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Consistent temperature sensitivity of labile soil organic carbon mineralization along an elevation gradient in the Wuyi Mountains, China

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ABSTRACT

Labile soil organic carbon (LOC) is an essential component in the global carbon (C) cycling due to its fast turnover and sensitivity to environmental changes. However, responses of the mineralization of LOC to current global warming are still not fully understood. In this study, we investigated LOC mineralization at 5, 15, 25 and 35 °C incubation temperatures through laboratory incubation of soil samples and estimated the temperature sensitivity of LOC mineralization at various temperature ranges (i.e. 5–15, 15–25, and 25–35 °C) in an evergreen broad-leaf forest (EBF), a coniferous forest (CF), a sub-alpine dwarf forest (SDF), and an alpine meadow (AM) along an elevation gradient in the Wuyi Mountains in southeastern China. Our results showed that mineralization of LOC significantly increased along the elevation gradient and with increasing incubation temperatures. The interaction of elevation and incubation temperatures was additive on LOC mineralization. Moreover, the temperature sensitivity (Q_{10}) of LOC mineralization significantly decreased with increasing incubation temperature ranges. However, elevation gradient had no statistically significant impact on Q_{10} within each incubation temperature range. Our results suggest that soil organic C (SOC) at high elevations is more vulnerable to global warming. Moreover, consistent Q_{10} of LOC mineralization along the elevation gradient indicates that locally, C quality maybe a minor factor in affecting LOC mineralization and it may be adequate to use a constant Q_{10} value to represent the response of LOC mineralization to warming in regional climate-C cycling models.

1. Introduction

Global mean temperature is predicted to increase another 0.3 to 4.8 °C by the end of this century (IPCC, 2013). Temperature, which has captured much attention in the global carbon (C) cycling, is undoubtedly one of the most important variables that can regulate mineralization of soil organic C (SOC) (Davidson and Janssens, 2006; Xu et al., 2012; Sierra et al., 2015). SOC decomposition is one of the two aspects that determine soil C balance in terrestrial ecosystems (Davidson et al., 2000; Wetterstedt et al., 2010). The potential loss of soil-stored C due to an increase in temperature may result in a buildup in atmospheric CO_2 concentration as well as a positive feedback on climate change (e.g. Xu et al., 2010b). However, accurate prediction of future climate change is greatly limited by our understanding of the land C cycling (Friedlingstein et al., 2006, 2014; Luo et al., 2016). There is thus an urgent need for more empirical knowledge of soil C decomposition and its temperature sensitivity (Q_{10}).

The process by which organic C (OC) are broken down and transformed into inorganic C is known as mineralization. Conceptually, SOC is usually divided into two fractions, labile OC (LOC) and recalcitrant OC (ROC), in laboratory studies (e.g. Fang et al., 2005b; Conant et al., 2008; Xu et al., 2010b). In comparison to ROC, LOC functions as a good indicator for predicting minor changes in SOC. LOC, a type of microbially degradable C associated with microbial growth (Zou et al., 2005), is considered to be the labile C pool. It is easily biodegradable and physically accessible by soil microbes and accounts for a small part of the SOC pool, typically less than 8% (Xu et al., 2010a). However, the rapid turnover of LOC is one of the main aspects in the flux of CO_2 between terrestrial ecosystems and the atmosphere. It might be a potential C source since microbial decomposition of SOC is sensitive to warming (Wetterstedt et al., 2010; Wang et al., 2013; Luo et al., 2016).

