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Concentration and mineralization of organic carbon in forest soils along a climatic gradient

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ABSTRACT

Forty-four percent of the organic carbon (OC) in the world's forests is stored in soils. However, the distribution and stability of OC in forest soils along a climatic gradient remain largely unclear, hindering our understanding and the accurate prediction of biogeochemical cycles in forest ecosystems in a changing world. To address these uncertainties, we measured OC and nitrogen (N) concentrations and mineralization of OC in soils from broadleaved and coniferous forests along a wide-ranging climatic gradient in China and related these to experimental N addition and climatic conditions. An 85-day incubation was conducted under 25 °C and 60% of soil moisture at field capacity to determine the mineralization of soil OC. We hypothesized that the concentrations of OC and N would be higher but the mineralization of OC would be lower in soils from colder and drier forests and that the mineralization would be positively responsive to N addition. In support of these hypotheses, the concentrations of OC and N decreased, while the mineralization of OC measured under standard laboratory condition increased, with mean annual precipitation (MAP) and temperature (MAT). These metrics were not affected by forest type or the interaction between forest type and site. Nitrogen addition increased the cumulative mineralized OC (C_m, g kg^{-1}) by 6–67%, and the effects varied with site and soil depth, but were similar between the broadleaved and coniferous forests. The C_m decreased with increasing soil OC concentration, C/N ratio and mineral N, while the rate constant of OC mineralization (k, day^{-1}) showed opposite relationships with these metrics. The addition of N did not change the slopes of the relationships of C_m and k with the C/N ratio, MAP, and MAT; however, it strengthened the negative relationship of C_m with OC and mineral N concentrations. The results from this study suggested that the mineralization of OC was limited by N availability in the studied forested soils, and the response of OC mineralization to N addition was independent of climatic conditions.

1. Introduction

Forty-four percent of the organic carbon (OC) in the world's forests is stored in the soil (Pan et al., 2011). Forest soils play an important role in regulating the response of global biogeochemical cycles to anthropogenic disturbance and global change (Hadden and Grelle, 2016; Keenan et al., 2014; Seidl et al., 2014). Therefore, understanding the distribution and stability of OC in forest soils along a climatic gradient would provide essential information for predicting OC dynamics at regional to global scales.

The stability of soil OC is often assessed by measuring the metrics of mineralization or decomposition of soil organic matter, in which a lower mineralization rate represents a higher stability (Fang et al., 2005; Fontaine et al., 2007; Schmidt et al., 2011). The mineralization of soil OC is usually determined by measuring CO_2 emissions during controlled incubation of soil samples at certain conditions (Fang et al., 2005; Fontaine et al., 2007; Schmidt et al., 2011; Cotrufo et al., 2015; Jenny et al., 1949; Karhu et al., 2010; Knorr et al., 2005; Powlson et al., 1987). As an important factor in land management, nitrogen (N) supply significantly affects OC mineralization by influencing the chemical properties of soil, microbial and enzymatic activities, and the quantity and availability of substrates (Hobbie, 2008; Leifeld et al., 2008; Min et al., 2011). The mineralization of OC in soils, however, responds inconsistently to N addition, with previous reports of increased (Menyailo et al., 2014; Tu et al., 2013) or decreased (Min et al., 2011; Tonitto et al., 2014) mineralization following N addition. This inconsistency

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may be a result of differences in the quality of the organic matter and soil properties (Du et al., 2014; Knorr et al., 2005; Leifeld et al., 2008), all of which greatly vary among sites and climatic conditions. Moreover, OC mineralization is highly dependent on climatic conditions (Doetterl et al., 2015; Fissore et al., 2008; Homann et al., 2007), but whether such dependence is affected by N addition or whether the response of OC mineralization to N addition is affected by climate remains untested in both observational and experimental studies. These uncertainties limit our understanding of the responses of ecosystems to global change and emphasize the need for further studies on the effects of N addition on OC stability in forest soils along climatic gradients.

The forest type is also an important factor that contributes to variations in soil OC cycling by affecting the quality and quantity of fresh litter or root inputs and thus controlling the composition and biodegradability of organic matter in soils (Augusto et al., 2015; Cools et al., 2014; Mueller et al., 2012; Reich et al., 1997). Coniferous needles generally have more recalcitrant carbon components than the leaves of broadleaved trees (Shirato and Yokozawa, 2006), resulting in different OC mineralization rates and various coupled relationships between OC cycling in forest soils (Quan et al., 2014). No consensus has yet been reached on the effects of forest type on OC mineralization in soils. For example, the mineralization of soil OC has been reported to be higher (Mueller et al., 2012; Reich et al., 1997; Xu et al., 2014) or similar (Augusto et al., 2015; Colman and Schimel, 2013; Mueller et al., 2012) in broadleaved forests compared to coniferous forests, including not only unexplained variability but also some variability contingent on whether mineral soil or organic horizons were measured, or on whether natural or plantation stands were compared. This range of observations provides some understanding of the effect of forest type on OC dynamics but highlights the uncertainty in such response, hindering the extrapolation of these results to a larger spatial scale and the identification of a universal pattern of influences.

In this study, we hypothesized that (H1) the concentrations of OC and N, and the mineralization of OC under standard temperature and soil moisture condition would be higher in broadleaved forests compared to those in coniferous forests, that (H2) the concentrations of OC and N would be higher but the mineralization under standard conditions lower in soils from colder and drier forests, and that (H3) the mineralization of OC under standard conditions would be positively responsive to N addition because most forests are limited by N availability. To test these hypotheses, we collected mineral soils from coniferous and broadleaved forests at 11 sites in China. These sites were located throughout China across a wide range of climatic gradient, which determines soil texture, the concentrations of OC and N, and the quality of soil organic matter. All these factors can directly affect soil OC mineralization. We measured the OC concentration and mineralization at a commonly used standard temperature (25 °C) and soil moisture (60% field capacity) condition. The effects of N addition and dependence on climatic conditions were also examined.

2. Materials and methods

2.1. Study sites and soil sampling

Soil samples were collected from 11 forested sites in China along a 22 °C gradient of mean annual temperature (MAT) and a 2000 mm gradient of mean annual precipitation (MAP) (Table 1, Fig. 1). Climatic data were available for all sites. Two adjacent tracts of broadleaved and coniferous forest stands were selected as replicates at two subsites (~3 km apart) at each site, except for Helan and Xishuangbanna, where only coniferous or broadleaved forest was selected. The age of the dominant species in our forest was over 80 years, which is considered as the mature forest (Keeton et al., 2007; Liu et al., 2014). The dominant species of each forest type at each site are shown in Table 1. Three plots (20 × 20 m in size) were established > 100 m apart in each adjacent tract of each forest. The plots in each forest had the same soil type and

Table 1
Description of each site used in this study along a climatic gradient in China.

