



The decomposition rates of leaf litter and fine root and their temperature sensitivities are influenced differently by biotic factors

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Abstract

Background and aims Determining the temperature sensitivities of the decomposition rates of leaf litter and fine root is important for predicting the impact of climate warming on above- and belowground carbon (C) cycles in forest ecosystems. However, the responses of leaf and root decomposition rates to temperature have rarely been examined together.

Methods Here, we present the results of paired leaf litter and fine root decomposition experiments at four forest sites spanning 32° latitude in eastern China.

Results The mean annual soil temperature explained the variances of the decomposition rates of the leaf litter (k_{Leaf} , $R^2 = 0.95$) and fine root ($k_{\text{Fine root}}$, $R^2 = 0.86$) across the different biomes well and exerted a positive effect on the $k_{\text{Leaf}}: k_{\text{Fine root}}$ ratio. As a result, the

sensitivity of the decomposition rate to temperature was significantly higher in the leaf litter ($Q_{10} = 2.17 \pm 0.07$) than in the fine root ($Q_{10} = 1.40 \pm 0.06$). The results of structural equation models indicated that the initial C:nitrogen (C:N) ratio exhibited negative effects, and phosphorus (P) cycling related enzymes activity exhibited positive effects on the $k_{\text{Fine root}}$ when the effects of temperature were controlled. Even when the variables of these biotic factors were added, the soil temperature still exerted a dominant effect on the k_{Leaf} . **Conclusions** Our results suggest that temperature directly influences the k_{Leaf} but indirectly affects the $k_{\text{Fine root}}$ through litter quality and soil decomposers.

Keywords Fine root · Leaf litter · Litter quality · Soil enzymes · Soil microbial biomass · Temperature sensitivity

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Introduction

The decomposition of above- and below-ground plant litter is a key component in terrestrial carbon (C) and nutrient cycling (Aerts 1997; Swift et al. 1979). Approximately half of the net primary productivity in forest ecosystems is returned to the soil by the decomposition of leaf litter (Cao et al. 2020; Wardle et al. 2004; Zhu et al. 2017). Although the contribution of fine root litter decomposition to C turnover is comparable to that of leaf litter (Gill and Jackson 2000), few studies on litter decomposition have focused on plant roots (Freschet et al. 2013).

Litter decomposition is driven by abiotic and biotic factors, including climate, litter quality and soil organisms (Chen et al. 2019; Moinet et al. 2020; Swift et al. 1979; Tresch et al. 2019). Among these factors, climate is commonly thought to be the primary factor determining decomposition rates at a regional scale (Berg et al. 1993; Meentemeyer 1978; Wall et al. 2008). Litter quality is assessed by determining the chemistry and nutrient concentrations, which strongly affect the decomposition rate (Aber et al. 1990; Hoerber et al. 2020). Because climate is considered a primary controller of the activity of decomposers, few studies have assumed that soil decomposers are direct factors influencing decomposition rates at the regional scale (Bradford et al. 2016). However, recent studies suggest that biotic factors may be more important than climate in controlling the decomposition rates of leaf litter and woody debris at regional and global scales (Bradford et al. 2014; Currie et al. 2010; Hu et al. 2018). Regardless of whether climatic factors dominate regional leaf litter decomposition, temperature and/or precipitation could directly control decomposition through soil biological processes and indirectly influence litter quality and decomposer activity (Liu et al. 2004; Petraglia et al. 2019; Wardle et al. 2004). However, the effects of climate and biotic factors on root decomposition rates have not been clearly identified at the regional scale (Gholz et al. 2000; Liu and Greaver 2010).

Global climate warming is likely to increase the decomposition rates of plant litter (Davidson and Janssens 2006). The temperature sensitivity parameter (Q_{10}) is often used to quantify the effect of increased temperature on the decomposition rates of litter, where Q_{10} is the change in the decomposition rate given a 10 °C change in temperature. Many ecosystem models typically assume that the Q_{10} value is a constant of 2.0 for all types of organic matter (Burke et al. 2003; Hyvönen et al. 2005). However, studies based on field observations (Gholz et al. 2000; Salinas et al. 2011) and lab incubated estimations (Craine et al. 2010; Fierer et al. 2005) stated that the Q_{10} value varied considerably in different types of litter. Litter quality and soil microbial enzyme kinetics govern not only the decomposition rates of litter but also their temperature sensitivities (Fierer et al. 2005; Mao et al. 2018). For example, root litter could be less sensitive than labile leaf litter to temperature (Giardina and Ryan 2000; Knorr et al. 2005). Given this assumption, the Q_{10} value of fine root decomposition should be lower than that of leaf litter,

but few studies have explored the decomposition rates of leaf litter and fine root and their temperature sensitivities together in the same species (Freschet et al. 2013; Gholz et al. 2000).

Here, we compared the decomposition rates of leaf litter and fine root of four dominant species in boreal, temperate, sub-tropical and tropical forest sites in eastern China based on approximately two-year decomposition experiments. The overall objective of this study was to examine the effects of biotic factors (litter quality and soil decomposers) and climate (soil temperature) on the decomposition of leaf litter and fine root. We hypothesized that (1) soil temperature could explain the spatial variance in the decomposition rates of both leaf litter and fine root; (2) the Q_{10} value of the leaf litter decomposition rate should be higher than that of the fine root decomposition rate; and thus (3) the quality of litter and the activity of soil decomposers could affect the decomposition rates of leaf litter and fine root, but the effect would be more significant for the fine root than for the leaf litter.

