

Soil microbial respiration rate and temperature sensitivity along a north-south forest transect in eastern China: Patterns and influencing factors

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Abstract:

Soil organic matter is one of the most important carbon (C) pools in terrestrial ecosystems, and future warming from climate change will likely alter soil C storage via temperature effects on microbial respiration. In this study, we collected forest soils from eight locations along a 3700 km north-south transect in eastern China (NSTEC). For 8 weeks these soils were incubated under a periodically changing temperature range of 6–30°C while frequently measuring soil microbial respiration rate (R_s ; each sample about every 20 min). This experimental design allowed us to investigate R_s and the temperature sensitivity of R_s (Q_{10}) along the NSTEC. Both R_s at 20°C (R_{20}) and Q_{10} significantly increased (logarithmically) with increasing latitude along the NSTEC suggesting that the sensitivity of soil microbial respiration to changing temperatures is higher in forest soils from locations with lower temperature. Our findings from an incubation experiment provide support for the hypothesis that temperature sensitivity of soil microbial respiration increases with biochemical recalcitrance (C quality-temperature hypothesis) across forest soils on a large spatial scale. Furthermore, microbial properties primarily controlled the observed patterns of R_{20} , whereas both substrate and microbial properties collectively controlled the observed patterns of Q_{10} . These findings advance our understanding of the driving factors (microbial versus substrate properties) of R_{20} and Q_{10} as well as the general relationships between temperature sensitivity of soil microbial respiration and environmental factors.

Keywords: latitude | soil organic matter | decomposition | temperature sensitivity | carbon quality-temperature hypothesis

Article:

*****Note: Full text of article below**

RESEARCH ARTICLE

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Key Points:

- Temperature sensitivity increased logarithmically with increase in latitude
- Carbon quality-temperature hypothesis is applicable to forest soils on a large scale
- Periodic temperature incubation and continuous measurement offer a new protocol

Supporting Information:

- Supporting Information S1
- Figure S1
- Figure S2
- Figure S3

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Soil microbial respiration rate and temperature sensitivity along a north-south forest transect in eastern China: Patterns and influencing factors

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Abstract Soil organic matter is one of the most important carbon (C) pools in terrestrial ecosystems, and future warming from climate change will likely alter soil C storage via temperature effects on microbial respiration. In this study, we collected forest soils from eight locations along a 3700 km north-south transect in eastern China (NSTEC). For 8 weeks these soils were incubated under a periodically changing temperature range of 6–30°C while frequently measuring soil microbial respiration rate (R_s ; each sample about every 20 min). This experimental design allowed us to investigate R_s and the temperature sensitivity of R_s (Q_{10}) along the NSTEC. Both R_s at 20°C (R_{20}) and Q_{10} significantly increased (logarithmically) with increasing latitude along the NSTEC suggesting that the sensitivity of soil microbial respiration to changing temperatures is higher in forest soils from locations with lower temperature. Our findings from an incubation experiment provide support for the hypothesis that temperature sensitivity of soil microbial respiration increases with biochemical recalcitrance (C quality-temperature hypothesis) across forest soils on a large spatial scale. Furthermore, microbial properties primarily controlled the observed patterns of R_{20} , whereas both substrate and microbial properties collectively controlled the observed patterns of Q_{10} . These findings advance our understanding of the driving factors (microbial versus substrate properties) of R_{20} and Q_{10} as well as the general relationships between temperature sensitivity of soil microbial respiration and environmental factors.

1. Introduction

Temperature is one of the key factors that influence soil microbial respiration rate (R_s) [Davidson and Janssens, 2006; Fang and Moncrieff, 2001; Ise and Moorcroft, 2006], as such R_s is predicted to change in a warmer world. The temperature sensitivity of R_s (Q_{10}) is influenced by various factors, in particular, substrate and microbial community properties, and therefore varies across landscapes at both small and large spatial scales [Davidson and Janssens, 2006; Plante *et al.*, 2010]. Even slight changes in R_s in response to the predicted warmer world might affect the global patterns of soil organic carbon (SOC) storage, with consequential feedbacks on global warming trends [Jiang *et al.*, 2013; Shibata *et al.*, 2005]. Therefore, understanding the mechanisms underlying the global effects of temperature on R_s and the patterns of Q_{10} is imperative for predicting carbon sequestration in a warmer world.

