

Effects of substrate availability on the temperature sensitivity of soil organic matter decomposition

ALEXANDER GERSHENSON*[†], NICHOLAS E. BADER[‡] and WEIXIN CHENG*

*Department of Environmental Studies, University of California, Santa Cruz, CA 95064, USA, [†]Department of Environmental Studies, San Jose State University, San Jose, CA 95192, USA, [‡]Department of Geology, Whitman College, Walla Walla, WA 99362, USA

Abstract

Soil carbon is a major component in the global carbon cycle. Understanding the relationship between environmental changes and rates of soil respiration is critical for projecting changes in soil carbon fluxes in a changing climate. Although significant attention has been focused on the temperature sensitivity of soil organic matter decomposition, the factors that affect this temperature sensitivity are still debated. In this study, we examined the effects of substrate availability on the temperature sensitivity of soil respiration in several different kinds of soils. We found that increased substrate availability had a significant positive effect on temperature sensitivity, as measured by soil Q_{10} values, and that this effect was inversely proportional to original substrate availability. This observation can be explained if decomposition follows Michaelis–Menten kinetics. The simple Q_{10} model was most appropriate in soils with high substrate availability.

Keywords: decomposition, microbial respiration, Q_{10} , rhizosphere, soil carbon, soil incubation, soil organic matter, substrate availability, temperature sensitivity

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Introduction

Soils contain at least twice as much of carbon as the atmosphere (Schimel, 1995), and annual CO_2 efflux from soil respiration is about 10 times the annual CO_2 flux from fossil fuel burning (Raich & Potter, 1995; Solomon *et al.*, 2007). Understanding the relationship between environmental changes and rates of soil respiration is critical for projecting changes in soil carbon fluxes in a changing climate (Houghton *et al.*, 2001). If climate warming from anthropogenic CO_2 stimulates microbial respiration of soil organic carbon (SOC), the extra CO_2 efflux from SOC may cause further warming, forming a positive feedback (Jenkinson *et al.*, 1991). The strength of this feedback largely depends on the realized temperature sensitivity of SOC decomposition. Therefore, the temperature sensitivity of SOC decomposition has been extensively studied, especially in recent years (e.g. Townsend *et al.*, 1997; Fierer *et al.*,

2003; Curiel Yuste *et al.*, 2004; Fang *et al.*, 2005; Knorr *et al.*, 2005; Tang *et al.*, 2005). Despite much research, the temperature sensitivity of SOC decomposition remains controversial (Davidson & Janssens, 2006; Kirschbaum, 2006; Hakkenberg *et al.*, 2008). Some studies have indicated that a warmer climate may accelerate rates of SOC decomposition and CO_2 emissions from SOC (Trumbore *et al.*, 1996; Holland *et al.*, 2000; Sanderman *et al.*, 2003), whereas others have provided evidence that supports the opposite, i.e., the response of SOC decomposition to warming is either transient or insensitive (Giardina & Ryan, 2000; Luo *et al.*, 2001; Melillo *et al.*, 2002).

The causes of this controversy may stem from confounding factors such as soil moisture and substrate availability (Davidson & Janssens, 2006; Kirschbaum, 2006). It is unclear whether soil carbon losses would change following an increase in temperature due to changing rates of soil organic matter (SOM) decomposition, and what role will increasing plant-derived carbon inputs play in changes in SOM decomposition (Davidson & Janssens, 2006). Under conditions of elevated CO_2 , several studies have shown increased net primary production (NPP) and soil respiration (Luo *et al.*, 1996;

Correspondence: Alexander Gershenson, Department of Environmental Studies, University of California, Santa Cruz, CA 95064, USA, tel. +1 831 252 3514, fax +1 408 924 5477, e-mail: agersh@gmail.com

Norby *et al.*, 2002; Bernhardt *et al.*, 2006), although the treatment effects appear to diminish with time. Fine root production, metabolism, and rhizodeposition has been demonstrated to be one of the major sinks of increased NPP under elevated CO_2 treatments (Matamala & Schlesinger, 2000; Norby *et al.*, 2004). A significant portion of these increased inputs is likely to result in higher rates of root exudation, providing increased amounts of labile carbon to soil microbes. Despite its importance, substrate availability is probably the least studied factor which affect the temperature sensitivity of SOC decomposition (Davidson *et al.*, 2006), in part because of methodological difficulties associated with quantifying substrate availability.

