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Insight into the temperature sensitivity of forest litter decomposition and soil enzymes in subtropical forest in China

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Abstract

Aims

With the continuing increase in the impact of human activities on ecosystems, ecologists are increasingly interested in understanding the effects of high temperature on litter decomposition since litter decomposition and the accompanying release of nutrients and carbon dioxide are key processes in ecosystem nutrient cycling and carbon flux. This study was conducted to evaluate the temperature sensitivity of forest litter decomposition and soil enzymes during litter decomposition in subtropical forest in China.

Methods

Two dominant litter types were chosen from Zijin Mountain in China: *Quercus acutissima* leaves from a broadleaf forest (BF) and *Pinus massoniana* needles from a coniferous forest (CF). The litter samples were incubated in soil microcosms at ambient control temperature (20°C) and 10°C warmer. During a 5-month incubation, chemical composition of litter samples, litter mass losses, and related soil enzyme activities were determined.

Important Findings

Three main results were found: (i) high temperature accelerated decomposition rates of both litter types, and the temperature sensitivities of litter decomposition for BF leaves and that for CF needles are equivalent basically, (ii) high temperature enhanced soil enzyme activities in the two forest types, and the temperature sensitivities of polyphenol oxidase were significantly higher than those of the other soil enzymes and (iii) the temperature sensitivities of nitrate reductase were significantly higher in the CF soil than in the BF soil, while there was no significant difference in the temperature sensitivities of the other soil enzymes between BF and CF. As a long-term consequence, the high-temperature-induced acceleration of litter decomposition rates in these subtropical forests may cause carbon stored belowground to be transferred in the atmosphere, which may alter the balance between carbon uptake and release, and then alter the global carbon cycle in the coming decades.

Keywords: broadleaf forest • coniferous forest • high temperature • litter decomposition • soil enzyme • temperature sensitivities

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INTRODUCTION

Coniferous forests (CFs) and broadleaf forests (BFs) are typical stages in the succession of subtropical forests. These forests play important roles in global carbon (C) dynamics due in part to their high productivity and nutrient turnover (He *et al.* 2007; Hughes *et al.* 1999). Meanwhile, leaf litter decomposition and the accompanying release of nutrients and carbon dioxide and formation of soil organic matter are fundamental processes in ecosystem nutrient cycling, C flux and humus formation (Hoorens *et al.* 2003). Thus, the study of the litter decomposition process in subtropical forests is important for understanding their functioning. With the continuing increase in anthropogenic greenhouse gases in the atmosphere, the global mean temperature is expected to rise by 1.8–4.0°C by the end of this century (IPCC 2007). Thus, the effects of high temperature on

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forest litter decomposition have recently received considerable interest because of its importance in the global C cycle and so could impact the rate of climate change in the coming decades (Coûteauxa *et al.* 1995). This study was thereby conducted to evaluate the temperature sensitivity of decomposition of different forest litter types in subtropical forest in China.

At present, there have been inconsistent results regarding the temperature sensitivities of the decomposition of different litter types. According to chemical kinetic theory, decomposition of recalcitrant matter or low-quality litters has higher activation energy and thus higher temperature sensitivity (Davidson and Janssens 2006). Studies on decomposing leaf litter (e.g. Fierer *et al.* 2005) and organic soils (e.g. Mikan *et al.* 2002) have supported this theory. Contradictory results, however, were obtained from different soil C fractions (e.g. Melillo *et al.* 2002). Other studies even suggested that the temperature sensitivities of young and old soil C fractions are equivalent (e.g. Conen *et al.* 2006). The controversy may be due to the fact that the observed temperature sensitivity in conditions where environmental constraints limit decomposition may be lower or higher than the intrinsic temperature sensitivity determined by the kinetic properties (Davidson and Janssens 2006; Karhu *et al.* 2010).

