie abandoned from agriculture 30 years ago and without grazing during the past 20 years. The grassland is dominated by three C_4 grasses: *Sorghastrum nutans*, *Andropogon gerardii*, and *Panicum virgatum*; and two C_3 forbs: *Ambrosia psilotachyia* and *Xanthocephalum texanum*. Mean annual temperature is 16.3°C with monthly mean temperature of 3.1°C in January and 28.0°C in July. Mean annual precipitation is 914 mm (averaged value from 1948 to 1998 from Oklahoma Climatological Survey). Annual precipitation showed the large variation for the study period with a range of 515–1,306 mm from 2002 to 2008 (Figure 2a,b). The soil belongs to the Nash–Lucien complex characterized by deep and moderately penetrable root zone, high available water holding capacity, and a neutral pH (USDA 1979). The rooting depth is around 60 cm according to our own data from ingrowth cores.

The experiment used a paired factorial design with warming as the main factor nested by clipping factor. Each treatment had six replicates (i.e., six pairs). Each pair had two plots of 2 × 2 m. One plot had been subjected to continuous warming since 21 November 1999, whereas the other was the control with ambient temperature. A single infrared heater (165 cm × 15 cm) having a radiation output of 100 W/m^2 (Kalglo Electronics Inc, Bethlehem, Pennsylvania, USA) was suspended 1.5 m above the ground in each warmed plot. The heating is on year around, 24 hr per day and 365 days per year in the field. The control plot had a "dummy" heater with same dimensions as the infrared heater suspended at a similar height to mimic the shading effects of the heater.

Each 2 m × 2 m plot was divided into four 1 m × 1 m subplots. Plants in two diagonal subplots were clipped at a height of 10 cm above the ground once a year to mimic hay harvesting, whereas the other two subplots were unclipped. With this experimental setup, we had four treatments: unclipping and control (ambient) temperature (UC), unclipping and warming (UW), clipping and control temperature (CC), and clipping and warming (CW). Since this study focused on temperature sensitivity of SOC decomposition and their warming effects, we only present the results in control and warmed plots (i.e., ambient temperature and warming treatments, respectively) under unclipped subplots and clipped subplots were not relevant for this study.

2.2 | Measurement protocols

2.2.1 | Soil temperature, moisture, and precipitation measurement

Soil temperature was monitored at the depth of 5 cm adjacent to each PVC collar at the time of soil respiration and soil C decomposition measurement using a thermocouple connected to a LI-6400 portable IRGA. At the same time, soil moisture content was also measured volumetrically using manual Time Domain Reflectometry (TDR) equipment (Soilmoisture Equipment Corp., Santa Barbara, California, USA) at the depth interval of 0–15 cm adjacent to each PVC collar. Precipitation was recorded at an Oklahoma Mesonet Station located about 200 meters away from the experimental site. We also occasionally measured soil moisture in deep PVC tubes.

2.2.2 | Soil respiration and SOC decomposition

Soil respiration (*Rs*) represents CO_2 release at the soil surface from microbial respiration during organic matter decomposition (i.e., SOC decomposition or microbial respiration) and rhizosphere respiration by live roots and their symbionts (root respiration, i.e., Zhou, Sherry, An, Wallace, & Luo, 2006; Bradford et al., 2008; Conant et al., 2011). To measure *Rs* (including SOC decomposition and rhizosphere respiration), PVC collars (referred to as the shallow collars, 5 cm depth) were inserted 2–3 cm into the soil permanently at the center of each subplot. Soil respiration was measured once or twice a month between 10:00 and 15:00 (local time), using a LI-COR 6400 portable photosynthesis system attached to a 6400-09 soil CO_2 flux chamber (LI-COR. Inc., Lincoln, Nebraska, USA). In October 2001, we installed deep soil collars (10 cm in diameter and 70 cm in depth of PVC tubes) at each plot to incubate soil under ambient and warming treatments. The 70-cm-long soil collars cutoff old plant roots and prevented new roots from growing inside the tubes. Our own data from ingrowth cores showed that roots in the system were very rare below 60 cm. The measurement time and frequency of SOC decomposition (i.e., microbial respiration) are same as those of *Rs*. The measurements of CO_2 efflux above these PVC tubes began immediately after installation to examine the transient response of dead root decomposition. After a specific period (5 months) when most of severed dead roots were decomposed, CO_2 efflux measured above those PVC tubes represents SOC decomposition. Using this approach, some confounding factors (e.g., root exudates, soil moisture, and microbial community) may affect the results of SOC decomposition to some degree. However, our analysis and results from other studies indicate that effects of experimental warming on soil physical properties, soil chemistry, and other soil characteristics are not substantial (Wan, Yuan, et al., 2002; Xu et al., 2010; Xue, Luo, Zhou, Sherry, & Jia, 2011). As a consequence, the confounding effects of these factors on Q_{10} values should be small. It is expected that microbial community may change in deep collars over time compared to intact soil because microbial species composition is sensitive to substrate supply (Cheng et al., 2017). However, changes in SOC decomposition and temperature sensitivity may largely result from altered microbial species composition, which is a major topic under way.

Apparent temperature sensitivity of SOC decomposition (Q_{10}) was estimated by fitting seasonal data of temperature and SOC decomposition rates to an exponential function $R_h = ae^{bT}$ for each year from 2002 to 2008 (Arrhenius, 1889), where R_h is soil C decomposition rate in the deep soil collars, coefficient *a* is the intercept of soil C decomposition when temperature is zero, and *b* is temperature response coefficient to estimate the temperature sensitivity by $Q_{10} = e^{10b}$.

Annual soil respiration and SOC decomposition for each treatment were estimated by summing the products of monthly mean soil respiration and SOC decomposition and the number of days between samples. It was corrected further for diurnal patterns in fluxes. Our measurements, collected between 10:00 and 15:00, were assumed to represent daytime averages based on diurnal patterns in the shallow and deep collars measured on Jun 28, 2004 (Data not shown). The calculated average daily efflux was 96.5% of the observed daytime average. The corrected daily flux was then multiplied by the number of days between measurements to compute the cumulative flux over the period (Bremer, Ham, Owensby, & Knapp, 1998).

2.2.3 | Soil C content

Soil samples were taken from deep collars and outsides in 2009. Soil C content was measured with a Shimadzu TC analyzer (Shimadzu Corporation, Kyoto, Japan) at Oklahoma State University, after carbonates were removed by 1N HCl for 24 h at room temperature.

