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Rhizosphere priming effect increases the temperature sensitivity of soil organic matter decomposition

BIAO ZHU and WEIXIN CHENG

Department of Environmental Studies, University of California, Santa Cruz, CA 95064, USA

Abstract

The temperature sensitivity of soil organic matter (SOM) decomposition has been a crucial topic in global change research, yet remains highly uncertain. One of the contributing factors to this uncertainty is the lack of understanding about the role of rhizosphere priming effect (RPE) in shaping the temperature sensitivity. Using a novel continuous ^{13}C-labeling method, we investigated the temperature sensitivity of RPE and its impact on the temperature sensitivity of SOM decomposition. We observed an overall positive RPE. The SOM decomposition rates in the planted treatments increased 17–163% above the unplanted treatments in three growth chamber experiments including two plant species, two growth stages, and two warming methods. More importantly, warming by 5 °C increased RPE up to threefold, hence, the overall temperature sensitivity of SOM decomposition was consistently enhanced (Q_{10} values increased 0.3–0.9) by the presence of active rhizosphere. In addition, the proportional contribution of SOM decomposition to total soil respiration was increased by soil warming, implying a higher temperature sensitivity of SOM decomposition than that of autotrophic respiration. Our results, for the first time, clearly demonstrated that root–soil interactions play a crucial role in shaping the temperature sensitivity of SOM decomposition. Caution is required for interpretation of any previously determined temperature sensitivity of SOM decomposition that omitted rhizosphere effects using either soil incubation or field root-exclusion. More attention should be paid to RPE in future experimental and modeling studies of SOM decomposition.

Keywords: priming effect, Q_{10} value, rhizosphere respiration, soil warming, substrate availability

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Introduction

The global CO_2 efflux from soils to the atmosphere is estimated at $98 \pm 12\,Pg\,C\,yr^{-1}$ in 2008 (Bond-Lamberty & Thompson, 2010), which is approximately 10 times the current anthropogenic CO_2 emissions from fossil fuel burning and deforestation. Therefore, any potential changes in the rate of soil CO_2 efflux would have major impacts on atmospheric CO_2 concentration and the earth's climate (Davidson & Janssens, 2006; Smith *et al*., 2008). However, CO_2 efflux from the soil surface is a combination of two distinct components: (1) rhizosphere respiration or *autotrophic* soil respiration, including root respiration and rhizomicrobial respiration by rhizosphere microbes utilizing materials released from live roots, and (2) microbial decomposition of soil organic matter (SOM) or *heterotrophic* soil respiration, including basal SOM decomposition and rhizosphere priming effect (RPE) in which root-derived labile carbon often stimulates microbial decomposition of original SOM (Kuzyakov, 2002; Cheng & Kuzyakov, 2005). Separating these two processes is necessary for assessing how environmental changes may alter the carbon balance in belowground ecosystems (Hanson *et al*., 2000; Kuzyakov, 2006), because the two processes may respond differently to variable environmental factors, such as temperature (Hartley *et al*., 2007; Moyano *et al*., 2007; Gaumont-Guay *et al*., 2008).

The temperature sensitivity of SOM decomposition underlies an important feedback mechanism in the global carbon cycle, yet remains a subject of debate (Davidson & Janssens, 2006; Kirschbaum, 2006; von Lutzow & Kogel-Knabner, 2009). Some studies indicate that a warmer climate accelerates soil CO_2 emissions (Holland *et al*., 2000; Knorr *et al*., 2005), while other studies suggest that the response of SOM decomposition to warming is either insensitive or transient (Giardina & Ryan, 2000; Melillo *et al*., 2002). One possible cause of this inconsistency is the confounding role of rhizosphere processes (Curiel Yuste *et al*., 2004; Bader & Cheng, 2007). Field soil warming experiments measure temperature sensitivity of either total soil CO_2 efflux that includes both rhizosphere respiration and SOM decomposition (Luo *et al*., 2001; Melillo *et al*., 2002) or SOM decomposition that was separated from total soil CO_2 efflux using root-exclusion method which neglected RPE (Hartley *et al*., 2007; Zhou *et al*., 2007;

Correspondence: Biao Zhu, tel. +1 831 331 3627, fax +1 831 459 4015, e-mail: biaozhu@gmail.com

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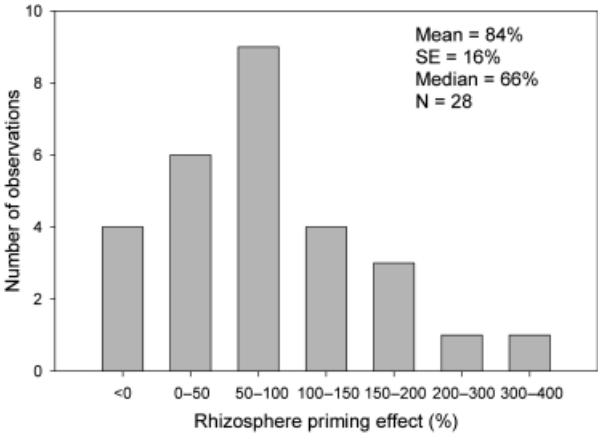

Fig. 1 Frequency distribution of rhizosphere priming effect (%, calculated as [(mean SOM decomposition in planted treatment−mean SOM decomposition in unplanted treatment)/mean SOM decomposition in unplanted treatment] × 100) based on a literature synthesis including 28 observations from 14 studies (Appendix SA1).

Schindlbacher *et al*., 2009). Laboratory soil incubation experiments often use root-free soils and exclude the rhizosphere component, implicitly assuming that rhizosphere processes have little influence on SOM decomposition rates (Holland *et al*., 2000; Conant *et al*., 2008). In both cases, the real response of SOM decomposition to warming is obscured by rhizosphere processes (Bader & Cheng, 2007). Therefore, the temperature sensitivity of SOM decomposition should be investigated with due attention paid to rhizosphere processes.

The importance of rhizosphere processes in controlling SOM decomposition and its feedback to climate change has increasingly been recognized (Dijkstra & Cheng, 2007a; Fontaine *et al*., 2007). Both abiotic and biotic factors, such as soil nutrient status (Liljeroth *et al*., 1994), soil moisture (Dijkstra & Cheng, 2007b), CO_2 concentration (Carney *et al*., 2007), light intensity (Kuzyakov & Cheng, 2001), plant phenology (Cheng *et al*., 2003) and biomass (Dijkstra *et al*., 2006), and rhizodeposition (Dijkstra & Cheng, 2007a) have been found to influence the magnitude of RPE. Practically, RPE is often expressed as the percent (%, Fig. 1) or amount (mg C kg soil^{-1} day^{-1}, Fig. 2b) of the difference in SOM decomposition rate between planted treatment and unplanted treatment. A compilation of recently published results indicates that SOM decomposition rate in the presence of live roots can be suppressed by 50% or stimulated by as much as threefold in comparison with soil incubations without live roots but under similar temperature and moisture conditions (Fig. 1,

