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Labile substrate availability controls temperature sensitivity of organic carbon decomposition at different soil depths

Xueyong Pang · Biao Zhu · Xiaotao Lü · Weixin Cheng

Abstract The decomposition of soil organic carbon (SOC) is intrinsically sensitive to temperature. However, the degree to which the temperature sensitivity of SOC decomposition (as often measured in Q_{10} value) varies with soil depth and labile substrate availability remain unclear. This study explores (1) how the Q_{10} of SOC decomposition changes with increasing soil depth, and (2) how increasing labile substrate availability affects the Q_{10} at different soil depths. We measured soil CO_2 production at four temperatures (6, 14, 22 and 30 °C) using an infrared CO_2 analyzer. Treatments included four soil depths (0–20, 20–40, 40–60 and 60–80 cm), four sites (farm, redwood forest, ungrazed and grazed grassland), and two levels of labile substrate availability (ambient and saturated by adding glucose solution). We found that Q_{10} values at ambient substrate availability decreased with increasing soil depth, from 2.0–2.4 in 0–20 cm to 1.5–1.8 in 60–80 cm. Moreover, saturated labile substrate availability led to higher Q_{10} in most soil layers, and the increase in Q_{10} due to labile substrate addition was larger in subsurface soils (20–80 cm) than in surface soils (0–20 cm). Further analysis showed that microbial biomass carbon (MBC) and SOC best explained the variation in Q_{10} at ambient substrate availability across ecosystems and depths ($R^2 = 0.37$, $P < 0.001$), and MBC best explained the variation in the change of Q_{10} between control and glucose addition treatment ($R^2 = 0.14$, $P = 0.003$).

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Overall, these results indicate that labile substrate limitation of the temperature sensitivity of SOC decomposition, as previously shown in surface soils, is even stronger for subsoils. Understanding processes controlling the labile substrate availability (e.g., with rising atmospheric CO_2 concentration and land use change) should advance our prediction of the fate of subsoil SOC in a warmer world.

Introduction

Changes in soil carbon, the largest terrestrial carbon pool, regulate the global carbon cycle, atmospheric CO_2 levels, and the global climate (Amundson 2001). The decomposition of soil organic carbon (SOC) is intrinsically sensitive to temperature (Davidson and Janssens 2006). Increased decomposition of SOC due to soil warming is an important potential feedback to climate change (Davidson and Janssens 2006; Luo and Zhou 2007; Smith et al. 2008). Therefore, accurate representation of the temperature sensitivity of SOC decomposition (often measured in Q_{10} value) in Earth System Models (ESMs) is crucial because it affects our predictions of the impact of climate change on soil carbon stock (Holland et al. 2000; Fang et al. 2005; Foereid et al. 2014). However, there is still no consensus on how the temperature sensitivity of SOC decomposition varies with biotic and abiotic factors (Davidson and Janssens 2006; Kirschbaum 2006; Smith et al. 2008; von Lützow and Kögel-Knabner 2009; Subke and Bahn 2010; Conant et al. 2011), such as soil depth (Fierer et al. 2003; Rey et al. 2008; Gillabel et al. 2010) and labile substrate availability (Davidson and Janssens 2006; Gershenson et al. 2009; Fissore et al. 2013).

In well-drained upland soils, the chemical composition and turnover time of SOC change significantly with increasing soil depth (Trumbore 2000; Rumpel et al. 2002; Schrumpf et al. 2013). Soil organic matter (SOM) consists of compounds of vastly different structures and properties. It is commonly perceived that the fraction of less reactive and more recalcitrant organic matter increases with increasing soil depth, meaning that the organic matter at depth is less

biodegradable and has more complicated structure than the organic matter at surface (Rumpel et al. 2002; Spielvogel et al. 2008; Hassouna et al. 2010). Kinetic theory predicts that the intrinsic temperature sensitivity of decomposition increases with increasing recalcitrance of the carbon compounds (Bosatta and Ågren 1999). Therefore, the intrinsic Q_{10} value of soil respiration is expected to increase with increasing soil depth. However, previous studies have shown inconsistent patterns of Q_{10} values of soil respiration with soil depth. Increase (Lomander et al. 1998; Fierer et al. 2003; Jin et al. 2008; Karhu et al. 2010), decrease (Winkler et al. 1996; MacDonald et al. 1999; Gillabel et al. 2010), or no changes (Fang et al. 2005; Leifeld and Fuhrer 2005; Rey et al. 2008) in apparent Q_{10} values with increasing soil depth have been observed in different studies. Much of the variation in the apparent temperature sensitivity of SOC decomposition may be related to the fact that labile substrate availability is often unaccounted for in these studies (Davidson and Janssens 2006; Gershenson et al. 2009; Conant et al. 2011). Therefore, in-depth studies are needed, particularly those in which labile substrates are added to a range of soil types and depths.

A theoretical relationship between labile substrate availability and the temperature sensitivity of SOC decomposition has been described using the Michaelis–Menten model (Michaelis and Menten 1913), which is well tested and widely used in studying enzymatic kinetics (Marx et al. 2005; German et al. 2012). The Michaelis–Menten equation for soil respiration can be written in the form $R = (V_{max}[C])/(K_m + [C])$, where R is soil respiration rate, V_{max} is the maximal rate of enzymatic activity, K_m is the dissociation constant (or 'half-saturation constant'), and $[C]$ is the concentration of organic carbon substrates. Both V_{max} and K_m are positively temperature dependent. When substrate concentration is at or above the saturation level, the temperature sensitivity of soil respiration approaches the temperature sensitivity of V_{max}, or the *intrinsic* temperature sensitivity. When substrate concentration is below the saturation level, the temperature sensitivity of K_m becomes important, and the overall temperature sensitivity of soil respiration (also defined as the *apparent* temperature sensitivity) decreases below that of V_{max}. Applying this equation to soil respiration offers a plausible mechanistic explanation for the current controversy concerning the role of substrate