A growing body of evidence indicates that litter decomposition is driven by exoenzymes (Moorhead and Sinsabaugh 2000; Schimel and Weintraub 2003), and the changes these undergo under high temperature can provide an explanation of the warming effects on litter decomposition. Thus, it is important to investigate the effects of high temperature on soil enzyme activities to understand their role in determining high temperature impacts on litter decomposition. To our knowledge, no previous studies have assessed the temperature sensitivity of soil enzymes during litter decomposition in subtropical forest in China, although little information exists on the variations in the temperature sensitivity of soil enzymes in other ecosystem (e.g. Wallenstein *et al.* 2009).

Microcosm experiments under controlled laboratory conditions have proven useful for investigating the various factors that influence litter decomposition (Naeem *et al.* 2000). Thus, this study was carried out through a microcosm experiment, in order (i) to determine the effects of high temperature on litter decomposition and soil enzyme activities and (ii) to evaluate the temperature sensitivity of decomposition of forest litters with different physicochemical properties and that of different types of soil enzymes that involved in litter decomposition in a subtropical BF (*Quercus acutissima*) and a CF (*Pinus massoniana*) in China.

MATERIALS AND METHODS

Site description

Three discrete sites, separated by ~50 m, were sampled in two types of forests, a BF (dominated by *Q. acutissima*) and a CF (dominated by *P. massoniana*), located in Zijin Mountain (32°5′N, 118°48′E), Nanjing, China, with an area of 24 km^2 and an altitude of 420 m. The study areas have a subtropical humid climate. Annual mean temperature is 15.4°C, while monthly mean temperature reaches a maximum of 28.2°C in July and decreases to a minimum of 1.9°C in January. The annual precipitation is 1 106.5 mm, and the rainy season comes in June and July.

Experimental design

In September 2008, *Q. acutissima* leaves and *P. massoniana* needles were collected from the forest floor of the aforementioned forest sites (initial litter characteristics are shown in Table 1). All litter samples were taken back to the laboratory and oven-dried at 70°C for 24 h to achieve constant weight for further study. Meanwhile, three soil samples from each forest type were also collected from topsoil layers. All soil samples were kept in sealed bags and immediately (after ~2 h) taken back to the laboratory. Soil samples were passed through a 2-mm sieve to remove leaves, plant roots and gravel. All soil samples were then homogenized by thorough mixing and kept in a refrigerator at 4°C until the start of incubation (within 1 d after sampling). The sieving and homogenization steps were performed to decrease the discrepancies caused by inhomogeneity of soil enzyme contents and to reduce the effects of serendipitous foreign materials on parameter determination.

To study litter decomposition, 1 g oven-dried litter was mixed with ~40 g soil in a 125-ml polypropylene specimen chamber. Soils of BF and CF were selected as the sources of microorganisms. BF leaves were incubated in the BF soil, and CF needles were incubated in the CF soil. The samples were then incubated separately and exposed to different temperatures, particularly to a normal temperature (20°C) and a high temperature (30°C) in a temperature-controlled incubator in the laboratory. In this study, 20°C was approximately the seasonally mean temperature of spring (leaf-growing season) and autumn (leaf-falling season), and 30°C was the high temperature treatment. As such, there were a total of four treatment combinations: BF at 20°C (20°C-BF), BF at 30°C (30°C-BF), CF at 20°C (20°C-CF) and CF at 30°C (30°C-CF). During the incubation, soil moisture content was monitored and maintained between 50% and 60% of gravimetric moisture content by adding water to the surface of soil samples. The length of incubation was 5 months.

Three replicate samples per treatment were systematically harvested each month after incubation. The soil adhering to litter samples were carefully removed, and the litter samples

Table 1: initial litter chemistry of BF leaves and CF needles

Composition	Leaves	Needles
Lignin (mg g^{-1})	301.40^{b}	385.35^{a}
Total carbohydrate (mg g^{-1})	485.29^{b}	526.75^{a}
N (mg g^{-1})	9.25^{a}	7.99^{b}
Lignin:N	32.57^{b}	48.21^{a}
C:N	52.44^{b}	65.90^{a}

Data with different superscript letters in a transverse row indicate a significant difference ($P < 0.05$) using *T*-test.