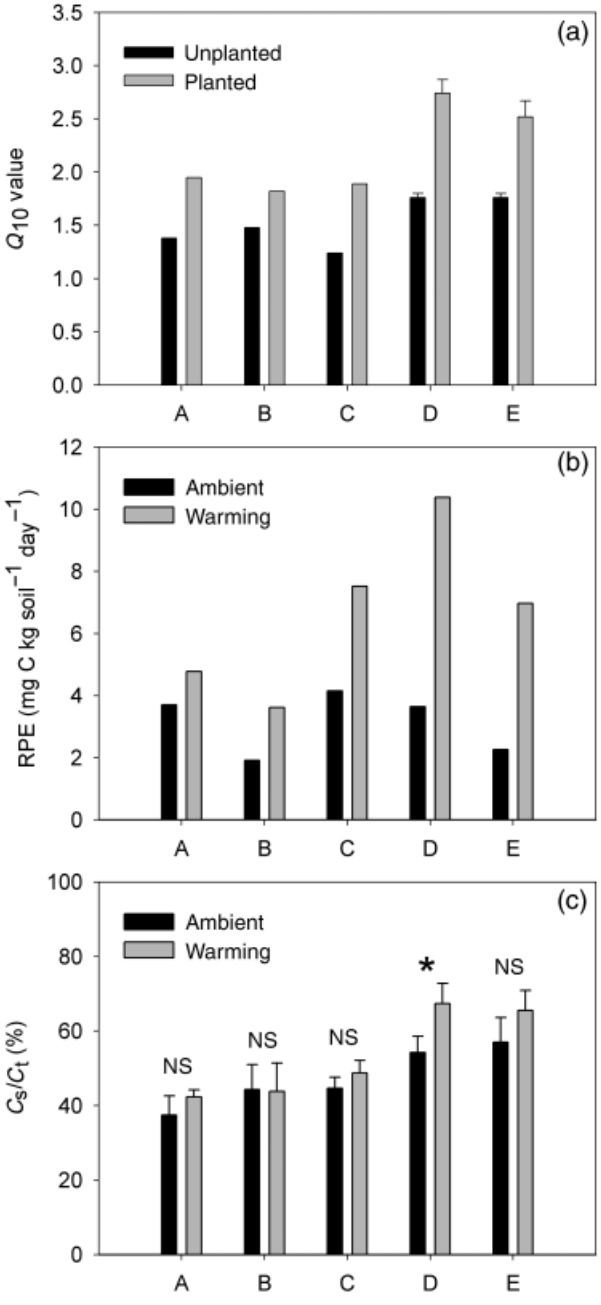

Fig. 2 (a) The temperature sensitivity of SOM decomposition (Q_{10} value) under both unplanted and planted treatments, (b) the rhizosphere priming effect (calculated as the difference in mean SOM decomposition rate between unplanted treatment and planted treatment) under both ambient and warming conditions, and (c) the proportional contribution of SOM decomposition to total soil respiration (C_s/C_t) under both ambient and warming conditions. The labels on *X*-axis stand for five different measurements: A, experiment-1, B, the first trapping in experiment-2, C, the second trapping in experiment-2, D, soybean in experiment-3, and E, sunflower in experiment-3. Error bars in (a) are standard errors for the two cases in experiment-3 (D and E). Error bars in (c) are 95% confidence intervals calculated by the IsoError model (Phillips & Gregg, 2001). ns, not statistically significant ($P > 0.05$), *Statistically significant ($P < 0.05$).

Appendix SA1). These results suggest that the magnitude of RPE can rival the level of commonly reported influence by temperature or moisture. However, mainly due to methodological difficulties, very little is known about how temperature controls RPE (Kuzyakov, 2010). Bader & Cheng (2007) observed large variations in RPE of *Populus fremontii* with air temperature among seasons, but the temperature control of RPE was confounded by other co-varying factors such as plant phenology and biomass. Kuzyakov *et al*. (2007) showed that the addition of labile root exudate components (glucose, malate or glutamate) into a rhizosphere model system stimulated *Lolium perenne* litter decomposition at 15 °C, but not at 25 °C. To the best of our knowledge, no studies have yet directly investigated the effect of soil temperature on RPE.

The relative temperature sensitivities of autotrophic and heterotrophic components of total soil respiration have been hotly debated in the literature (Boone *et al*., 1998; Baath & Wallander, 2003; Hartley *et al*., 2007). Some studies showed that seasonally derived temperature sensitivity was higher for autotrophic soil respiration than for heterotrophic soil respiration (Boone *et al*., 1998; Zhou *et al*., 2007), while other studies suggested that temperature sensitivity of autotrophic soil respiration was equal to (Baath & Wallander, 2003; Schindlbacher *et al*., 2009) or lower than (Bhupinderpal-Singh *et al*., 2003; Hartley *et al*., 2007) that of heterotrophic soil respiration. A possible cause of this debate is the often used destructive method of root-exclusion (e.g. trenching) which can produce variable results because of confounding factors inherent of the method (Hanson *et al*., 2000; Subke *et al*., 2006). In order to overcome this method limitation, isotope methods (e.g. continuous ^{13}C-labeling and radiocarbon) have been recommended by some recent reviews (Kuzyakov, 2006; Trumbore, 2006). However, empirical studies of this issue using continuous ^{13}C-labeling remain scarce.

Here we report results from three separate experiments designed to address the questions raised above: (1) does RPE change the temperature sensitivity of SOM decomposition; (2) is RPE sensitive to soil temperature; and (3) does heterotrophic soil respiration have a different temperature sensitivity than autotrophic soil respiration. In order to answer these three questions, we grew sunflower (*Helianthus annuus* L.) and soybean (*Glycine max* L. Merr.) in a sandy loam soil collected from a farm (surface 0–30 cm) in a continuous ^{13}C-labeling growth chamber. Experiment-1 was the first attempt to answer these three questions based on one measurement when sunflower was at flowering stage. Experiment-2 was conducted to see if results obtained in experiment-1 are dependent on plant phenology based on two measurements when sunflower was at vegetative and flowering stages. Experiment-3 was designed to further test the generality of these results by including two plant species (soybean and sunflower) and using a different warming method.