availability in affecting the temperature sensitivity of SOC decomposition (Davidson and Janssens 2006). Although empirical validation of the Michaelis–Menten model for soil respiration using surface soils has been reported (Larionova et al. 2007; Gershenson et al. 2009; Curiel Yuste et al. 2010; Zhu and Cheng 2011b; Fissore et al. 2013), little experimental evidence come from subsurface soils. Subsurface soils contain more carbon than surface soils at the global scale (Jobbágy and Jackson 2000), have a greater amount of mineral-associated or physically-protected organic carbon (Schrumpf et al. 2013), and play a crucial role in the global carbon cycle (Rumpel and Kögel-Knabner 2011). Therefore, in-depth studies of the temperature sensitivity of subsurface soils in general and the mechanistic relationship between the substrate status and the temperature sensitivity of subsoils in particular are needed.

In this study, we aimed to explore (1) how the Q_{10} of SOC decomposition changes along the soil profile, and (2) how the Q_{10} of SOC decomposition responds to a saturated labile substrate level (through glucose addition) at different soil depths. We collected soils at four different depths (0–20, 20–40, 40–60, and 60–80 cm) from four ecosystems (farm, redwood forest, ungrazed grassland, and grazed grassland), and measured the temperature sensitivity of SOC decomposition at ambient (without glucose addition) and saturated (with glucose addition) labile substrate availability. We chose glucose because it has been widely demonstrated as a readily available common substrate for most soil microbes (Anderson and Domsch 1978; Cheng et al. 1996). The soil respiration after addition of glucose at or above the saturation level has been called the substrate-induced respiration. Studies (Anderson and Domsch 1978; Lin and Brookes 1999) have shown that substrate-induced respiration remains nearly constant during the initial 4 h period before any microbial growth is noted.

We have two specific hypotheses in this study. First, at ambient substrate condition (without glucose addition), increasing soil depth leads to increasing intensity of physico-chemical protection of SOC and decreasing amount of labile substrate for microbial respiration (Rumpel and Kögel-Knabner 2011; Schrumpf et al. 2013). This increasing substrate limitation causes decreasing apparent temperature sensitivity of SOC decomposition with increasing depth (Gillabel et al. 2010). Second, if the kinetics of

soil respiration can be adequately approximated by the Michaelis–Menten equation, Q_{10} of the substrate-induced respiration should be significantly higher than that of the basal respiration without substrate addition, because the canceling effect of the temperature sensitivity of K_m on the temperature sensitivity of soil respiration is negligible when the substrate is saturated and much higher than $K_m([C] \gg K_m$, Davidson and Janssens 2006; Larionova et al. 2007; Gershenson et al. 2009). Moreover, the change in Q_{10} after substrate addition is more significant in subsurface soils where organic carbon is more protected and less available for microbial respiration (Rumpel and Kögel-Knabner 2011). In short, we hypothesized that (1) the Q_{10} of microbial respiration at ambient substrate availability decreases with increasing soil depth, and (2) the Q_{10} of microbial respiration increases with glucose addition, particularly for subsurface soils.

Materials and methods

Soil sampling and experimental setup

Soil samples were collected from four ecosystems in the Natural Reserve on the campus of University of California, Santa Cruz. Santa Cruz has a Mediterranean climate, with cool wet winters and warm dry summers. The four sites include an organic farm which has been planted with various crops and vegetables (sunflower, strawberry, lettuce, etc.) since its conversion from grassland in 1974, a redwood (*Sequoia sempervirens*) forest which was logged about 90 years ago and has not experienced fire since then, an ungrazed grassland dominated by non-native annual grasses, and a cow-grazed grassland with more native perennial forbs (Gershenson et al. 2009). We chose these four sites to test whether the depth control of substrate-induced temperature sensitivity of SOC decomposition varies across landuse changes (cropland, forest, ungrazed and grazed grassland). At each site, we collected soils from four randomly chosen locations within 100 m; each of these four locations was considered as a field replicate. At each location, we dug a soil pit and collected soils at four depths (0–20, 20–40, 40–60 and 60–80 cm). All soils were limestone-derived sandy soils in the region, with pH values from 4 to 6 and without detectable carbonates

Table 1 Soil organic C (SOC, g kg^{-1}), total N (g kg^{-1}), C:N ratio, 0.5 M K$_2$SO$_4$ extractable organic C (EOC, mg kg^{-1}), microbial biomass C (MBC, mg kg^{-1}), EOC:SOC (%) and MBC:SOC (%) of soils from different layers of farm, redwood forest, ungrazed grassland, and grazed grassland ecosystems (mean ± SE, n = 4). Means with different letters (a, b, c or d) indicate statistically significant ($P < 0.05$) difference between the two mean values at different depths based on Student t-test

