Q₁₀ values vary with different kinetic properties of C mineralization

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A R T I C L E   I N F O

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A B S T R A C T

Temperature response quotient (Q₁₀) is a critical parameter for evaluating global additional carbon (C) release with climate change. However, its value is usually derived from time span or instantaneous rate or cumulative amount of C flux, giving a very one-sided account of thermal sensitivity of C cycling. Through a 117-day laboratory incubation study, we estimated Q₁₀ values simultaneously with the labile (a₀) and recalcitrant C proportions and their rate constants, and then tested for any variances of these kinetic properties in different vegetation stands, soil horizons, aeration statuses, and thermal settings (i.e., diurnally-varying, constant low and constant high temperatures). A regularly varying temperature regime increased the exploitation of labile C resources (i.e., high a₀) and required longer time spans (i.e., low rate constants). The constant high temperature induced the exhaustive depletion of the labile C pool and motivated a very rapid and short-term C mineralization process. The constant low temperature treatment was characterized by the lowest a₀ but by medium rate constants because low temperature slowed the C mineralization processes but retained high level of the original C processing diversity. Therefore, a₀ and the rate constants showed discrepancies in their temperature sensitivities as revealed by pairwise comparisons of temperature regimes. Such discrepancies were also supported by pairwise comparisons of aeration statuses, forest stands and soil horizons. The Q₁₀ bias between C mineralization a₀ and rate constants in this laboratory experiment is attributed to the inherently distinct properties of these two parameters, as a₀ and its Q₁₀ are closely correlated with the sizes of the easily available C pool, while rate constants and their Q₁₀ variances explain the temporal scale of the same C mineralization process. Our findings suggest a combined application of a₀ and rate constants for exploring the temperature sensitivity of C mineralization in future studies.

1. Introduction

The temperature response quotient (Q₁₀) is a critical indicator of the thermal sensitivity of C (decomposition) and is broadly used to estimate the additional global C release induced by climate change (Davidson and Janssens, 2006; Kirschbaum, 1995; Luo et al., 2001; Phillips et al., 2016). Q₁₀ evaluation is usually based on instantaneous CO₂ flux rates (Chang et al., 2012; Fang and Moncrieff, 2001; Karhu et al., 2014; Sun et al., 2016; Waldrop et al., 2010), time spans needed for an identical amount of C mineralization (Bracho et al., 2016; Wang et al., 2013; Zhu and Cheng, 2011), cumulative C flux over a given time period (Conant et al., 2008; Hamdi et al., 2013; Nakajima et al., 2016; Wang et al., 2013). For instance, the “equal-time” approach always leads to great discrepancies in the degradation of fast- vs. slow-turnover C pools among samples along with increasing incubation temperature and time, while the “equal-C” approach can underestimate the contribution of more recalcitrant substrates (Hamdi et al., 2013). Although a first-order model has been applied to disentangle the C mineralization process to quantify the sizes of various labile and recalcitrant pools as well as their decomposition rate constants, the temperature sensitivity of the above-mentioned kinetic parameters of C mineralization has seldom been investigated (Braakhekke and de Bruijn, 2007; Bracho et al., 2016; Rey

However, the Q₁₀ values derived from various experimental methods can be confounded by the different qualities and retention times of the co-existing labile and recalcitrant components (Conant et al., 2008; Hamdi et al., 2013; Nakajima et al., 2016; Wang et al., 2013). For example, the “equal-time” approach always leads to great discrepancies in the degradation of fast- vs. slow-turnover C pools among samples along with increasing incubation temperature and time, while the “equal-C” approach can underestimate the contribution of more recalcitrant substrates (Hamdi et al., 2013). Although a first-order model has been applied to disentangle the C mineralization process to quantify the sizes of various labile and recalcitrant pools as well as their decomposition rate constants, the temperature sensitivity of the above-mentioned kinetic parameters of C mineralization has seldom been investigated (Braakhekke and de Bruijn, 2007; Bracho et al., 2016; Rey...
et al., 2008; Sun et al., 2016). Although Rey and Jarvis (2006) found that the labile C proportion (a₀) did not vary among 4, 10, 20 and 30 °C, their experimental data were only derived from upper mineral soils, whose estimated labile fraction from the two-compartment model might be too small (1–9%) to detect substantial differences. The C pool sizes were reported to vary with the substrate quality, the microbial community composition and the environmental conditions (Braakhekke and de Bruijn, 2007; Coûteaux et al., 2002; Erhagen et al., 2015). In principle, a change in temperature can induce shifts in functional microorganisms and in enzyme activities, modify the primary resource decomposition pathways and the secondary material production, and, finally, affect the sizes of the labile or recalcitrant C pools (Dalias et al., 2001; Razavi et al., 2016). Thus, the kinetic parameters of various soil C pools should be fitted to the observational data to determine the temperature sensitivity of the C mineralization, including the rate constants and the relative sizes of the C pools of varying decomposability (Davidson and Janssens, 2006).