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Consequently, temperature sensitivity (Q_{10}) of SOC mineralization has received much attention (e.g. Fang et al., 2005b; Davidson and Janssens, 2006; Sierra et al., 2015). In climate-C modeling studies, Q_{10} of SOC decomposition is always considered to be a constant constraint in prediction of the impact of climate change on soil C stock (Luo et al., 2016). However, many empirical studies have proposed to use different Q_{10} values to represent mineralization of LOC and ROC to temperature changes in models (e.g. Liski et al., 2000; Melillo et al., 2002; Conant et al., 2008; Hartley and Ineson, 2008; Xu et al., 2010b, 2012). Moreover, one of the opinions in the SOC mineralization-temperature relationship studies is that the mineralization of LOC is sensitive to temperature variation (Liski et al., 2000; Fang et al., 2005b). To better project future climate change, we undoubtedly need more knowledge on Q_{10} of LOC mineralization and to find out whether LOC's mineralization is in accordance with the "C quality-temperature hypothesis", which suggests that Q_{10} of C mineralization is inversely related to the C quality of the SOC (Bosatta and Agren, 1999; Davidson and Janssens, 2006).

Soils in boreal forests and tundra at high latitudes are believed to expect a high loss of C under current global warming due to the predicted experience of the greatest temperature rise in these regions (Dorrepaal et al., 2009). Elevational gradient of temperature changes in mountains can be similar to that caused by latitudes (Smith et al., 2002), which make mountains important regions in climate change research. In this study, we aimed to: (1) assess the mineralization rates of LOC and (2) estimate the temperature sensitivity of LOC mineralization along the elevation gradient in the Wuyi Mountains. The Wuyi Mountains have a typical vertical, well-reserved zonation of vegetation communities in the subtropics in the southeastern China (Wang et al., 2009; Xu et al., 2010b). The elevational temperature gradient, which could resemble those observed along latitudinal gradients (Niklinska and Klimek, 2007), provides us an ideal model ecosystem to investigate the mineralization of LOC.

2. Materials and methods

2.1. Site description

The experimental sites are located in the Wuyishan National Reserve Area in Fujian Province, China (27°33′—27°54′N, 117°27′—117°51′E), a 56,527 ha forested area in the southeast of China. Mean annual temperature (MAT) is 15 °C and mean annual precipitation (MAP) is 2,000 mm. The four typical, different vegetation types along the elevation gradient are evergreen broad-leaf forest (EBF), coniferous forest (CF), sub-alpine dwarf forest (SDF), and alpine meadow (AM). See detailed site information in Table 1.

2.2. Experimental design and soil sampling

Four replicate plots (50 × 60 m) at each vegetation type (EBF, CF, SDF and AM) were set along the elevation 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 (0–25 cm in depth) in all the subplots in November 2016 using a 2 cm-diameter soil corer. Ten soil cores were taken from each subplot and pooled together, as a replicate. Samples were immediately sieved (< 2 mm) to remove soil fauna, rocks and fine roots, thoroughly hand-mixed and placed in plastic bags and transported in several coolers to the ecological laboratory at the Nanjing Forestry University.

2.3. Methods

The LOC content was estimated using a sequential fumigation-incubation method according to Zou et al. (2005) and Liu and Zou (2002). Brief procedures were as follows: 30 g of fresh soil samples were fumigated for 36 h with purified chloroform in a desiccator with

Table 1
Site conditions and soil characteristics along the elevation gradient.

Site	Elevation (m)	MAT (°C)	MAP (mm)	T_{soil} (°C)	M_{soil} (%)	MBC (mg g^{-1})	SOC (mg g^{-1})	TN (mg g^{-1})	C:N	pH	Litter mass (t hm^{-2} y^{-1})	Fine root biomass (kg m^{-3})	Dominant species
EBF	500	18.5	1,700	15.12 ± 0.05	21.91 ± 1.01	1.09 ± 0.09d	38.50 ± 1.77c	5.10 ± 0.10c	7.55 ± 0.32b	4.65 ± 0.03a	5.63 ± 0.51b	1.90 ± 0.16c	*Castanopsis carlesii, Castanopsis eyrei*
CF	1,150	14.5	2,000	13.73 ± 0.08	28.93 ± 0.52	1.60 ± 0.12c	39.85 ± 2.76c	5.11 ± 0.58c	7.80 ± 0.50b	4.31 ± 0.08b	8.08 ± 0.65a	2.05 ± 0.15c	*Pinus taiwanensis, Oligostachyum oedogonatum*
SDF	1,750	11.2	2,200	11.04 ± 0.14	40.43 ± 0.64	2.07 ± 0.05b	59.46 ± 2.90b	7.06 ± 0.28b	8.42 ± 0.45b	4.58 ± 0.05a	2.92 ± 0.46c	2.74 ± 0.21b	*Symplocos paniculata, Stewartia sinensis*
AM	2,150	9.7	3,100	10.63 ± 0.02	52.96 ± 0.83	3.19 ± 0.04a	102.59 ± 3.58a	10.60 ± 0.56a	9.68 ± 0.56a	4.78 ± 0.11a	1.94 ± 0.22d	5.48 ± 0.10a	*Calamagrostis brachytricha, Miscanthus sinensis, Lycopodium clavatum*