Two types of soil factors regulate the response of soil organic matter (SOM) decomposition to temperature—microbial community and abiotic soil properties. Differences in microbial community structure as well as microbial biomass have been shown to influence soil microbial respiration [Malcolm *et al.*, 2008; Rousk *et al.*, 2012]. Moreover, multiple abiotic soil properties, such as oxidation reduction potential (ORP), electrical conductivity (COND), pH [Shen *et al.*, 2013], permeability, hydraulic conductivity [Gabriel and Kellman, 2014; Moyano *et al.*, 2013], and substrate for microbial metabolism [Blagodatskaya *et al.*, 2014b; Zhang *et al.*, 2013], might influence soil microbial respiration, as these soil properties regulate microbial activity. Although some studies have focused on these aspects, the dominant factors influencing soil microbial respiration at large spatial scales still remain unclear, particularly the relative contribution of soil microbes and soil substrate properties [Blagodatskaya *et al.*, 2014a; Briones *et al.*, 2014; Xu *et al.*, 2015].

Table 1. Information About the Eight Soil Sampling Sites Along the North-South Transect in Eastern China

Sampling Sites	Longitude (E)	Latitude (N)	MAT ^b (°C)	MAP (mm)	Vegetation Types	Dominant Species	Soil Type
HZ ^a	123°01'12"	51°46'48"	-3.67	472.96	Cold-temperate coniferous forest	<i>Larix gmelinii</i> Rupr, <i>Pinus sylvestris</i> L., <i>Betula platyphylla</i> Suk.	Grey forest soil
LS	128°53'51"	47°11'06"	0.01	648.34	Temperate conifer broadleaf mixed forest	<i>L. gmelinii</i> Rupr, <i>P. koraiensis</i> Siebold, <i>B. platyphylla</i> Suk.	Dark brown soil
CB	128°05'27"	42°24'16"	2.79	691.00	Temperate conifer broadleaf mixed forest	<i>L. gmelinii</i> Rupr, <i>P. koraiensis</i> Siebold, <i>Quercus Mongolica</i> Fisch.	Dark brown soil
DL	115°25'24"	39°57'27"	6.55	539.07	Warm temperate deciduous broad-leaved forest	<i>P. tabulaeformis</i> Carr, <i>Q. wutaishanica</i> Mayr, <i>L. principis-rupprechtii</i> Mayr	Brown soil
TY	112°04'39"	36°41'43"	5.98	644.38	Warm temperate deciduous broad-leaved forest	<i>Q. wutaishanica</i> Mayr, <i>P. tabulaeformis</i> Carr, <i>Populus davidiana</i> Dode.	Cinnamon soil
JL	114°26'28"	24°35'05"	18.22	1769.93	Subtropical evergreen broad-leaved forest	<i>S. superba</i> Gardn, <i>Castanopsis fabri</i> Hance, <i>C. carlesii</i> Hayata.	Red earth
DH	112°32'14"	23°10'25"	21.83	1927.00	South subtropical evergreen broad-leaved forest	<i>Schima. Superba</i> Gardn, <i>Cryptocarya. Chinensis</i> Hems!, <i>P. massoniana</i> Lamb.	Laterite
JF	108°51'26"	18°44'18"	23.15	2265.80	Tropical mountain rainforest	<i>Schoepfia. Jasminodora</i> Sieb, <i>Ficus. vasculosa</i> Wall, <i>Madhuca. Hainanensis</i> Chun.	Lateritic yellow earth

^aHZ, Huzhong; LS, Liangshui; CB, Changbai; DL, Dongling; TY, Taiyue; JL, Jiulian; DH, Dinghu; JF, Jianfeng.

^bMAT, mean annual temperature; MAP, mean annual precipitation.