Ecosystem	Layer (cm)	SOC	Total N	C:N	EOC	MBC	EOC:SOC	MBC:SOC
Farm	0–20	10.9 ± 0.2a	1.1 ± 0.0a	9.7 ± 0.2a	56 ± 3a	109 ± 4a	0.51 ± 0.03a	1.00 ± 0.02a
	20–40	8.3 ± 1.1b	0.9 ± 0.1b	9.0 ± 0.4a	54 ± 4a	63 ± 10b	0.70 ± 0.13a	0.75 ± 0.04b
	40–60	4.5 ± 0.5c	0.6 ± 0.0c	7.9 ± 0.2b	41 ± 3b	16 ± 2c	0.94 ± 0.14ab	0.36 ± 0.05c
	60–80	3.0 ± 0.5c	0.4 ± 0.1c	7.0 ± 0.2c	35 ± 3b	4 ± 1d	1.24 ± 0.17b	0.12 ± 0.01d
	P value	<0.001	<0.001	0.122	0.01	<0.001	<0.05	<0.001
Redwood forest	Oi*	na	15.0 ± 0.6a	na	1944 ± 122	3631 ± 679a	na	na
	0–20	77.2 ± 4.9a	4.7 ± 0.3b	16.5 ± 0.5a	114 ± 16a	499 ± 76b	0.15 ± 0.02a	0.64 ± 0.07a
	20–40	42.1 ± 5.5b	2.8 ± 0.3c	15.1 ± 0.9a	75 ± 11ab	236 ± 37c	0.20 ± 0.06a	0.56 ± 0.03a
	40–60	26.2 ± 3.9bc	1.7 ± 0.3 cd	15.9 ± 1.7a	62 ± 12b	131 ± 20d	0.27 ± 0.09a	0.51 ± 0.08a
	60–80	18.7 ± 2.2c	1.0 ± 0.1 cd	16.0 ± 1.6a	53 ± 9b	83 ± 9d	0.29 ± 0.06a	0.45 ± 0.02a
	P value	<0.001	<0.001	0.894	0.018	<0.001	0.385	0.134
Ungrazed grassland	0–20	16.2 ± 3.9a	1.4 ± 0.3a	11.0 ± 0.4a	55 ± 2a	398 ± 37a	0.27 ± 0.12a	1.83 ± 0.14a
	20–40	10.1 ± 1.9ab	1.0 ± 0.2a	9.9 ± 0.7a	63 ± 11a	151 ± 17b	0.36 ± 0.23ab	0.99 ± 0.14ab
	40–60	8.3 ± 0.5ab	0.8 ± 0.0a	10.4 ± 0.6a	59 ± 6a	80 ± 9bc	0.42 ± 0.22ab	0.74 ± 0.13b
	60–80	5.9 ± 1.0b	1.0 ± 0.3a	8.9 ± 0.5a	71 ± 15a	33 ± 7c	0.57 ± 0.19a	0.64 ± 0.10b
	P value	0.057	0.333	0.158	0.7	<0.001	<0.05	0.012
Grazed grassland	0–20	20.8 ± 4.0a	1.7 ± 0.2a	11.7 ± 0.7a	44 ± 14a	366 ± 47a	0.42 ± 0.12a	2.91 ± 0.66a
	20–40	14.8 ± 3.6ab	1.2 ± 0.2ab	11.6 ± 1.1a	35 ± 16a	146 ± 39b	0.66 ± 0.10a	1.67 ± 0.43b
	40–60	10.8 ± 2.3ab	0.9 ± 0.1b	11.0 ± 1.3a	33 ± 10a	74 ± 14c	0.70 ± 0.04a	0.97 ± 0.13b
	60–80	7.9 ± 0.9b	0.8 ± 0.0b	10.5 ± 0.8a	41 ± 9a	49 ± 8c	1.33 ± 0.44a	0.46 ± 0.05b
	P value	0.046	0.007	0.808	0.928	<0.001	0.735	<0.001

na not available

(Gershenson et al. 2009; Zhu and Cheng 2011a). Organic C content ranged from 10.9 to 77.2 mg g^{-1} dry soil at 0–20 cm layer and gradually dropped to 3.0 to 18.7 mg g^{-1} dry soil at 60–80 cm layer across the four ecosystems (Table 1).

All soil samples were brought to the laboratory, picked free of roots, hand homogenized, and passed through a 4 mm sieve. Each sample was divided into eight 150 g aliquots; each aliquot was placed in a separate 150 cm^3 (5 cm in diameter and 20 cm in length) copper tube, which was covered with white paint to minimize the potential impact of copper on microbial activity (Fig. S1). We closed both ends of the copper tube using synthetic rubber stoppers connected with plastic tubing for air circulation. The stopper at the air inlet end was further connected with a semi-rigid polyethylene tube perforated with many small pin holes. The polyethylene tube was placed at the center of the copper tube for homogenously adding

water or glucose solution into the soil sample inside the copper tube before respiration measurement. Separate copper tubes were treated with two labile substrate treatments (Gl+ for added glucose and CK for ambient substrate), and submerged into four temperature-controlled water baths (6, 14, 22 and 30 °C, Fig. S1). The four temperatures are within the natural temperature range experienced by these soils in the region. We added 100 g L^{-1} glucose solution to Gl+ samples using a 20 ml syringe at a calculated amount (10–15 ml per sample, or 3.69–5.54 mg C g^{-1} soil) that gave soil water at 100 % holding capacity and saturated carbon substrate concentration (Cheng and Coleman 1989). Deionized water (DI) was added to ambient substrate replicates in the same manner to avoid differences in soil moisture. We took precautions to minimize the disturbance due to soil sampling and processing. In order to best reflect natural differences in substrate availability among soil depths,

we (1) gently processed and sieved the fresh soils using 4.0 mm screen which minimally disrupted soil aggregates; (2) carried out respiration measurements within 3 h from the initial collection of the soil samples to minimize the loss of naturally available substrate to respiration, and (3) did one soil pit (or field replicate) of one ecosystem type per day in order to keep soils fresh and finish the above tasks within the required time period. The experiment is a full factorial design, including four ecosystems, four soil depths, four temperatures, two substrate concentrations, and four field replicates.

Soil respiration measurement

We measured soil respiration rate using the methodology described by Cheng and Virginia (1993) and Gershenson et al. (2009) with critical improvement for subsurface soils. The use of the copper tube allows a much higher amount of soil sample than the original method (150 vs. 20 g), and significantly improves the sensitivity of the measurement, especially for subsurface soils with much lower respiration rates. The copper tube also maintains better thermal equilibrium with water bath temperature than does a glass flask, and the perforated polyethylene tube inside the copper tube ensures homogeneous distribution and faster diffusion of substrates through the soil column.