Furthermore, the temperature sensitivity of C mineralization not only varies in those kinetic properties, which are partially determined by soil properties (Xu et al., 2016), but also changes with environmental conditions, such as constant vs. varying temperature regimes (Conant et al., 2008; Fang et al., 2005; Nakajima et al., 2016; Xia et al., 2009; Zhu and Cheng, 2011), the aeration statuses (Blagodatskaya et al., 2014; Devêvre and Horwáth, 2000; Diakova et al., 2016), the forest stands (Guo et al., 2016; Gutiérrez-Girón et al., 2015; Rey and Jarvis, 2006), and the soil horizons (Laganière et al., 2015; Xu et al., 2014). These constraints, especially the temperature and the aeration status, are fixed as constant in most studies, and a continuously changing vs. constant environmental comparison has rarely been scrutinized (Conant et al., 2008; Hartley et al., 2008; Pettersson and Bååth, 2003; Ranneklev and Bååth, 2001).

Together, we hypothesized that Q₁₀ values would vary with the different kinetic properties of C mineralization and would be strongly influenced by the temperature setting, the aeration status, the forest stand or the soil horizon. To test this hypothesis, we conducted an incubation study to test for any variances in the temperature dependence of the decomposition potential and the rate constants of the labile and recalcitrant C pools in terms of the environmental variables noted above.

2. Materials and methods

On 4 Sep 2013, we randomly collected samples from soil horizons O (S₀) (0–5 cm) and A (S₄) (5–15 cm) in 10 plots (five samples pooled into a single composite sample for each 10-m × 10-m plot) in both a deciduous forest (F₉) and an evergreen coniferous forest (F₇) on Changbai Mountain (Jilin, China) (Table 1).

Soil samples were thoroughly mixed and freshly sieved through a 5-mm sieve and then stored at 4 °C until use. The aboveground parts (i.e., stalk and leaf) of maize residues (C = 42.16%; N = 0.80%) were dried at 60 °C to a constant weight and passed through a 5-mm sieve. The soils were thoroughly mixed with the maize residue at a rate of 5 g C residue per 10 g soil (DW) (< 5 mm). The large amount of residue was used as a standard organic material (Coûteaux et al., 2002), ensuring a relatively constant supply of available C for microbial growth over the period of this laboratory experiment. The soil mixture was then packed into bottom-sealed PVC columns (inner diameter of 5 cm and height of 16 cm) at 60% water holding capacity; this was replicated 3 times. Sterilized ultrapure water was added to the soil mixture every 2–3 days to maintain the constant weight in each column over the course of the laboratory incubations.

The experimental temperature regimes included the constant low (CLT) at 10 °C, the constant high (CHT) at 30 °C, and the regularly varying (VT) between 10 and 30 °C with 4 programmed stages per day: stage 1, 10 °C for 6 h; stage 2, increasing smoothly from 10 to 30 °C for 6 h; stage 3, 30 °C for 6 h; stage 4, decreasing smoothly from 30 to 10 °C for 6 h. The soil microcosms were aerated using a pump that was automatically controlled by a timer that periodically switched the pump on for 2 min and then off for 1 min. The CO₂ subsamples were collected separately on days 0, 1, 2, 4, 8, 16, 22, 40, 67 and 117.