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were then oven-dried at 70°C for 24 h to achieve constant weight for chemical analyses and determination of mass losses. The soil samples for each replicate were also retained, stored in sealed bags and refrigerated at 4°C in preparation for determination of soil enzyme activities.

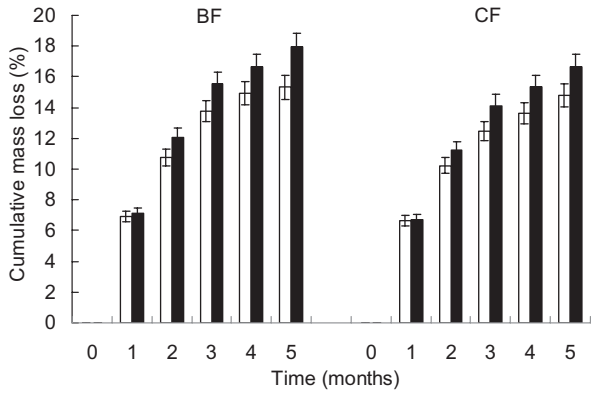

Figure 1: changes in cumulative mass losses of the two litter types during litter decomposition. Symbols: open square, 20°C; filled square, 30°C. Error bars indicate standard error (n = 3).

Chemical analysis and soil enzyme activity determination

Litter samples were analyzed to determine lignin, total carbohydrate and nitrogen (N) concentration and litter mass losses. Lignin concentration was determined by a gravimeter using hot sulfuric acid digestion (Osono and Takeda 2002). Total carbohydrate concentration was estimated by the phenol–sulfuric acid method (Osono and Takeda 2002). N concentration was determined with Kjeldahl digestion (Bremner 1996).

Soil samples were analyzed to determine related soil enzyme activities. The activities of soil enzymes involved in cellulose, lignin, N and phosphorus (P) decomposition were determined spectrophotometrically with little modification: cellulase (E.C. 3.2.1.4) activity was determined using 0.5% carboxymethylcellulose solution as substrate with incubate at 50°C for 30 min (pH 5.5; glucose concentration was determined by colorimetric assay at 540 nm; Ghose 1987); invertase (E.C. 3.2.1.26) activity was determined using 10% sucrose solution as substrate with incubate at 37°C for 24 h (pH 5.5; glucose concentration was determined by the spectrophotometer at 508 nm; Ohshima *et al.* 2007); polyphenol oxidase (E.C. 1.10.3.1) activity was determined using 50 mM l^{-1} pyrocatechol solution as substrate with incubate at 30°C for 10 min (pH 5.8; the color was determined colorimetrically at 410 nm; Perucci *et al.* 2000); catalase (E.C. 1.11.1.6) activity was determined using 8.8 mM H_2O_2 solution as substrate with incubate at room temperature for 10 min (the color was determined colorimetrically at 505 nm; Trasar-Cepeda *et al.* 1999); nitrate reductase (E.C. 1.7.99.4) activity was determined using 200 mM KNO_3 solution as substrate with incubate at room temperature for 30 min (pH 7.5; NO_2^- concentration was determined

Table 2: three-way ANOVAs on the effects of temperature (T), sampling date (D) and forest type (F) on lignin, TC, N, lignin:N, C:N and litter mass loss

		Lignin	TC	N	Lignin:N	C:N	Mass loss
T	*F*	0.014	0.001	0.92	0.15	0.319	19.135
	P	0.906	0.978	0.356	0.705	0.583	**0.001*** **
D	*F*	0.087	0.158	1.281	0.299	0.587	358.652
	P	0.993	0.973	0.334	0.904	0.71	**<0.001*** **
F	*F*	529.948	294.842	21.078	131.903	59.46	0.09
	P	**<0.001*** **	**<0.001*** **	**<0.001*** **	**<0.001*** **	**<0.001*** **	0.767
T × D	*F*	0.002	0.001	0.238	0.022	0.081	1.974
	P	1.000	1.000	0.938	1.000	0.994	0.155
T × F	*F*	0.004	0.026	0.352	0.048	0.180	0.002
	P	0.953	0.873	0.56	0.828	0.676	0.967
D × F	*F*	0.910	0.996	0.62	0.512	0.394	0.281
	P	0.506	0.460	0.687	0.762	0.843	0.915
T × D × F	*F*	0.176	0.044	0.635	0.001	0.502	0.407
	P	0.967	0.999	0.677	1.000	0.769	0.835