In addition, the reasons for observed global patterns of Q_{10} , a representation of soil microbial respiration response to changing temperature [Davidson and Janssens, 2006], are also still debated. Two important hypotheses addressing the global patterns of Q_{10} have been developed in the past decades. First, Kirschbaum [1995] hypothesized that R_s is more sensitive to temperature in regions with historically low temperature climate than in regions with a high temperature climate (i.e., Q_{10} is stronger in low temperature regions compared to that in high temperature regions). Overall, large spatial scale experimental evidence for a latitudinal gradient is scarce, although support for this hypothesis has been obtained from incubation experiments [Conant et al., 2011; Kirschbaum, 1995] as well as small spatial scale regional studies performed using elevation gradients [Whitby and Michael, 2013]. Second, the carbon (C) quality-temperature (CQT) hypothesis [Bosatta and Ågren, 1999] predicts that R_s of low-quality substrates will have a stronger temperature dependency than high-quality substrates. R_s is regulated by microbial enzyme kinetics, and soil microbial respiration increases with a decrease in SOM quality. Differences in definitions and measurements of C quality in SOM [Li et al., 2015; Plante et al., 2010; Wagai et al., 2013] have resulted in inconsistent support for the CQT hypothesis, with studies finding that Q_{10} increases [Craine et al., 2010; Gershenson et al., 2009], has no relationship [Conen et al., 2006; Fang et al., 2005], or decreases with the carbon quality of the substrate [Liski et al., 1999; Sierra, 2012]. The discrepancies in these studies might possibly be a virtue of the different definitions of C quality by physical or chemical methods [Bosatta and Ågren, 1999; Plante et al., 2010; Wagai et al., 2013]. Min et al. [2014] and Sierra [2012] reported the temperature sensitivity of soil organic matter decomposition using the Arrhenius equation, which implied that a substrate of low quality requires high amounts of energy to be degraded, and its decomposition rate is slow. In other word, the decomposition rate was positively related to SOM quality, or the higher decomposition rate indicated higher qual-

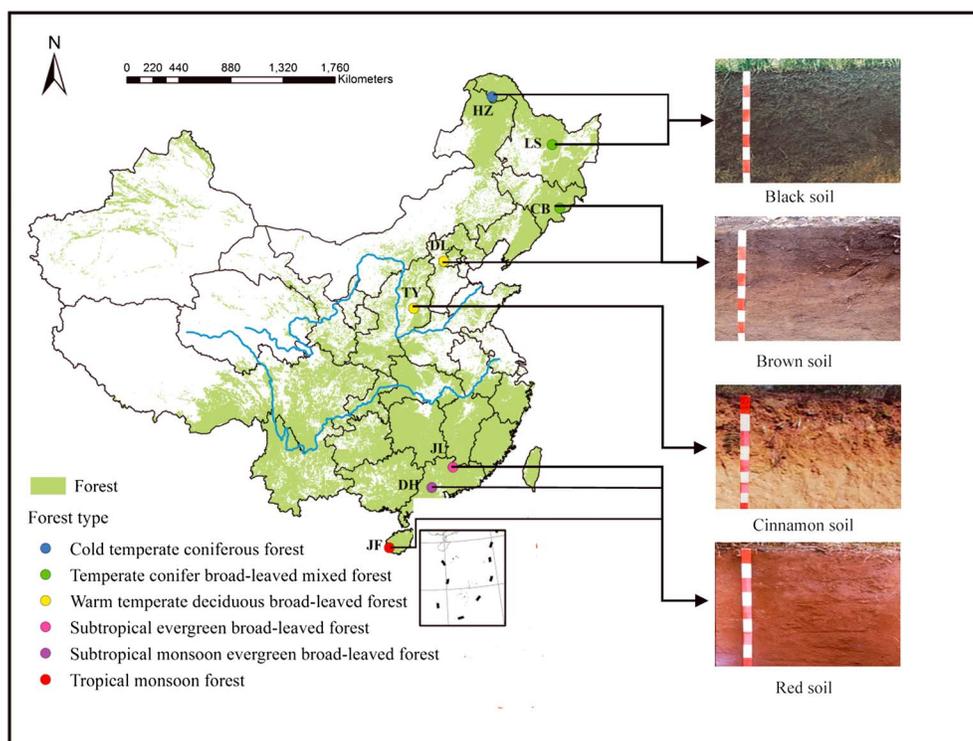


Figure 1. Site locations along the north-south transect of eastern China. The eight sites were located in forests which were typical representations of that forest type. HZ, Huzhong; LS, Liangshui; CB, Changbai; DL, Dongling; TY, Taiyue; JL, Jiulian; DH, Dinghu; JF, Jianfeng. The eight sampling sites were categorized as black soil (HZ and LS), brown soil (CB and DL), cinnamon soil (TY), and red soil (JL, DH, and JF) according to the genetic type of soils in China. The colored illustrations are inserted according to soil types in the right.

