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Temperature sensitivity increases with soil organic carbon recalcitrance along an elevational gradient in the Wuyi Mountains, China

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ABSTRACT

No consensus exists regarding soil organic carbon (SOC) lability and the temperature sensitivity of its decomposition. This lack of clear understanding limits the accuracy in predicting the long-term impacts of climate change on soil carbon (C) storage. In this study, we determined the temperature responses of labile and recalcitrant organic carbon (LOC vs. ROC) by comparing the time required to decompose a given amount of C at different incubation temperatures along an elevational gradient in the Wuyi Mountains in southeastern China. Results showed that the temperature sensitivity increased with increasing SOC recalcitrance ($Q_{10\text{-labile}} = 1.39 \pm 0.04$ vs. $Q_{10\text{-recalcitrant}} = 3.94 \pm 0.30$). $Q_{10\text{-labile}}$ and $Q_{10\text{-recalcitrant}}$ values significantly increased with increasing soil depth. The effect of elevational vegetation change was significant for $Q_{10\text{-recalcitrant}}$ but not for $Q_{10\text{-labile}}$, though they increased along the elevational gradient. The response of ROC pools to changes in temperature would accelerate the soil-stored C losses in the Wuyi Mountains. Kinetic theory suggested that SOC decomposition was both temperature- and quality-dependent due to an increased temperature. This would promote more CO_2 release from recalcitrant soil organic matter (SOM) in cold regions, resulting in a greater positive feedback to global climate change than previously expected. Moreover, the response of ROC to changes in temperature will determine the magnitude of the positive feedback due to its large storage in soils.

1. Introduction

The response of soil organic carbon (SOC) decomposition to current global warming is still not clearly understood (Davidson and Janssens, 2006). Of the dozens of variables (Ågren and Wetterstedt, 2007) that can regulate the decomposition of SOC, temperature has undoubtedly captured more than its share of attention. Though accessing the temperature-driven changes is challenging (Conant et al., 2008a), it has promoted many studies to investigate the SOC decomposition–temperature relationship. The temperature coefficient, Q_{10}, is used to measure temperature sensitivity of SOC decomposition. This type of measurement has received considerable interest (e.g. Davidson et al., 2000; Giardina and Ryan, 2000; Fang et al., 2005) due to its importance in the global C cycle and potential feedback to climate change (e.g. Luo et al., 2001; Davidson and Janssens, 2006).

Despite much research, however, no consensus exists regarding the temperature sensitivity of SOC decomposition partly due to SOC being composed of several discrete pools with different lability (Smith et al., 1997), such as the fast, slow and passive pools in the well-known CENTURY model (Parton et al., 1987). In laboratory studies (e.g. Liski et al., 2000; Fang et al., 2005; Fierer et al., 2005; Conant et al., 2008a), however, SOC is always conceptually broken into two fractions: labile organic carbon (LOC) and recalcitrant organic carbon (ROC). In general, LOC is defined as being high-lability and easily decomposed by microbes (Shaver et al., 2006) while ROC is considered to be high recalcitrance and resistant to decay (Hartley and Ineson, 2008). Different C pools exhibit a wide range of inherent kinetic properties in terms of temperature sensitivity of decomposition (Davidson and Janssens, 2006). For example, previous studies suggest that the temperature sensitivity of LOC may be greater than (Fierer et al., 2005; Conant et al., 2008a), equivalent to (Fang et al., 2005; Conen et al., 2006), or less than (Liski et al., 2000; Melillo et al., 2002) that of the ROC. Therefore, the amount of soil-stored C is likely to change in response to climatic warming (Vanhala et al., 2007) largely because soil

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C balance, the difference between the net primary production (NPP) of vegetation and the decomposition of SOC, is sensitive to temperature changes (Davidson et al., 2000; Holland et al., 2000).

A decline in decomposition rate was commonly observed with increasing incubation time (Fang et al., 2005). Kinetic theory indicates that Q_{10} of SOC is both temperature- and quality-dependent, which is represented by the activation energy (Fissore et al., 2009). However, the decline in decomposition rates often results in temperature-induced differences in the quantity and quality of respired C (Reichstein et al., 2000; Conant et al., 2008b). The intrinsic temperature sensitivities of the labile C (high quality) vs. the recalcitrant (low quality) are thus confounded. In this study, we determined the temperature responses of SOC by comparing the time required to decompose a given amount of C at different incubation temperatures according to Conant et al. (2008a), separating the temperature sensitivity of the labile C apart from that of the recalcitrant C. One of the advantages of this analytical method is to eliminate the potential problem: fixed incubation duration leading to comparison of different C pools with different intrinsic temperature sensitivities (Rey and Jarvis, 2006; Conant et al., 2008a).