Abbreviation: TC = total carbohydrate. *P* values ≤0.05 are in bold face. *, ** and *** indicate significant differences at the 0.05, 0.01 and 0.001 probability level, respectively.

Table 3: decomposition coefficient (k, month^{-1}) of the two litter types during a 5-month litter decomposition

Treatments	Leaves	Needles
Normal temperature (20°C)	0.0336^{b}	0.0311^{b}
High temperature (30°C)	0.0401^{a}	0.0364^{ab}

Data with different superscript letters indicate a significant difference ($P < 0.05$) using Tukey's Honestly Significant Differences test.

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by the spectrophotometer at a wavelength of 520 nm; Daniel and Curran 1981); urease (E.C. 3.5.1.5) activity was determined using 10% urea solution as substrate with incubate at 37°C for 24 h (pH 6.7; NH_4^+-N concentration was determined by the spectrophotometer at a wavelength of 578 nm; Nannipieri *et al.* 1980) and acid phosphatase (E.C. 3.1.3.2) activity was determined using 0.5% disodium phenyl phosphate solution as substrate with incubate at 37°C for 24 h (pH 5.0; phenol concentration was determined by the spectrophotometer at 570 nm; Kandeler *et al.* 1999). Soil enzyme activities were assayed within 4–5 d after sampling.

Table 4: the Q_{10} values of decomposition of the two litter types and soil enzymes in the two forest types after a 5-month incubation

LD	Catalase	Cellulase	INV	NR	ACP	PPO	Urease
BF	1.1935^{c}	1.2265^{bc}	1.1183^{cd}	1.0429^{d}	1.0548^{d}	1.1047^{cd}	1.6757^{a}	1.0941^{cd}
CF	1.1704^{c}	1.1290^{cd}	1.1437^{cd}	1.0576^{d}	1.3511^{b}	1.1199^{cd}	1.8269^{a}	1.1191^{cd}

Abbreviations: ACP = acid phosphatase, INV = invertase, LD = litter decomposition, NR = nitrate reductase, PPO = polyphenol oxidase. Data with different superscript letters indicate a significant difference ($P < 0.05$).

Statistical analyses

The constant potential mass loss over time was calculated by the following exponential equation (Olson 1963):

$$x_t = x_0 e^{-kt}, \quad (1)$$

where x_0 is the original mass of the litter, x_t is the amount of litter remaining after time t and k is the litter decomposition coefficient (month^{-1}).

The temperature sensitivity of decomposition of the two litter types was estimated by the Q_{10} values (Karhu *et al.* 2010; Kirschbaum 1995):

$$Q_{10} = \left(\frac{k_2}{k_1}\right)^{\left[\frac{10}{T_2 - T_1}\right]}, \quad (2)$$

where k_2 and k_1 were the litter decomposition coefficients at T_2 and T_1, respectively. In this study, T_2 = 30°C and T_1 = 20°C.