Materials and methods

Study sites

This research was conducted at four locations spanning 32° latitude in eastern China, with approximately a 10° latitude interval between each site (Table 1). From north to south, the four forest sites were established in Genhe (50.94°N, 121.50°E; the boreal site), Donglingshan (39.96°N, 115.43°E; the temperate site), Guniujiang (30.03°N, 117.36°E; the sub-tropical site) and Jianfengling (18.73°N, 108.90°E; the tropical site). The vegetation types of these forest sites are boreal coniferous forest, temperate broadleaved and conifer mixed forest, sub-tropical evergreen broadleaved forest, and tropical mountain rainforest, respectively (Table 1). The mean annual temperature ranges from −5.4 to 24.7 °C, the mean annual precipitation ranges from 481 to 2265 mm, and the elevation ranges from 350 to 1400 m (Du et al. 2013). The growing season is short in the boreal (June to August) and the temperate (May to September) sites, and lasts a whole year in the subtropical and the tropical sites. *Larix gmelinii* and *Quercus liaotungensis* are the dominant species in the boreal site and the temperate site, respectively. The dominant species in the sub-tropical site are *Castanopsis eyrei*,

Cyclobalanopsis myrsinaefolia, *C. glauca* and *Lithocarpus brevicaudatus*. There is no specific dominant species in the tropical site, and the most common species belong to Lauraceae and Fagaceae. More detailed site information can be found in Table 1, or see Zhu et al. (2020).

Litter bag decomposition experiment

Three replicated forest plots ($20 \times 20 \text{ m}^2$) at each forest site were established to simultaneously explore the decomposition of the leaf litter and fine root (with the same species at each site). From November 2012 to June 2015, a litterbag experiment was conducted to quantify the decomposition rates of the leaf litter and fine root in the four selected forests. We selected the leaf litter and fine root of *L. gmelinii* in the boreal forest, *Q. liaotungensis* in the temperate forest, *C. eyrei* in the sub-tropical forest, and *C. chinensis* in the tropical forest. To reduce the uncertainty of the “home field advantage” effect for local species of litter on the decomposition process, transplanted treatment was not involved in our experiment (Vivanco and Austin 2008; Tian et al. 2018; Wang et al. 2020). In October 2012, fresh senescent leaves of each litter species were collected from litter traps (five $1 \times 1 \text{ m}^2$ traps in each forest plot). Then, we sorted the fine root from the selected species for the decomposition experiments at each site. As it was difficult to distinguish the dead roots from the root system, we used the fine roots (diameter $< 2 \text{ mm}$) with no signs of senescence to perform this study (Tian et al. 2018). We cut all the fine roots to a length of approximately 5 cm to reduce the uncertainty of the external shape on the decomposition rates. Five grams of the leaf litter samples ($40 \text{ }^\circ\text{C}$, 48 h) and 4 g of the fine root samples ($50 \text{ }^\circ\text{C}$, 72 h) were placed separately in 0.50 mm (0.2 mm for the *Larix* leaf litter) nylon mesh bags ($10 \times 10 \text{ cm}^2$) and sealed. We explored 3 subplots ($2 \times 2 \text{ m}^2$) for both the leaf litter and fine root from each forest plot for placing the leaf litter bags.

Five litterbags of leaves and three of fine roots were collected at each sampling event. The sampling frequency of each site was not the same due to the duration of the growing season. To determine dry mass, the retrieved leaf litter was oven-dried at $65 \text{ }^\circ\text{C}$ for 48 h, and the fine root was also oven-dried at $65 \text{ }^\circ\text{C}$ but for 72 h. After oven-drying, the residual litter was ground (0.15 mm sieve) for C, nitrogen (N), cellulose and lignin analysis.

The soil temperature at a depth of 5 cm was measured every hour using an EM50 data logger (Decagon Devices, USA) for each site during the study period (Fig. 1). The initial C and N concentrations of the leaf litter and fine root were determined using an elemental analyzer (2400 II CHN Elemental Analyzer; Perkin-Elmer, Boston, MA, USA). The initial contents of lignin and cellulose were measured using the acid detergent lignin method (Graca et al. 2005).

Soil microbial biomass and enzyme activity

From north to south, we conducted centralized soil sampling at our experimental sites in August and September 2015. In each plot, we sampled three soil samples in the 0–10 cm soil depth in the leaf litter subplots. The soil samples were placed in a sterile plastic bag and stored in an ice box for transport to the laboratory. In the laboratory, the samples were passed through a 2-mm sieve and then stored at $-18 \text{ }^\circ\text{C}$, and the analyses were finished within 2 weeks. The soil microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN) were determined by classical chloroform fumigation extraction and then analyzed by the indigotic colorimetry method (Brookes et al. 1982). The correction factors of MBC and MBN were 0.30 and 0.45, respectively.