2.2.4 | Soil ^{14}C isotopic data

CO_2 sampling was carried out within an air-tight PVC collar in each subplot from April 27 to 29, 2010. The collars were made from PVC pipe with a diameter of 5 in. It was constructed using a plastic Petri dish (15 cm in diameter) as a lid (top collar). The Petri dish was attached by silicone to create a permanent air-tight seal. 30 ml vials containing 4 ml of 0.25 M NaOH was placed on the ground surface at each bottom collar. The lid of the vial was removed and the top collar was placed over the ground collar. Vacuum grease was used to create a temporary air-tight seal between the ground and top collars and a hose clamp was used to keep the two collars from separating. Control vials were placed between the control and warming plots on a Petri dish with a top collar over it. Vacuum grease was used to seal the top collar to the Petri dish. After approximately 48 hr, the top PVC collar was removed and the lid was placed on each vial. The vials were then brought back to the laboratory. One milliliter solution was taken out of each vial to determine the amount to CO_2 absorbed by titration. To make sure that all NaOH had reacted with CO_2 to keep pH ≈ 7 for the ^{14}C measurement, the lids of the vials were removed to allow the solution to trap atmospheric CO_2 for 5 days. After 5 days, 0.1 ml solution was taken out of each vial into a conical flask with phenolphthalein solution (Levin, Hammer, Kromer, & Meinhardt, 2008). Samples were then oven-dried at 80°C for 48 hr. Samples (about 22 mg) were stored in the mini-centrifuge tubes for ^{14}C analyses. ^{14}C measurements were done by Accelerator Mass Spectrometry (AMS, National Electrostatics Corporation, Middleton, WI) at the University of Arizona, Tucson, AZ. Controls were used to absorb atmospheric CO_2 with ^{14}C compared with those under treatments. C age was calculated based on Levin et al. (2008). We excluded the impact of atmospheric CO_2 on C age according to titration results. The comparison between control with atmospheric CO_2 from the laboratory and the treatments in the field with CO_2 efflux from soil and atmospheric CO_2 from the laboratory may offset the effects of atmospheric CO_2.

2.3 | Model description and parameter estimation

2.3.1 | Model description

To quantify relative changes in various SOC fractions (i.e., active, slow, and passive) and their residence times in the deep collars, the modified terrestrial ecosystem (TECO) model with a 5-pool compartmental structure was used (Figure 1), which has been extensively applied to C cycle research through integration of experimental data with models (Luo et al., 2003; Weng & Luo, 2011; Zhou et al., 2010). Although plants were excluded in the deep collar, they grew outside the collar and litter dropped into the deep collars and then became soil C content. Specifically, C enters the ecosystem via canopy photosynthesis and is partitioned into shoots (root excluded). Dead shoot materials are transferred to litter, and are decomposed by microbes. Part of the litter C is respired and the remainder is converted into slow and passive soil C pools. C transfer coefficients are rate constants that determine 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 is represented by the following first-order ordinary differential equation:

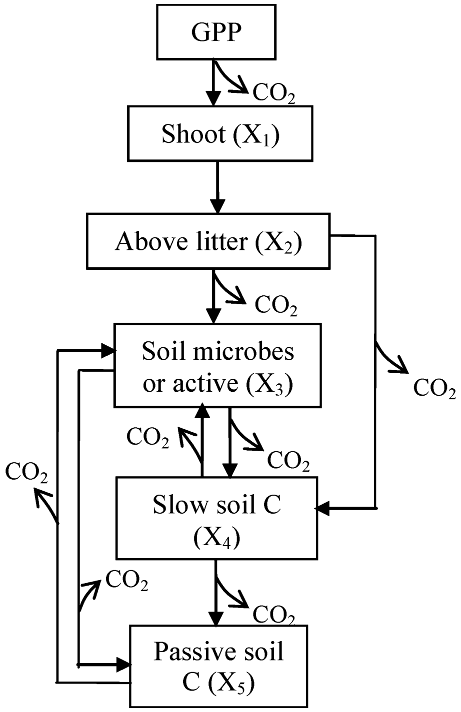

FIGURE 1 Carbon pools and pathways of C flux for deep-tubes soil C decomposition in the modified terrestrial ecosystem model

TABLE 1 Description of carbon (C) transfer coefficients among C pools and temperature sensitivity of soil C decomposition (Q_{10}) in field incubation of 70-cm deep soil collars shown in Figure 3

Parameters	Intervals	Description
c_1	5.00×10^{-4}–7.07×10^{-3}	From pool "shoots" (X_1) to pools "aboveground litter" (X_2)
c_2	5.48×10^{-4}–5.28×10^{-3}	From pool "aboveground litter" (X_2) to pools "soil microbes" (X_3) and slow soil C" (X_4)
c_3	2.80×10^{-4}–4.25×10^{-3}	From pool "soil microbes or active" (X_3) to pools "slow soil C" (X_4) and "passive soil C" (X_5)
c_4	3.28×10^{-5}–3.19×10^{-4}	From pool "slow soil C" (X_4) to pools "soil microbes or active" (X_3) and "passive soil C" (X_5)
c_5	1.07×10^{-6}–3.24×10^{-5}	From pool "passive soil C" (X_5) to pool "soil microbes or active" (X_3)
Q_{10}	0.7–4.0	Intrinsic temperature sensitivity of SOC decomposition

Unit for c_i is g g^{-1} day^{-1}.

$$\begin{aligned}\frac{\mathrm{d}X(t)}{\mathrm{d}t} &= \xi(t)ACX(t) + BU(t)\\ X(0) &= X_0\end{aligned} \tag{1}$$

where $X(t) = (X_1(t), X_2(t), \ldots X_5(t))^{\mathrm{T}}$ is a 5 × 1 vector describing *C* pool sizes, *A* and *C* are 5 × 5 matrices given by

$$A = \begin{Bmatrix} -1 & 0 & 0 & 0 & 0\\ 1 & -1 & 0 & 0 & 0\\ 0 & 0.40 & -1 & 0.42 & 0.45\\ 0 & 0.05 & 0.296 & -1 & 0\\ 0 & 0 & 0.004 & 0.03 & -1 \end{Bmatrix} \tag{2}$$
$$C = \mathrm{diag}(c)$$

where a_{ij} in *A* matrix is *C* partitioning coefficients to different pools, diag (*c*) denotes a 5 × 5 diagonal matrix with diagonal entries given by vector $c = (c_1, c_2, \ldots, c_5)^{\mathrm{T}}$. Components c_i (i = 1, 2,… 5) represent *C* transfer coefficients associated with pools X_i (i = 1, 2, …, 5) (Table 1). $B = (0.25\ 0\ 0\ 0\ 0)^{\mathrm{T}}$ is a vector that partitions the photosynthetically fixed C to shoots (no roots in deep soil collars). *U*(.) is system input of photosynthetically fixed C given by a canopy photosynthetic model. X_0 = [110 106 107 1,531 998] represents an initial condition, estimated by the method used in Luo, Wu, et al.(2001) based on an initial steady-state C balance in the TECO model and experimental data at the start of this study. ξ(.) is a scaling function accounting for temperature and moisture effects on C decomposition: $\xi(.) = F_T F_W$. F_T describes temperature effects on plant respiration and decomposition of litter and SOC as $F_T = R_{10} \times Q_{10}^{(T-10)/10}$, where R_{10} is SOC decomposition rate at 10°C, Q_{10} represents the intrinsic temperature sensitivity of SOC decomposition. F_W represents the effects of soil water content (*W*) as follows:

$$F_W = \begin{cases} 1.0 - 5 \times (0.2 - W) & W < 0.2\\ 1 & W \geq 0.2 \end{cases} \tag{3}$$

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

$$R_H = \sum_{i=3}^{10} \left[\left(1 - \sum_{j=8}^{10} a_{j,i}\right) c_{i,i} X_i\right] \quad i = 3, 4, \ldots 10 \tag{4}$$

Equation (4) is called as a mapping function to match the modeling estimates with measurements.