Before the CO₂ flux was detected, the timer was bypassed, and the pump was switched on to continuously circulate CO₂-free air through a soda lime column to remove atmospheric CO₂ inside the soil microcosms over 1 h, and then, the CO₂ flux rate under continuous aeration status (C₀) was determined using the method described by Gershenson et al. (2009). Subsequently, the timer was set to its original status (see above); the CO₂ flux per column was trapped in a 0.5-M NaOH solution, which was saved in a closely sealed glass vial at room temperature, and the C content was immediately measured with a TOC/TN analyzer (Multi N/C 3000, Analytik Jena, Germany) (Zhu and Cheng, 2011). This intermittent aeration status was defined as “I₁₀”. In particular, under the V₁₀, the CO₂ samples were collected separately for each programmed temperature stage (see above).

A flow diagram illustrating Q₁₀ determination and a description of C mineralization parameters are provided in the Flow diagram SI-1 and Table SI-2, respectively. The effects of the temperature regime (CLT, CHT and VT), the air-flow status (C₀ and I₁₀), the forest stand (F₉ and F₇) and the soil horizon (S₀ and S₄) on the C mineralization parameters and their Q₁₀ values were analyzed with a factorial ANOVA in Statistica 10.0 (StatSoft Inc., Tulsa, Okla., USA). Post hoc analyses for the ANOVAs were performed using Scheffe test. All data met the assumptions of variance homogeneity and residual normality for conducting ANOVAs.

3. Results and discussion

Consistent with previous studies (Bracho et al., 2016; Dalias et al., 2001; Sun et al., 2016), we found that the temperature sensitivity of the C mineralization varied not only with the rate constants (k) but also with the labile C pool size (a₀) in this laboratory experiment (Fig. 1A–F). Furthermore, the a₀ and the rate constants showed discrepancies in their temperature sensitivities as revealed by pairwise comparisons of the temperature regimes, the aeration statuses, the forest stands and the soil horizons. All these results support the hypothesis that distinct thermal sensitivities exist among different kinetic parameters of C mineralization.

3.1. Temperature regime

The kinetic parameters of C mineralization varied substantially between temperature settings (Tables SI-2 and SI-3). As previously reported (Bárcenas-Moreno et al., 2009; Hamdi et al., 2013; Ranneklev and Bååth, 2001), the varying temperature regime (V₁₀) can promote the optimal growth of most mesophilic microbial groups. In addition, highly diversified microbial pathways increase the exploitation of C resources and the size of the labile C pool (Bracho et al., 2016; Sun et al., 2016). Thus, the greatest potential C mineralization (i.e., the highest a₀) under the V₁₀ was reasonable in the current study (Tables SI-2 and SI-3). At the same time, such a high diversity of active microbial species under the V₁₀ should be associated with the most complicated and multiple alternative C-decomposing processes, requiring the longest time spans (i.e., the lowest rate constants) (Tables SI-2 and SI-3).

The constant 30 °C under the CHT induced more exhaustive combustion of available C (i.e., highest a₀) than the CLT (Tables SI-2 and SI-3). At the same time, however, the CH₄ might adversely affect and thus reduce the abundances of undesireable psychrophilic microorganisms according to previous studies (Ranneklev and Bååth, 2001; van Gestel et al., 2013). This “sieved” and “simplified” microbial community caused the C mineralization process to complete in a very short time (i.e., the highest rate constants) (Tables SI-2 and SI-3). Similarly, as observed by Sun et al. (2016) and Bracho et al. (2016), the turnover time of the decomposing C pools is always negatively
influenced by an increase in temperature. In contrast, although C mineralization processes are always very slow and incomplete at low temperatures (Hartley et al., 2008; Ranneklev and Bååth, 2001; van Gestel et al., 2013), the constant 10 °C under the CLT should preserve the high level of the original C-processing diversity. Thus, the CLT treatment was characterized by the lowest $a_0$ but by medium rate constants (Tables SI-2 and SI-3).

As a result, we found that the $Q_{10}(a_0)$ values were, on average, the highest with L-V (i.e., CLT vs. VT) (3.65), medium with L-H (i.e., CLT vs. CHT) (1.70), and the lowest with V-H (i.e., VT vs. CHT) (0.94) ($p < 0.001$) (Fig. 2A). However, the mean $Q_{10}(k)$ values in reverse order were as follows: L-V (0.78–1.13) < L-H (1.06–1.33) < V-H (2.28–2.52) ($p < 0.001$) (Fig. 2A).