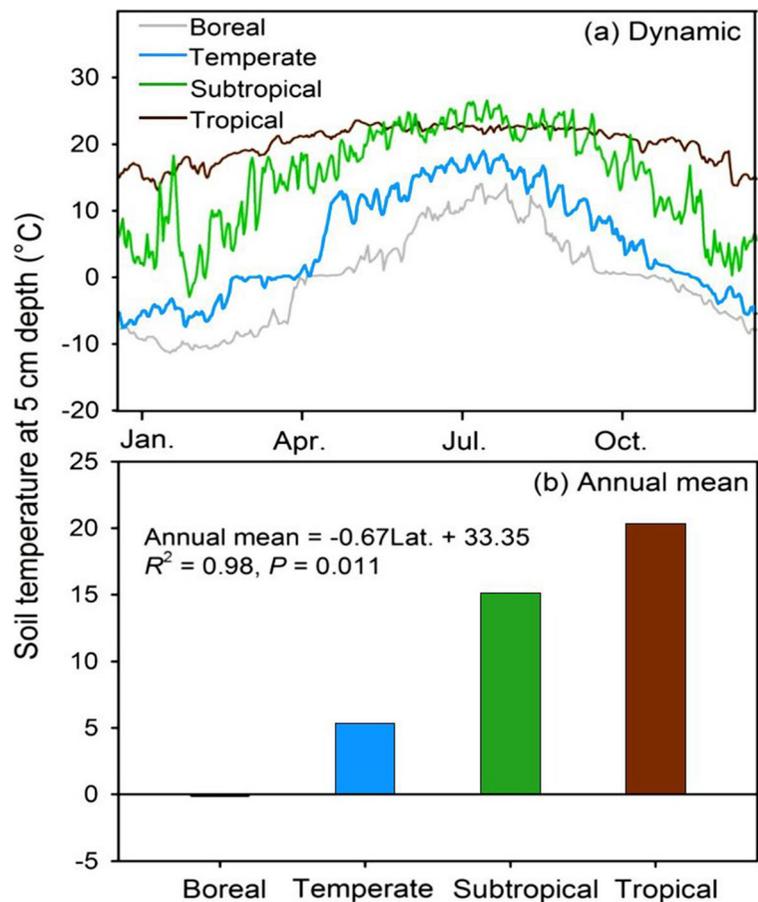
To detect the effect of the potential activity of soil extracellular enzymes on the litter decomposition rate, the activities of β -1,4-glucosidase (BG), β -D-1,4-cellobiosidase (CB), β -1,4-N-acetylglucosaminidase (NAG), acid phosphatase (AP), leucine aminopeptidase (LAP), phenol oxidase (POX) and peroxidase (PER) were measured in this study. The hydrolytic (BG, CB, LAP, NAG and AP) enzymes could promote the decomposition of easily decomposable organic matters (e.g., cellulose and hemicellulose) and macromolecular substances (e.g., protein and nucleic acid) in the decomposition process of litter, and oxidative (POX and PER) enzymes play a main role in degrading the difficult-to-decompose organic matters (e.g., peroxide and phenolics) (Sinsabaugh 2010). These soil extracellular enzymes were related to labile-carbon-cycling (BG and CB), recalcitrant-carbon-cycling (POX and PER), nitrogen-cycling (NAG and LAP) and phosphorus-cycling (AP). The activities of these enzymes were determined according to the protocol described by German et al. (2011) and Bach et al. (2013). In brief, 1.5 g of fresh soil was weighed and suspended in 125 ml of 50 mM sodium acetate buffer (pH = 5.3). Fifty μl

Table 1 Basic information of the sampling sites

Sites	Lat. (°N)	Lon. (°E)	Ele. (m)	MAT (°C)	MAP (mm)	Growing season (months)	Soil type	Forest type	Dominant species	Litter species
Boreal	50.94	121.50	825	-5.4	481	6–8	Brown soil	Boreal coniferous forest	<i>Larix gmelinii</i>	<i>Larix gmelinii</i>
Temperate	39.96	115.43	1150	5.4	505	5–9	Brown soil	Temperate deciduous broadleaved forest	<i>Quercus liaotungensis</i>	<i>Quercus liaotungensis</i>
Subtropical	30.03	117.36	375	9.2	1650	1–12	Brown earth	Subtropical evergreen broadleaved forest	<i>Castanopsis eyrei</i> , <i>Cyclobalanopsis myrsinaefolia</i> , <i>Cyclobalanopsis glauca</i> , <i>Lithocarpus brevicaudatus</i>	<i>Castanopsis eyrei</i>
Tropical	18.73	108.90	870	24.7	2265	1–12	Yellow soil	Tropical mountain rainforest	Fagaceae and Lauraceae ^a	<i>Cryptocarya chinensis</i>

^a There is no specific dominant species in the stand of tropical forest, and the most common species belong to Fagaceae and Lauraceae. Lat.: latitude; Lon.: longitude; Ele.: elevation; MAT: mean annual temperature; MAP: mean annual precipitation

Fig. 1 Seasonal variation (a) and mean value (b) of the soil temperature at a depth of 5 cm in the four forests



enzyme specific substrate and 200 μl of soil suspension were combined in each well of the 96-well micro-plate, 50 μl of sodium acetate buffer and 200 μl of soil suspension were combined in sample control well, and 50 μl of enzyme specific substrate and 200 μl of sodium acetate buffer were combined in substrate control well. For hydrolytic enzymes, 50 μl of the standard substrate of 4-methylumbelliferyl or 7-amino-4-methylcoumarin (10 μM) and 200 μl of soil suspension were combined in quench control well, and the concentration of enzyme specific substrate was 200 μM . For oxidative enzymes, 25 mM L-DOPA was used as enzyme specific substrate. The hydrolytic enzymes with 8 replicates and the oxidative enzymes with 16 replicates were incubated at 25 °C in the dark for 2.5 h and 24 h, respectively. A micro-plate reader (Biotek Synergy 2, Winooski, VT, USA) was used to measure the absorbance of oxidative enzymes (450 nm) and fluorescence of hydrolytic enzymes (360 nm and 460 nm) (Jing et al. 2017).