In addition to soil C decomposition rates, we also infused aboveground biomass, litter mass, and soil C content described in Niu, Sherry, Zhou, Wan, and Luo (2010) to constrain C transfer coefficients (i.e., inverse of *C* residence time) and temperature sensitivity (Q_{10}) of SOC decomposition. The modified TECO model used gross primary productivity (GPP) as *C* input, which was given by a canopy photosynthetic model in ambient temperature and warming treatments (Weng & Luo, 2008). Pool-weighted mean residence times (MRTs) are calculated by proportion of active, slow, and passive pool sizes to total pool size and their respective MRT as below.

$$\begin{aligned}\text{Pool-weighted MRTs} = \frac{P_{\text{Labile}}}{P_{\text{Total}}} \times \text{MRT}_{\text{Labile}} + \frac{P_{\text{Slow}}}{P_{\text{Total}}} \times \text{MRT}_{\text{Slow}}\\ + \frac{P_{\text{Passive}}}{P_{\text{Total}}} \times \text{MRT}_{\text{Passive}}\end{aligned} \tag{5}$$

where P_{Total} is total pool size (i.e., $P_{\text{Active}} + P_{\text{Slow}} + P_{\text{Passive}}$), P_{Active}, P_{Slow}, and P_{Passive} are pool sizes of active, slow, and passive *C*, respectively, and $\text{MRT}_{\text{Active}}$, MRT_{Slow}, and $\text{MRT}_{\text{Passive}}$ are *C* residence times of active, slow, and passive *C*, respectively.

2.3.2 | Parameter estimation

A Bayesian probabilistic inversion approach was employed to optimize *C* transfer coefficients (c_i, i = 1, 2, …5) and temperature sensitivity of SOC decomposition (Q_{10}). A detailed description of the Bayes' theorem was given by McCarthy (2007), Xu, White, Hui, and Luo (2006), and Zhou et al. (2010) as well as Text S1. Here, we only provided a brief overview.

To apply Bayes' theorem, we first specified the prior probability density function (PDF) *p*(*c*) by giving a set of limiting intervals for parameters *c* with uniform distribution, 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 ($e(t)$).

$$p(Z|c) \propto \exp\left\{\frac{1}{2\sigma^2} \sum_{t \in \mathrm{obs}(Z_i)} [Z_i(t) - \varphi_i X(t)]^2\right\} \tag{6}$$

where constant σ^2 are the error variances of soil C decomposition, aboveground biomass, and litter mass, $Z_i(t)$ are the observed soil C decomposition rates, aboveground biomass, and litter mass at time t, $\varphi_i X(t)$ are the modeled values, which are a product of *X*(*t*) from Equation (1) and c from Equation (2). Then, with Bayes' theorem, the PPDF of parameters c is given by $p(c|Z) \propto p(Z|c)p(c)$. The Bayesian inversion model was coded by MATLAB 9.0 (The MathWorks Inc. Natick, MA, USA, Text S2).

2.4 | Statistical analysis

Repeated measured analysis of variance (ANOVA) was used to examine the statistical significance of warming on soil respiration and soil C decomposition. All statistical analyses were conducted using SAS software (SAS Institute Inc., Cary, NC, USA). Difference and interactions between the treatments were compared according to Duncan's multiple range test or Student's *t*-test at a probability level of 5%. The significant effects of warming on C transfer coefficients (c_i, i = 1, 2, …5) and slopes of the relationships were examined by a *t*-test method as described by Zhou et al. (2006).

3 | RESULTS

Experimental warming, on average, increased the daily mean air temperature by 1.1°C and daily mean soil temperature by 1.6°C, and decreased mean soil moisture by 5.4% from 2002 to 2008 (Figure 2c,d). Soil moisture at the deep collars was not significantly different from that near the collars (Figure 2e). Warming significantly