### 3.2. Aeration status

Anaerobic processes can increase C use efficiency and substrate quality by accumulating fermentation products and accelerating the conversion of C from resistant into active pools (Devêvre and Horwáth, 2000; Guntiñas et al., 2009; Lin et al., 2016). Diakova et al. (2016) also observed that certain microbial groups are capable of adjusting to the absence of oxygen and thriving under anaerobic conditions. Therefore,
it is reasonable that the negative impact of lower O\textsubscript{2} availability on the labile C potential (a\textsubscript{0}) under intermittent aeration (I\textsubscript{g}) was offset compared to the continuous aeration status (C\textsubscript{0}) (Tables SI-2 and SI-3). Moreover, the Q\textsubscript{10}(a\textsubscript{0}) exhibited no difference between I\textsubscript{g} (2.04) and C\textsubscript{0} (2.16) (p = 0.069) (Fig. 2B).

However, the stimulus of phenol oxidase activity with greater O\textsubscript{2} availability accelerates and shortens the decomposition processes of recalcitrant C compounds, and less accumulation of resistant C compounds reduces the physical protection to existing C pools (Pissore et al., 2009). Thus, we found that the rate constants were higher under C\textsubscript{0} than I\textsubscript{g} (Tables SI-2 and SI-3) and varied with temperature to a larger extent under C\textsubscript{0} (1.90–2.11) than I\textsubscript{g} (0.85–1.21) (Fig. 2B) (p < 0.001).

3.3. Forest stand

Compared to the F\textsubscript{0}, the F\textsubscript{3} was characterized by larger C and N abundances, higher soil microbial biomass carbon (SMBC)/C ratios, and lower C/N ratios (Table 1). Similarly, Rey and Jarvis (2006) maintained that deciduous soils harbor more decomposable deciduous litter and induce high levels of microbial activity. In particular, the mean residence time of bulk soil organic C is significantly lower in the N-rich deciduous stand than in the N-dominated evergreen-dominated pine ecosystem (Yuste et al., 2007). Furthermore, stronger positive responses to temperature are always observed in soils with higher C/N ratios (Karhu et al., 2014) as well as the presence of N-limited microbial decomposers (Nottingham et al., 2015; Wang et al., 2011). In brief, consistent with the previous statements that higher Q\textsubscript{10}(k) values always accompany lower qualities of C pools (Fierer et al., 2006; Hamdi et al., 2013), our results confirmed that higher rate constants (Tables SI-2 and SI-3) as well as larger temperature responses accompanied F\textsubscript{3} (1.51–1.79) than F\textsubscript{0} (1.23–1.53) (Fig. 2C).

Unlike Q\textsubscript{10}(k), Q\textsubscript{10}(a\textsubscript{0}) exhibited no difference between F\textsubscript{0} (2.04) and F\textsubscript{3} (2.15) (p = 0.111) (Fig. 2C). A comparable response to experimental warming was observed by Lagnièrè et al. (2015), who confirmed that soils with greater C/N ratios have identical Q\textsubscript{10} values of cumulative C mineralization to those with lower C/N ratios. Furthermore, a lower Q\textsubscript{10} (relative increase in decomposition rate per 10 °C increase) has been observed in pine than in deciduous soil (Yuste et al., 2007). The Q\textsubscript{10} value can be negatively correlated with potential C mineralization but positively correlated with pH (Gutiérrez-Girón et al., 2015). Higher pH values (Table 1) combined with greater C availability in F\textsubscript{3} might induce an increase in bacterial activity and result in more rapid depletion of the labile C pool and the formation of the recalcitrant C fraction to a greater extent. As Lagnièrè et al. (2015) maintained, the faster a substrate is initially mineralized, the more recalcitrant C compounds will remain. In addition, the adaptation of the microbial decomposers can play an important role in counteracting the temperature sensitivity of C mineralization (Bai et al., 2017; Lagnièrè et al., 2015; Yuste et al., 2007): a greater dominance of slow, K-strategic growth in the coniferous soils compared to the deciduous soils can be a confounding factor in reducing the temperature sensitivity of the labile C pool.