The aim of this study was to examine the responses of labile vs. recalcitrant SOC pools to temperature and the impact of soil depth and vegetation communities on the Q_{10} values along an elevational gradient in the Wuyi Mountains. Elevational gradients of temperature changes in mountains can be similar to that caused by latitudinal gradients (Smith et al., 2002), which make mountains important regions in climate change research. The Wuyi Mountains have a clear vertical zonation of vegetation communities (Wang et al., 2009) in the subtropics in southeastern China. The temperature gradients, which could resemble those observed along latitudinal gradients (Niklińska and Klimek, 2007), provide an ideal model ecosystem to investigate C decomposition. Moreover, the increase of recalcitrant C with increasing soil depth (Fierer et al., 2003; Yang et al., 2010) helps test the C quality-dependent hypothesis of Q_{10}.

2. Materials and methods

2.1. Site description

The experimental sites were located in the Wuyishan National Nature Reserve Area in Fujian Province (27°33′–27°54′N, 117°27′–117°51′E), a 56,527 ha forested area in the southeast of China (Wang et al., 2009).For this area, the annual mean temperature was 15.0 °C, relative humidity was 83.5%, fog days were 100 days, and precipitation was 2000 mm. There were four typical vegetation types along the elevation gradient: evergreen broad-leaf forest (EBF), coniferous forest (CF), sub-alpine dwarf forest (SDF), and alpine meadow (AM). Detailed site description is shown in Table 1.

2.2. Experimental design and soil sampling

Four plots (50 × 60 m) with different vegetation types (EBF, CF, SDF and AM) were set along an elevational gradient in the Wuyi Mountains. Each 50 m × 60 m plot was divided into four 25 m × 30 m subplots. Soil samples were randomly collected (0–10 cm, 10–25 cm, 25–40 cm depths) from all the subplots in March, 2006 using a 2 cm–diameter soil corer. Twenty soil cores were taken from each subplot at each soil depth and pooled together, as a replicate. Samples were immediately sieved (<2 mm) to remove soil fauna, rocks and fine roots, thoroughly hand-mixed, placed in plastic bags and transported in several coolers to the ecological laboratory at the Nanjing Forestry University.

2.3. Soil organic carbon decomposition

Once the soil samples reached the lab, they went through a five-day pre-incubation. Soil samples (100 g) were then incubated in 1 L Mason jars at two different temperatures (15 and 25 °C) under aerobic conditions. Controls, with no soil samples, were also incubated at the same time. Small vials (50 ml, with lids removed) containing 30 ml of 1 M NaOH solution were placed in each Mason jar to trap respired CO_2 (De Vene and Hofman, 2000; Liu and Zou, 2002). Samples were taken after 7, 14, 21, 35, 49, 63, 77, 91, 105, 126, 147, 168, 189, 210, 231, 259, 287, 315, 343, and 371 days by removing the NaOH vials. The amount of CO_2 was determined by titration of the NaOH with 1 M HCl to pH 8.3 in the presence of $BaCl_2$. Mason jars were flushed with compressed air to allow replenishment of O_2 after each interval and deionized water was added to maintain moisture at 60% of field capacity.

The temperature sensitivity (Q_{10}) of the LOC and ROC pools were calculated according to Conant et al. (2008a):

$$Q_{10} = (t_c/t_w)^{10/(t_w-t_c)}$$

where t_c and t_w are the time required to respire a given amount of soil C at relatively cold (15 °C) and warm (25 °C) temperatures during incubation. The Q_{10} values for the labile C pool were estimated by dividing the time taken to respire the first 1% of initial C at 15 °C by that at 25 °C. For the ROC pool, Q_{10} values were determined using the time taken to respire an additional 1% of initial C after 8% of initial C was decomposed (Fig. 1). The 8% of initial soil C was chosen based on results from a previous study that demonstrated that LOC (estimated by a sequential fumigation–incubation method according to Zou et al. (2005)) commonly takes up 3.40%–7.46% of SOC in the soils from the Wuyi Mountains (Xu et al., 2008).