ity of substrate. Referring to the result of *Min et al.* [2014] and *Sierra* [2012], we assumed that SOM quality may be defined as the relative rate of R_s ($\mu\text{gCg}^{-1}\text{d}^{-1}$), which was the overall quality (availability and lability) of substrates that were catabolized by decomposer organisms at a given time; then, we may compare different research results without considering their different classifications of C quality. Therefore, a clear uniform definition of C quality is needed as a method to distinguish microbial accessible parts from bulk SOM and to assess the temperature effects on the decomposition of easily soluble C pools and microbial properties. In addition, further studies, especially at large spatial scales, are required to investigate both the related hypotheses.

The north-south transect of eastern China (NSTEC), which includes a range of forest types from tropical to cold temperate. There are big differences in mean annual precipitation, in soil C, N concentrations, in vegetation type and so on (Table 1 and Table S1 in the supporting information), and consequently associated magnitudes of elemental/resource fluxes. There must be huge differences in the magnitude of annual organic matter input and decomposition, which provides an optimal gradient for investigating the spatial patterns of R_s and Q_{10} and for studying the above hypotheses (higher Q_{10} in colder zones and CQT). In this study, we collected forest soils from eight locations along the NSTEC. By conducting an 8 week incubation experiment with periodically changing temperature, we investigated R_s and Q_{10} with two main objectives: (1) to determine the spatial patterns of R_s and Q_{10} across large spatial scales and provide incubation experiment for the two above mentioned hypotheses and (2) to explore the relative importance of microbial and abiotic soil properties on the spatial variation of R_s and Q_{10} .

2. Materials and Methods

2.1. Site Description

NSTEC ($108^{\circ}51'26''$ – $123^{\circ}01'12''\text{W}$, $18^{\circ}44'18''$ – $51^{\circ}46'48''\text{N}$) is a unique forest belt, along the thermal gradient spanning cold-temperate, temperate, subtropical, and tropical forests [*Zhang and Yang*, 1995]. Eight sampling

sites were established in typical forests along the NSTEC (Figure 1). The mean annual temperature at these sites ranged from -3.67°C to 23.15°C ; the mean annual precipitation ranged from 473.0 mm to 2265.8 mm (Table 1). Anthropogenic disturbances were reduced by establishing the sampling plots within well-protected national nature reserves in China at each site, where the vegetation is relatively homogenous and strongly representative of the given forest type. Besides, soil properties from the eight sites along the NSTEC were significantly different among each other (Table S1).

2.2. Field Sampling and Pretreatment

Field sampling was conducted between July and August 2013. Four experimental plots (30×40 m) were established in each forest site. Soil samples (0–10 cm depth) were collected from four randomly chosen locations in each plot and combined to form one composite sample per plot. Soil samples were sieved (2 mm diameter), and roots and visible organic debris were removed manually. For each plot, homogenized soil was divided into three subsamples for testing: (1) approximately 200 g of fresh soil frozen at -80°C to test basic soil microbial properties, (2) approximately 100 g air-dried soil to test soil biochemistry and physical properties, and (3) 5 kg fresh soil stored at 4°C for incubation experiments. Soil and microbial properties were measured to investigate how they influenced R_s or Q_{10} among the NSTEC.

In the laboratory, soil water content, soil water holding capacity (WHC, %), and other properties were measured. The contents of SOC and total nitrogen were measured using an elemental analyzer (Elementar Vario Max, Germany). Phospholipid fatty acid content was measured using the mild alkaline methyl esterification method and gas chromatography and mass spectrometry (Thermo ISQ TRACE GC system Ultra ISQ, Germany) [Xu *et al.*, 2015] (self-communicated data from Dr. Xu Zhiwei) (Tables 1 and S1). The details of measurement of soil pH, ORP, COND, dissolved organic C (DOC), and dissolved organic nitrogen (DON) could be seen in section 2.4.2.