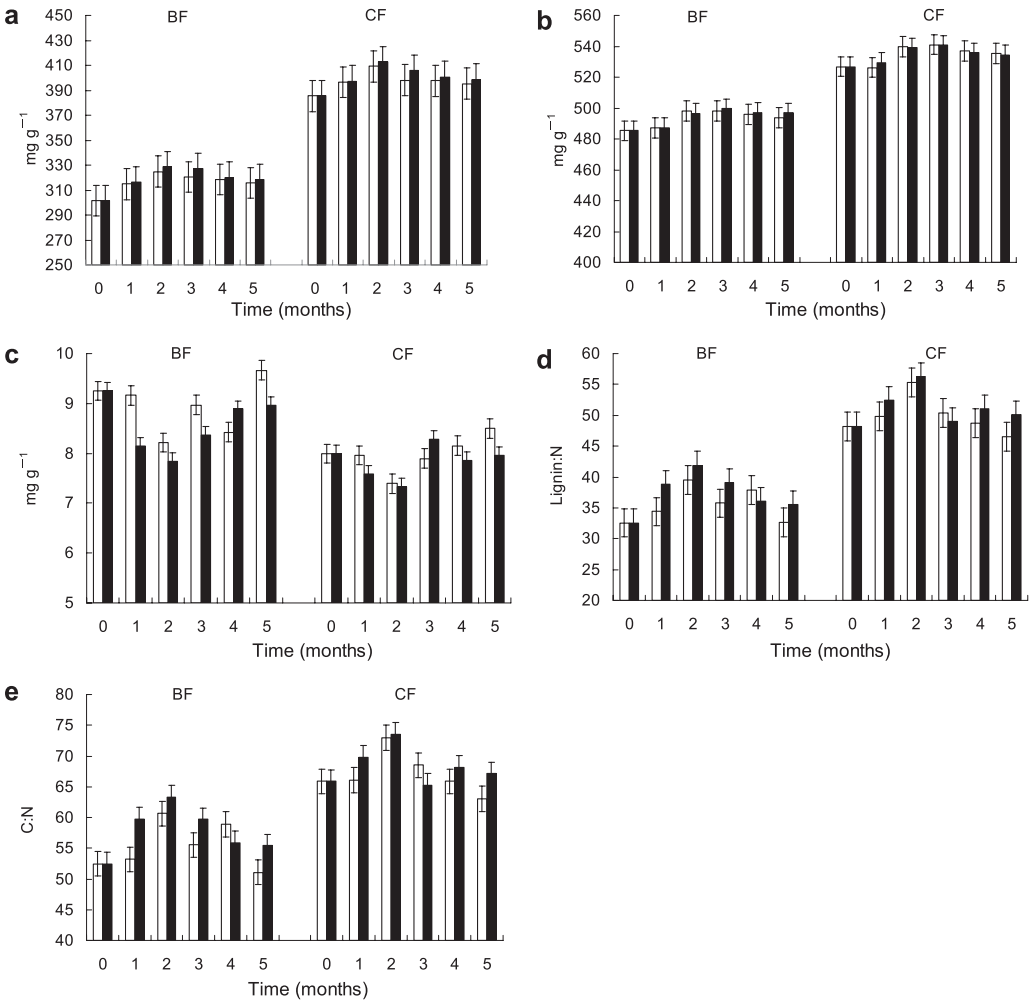

Figure 2: changes in lignin concentration (**a**), total carbohydrate concentration (**b**), N concentration (**c**), the ratios of lignin:N (**d**) and C:N (**e**) of the two litter types during litter decomposition. Symbols: open square, 20°C; filled square, 30°C. Error bars indicate standard error (n = 3).