2.4. Microbial biomass C, water-soluble organic C and soil properties

Microbial biomass carbon (MBC) was measured by a chloroform fumigation–extraction method (Vance et al., 1987; Liu and Zou, 2002). MBC concentration in the extracted solutions was measured by a TOC Analyzer (Shimazu, TOC-Vcph, Japan). Water-soluble organic carbon (WSOC) was extracted from 30 g of fresh soil with an addition of 60 ml of deionized water. The mixture was shaken for 0.5 h at 250 rpm at 25 °C, and centrifuged for 10 min at 15,000 rpm (Jiang et al., 2006). Then, the supernatant liquid was filtered through a 0.45 μm filterable membrane. WSOC in extracts was measured by a TOC Analyzer (Shimazu, TOC-Vcph, Japan). Soil organic carbon (SOC) was determined by combustion with an elemental analyzer (Model CNS, Elementar Analysen Systeme GmbH, Germany). Soil temperature and soil moisture (m:m) were measured by watchdog weather stations (Spectrum Technologies, Inc., IL, USA) at soil depths of 5, 15, and 30 cm. Soil pH values were measured with a Calomel electrode on a paste of 1:1 (w:v) of fresh soil and deionized water.

2.5. Statistical analysis

We used a paired t-test to compare calculated Q_{10} values. Two-way ANOVA analyses were performed to examine the effect of soil depth and elevational (vegetation) changes for the $Q_{10\text{-labile}}$ and $Q_{10\text{-recalcitrant}}$ values. All statistical analyses were conducted using SPSS 15.0 software (SPSS Institute Inc., Chicago, IL, USA).

Table 1
Site conditions.

Site	Elevation (m)	MAT (°C)	MAP (mm)	Soil depth (cm)	Soil temperature (°C)	Soil moisture (%)	pH	Dominant species
EBF	500	18.5	1700	0–10	16.39 ± 0.23	26.69 ± 0.59	4.51 ± 0.04	*Castanopsis carlesii*, *Castanopsis eyrei*
				10–25	15.80 ± 0.18	23.23 ± 0.47	4.78 ± 0.04	
				25–40	15.13 ± 0.20	17.31 ± 0.88	4.85 ± 0.05	
CF	1150	14.5	2000	0–10	13.48 ± 0.11	42.98 ± 0.12	3.94 ± 0.06	*Pinus taiwanensis*, *Oligostachyum oedogonatum*
				10–25	13.29 ± 0.12	33.28 ± 0.30	4.68 ± 0.13	
				25–40	13.14 ± 0.17	25.56 ± 0.64	4.71 ± 0.05	
SDF	1750	11.2	2200	0–10	12.96 ± 0.24	45.80 ± 0.21	4.33 ± 0.08	*Symplocos paniculata*, *Stewartia sinensis*
				10–25	12.44 ± 0.17	40.50 ± 0.73	4.83 ± 0.05	
				25–40	12.03 ± 0.16	36.49 ± 0.48	4.90 ± 0.02	
AM	2150	9.7	3100	0–10	12.10 ± 0.16	58.40 ± 0.36	4.50 ± 0.10	*Calamagrostis brachytrich*, *Miscanthus sinensis*, *Lycopodium clavatum*
				10–25	11.91 ± 0.09	52.98 ± 0.42	5.06 ± 0.25	
				25–40	11.73 ± 0.05	41.53 ± 0.84	5.04 ± 0.04	

Note: MAT, mean annual temperature; MAP, mean annual precipitation. EBF: evergreen broad-leaf forest; CF: coniferous forest; SDF: sub-alpine dwarf forest; AM: alpine meadow. Datasets of MAT and MAP are obtained from He et al. (1994), Zheng and Fang (2004) and Wang et al. (2009).

3. Results

The decomposition rates of SOC declined by an average of 88.13% over the entire incubation period along the elevational (vegetation) gradient, indicating that the LOC pool was progressively depleted. The results were in line with the existence of a small LOC pool and a large ROC pool. The cumulative proportion of C respired leveled off with increasing incubation time (e.g. Fig. 1b). After 371 days of incubation, at least 9.37% of the initial C had been decomposed. The dynamics of SOC decomposition followed a two-phase (relatively fast and slow) pattern with significantly different decomposition rates (Fig. 1a).

The temperature sensitivity increased with decreasing SOC lability. During the course of incubation, the estimated mean Q_{10} for CO_2 that evolved from the labile C pool (1.39 ± 0.04; mean ± SE; $n = 12$) was significantly less than the mean Q_{10} for CO_2 respired from the ROC pool (3.94 ± 0.30; mean ± SE; $n = 12$; $P < 0.000$) across the soil layers along the elevational gradient (Fig. 2). The data also indicated that temperature sensitivity of organic C decomposition varies with its quality since the two-phase pattern during incubation represents the decomposition of labile and recalcitrant C, respectively.