Briefly, an air pump forces ambient air through a soda-lime column, thereby producing CO_2-free air. The CO_2-free air travels through a copper coil submerged in the water bath to equilibrate air temperature with water bath temperature, and then enters a manifold, from which individual tubes lead to individual sample inflow tubes. The flow of air to each sample is controlled by a needle valve to ensure a constant flow rate (80 ± 5 mL min^{-1}). One of the outlets was connected to an empty copper tube without soil and was used as a blank. Prepared copper tubes with soil samples were allowed to acclimate to water bath temperature for 1 h before respiration measurements occurred. Previous studies (Gershenson et al. 2009; Zhu and Cheng 2011b) showed that 1 h was adequate for respiration of these soils to equilibrate at such temperatures. We measured soil respiration by connecting a LiCOR IRGA 6262 (LiCOR Biosciences, Lincoln, NB, USA) and a mass flow meter to the outflow tube of each sample, and recorded the flow rate and the concentration of CO_2 in the sample.

Respiration measurement for one sample lasted approximately 2 min, which ensures both the accuracy of each measurement and finishing all measurements during the initial stable phase of the substrate-induced respiration (0–5 h after glucose addition).

Four water baths were set up with temperatures of 6, 14, 22 and 30 °C. Temperature in the 6 and 14 °C were automatically maintained by chilled water (about 3 °C) circulated through heat exchangers made of copper tubing and pumps (Fig. S1). The automatic control was accomplished by monitoring water temperature at 1 min intervals using calibrated thermocouples (Omega thermocouple type-T, Stamford, CT, USA) connected to a datalogger (Campbell Scientific CR10X, Logan, UT, USA) which triggers on–off controls of the two circulating pumps. The chilled water was supplied by an automated water chiller (ADVANTAGE M1-.5A, Greenwood, IN, USA) with a temperature control accuracy of ± 0.1 °C. Temperature in the 30 °C water bath was maintained using a processor-controlled temperature regulator (VWR 1122 Polyscience 1122 Heating Circulator, Manasquan, NJ, USA). Temperature in the 22 °C treatment (close to the room temperature) was regulated manually by adding cold or warm water as needed. We also verified the temperature in each water bath by manual measurements every 10 min using a mercury thermometer.

Analysis of soil organic C, total N, extractable organic C, and microbial biomass C

We dried (105 °C and 48 h in an oven) and ground a subsample (20 g) of the soils from each replicate. Ground soil samples were analyzed for C and N % on a Carlo Elba 1108 elemental analyzer. We also measured microbial biomass carbon (MBC) using the chloroform fumigation-extraction method with a slight modification (Vance et al. 1987). In brief, two 50 g subsample of each moist soil were weighed to measure microbial biomass carbon. One subsample was fumigated for 48 h at 22 °C with ethanol-free $CHCl_3$ and the other subsample was kept as unfumigated. These two subsamples were then extracted with 60 ml 0.5 M K_2SO_4 for 2 h by reciprocating shaker and filtered. Organic C in extracts was determined with a Shimadzu TOC-5050A analyzer equipped with a Shimadzu ASI-5000A autosampler. Microbial biomass C was calculated as follows: microbial

biomass $C = E_C/k_{EC}$, where E_C is the difference between organic C extracted from fumigated soils and that from non-fumigated soils and $k_{EC} = 0.45$ (Beck et al. 1997). Admittedly, the extraction efficiency, k_{EC}, might vary to some degree across ecosystems and soil depths. But, accurate determination of each k_{EC} value would require excessive amount of work beyond the focus of this study. Extractable organic carbon in the unfumigated samples was used as an indication of the ambient labile carbon substrate availability.

Calculations and statistical analysis

In order to determine the dry weight of samples, we took a sample of each replicate, dried it at 105 °C for mineral soil samples and 70 °C for the forest organic horizon samples, and determined gravimetric water content. The samples were weighed to nearest 0.01 g before and after drying on an analytical balance. We compared soil properties between different soil horizons within each soil type using one-way ANOVA (analysis of variance) and Tukey's post hoc test (Table 1).

We used the following equation (Gershenson et al. 2009) to calculate the respiration rate of each soil sample (Table S1):

$$R_r = 0.536 \times \frac{(C \times R_f)}{W_s} \qquad (1)$$

where R_r is soil respiration rate in mg CO_2-C g^{-1} SOC h^{-1}, C is the recorded CO_2 concentration in μmol CO_2 mol^{-1}, R_f is the recorded flow rate in mL h^{-1}, and W_s is the gram dry weight of the sample.

We fitted the measured respiration rates for the CK and Gl+ treatments to the van't Hoff equation (1899):

$$R_r = \alpha e^{\beta T} \qquad (2)$$

where α and β are fitted parameters. We determined the Q_{10} value for each treatment combination using the equation:

$$Q_{10} = e^{\beta 10} \qquad (3)$$

we used multi-factor ANOVA to assess the effects of Ecosystem (main factor), Depth (split-plot design), Substrate (repeated-measure), and their interactions on the temperature sensitivity of SOC decomposition (Q_{10}, Table 2). In addition, we used Pearson correlation (Table S2) and multiple linear regression (stepwise, Table S3) to explore the relationships between soil properties and the Q_{10} at ambient substrate condition (Q_{10}) as well as the change in Q_{10} with substrate addition (ΔQ_{10}) across ecosystems and depths. Curve fitting was performed using Origin 8.0 (Origin Inc.) and statistical analysis was performed using PASW Statistics 18v (SPSS Inc.).