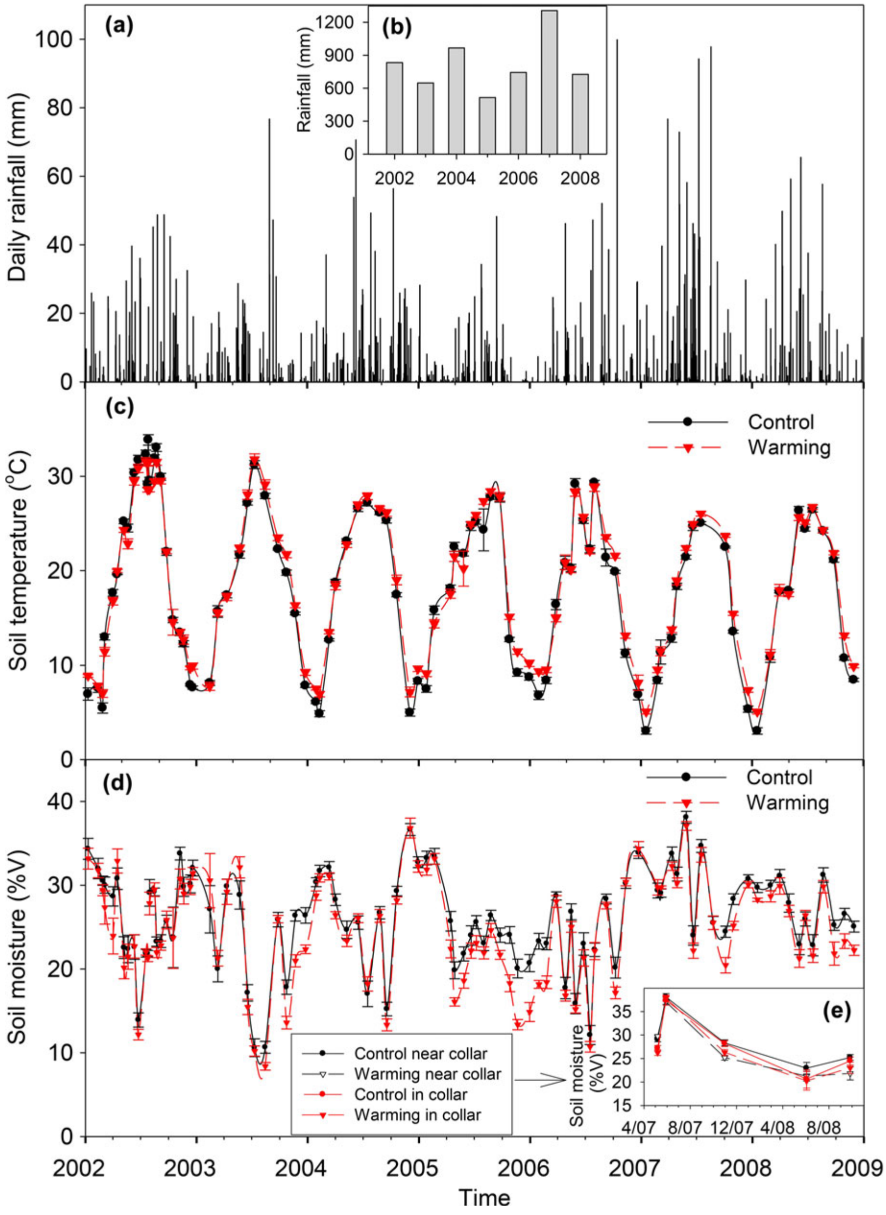

FIGURE 2 Daily (a) and annual (b, inserted figure) rainfall at the experimental site, and seasonal and inter-annual variability of soil temperature at the depth of 5 cm (c) and soil moisture of 0–15 cm (d) from 2002 to 2008 under control and warming treatments in the long-term warming experiment. Inserted panel e compared soil moisture near collar where we usually did with those in collar under control and warming in 2007 and 2008, showing non-significant effect. Vertical bars represent the standard error of the mean ($n = 6$)

increased soil carbon (C) decomposition from the deep collars (70 cm) and soil respiration from the shallow collars (5 cm) by 11.7% and 11.4%, respectively ($p < .05$, Figure 3), but occasionally decreased them during the summer drought (Figure 3a,b). Annual soil C decomposition rate from deep soil collars decreased linearly from 2002 to 2008 (Figure 4a) as did its percentage relative to annual soil respiration (Figure 4b), but annual soil respiration from the shallow collars did not show this trend (Figure 3b). Compared to those near the collars, SOC content in deep soil collars decreased by 14.8 ± 5.7% and 13.5 ± 5.2% at the depth of 15 cm in ambient temperature and warming treatments, respectively (Figure 4c). The ^{14}C isotope measurements of CO_2 efflux from soil showed that C ages of soil C decomposition in the deep collars were 23.03 ± 0.89 and 39.55 ± 0.74 years under the ambient temperature and the warming treatment, respectively, which were significantly higher compared to those near the collars with values of 4.29 ± 0.05) and 5.07 ± 0.43, respectively ($p < .05$, Figure 4d).

The posterior PDFs of parameters showed that all parameters were relatively well constrained by experimental data, except soil passive C pool (Figure S1). The modeled SOC decomposition rates agreed with the observed ones well (Figure S2). Our results from DC demonstrated that slow C and pool-weighted MRTs (i.e., fraction of each pool to total pool size × their respective MRT) increased linearly over years (Figure 5a,b), but MRTs of active and passive soil C pools did not show a significant trend from 2002 to 2008 (Figure 5c,d). The increased MRTs over time were supported by the increased C age from the ^{14}C isotope data in the deep collar compared to that in the shallow collar (Figure 4d).

The modeling analysis of soil C pools exhibited that the active soil C pool decreased significantly in the first 2 years and then remained a relatively low constant level (Figure 5g), while slow and passive C pools continuously declined over time (Figure 5e,f vs. Figure S3 from soil respiration data). Parallel increases in pool-weighted MRTs with the temperature sensitivity of soil C

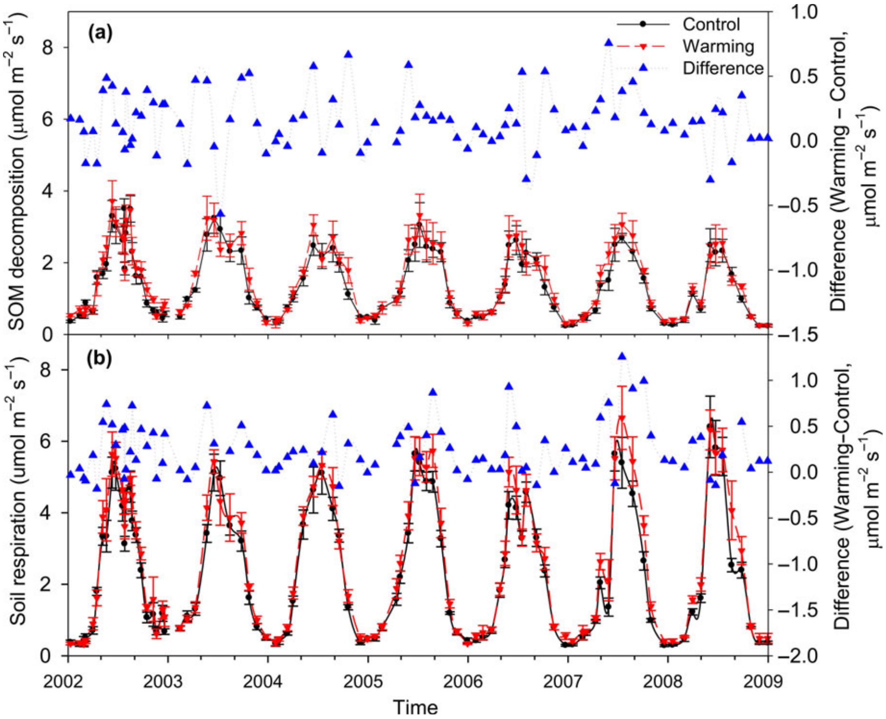

FIGURE 3 Seasonal and inter-annual variability of soil C decomposition (a, measurements of CO_2 efflux above 70 cm deep soil collars) and soil respiration (b, measurements of soil surface CO_2 efflux above the 5 cm shallow collars) from January 2002 to December 2008 under ambient and warming treatments in the long-term warming experiment. The dotted line with blue triangles represents the differences of soil C decomposition (a) and soil respiration (b) between warming and control from 2002 to 2008