Data analysis

The decomposition rates (k , yr^{-1}) of the leaf litter and fine root were estimated from the rate of litter mass loss over the decomposition time (Olson et al. 1963):

$$\frac{M_t}{M_0} = \exp^{-kt} \quad (1)$$

where M_0 is the biomass amount of the original litter; M_t is the biomass remaining at time t ; k is the decomposition rate for the leaf litter or fine root; and t is the decomposition time (in years). The residual rate of the leaf litter and fine root was calculated as the ratio (%) of M_t and M_0 . Then, we used Eq. (2) to describe the relationship between k and the mean annual soil temperature (T , °C) for the leaf litter and fine root in our forest sites:

$$k = k_0 \exp^{-K_{Tem} \cdot T} \quad (2)$$

where k_0 is the regression intercept, representing the k value at 0 °C, and K_{Tem} is the temperature sensitivity coefficient (regression slope, °C⁻¹). We used Q_{10} instead of K_{Tem} to describe the temperature sensitivity of decomposition rates for the leaf litter and fine root. The Q_{10} value is an increase in the decomposition rate for a 10 °C increase in soil temperature, and it was calculated from the K_{Tem} value (Eq. 3):

$$Q_{10} = \exp^{10K_{Tem}} \quad (3)$$

The effects of latitude and organs (leaf or fine root) on the decomposition rates were analyzed using two-way analysis of variance (ANOVA). The least significant difference (LSD) test was used to determine the paired differences when possible. Differences in the initial litter quality, including the contents (%) of C, N, lignin and cellulose as well as the ratios of C:N and lignin:N, between the leaf litter and fine root were measured by a t -test at $P < 0.05$. The latitude trend of the soil microbial biomass and enzyme activities (microbial biomass C and N and the BG, CB, NAG, AP, LAP, POX and PER enzyme activities) was analyzed using one-way ANOVA. Analysis of covariance (ANCOVA) was used to investigate the difference in the Q_{10} (or k_0) values between leaf litter and fine root. We also used a simple linear regression to analyze the relationship between the k value and the mean annual precipitation (mm).

We fitted a structural equation model (SEM) to infer the relative importance of the climate (mean annual soil temperature), litter quality (C:N and Lignin:N ratios) and soil decomposer-related variables (MBC, BG, CB, NAG, AP, LAP, POX and PER enzyme activities) on the decomposition rates of the leaf litter and fine root (Lefcheck and Duffy 2015). Soil decomposer-related variables were divided into four categories based on their role in the decomposition process, including (1) the amount of soil microbiome (MBC), (2) carbon-cycling related enzymes (BG, CB, POX and PER), (3) nitrogen-cycling related enzymes (NAG and LAP) and (4) phosphorus-cycling related enzymes (AP). We first considered an initial SEM that included all plausible pathways (Fig. S1). We then fitted the final SEM as linear models and calculated the standardized coefficient for each path from each linear model. The activities of carbon-cycling related enzymes, nitrogen-cycling related enzymes and phosphorus-cycling related enzymes were dimension-reduced by Principal component analysis (PCA) before they were incorporated into the model. The model fit was estimated using the chi-square, Akaike information criterion (AIC), Bayesian information criterion (BIC) values, and Comparative fit index (CFI) (Schermelleh-Engel et al. 2003). SEM was conducted using the ‘sem’ package in R version 3.5.1 (R Core Team 2018).

Results

The soil temperature at 5 cm in the different climate biomes is given in Fig. 1. As expected, the mean annual soil temperature decreased steadily with latitude from the tropical site (20.8 °C) to the boreal site (-0.2 °C) at a decreasing rate of 6.8 °C per 10° latitude.

The relationships between the residual rates of the leaf litter and fine root against the decomposition time could be well described by exponential equations (R^2 ranged from 0.88 to 0.98, Eq. 1, Fig. S2). The leaf litter decomposition rate (k_{Leaf}) increased significantly, from $0.14 \pm 0.01 \text{ year}^{-1}$ in the boreal forest to $0.71 \pm 0.08 \text{ year}^{-1}$ in the tropical forest. The fine root decomposition rate ($k_{\text{Fine root}}$) also increased significantly, from $0.22 \pm 0.02 \text{ year}^{-1}$ in the boreal and temperate forests to $0.42 \pm 0.06 \text{ year}^{-1}$ in the tropical forest ($F = 114.1$, $P < 0.001$, Table 2). The k_{Leaf} was significantly higher than the $k_{\text{Fine root}}$ in the temperate, sub-tropical and tropical sites but lower in the boreal site ($P < 0.05$; Fig. 2). At the regional scale, the decomposition rates of the leaf litter and fine root had a significant correlation ($R^2 = 0.75$, $P < 0.001$), but this correlation did not occur at the local scale in the current study (Fig. 2). Although the decomposition rates between the leaf litter and fine root varied similarly along the latitudinal gradient, the degree of their changes was different. The $k_{\text{Leaf}}:k_{\text{Fine root}}$ ratio decreased gradually and significantly with latitude: tropical (1.70 ± 0.01) > sub-tropical (1.57 ± 0.06) > temperate (1.31 ± 0.10) > boreal (0.64 ± 0.01) site (Fig. 2).

Both the k_{Leaf} and $k_{\text{Fine root}}$ were positively and significantly related to the mean annual soil temperature (Fig. 3). An exponential regression of the k value over the mean annual soil temperature could explain 95 % and 86 % of the variability in the k_{Leaf} and $k_{\text{Fine root}}$, respectively (Fig. 3). We therefore defined the coefficient of the exponential regression as the temperature sensitivity parameter ($K_{\text{Tem.}}$) and derived the Q_{10} parameter. The $K_{\text{Tem.}}$ of the leaf litter ($0.077 \pm 0.003 \text{ } ^\circ\text{C}^{-1}$) was significantly higher than that of the fine root ($0.034 \pm 0.004 \text{ } ^\circ\text{C}^{-1}$) ($F = 78.7$, $P < 0.001$), from which we calculated the Q_{10} values of 2.17 ± 0.07 and 1.40 ± 0.06 , respectively (Fig. 3a). The $k_{\text{Leaf}}:k_{\text{Fine root}}$ ratio increased with the mean annual soil temperature across the sites (Fig. 3). In addition, both the k_{Leaf} and $k_{\text{Fine root}}$ were positively and significantly related to the mean annual precipitation, and the $k_{\text{Leaf}}:k_{\text{Fine root}}$ ratio increased with the mean annual precipitation across the sites (Fig. S3).