A theoretical relationship between substrate availability and the temperature sensitivity of SOC decomposition has been described using the Michaelis–Menten model (Michaelis & Menten, 1913) which is well tested and widely used in studying enzymatic kinetics (Davidson *et al.*, 2006). 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 concentrations are above the saturation level so that $[C] \gg K_m$, the temperature sensitivity of soil respiration reduces to the temperature sensitivity of V_{\max} , or the intrinsic temperature sensitivity. At substrate concentrations below the saturation level, the temperature sensitivity of K_m becomes important, and the overall temperature sensitivity of soil respiration (also defined as apparent temperature sensitivity) decreases. Applying this enzymatic equation to soil respiration offers a plausible mechanistic explanation for the current controversy concerning the role of substrate availability in assessing temperature sensitivity of SOC decomposition (Davidson *et al.*, 2006). However, empirical validation of this approach is lacking.

In this study, we apply the Michaelis–Menten equation to soil respiration. Soil microbial metabolism is normally C-limited, except for a small fraction of microbes that inhabit the exuding surface of young roots (Cheng *et al.*, 1996). The C-limitation of soil microbial activity has been demonstrated by the 2–6-fold increases in soil respiration immediately after the addition of a readily available substrate (glucose is the most commonly used) at or above the saturation level (Anderson & Domsch, 1978; Cheng *et al.*, 1996). The soil respiration after substrate addition has been called the substrate-induced respiration, which remains

nearly constant during the initial 4 h period before any microbial growth is noted (Lin & Brookes, 1999). We hypothesized that if the kinetics of soil respiration can be adequately approximated by the Michaelis–Menten equation, Q_{10} of substrate-induced respiration should be significantly higher than that of the basal respiration without substrate addition, because the canceling effect of K_m on the apparent Q_{10} is greatly reduced by substrate saturation. We used a short-term incubation technique using glucose as a simple analog for increased labile carbon inputs. We assumed that due to the short duration of the incubation, the influence from decomposition of recalcitrant SOM pools was negligible, thus allowing us to separate the effect of concentration from the effect of intrinsic temperature sensitivity of different pools of SOM.

The ratio of basal respiration rate to substrate-induced respiration rate is indicative of the C availability in the soil sample, thus called Carbon Availability Index (CAI). When initial substrate availability (and thus CAI) is low, the temperature sensitivity of the dissociation constant K_m is more dominant, and we would expect to see the greatest difference in Q_{10} between baseline and added substrate conditions. Thus, our second hypothesis was that CAI would be negatively correlated with the net increase of the Q_{10} value of the substrate-induced respiration above that of the basal respiration. We tested these two hypotheses using three kinds of freshly sampled soils. Our results are relevant to global change research, as they are directly related to the positive feedback between SOC decomposition and global climate warming, and the implications of increased soil carbon availability under CO_2 -enriched conditions (Matamala & Schlesinger, 2000; Norby *et al.*, 2004).

Methods

Soil sampling

Soil samples were collected from three sites on the University of California campus in Santa Cruz, California. All soils are characteristic of the area, limestone-derived sandy soils. Santa Cruz has a Mediterranean climate, with cool wet winters and warm dry summers. The first site is an annual grassland dominated by non-native grasses and perennial native forbs; the second site is on an organic farm, which had been established 25 years earlier on a similar annual grassland; the third site is in a second-growth redwood forest that had been logged about 90 years earlier. Within each site, we collected soils from four randomly chosen locations; each of these four locations was considered a replicate. At each location, we collected bulk soil (grassland-Ga,

redwood forest-RW, and organic farm-Farm), which we defined as soil from the upper 30 cm that did not adhere to roots. Roots were present through the entire profile. For the grassland soil, we also collected a subsurface soil (Gb) from between 30 and 50 cm depth underneath most of the fine roots.