# Site	Location	Province	MAP (mm)	MAT (°C)	Soil types	Sampling depth	Forest types and dominant species	
							Broadleaved forest	Coniferous forest
1	Helan	Ningxia	300	3.5	Alfisols	0–10 cm, 10–20 cm		*Picea crassifolia, Pinus tabuliformis, Juniperus rigda*
2	Beijing	Beijing	575	7.5	Alfisols	0–10 cm, 10–20 cm	*Populus davidiana, Betula platyphylla Suk, Quercus liaotungensis*	*Pinus tabuliformis, Larix principis-rupprechtii*
3	Huanglong	Shaanxi	611.8	8.6	Inceptisols	0–10 cm, 10–20 cm	*Betula platyphylla Suk, Quercus liaotungensis*	*Pinus tabuliformis*
4	Guyuan	Ningxia	676	5.8	Alfisols	0–10 cm, 10–20 cm	*Betula platyphylla Suk, Quercus liaotungensis*	*Pinus armandi, Larix principis-rupprechtii*
5	Harbin	Heilongjiang	723.8	2.8	Alfisols	0–10 cm, 10–20 cm	*Betula platyphylla Suk*	*Pinus koraiensis Sieb. et Zucc.*
6	Bijie	Guizhou	877	13	Inceptisols	0–10 cm	*Castanopsis Spach, Populus davidiana, Cinnamomum parthenoxylon (Jack) Nees*	*Cunninghamia lanceocycla Mitf, Pinus yunnanensis, Keteleeria davidiana (Bertr.) Beissn*
7	Changsha	Hunan	1422	17	Ultisols	0–10 cm, 10–20 cm	*Liquidambar formosana Hance, Cinnamomum camphora*	*Pinus massoniana, Cunninghamia lanceocycla Mitf*
8	Taihe	Jiangxi	1726	17.8	Ultisols	0–10 cm, 10–20 cm	*Schima superba*	*Pinus massoniana, Cunninghamia lanceocycla Mitf*
9	Xishuangbanna	Yunnan	1795	19	Ultisols	0–10 cm, 10–20 cm	*Dysoxylum excelsum Bl, Pometia pinnata, Pittosporopsis kerrii Craib*	
10	Wuyishan	Fujian	1800	16	Ultisols	0–10 cm, 10–20 cm	*Idesia polycarpa, Castanopsis fargesii*	*Cunninghamia lanceolata Pinus tanwanensis*
11	Wuzhishan	Hainan	2419	22.5	Ultisols	0–10 cm, 10–20 cm	*Lithocarpus fenzelianus, Castanopsis tonkinensis*	*Pinus fenzeliana, Keteleeria hainanensis,*

Soil was classified according to Soil Survey Staff in USDA (1992).

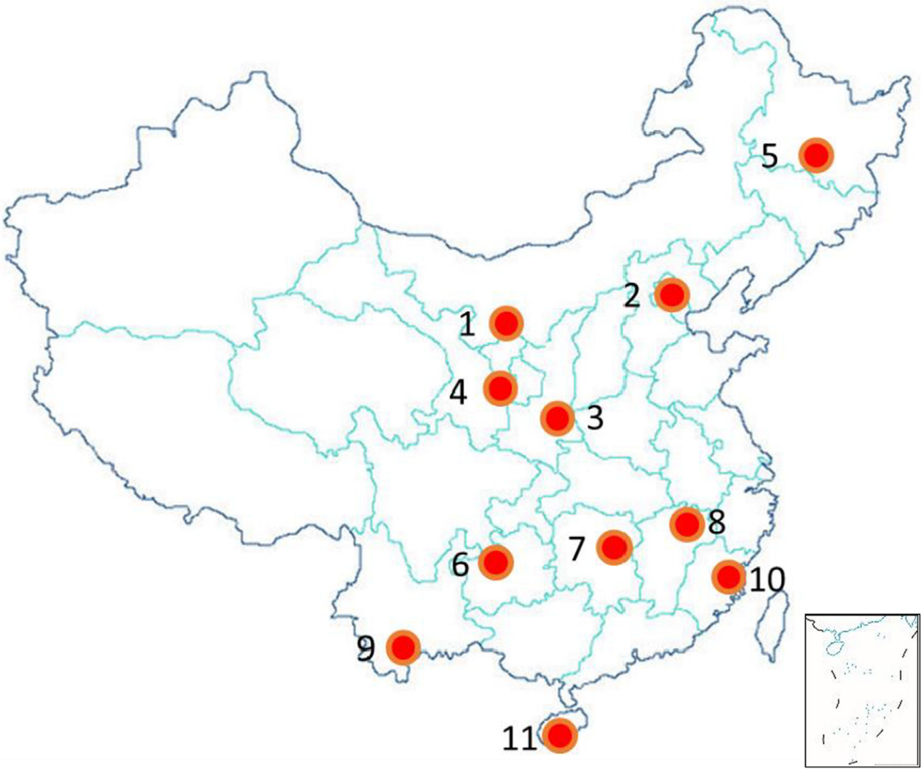

Fig. 1. Location of the study sites. Site 1, Helan; Site 2, Beijing; Site 3, Huanglong; Site 4, Guyuan; Site 5, Harbin; Site 6, Bijie; Site 7, Changsha; Site 8, Taihe; Site 9, Xishuangbanna; Site 10, Wuyishan; Site 11, Wuzhishan. The details of each site were present in Table 1. All the forests are secondary forests but are mature for each site.

similar physiographic conditions and slope gradients. Five subplots were randomly established in each plot. Mineral soil samples were collected from 0 to 10 and 10–20 cm depths using a soil-coring kit (5.0 cm in diameter) in each of the five subplots and combined as a composite sample for each plot for each depth. Samples at Bijie were only collected from the 0–10 cm depth. The organic layers were removed prior to sampling. Visible pieces of organic material were removed, and the moist field samples were transported to the laboratory. The samples were carefully sieved through a 2-mm sieve to remove roots and rocks and air-dried to measure field capacity and to prepare for the measurement of OC mineralization. Subsamples of the air-dried soils were ground to pass through a 0.25-mm sieve to measure the OC and N concentrations.