To explore the effects of other environmental factors on the decomposition rates of the leaf litter and fine root, we measured the initial litter quality and soil decomposer-related factors. The variation in the initial litter quality (concentrations of C and N, contents of lignin and cellulose, and ratios of C:N and lignin:N) with site and organ is shown in Table 3. The initial C concentration of the litter varied slightly across the sites and organs, ranging from 46.8–48.8 %. The lignin contents of the leaf litter in the boreal and temperate forests were significantly lower than those of the fine root, but the result in the tropical forest was the opposite (Table 3). The initial N concentration of the litter exhibited considerable variation among the sites and organs. First, the N concentration of the leaf litter was significantly higher than that of the fine root in all forest sites. Second, with latitude increasing, the initial N concentrations of both the leaf litter and fine root decreased steadily in the sites (Table 3). As a result, the C:N ratio and lignin:N ratio of the leaf litter decreased significantly, from 42.5 ± 0.5 and 15.9 ± 1.2 in the boreal forest to 18.4 ± 0.1 and 13.2 ± 2.0 in the tropical forest, respectively. Similarly, these ratios in the fine root decreased from 56.3 ± 0.2 and 28.8 ± 1.0 in the boreal forest to 30.6 ± 0.4 and 14.2 ± 1.0 in the tropical forest, respectively.

The activities of all enzymes and microbial biomass in the surface soil varied significantly with site (Table S1). In brief, the activities of the BG, CB, NAG and LAP enzymes as well as the MBC and MBN were higher in the boreal forest than in the temperate, sub-tropical and tropical forests. In contrast, the enzyme activities of AP, POX and PER were lower in the temperate and boreal forests and higher in the tropical and subtropical forests.

Finally, we fitted an SEM to infer the effects of climatic factors, litter-quality related factors and soil decomposer traits on the decomposition rates of the leaf litter (Fig. 4a) and fine root (Fig. 4b). The two SEMs indicated that the mean annual soil temperature had a positive effect on the decomposition rate of leaf litter through increased soil phosphorus-cycling related enzymes activities ($\beta = 0.63$), and a positive effect on the decomposition rate of fine root through reduced C:N ratio of the initial fine root ($\beta = -0.90$) and increased soil phosphorus-cycling related enzymes activities ($\beta = 0.63$). The initial C:N ratio exhibited negative effects ($\beta = -0.60$), and soil phosphorus-cycling related enzymes activities ($\beta = 0.48$) exhibited positive effects on the $k_{\text{Fine root}}$. Even when the variables of litter quality and soil decomposer traits were under control, the soil

Table 2 Results of the two-way ANOVA for the effects of the site and organ (leaf litter or fine root) treatments and their interactions on the litter decomposition rate (k)

Source	Sum of squares	df	Mean square	F	P
Model	3.835	8	0.479	297.6	<0.001
Site	0.551	3	0.184	114.1	<0.001
Organ	0.083	1	0.083	51.5	<0.001
Interaction	0.116	3	0.039	24.0	<0.001
Error	0.026	16	0.002		
Total	3.861	24			

temperature still exerted a dominant effect on the k_{Leaf} ($\beta = 0.90$), but not on $k_{\text{Fine root}}$. The mean annual soil temperature had a negative effect on soil carbon-cycling related enzymes and nitrogen-cycling related enzymes activities through soil microbial biomass carbon ($\beta = -0.69$), but these parameters had no significant effect on the decomposition rates of the leaf litter and fine root.

Discussion

Exploring the temperature sensitivity of litter decomposition rates requires that the temperature range be

broadly distributed (Salinas et al. 2011). We observed a 21 °C transect in the mean annual soil temperature between our boreal and tropical sites. Overall, the k_{Leaf} and $k_{\text{Fine root}}$ decreased steadily and significantly with latitude. The mean annual soil temperature accounted for 95 % and 86 % of the variation in the k_{Leaf} and $k_{\text{Fine root}}$, respectively. We calculated a Q_{10} value of 2.17 ± 0.07 (corresponding to a temperature coefficient of $0.077 \pm 0.003 \text{ } ^\circ\text{C}^{-1}$, Fig. 3) for the k_{Leaf} and 1.40 ± 0.06 ($0.034 \pm 0.004 \text{ } ^\circ\text{C}^{-1}$) for the $k_{\text{Fine root}}$, these results are comparable with those observed in several lab-based estimations (Reichstein et al. 2000; Fierer et al. 2005) and lower than the value of 3.06 reported by Salinas

Fig. 2 Bivariate correlations between the decomposition rates of the leaf litter and fine root across the four forests. The ratio of leaf litter to fine root decomposition is shown in the inset