All soil samples were brought to the laboratory, quickly picked free of visible roots, homogenized, and passed through a 2 mm sieve. Each sample was divided into eight 20 g aliquots; each aliquot was placed in a separate 125 mL Erlenmeyer flask. The flasks were divided among four temperature treatments (0, 10, 22, and 30 °C) and either treated with two glucose treatments (GI+ for added glucose and GI- for ambient substrate). We added a 60 g L⁻¹ glucose solution to the GI+ samples using a 10 cc syringe with a needle tip. Care was exercised to ensure even distribution of glucose without saturating the soil with liquid, which would restrict CO₂ evolution from the sample. Two of the samples (one redwood and one farm) were excluded from the analysis due to saturated conditions. Deionized water (DI) was added to ambient substrate replicates in the same manner in order to avoid confounding influences of soil moisture. The experiment was started <3 h from the initial collection of the samples in order to ensure minimal loss of naturally available substrate to respiration.

Measuring soil respiration

We measured soil respiration using the methodology described in Cheng & Virginia (1993). Briefly, an air pump forces ambient air through a soda-lime column, thereby producing CO₂-free air. The air then travels through a copper coil submerged in a water bath, in order to equilibrate the air temperature with the temperature of the water bath. The air 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 in order to ensure a constant flow rate (the average flow rate for all samples was 83.5 ± 7.5 mL min⁻¹). One of the outlets was not connected to the samples and was used as a reference. 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 CO₂ in the sample. Respiration measurement for one sample lasted approximately 2 min. The rate of substrate-induced respiration remained constant during the measurement period.

Four water baths were set up with temperatures of 0, 10, 22, and 30 °C. Temperature in the 0 °C water bath was maintained by continuous inputs of ice into the

water. Temperature in the 10 °C water bath was regulated using an automated water chiller. Temperature in the 22 °C water bath was the ambient temperature of the laboratory. Temperature in the 30 °C treatment was maintained using a processor-controlled temperature regulator. All temperatures were manually verified every 10 min. Each water bath was equipped with a multiflask suspension system, which allowed Erlenmeyer flasks to be suspended in the water bath, with the stopper and inflow and outflow tubes above the water. After the flasks were filled with the soil samples and were given either the glucose or the DI water addition, they were suspended in the water baths and connected to the CO₂-free air manifold in order to ensure supply of fresh air for the sample. The flasks were allowed to acclimate to the water bath temperature for 1 h. After 1 h, each flask was connected in turn to the flow meter and IRGA assembly, and the flow rate and CO₂ concentration were recorded.

Calculations

In order to determine the dry weight of the samples, we took a sample of each replicate, dried it at 105 °C, and determined water content. The sample was weighed before and after drying on an analytical balance. In order to calculate the respiration rate of the soil samples we used the formula

$$R_r = 0.536 \frac{(CR_f)}{W_s}, \quad (1)$$

where R_r is soil respiration in $\mu\text{g C kg}^{-1}$ dry soil h^{-1} , C is the recorded CO₂ concentration in $\mu\text{mol CO}_2 \text{ mol}^{-1}$, R_f is the recorded flow rate in mL h^{-1} , and W_s is gram dry weight of the sample.

We fitted the measured respiration rates for the GI+ and GI- treatments to the van't Hoff equation (1898) using SIGMAPLOT 10.0 DYNAMIC FIT MODULE (Systat Software Inc.)

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

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

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

We then compared the GI- and GI+ treatments within each soil type using a two-tailed two-sample t -test. We conducted comparisons between individual soil type pairs using a two-tailed two-sample t -test, and compared all soils between each other using an ANOVA. Curve fitting was performed using SIGMAPLOT 10.0 (Systat Inc.) and statistical analysis was performed using SYSTAT 12.0 (Systat Inc.)