2.2. Soil analysis

The field capacity of each sample was determined using the method proposed by Fissore et al. (2008). The concentrations of OC and N were measured using the Walkley-Black and Kjeldahl methods, respectively (Page, 1982). The mineral N concentration was measured using a continuous flow analyzer (AutoAnalyzer-AA3, Seal Analytical, Germany) following extraction by 2 mol L^{-1} KCl.

We measured the OC mineralization at a commonly used standard temperature (25 °C) (Cotrufo et al., 2015; Jenny et al., 1949; Karhu et al., 2010; Knorr et al., 2005; Powlson et al., 1987). Briefly, 10 g of air-dried soils was adjusted to 60% field capacity in 250-mL jars and pre-incubated for five days to remove the flush of C mineralization caused by rewetting. The samples were then incubated in the dark. A 10-mL glass vial containing 5 mL of 1 M NaOH was placed in each jar to trap the released CO_2. The soil moisture during incubation was adjusted by adding deionized water to maintain the initial weight. Six empty jars with no soil were prepared as controls. The amount of CO_2 trapped was determined by titration against HCl. The emission of CO_2 was measured at 4, 8, 15, 22, 29, 36, 43, 50, 57, 64, 71, 78, and 85 days of incubation. At each sampling, the vials were replaced with another set of vials containing fresh NaOH, and the jars were returned to the incubator. The caps of the jars were periodically opened during sampling to replenish the oxygen supply in the headspace. The cumulative mineralized OC (C_m, g kg^{-1} OC) following 85 days of incubation was calculated as the sum of the mineralized OC at each sampling. The cumulative mineralized OC was the C loss during the mineralization.

To investigate the effects of N supply on OC mineralization, we added NH_4NO_3 to 10 g of soil at a rate of 0.1 g N kg^{-1} soil. The soils with added N were then incubated to determine the OC mineralization using the same procedure previously described.

2.3. Data analysis

We used a first-order model (natural growth equation) to fit the OC mineralized (OC loss) over time as follows (Wang et al., 2014; Tian et al., 2016):

$$C_t = C_p \times (1 - e^{(-k \times t)}) \tag{1}$$

where C_t is the cumulative mineralized OC (g kg^{-1} OC) at time t (d), C_p is the potentially mineralizable OC (g kg^{-1} OC), which represented only a small proportion of soil OC (with a mean of 3.2% OC and range of 0.5–13% OC) (data not shown), and k is the rate constant of OC mineralization (day^{-1}).

All variables were compared by mixed-effect analyses of variance (ANOVAs) to test the effects of soil depth, site and forest type. Only one forest type was included at Helan and Xishuangbanna, and the soil was collected from only one depth at Bijie (Table 1); thus, these three sites were excluded from the ANOVAs. The independent variables in the models were soil depth, site, forest type, and their interaction. An additional model examined the effects of N addition on the C_m and k of OC mineralization. The independent variables in the models were N addition, soil depth, site, forest type, and their interactions. A result was significant when $P < 0.05$. The relationships among the variables were determined via correlation analysis. The dependence of OC mineralization measured under standardized temperature and moisture conditions on climate (MAP or MAT) and its response to N addition were determined using a simple regression analysis. All data were

Table 2
ANOVA results (P values) of soil depth (D), forest types (F), sites (S), nitrogen addition (N) and their interactions on soil organic carbon (OC), nitrogen (N), C/N ratios, mineral N concentration (Min-N), cumulative mineralized organic carbon (C_m) and the mineralization rate constant (k) of OC mineralization measured under the standard temperature and soil moisture condition.

Sources of variation	OC	N	C/N	Min-N	C_m	k
D	**< 0.0001**	**< 0.0001**	**0.0226**	**< 0.0001**	0.1726	**< 0.0001**
F	0.2060	0.5038	0.9849	0.7421	0.8290	0.2369
S	**< 0.0001**	**< 0.0001**	**0.0056**	**< 0.0001**	**< 0.0001**	**< 0.0001**
F × D	0.7249	0.1910	0.2674	0.9741	0.8944	0.2977
S × D	**< 0.0001**	**0.0007**	**0.0004**	**< 0.0001**	**0.0351**	**0.0194**
S × F	0.4567	0.1268	**0.0006**	**0.0017**	**0.0604**	**0.0026**
F × S × D	0.5316	0.3935	0.6090	0.5830	0.1448	0.6907
N					**0.0012**	**0.0006**
D × N					0.2195	0.9853
F × N					0.9563	0.1948
S × N					0.6199	0.2846
F × D × N					0.9144	0.7790
S × D × N					0.9765	0.9400
S × F × N					0.9986	0.8751
F × S × D × N					0.9956	0.5567
R^2	0.727	0.784	0.452	0.694	0.419	0.530
RMSE	10.20	0.71	2.67	6.85	13.40	0.01

R^2 and RMSE are coefficient of determination and root mean square error of the overall model.

analyzed using JMP 10.0 (SAS Institute, Cary, USA).

3. Results

3.1. Concentration of OC in forest soils along a climatic gradient

The concentrations of OC and N were significantly affected by soil depth and site, with higher concentrations at the 0–10 cm depth compared to those at the 10–20 cm depth, and higher concentrations at the colder or drier sites (Table 2, Fig. 2). When tested across sites, soil OC concentration was 53% and 58% higher at 0–10 cm soil depths compared to that at 10–20 cm soil depths in broadleaved and coniferous forests, and soil N concentration was 41% and 34% higher, respectively. Furthermore, OC and N concentrations were significantly higher in Helan, Guyuan and Harbin but lower in Changsha, Taihe and Xishuangbanna either across or within soil depths or forest types (Fig. 2). However, OC and N concentrations were not affected by forest type (*P* = 0.206 and 0.504) or its interaction with site (*P* = 0.457 and 0.127, Table 2). For example, at the 0–10 cm depth, the soil OC concentration was 32.2 and 32.7 g kg^{-1} in broadleaved and coniferous forests, respectively; at the 10–20 cm depth, the soil OC concentration was 21.1 and 20.6 g kg^{-1}, respectively. This pattern was observed across or within most sites (Fig. 2). Moreover, OC and N concentrations decreased with MAP and MAT (Fig. 3), indicating that climate significantly controlled the concentrations of OC and N in the forest soils.