2.3. Design of Incubation Experiment

2.3.1. Incubation With Periodically Changing Temperature

Most incubation experiments are conducted with a single constant incubation temperature [Fierer *et al.*, 2005; Gershenson *et al.*, 2009; Rousk *et al.*, 2012; Wagai *et al.*, 2013] or by placing different soil samples at different constant temperatures along a temperature gradient [Weedon *et al.*, 2013; Xu *et al.*, 2012], which had relative few data to calculate Q_{10} and might influence the accuracy of Q_{10} . In addition, soils incubated at an appropriate temperature might consume more substrate than at higher or lower temperatures. The disadvantages of traditional incubation experiments were overcome here by developing a new experimental design where soil samples were incubated under continuously and periodically changing temperature conditions from 6°C to 30°C (we assumed all soils would experience the temperature range 6 (in the cold middle night) to 30°C (in the hot afternoon) under future global warming scenarios) daily during the 56 days of incubation. Simultaneously, R_s and soil temperature were continuously measured under a model of varying temperature in 12 h according to the designated program (for details see Figures S1 and S2) [He *et al.*, 2013]. Measuring R_s more frequently at intervals of several minutes allows better exploration of the relationship between R_s and changing temperatures as well as a more accurate Q_{10} . Soil chemistry, microbial community, and substrate properties were measured by conducting destructive sampling at different incubation times in order to determine their influence on R_{20} and Q_{10} .

2.3.2. Incubation Experiment

For each treatment, 40 g of fresh soil and 10 g quartz sand were mixed together (preventing soil from caking), adjusted to 55% WHC, and placed in 150 mL polyethylene plastic bottle. Each forest soil had 15 replicates, 3 replicates for the repeated measurements of R_s throughout the incubation period and 12 replicates for four separate destructive sampling times to measure soil chemistry, microbial community, and substrate properties. In all, 120 incubation soil samples were used for the eight forest soils. All soil samples were first preincubated at 20°C for 1 week and then placed in an incubator with automatic temperature regulation. Considering the diurnal dynamics of air temperature and limit of the device, four incubation temperatures (6, 14, 22, and 30°C) were established, and each temperature was maintained for 6 h within a day (Figure S1). In order to maintain constant soil moisture levels, water loss was checked, and soil water content was adjusted on the basis of weight at intervals of 3–4 days. Repeated R_s measurements were conducted after 0, 7, 14, 21, 42, and 56 days of incubation. Soil substrate (DON and DOC), microbial (microbial biomass carbon (MBC), microbial biomass nitrogen (MBN)), and chemical properties (pH, ORP, and COND) were measured after 0, 14, 42, and 56 days of incubation.