Table 1 Respiration rates ($\mu\text{g CO}_2\text{-C kg}^{-1}\text{ soil h}^{-1}$) of redwood (RW) surface soil (0–30 cm), organic farm (Farm) surface soil (0–30), grassland A horizon (Ga) soil (0–30 cm), and grassland B-horizon (Gb) soil (30–50 cm) at four temperatures with (Gl +) and without (Gl–) glucose addition

T (°C)	RW			Farm			Ga			Gb		
	Gl–	Gl +	CAI	Gl–	Gl +	CAI	Gl–	Gl +	CAI	Gl–	Gl +	CAI
0	7.11 (1.56)	9.09 (1.11)	0.78 (0.08)	1.13 (0.16)	7.16 (0.29)	0.16 (0.02)	6.62 (0.11)	18.77 (0.79)	0.35 (0.01)	1.70 (0.21)	3.11 (0.44)	0.55 (0.11)
10	24.13 (2.83)	40.52 (4.03)	0.60 (0.03)	7.08 (0.48)	33.31 (2.16)	0.21 (0.01)	19.17 (1.46)	74.94 (4.58)	0.26 (0.00)	3.64 (0.13)	8.10 (0.90)	0.45 (0.04)
22	50.94 (3.21)	97.40 (11.71)	0.52 (0.04)	12.97 (0.76)	82.36 (4.84)	0.16 (0.00)	47.73 (2.94)	195.13 (10.84)	0.24 (0.00)	8.28 (0.69)	22.18 (3.11)	0.37 (0.02)
30	87.06 (8.77)	163.13 (16.56)	0.53 (0.01)	21.93 (1.66)	148.06 (10.35)	0.15 (0.00)	66.60 (3.86)	314.68 (18.38)	0.21 (0.00)	9.40 (0.62)	41.94 (5.86)	0.22 (0.02)

Each value is the mean of four replicates for Ga and Gb ($n = 4$) and three replicates for RW and Farm ($n = 3$), with a standard error in parentheses. Carbon availability index (CAI) for each soil was calculated as Gl–:Gl + ratio.

We calculated the increase in Q_{10} between the Gl + and Gl– treatments (ΔQ_{10}) as a simple difference, i.e. $Q_{10}(\text{Gl}+) - Q_{10}(\text{Gl}-)$.

CAI was calculated as

$$\text{CAI} = \frac{R_{\text{Gl}-}}{R_{\text{Gl}+}}, \quad (4)$$

where $R_{\text{Gl}-}$ and $R_{\text{Gl}+}$ are the respiration rates at 22 °C in the ambient-substrate and added-glucose treatments, respectively (Cheng *et al.*, 1996).

Results

We observed wide variation in soil respiration dependent on soil type (Table 1). Substrate addition strongly affected soil respiration rates, in some cases by an order of magnitude. We have found that substrate availability has strong significant effects on the Q_{10} value of soil respiration for surface grassland soils (Ga, $P < 0.01$), subsurface grassland soils (Gb, $P < 0.01$), farm surface soils (Farm, $P < 0.01$), and marginally significant effects for redwood soils (RW, $P < 0.075$), with Gl + Q_{10} values being significantly higher than Gl– treatments (Fig. 1). We found significantly higher Q_{10} values for RW vs. both grassland soils under Gl– conditions ($P < 0.01$), and farm Q_{10} values were significantly higher than RW values under Gl + conditions; however, there was no difference observed between RW and Ga Q_{10} values under Gl + conditions ($P = 0.544$) and between RW and farm soils under Gl– conditions ($P = 0.289$). The Q_{10} values of farm soils were significantly higher than Ga soils under both Gl– and Gl + conditions ($P < 0.01$). Subsurface grassland soils exhibited the lowest Q_{10} values under Gl– conditions, but had the highest Q_{10} values with added substrate, which were significantly greater ($P < 0.01$) than those of other soils, and marginally