Results

Soil properties among ecosystems and depths

Most of soil properties were significantly different among ecosystems and soil depths (Table 1). Organic C and total N both decreased with soil depth in all four ecosystems, while C:N ratio only declined in the farm soil and did not change with soil depth in the forest and two grassland soils. Extractable organic carbon (EOC, as measured in unfumigated samples) declined slightly in farm and redwood forest soils, but remained stable in two grassland soils with depth. Microbial biomass carbon (MBC) decreased dramatically with soil depth in all four ecosystems. Moreover, the ratio of EOC to SOC showed increasing trend with soil depth (not significant in redwood forest and grazed grassland), while the ratio of MBC to SOC declined progressively with soil depth (not significant in redwood forest).

Soil respiration and Q_{10} under ambient substrate condition

We observed large variations in soil respiration rate among ecosystems and soil depths. Soil respiration rate per unit soil organic carbon (μg CO_2-C g^{-1} C h^{-1}) under ambient substrate condition (CK) at each depth increased exponentially with temperature (Table S1). The temperature sensitivity (Q_{10}) under ambient substrate condition significantly decreased with increasing soil depth (Table 2; Fig. 1). In the farm soil, Q_{10} was significantly higher in 0–20 cm layer than in both 40–60 cm and 60–80 cm layers ($P < 0.05$), but was not different between 0–20 cm and 20–40 cm depth (Fig. 1a). In redwood forest soil, Q_{10} of the Oi organic layer was significantly higher than that of the top 0–20 cm mineral soil ($P < 0.001$), and Q_{10} of 0–20 cm layer was significantly higher than that of the following three depths (20–40, 40–60, and

Table 2 ANOVA analyses of Q_{10} values for the effect of Ecosystem (four ecosystem types, main factor), Depth (four depth intervals, split-plot design), Substrate (before and after glucose addition, repeated-measure design), and their interactions

	df	SS	MS	F	P
Ecosystem	3	1.46	0.49	10.04	<0.001
Depth	3	2.89	0.96	19.87	<0.001
Substrate	1	2.97	2.97	289.23	<0.001
Ecosystem × depth	9	0.34	0.04	0.79	0.627
Ecosystem × substrate	3	0.25	0.08	8.04	<0.001
Depth × substrate	3	0.14	0.05	4.39	0.008
Ecosystem × depth × substrate	9	0.17	0.019	1.86	0.081

SS Sum of squares, *MS* Mean square

60–80 cm, $P < 0.05$, Fig. 1b). In the ungrazed grassland soil, the only significant difference in Q_{10} was between 0–20 and 60–80 cm layers ($P < 0.01$, Fig. 1c), whereas in the grazed grassland soil, Q_{10} of the top two depths (0–20 and 20–40 cm) was significantly higher than Q_{10} of the deeper two layers (40–60 and 60–80 cm, $P < 0.001$, Fig. 1d).

Responses of soil respiration and Q_{10} to labile substrate saturation

Labile substrate saturation strongly affected soil respiration rates. After adding a saturated level of glucose solution (Gl+), soil respiration rate significantly increased, with the magnitude depending on ecosystems and depths (Table S1). Labile substrate saturation also had significant impacts on the temperature sensitivity of soil respiration (Table 2, Fig. 1): it significantly increased Q_{10} of soil respiration in most soil depths of the four ecosystems ($P < 0.001$), except for Oi and 0–20 cm layers of the redwood forest soil (Fig. 1b), and 0–20 and 20–40 cm layers of the ungrazed grassland soil (Fig. 1c). In addition, the increase in Q_{10} after glucose addition was significantly stronger in subsurface soils (20–80 cm) than in surface soils (0–20 cm). For example, adding glucose resulted in 13.2, 11.1, 11.3 and 2.4 % increases in Q_{10} in the 0–20 cm layer, but 18.7, 9.4, 28.9 and 22.7 % increases in Q_{10} in the 60–80 cm layer of farm, redwood forest, ungrazed grassland, and grazed grassland soils, respectively (Figs. 1, 2). Within each ecosystem, the glucose-induced Q_{10} change was not significantly different among the three subsoil layers (20–40, 40–60, and 60–80 cm), but it was significantly

higher in all three subsoil layers than in the topsoil (0–20 cm), except for the redwood forest soil (Fig. 2).

Relationships between soil properties and Q_{10}

We used multi-factor ANOVA to assess the effect of ecosystem, depth (split-plot), substrate (repeated-measure), and their interactions on Q_{10} (Table 2). The effect of depth on Q_{10} was significant ($P < 0.001$) and consistent across all ecosystems (no depth by ecosystem interaction, $P = 0.627$). Additionally, the effect of substrate on Q_{10} was significant ($P < 0.001$), but it was stronger at depth than at surface (significant substrate by depth interaction, $P < 0.01$) and weaker in the forest than in the other ecosystems (significant substrate by ecosystem interaction, $P < 0.001$). Finally, the insignificant three-way interaction ($P = 0.081$) indicates that the stronger substrate-induced Q_{10} at depth (or the substrate-depth interaction on Q_{10}) was observed in all four ecosystems.