3.2. Mineralization of OC in soils along a climatic gradient

The mineralization of soil OC measured at a standard temperature and soil moisture condition was significantly affected by site (Table 2,

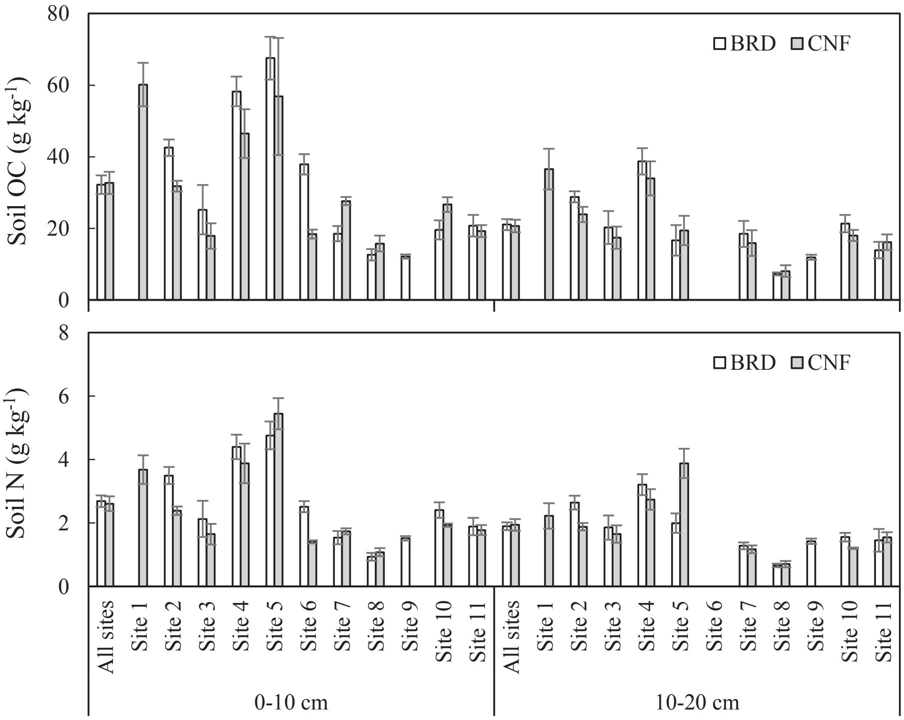

Fig. 2. Concentrations of soil organic carbon (OC) and nitrogen (N) as affected by sites and forest types at the 0–10 and 10–20 cm soil depths along a climatic gradient in China. Error bars are standard errors of the means. BRD: broadleaved forest; CNF: coniferous forest. Site 1, Helan; Site 2, Beijing; Site 3, Huanglong; Site 4, Guyuan; Site 5, Harbin; Site 6, Bijie; Site 7, Changsha; Site 8, Taihe; Site 9, Xishuangbanna; Site 10, Wuyishan; Site 11, Wuzhishan.

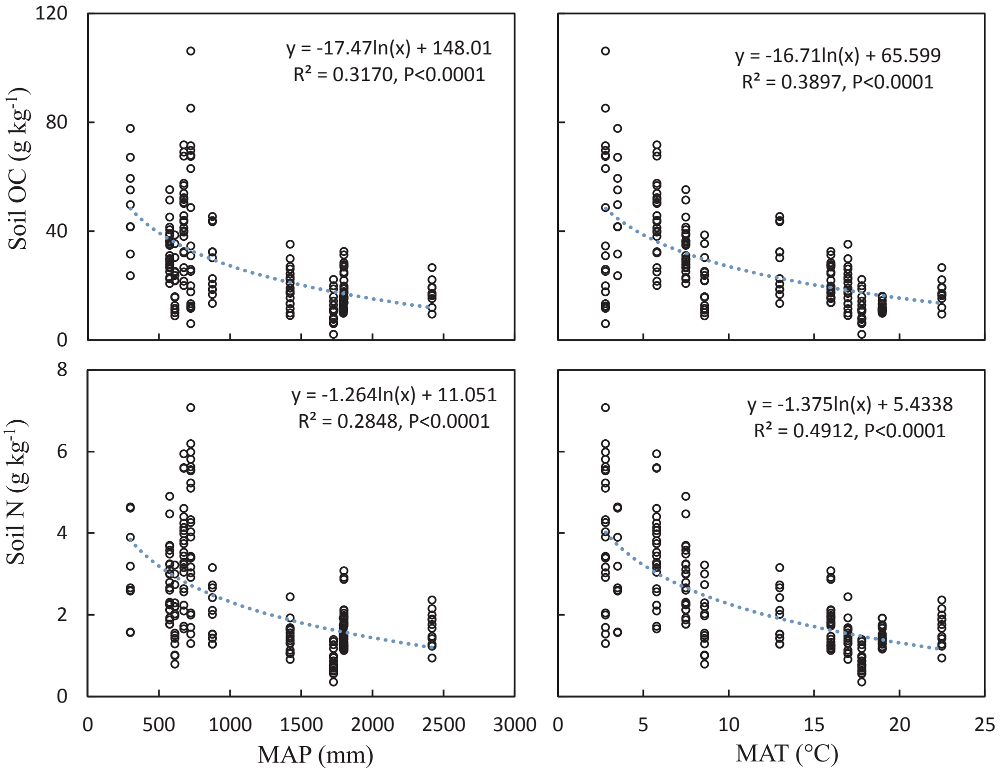

Fig. 3. Relationships of concentrations of soil organic carbon (OC) and nitrogen (N) to mean annual precipitation (MAP) and temperature (MAT) across sites, forest types and soil depths.

Fig. 4). Averaged across the forest types and soil depths, C_m and k ranged from 14.1 to 37.9 g kg^{-1} OC ($P < 0.0001$) and 1.21×10^{-2} to 2.28×10^{-2} day^{-1} ($P < 0.0001$) among the 11 sites, respectively. C_m was significantly higher at Huanglong, Harbin, Taihe, Xishuangbanna and Wuzhishan compared to that at the other sites, while k was significantly lower at Wuyishan compared to that at the other sites (Fig. 4). C_m and k were significantly higher at the 0–10 cm soil depth compared to those at the 10–20 cm soil depth but were not affected by