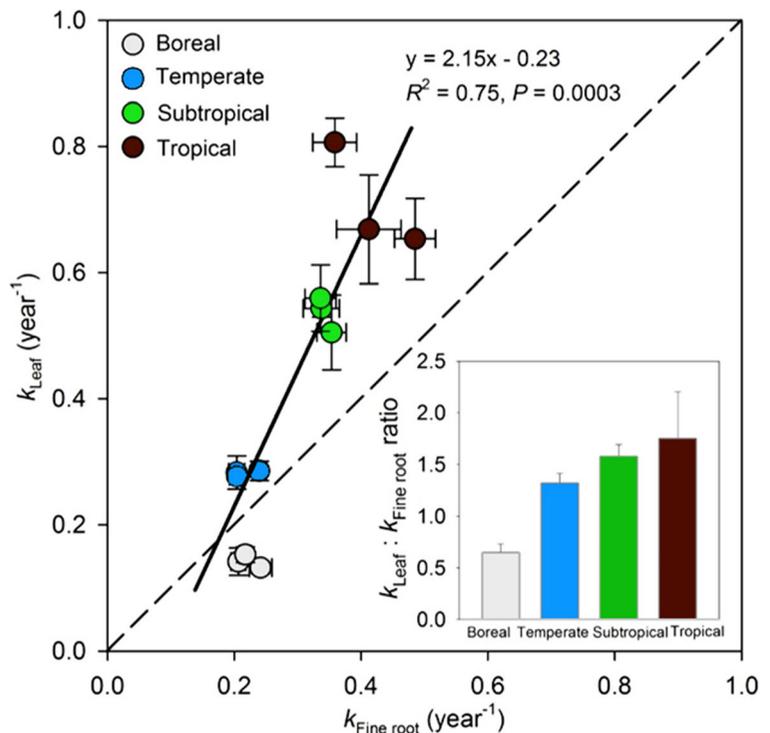
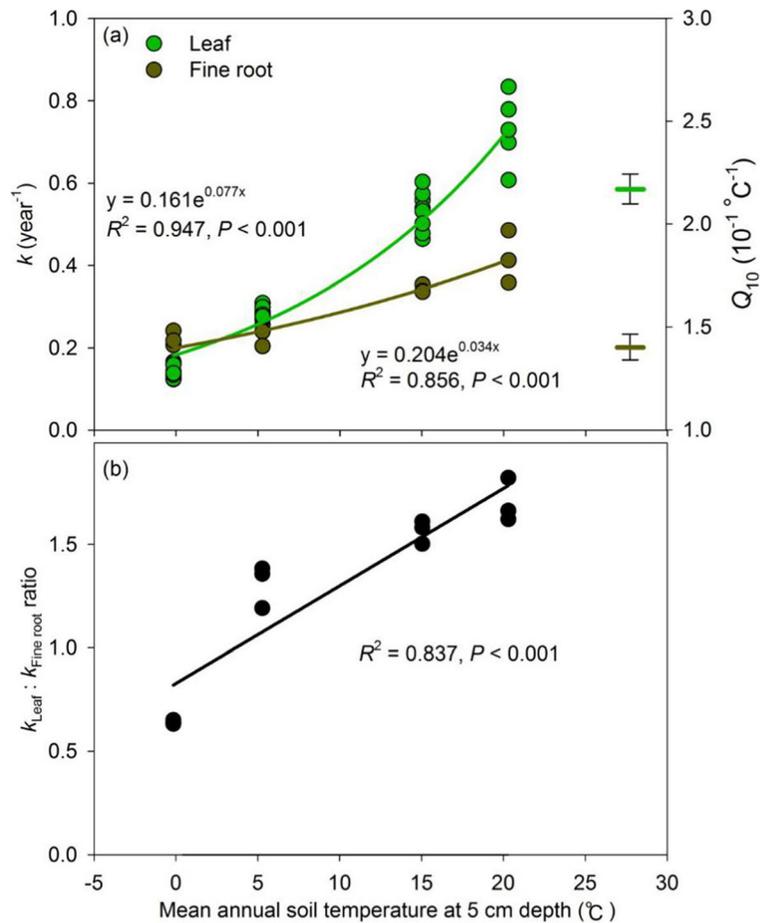


Fig. 3 Relationships between the decomposition rates of the leaf litter and fine root (a) and the $k_{\text{Leaf}}:k_{\text{Fine root}}$ ratio (b) and the mean annual soil temperature at a depth of 5 cm



et al. (2011) from a transplanted and elevation-based leaf litter decomposition experiment in Peruvian tropical mountain forests. The relatively narrow temperature range (11.1–23.9 °C) and “home field advantage” of the local leaf litter in their study may result in a higher estimated Q_{10} value (Vivanco and Austin 2008).

Studies on the decomposition rates of above- and belowground litter in the same species have been relatively rare (Freschet et al. 2013; Gholz et al. 2000) estimated Q_{10} values of 2.6 in leaf litter and 2.1 in fine root from two species transplanted along a latitudinal gradient in the United States. Although we incubated only one species of the paired leaf litter and fine root across the four forest sites, the k values of both leaf litter and fine root were strongly correlated with the soil temperature. Together with these results, our finding of different temperature sensitivities of leaves and fine roots contrasts with the commonly used assumption in coupled climate-carbon models that the Q_{10} value for

the decomposition of both above- and belowground organic matter is approximately 2.0 (Hyvönen et al. 2005; Friedlingstein et al. 2014). We estimated a two-fold variation in the decomposition rate between the leaf litter and fine root (Fig. 2) and in their Q_{10} values (Fig. 3). The different litter qualities of leaves and fine roots could be a major reason for their different decomposition rates at the local scale (Table 3; Melillo et al. 1982; Berg et al. 1993). The lack of representation for variations in the k and Q_{10} values between leaves and fine roots and among the different forest types could partly explain why models cannot capture the spatial distribution of soil organic matter well (Todd-Brown et al. 2013).

Since the leaf litter had a higher temperature sensitivity than the root, the $k_{\text{Leaf}}:k_{\text{Fine root}}$ ratio was positively correlated with the mean annual soil temperature (Fig. 3b). To demonstrate whether this result is universal, we collected 62 data points from 38 published

Table 3 Initial quality of the leaves and fine roots of the selected litter species across the sampling sites