Materials and methods

Experimental setup

The three experiments were separately conducted in a continuous ^{13}C-labeling growth chamber with very similar experimental setup (Table 1). Surface (0–30 cm) soils (sandy loam)

Table 1 Differences in setup and measurements of the three experiments

Settings	Experiment-1	Experiment-2	Experiment-3
Experiment period	2007 (51 days)	2008 (57 days)	2009 (50 days)
Soil characteristics			
Total C (%)	0.94	1.49	1.17
Total N (%)	0.11	0.14	0.13
C : N	8.8	10.5	8.8
$\delta^{13}C$ (‰)	−25.84	−26.65	−25.72
Growth chamber settings			
Air temperature (°C)	18–28	15–25	15–25
Soil warming magnitude (°C)	2.7	4.5	5
$\delta^{13}C$ of CO_2 (‰ ± SD)	−15.7 ± 0.4	−17.8 ± 0.3	−16.8 ± 0.2
Soil respiration measurements			
CO_2 trapping time (hours)	48	24	24
Days after sowing	49–51	42–43 (first) 56–57 (second)	47–48 (ambient) 49–50 (warming)
Plant phenology	Flowering	Vegetative (first) Flowering (second)	Flowering

were collected from three different locations of a farm on the campus of University of California, Santa Cruz. Various crops and vegetables (mostly C_3 plants, sunflower, soybean, strawberry, lettuce, etc.) have been grown in the farm since it was converted from a meadow in 1974. The soils had pH values around 5.8 and slightly different C%, N%, C : N, and $\delta^{13}C$ values. All soils were homogenized by sieving through a 4-mm screen and air-dried before use. A nylon bag filled with 2000 g sand was placed at the bottom of each polyvinyl chloride pot (diameter 15 cm, height 40 cm, capped at bottom) to improve air circulation, and then 8000 g air-dried soil was packed into each pot at a similar bulk density. We used 16 pots in experiments 1 and 2 with four replicates for each treatment: ambient-unplanted, ambient-sunflower, warming-unplanted, and warming-sunflower; while we used 15 pots in experiment-3 with five replicates for each treatment: unplanted, soybean, and sunflower. We lost one replicate in some treatments due to trapping failure (leakage) and the final replicate number ranges from three to five (Table 3). All filled pots were rewetted to 25% gravimetric soil moisture content (equivalent of 80% water holding capacity) and preincubated at room temperature (22 °C) for 5 days before sowing. For planted treatments, we planted four seeds of sunflower (variety Sunbright F1) or soybean (variety Envy) and thinned to one individual plant per pot after seedling emergence. We chose these plant–soil combinations because (1) our previous work (Dijkstra *et al*., 2006; Dijkstra & Cheng, 2007b) showed that these plant–soil combinations produced RPE at a medium level (0–150%), the most frequently observed range among all previous studies (Fig. 1), (2) this is the first study on the response of RPE to soil warming, thus previous experiences on these plant–soil combinations can ensure a successful execution of the experiments, and (3) the capacity of the labeling growth chamber would not allow us to include more treatment combinations.

Lighting inside the growth chamber was maintained at 800 μmoL m^{-2} s^{-1} for 12 h day^{-1} and relative humidity was kept at 40%. Air temperature inside the growth chamber was slightly different among experiments (Table 1). For the warming treatments in experiments 1 and 2, we continuously warmed the soil throughout the experimental period by using automatically controlled electric heating cables (Briskheat SL-5-120-B, Columbus, OH, USA) buried in the pots. Temperature in each pot was monitored every 2 min using calibrated thermocouples (Omega thermocouple type-T, Stamford, CT, USA) at 15 cm depth and recorded by a datalogger (Campbell Scientific CR10X, Logan, UT, USA). This warming method achieved a control accuracy of ± 0.2 °C. In experiment-3, we temporarily warmed the whole plant–soil system for 48 h (48–50 days after sowing) by changing the temperature settings of the growth chamber. Soil respiration was measured twice for each of the 15 pots in experiment-3: 47–48 days after sowing (ambient temperature) and 49–50 days after sowing (elevated temperature). Thus, all of the 15 pots in experiment-3 were temporarily warmed for 2 days with 1-day prewarming before the measurement, while only half of the 16 pots in experiments 1 and 2 (i.e. warming-unplanted treatment and warming-sunflower treatment) were continuously warmed for the entire duration of the two experiments. The warming magnitude was 2.7, 4.5, and 5 °C above 'ambient' for experiments 1, 2, and 3 respectively. Gravimetric water content in each pot was maintained at 25% throughout the experimental period by frequent weighing and watering with deionized water. Anaerobic conditions were prevented by forcing ambient air through each pot for 30 min every 6 h using an aeration pump.

We continuously labeled plants with naturally ^{13}C-depleted CO_2. By regulating the flow of ^{13}C-depleted CO_2 from a tank and setting CO_2-free air (ambient air passed through a soda lime column removing the CO_2) flow rate proportional to the growth chamber leakage rate, we maintained a relatively constant concentration (400 ± 5 ppm, measured by a LI-820 CO_2 analyzer every 2 min) and $\delta^{13}C$ value (Table 1) of CO_2 inside the growth chamber when lights were on. To check whether the $\delta^{13}C$ value of CO_2 inside the growth chamber was constant throughout the experimental period, we trapped the growth chamber CO_2 through a glass airstone in a test tube filled with 50 mL of 0.1 M NaOH solution every 3 days when the lights were on, and then analyzed the $\delta^{13}C$ value of $SrCO_3$ precipitate formed after adding 1 mL of 0.3 M $SrCl_2$ solution (Harris *et al*., 1997). The day-to-day variability of the $\delta^{13}C$ value of CO_2 inside the growth chamber was < 0.4‰ (Table 1). Note that the $\delta^{13}C$ value of CO_2 inside the growth chamber was dependent on the $\delta^{13}C$ value of CO_2 from the tanks (−36 to −38‰) and thus differed slightly among the three experiments. For details about this continuous ^{13}C-labeling method, please see Cheng & Dijkstra (2007).

Measurements

We measured total soil respiration using a closed-circulation CO_2 trapping system (Cheng *et al*., 2003). Briefly, we sealed each pot at the base of the plant with nontoxic silicone rubber and removed CO_2 inside each pot by circulating the isolated air through a soda lime column for 1 h. Then CO_2 produced during a 24 or 48-h period in each sealed pot was trapped in a 400 mL 0.5 M NaOH solution by periodic air circulation for 30 min at a 6-h interval. The CO_2 trapping efficiency with this system was greater than 99%, eliminating preferential sorption of $^{13}CO_2$ vs. $^{12}CO_2$. Blanks were included to correct for handling errors. An aliquot of each NaOH solution was analyzed for total inorganic C and another aliquot was precipitated as $SrCO_3$ and then analyzed for $\delta^{13}C$ (Harris *et al*., 1997). The $\delta^{13}C$ values measured in $SrCO_3$ were corrected for contamination from carbonate in the NaOH stock solution and from sample handling (Cheng *et al*., 2003). We separated total soil respiration (C_t) into SOM decomposition (C_s), and rhizosphere respiration (C_r) using a two-source mixing model:

$$C_s = C_t(\delta^{13}C_r - \delta^{13}C_t)/(\delta^{13}C_r - \delta^{13}C_s), \quad [1]$$

$$C_r = C_t - C_s, \quad [2]$$

where $\delta^{13}C_r$ is the $\delta^{13}C$ value of rhizosphere respiration which was inferred from the $\delta^{13}C$ value of root biomass adjusted by a difference based on a sand-perlite mixture experiment. Briefly, in a separate experiment with sunflower and soybean growing in C-free sand-perlite mixture, we found that CO_2 from rhizo-

sphere respiration was ^{13}C-depleted relative to root biomass (1.0‰ for sunflower and 1.7‰ for soybean; Zhu & Cheng, unpublished results). $\delta^{13}C_t$ is the measured $\delta^{13}C$ value of total soil respiration, and $\delta^{13}C_s$ is the mean $\delta^{13}C$ value of CO_2 from SOM decomposition measured in unplanted treatment.