Note: MAT: mean annual soil temperature; MAP: mean annual precipitation, T_{soil}: soil temperature; M_{soil}: soil moisture; MBC: microbial biomass carbon; SOC: soil organic carbon; TN: total nitrogen. Values are mean ± SE. Different lower case letters indicate statistically significant difference along the elevation gradient. EBF: evergreen broad-leaf forest; CF: coniferous forest; SDF: sub-alpine dwarf forest; AM: alpine meadow.

Table 2
Results of two-way ANOVA (*F* tests) for responses of the rates and temperature sensitivity (Q_{10}) LOC mineralization to elevation and incubation temperatures (5, 15, 25, and 35 °C, for rates) or incubation temperature ranges (5–15, 15–25, and 25–35 °C, for Q_{10}). ***: < 0.001.

	Elevation		Temperature		Elevation × Temperature	
	df	*F*, *P*	df	*F*, *P*	df	*F*, *P*
Rates	3	750.33***	3	1937.38***	9	85.81***
Q_{10}	3	1.22	2	64.37***	6	0.41

moist paper towels. Control (unfumigated) soil samples were placed in another desiccator for 36 h. Then, chloroform was excluded from the fumigated soil samples and all soil samples were inoculated with 1 g of unfumigated soil. Each of the fumigated soil samples, control and blank, along with a small plastic bottle (50 ml, with lid removed) containing 15 ml of 1 M NaOH was placed in a 1 l Mason jar, and incubated at 60% of water holding capacity (WHC) under different temperatures (5, 15, 25, and 35 °C) for 10 days as a cycle. 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 between each interval and deionized water was added to maintain moisture. The sequential fumigation-incubation had a total of 6 cycles in this study. The LOC content was calculated according to (Stanford and Smith, 1972; Zou et al., 2005):

$$M_t = C_{LOC}(1 - e^{-kt}), (t = 1, 2, \ldots\ldots, n); \quad (1)$$

where M_t is the accumulated CO_2-C during incubation; C_{LOC} is the estimated pool size of LOC; k is the potential turnover rate which could be estimated using linear regression with the following equation:

$$Ln(C_t) = Ln(kC_{LOC}) - kt, (t = 1, 2, \ldots\ldots, n); \quad (2)$$

where C_t is the CO_2-C for each single incubation cycle; k is the slope; $Ln(kC_{LOC})$ is the intercept (a), and $C_{LOC} = e^a/k$. The mineralization rate (mg kg^{-1} d^{-1}) is calculated as:

$$R = C_{LOC}/10t, (t = 1, 2, \ldots\ldots, n). \quad (3)$$

By definition, the temperature sensitivity of SOC mineralization is the change in mineralization rates with temperature under otherwise constant conditions (Fang et al., 2005b). It is estimated as:

$$Q_{10} = (r_2/r_1)^{10/(T_2 - T_1)}; \quad (4)$$

where r_2 and r_1 are mineralization rates at high and low incubation temperatures, T_2 and T_1, respectively. The Q_{10} values were obtained for soil LOC from each elevation site at three ranges of temperature: low (5–15 °C, Q_{10L}), medium (15–25 °C, Q_{10M}), high (25–35 °C, Q_{10H}).