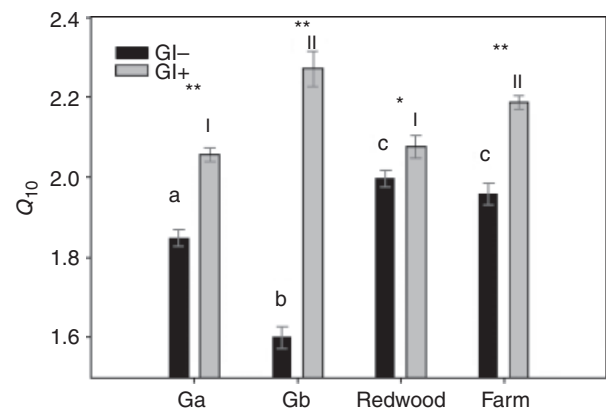


Fig. 1 Differences in Q_{10} between added substrate (Gl +) and ambient substrate (Gl–) treatments among four soils from three locations. Letters indicate significant ($P < 0.01$) differences between different soils, asterisks indicate significant ($*P < 0.075$, $**P < 0.01$) differences between ambient and added substrate temperature sensitivity. Error bars represent ± 1 SE, $n = 4$ for grassland soils, $n = 3$ for redwood and farm soils.

ally greater than those of farm soils under substrate-saturated conditions ($P = 0.12$). The results of an ANOVA show a significant effect of both soil type and added substrate on Q_{10} values ($P < 0.001$).

In order to further examine the relationship between changes in Q_{10} and substrate availability, we related the increase in Q_{10} to the CAI both within the different fractions of the grassland soils, and between the grassland, redwood, and farm bulk soils. There was no significant relationship between CAI and changes in Q_{10} among the replicates within each soil type. Likewise, we found no significant relationship when we compared all four soil types together, largely due to significant outlier values of Gb soils. However, we

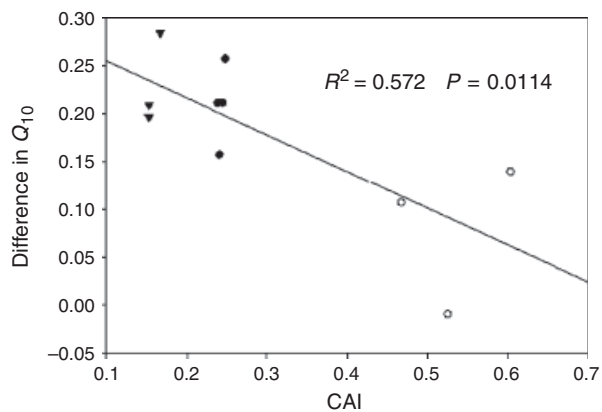


Fig. 2 The relationship between ΔQ_{10} and initial carbon availability [Carbon Availability Index (CAI)] at 22 °C in surface soils from farm (Δ), Ga (filled circles), and redwood (RW) (open circles).

Table 2 R^2 for the fit of the van't Hoff exponential equation to the respiration curves and carbon availability index (CAI) at 22 °C

Soil type	$R^2_{\text{Gl-}}$	$R^2_{\text{Gl+}}$	$R^2_{\text{Gl- vs. Gl+}}$	CAI (22 °C)
Ga	0.974 ± 0.008	0.988 ± 0.003	$P = 0.017$	0.24
Gb	0.926 ± 0.024	0.999 ± 0.001	$P = 0.001$	0.37
Farm	0.978 ± 0.007	0.994 ± 0.001	$P = 0.015$	0.16
RW	0.991 ± 0.007	0.991 ± 0.002	$P = 0.988$	0.52

P-values were computed for the differences between Gl- and Gl+ treatments.

found that soils with higher CAI exhibited a smaller change in Q_{10} when we compared the surface soils of each site (Fig. 2) ($R^2 = 0.572$, $P = 0.0114$), and surprisingly when we compared just the Gb and Ga soils, we found an opposite relationship, which was highly significant ($R^2 = 0.88$, $P < 0.01$).

In all soil types, soil respiration was adequately described by a simple exponential relationship with temperature. However, the substrate-saturated (Gl+) soils fit the exponential model better, with equal or higher R^2 compared with the Gl- soils (Table 2). We also found that CAI explained 38% of the variance of the R^2 values of the exponential function in Gl- treatments in surface soils ($R^2 = 0.38$, $P = 0.057$), with higher CAI values corresponding to better fitting of the data to the exponential model. The goodness of fit of the Gl- data to the simple exponential equation was a significant predictor of the effect that substrate had on the change in the Q_{10} values across all samples from all sites ($R^2 = 0.815$, $P < 0.001$); the sensitivity of Q_{10} to substrate was inversely proportional to the goodness of fit.