The temperature sensitivity (Q_{10}) of SOM decomposition was calculated using this equation:

$$Q_{10} = (C_{s\_w}/C_{s\_a})^{(10/\Delta T)}, \quad [3]$$

where C_{s_w} and C_{s_a} are the mean SOM decomposition rates (C_s) under warming and ambient conditions, respectively. ΔT is the difference in mean soil temperature between ambient and warming treatments.

Immediately after final CO_2 trapping, we separated plants into shoots and roots, homogenized soils (including those attached to roots but fell after shaking for planted pots), and took a representative fresh soil sample (400 g) from each pot. Virtually all soil volume in the planted pots was occupied by roots at harvesting and thus there was nearly no 'root-free' soil. Fine roots were removed from soil samples from planted pots by hand-picking. Then all soil samples were analyzed for soil moisture, microbial biomass carbon and extracellular enzyme activity (in experiment-1), and substrate-induced respiration (in experiment-3), within 2 days. We dried (60 °C and 24 h in an oven), weighed and ground all plant samples, and dried (80 °C and 48 h in an oven) and ground a subsample of the soil (20 g) from each pot. Ground plant and soil samples were then analyzed for C%, N%, $\delta^{13}C$ and $\delta^{15}N$ on a continuous flow isotope ratio mass spectrometer (PDZ Europa Hydra 20-20, Cheshire, UK).

In order to explore the role of soil microbes in SOM decomposition, we measured microbial biomass carbon and potential activity of five extracellular enzymes of fresh soil samples collected after CO_2 trapping in experiment-1, using the chloroform fumigation-extraction method (Vance *et al*., 1987) and a standard soil enzyme method (Waldrop & Firestone, 2006) respectively. The five enzymes are α-glucosidase which degrades starch, cellobiohydrolase and β-glucosidase which degrades cellulose, xylosidase which degrades hemicellulose, and NAGase which degrades chitin and N-acetylglucosamine-containing polymers.

In order to investigate the effect of substrate availability on temperature sensitivity of SOM decomposition, we measured substrate-induced respiration of fresh soil samples collected after final CO_2 trapping in experiment-3, using the method of Gershenson *et al*. (2009). Briefly, fresh soil samples from each pot were divided into four 20 g aliquots and each aliquot was placed into a 125 mL flask. The four flasks were divided among two temperature treatments (15 and 25 °C) and two glucose treatments (control and glucose addition). We added a 60 g L^{-1} glucose solution to glucose addition samples and deionized water to control samples using a 10 mL syringe with a needle tip to maintain soil moisture at approximately 120% water holding capacity for all samples. Then we incubated the soil samples in two water baths with temperature of 15 and 25 °C respectively for 1 h, and measured soil respiration using the methodology described in Gershenson *et al*. (2009). The substrate-induced respiration measurements were executed within 4 h from the initial collection of soil samples to ensure minimal loss of naturally available substrate to respiration.

Statistical analyses

For plant biomass and $\delta^{13}C$ values (Table 2), we used independent-samples *t*-test to compare data between ambient and warming treatments in experiments 1 and 2. For CO_2-C efflux rate and $\delta^{13}C$ value of total soil respiration (C_t) and its autotrophic (C_r) and heterotrophic (C_s) components (Table 3), we used analyses of variance (ANOVA) to assess the effects of temperature, plant and their interaction in experiments 1 and 2, and paired-samples *t*-test to compare data between ambient and warming conditions for all three treatments (unplanted, soybean, and sunflower) in experiment-3. The statistical significance of the impact of RPE on the Q_{10} value of C_s or the difference in the Q_{10} value of C_s between unplanted treatment and planted treatment (Fig. 2a) was based on the interaction between temperature and plant on C_s in the ANOVA results in experiments 1 and 2, and independent-samples *t*-test of the

Table 2 Plant biomass (g pot^{-1}) and $\delta^{13}C$ values (‰) of sunflower and soybean

	Plant biomass (g pot^{-1})			$\delta^{13}C$ (‰)		
Treatment	Shoot	Root	Total	Shoot	Root	Total
Experiment-1						
Ambient ($n = 3$)	29.00(1.24)	6.15(0.38)	35.15(1.50)	−37.68(0.19)	−37.98(0.27)	−37.73(0.21)
Warming ($n = 4$)	33.36(1.12)	5.83(0.17)	39.19(1.21)	−37.06(0.19)	−37.31(0.13)	−37.10(0.17)
P−value	0.049	0.446	0.088	0.073	0.057	0.064
Experiment-2						
Ambient ($n = 3$)	20.26(0.24)	4.29(0.06)	24.55(0.18)	−40.79(0.16)	−39.50(0.43)	−40.56(0.21)
Warming ($n = 3$)	23.98(1.36)	4.50(0.18)	28.48(1.50)	−40.17(0.36)	−39.44(0.48)	−40.04(0.36)
P-value	0.054	0.315	0.060	0.183	0.931	0.280
Experiment-3						
Soybean ($n = 4$)	18.55(2.01)	3.38(0.44)	21.93(2.42)	−36.98(0.19)	−36.09(0.31)	−36.84(0.21)
Sunflower ($n = 4$)	13.71(1.76)	3.68(0.45)	17.39(2.20)	−38.83(0.25)	−38.94(0.13)	−38.85(0.22)

Values represent means of three or four replicates with standard error in parenthesis and *P*-values of independent-samples *t*-test.

Table 3 CO_2-C efflux rate (mg C kg soil^{-1} day^{-1}) and δ^{13}C values (‰) of total soil respiration (C_t) and its SOM-derived or heterotrophic (C_s) and root-derived or autotrophic (C_r) components