SOC and total nitrogen (TN) were determined by combustion with an elemental analyzer (Model CNS, Elementar Analysen Systeme GmbH, Germany). Soil temperature and moisture were measured by watchdog weather stations (Spectrum Technologies, Inc., IL, USA) at the 15 cm soil depth. Soil pH values were measured with a Calomel electrode on a paste of 1:1 (w:v) of fresh soil and deionized water. Plant litter was collected by tents (1 mm × 1 mm in mesh size) in EBF, CF, and SDF and by clipping in AM. Plant litter mass was determined by weight in the laboratory after being oven-dried at 65 °C for 48 h. Fine root biomass (≤ 2 mm in diameter) was seasonally estimated with soil cores (Davis et al., 2004; Xu et al., 2014).

2.4. Statistical analysis

Two-way ANOVA was performed to examine the effects of elevation and incubation temperatures or temperature ranges on the mineralization rates of LOC, Q_{10} values. One-way ANOVA was used to examine the effect of elevation on soil properties, litter mass and fine root biomass.

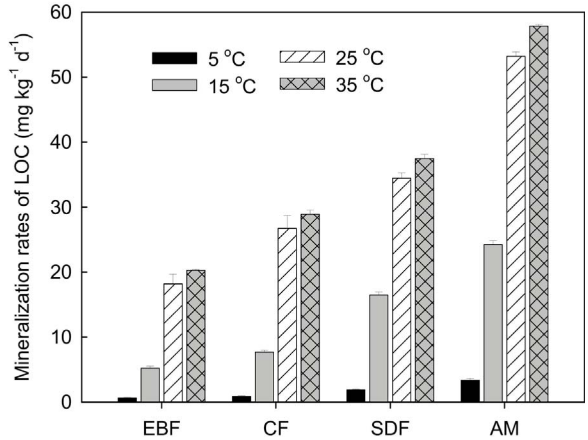

Fig. 1. Mean mineralization rates of LOC along the elevation at different incubation temperatures (values are mean ± SE, n = 4).

Linear regression analyses were used to evaluate the relationships of the rates of LOC mineralization with litter mass and fine root biomass. All statistical analyses were conducted using R 3.3.2 (R Development Core Team, 2016).

3. Results

Along with the increasing elevation, MAT and soil temperature decreased and MAP and soil moisture increased. While SOC, TN, and fine root biomass significantly increased along the elevation, C:N ratio was significantly higher in AM, litter mass was significantly higher in CF, and pH value was significantly lower in CF (Table 1).

Elevation gradient and incubation temperatures had significant impacts on the mineralization of LOC (all $P < 0.001$, Table 2, Fig. 1). The mean mineralization rates of LOC substantially increased along the elevation gradient from EBF, CF, SDF to AM. The mineralization rates of LOC also significantly increased with increasing incubation temperatures. Soils differed greatly in their C loss during incubation, for example, ranging from 18.17 ± 1.49 mg kg^{-1} d^{-1} in EBF to 53.21 ± 0.66 mg kg^{-1} d^{-1} in AM at 25 °C (Fig. 1). The interaction of elevation and incubation temperatures was additive on LOC mineralization ($P < 0.001$, Table 2). The mineralization of LOC was positively regulated by microbial biomass C (all $P < 0.001$, Fig. 2) and by fine root biomass (all $P < 0.001$, Fig. 3a) but negatively regulated by litter mass (all $P < 0.01$, Fig. 3b) at each incubation temperature.