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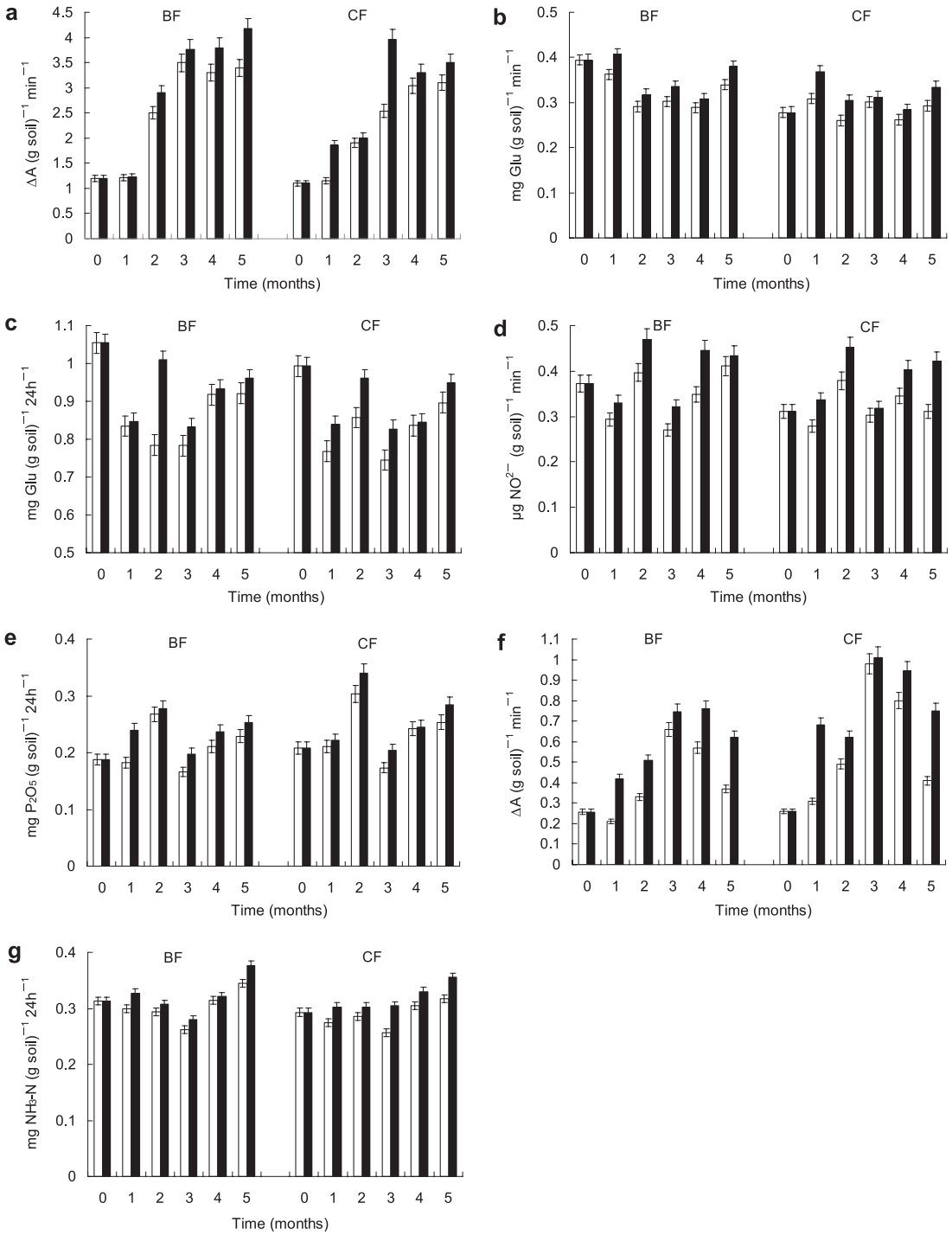

Figure 3: changes in soil enzyme activities in the two forest types during litter decomposition. Legend: (**a**) catalase; (**b**) cellulase; (**c**) invertase; (**d**) nitrate reductase; (**e**) acid phosphatase; (**f**) polyphenol oxidase; (**g**) urease. Symbols: open square, 20°C; filled square, 30°C. Error bars indicate standard error (n = 3).

The temperature sensitivity of soil enzymes in the two forest types was also estimated by the Q_{10} values (Wallenstein *et al.* 2009).