3.4. Soil horizon

The contradictory Q\textsubscript{10} tendency of different kinetic parameters was also obtained via the pairwise comparisons of the soil horizons, i.e., the average Q\textsubscript{10}(a\textsubscript{0}) values decreased dramatically from the top organic horizon (S\textsubscript{0}) (2.45) to the subsurface mineral soil (S\textsubscript{1}) (1.74) (p < 0.001), while the Q\textsubscript{10}(k) varied little between the S\textsubscript{0} (1.42–1.69) and the S\textsubscript{1} (1.33–1.63) (p > 0.05) (Fig. 2D).

The cumulative C decomposition Q\textsubscript{10} for the mineral horizon can be lower than the overall organic horizon, and such reduced C mineralization temperature sensitivity in the mineral soil is probably due to the protective mechanism of increased metal Fe availability (Lagnièrè et al., 2015) or the highly occluded organic C within the mineral matrix (Nottingham et al., 2015). Additionally, as concluded by Bracho et al. (2016), the deeper mineral soil always maintains a smaller labile C pool compared to the top organic layer. Accordingly, a smaller a\textsubscript{0} (Tables SI-2 and SI-3) and its temperature sensitivity (Fig. 2D) accompanied S\textsubscript{A} rather than S\textsubscript{0}.

In contrast, the soil horizon had contrasting effects on rate constants k\textsubscript{1} and k\textsubscript{2} (Tables SI-2 and SI-3), and did not influence Q\textsubscript{10}(k) values (Fig. 2D). In general, the surface soil is dominated by more labile C substrates and deeper horizons by relatively recalcitrant compounds (Kim et al., 2012); more chemical complexity results in higher temperature dependencies (Mikan et al., 2002; Nottingham et al., 2015). However, the Q\textsubscript{10} derived from the times required for a given amount of C mineralization can be approximately 20% higher in the organic layer than in the subsurface mineral soil (Xu et al., 2014). In fact, different temperature sensitivities of enzyme kinetic parameters V\textsubscript{max} and K\textsubscript{m} under low substrate availabilities can lead to a canceling effect, i.e., V\textsubscript{max} and K\textsubscript{m} cancel each other out with increasing temperature, especially at intermediate temperatures (e.g., 15–25 °C) that favor mesophilic microorganisms (Blagodatskaya et al., 2016; Razavi et al., 2015). Thus, a highly available substrate in the organic layer can cause a higher temperature sensitivity of C decomposition compared to the mineral soil horizon because the top organic soil C
substrate is the least limiting ($S_l > S_m$), and the canceling effect between the $V_{max}$ and the $K_m$ is significantly reduced (Xu et al., 2014). The mechanisms underlying the soil horizon influences upon the rate constants of C mineralization and their $Q_{10}$ values need further investigation.

4. Concluding remarks

The inconsistent effects of environmental variables on the $Q_{10}$ values of the C mineralization rate constants and the $a_0$, which have been partially verified previously (Colman and Schimel, 2013), were confirmed in this incubation study. This $Q_{10}$ bias between the labile C pool fractions and the C decomposition rate constants is attributed to their inherently distinct properties because the former represents the available C potential capacity, whereas the latter indicates how rapidly a particular process occurs and is completed (Kirschbaum, 1995). We infer that the $a_0$ and its $Q_{10}$ are closely correlated with the substrate quality and the size of the easily available C pool, while the rate constants and their $Q_{10}$ variances explain the complexity and the temporal scale of the same C mineralization process, which are both probably determined by the sorting of the microbial community as affected by the environmental variables. Although incubation experiments tightly control environmental conditions, their $Q_{10}$ values of C mineralization may differ from those in the field, where the synthetic C is supplied by plants (Bracho et al., 2016; Schindlbacher et al., 2008; Yuste et al., 2007). Our findings call for urgent attention to and further verification of the combined application of $a_0$ and rate constants for exploring the sensitivity of C mineralization to global warming, especially in terms of varying environmental conditions such as temperature and aeration in field studies.

Declaration of interest

The authors have no conflicts of interest to declare.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at http://dx.doi.org/10.1016/j.jpedobi.2017.05.008.

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