Both the soil depth and elevational gradient played essential roles in the sensitivity of soil C decomposition (Table 2). Soil depth had a significant effect for the variance in Q_{10} values for both the labile and the recalcitrant C pools. Overall, $Q_{10\text{-labile}}$ and $Q_{10\text{-recalcitrant}}$ values were higher in the subsoil (25–40 cm) compared to the topsoil (0–10, 10–25 cm). Elevational changes in vegetation communities had a significant effect for $Q_{10\text{-recalcitrant}}$ values, but not for $Q_{10\text{-labile}}$ values. The percentages of MBC to SOC and WSOC to SOC declined significantly with increasing soil depth. For example, MBC/SOC ratios decreased 3.6 times from 3.08 (±0.31; 0–10 cm) to 0.85 (±0.30; 25–40 cm) in SDF. However, no significant differences were found for the percentages of MBC to SOC and

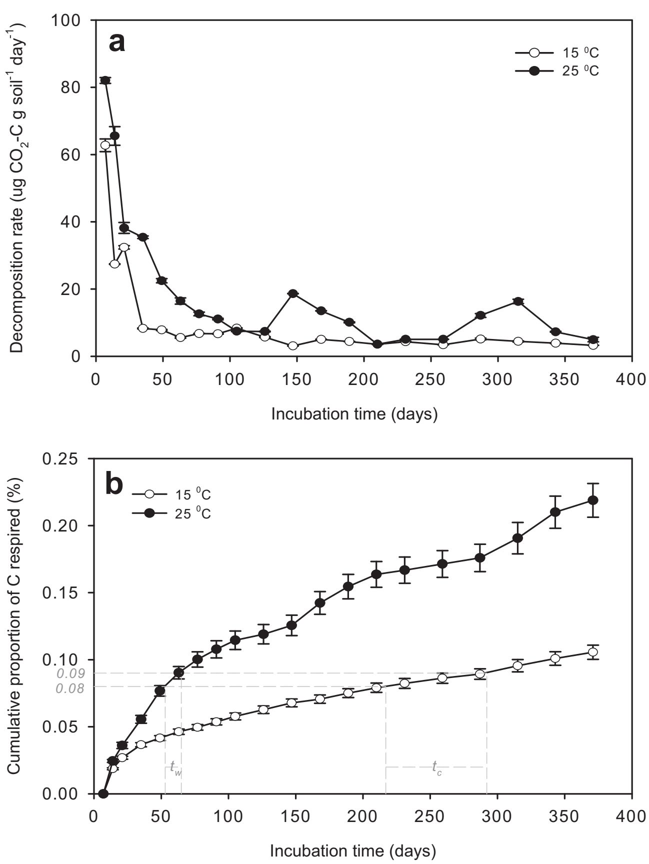

Fig. 1. SOC decomposition rates declined over incubation time (a), Q_{10} values of SOC decomposition determined by comparing the time required to decompose a given amount of carbon at different incubation temperatures (b). (data from CF, 25–40 cm).

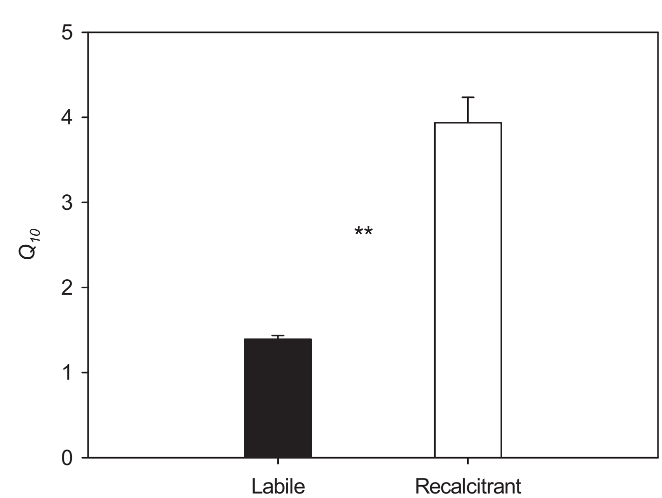

Fig. 2. The mean temperature sensitivity (Q_{10}) of labile and recalcitrant carbon pools (Values are mean ± SE; $n = 12$; **: $P < 0.000$).

Table 2
Results of two-way ANOVA for Q_{10} values of different carbon pools and soil properties in the four elevational vegetation communities.