In order to explore what soil properties drive the variations of Q_{10} under ambient substrate condition (Q_{10}) and change in Q_{10} with substrate addition (ΔQ_{10}) across ecosystems and depths, we further carried out Pearson correlation analysis and multiple linear regression (stepwise) analysis. Q_{10} values at ambient substrate condition of all 64 samples were positively correlated to total N ($r = 0.47$, $P < 0.001$) and microbial biomass C ($r = 0.51$, $P < 0.001$), indicating that these two soil properties are important in modulating the temperature sensitivity of SOC decomposition (Table 3). ΔQ_{10} values were negatively correlated with total N ($r = -0.41$, $P < 0.001$), microbial biomass C ($r = 0.37$, $P = 0.003$), C:N ratio

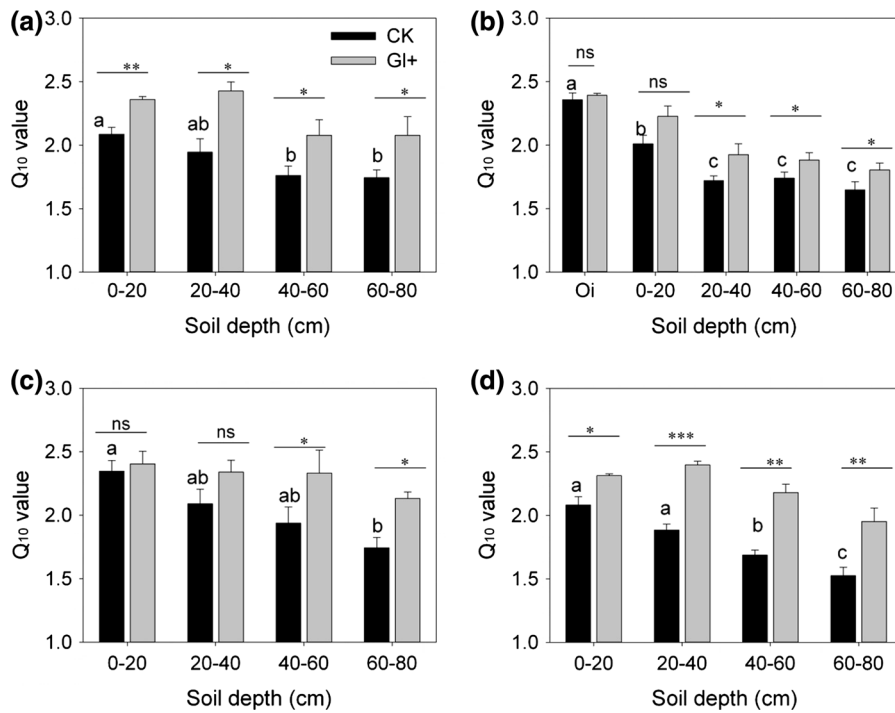**Fig. 1** Difference in Q_{10} (mean ± SE, n = 4) of soil respiration between ambient substrate (CK) and added substrate (Gl+) treatments in 0–20, 20–40, 40–60 and 60–80 cm soil layers of farm (**a**), redwood forest (**b**), ungrazed grassland (**c**), and grazed grassland (**d**) ecosystems. *Different letters* indicate significant ($P < 0.05$) differences in Q_{10} at ambient substrate (CK) among different soil layers. *Asterisks* indicate significant (*ns* not significant, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$) differences in Q_{10} between ambient (CK) and added (Gl+) substrate treatments for each soil layer

Fig. 2 Relative changes of Q_{10} after glucose addition in 0–20, 20–40, 40–60 and 60–80 cm soil layers from farm (**a**), redwood forest (**b**), ungrazed grassland (**c**), and grazed grassland (**d**) ecosystems, respectively. *Different letters* indicate significant ($P < 0.05$) differences among different soil depths
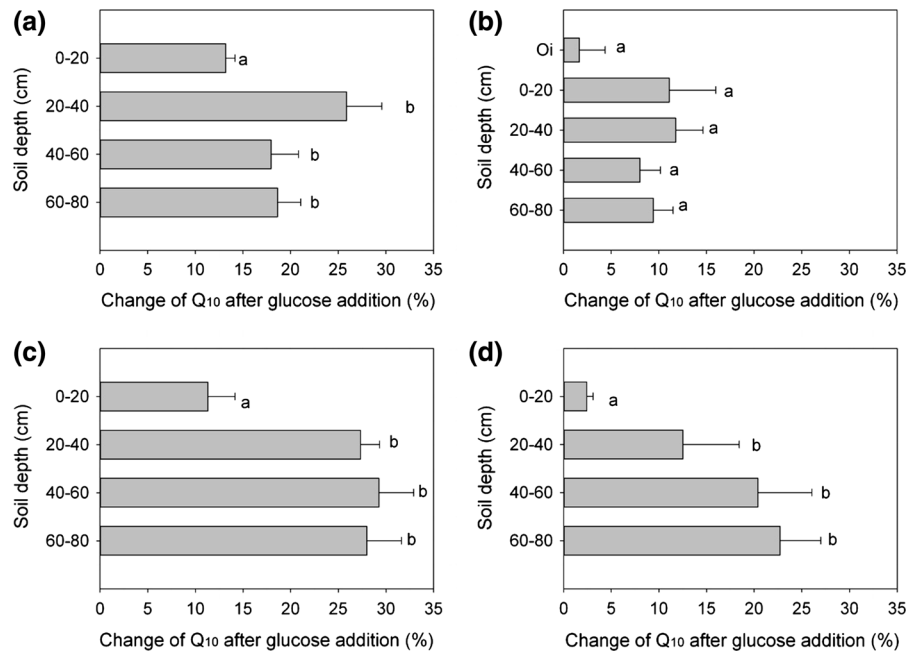
($r = 0.31$, $P = 0.014$), and SOC ($r = 0.30$, $P = 0.017$). However, when the interactions between soil variables were accounted for in the stepwise multiple linear regression analysis, only microbial biomass C and SOC explained statistically significant portion of the overall variations of Q_{10} values under ambient substrate condition ($R^2 = 0.39$, $P < 0.001$), and only microbial biomass carbon was statistically significant in its contribution to the variations of ΔQ_{10} ($R^2 = 0.14$, $P = 0.003$) across ecosystems and soil depths.