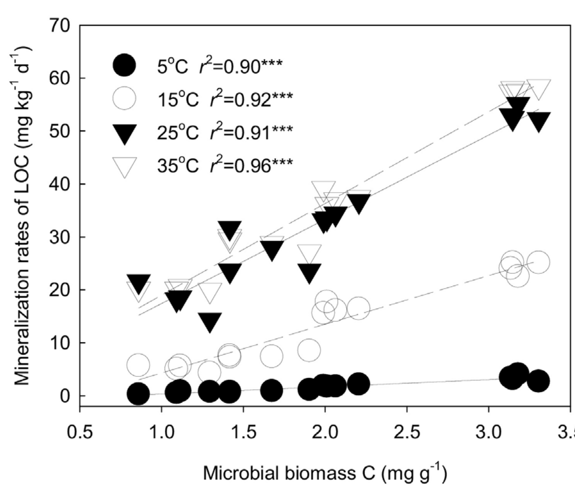

Fig. 2. Relationships between microbial biomass C and the mineralization rates of LOC at different incubation temperatures. ***: $P < 0.001$.

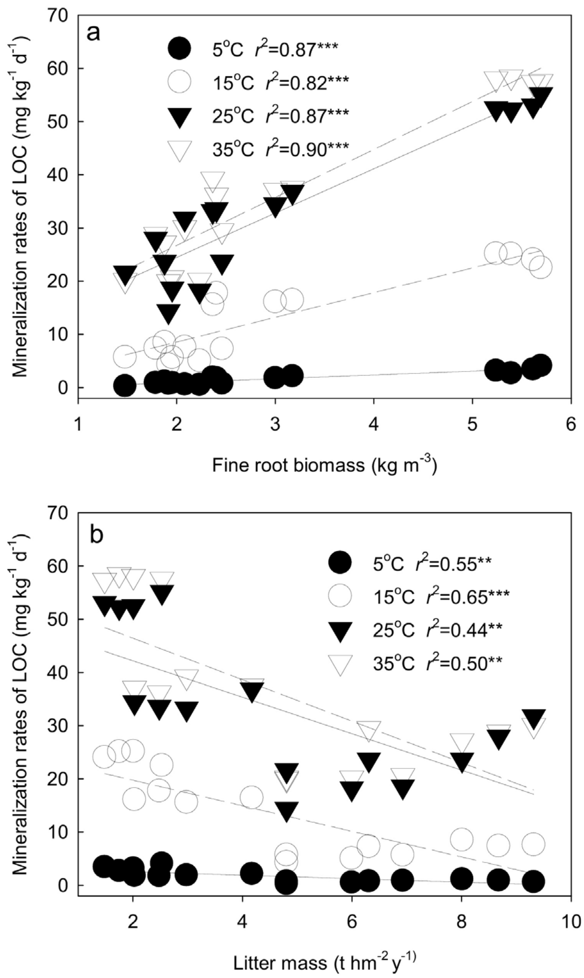

Fig. 3. Relationships of fine root biomass (a) and litter mass (b) with the mineralization rates of LOC at different incubation temperatures. **: $P < 0.01$; ***: $P < 0.001$.