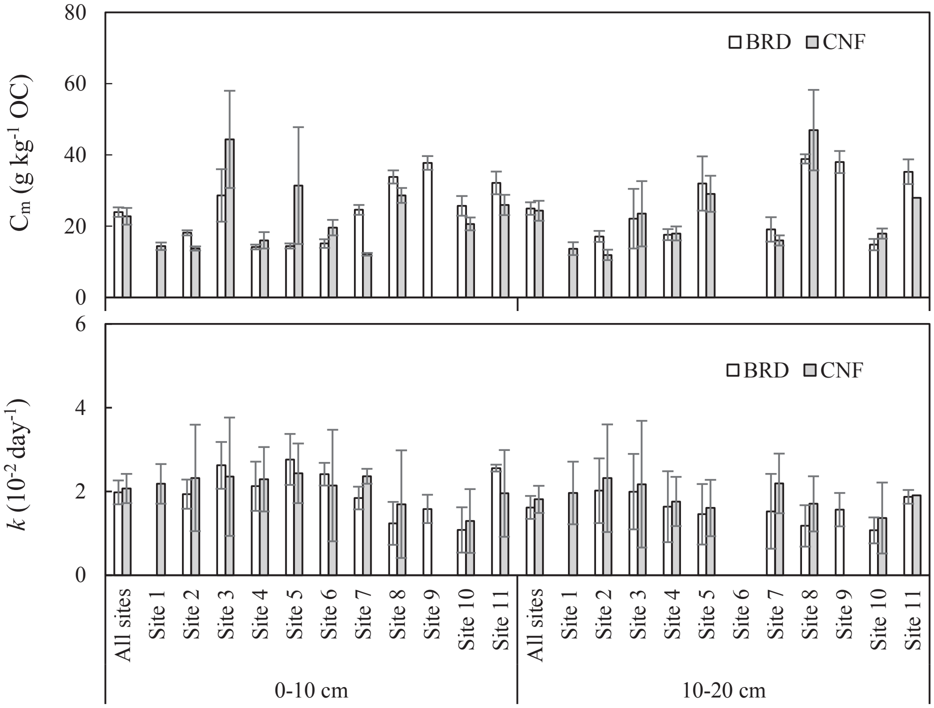

Fig. 4. Cumulative mineralized organic carbon (C_m) and the mineralization rate constant (k) of soil organic carbon (OC) mineralization as affected by sites and forest types at the 0–10 and 10–20 cm soil depths along a climatic gradient in China. Error bars are standard errors of the means. BRD: broadleaved forest; CNF: coniferous forest. Site 1, Helan; Site 2, Beijing; Site 3, Huanglong; Site 4, Guyuan; Site 5, Harbin; Site 6, Bijie; Site 7, Changsha; Site 8, Taihe; Site 9, Xishuangbanna; Site 10, Wuyishan; Site 11, Wuzhishan.

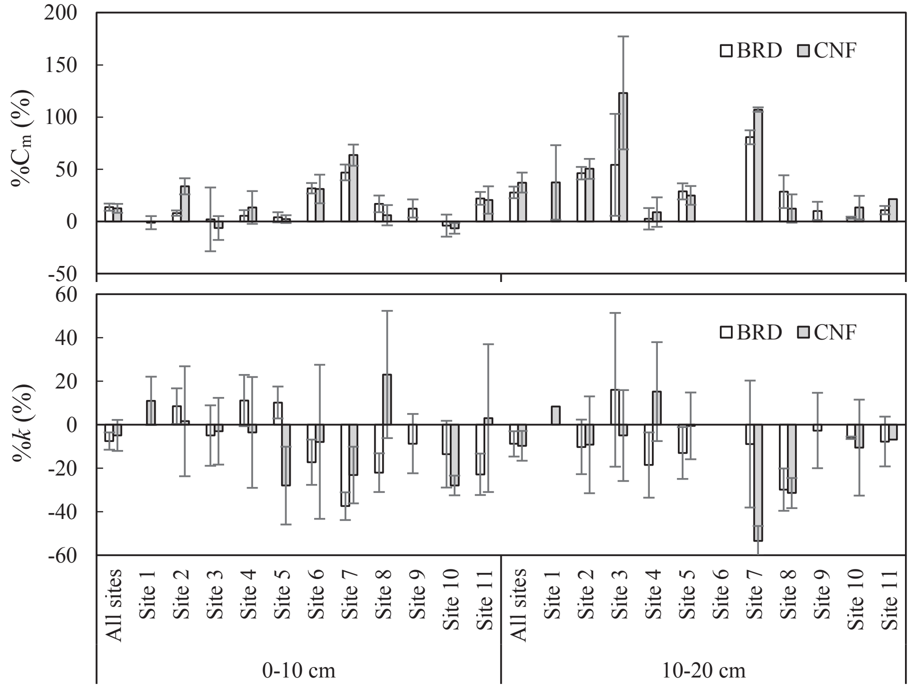

Fig. 5. Percent changes of cumulative mineralized organic carbon (%C_m) and the mineralization rate constant (%k) after nitrogen (N) addition as affected by sites and forest types at the 0–10 and 10–20 cm soil depths along a climatic gradient in China. Error bars are standard errors of the means. BRD: broadleaved forest; CNF: coniferous forest. Site 1, Helan; Site 2, Beijing; Site 3, Huanglong; Site 4, Guyuan; Site 5, Harbin; Site 6, Bijie; Site 7, Changsha; Site 8, Taihe; Site 9, Xishuangbanna; Site 10, Wuyishan; Site 11, Wuzhishan. The values of %C_m and %k were calculated as the percent difference between N addition and control treatments. The OC mineralization was measured under 25 °C and 60% field capacity.

forest type.

C_m and k were not affected by forest type, and C_m was not affected by soil depth, while k was significantly higher at the 0–10 cm depth compared to that at the 10–20 cm depth either across or within most sites (Table 2, Fig. 4). Averaged across all sites, C_m was 24.0 and 25.0 g kg^{-1} OC at the 0–10 and 10–20 cm soil depths ($P = 0.6441$), respectively, for the broadleaved forests and 22.8 and 24.3 g kg^{-1} OC ($P = 0.6704$), respectively, for the coniferous forests (Fig. 4). Similarly, the k values were 1.98×10^{-2} and 1.62×10^{-2} day^{-1} at the 0–10 and 10–20 cm soil depths ($P = 0.0044$), respectively, for the broadleaved forests and 2.07×10^{-2} and 1.81×10^{-2} day^{-1} ($P = 0.0623$), respectively, for the coniferous forests (Fig. 4). Furthermore, these response patterns of C_m and k to forest type were observed at most sites (Fig. 4).