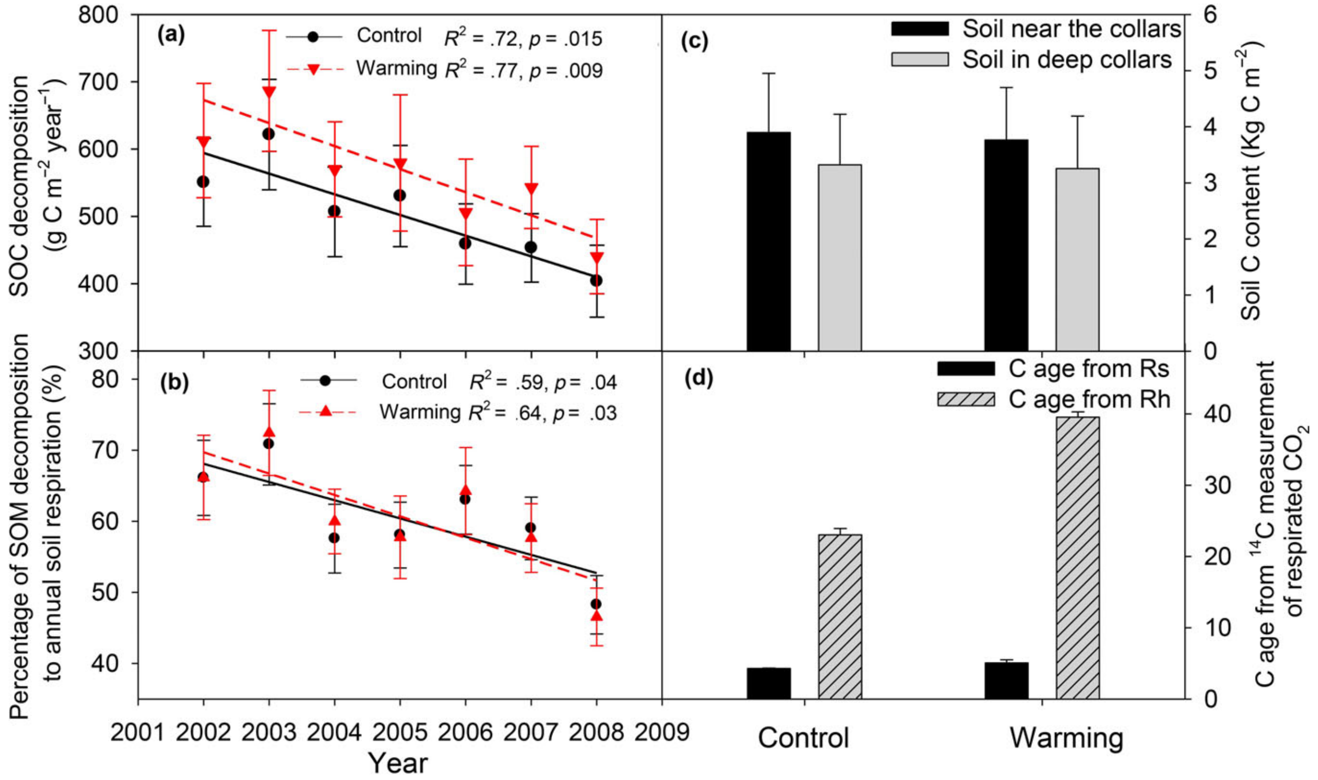

FIGURE 4 Annual soil C decomposition rates (a, measurements of CO_2 efflux above 70 cm deep soil collars) and percentage of soil C decomposition to annual soil respiration (b, measurements of soil surface CO_2 efflux above 5 cm shallow collars) from January 2002 to December 2008 under ambient and warming treatments in the long-term warming experiment. The results show that both soil C decomposition in deep collars and its percentage to soil respiration reduced over time, indicating the decreasing stock of soil organic C in the deep cores. Panels *c* and *d* show soil C content from direct measurements in shallow and deep collars (c) and C ages calculated from ^{14}C measurement of respired CO_2 from SOC decomposition and soil respiration (d) under ambient and warming treatments in 2008. Vertical bars represent the standard error (±*SE*) of the mean (n = 6 for soil C content, soil C decomposition, and percentage of soil C decomposition to annual soil respiration, and n = 3 for ^{14}C isotopic data due to expensive measurements). *Rs*—Soil respiration from the shallow collars, R_h—Soil C decomposition in the deep collars