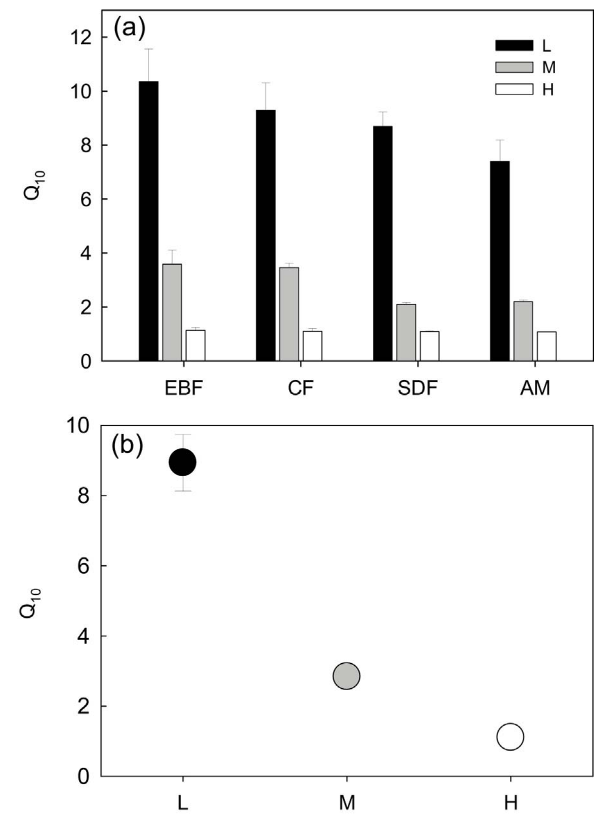

Fig. 4. Q_{10} values of LOC mineralization along the elevation gradient under different incubation temperature ranges (a, values are mean ± SE, n = 4). L, M, H indicate temperature ranges (L: 5–15 °C; M: 15–25 °C; H: 25–35 °C). Panel (b) shows mean Q_{10} values of different incubation temperature ranges (values are mean ± SE, n = 16).

The Q_{10} of the mineralization of LOC was sensitive to temperature changes ($P < 0.001$, Fig. 4) but not the elevation gradient ($P > 0.05$, Table 2). The temperature sensitivity (Q_{10}) of LOC mineralization significantly decreased with increasing incubation temperature ranges: $Q_{10L} > Q_{10M} > Q_{10H}$ ($P < 0.001$, Table 2, Fig. 4b). However, no statistically significant differences were found in Q_{10} values along the elevation gradient ($P > 0.05$, Table 2).

4. Discussion

In our study, the mineralization rates of LOC significantly increased with the increasing elevation and the incubation temperatures. The mineralization of LOC was the transformation of organic C into inorganic C by heterotrophs. The process largely depends on substrate quality (Niklinska and Klimek, 2007), which in turn controlled by vegetation community (Raich and Tufekciogul, 2000). Soil decomposability (quality), one of the dominant factors that control decomposition rates (Hobbie and Gough, 2004; Shaver et al., 2006), increased along the elevation gradient. For example, LOC content significantly increased with increasing elevation, supporting the high lability of labile C pools with high decomposability at higher elevations. Moreover, the TN increased significantly with increasing elevation, which may facilitate mineralization of LOC. Many studies had reported substantial vegetation effect on microbial decomposition of LOC through C input associated with litter and fine roots (e.g. Hobbie and Gough, 2004; Fornara et al., 2009). Different vegetation types along the elevation may have a strong impact on the quality of fine roots and litter that eventually became organic matter (Hobbie and Gough, 2004). In accordance with those findings, our results showed that the mineralization of LOC positively correlated with fine root biomass and negatively with litter mass at each incubation temperature. Fine roots were one of the labile C pools in the soil (Cheng and Kuzyakov, 2005), which had rapid decomposition rates (Kuzyakov et al., 2007). Plant litter, cut into small pieces by soul fauna, also was an important C source (Loya et al., 2004). Though the values of litter mass in EBF and CF were higher, it might be the decomposability of litter rather than the quantity, closely relating to soil C mineralization. For instance, litter in CF was resistant to decomposition due to the richness in waxes, resins and lignin (Swift et al., 1981; Niklinska and Klimek, 2007).