	CO_2-C efflux (mg C kg soil^{-1} day^{-1})			δ^{13}C (‰)		
Treatment	C_t	C_s	C_r	$\delta^{13}C_t$	$\delta^{13}C_s$	$\delta^{13}C_r$
(A) Experiment-1						
Ambient, unplanted ($n = 3$)		3.22 (0.03)			−23.26 (0.14)	
Ambient, sunflower ($n = 3$)	18.51 (0.48)	6.92 (0.20)	11.59 (0.53)	−32.88 (0.22)	−23.34 (0.08)*	−38.59 (0.18)†
Warming, unplanted ($n = 3$)		3.51 (0.09)			−23.42 (0.10)	
Warming, sunflower ($n = 4$)	19.62 (0.67)	8.29 (0.27)	11.33 (0.42)	−32.14 (0.06)	−23.34 (0.08)*	−38.59 (0.18)†
ANOVA *P*-values						
Temperature	0.266	0.002	0.713	0.013	0.189 (unplanted)	
Plant		0.000				
Temperature × Plant		0.024				
(B) The first trapping in Experiment-2						
Ambient, unplanted ($n = 4$)		9.38 (0.11)			−26.47 (0.10)	
Ambient, sunflower ($n = 3$)	25.58 (1.35)	11.30 (0.53)	14.28 (1.06)	−34.31 (0.25)	−26.55 (0.07)*	−40.47 (0.29)†
Warming, unplanted ($n = 4$)		11.18 (0.10)			−26.64 (0.10)	
Warming, sunflower ($n = 3$)	33.83 (0.48)	14.80 (0.50)	19.03 (0.96)	−34.37 (0.29)	−26.55 (0.07)*	−40.47 (0.29)†
ANOVA *P*-values						
Temperature	0.004	0.000	0.030	0.871	0.283 (unplanted)	
Plant		0.000				
Temperature × Plant		0.023				
(C) The second trapping in Experiment-2						
Ambient, unplanted ($n = 4$)		8.78 (0.26)			−26.10 (0.16)	
Ambient, sunflower ($n = 3$)	28.98 (0.37)	12.92 (0.15)	16.06 (0.26)	−34.15 (0.04)	−26.29 (0.11)*	−40.47 (0.29)†
Warming, unplanted ($n = 4$)		9.67 (0.14)			−26.48 (0.08)	
Warming, sunflower ($n = 3$)	35.36 (0.60)	17.19 (0.11)	18.17 (0.62)	−33.57 (0.13)	−26.29 (0.11)*	−40.47 (0.29)†
ANOVA *P*-values						
Temperature	0.001	0.000	0.035	0.012	0.07 (unplanted)	
Plant		0.000				
Temperature × Plant		0.000				
(D) Soybean in Experiment-3						
Ambient, unplanted ($n = 5$)		13.41 (0.53)			−26.84 (0.15)	
Ambient, soybean ($n = 4$)	31.48 (0.80)	17.05 (0.32)	14.43 (0.65)	−31.77 (0.12)	−26.69 (0.10)*	−37.79 (0.31)†
Warming, unplanted ($n = 5$)		17.81 (0.66)			−26.54 (0.10)	
Warming, soybean ($n = 4$)	41.97 (1.66)	28.19 (0.50)	13.79 (1.26)	−30.31 (0.20)	−26.69 (0.10)*	−37.79 (0.31)†
Paired-samples *t*-test *P*-values	0.002	0.000 (for both)	0.416	0.001	0.124 (unplanted)	
(E) Sunflower in Experiment-3						
Ambient, unplanted ($n = 5$)		13.41 (0.53)			−26.84 (0.15)	
Ambient, sunflower ($n = 4$)	27.52 (1.03)	15.68 (0.79)	11.84 (0.68)	−32.39 (0.26)	−26.69 (0.10)*	−39.94 (0.13)†
Warming, unplanted ($n = 5$)		17.81 (0.66)			−26.54 (0.10)	
Warming, sunflower ($n = 4$)	37.90 (1.47)	24.78 (0.71)	13.12 (1.00)	−31.26 (0.21)	−26.69 (0.10)*	−39.94 (0.13)†
Paired-samples *t*-test *P*-values	0.001	0.000 (for both)	0.036	0.002	0.124 (unplanted)	

*Average of all unplanted pots under both ambient and warming conditions ($n = 6$ in experiment-1, 8 in experiment-2 or 10 in experiment-3)

†Average of all roots under ambient and warming conditions ($n = 7$ for sunflower in experiment-1, 6 for sunflower in experiment-2 or 4 for both sunflower and soybean in experiment-3) and adjusted by a difference in δ^{13}C value between root biomass and rhizosphere respiration (1.7‰ for soybean and 1.0‰ for sunflower, B. Zhu and W. Cheng, unpublished results). Note that the same four pots planted with soybean or sunflower were trapped twice under ambient and temporary warming conditions in experiment-3, so the δ^{13}C values are average of four replicated plants harvested after final trapping.

Values represent means of three to five replicates with standard error in parenthesis and *P*-values of ANOVA or paired-samples *t*-test.

Q_{10} value of C_s in experiment-3. The RPE (Fig. 2b) was calculated as the difference in mean C_s between unplanted treatment and planted treatment, which prevented us from calculating SD (or SE) of RPE (Kuzyakov, 2010). For the proportional contribution of SOM decomposition to total soil respiration (C_s/C_t, Fig. 2c), the mean value and 95%

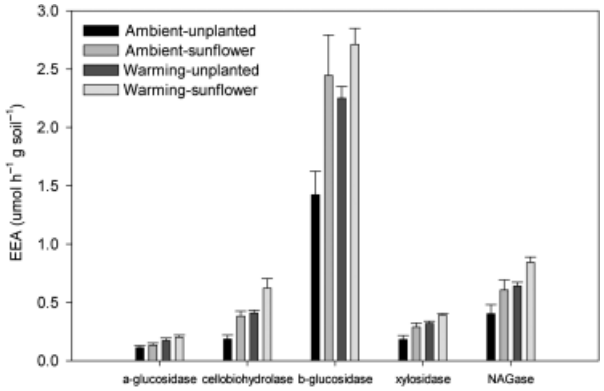

Fig. 3 Extracellular enzyme activities (EEA, mean + SE) among different treatments in experiment-1. ANOVA *P*-values of the effects of temperature, planting and temperature-planting interaction are 0.01, 0.24, and 0.87 for α-glucosidase, <0.01, <0.01, and 0.89 for cellobiohdyrolase, 0.03, <0.01, and 0.21 for β-glucosidase, <0.01, <0.01, and 0.49 for xylosidase, and <0.01, 0.01, and 0.99 for NAGase.

confidence interval were calculated using the IsoError model (Phillips & Gregg, 2001). IsoError is a two-source linear mixing model that accounts for the variability in the isotopic signatures for the two sources ($^{13}C_s$ and $^{13}C_r$) as well as the mixture ($^{13}C_t$). For microbial biomass carbon (data not shown) and extracellular enzyme activity (Fig. 3) measured in experiment-1, we used ANOVA to assess the effects of temperature, plant and their interaction. For substrate-induced respiration measured in experiment-3 (Fig. 4), we used ANOVA (post hoc Tukey test) to compare Q_{10} values at ambient substrate condition among the three soils (i.e. the original-substrate effect, Fig. 4b), and paired-samples *t*-test to compare Q_{10} values between original-substrate condition (control) and added-substrate condition (glucose) for each soil (i.e. the added-substrate effect, Fig. 4b). We used SPSS 15.0 to perform all statistical analyses and set the significance level at $P<0.05$.