Data were checked for deviations from normality and homogeneity of variance before analysis. An analysis of variance was applied to assess significant differences between various treatments using DPS (version 7.05). Correlations were determined using the simple Pearson product-moment correlation coefficient. Statistically significant differences were set with P values <0.05, unless otherwise stated. Three-way

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Table 5: three-way ANOVAs on the effects of temperature (T), sampling date (D) and forest type (F) on soil enzyme activities

		Catalase	Cellulase	INV	NR	ACP	PPO	Urease
T	*F*	6.982	40.170	11.977	33.391	18.438	32.397	26.214
	P	**0.020***	**<0.001*****	**0.004****	**<0.001*****	**0.001*****	**<0.001*****	**<0.001*****
D	*F*	25.990	26.921	7.006	22.201	39.406	23.892	24.123
	P	**<0.001*****	**<0.001*****	**<0.001*****	**<0.001*****	**<0.001*****	**<0.001*****	**<0.001*****
F	*F*	8.704	31.181	2.482	2.865	12.749	28.203	3.405
	P	**0.011***	**<0.001*****	0.139	0.114	**0.003****	**<0.001*****	0.088
T × D	*F*	6.119	4.317	6.595	10.576	8.058	4.454	10.306
	P	**0.004****	**0.016***	**0.003****	**<0.001*****	**0.001*****	**0.014***	**<0.001*****
T × F	*F*	0.729	3.158	1.882	1.906	0.989	2.989	1.526
	P	0.550	0.054	0.173	0.169	0.423	0.062	0.246
D × F	*F*	11.798	3.448	1.670	2.603	8.080	3.373	3.752
	P	**<0.001*****	**0.033***	0.218	0.076	**0.001*****	**0.036***	**0.026***
T × D × F	*F*	0.162	0.310	2.338	0.522	0.132	0.550	0.529
	P	0.953	0.865	0.126	0.722	0.967	0.704	0.717

Abbreviations: ACP = acid phosphatase, INV = invertase, NR = nitrate reductase, PPO = polyphenol oxidase. *, ** and *** indicate significant differences at the 0.05, 0.01 and 0.001 probability level, respectively. *P* values ≤0.05 are in bold face.

ANOVAs were applied to test the effects of temperature, sampling date and forest type on soil enzyme activities using SPSS (version 13.0).

RESULTS

Litter decomposition

After a 5-month period of litter decomposition, the cumulative mass losses were 15.31% for 20°C-BF, 17.94% for 30°C-BF, 14.78% for 20°C-CF and 16.65% for 30°C-CF (Fig. 1), and ANOVAs showed that temperature affected litter mass losses significantly (Table 2; $P < 0.001$). Correspondingly, litter decomposition coefficients (k values) were in the order of 0.0401 (30°C-BF), 0.0364 (30°C-CF), 0.0336 (20°C-BF) and 0.0311 (20°C-CF)(Table 3). But there was no significant difference in the Q_{10} values of litter decomposition between BF leaves and CF needles (Table 4; $P > 0.05$).

Lignin concentration, lignin:N ratio and C:N ratio of both litter types increased slightly in the first 2 months but then decreased in the latter 3 months during litter decomposition (Fig. 2a, d and e). Total carbohydrate concentration of both litter types did not significantly change during litter decomposition under either temperature condition (Fig. 2b). N concentration of both litter types showed a similar trend, with a slight decrease in the first 2 months and a slight increase in the latter 3 months (Fig. 2c). No significant relationship was found between lignin concentration, total carbohydrate concentration, N concentration, lignin:N and C:N with mass losses of the two litter types during decomposition ($P > 0.05$). ANOVAs indicated that there was significant difference in lignin, total carbohydrate, N, lignin:N and C:N between BF leaves and CF needles (Table 2; $P < 0.001$).

Soil enzyme activities

High temperature enhanced soil enzyme activities in the two forest types (Fig. 3), and ANOVAs revealed that temperature, sampling date and the interactions of temperature and sampling date affected soil enzyme activities significantly (Table 5; $P < 0.05$). Polyphenol oxidase and acid phosphatase activities were significantly higher in the CF soil than in the BF soil (Fig. 3e and f; Table 5; $P < 0.001$), and the activities of some other soil enzymes (i.e. catalase and cellulase) were higher in the BF soil than in the CF soil (Fig. 3a and b; Table 5; $P < 0.05$). The Q_{10} values of polyphenol oxidase were significantly higher than those of the other soil enzymes (i.e. catalase, cellulase, invertase, urease, nitrate reductase and acid phosphatase) in the two forest types (Table 4; $P < 0.05$). The Q_{10} values of nitrate reductase were significantly higher in the CF soil than in the BF soil (Table 4; $P < 0.05$), while there was no significant difference in the Q_{10} values of the other soil enzymes (i.e. catalase, cellulase, invertase, urease, polyphenol oxidase and acid phosphatase) between BF and CF (Table 4; $P > 0.05$).