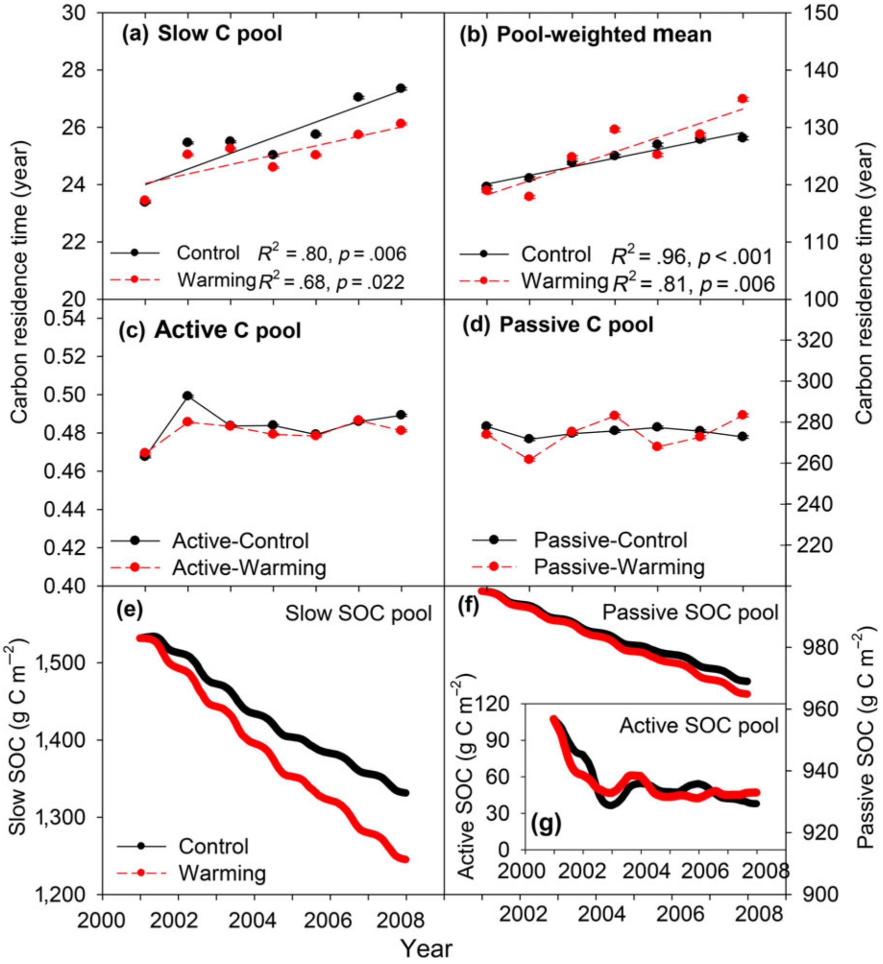

FIGURE 5 Mean residence time (MRT) of slow (a), pool-weighted mean (b), active (c), and passive (d) C pools from the data assimilation analysis for each year of data under ambient and warming treatments in a tallgrass prairie ecosystem. Panels *e* and *f* show changes in slow (e) and passive (f) C pools under ambient and warming treatments from January 2002 to December 2008. Inserted panel *g* shows changes in active soil organic carbon pool under ambient and warming treatments from 2002 to 2008. Pool-weighted mean MRT was calculated by proportion of active, slow, and passive C pool sizes to total pool size and their respective MRT. Slow and pool-weighted mean MRTs showed linear increase from 2002 to 2008. Active and passive MRTs did not show significant change over time. Vertical bars represent standard error (±*SE*) of 40,000 samples from Metropolis–Hastings simulation

decomposition over time (Figures 5 and 6b) caused linear relationships between them under both ambient and warming treatments (Figure 6c). The intrinsic temperature sensitivity of SOC decomposition from DC (Figure 6a) was relatively low compared to that from exponential function with measured SOC decomposition rates and soil temperature, but the trends were similar under both ambient temperature and warming treatments (Figure 6b). However, warming significantly decreased the slope of the relationships between the temperature sensitivity and SOC residence times in comparison with that under ambient temperature ($p < .05$, Figure 6). Therefore, all of these changes showed a conceptual framework in which soil C and its components (i.e., young and old fractions), temperature sensitivity of soil C, and C residence time changed over time as well as warming effects in the deep and shallow collars (Figure 7).

4 | DISCUSSION

Predicting ecosystem responses to warming and assessing the climate-C cycle feedback strongly relies on our understanding of the warming-induced effects on SOC decomposition, especially for this large pool of old soil organic matter (Bradford et al., 2016; Cox et al., 2000; Davidson et al., 2006; Friedlingstein et al., 2006). Our results showed that warming significantly increased soil carbon (C) decomposition and soil respiration, likely resulting from enhanced oxidation of soil C compounds in the warmed plots compared to that in the control (Figure 3, Lin, Rygiewicz, Ehleringer, Johnson, & Tingey, 2001; Rustad et al., 2001). However, soil C decomposition and SOC content in deep soil collars decreased from 2002 to 2008 (Figure 4a,c). The decreases in soil C decomposition rates in the deep collars likely resulted from depletion of active C pool with short residence times at first, leading to relatively increased fractions of old SOC (i.e., slow and passive C pools) with long residence times in soil over time. Age of SOC can be quantitatively represented by C residence times (Bosatta & Ågren, 1999; Trumbore, 1997), which are generally distinct among three soil C pools (i.e., active, slow, and passive) in most modeling studies.

Our modeling analysis showed that active soil C pool reduced significantly in the first 2 years and then retained a relatively low level (Figure 5g), whereas slow and passive C pools continuously decreased over time (Figure 5e,f vs. Figure S3 from soil respiration data). The constant active C pool after 2 years reflected a balance between loss via decomposition and production via conversion of litter and old SOC from slow and passive pools (Waldrop & Firestone, 2004). The constant C content in the active pool is likely to be maintained for years since pool sizes of slow and passive C are much larger than those of active C (Figure 4, Trumbore, 1997). Although we defined the slow or passive C, respectively, as a single pool, each