Parameter	Boreal		Temperate		Subtropical		Tropical	
	Leaf	Fine root	Leaf	Fine root	Leaf	Fine root	Leaf	Fine root
C (%)	48.8±0.1a	47.4±0.1b	46.8±0.0a	47.3±0.2a	48.7±0.1a	47.4±0.0b	48.2±0.0a	47.6±0.0b
N (%)	1.2±0.0a	0.8±0.0b	1.3±0.0a	0.9±0.0b	1.4±0.0a	1.0±0.0b	2.6±0.0a	1.6±0.0b
Lignin (%)	18.2±1.2a	24.2±0.8b	11.9±2.2a	23.5±5.3b	19.4±4.2a	18.7±3.5a	34.6±5.1a	22.0±1.2b
Cellulose (%)	12.3±1.0a	15.7±1.6a	17.4±3.1a	21.8±6.6a	20.7±6.9a	25.3±2.1a	13.3±2.9a	15.0±0.8a
C:N	42.5±0.5a	56.3±0.2b	37.1±0.3a	50.7±0.5b	35.8±0.3a	47.8±0.2b	18.4±0.1a	30.6±0.4b
Lignin:N	15.9±1.2a	28.8±1.0b	9.5±1.8a	25.3±5.8b	14.3±3.2a	18.8±3.6b	13.2±2.0a	14.2±1.0a

papers that reported decomposition rates of leaf litter and fine root from the same species across diverse biomes (Table S2). The negative relationship observed between the $k_{\text{Leaf}}:k_{\text{Fine root}}$ ratio and latitude (Fig. 5a) or altitude (Fig. 5b) in the global biomes confirmed that the effect of temperature on the decomposition rate was different between the leaf litter and fine root. This result suggests that leaf litter has a higher temperature sensitivity than fine root (Gholz et al. 2000). This conclusion was supported by the SEMs, where the influence of temperature on the leaf litter decomposition was direct (Fig. 4a), but the effect of temperature on the fine root was mediated by the litter quality and soil decomposer traits (Fig. 4b).

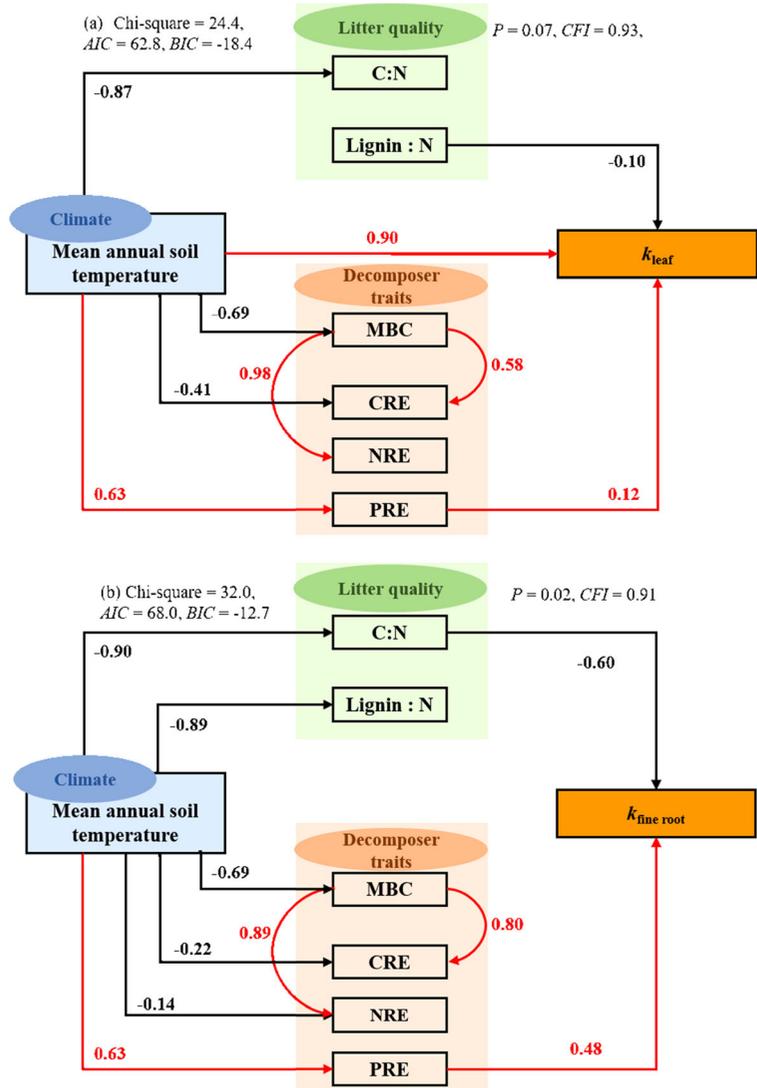
At the local scale, all soil carbon-related, nitrogen-related and phosphorus-related enzyme activities as well as the microbial biomass tended to exhibit positive effects on leaf litter and fine root decomposition (Zhu et al. 2013; Hu et al. 2017; He et al. 2019). However, these decomposer-related indicators were closely correlated with climatic factors at the regional scale (Hendriksen et al. 2016). In this study, the SEMs demonstrated that soil carbon-cycling and nitrogen-cycling related enzymes activities and soil microbial biomass carbon were significantly and negatively correlated with the mean annual soil temperature, but temperature positively affected the soil phosphorus-cycling related enzymes activities (Fig. 4). These results were consistent with the results of studies in eastern Chinese forests (Xu et al. 2017) and grasslands (Peng and Wang 2016). However, soil microbial biomass carbon, carbon-cycling and nitrogen-cycling related enzymes activities were not significant predictors of the decomposition rates of the leaf litter and fine root. These results suggested that the prediction of soil microbial biomass

carbon, carbon- and nitrogen-cycling related enzymes activities on the decomposition rates of the leaf litter and fine root were weaker than litter quality and phosphorus-cycling related enzymes activities.

The mean annual soil temperature directly and predominantly affected the leaf litter decomposition but not the fine root decomposition (Fig. 5). Although spatial variation in the mean temperature dominated the variation in the k value, the initial C:N ratio exhibited significant negative effects, and the activities of phosphorus-cycling related enzymes exhibited significant positive effects on the $k_{\text{Fine root}}$. However, the temperature sensitivities of the k_{Leaf} and $k_{\text{Fine roots}}$ were different. When the concept of temperature sensitivity is used in process models, the difference between above- and below-ground organic matter should be considered (Wang et al. 2010, 2014; Freschet et al. 2013).