Vegetation	Depth (cm)	$Q_{10\text{-Labile}}$	$Q_{10\text{-Recalcitrant}}$	MBC/SOC (%)	WSOC/SOC (%)	SOC (mg g^{-1})	C:N
EBF	0–10	1.27 ± 0.04	2.07 ± 0.12	1.67 ± 0.19	0.20 ± 0.02	48.67 ± 1.94	8.91 ± 0.67
	10–25	1.28 ± 0.17	2.76 ± 0.11	1.58 ± 0.70	0.17 ± 0.02	28.32 ± 1.77	6.00 ± 0.16
	25–40	1.42 ± 0.03	3.83 ± 0.29	1.59 ± 0.57	0.06 ± 0.02	27.50 ± 6.36	5.85 ± 0.88
CF	0–10	1.30 ± 0.11	2.53 ± 0.24	2.05 ± 0.35	0.39 ± 0.04	50.12 ± 5.80	9.36 ± 1.67
	10–25	1.31 ± 0.13	4.17 ± 0.62	1.40 ± 0.36	0.27 ± 0.03	29.57 ± 2.60	6.49 ± 0.44
	25–40	1.49 ± 0.08	4.76 ± 0.38	1.26 ± 0.21	0.10 ± 0.03	29.02 ± 1.72	6.41 ± 0.37
SDF	0–10	1.36 ± 0.02	3.39 ± 0.11	3.08 ± 0.31	0.29 ± 0.04	74.00 ± 4.24	9.17 ± 0.47
	10–25	1.41 ± 0.07	4.54 ± 0.16	1.35 ± 0.41	0.22 ± 0.05	44.92 ± 1.67	7.54 ± 0.53
	25–40	1.56 ± 0.21	4.99 ± 0.38	0.85 ± 0.30	0.17 ± 0.02	31.27 ± 2.66	6.17 ± 0.35
AM	0–10	1.34 ± 0.04	4.13 ± 0.21	3.11 ± 0.50	0.24 ± 0.07	129.56 ± 12.35	12.00 ± 1.95
	10–25	1.42 ± 0.06	5.01 ± 0.19	1.44 ± 0.30	0.14 ± 0.01	103.61 ± 14.37	10.97 ± 2.19
	25–40	1.76 ± 0.05	5.05 ± 0.13	1.24 ± 0.31	0.16 ± 0.06	40.32 ± 5.79	7.41 ± 0.44
Source of variation							
Depth		**	**	**	**	**	**
Elevation		n.s.	**	n.s.	n.s	**	*
Elevation × depth		*	n.s.	*	*	**	n.s.

Note: values are mean ± SE, $n = 4$ (n.s. = not significant; $^{**}P < 0.01$). The statistical difference between each pair of labile and recalcitrant carbon pools is significant ($P < 0.01$). MBC: microbial biomass carbon; WSOC: water-soluble organic carbon. EBF: evergreen broad-leaf forest; CF: coniferous forest; SDF: sub-alpine dwarf forest; AM: alpine meadow.

WSOC to SOC at the same soil depth in different vegetation communities. SOC and C:N ratios were greatly influenced by both soil depth and elevational vegetation changes (Table 2), showing a significant increase along the elevational gradient and a decrease with increasing soil depth.

4. Discussion

In our study, C decomposition from all soil samples followed the same pattern as shown in Fig. 1a. This data showed in the CF in the 25–40 cm soil depth, the decomposition rates dropped dramatically by day 60, remaining low and relatively constant through day 371. The rapid drop of decomposition rates, which was also found in similar studies (Conant et al., 2008a; Hartley and Ineson, 2008), was probably driven by the progressive depletion of labile C of SOC being incubated. Since the incubated soil samples were removed from the plant–soil system, the LOC pool decomposed rapidly with no replacement. The leveling off of the cumulative decomposition curves of SOC (Fig. 1b) was consistent with previous findings (e.g. Fang et al., 2005; Conant et al., 2008a). With the increase contribution of ROC in decomposition of SOC (Fang et al., 2005; Vanhala et al., 2007), the decomposition rates decreased and stabilized. Changes in the lability (quality) of SOC were believed to be the dominant factor regulating the decline in decomposition rates under constant temperature and moisture conditions (Kirschbaum, 2006; Conant et al., 2008b), though changes in the microbial community were likely to occur under different incubation temperatures (Fang et al., 2005).