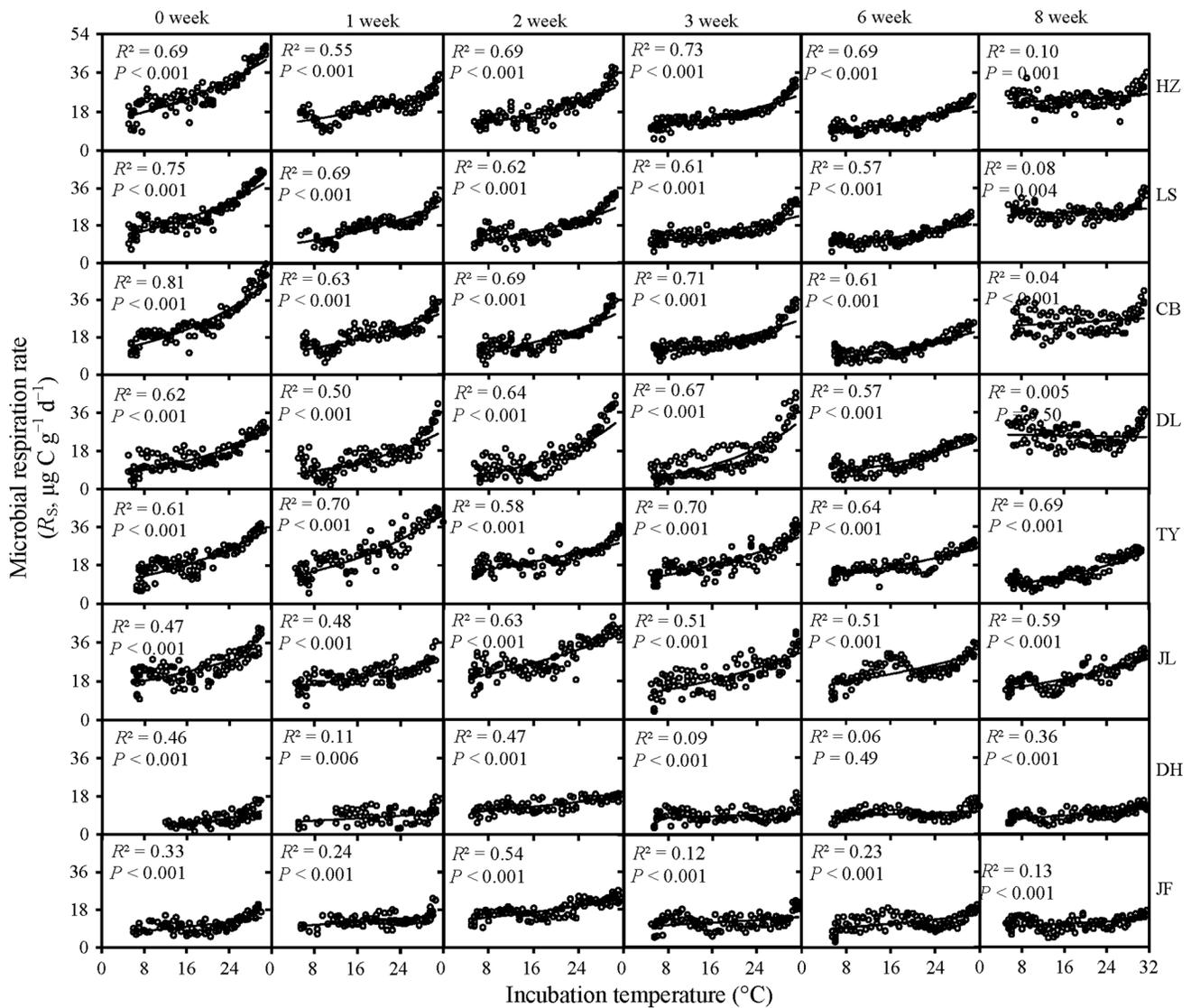


Figure 2. Changes in soil microbial respiration rate (R_s , $\mu\text{g C g}^{-1} \text{d}^{-1}$) with incubation temperature. HZ, Huzhong; LS, Liangshui; CB, Changbai; DL, Dongling; TY, Taiyue; JL, Jiulian; DH, Dinghu; JF, Jianfeng.

2.4. Measurements of R_s , Soil Microbial Content, and Chemical Properties

2.4.1. Measurements of R_s

Traditionally, scientists establish 3–6 specific temperature gradients to determine R_s and then calculate Q_{10} [Craine *et al.*, 2010; He *et al.*, 2013; Wang *et al.*, 2015; Wetterstedt *et al.*, 2010]. In this study, a continuous measurement apparatus was used to measure (at intervals of 20 min for each sample) the dynamics of R_s over 12 h at each incubation time point by using an automatic poikilothermia system and raising the temperature from 6 to 30°C at four incremental temperatures in this 12 h period; this method was modified from He *et al.* [2013] by involving an automatic temperature regulator (Julabo, Germany; Figure S2). Further, a button thermometer (DS1922L; DALLAS, USA) was used to measure the actual soil temperature while measuring R_s , providing accurate paired data for R_s and soil temperature to calculate Q_{10} .