3.3. Effects of N addition on OC mineralization in soils

Nitrogen addition increased C_m by 6–67% ($P = 0.0005$), with a greater increase occurring in Changsha and Huanglong and a lesser increase occurring in Guyuan and Wuyishan (Fig. 5). Furthermore, the increase was similar between the two types of forest but was greater at the10–20 cm depth than at the 0–10 cm depth. For example, N addition resulted in 14 and 13% increases in C_m in broadleaved and coniferous forests at the 0–10 cm depth and in 28 and 37% increases at the 10–20 cm depth, respectively. The effects of N addition on k varied by site ($P = 0.0002$), with an 11% increase at Helan but a 0–32% decrease at the other sites (Fig. 5). However, the effect of N addition on k was not influenced by soil depth or forest type (Table 2). For instance, when tested across sites, N addition resulted in 8 and 5% decreases in the k value of broadleaved and coniferous forests at the 0–10 cm depth and 9 and 10% decreases at the 10–20 cm depth, respectively.

3.4. Dependence of OC mineralization on soil OC and climate

Pooled across all sources of variation, C_m decreased but k increased with increasing soil OC, C/N ratio and mineral N (Fig. 6). The addition of N did not change the slopes of the relationships of C_m and k with C/N ratios but strengthened the negative relationship of C_m with OC and mineral N concentrations (Table 3). For example, the slopes of the relationships of C_m with OC and mineral N concentrations decreased from -0.44 to -0.62 and from -0.058 to -0.237, respectively, following N addition (Table 3). We further observed that changes in C_m following N addition decreased with increasing soil OC and mineral N concentrations (Fig. 7). Therefore, the OC mineralization was limited by the N availability in the mature forest soils.

The C_m and k of OC mineralization were correlated with climatic conditions, with C_m increasing but k decreasing with MAP and MAT (Table 3). However, the slope of the relationship between C_m and MAP or MAT was not affected by N addition (Table 3), implying that such dependence was stable with respect to N supply. Similarly, the response of OC mineralization to N addition (%C_m or %k) was not correlated with MAP or MAT (Table 3). Therefore, the response of OC mineralization to N addition was independent of the climatic gradient in the studied mature forests.

4. Discussion

Documenting the concentration and mineralization of OC in forest soils along a climatic gradient is essential for accurately predicting OC dynamics and storage in forest soils in a changing world. We demonstrated that climatic conditions, forest types, and N addition interactively regulate the concentrations and mineralization of OC and N in forest soils. Across the climatic gradient in this study, the concentrations of OC and N and the mineralization of OC at the standard condition were similar between the broadleaved and coniferous forests but significantly varied by site. Soil OC and N concentrations were higher in soils from colder or drier sites, while C_m increased but k decreased with MAP and MAT, refuting H1 but supporting H2. The cumulative mineralization of OC increased with N addition, and changes in C_m following N addition decreased with increasing soil OC and mineral N concentrations, indicating that the decomposition of soil organic matter in the mature forests was limited by N availability in accordance with H3.

4.1. Concentrations of OC and N in forest soils along a climatic gradient

The higher OC and N concentrations at the 0–10 cm depth compared to those at the 10–20 cm depth mainly resulted from the accumulation

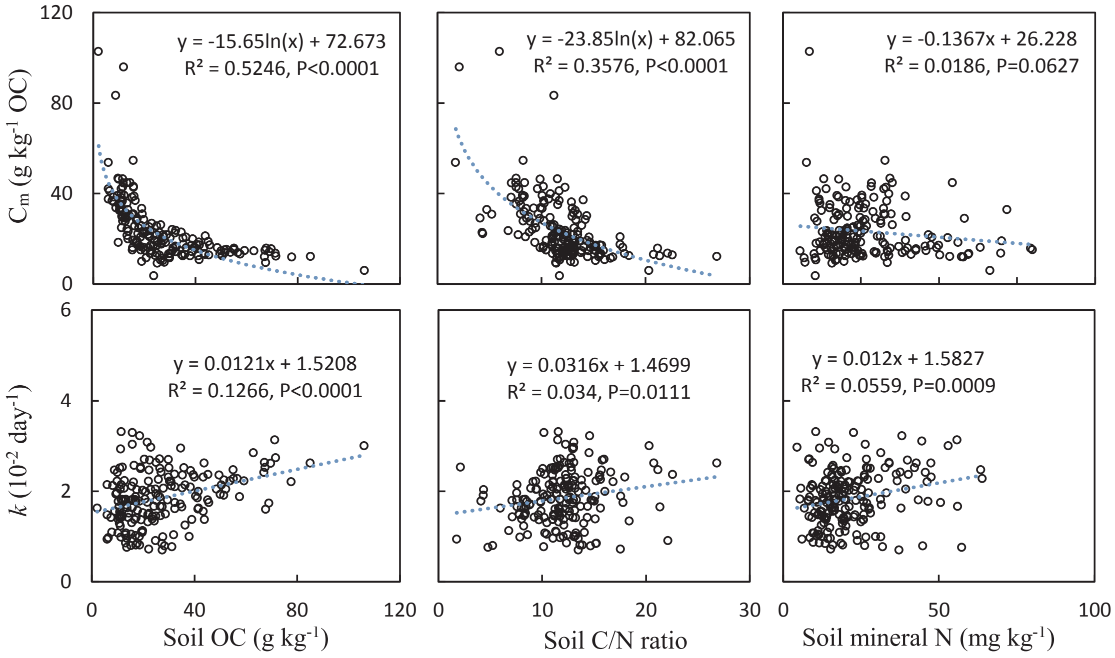

Fig. 6. Relationships of cumulative mineralized organic carbon (C_m) and the mineralization rate constant (k) of soil organic carbon (OC) mineralization to soil OC, C/N ratios and mineral nitrogen (N) across sites, forest types and soil depths. The OC mineralization was measured under 25 °C and 60% field capacity.

of organic materials on the land surface and incorporation with soil particles in the topsoil. The variations in OC and N concentrations among the sites may have been due to the effect of climatic conditions on forest soils. The decreases in OC and N concentrations with MAT (Fig. 3b and d) were consistent with the regional distributional pattern of OC in Chinese forests (Yang et al., 2014) and with previous observations elsewhere (Amundson, 2001; Fissore et al., 2008; Homann et al., 2007; Jobbágy and Jackson, 2000). High MATs and MAPs are generally associated with high ecosystem productivity and therefore provide higher inputs of fresh organic materials to soils (Del Grosso et al., 2008; Knapp and Smith, 2001; Nemani et al., 2003; Reich et al., 2014). High MATs and MAPs, however, can also increase microbial decomposition and turnover rates and thus increase the loss of OC and N (Fissore et al., 2008; Hagerty et al., 2014; Schimel et al., 1994), which is consistent with the linear increase in C_m with MAT and MAP (Table 3), accounting for the response pattern of OC and N to climate determined in this study (Fig. 3).