Results

Plants appeared normal with no obvious signs of pests or pathogens. In experiments 1 and 2, soil warming slightly increased plant biomass as well as plant $\delta^{13}C$ values (Table 2). We successfully labeled plants with ^{13}C-depleted CO_2. Overall, the difference between the mean $\delta^{13}C$ value of plant tissues and that of CO_2 from SOM decomposition was 10–14‰ (Tables 2 and 3). Soil warming did not significantly change the $\delta^{13}C$ value of CO_2 from SOM decomposition in unplanted pots or the $\delta^{13}C$ value of roots. Thus, for separating SOM-derived CO_2 from root-derived CO_2 using the two-source mixing model [Eqns (1) and (2)], the mean $\delta^{13}C$ value of CO_2 from SOM decomposition in unplanted pots in both temperature treatments was used as the end-member for SOM-derived CO_2 ($\delta^{13}C_s$); and the mean $\delta^{13}C$ value of roots in both temperature treatments plus

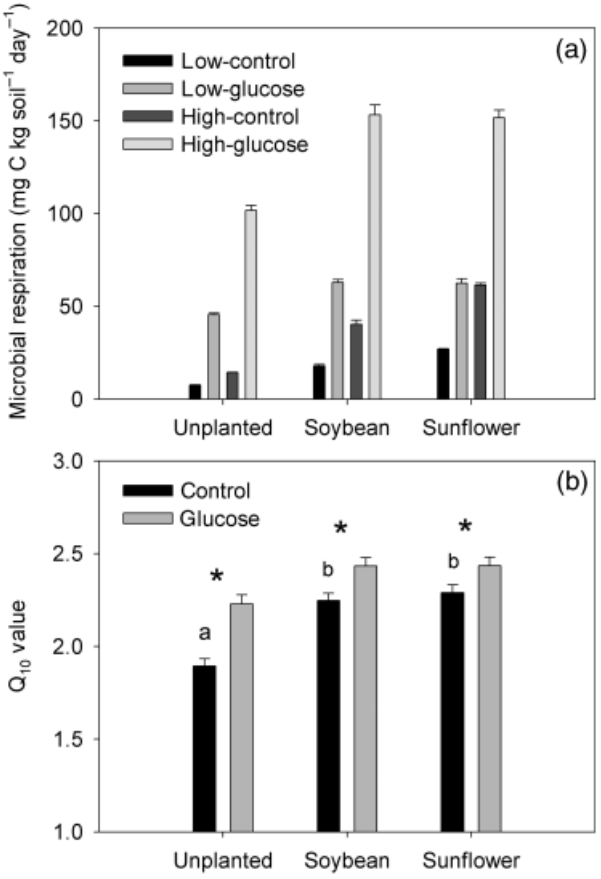

Fig 4 (a) Microbial respiration (overall CO_2 production) among four different temperature-substrate treatment combinations which include two temperature conditions (15 °C – low, 25 °C – high) and two substrate levels (original-substrate – control, added-substrate – glucose) for soils from the three planting treatments (unplanted, soybean, and sunflower) in experiment-3. (b) Q_{10} values of microbial respiration for both original-substrate (control) and added-substrate (glucose) treatments for soils from the three planting treatments (unplanted, soybean, and sunflower) in experiment-3. Different letters indicate significant ($P<0.05$) differences in Q_{10} value at ambient substrate condition (control) among the three soils (i.e. the original-substrate effect), while * indicate significant ($P<0.05$) differences in Q_{10} value between original-substrate (control) and added-substrate (glucose) conditions for each soil (i.e. the added-substrate effect). Note that some error bars (standard error) are too small to be visible.

an adjustment for ^{13}C-depletion (1.7‰ for soybean and 1.0‰ for sunflower) was used as the end-member for root-derived CO_2 ($\delta^{13}C_r$).

Soil warming significantly stimulated total soil respiration in planted pots ($P<0.05$), with an exception in experiment-1 (Table 3). Similarly, soil warming significantly enhanced rhizosphere respiration in planted pots ($P<0.05$, Table 3), except for experiment-1 and soybean in experiment-3. More importantly, warming, planting, and the interaction of warming and planting all significantly

increased SOM decomposition in experiments 1 and 2 (ANOVA, $P<0.05$, Table 3). The statistical significance of the interaction between warming and planting on SOM decomposition indicated that the presence of plants through RPE significantly increased the temperature sensitivity of SOM decomposition in experiments 1 and 2 (Fig. 2a). Furthermore, this priming-enhanced temperature sensitivity of SOM decomposition was also demonstrated to a larger degree in experiment-3 with temporary warming of the whole plant–soil system. The temperature sensitivity of SOM decomposition as measured by Q_{10} values in soybean and sunflower treatments was significantly higher than that in the unplanted treatment in experiment-3 (Independent-samples *t*-test, $P<0.05$, Fig. 2a). The consistently higher Q_{10} values (from 0.3 to 0.9 higher) of SOM decomposition in the planted treatment than in the unplanted treatment under the same soil temperature and moisture conditions across the five comparisons (Fig. 2a) indicated that rhizosphere processes imposed significant controls on the temperature sensitivity of SOM decomposition.

RPE, calculated as the difference in mean SOM decomposition rate between the planted treatment and the unplanted treatment under the same soil temperature and moisture conditions, was consistently higher in the warming treatment than in the ambient treatment (Fig. 2b). The magnitude of this warming-enhanced RPE was especially large in experiment-3 where RPE was almost tripled by 5 °C temporary warming of the entire plant–soil system. This indicated that the magnitude of RPE was highly sensitive to temperature changes.

The proportional contribution of SOM decomposition to total soil respiration (C_s/C_t) ranged from 37% to 67% among all measurements (Fig. 2c). Generally, soil warming tended to increase C_s/C_t except for the first trapping in experiment-2 where C_s/C_t did not differ between the ambient treatment and the warming treatment. Because the IsoError model was used to estimate the confidence interval of C_s/C_t, the soil warming effect on C_s/C_t was only statistically significant ($P<0.05$) for soybean treatment in experiment-3 where RPE was large in magnitude and highly sensitive to temperature (Fig. 2c). These results indicated that the temperature sensitivity of SOM decomposition could be equal to or higher than that of rhizosphere respiration, depending on the magnitude and temperature sensitivity of RPE.

Discussion

Effects of RPE on temperature sensitivity of SOM decomposition

Our results, for the first time, clearly showed that RPE increased the temperature sensitivity of SOM decomposition. For unplanted treatments in experiments 1 and 2, Q_{10} values ranged between 1.2 and 1.5 (Fig. 2a), which is similar to most reported values from continuous warming experiments, but lower than the commonly reported values determined in short-term laboratory experiments in this temperature range (Davidson *et al*., 2006). This is possibly caused by either faster depletion of labile substrates in the warmed pots than in the ambient pots (Conant *et al*., 2008; Curiel Yuste *et al*., 2010) or microbial acclimation to warming (Bradford *et al*., 2008; Curiel Yuste *et al*., 2010). However, for planted treatments in experiments 1 and 2, Q_{10} values were close to 2.0 and significantly higher than those in unplanted treatments (Fig. 2a). Moreover, for unplanted treatment in experiment-3, the temporary warming-derived Q_{10} value was 1.8 (Fig. 2a), close to the commonly reported value of 2.0. This may be explained by little difference in substrate availability in the same soils between ambient condition and warming condition (measured on the same five pots 2 days later) and less microbial acclimation during this short period. Interestingly, for planted treatments (soybean and sunflower) in experiment-3, the short-term warming-derived Q_{10} values were significantly higher than that for the unplanted treatment (2.5–2.7 vs. 1.8, Fig. 2a). Overall, all five measurements consistently demonstrated that the presence of the rhizosphere priming increased the temperature sensitivity of SOM decomposition.