It should be noted that there were many factors that may cause uncertainties in our results, as following: (1) there were clear seasonal precipitation patterns across our sites (Du et al. 2013). These forest sites have distinct growing and nongrowing seasons (Fig. 1), even the tropical mountain rainforest site (Wang et al. 2018). Not only the mean annual soil temperature has a positive effect on the decomposition rates of leaf litter and fine root, but mean annual precipitation also has a positive effect on the decomposition rates of leaf litter and fine root. Due to the high autocorrelation between temperature and precipitation at this regional scale (Table 1), we did not detect the relationship between precipitation and the decomposition rate in our models, despite the importance of soil moisture content for decomposition (Fig. S3) (Howard and Howard 1979). This missing information may have resulted in some uncertainties in our results. (2) the litter of the most dominant species in

Fig. 4 Structural equation models of climate, litter quality and soil decomposer traits as predictors of the decomposition rates of leaf litter (a) and fine root (b). Solid red and solid black arrows represent positive and negative paths, respectively ($P < 0.05$). C, carbon; N, nitrogen; MBC, soil microbial biomass carbon; CRE, carbon-cycling related enzymes (BG, CB, POX and PER); NRE, nitrogen-cycling related enzymes (NAG and LAP); PRE, phosphorus-cycling related enzymes (AP)

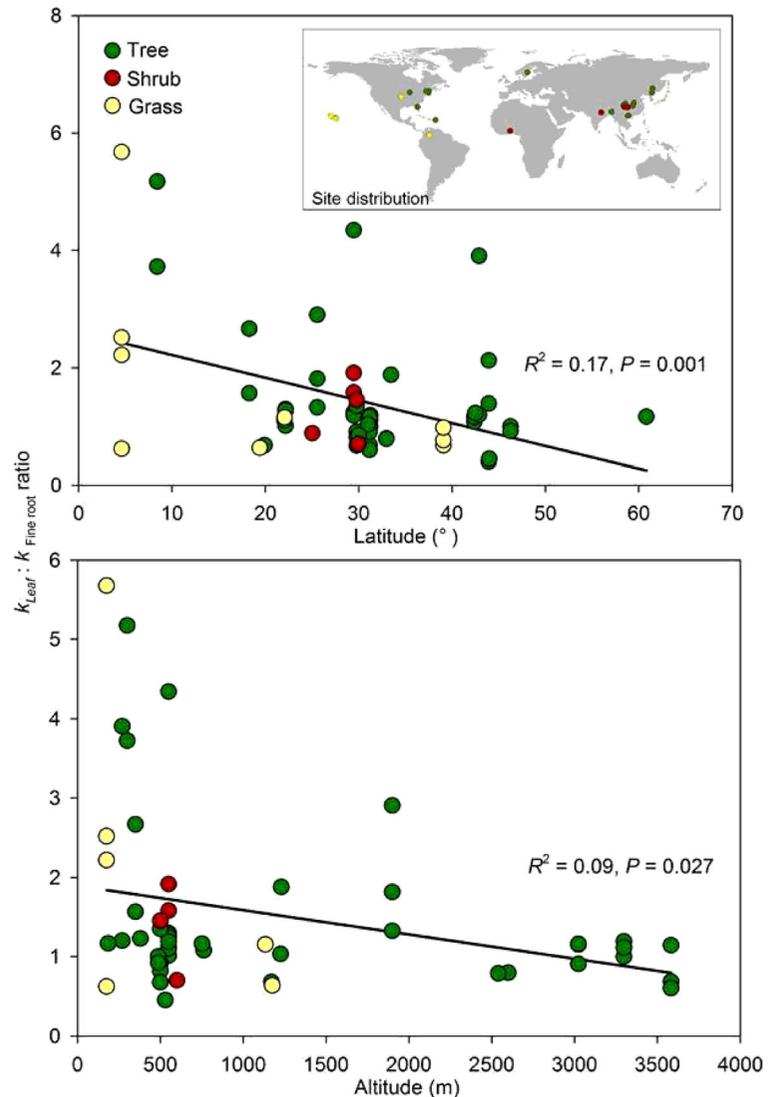


each site was incubated. Non-transplanted litter and insufficient replicates of litter species may lead to uncertainties (mainly from litter quality) in the decomposition rates of leaf litter and fine root. (3) soil temperature at a depth of 5 cm was continuously measured at each site during the study period, but the soil physical and chemical properties (e.g. soil pH and soil moisture) and enzyme activity were not monitored synchronously at each sampling event. The lack of analysis of the parameters related to litter decomposition at different decomposition stages may cause uncertainties in evaluating the factors influencing the decomposition rates of litter.

Conclusions

We exploited a litter decomposition experiment with a large latitudinal gradient (from 18 °N to 51 °N) to explore the environmental drivers of decomposition rates of both leaf litter and fine root along an approximately 30 °C transect in the mean annual soil temperature. We defined the sensitivity of the decomposition rate (k) to temperature, calculating the Q_{10} values of 2.17 for the leaf litter and 1.40 for the fine root. As a result, the $k_{\text{Leaf}}:k_{\text{Fine root}}$ ratio was positively correlated with the mean annual soil temperature and precipitation, resulting in different

Fig. 5 Global patterns of the $k_{\text{Leaf}}:k_{\text{Fine root}}$ ratio versus latitude (a) and altitude (b) across three biomes. The insert map shows the spatial distribution of the 62 sites collected from the 37 published studies (Table S2)



effects of climatic factors on the leaf litter and fine root decomposition. The SEMs indicated that the mean annual soil temperature directly influences the k_{Leaf} but indirectly affects the $k_{\text{Fine root}}$ through litter quality and soil decomposers.

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