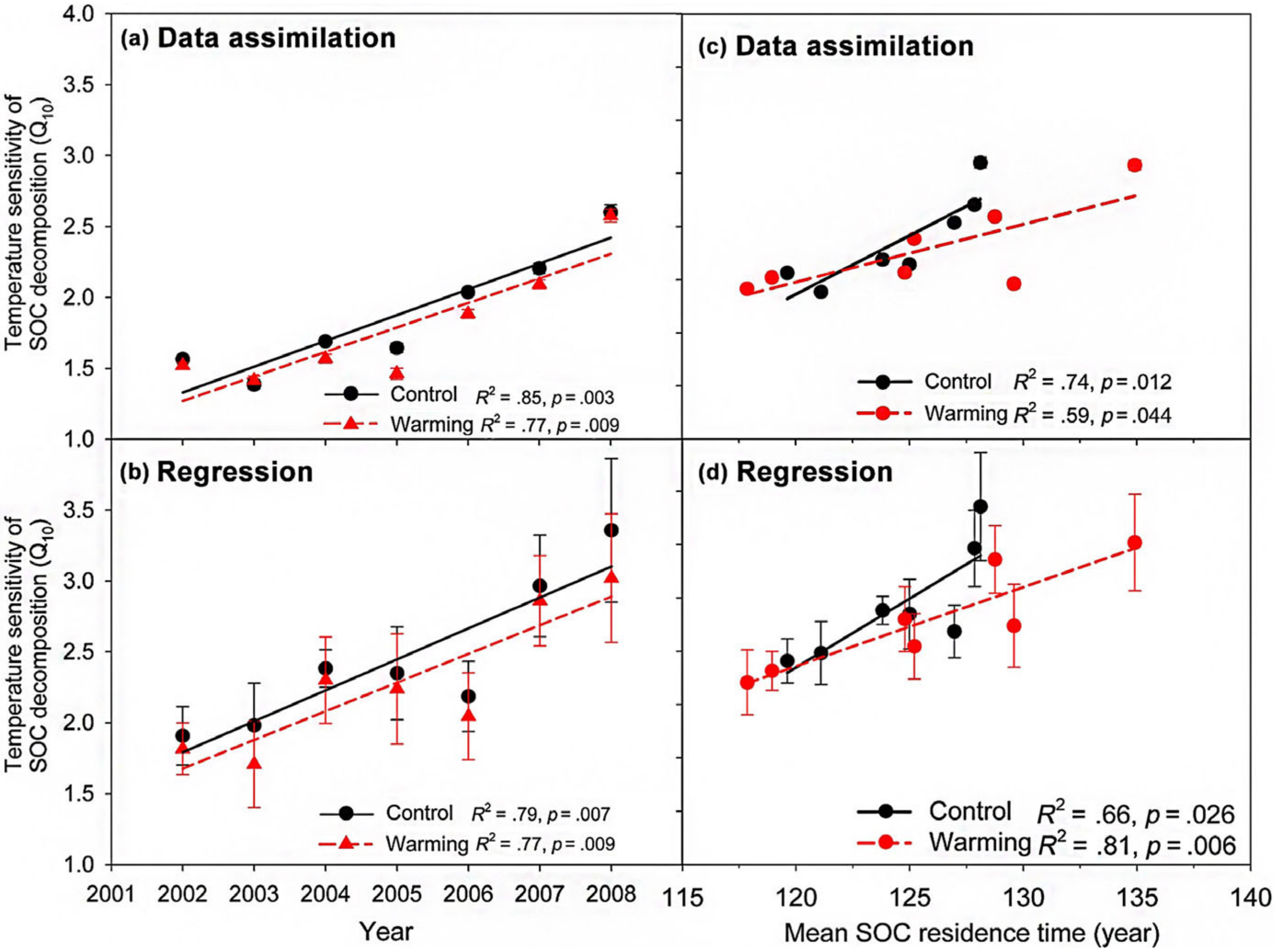

FIGURE 6 The estimated intrinsic temperature sensitivity of soil organic carbon (SOC) decomposition from data assimilation (a) and apparent temperature sensitivity ($Q_{10} = e^{10b}$) from exponential function $R_h = ae^{bT}$ (b) under ambient and warming treatments from 2002 to 2008 in a tallgrass prairie ecosystem. The differences between Q_{10} slopes under ambient temperature and warmed treatments are not significant for both methods ($p = .42$ (a) and $p = .65$ (b), respectively). Panels c and d show the relationships of pool-weighted mean soil SOC residence times with the estimated intrinsic Q_{10} from data assimilation (c) and apparent Q_{10} from exponential function under ambient and warming treatments at the same study period. Their slopes of temperature sensitivity with mean residence times are significantly affected by warming ($p = .009$ (c) and $p = .04$ (d), respectively). Vertical bars represent standard error (±*SE*)

likely is a continuum of C compounds with a range of C residence times. As less old C components in slow pools were converted into active pool in deep than shallow collars, MRTs in slow pools increased with time. Since passive C pool in soil has very slow decomposition rate with long C residence time (> 100 yrs, Figure 5d), its conversion into active C pool might be small and possibly negligible compared to slow C pool. Warming accelerated loss of C from slow and passive pools (Figure 5e,f), resulting in increases in pool-weighted MRTs (Figure 5b) although MRTs of slow C pool increased slightly less under the warming than ambient treatments (Figure 5a). The latter is possibly due to an increase in the ratio of oxidative to hydrolytic enzyme activities for the enhanced degradation of more old SOC, since oxidase enzymes enhanced the degradation of the old SOM (e.g., phenolic compounds) under climatic warming (Figure 5e,f; Kirk & Farrell, 1987; Waldrop & Firestone, 2004). In addition, warming-induced changes in physiochemical processes controlling C stabilization and destabilization may also regulate warming effects on C residence time (Figure 5b, Waldrop & Firestone, 2004).

In this study, the estimated temperature sensitivity of SOC decomposition increased significantly over time from 2002 to 2008 (Figure 6a). However, warming did not significantly affect the temperature sensitivity ($p = .42$, Figure 6a), possibly resulting from acclimatization of soil microbes or changes in microbial communities at higher temperature (Bradford et al., 2008; Luo, Wan, et al., 2001; Zhou et al., 2012). Our results showed that apparent temperature sensitivity had the same trend over time as the intrinsic one from DC with higher values for the apparent ones (Figure 6a,b). This is because temperature-sensitive processes (e.g., enzyme activity) may relieve environmental constraints to SOC decomposition, resulting in the subsequent increase in substrate availability in the soils (Davidson & Janssens, 2006).

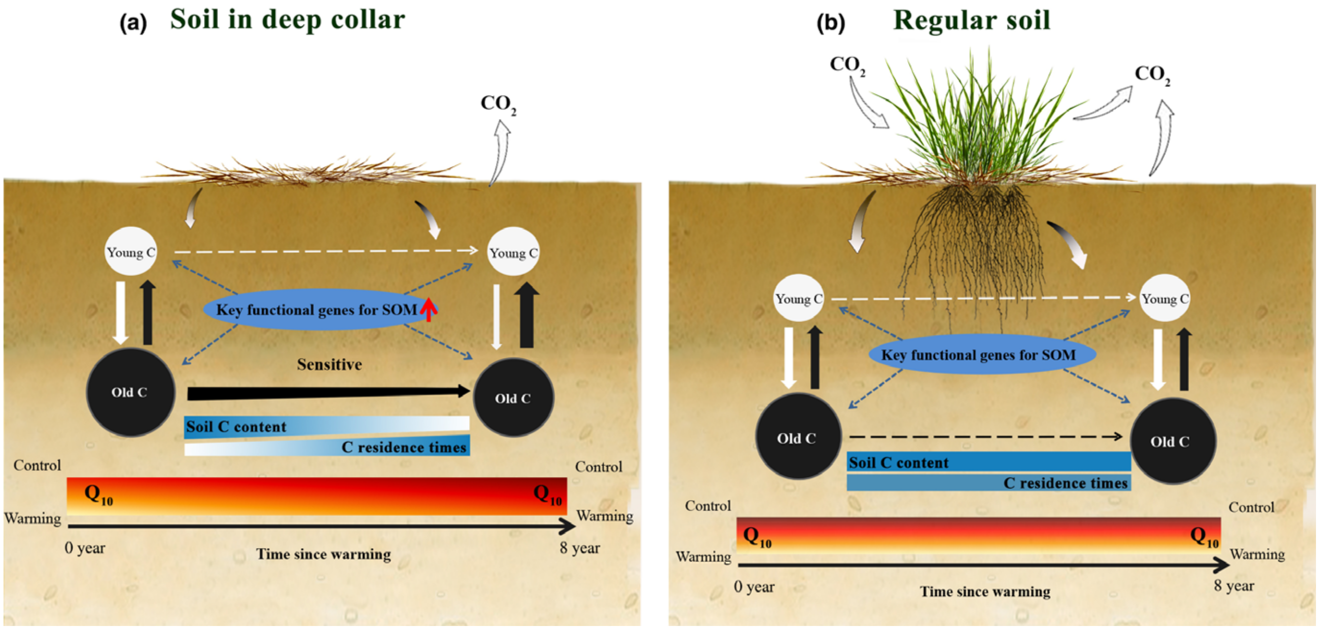

FIGURE 7 Potential mechanisms of higher temperature sensitivity of old SOC than young components. The diagram showed that soil C and its components (i.e., young and old fractions), temperature sensitivity of soil C, and C residence time varied over time as well as warming effects on soil in deep collars (a) and near the collars (b). The cycle represents the pool sizes of young and old C. Q_{10}, temperature sensitivity of SOC