Discussion

Our results support our two hypotheses and the applicability of the Michaelis–Menten model to soil respiration. Addition of a readily available C substrate significantly increases Q_{10} values for all soil types as compared with the Q_{10} values without glucose addition ($P < 0.01$ – 0.075) (Fig. 1), presumably because substrate saturation eliminated the canceling effect of K_m on the measured Q_{10} values. In addition, we observed a negative relationship between CAI and change in Q_{10} (ΔQ_{10}) in surface soils across the sites (Fig. 2). CAI explains approximately 57% of the variance in ΔQ_{10} across three sites. This supports the hypothesis that without substrate addition, soils with higher indigenous carbon availability tend to produce Q_{10} values closer to their intrinsic Q_{10} values than soils with lower C availability, because the canceling effect of K_m on the apparent Q_{10} value is less important under high substrate concentrations than under low substrate concentrations. Our observations may allow us to clarify the relationship between substrate availability and temperature sensitivity of SOC decomposition. For instance, Kirschbaum (1995, 2000) has shown that Q_{10} of SOC decomposition has an empirical relationship with t , the measurement temperature: $Q_{10} = \exp[2415/(t + 32)^2]$; indicating that Q_{10} value decreases as the measurement temperature increases. If we apply the Michaelis–Menten model, then these results are logically consistent: because K_m is sensitive to temperature and increases as measurement temperature increases, apparent Q_{10} decreases as the measurement temperature increases. This mechanistic explanation extends the logic predicted from the Arrhenius equation as described by Davidson & Janssens (2006).

A related issue, also debated, is whether the temperature sensitivity of SOC decomposition varies with substrate quality (e.g. labile vs. recalcitrant). Based on thermodynamic considerations as given in Arrhenius equation, the decomposition of recalcitrant SOC should have higher temperature sensitivity than labile SOC because recalcitrant SOC requires higher activation energy (Bosatta & Ågren, 1999; Ågren, 2000). Some empirical studies indeed suggest that the decomposition of recalcitrant carbon is more sensitive to temperature changes than labile carbon (Waldrop & Firestone, 2004; Conant *et al.*, 2008; Hartley & Ineson, 2008), but other studies report either equivalent temperature sensitivity for both components (Conen *et al.*, 2006) or lower temperature sensitivity for recalcitrant carbon (Luo *et al.*, 2001; Melillo *et al.*, 2002). The real causes of this inconsistency are unclear at this stage. In our experiment, the higher Q_{10} values in the glucose (a truly labile substrate) treatment may seem to indicate

that the temperature sensitivity of more labile substrates is higher than that of recalcitrant substrates. However, in the context of the Michaelis–Menten equation, the higher Q_{10} can be explained solely as a function of substrate availability. The inconsistency among measured temperature sensitivities of labile and recalcitrant substrates may stem from the common practice of omitting the role of substrate availability in influencing temperature sensitivity. As we have shown, temperature sensitivity at different substrate concentrations may be much different, especially if CAI is low, a condition common to many soils (Insam & Haselwandter, 1989; Cheng *et al.*, 1996).

Because of the potential difference between the respiration rate of labile and recalcitrant components of SOC, we assume that the measured soil CO_2 efflux predominantly originates from relatively labile substrate similar to glucose. There are several lines of evidence that supports this assumption. First, soil CO_2 production during short-term incubation is primarily controlled by the labile pool more than the total SOC pool (Franzluebbers *et al.*, 2001). Second, changes of soil respiration are often positively correlated to labile substrate input such as litterfall and root growth (Nadelhoffer & Raich, 1992). Third, studies using carbon isotopes (^{13}C and ^{14}C) have indicated that the majority of soil CO_2 comes from fast-cycling young soil carbon fractions (Conen *et al.*, 2006; Czimczik & Trumbore, 2007; Follett *et al.*, 2007). Fourth, it is commonly accepted that soil microorganisms are not capable of directly metabolizing structurally complex recalcitrant substrates without the help of extracellular enzymes that carry out the critical step of depolymerization. Therefore, the results of our study may not directly apply to the temperature sensitivity of depolymerization.