In this study, soil OC and N concentrations were similar between the two types of forest, in contrast with our expectation that OC and N would be higher in soils from broadleaved forests compared to coniferous forests, as organic materials from broadleaved forests tend to be more degradable than those from coniferous forests (Gholz et al., 2000;

Table 3
Linear relationship (Y = a + b × X) of cumulative mineralized organic carbon (OC) (C_m) and the mineralization rate constant (k) of OC mineralization measured under standard temperature and soil moisture condition to soil OC concentration, C/N ratio, mineral nitrogen (Min-N), mean annual precipitation (MAP) and temperature (MAT) in control (CK) and nitrogen addition (N) treatments across soil depths, sites and forest types.

X	Y	N treatment	a	SE(a)	b	SE(b)	RMSE	R^2	*P*
OC	C_m	CK	35.94	1.50	−0.440	0.046	11.2	0.33	< 0.0001
		N	45.69	1.76	−0.620	0.055	12.4	0.42	< 0.0001
	k	CK	1.54	0.08	0.012	0.002	0.58	0.13	< 0.0001
		N	1.22	0.09	0.017	0.003	0.66	0.16	< 0.0001
C/N	C_m	CK	49.76	2.97	−2.148	0.238	11.4	0.30	< 0.0001
		N	57.10	3.74	−2.375	0.302	14.0	0.26	< 0.0001
	k	CK	1.49	0.16	0.032	0.013	0.60	0.03	0.0111
		N	1.45	0.19	0.019	0.015	0.71	0.01	0.2096
Min-N	C_m	CK	25.25	2.07	−0.058	0.084	13.6	0.00	0.4876
		N	34.09	2.56	−0.237	0.102	16.1	0.03	0.0221
	k	CK	1.60	0.09	0.013	0.004	0.60	0.06	0.0005
		N	1.49	0.11	0.008	0.004	0.71	0.02	0.0597
MAP	C_m	CK	15.27	2.04	0.007	0.002	12.9	0.11	< 0.0001
		N	19.67	2.49	0.008	0.002	15.6	0.09	< 0.0001
	k	CK	2.30	0.09	−0.0003	0.000	0.58	0.13	< 0.0001
		N	2.22	0.10	−0.0005	0.000	0.66	0.16	< 0.0001
MAT	C_m	CK	15.93	2.06	0.677	0.154	13.0	0.09	< 0.0001
		N	19.23	2.49	0.813	0.185	15.5	0.10	< 0.0001
	k	CK	2.21	0.09	−0.028	0.007	0.58	0.09	< 0.0001
		N	2.16	0.10	−0.042	0.008	0.68	0.13	< 0.0001

R^2 and RMSE are coefficients of determination and root mean square error of the overall model.

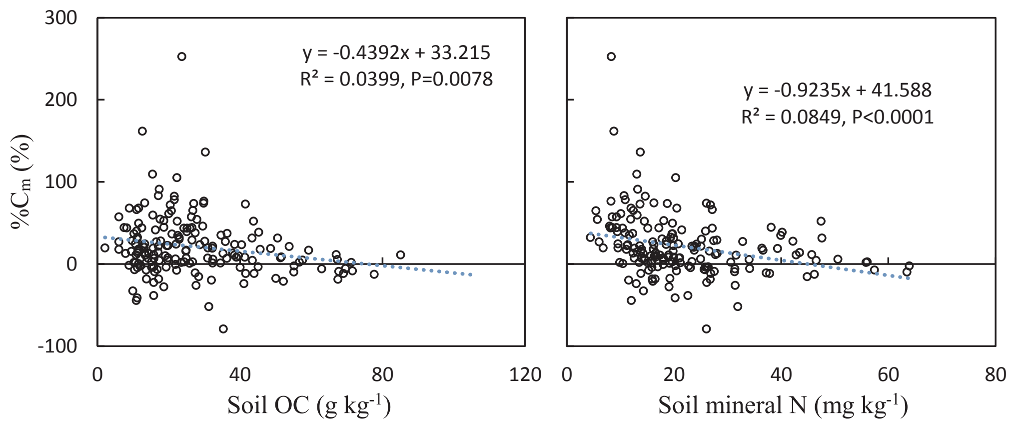

Fig. 7. Relationships of percent change of cumulative mineralized organic carbon (%C$_m$) after nitrogen (N) addition to soil organic carbon (OC) and mineral N concentrations across sites, forest types and soil depths. The value of %C$_m$ was calculated as the percent difference between N addition and control treatments. The OC mineralization was measured under 25 °C and 60% field capacity.

Shirato and Yokozawa, 2006; Silver and Miya, 2001). We ascribed the lack of a response of soil OC and N concentrations to forest types to the lignified roots and reduced exudates of the topsoil in the studied mature forests. An alternative explanation might be the high aggregation of soil particles in these mature forest soils. In this study, macroaggregates (> 0.25 mm) accounted for 72% and 67% of the total soil mass for the broadleaved and coniferous forests across all 11 sites (unpublished data), respectively, suggesting that aggregation of soil particles may have reached an equilibrium (when the proportions of each aggregate fraction do not change over time), at which point they may no longer be influenced by forest type. Broadleaved and coniferous forests may therefore have similar soil structures and thus provide similar protection to organic matter from microbial decomposition, accounting for the similarity of the OC and N concentrations between the two forest types but variation among the sites, as soil structure determines the accumulation and turnover of OC and N (Christensen, 2001; Six et al., 2000; Six and Paustian, 2014).

4.2. OC mineralization in forest soils along a climatic gradient

The variations in OC mineralization among the sites were likely a result of the differences in both the biodegradability of OC, determined by the quality and quantity of the substrates (Kemmitt et al., 2008; Marschner and Kalbitz, 2003; Tian et al., 2015), and soil mineralogy (Doetterl et al., 2015). Differences among the sites resulted in significant variations in the OC concentrations, C/N ratio, chemical composition, stoichiometry, and degradability of leaves and litter and therefore in the quantity and quality of the substrates for microbial decomposition in the soils. This explanation was supported by the decreases in C$_m$ of OC mineralization with soil OC and mineral N concentrations and C/N ratio (Fig. 6), while these metrics significantly varied by site (Table 2, Fig. 2). Variations in soil mineralogy among the sites determined the association of OC with soil minerals and thus their mineralization (Fissore et al., 2008; Doetterl et al., 2015).