DISCUSSION

Litter decomposition

Some investigators revealed that the decomposers in the CF are often dominated by fungi (Schimel *et al.* 2007), and high temperature may increase fungal–bacterial biomass ratio (Zhang *et al.* 2004, 2005). Meanwhile, 'temperature–quality hypothesis' suggested that decomposition of low-quality organic matter involves higher activation energies and that low-quality organic matter therefore would be more temperature sensitive than high-quality organic matter (Davidson and Janssens 2006). Thus, the effects of high temperature on litter decomposition in the CF were presumably more

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significant than in the BF according to the above results. However, there was no significant difference in the Q_{10} values of litter decomposition between BF leaves and CF needles, suggesting that the temperature sensitivities of litter decomposition for BF leaves and that for CF needles are equivalent basically, which is inconsistent with previous reports (Davidson and Janssens 2006; Fierer *et al.* 2005; Melillo *et al.* 2002; Mikan *et al.* 2002). The reason may be mainly attributed to differences in the litter types, testing temperature range, native soil microbial community or different time scales of these studies (Kuperman 1999).

Soil enzyme activities

Some studies suggested that monitoring soil enzymes could also be a useful approach for estimating microbial activities related to litter decomposition (e.g. DeForest 2009; Sinsabaugh *et al.* 2005). Thus, changes in soil enzyme activities under high temperature could explain their effects on litter decomposition. This study showed that high temperature accelerated either enzyme activities or enzyme secretion (or both) in soils of the two forest types, suggesting that C, N and P mineralization increased under high temperature. The results also suggested that the high-temperature-accelerated litter decomposition may be due to the enhanced soil enzyme activities. As a long-term consequence, the high-temperature-induced acceleration of litter decomposition rates in these subtropical forests may cause C stored belowground to be transferred in the atmosphere, which may alter the balance between C uptake and release, and then alter the global C cycle in the coming decades. Acid phosphatase activities in the CF soil were higher than those in the BF soil, probably because the pH values of the CF soil are closer to the optimum value for acid phosphatase activities. Polyphenol oxidase activities in the CF soil were significantly higher than those in the BF soil, possibly because the litter of the CF contained more polyphenols (Kalbitz *et al.* 2003; Palm and Sanchez 1991). The activities of some other soil enzymes (i.e. catalase and cellulase) in the BF soil were higher than those in the CF soil, possibly due to the higher microbial activities in the BF soil.

This study first assessed the temperature sensitivity of soil enzymes in subtropical forest in China. The temperature sensitivities of polyphenol oxidase were significantly higher than those of the other soil enzymes in this study, partly due to the fact that lignin is the most in abundance of all the naturally produced organic chemicals in forest litter (Kirk and Farrell 1987). Another reason may be that lignin may be more sensitive to warming than many other plant-derived compounds in forest soils (Feng *et al.* 2008), likely because of its chemical complexity and the higher activation energy required to decompose it by micro-decomposers (Davidson and Janssens 2006). The temperature sensitivities of nitrate reductase were significantly higher in the CF soil than in the BF soil, likely due to the fact that the micro-decomposers in the CF soil were limited more by N than in the BF soil (Schimel *et al.* 2007; Tietema 1998), and the increased temperature significantly enhances the activities of soil nitrifying bacteria, resulting in significant increases in the amounts of mineralized organic matter and produced NH_4-N and NO_3-N (Magdoff *et al.* 1990).

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