Discussion

We compared the temperature responses of SOC decomposition with increasing soil depth in four ecosystems with ambient substrate and adding readily available substrate (glucose) at the saturated level. The temperature sensitivity of microbial respiration (Q_{10}) at ambient substrate decreased with soil depth (Fig. 1). This decreasing trend seemed to be related to total soil N and microbial biomass C since both variables were significantly positively correlated with Q_{10} values at different depths (Table 3). Moreover, glucose addition increased Q_{10} at most soil depths, and this substrate-induced change in Q_{10} was higher in subsurface soils (20–80 cm) than in surface soils (0–20 cm) (Fig. 2). Taken together, our results provide strong

Table 3 Person correlation coefficients (r) between Q_{10} values under ambient substrate condition (Q_{10}) and soil properties (SOC, TN, C:N, EOC, MBC); and between the net change in Q_{10} values as a response to glucose addition treatment (ΔQ_{10}) and soil properties. Statistically significant ($P < 0.05$) correlations are indicated by the bold numbers

	Q_{10}		ΔQ_{10}	
	r	P	r	P
SOC	0.14	0.266	**−0.30**	**0.017**
TN	**0.47**	**<0.001**	**−0.41**	**<0.001**
C:N	0.05	0.722	**−0.31**	**0.014**
EOC	0.13	0.314	−0.21	0.104
MBC	**0.51**	**<0.001**	**−0.37**	**0.003**

Data are from four depths and four replicates, with four ecosystems together (n = 64)

SOC (soil organic carbon content, g kg^{-1}), *TN* (total N, g kg^{-1}), *C:N* (soil C:N ratio), *EOC* (0.5 M K$_2$SO$_4$ extractable organic C, mg kg^{-1}), *MBC* (microbial biomass C, mg kg^{-1})

experimental evidence for the role of labile substrate availability in controlling the temperature sensitivity of SOC decomposition, particularly for subsurface soils.

Q_{10} of SOC decomposition at ambient substrate condition decreases with depth

Consistent with our first hypothesis, the temperature sensitivity of SOC decomposition under ambient substrate condition significantly decreased with increasing soil depth in all four ecosystems (Fig. 1). Based on the Arrhenius equation, the more complicated chemical structure of a reactant, the higher activation energy the reaction needs (Arrhenius 1889; Bosatta and Ågren 1999). The Arrhenius equation also shows that reactants with higher activation energies (i.e., less reactive and more recalcitrant) should have higher temperature sensitivities (Bosatta and Ågren 1999; Davidson and Janssens 2006). In general, with increasing soil depth, organic matter becomes increasingly chemically recalcitrant (Rumpel et al. 2002; Lorenz and Lal 2005; Spielvogel et al. 2008). Therefore, the temperature sensitivity of SOC decomposition should theoretically increase with depth (Lomander et al. 1998; Fierer et al. 2003; Karhu et al. 2010). However, our results did not support this prediction, suggesting mechanisms other than chemical recalcitrance are needed to explain our results.

Results in the published literature point to two possible explanations as to why the temperature sensitivity of SOC decomposition decreases with depth in this study: (1) increase in physical protection of SOC and (2) change in microbial community structure with depth. First, the physical protection of SOC due to aggregation or association with soil minerals tends to increase with depth (Kögel-Knabner et al. 2008; Schrumpf et al. 2013), which may lead to a physical disconnect between microbes and substrates and a lower temperature dependence of microbial respiration in subsoils (Gillabel et al. 2010; Conant et al. 2011). Although physical protection of SOC was not directly measured in this study, MBC and total N contents may indicate the intensity of physical protection of SOC for microbial decomposition. These two variables showed declining trends with depth (Table 1) and positive correlations with Q_{10}, and best explained the variations in Q_{10} across ecosystems and depths (Table 3). Therefore, the increasing substrate

limitation for microbes due to physical protection of SOC may be one of the mechanisms driving the decreasing Q_{10} at ambient substrate condition with depth. Second, distinct microbial communities at different depths (Eilers et al. 2012; Stone et al. 2014) may have different thermal optima due to physiological adaptations to specific temperature regimes (Stark and Firestone 1996; Balser and Wixon 2009), which may partly account for the different temperature sensitivity of microbial respiration at different depths. Our correlation analysis indicate that microbial biomass C is an important variable in modulating Q_{10} values at different depths. It is likely that the changes in microbial biomass at different depths are also associated with changes in community composition which may directly contribute to the difference in Q_{10} values. Considering that these two proposed explanations are solely based on results in the literature. Further studies are needed to pinpoint the specific mechanisms (the physical protection of SOC, microbial community structure, or other factors such as soil moisture or nutrients) responsible for the decrease in Q_{10} values with depth observed in this study.

Glucose-induced increase in Q_{10} of SOC decomposition with depth

Soil microbial communities are generally carbon-limited (Cheng et al. 1996; Cleveland et al. 2007). We observed not only an increase in overall respiration rates (Table S1), but also an increase in Q_{10} values in added substrate treatments (Fig. 1). This result has been reported in previous studies using surface soils (e.g., Gershenson et al. 2009; Zhu and Cheng 2011b). Moreover, the effect of glucose addition on Q_{10} differed among soil depths (Fig. 2). We observed a larger increase of Q_{10} values in subsurface soil than that in surface soil following addition of a readily available substrate except in the redwood forest soil (Fig. 2). This result supports our second hypothesis, indicating that the temperature sensitivity of soil microbial respiration at deeper depths is more responsive to changes in labile substrate availability than the topsoil. Based on Michaelis–Menten model of soil respiration, adding a readily available carbon substrate at a saturate concentration should eliminate the canceling effect of K_m on the measured Q_{10} values (Davidson and Janssens 2006), and result in an increase of observed Q_{10} values. As a response to glucose addition, the larger increases in Q_{10} values for the subsoil than the topsoil in our study (Figs. 1, 2) indicate that the canceling effect of K_m on the measured Q_{10} value was much stronger for the subsoil than for the topsoil. The mechanism responsible for the lack of difference in the glucose-induced Q_{10} between topsoil and subsoil in the redwood forest ecosystem is unclear and awaits further investigation.