The quality of substrates generally differs between the broadleaved and coniferous forests, as indicated by the different C/N ratios. The leaf litter and roots of the coniferous trees generally have higher C/N ratios (and lignin/N ratios) and more recalcitrant C components compared to the litter from broadleaved trees (Gholz et al., 2000; Shirato and Yokozawa, 2006; Silver and Miya, 2001). Because of their lower recalcitrance, soil organic matter derived from leaves, roots, and litter from broadleaved forests is hypothesized to be more apt to decompose than that of coniferous forests. In contrast to our expectation, however, the OC mineralization was similar between the two types of forest, possibly because of the similar quantity and quality of OC between them. This result was partly supported by the similar OC concentrations and C/N ratios between the broadleaved and coniferous forests (Table 2, Fig. 2). Alternatively, the highly and consistently aggregated soils in the broadleaved and coniferous forests might provide similar protection to soil organic matter, leading to similar OC mineralization between the forest types. We further observed that C$_m$ decreased with increasing soil OC concentration, indicating that the quality and proportional quantity of the substrates for microbial decomposition decreased with soil OC concentrations. This might occur because the higher OC promotes soil aggregation, which protects OC from microbial decomposition (Bronick and Lal, 2005; Paul et al., 2003).

In most biogeochemical models, forest type was differentiated because of significantly variations of quality and quantity of soil organic materials between broadleaved and coniferous trees (Mueller et al., 2012; Reich et al., 1997). Our results showed that concentrations of OC and N and the mineralization of OC measured under standard laboratory condition were not affected by forest type or the interaction between forest type and site. Therefore, averaged parameters across forest types could be used to assess or predict the distribution and dynamics of OC and N in mature forest soils, which would simplify the selection of parameters in modeling biogeochemical cycles of soil C at relatively large spatial scales.

4.3. Effects of N addition on OC mineralization

We demonstrated that N addition increased the C$_m$ but decreased the k of OC mineralization (Fig. 5), indicating that N addition enhanced OC mineralization. Our results were consistent with observations that N addition increased OC mineralization in forest soils because of a decrease in the soil C/N ratio and a shift in the ratio of bacterial to fungal biomass (Menyailo et al., 2014; Tu et al., 2013). Furthermore, the effects of N addition varied with site and soil depth, probably because of the variation in available N among sites and depths. In this study, mineral N was 90% higher at 0–10 cm soil depths compared to that at 10–20 cm soil depths across sites and forest types ($P < 0.0001$, Table 2). Furthermore, mineral N was relatively lower at Changsha and Huanglong compared to that at other sites, corresponding to the relatively greater increase in C$_m$ at these two sites. This explanation was further evidenced by our observation that the response of C$_m$ to N addition (%C$_m$) decreased with mineral N concentration in soils ($P < 0.0001$) (Fig. 7). Therefore, OC mineralization was limited by N availability and would be enhanced by additional N supply in these mature forest soils. It is important to note that the response to N added to soil prior to incubation provides a meaningful understanding of the mechanisms of response but should not be taken as representative of how an ecosystem would respond to N addition, as indirect effects via changes in tissue chemistry and plant composition are also important in the latter context.

4.4. Dependence of OC mineralization on climate

Climate influences soil mineralization mainly by directly affecting decomposition and indirectly affecting the quality of substrates (Doetterl et al., 2015; Fissore et al., 2008; Homann et al., 2007). Climate can directly affect soil OC mineralization by influencing microbial activity and the availability of a substrate to decomposers. Generally, higher MAP and MAT increase microbial activity (Manzoni et al., 2012; Schindlbacher et al., 2011) and the availability of soil OC (Billings and Ballantyne, 2013; Li et al., 2012), thus resulting in a higher mineralization of OC (Laudicina et al., 2015; Xu et al., 2006). These direct effects are supported by our observation that OC mineralization increased with MAT and MAP (Table 3), indicating a higher quality of OC and thus a lower stability at wetter or warmer sites. Ecosystem productivity, the input of organic material into soils and thus the turnover rates of these new inputs are higher at wetter or warmer sites (Del Grosso et al., 2008; Knapp and Smith, 2001; Nemani et al., 2003; Reich et al., 2014), resulting in higher proportions of labile or decomposable fractions of soil organic matter and higher C_m in the soils. This explanation is consistent with the decrease in soil C/N ratios with MAP or MAT found in our study ($P = 0.0192$ and 0.0005, respectively) and observed at a global scale by Xu et al. (2016) ($C/N = 16.92–0.34 \times MAT$, $P < 0.001$, $n = 130$), as the C/N ratios may be used as an index for predicting OC mineralization, representing higher decomposition rates at lower C/N ratios (Fig. 6) (Bragazza et al., 2006; Hu et al., 2001; Moorhead et al., 2012).

5. Conclusions

In this study, we examined the distribution of OC and N concentrations, and the mineralization of OC in forest soils along a climatic gradient. Our results showed that the concentrations of OC and N were similar between broadleaved and coniferous forests but significantly varied by site. The concentrations were higher at colder or drier sites and decreased with MAP and MAT. Similarly, the mineralization of soil OC was not affected by forest types but significantly varied by site, with C_m and k ranging from 14.1 to 37.9 $g\,kg^{-1}$ OC and 1.21×10^{-2} to 2.28×10^{-2} day^{-1} among the 11 sites, respectively. Nitrogen addition increased the cumulative mineralized OC (C_m) by 6–67%, and the effects varied with site and soil depth but were similar between broadleaved and coniferous forests. C_m decreased with increasing soil OC, C/N ratio and mineral N but increased with MAP and MAT, while k showed the opposite relationships with these metrics. The addition of N did not change the slopes of the relationships of C_m and k in topsoil with the C/N ratio and MAP and MAT; however, it strengthened the negative relationships of C_m with OC and mineral N. We therefore concluded that OC mineralization was limited by N availability in the studied mature forest soils, and the response of OC mineralization to N addition was independent of the climatic gradient.

In this study, we determined soil OC mineralization at a commonly used standard temperature (25 °C) and soil moisture (60% field capacity), which may have underestimated the results for soils from warmer sites but overestimated results for soils from colder sites. Given that we collected soils across a wide range of natural conditions, which greatly varied in terms of temperature and precipitation, linking the *in-situ* OC mineralization and potential mineralization rates under standard conditions merits further research to provide an accurate estimation of the C cycle in forested soils.

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