Parallel increases in pool-weighted MRTs with the temperature sensitivity of soil C decomposition over time (Figures 5 and 6b) caused linear relationships between them under both ambient and warming treatments (Figure 6c). As active C was depleted in the deep collars, the remaining soil C was becoming more old and decomposed with a higher sensitivity to temperature over time although decomposition rate is low (Figure 7). This result was supported by the direct measurements of SOC content and estimated MRTs from ^{14}C isotopic of CO_2 efflux (Figure 4c,d). However, warming significantly decreased the slope of the relationship between the temperature sensitivity and SOC residence times in comparison with that under ambient temperature ($p < .05$, Figures 6 and 7). The deviation induced by warming indicates that the relationship of increased temperature sensitivity with SOC residence time is not unimodally governed by biochemical reactions (Davidson & Janssens, 2006; Suseela, Tharayil, Xing, & Dukes, 2013), but is also modulated by other abiotic and biotic processes, such as substrate availability, environmental conditions, aggregate protection, microbial enzyme production, and/or microbial efficiency (Conant et al., 2011). In addition, warming can typically reduce soil moisture and could have exacerbated differences of soil moisture between the treatments, potentially leading to biases and increasing uncertainties, especially during dry and wet periods (Figure 2d; Luo, Wan, et al., 2001; Luo, Wu, et al., 2001; Zhou et al., 2007). Soil C pools become depleted faster under warming in the deep than shallow collars, which would reduce the long-term response of microbial activity to experimental warming. Moreover, respiratory acclimation or adaptation is possibly affected by changes in the composition of microbial community, substrate quality and quantity, and microbial C resource utilization patterns (Bradford et al., 2008; Davidson & Janssens, 2006; Luo, Wan, et al., 2001; Waldrop & Firestone, 2004), which are concomitant and jointly affect temperature sensitivity of soil C decomposition in field incubation (Biasi et al., 2005; Davidson & Janssens, 2006; Larionova, Yevdokimov, & Bykhovets, 2007). In the same deep collars, Cheng et al. (2017) found that microbial communities in the warmed soil had a higher abundance of key functional genes in decomposing old organic matter compared to those in the control. The relative impacts of substrate supply per se and microbial communities on temperature sensitivity of soil C decomposition are yet to be assessed.

Our long-term field incubation experiment avoids soil disturbance of sieving, mixing, drying, and rewetting, which usually occur in laboratory incubation, and thus the results may be more representative to soil C decomposition in situ. When more than 50% of active SOC was depleted after 1-year field incubation (Figure 5g), the age of SOC increased significantly as pool-weighted MRTs increased over years (Figure 5b). While the deep collars caused minor changes in soil moisture and nutrient availability, such minor changes unlikely alter our results and conclusions (Figure 2e, Wan, Luo, & Wallace, 2002). In short-term laboratory incubation, however, the activity of small, active SOC pools usually mask the effects of large, old pools that dominate feedback from soil to atmosphere over timescales of decades to centuries. Data integration and transect studies are complicated by variation in other potentially controlling factors (Knorr et al., 2005; Liski et al., 1999; Zhou, Talley, & Luo, 2009). Our novel approach, combining long-term field incubation with DC and warming experiment, reflects changes in SOC quality over time and provide realistically qualitative information on temperature sensitivity of different SOC fractions. The long-term field experiment had enough time for active SOC pools to be depleted (~ 2 years) before the temperature sensitivity of the old SOC decomposition, which dominate feedback from soil to atmosphere over the timescales of decades or longer, became quantifiable (Cheng et al., 2017; Davidson & Janssens, 2006; Hopkins et al. 212). Thus, our study avoids biases in short-term laboratory incubation studies, in which soil C release was dominated by active C decomposition. More importantly, the DC approach used in this study can quantify different fractions of SOC by residence times, which are conceptually characterized in terms such as age, liability, or stability in most studies. The estimated residence times (or inverse of transfer coefficients) can be directly used in Earth system models. The DC technique also allowed us to estimate intrinsic temperature sensitivity to avoid confounding effects of temperature and moisture in most studies. For example, in the soils near the deep collars, the temperature sensitivity of SOC decomposition might be strongly dominated by a labile C pool fed through a continuous input of root litter but not in deep soil, which may weaken priming effects (Cheng et al., 2014). The information used by DC contained not only in SOC decomposition, but also other data sets such as plant biomass, soil C content, and litter mass to constrain estimation of residence times and temperature sensitivity with high accuracy (Weng & Luo, 2011).

This study, for the first time to the best of our knowledge, has quantified the relationships between temperature sensitivity of soil C decomposition and C residence time toward understanding the soil-climate feedback (Figures 6 and 7). Our results showed that decomposition of old SOC was more sensitive to temperature change than active SOC. Since the long-lived components of SOC are the major part in the soil, the effects of future climate change on decomposition of this large, old fraction is critical for the regulation of potential feedbacks to climate change in the long term (Cox et al., 2000; Davidson & Janssens, 2006; Hopkins et al., 2012). An increase in only temperature sensitivity of old SOC decomposition will significantly induce the respiratory CO_2 release as predicted by Rothamsted C Model and other SOC decomposition models in comparison with a fixed-Q_{10} value for all soil C components in European soils (Fang, Smith, Moncrieff, & Smith, 2005; Hartley & Ineson, 2008). If this relationship holds over larger spatial and temporal scales, ecosystems with long MRTs of soil C as mixed forests and shrubland (Zhou & Luo, 2008) might respond to global warming more than ecosystems with short MRTs. Thus, the temperature sensitivity of different SOC fractions strongly regulates the capacity of future ecosystems to act as sinks or sources for anthropogenic CO_2 and ecosystem feedbacks to climate change.

In summary, our field incubation combined with DC showed that temperature sensitivity of soil C decomposition was linearly correlated with pool-weighted MRTs of soil C by application of DC to the observational data, indicating a greater temperature sensitivity of old soil C decomposition than that of active fraction. The greater temperature sensitivity of the old, long-lived fraction may affect its decomposition in a warmer climate, possibly causing a stronger positive C-cycle feedback to climate warming as previously projected by Earth system models (Figure 7). Furthermore, the response of SOC decomposition to temperature over centurial timescales is dominated by the slow and passive pools and likely to be stronger than is suggested by fixed-Q_{10} coupled climate-C cycle models. The capacity of future ecosystems to act as sinks or sources for anthropogenic CO_2 will be determined by feedbacks among ecosystem processes, which are strongly regulated by the temperature sensitivity of different SOC fractions.

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AUTHOR CONTRIBUTIONS

X.H.Z. collected soil respiration and SOC decomposition data and did statistical analysis. He also synthesized data, conducted data assimilation, and wrote the manuscript. Y.Q.L. conceived, designed, and oversaw the experiment. X.X. measured percentage soil C content (%) and the age of respired CO_2 based on ^{14}C isotopic data. G.Y.Z discussed and revised the manuscript together.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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