A number of emprical studies (Larionova et al. 2007; Gershenson et al. 2009; Curiel Yuste et al. 2010; Zhu and Cheng 2011b; Fissore et al. 2013) have identified the control of temperature sensitvitiy of microbial respiration by labile substrate availability (Davidson and Janssens 2006; Davidson et al. 2006). Larionova et al. (2007) showed that the temperature dependence of microbial respiration is dependent on the concentration of readily decomposable carbon (including native soil carbon and added glucose carbon) by adding increasing levels of glucose to two surface soils (forest and cropland). Three following studies (Gershenson et al. 2009; Curiel Yuste et al. 2010; Zhu and Cheng 2011b) found a rise in the temperature dependence of microbial respiration from the control (no glucose addition) to the saturated-glucose-addition treatment for various surface soils (bulk soil, rhizosphere soil, labile substrate-depleted soil) from a number of ecosystems (forest, grassland, cropland). Fissore et al. (2013) further reported lower temperature dependence of SOC decomposition for labile substrate-depleted soils through extended incubation than for non-depleted soils or substrate-depleted soils amended with saturated glucose. All these studies provide strong evidence for the role of labile substrate supply in controlling the temperature sensitivity of microbial respiration in surface soils (top 20 or 30 cm). Our current study moves a step forward by showing that the decomposition of subsurface SOC is even more responsive to labile substrate supply than that of surface SOC. To best reflect natural differences in labile substrate availability along the soil profile, we incubated freshly sampled and carefully processed soils in this study. However, any processing of soil, no matter how careful, will tend to release labile carbon, particularly for subsurface soils with higher intensity of physico-chemical protection. Therefore, labile substrate limitation for the temperature sensitvitiy of SOC decomposition is likely underestimated in this study.

Soil carbon stocks are comprised of pools with turnover times varying from days to decades, centuries and beyond. There has been apparently contradictory results on the relative temperature sensitivity of fast- vs. slow-cycling SOC (reviewed in Conant et al. 2011). For example, two field studies (Trumbore et al. 1996; Fissore et al. 2009) have used ^{14}C methods to show that the turnover of older carbon is less sensitive to warming than kinetic theory would predict (or the *intrinsic* temperature sensitivity). In contrast, some incubation methods have shown the opposite (Conant et al. 2008; Karhu et al. 2014). Recent syntheses (e.g., Davidson and Janssens 2006; Conant et al. 2011) highlighted that environmental constraints on decomposition can reduce substrate availability and dampen the intrinsic temperature sensitivity of SOC decomposition. This study illustrated the impact of labile substrate availability on the short-term response of microbial respiration to warming, particularly for subsurface soils. Taken together, it has been increasingly recognized that the persistence of SOC in a warmer world is largely determined by processes influencing SOC availability for decomposition (Conant et al. 2011; Schmidt et al. 2011).

Implications for soil carbon dynamics under global change

Results from our study indicate that SOC in subsoils is vulnerable to warming, particularly when labile substrate availability also increases. This vulnerability may stem from the distinctive substrate kinetics associated with deeper soils (i.e., K_m of microbial metabolism and its temperature sensitivity). Therefore, any global environmental change (e.g., elevated CO_2, land use change) that increases the labile substrate availability of deep soils may result in potential loss of carbon from soils to the atmosphere in a warming world. Our finding is based on the short-term response of microbial respiration to warming with and without labile substrate addition. Ultimate change in soil carbon storage in response to warming in combination with substrate alteration awaits further investigation which may consider whether priming (enhanced native SOC decomposition by substrate-induced microbial activity) occurs and persists (Kuzyakov 2010), how added substrate is stabilized in soil (Fissore et al. 2013), and the temperature dependence of these two processes.

Given the fact that more than half of SOC is stored in subsurface soils globally (Jobbágy and Jackson 2000) and the entire soil profile is likely to experience the similar magnitude of warming (but different diurnal and season regimes of temperature) as the surface soil in this century (Jungqvist et al. 2014), there is an urgent need to investigate the vulnerability of subsurface soil carbon to global environmental change in future experimental and modeling studies (Rumpel and Kögel-Knabner 2011). A number of empirical studies have found contrasting patterns of the temperature sensitivity of SOC decomposition (Q_{10}) along the soil profile (Winkler et al. 1996; Fierer et al. 2003; Rey et al. 2008). This study showed that labile substrate availability may help explain the variation in Q_{10} along the soil profile. Further in-depth studies on the processes controlling labile substrate availability, as well as the downstream processes such as priming of native SOC and stabilization of added C, could improve our understanding of the long-term fate of soil carbon in a warming world.

Conclusion

This study provided new empirical evidence illustrating the importance of microbial substrate availability in controlling the temperature sensitivity of SOC decomposition along the soil profiles in four contrasting ecosystems. We showed that the Q_{10} at ambient substrate availability significantly decreased with increasing soil depth. Moreover, for the first time, we found that saturated C substrate addition led to significantly higher Q_{10} in most soil depths, and the increase in Q_{10} as a response to substrate addition was larger in deeper soils than in the surface soils. These results clearly indicated that substrate availability plays an important role in controlling the temperature sensitivity of SOC decomposition, especially in subsoils. In order to improve our prediction of the fate of the large carbon stock stored in subsoils in a warming world, future studies need to focus on key mechanisms controlling substrate availability and its response to temperature change.

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