We shall discuss this result with some potential uncertainties. First, soils used in this study were disturbed by sieving, air-drying, packing, and rewetting. All these disturbances might have released some labile carbon substrates for microbial respiration and rhizosphere priming, which might, in some way, biased the temperature sensitivity. In order to minimize this possible disturbance effect, we did 5-day preincubation before sowing seeds and did not measure soil respiration until 40 days after sowing. A previous study (Dijkstra & Cheng, 2007a) showed that RPE of two tree species on decomposition of three different soils persisted throughout a 395-day experimental period, until well after the initial disturbance-induced labile carbon substrates were depleted by respiration. Therefore, it is unlikely that the disturbance during soil preparation significantly affects our results on RPE. Second, we assumed that the proportional respiration from different SOM fractions and the $\delta^{13}C$ values of SOM-derived CO_2 are the same with and without the presence of roots. However, different SOM components may have different $\delta^{13}C$ values. The proportional respiration originating from different SOM components may be different between rooted and root-free soil, which could lead to different $\delta^{13}C$ values of SOM-derived CO_2 between unplanted and planted treatments. This is a

common issue to all studies that employ the two-source isotope partitioning approach (Phillips & Gregg, 2001; Werth & Kuzyakov, 2010). But it should be the least concern for this study because the $\delta^{13}C$ value of SOM-derived CO_2 remained unchanged regardless of temperature treatments (Table 3). Even if the $\delta^{13}C$ value of SOM-derived CO_2 did change to some level when comparing planting treatments, based on Eqn (1) in the two-source mixing model, a change in the $\delta^{13}C$ value of SOM-derived CO_2 ($\delta^{13}C_s$) would only change the estimate of SOM decomposition (C_s) to an equal extent between ambient treatment and warming treatment, and thus would neither change the temperature sensitivity of SOM decomposition nor our main conclusion (Fig. 2a). Therefore, our main conclusion is basically sound.

A mechanistic hypothesis for PRE-enhanced temperature sensitivity of SOM decomposition

Our finding of a consistently higher temperature sensitivity of SOM decomposition with the presence of roots (with RPE) is novel. While the exact mechanisms behind this phenomenon are unknown and need further investigation, here we propose a mechanistic hypothesis to explain this observation based on some ancillary data we collected: root-derived labile carbon compounds in the form of rhizodeposition activate soil microbes which produce more extracellular enzymes and increase SOM-derived substrate availability, which consequently lead to higher temperature sensitivity of SOM decomposition, if SOM decomposition follows Michaelis–Menten kinetics.

How does root-derived substrate input into the soil lead to higher SOM-derived substrate availability for microbial respiration? One possible mechanism is related to soil extraceullar enzyme activities. Labile carbon compounds released by roots can stimulate growth of active microbes as well as activate dormant microbes in the rhizosphere. These activated microbes may accelerate SOM decomposition either through co-metabolisms with root exudates (Kuzyakov, 2002) or via producing more polymer-degrading enzymes which increase the breakdown of insoluble macromolecules into smaller, soluble molecules. Therefore, these extracellular enzymes enhance labile SOM-derived substrates that can be assimilated by living microbes and respired as SOM-derived CO_2 (Schimel & Weintraub, 2003; Wallenstein & Weintraub, 2008). In order to test this possibility, we used a standard soil enzyme method (Waldrop & Firestone, 2006) and measured the potential activity (indicative of overall enzyme concentrations) of five soil extracellular enzymes in experiment-1. Although neither warming nor planting significantly changed microbial biomass carbon (data not shown), planting with sunflower significantly increased activities of four soil extracellular enzymes (cellobiohydrolase, β-glucosidase, xylosidase, and NAGase, but not α-glucosidase, Fig. 3).

How does higher substrate availability lead to higher temperature sensitivity of SOM decomposition? This can be explained if SOM decomposition follows Michaelis–Menten kinetics (Davidson *et al*., 2006): $R = (V_{max}[C])/(K_m + [C])$, where R is SOM decomposition rate, V_{max} is the maximal rate of enzymatic activity, K_m is the half-saturation constant, and $[C]$ is the concentration of SOM-derived organic carbon substrates. Both V_{max} and K_m are temperature dependent. Based on this theory, when substrate availability is low or $[C]$ is comparable to K_m, the temperature dependence of K_m partly cancels out the temperature dependence of V_{max} and thus the overall temperature sensitivity of SOM decomposition (also defined as the *apparent* temperature sensitivity) decreases. However, when substrate availability is high or $[C] \gg K_m$, the temperature sensitivity of SOM decomposition is largely determined by that of V_{max} (also defined as the *intrinsic* temperature sensitivity) and thus increases. These predictions have been empirically supported by previous studies (Larionova *et al*., 2007; Gershenson *et al*., 2009; Curiel Yuste *et al*., 2010), and are also supported by substrate-induced respiration data in experiment-3 (Fig. 4). We found that (1) adding glucose significantly increased Q_{10} values of microbial respiration (overall CO_2 efflux) as compared with Q_{10} values without glucose addition, which can be referred to as 'added-substrate effect', and (2) without glucose addition, planted soils with higher indigenous carbon substrate availability tended to produce apparent Q_{10} values closer to their intrinsic Q_{10} values than unplanted soils with lower indigenous carbon substrate availability, which can be referred to as 'original-substrate effect'.

Relative temperature sensitivities of autotrophic and heterotrophic soil respiration

Our results, based on a novel continuous ^{13}C-labeling method to partition soil respiration, showed that heterotrophic soil respiration was more temperature-sensitive than autotrophic soil respiration, because soil warming increased the ratio of C_s/C_t (Fig. 2c), especially for the soybean treatment in experiment-3. However, regarding whether autotrophic (root-derived, C_r) and heterotrophic (SOM-derived, C_s) components of soil respiration (C_t) respond similarly to temperature, published results have been highly controversial (Boone *et al*., 1998; Baath & Wallander, 2003; Hartley *et al*., 2007).

Evidence for higher temperature sensitivity of C_r than of C_s mostly comes from seasonally coupled measurements of temperature, C_t, and C_s using root-exclusion method. Studies using this approach (Boone *et al*., 1998; Zhou *et al*., 2007; Gaumont-Guay *et al*., 2008) generally found much higher seasonally derived Q_{10} values for C_r (2.5–5.0) than for C_s (1.5–3.0). It has been pointed out that seasonally derived Q_{10} values are confounded by other variables that affect C_r and/or C_s and co-vary with temperature, such as light and photosynthesis, root dynamics, soil moisture and substrate availability (Curiel Yuste *et al*., 2004; Mahecha *et al*., 2010). For example, when high temperature during temperate zone summers is accompanied with high root biomass and photosynthesis, seasonally derived Q_{10} value of C_r can be erroneously high (e.g. 4.6, Boone *et al*., 1998).