We observed significant differences between the dynamics of grassland A and B horizon soils. The increased Q_{10} in the Gl+ treatment (ΔQ_{10}) is significantly greater in B-horizon soils than in A-horizon soils ($P = 0.001$). Surprisingly, the CAI of the B-horizon soil is higher than that of the A-horizon soil (Table 1). A closer examination of the changes of CAI at different temperatures renders some clue for the causes of this contrasting phenomenon. As incubation temperature increases, the decreasing trend of CAI largely stops at the last temperature change from 22 to 30 °C for the three surface soils except for the B-horizon soil in which CAI further decreases by approximately 50%. This indirectly indicates that the temperature sensitivity of K_m for the B-horizon soil is substantially higher than the surface soils, therefore, resulting in a much stronger response in Q_{10} to glucose addition. Furthermore, the intrinsic Q_{10} value (or the Q_{10} determined with glucose

addition) for the B-horizon soil is the highest among soils tested here. These results suggest that the overall metabolism of the B-horizon soil is characterized with higher Q_{10} values for both V_{max} and K_m than surface soils, therefore, it exhibits both the lowest Q_{10} value without glucose addition and the highest Q_{10} value with glucose addition. Our second hypothesis assumed that the values of V_{max} and K_m would be similar for all soils; however, it is likely that the microbial communities in subsurface soils are significantly different than ones in the surface root-dominated horizons. Although we are unable to explain the exact mechanisms for this difference between the soils, the difference in substrate quality between surface soils and subsurface soils can be a possible cause of this contrasting result. While we did not directly examine substrate quality in this experiment, it likely plays a role (Fontaine *et al.*, 2007) in the differential responses to substrate additions between more labile carbon-dominated surface and more recalcitrant carbon-dominated subsurface soils.

Soil microbial communities have been shown to be carbon-limited. (Cheng *et al.*, 1996; Cleveland *et al.*, 2007). In all examined cases, we observed not only an increase in overall respiration rates, but an increase in Q_{10} values in added substrate treatments. The factor that appears to influence this change is the substrate limitation of respiration in the 22 and 30 °C treatments under ambient substrate conditions, which influences the goodness of fit of the Q_{10} model (Table 2). This substrate availability-driven limitation to temperature responses can explain the issues of the difference between ‘apparent temperature sensitivity’ and ‘intrinsic temperature sensitivity’ discussed by Davidson & Janssens (2006) in their recent review. Redwood soils had the highest values of carbon availability, and did not exhibit a large change in Q_{10} values under added substrate conditions. It is likely that in redwood soils, the ambient concentration of substrate is high enough that the temperature sensitivity of the half-saturation constant has little effect on the overall sensitivity of respiration to temperature under ambient conditions. Substrate availability plays a significant role in the applicability of simple exponential models to estimate the response of SOM decomposition dynamics to temperature. The effect of substrate availability on temperature sensitivity of SOM decomposition is strongly related to the initial substrate availability of the soil. Simple exponential models are likely less appropriate for soils with low carbon availability, such as mineral soils, due to the increasing influence of the substrate on the overall sensitivity of respiration, although in our cases such models fit the observations well.

Anthropogenic carbon emissions into the atmosphere, and the resultant elevated CO_2 levels, are likely

to increase NPP, and consequently labile carbon inputs into the soil through increased fine root turnover and rhizodeposition (Norby *et al.*, 1987, 2004; Matamala & Schlesinger, 2000; Uselman *et al.*, 2000). Some have suggested that increases in atmospheric CO₂ may potentially alter the composition of such rhizodeposits (Phillips *et al.*, 2006). Global temperatures are likewise projected to increase, with the majority of the increase projected for mid- and high-latitude ecosystems (Meehl *et al.*, 2007). Although there is still no clear understanding of how different quality substrates will respond to increasing temperatures (Davidson & Janssens, 2006), temperature sensitivity may increase under conditions of higher substrate availability, because the canceling effect of the temperature sensitivity of K_m becomes less important under higher substrate availability. Future experiments that explicitly include both substrate availability and substrate quality may be the most successful at interpreting observed decomposition dynamics at different temperatures.

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