In accordance with kinetic theory based on chemical reactions, our results showed that the ROC was much more temperature-sensitive than the LOC (3.94 ± 0.30 vs. 1.39 ± 0.04, Fig. 2) in the Wuyi Mountains. The temperature sensitivity of SOC decomposition significantly increased with substrate recalcitrance, similarly to the results from many previous studies (e.g. Fierer et al., 2005; Conant et al., 2008a,b; Hartley and Ineson, 2008). This is a reasonable supposition given that temperature sensitivity of chemical reactions is inversely proportional to the reaction rates (Davidson and Janssens, 2006). Observed differences in temperature response of SOC decomposition indicated a shift to the decay of biochemically-recalcitrant C over time since 8% of the initial soil C was respired. Moreover, sensitivity of the decomposition of SOC to warming was quality-dependent (Wetterstedt et al., 2009), suggesting the high Q_{10} values for decomposition of SOC with high recalcitrance. The effects of warming on soil C balance fundamentally relied on the net release of CO_2 from recalcitrant C. Due to the large proportion of ROC stored in the soils (difference between 1 and MBC/TOC, Table 2) and their high temperature sensitivity in the Wuyi Mountains, the response of the ROC pool to changes in temperature would accelerate soil-stored C losses. Similar to tropical soils (Six et al., 2002; Davidson and Janssens, 2006), subtropical soils are expected to release more C due to the large amount of recalcitrant C stored in soil organic matter (SOM), resulting in a positive feedback to global climate change.

Soil depth had a significant effect on the $Q_{10\text{-labile}}$ and $Q_{10\text{-recalcitrant}}$ values (Table 2). With increasing soil depth, the proportion of labile C decreased and that of recalcitrant C increased (Fang et al., 2005), indicating a decreasing SOC quality. Our results showed that the percentage of MBC to SOC and WSOC to SOC decreased substantially with depth (Table 2), suggesting a dramatic decrease in substrate quality and an increasing effect of recalcitrant C on the Q_{10} values. Kinetic theory indicates higher temperature sensitivity for the recalcitrant C than the labile C (Fissore et al., 2009). So, the $Q_{10\text{-labile}}$ and $Q_{10\text{-recalcitrant}}$ values increased significantly with increasing soil depth. Interestingly, C:N ratios significantly decreased with increasing soil depth (Table 2). This may possibly reflect a greater degree of breakdown (Yang et al., 2010) and the accumulation of old, recalcitrant SOM stored in deeper soil layers (Callesen et al., 2007). During decomposition, LOC was largely respired as CO_2 while nitrogen was immobilized in microbes and decay products (Yang et al., 2010), resulting in more old, recalcitrant SOM with lower C:N ratios with increasing soil depth (Callesen et al., 2007).

One unexpected result from our study was that $Q_{10\text{-labile}}$ values showed an insignificant increase along the elevational vegetation change (Table 1). This may result from the nature of LOC that it was so easily broken down by microbes that little activation energy was needed. Since Q_{10} of SOC decomposition was represented by the activation energy according to kinetic theory, small differences in energy usage during labile C decay may indirectly result in non-significant $Q_{10\text{-labile}}$ values for the four studied elevations. Niklińska and Klimek's study (2007) also found no significant differences in Q_{10} values along an elevational gradient in Poland. In contrast to LOC, elevational change had a significant effect on $Q_{10\text{-recalcitrant}}$ values. These values showed a positive relationship with increasing elevation (Table 2). Radiocarbon dating of soil-respired CO_2 has shown that the contribution of old, recalcitrant SOC to total soil respiration tends to increase with increasing latitudes (Trumbore, 2000; Schuur and Trumbore, 2006). Since the elevational temperature gradient was comparable to those observed along latitudinal gradients (Niklińska and Klimek, 2007), the increase in $Q_{10\text{-recalcitrant}}$ values along the elevational gradient may be attributed to increasing C recalcitrance. Soils at higher elevations contained significantly more ROC (difference between 1 and MBC/TOC, Table 2) partly because C decomposition was limited by low soil temperatures and often wet conditions (Table 1; Garten et al., 1999; Kautz et al., 2004). However, an estimated temperature increase of 1.1 °C–6.4 °C at the end of this century would intensify the decomposition of SOC in the Wuyi Mountains, especially for the soil-stored recalcitrant C. Globally, it is likely that increased temperature would promote more CO_2 release from recalcitrant SOM in cold regions, resulting in a greater positive feedback to global climate change than previously expected. Moreover, the response of ROC to future temperature change will determine the magnitude of the positive feedback due to its large storage pool in soils.

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