Cases of higher temperature sensitivity of C_s than of C_r have been reported from a wheat/maize field soil warming experiment that used trenching to separate C_s from C_r (Hartley *et al*., 2007), and from two boreal forest field studies that compared responses of C_s and C_r (separated by girdling or trenching) to temperature changes at relatively short time scales (20-day in Bhupinderpal-Singh *et al*., 2003; diurnally in Gaumont-Guay *et al*., 2008). Higher temperature sensitivity of C_s than of C_r is logical if C_r is tightly coupled with aboveground photosynthesis (Hogberg *et al*., 2001; Kuzyakov & Cheng, 2001) and is largely controlled by belowground carbon allocation, which often shows a transient response to warming (Atkin & Tjoelker, 2003; Burton *et al*., 2008). In our study, soil warming tended to increase the ratio of C_s/C_t (Fig. 2c), suggesting a higher temperature sensitivity of C_s than of C_r. However, likely because we used the conservative method for estimating the confidence interval of C_s/C_t (IsoError model, Phillips & Gregg, 2001), the soil warming effect on C_s/C_t was statistically significant ($P<0.05$) only for the soybean treatment in experiment-3 where RPE was large in magnitude and highly sensitive to warming (Fig. 2b).

Additionally, many studies have demonstrated that there is no significant difference in temperature sensitivity between C_s and C_r. For example, Baath & Wallander (2003) and Moyano *et al*. (2007) used similar physical barrier methods (specially designed microcosms in a growth chamber and micro-pore meshes in a barley field) for C_t partitioning and found no significant difference in Q_{10} values among different components of total soil respiration. Using ^{13}C-isotope (Dorrepaal *et al*., 2009) or trenching (Schindlbacher *et al*., 2009) methods for C_t partitioning and field soil warming for Q_{10} determination, these two recent studies also reported equal responses of C_s and C_r to warming. We used a novel continuous ^{13}C labeling method for C_t partitioning and soil warming for Q_{10} determination in this study. In the first trapping of experiment-2, when sunflower was small and at vegetative stage and RPE was low in magnitude, there was no difference in C_s/C_t ratio between ambient condition and warming condition (Fig. 2c), indicating similar temperature sensitivity between C_s and C_r.

Overall, our results suggest that heterotrophic soil respiration may be more or equally sensitive to temperature than autotrophic soil respiration, depending on the magnitude and temperature sensitivity of RPE. New methods (e.g. apply the continuous ^{13}C labeling method to the field with less disturbed soils and at longer time scales) are recommended in future studies to further investigate this issue.

Implications for the debate on the temperature sensitivity of SOM decomposition

Our results challenge the reliability and the applicability of many existing temperature sensitivity assessments which omitted RPE. First, laboratory soil incubation experiments do not include roots and ignore the important part of the rhizosphere (e.g. Holland *et al*., 2000; Conant *et al*., 2008). Our results clearly demonstrate that the presence of roots can change both the magnitude and the temperature sensitivity of SOM decomposition through RPE. Therefore, serious caution is needed when extrapolating results from studies using soil incubation without roots to real field conditions where roots and soils are always interacting with each other. Second, earlier field soil warming experiments (e.g. Luo *et al*., 2001; Melillo *et al*., 2002) measured total soil respiration from both ambient and heated plots. If SOM decomposition and rhizosphere respiration have different temperature sensitivities, as demonstrated by our results, the real temperature sensitivity of SOM decomposition is confounded by the temperature sensitivity of rhizosphere respiration (Curiel Yuste *et al*., 2004; Bader & Cheng, 2007). The results from these experiments should be interpreted with caution. Third, recent field soil warming experiments partitioned total soil respiration into SOM- and root-derived components using root-exclusion methods in both ambient and heated plots, but ignored RPE in the partitioning process by assuming that SOM decomposition in control (rooted) plot is equal to that in root-excluded plot (e.g. Hartley *et al*., 2007; Zhou *et al*., 2007; Schindlbacher *et al*., 2009). However, because RPE can be large in magnitude and sensitive to temperature as indicated by the results of our current study and previous studies (Cheng & Kuzyakov, 2005; Dijkstra & Cheng, 2007a), the real temperature sensitivity of SOM decomposition should not be determined by using any root-exclusion method. Therefore, in design of future laboratory or field experiments, we recommend

consideration of RPE in separating SOM decomposition from rhizosphere respiration by using isotope methods (e.g. continuous ^{13}C-labeling or ^{14}C isotopes).

Our results also have important implications for the positive feedback between SOM decomposition and climate change (Davidson & Janssens, 2006). If our finding that root-derived carbon inputs increase the temperature sensitivity of original SOM decomposition is a general phenomenon, the positive feedback between SOM decomposition and climatic warming will be even higher than previous estimates based on results mostly from root-free soil incubation experiments. Models failing to consider root–soil interactions, i.e., RPE, underestimate soil carbon decomposition in response to future warming. It should be noted that our results of RPE are from two crop species grown in a growth chamber at relatively short time scales (50–60 days). Although Dijkstra & Cheng (2007a) showed that RPE of two tree species on the decomposition of three soils persisted throughout the 395-day period, how RPE affect the magnitude and temperature sensitivity of SOM decomposition under field conditions and at longer time scales (seasons and years) requires further investigation. Nevertheless, our results clearly highlight the need to pay due attention to root–soil interactions or RPE in future studies which aim to more accurately predict the temperature sensitivity of SOM decomposition and its feedback to climate change.

Conclusions

In conclusion, results from three independent growth chamber experiments demonstrated that root–soil interactions via RPE significantly and consistently increased the temperature sensitivity of SOM decomposition. We proposed a mechanistic hypothesis to explain this observation: the presence of roots via RPE activated soil microbes and increased SOM-derived substrate availability, which further increases the temperature sensitivity of SOM decomposition if SOM decomposition follows Michaelis–Menten kinetics. Soil warming substantially intensified RPE on SOM decomposition, and increased the proportional contribution of SOM decomposition to total soil respiration, suggesting a higher temperature sensitivity of SOM decomposition than that of autotrophic respiration. Taken together, these results clearly showed that root–soil interactions via RPE play a pivotal role in determining the temperature sensitivity of SOM decomposition. Results of the temperature sensitivity of SOM decomposition from previous laboratory soil-incubation or field root-exclusion experiments which ignored RPE should be interpreted with caution. More attention should be paid to root–soil interactions or RPE in future experimental and modeling studies of SOM decomposition.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix SA1. A synthesis of rhizosphere priming effect on SOM decomposition (28 observations from 14 studies, an update based on Cheng & Kuzyakov, 2005).

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