On the other hand, in line with previous studies, our results showed that the mineralization rates of LOC were significantly influenced by temperatures and comparable with, for example, the rates found across a network of European forest sites (e.g. Reichstein et al., 2005; Davidson and Janssens, 2006; Rey and Jarvis, 2006). This is because the decomposition process was microbially mediated and microbes themselves were temperature sensitive (Xu et al., 2010b; Zhou et al., 2012). Temperature had been found to be the major factor in controlling the mineralization of LOC in soil (e.g. Howard and Pja, 1993; Fang et al., 2005a; Xu et al., 2010b). It significantly influenced a range of soil parameters in the simulated rhizosphere, such as the amount of microbes in the soil (Kuzyakov et al., 2007), and the intensity of microbial activity. Soils at higher elevations contained significantly more organic C (Garten et al., 1999; Kautz et al., 2004) partly because the decomposition of LOC was limited by low soil temperatures and often wet conditions. SOC was found more decomposable at lower elevations (Giardina and Ryan, 2000) because SOC is both different in quality and exposed to contrasting environmental conditions (Rasse et al., 2006). In the Wuyi Mountains, EBF and CF at low elevations experienced relatively high temperatures and lower moistures, which caused great C losses. The high mineralization rates and high SOC contents at high elevations seemed to be contradictory. However, decomposition was only one of the processes of C turnover. The rate of C sequestration at high elevations was supposed to be high because we had increasing LOC and SOC contents with increasing elevation.

Significant differences in Q_{10} values were found between incubation temperature ranges. The highest Q_{10} coefficient was found for the low temperature range (5–15 °C), negatively correlated with incubation temperature ranges as found by Hamdi et al. (2013). Our estimates of Q_{10} ranging from 0.86 to 19.69 with 94% of the values falling with the range 0–10 are comparable with a synthesis of laboratory incubation studies with Q_{10} ranging from 0.5 to 344 with approximately 98% of the values falling with the range 0–10 (Hamdi et al., 2013). Our findings, the temperature sensitivity of LOC mineralization were not constant across the temperature ranges, is in consistent with predictions from chemical thermodynamics (Katterer et al., 1998; Davidson and Janssens, 2006; Martin et al., 2009). Q_{10} values, derived from LOC mineralization, declined with increasing temperature ranges because substrate-availability differences from 5 to 15 °C was the largest and the differences decreased with increasing incubation temperature ranges (Belaytedla et al., 2009). Our results also support that the effect of temperature on the mineralization rates was more intense at relatively lower temperature ranges (Kirschbaum, 1995; Sjogersten and Wookey, 2002). The mean Q_{10} value for the high temperature range (25 to 35 °C) was close to 1.0. It indicates that temperature around 30 °C was the particular thermal niche for the microbial activity in the Wuyi Mountains, outside of which microbial activity could be limited. Importantly, our results suggest that soils at higher elevations may release more CO_2 to the atmosphere in the Wuyi Mountains because an estimated temperature increase of 1.1–5.6 °C at the end of this century (IPCC, 2013) falls into the low incubation temperature ranges (5–15 °C) for the AM (MAT is 9.7 °C). This potential temperature increase makes soils at high elevations more vulnerable to global changes.

It was unexpected that Q_{10} values along the elevation gradient were constant within each incubation temperature range. Kinetic theory indicates that Q_{10} of SOC mineralization is inversely related to the C quality (Fissore et al., 2009). Interestingly, C:N ratio, as one of the indicators of C quality, was found significantly higher in AM. This is not contradictory to the kinetic theory since numerically, the differences between C:N ratios along the elevation gradient is small. For example, the mean C:N ratio in the Wuyi Mountains (8.4) is much lower than in the Beskidy Mountains (22.0) in southern Poland (Niklinska and Klimek, 2007) and nitrogen may not limit the mineralization of C in the Wuyi Mountains. On the other hand, we know little about the roles of microbes played in LOC mineralization, which is undoubtedly important but insufficiently studied. Consistent Q_{10} of LOC mineralization along the elevation gradient indicates that locally, C quality maybe a minor factor in affecting LOC mineralization and it may be adequate to use a constant Q_{10} value to represent the response of LOC decomposition to warming in regional climate-C cycling models. Further research of the effect of microbial community on the Q_{10} of SOC mineralization is highly needed toward more realistic projections of soil C dynamics by Earth system models.

Authorship

All authors contributed intellectual input and assistance to this study and manuscript preparation. X.X. conceived the idea and designed the experiment. Q.L. collected and analyzed the data with help from X.X. Q.L. and X.X. wrote the paper with input from all authors.

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