R_s was first calculated from the slope of the CO_2 concentration and conversion factors as follows [He *et al.*, 2013]:

$$R_s = \frac{C \times V \times \alpha \times \beta}{m} \quad (1)$$

Table 2. Two-Way Analysis of Variance for the Changes in Soil Microbial Respiration Rate at 20°C (R_{20}), Temperature Sensitivity (Q_{10}), R^2 (The Goodness of the Fitted Exponential Equation to Depict the Sensitivity of Soil Microbial Respiration Rate to Changing Temperature) With Latitude and Incubation Time

Factors	R_{20}		Q_{10}		R^2	
	F	P	F	P	F	P
Latitude (L)	319.88	<0.001	184.77	<0.001	19.81	<0.001
Incubation time (T)	119.82	<0.001	186.27	<0.001	2.30	0.084
$L \times T$	50.71	<0.001	43.82	<0.001	1.64	0.045

where R_s is the soil microbial respiration rate ($\mu\text{gC g}^{-1} \text{h}^{-1}$); C is the slope of the change in CO_2 concentration; V is the volume of the incubation bottle and gas tube; m is the soil weight (g); α (12/44, from CO_2 to C) is the conversion coefficient for CO_2 mass; and β (3600, from second to hour) is a conversion coefficient for time. The value of R_s ($\mu\text{gC g}^{-1} \text{h}^{-1}$) was obtained using the conversion coefficient of α and β , since the original measurement from the equipment was CO_2 concentration.

Changes in R_s with temperature were well fit by exponential models (Figure 2); therefore, the Q_{10} values were calculated using the following exponential equations [Lloyd and Taylor, 1994]:

$$R_s = A \times e^{b \times T} \quad (2)$$

$$Q_{10} = e^{10 \times b} \quad (3)$$

where R_s is the microbial respiration rate ($\mu\text{gC g}^{-1} \text{d}^{-1}$), T is temperature ($^{\circ}\text{C}$), and A and b are the exponential parameters that describe the intercept and slope of the line, respectively.

All CO_2 concentration values which were used to calculate R_s and Q_{10} were collected under experimental rising temperature. Besides, we calculated R_{20} by fitting exponential equations at 20°C.

Min *et al.* [2014] and Sierra [2012] theoretically and empirically reported the temperature sensitivity of organic matter decomposition in the Arrhenius equation, which implied that a substrate of low quality requires high amounts of energy to be degraded, and its rate of decomposition is slow. That is, the decomposition rate was positively proportional to SOM quality; the higher decomposition rate indicated higher quality of substrate. So in this study, SOM quality was defined as the relative rate of R_s . In other words, the C quality of soil microbial respiration was equal to A ($\mu\text{gC g}^{-1} \text{d}^{-1}$) in equation (2), which was the y intercept of the first-order exponential equation relating decomposition rate to temperature, i.e., the overall quality (availability and lability) of substrates that were catabolized by decomposer organisms at a given time. Other studies have described substrate C quality in a similar manner [Bosatta and Ågren, 1999; Fierer *et al.*, 2005; Xu *et al.*, 2012].

2.4.2. Measurements of Soil Microbial Biomass and Chemical Properties

Soil substrate, microbial community, and chemical properties (DON, DOC, microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), pH, ORP, and COND) were measured at 0, 14, 42, and 56 days after incubation. The chloroform-fumigation method was used to estimate the MBN ($(Kn = 1.85)$) [Brookes *et al.*, 1985], and the extractable N of nonfumigated samples was treated as soil DON. A modified fumigation-extraction method was used to measure soil MBC ($(Kc = 2.22)$) [Baumann *et al.*, 1996] and DOC. In detail, both the fumigation and nonfumigation soil samples were extracted with 50 mL K_2SO_4 solution and shaken simultaneously for 1 h. After shaking, the suspensions were allowed to settle for 10 min, and the supernatants were filtered through a membrane having a pore size of 0.45 μm . The supernatants of C and N were measured using a total organic carbon (TOC) instrument (liquid TOC II; USA) and continuous flow analyzer (Futura, France), respectively. Furthermore, the samples for pH, ORP, and COND were extracted with 25 mL ultrapure water (slurry of soil and ultrapure water, 1:2.5) and shaken simultaneously for 1 h. After shaking, the suspensions were allowed to settle for 10 min, and the supernatants were poured into two slots of "Ultrameter II" (Myron L Company, USA) to measure pH, ORP, and COND (Tables S1 and S2).

2.5. Statistical Analysis

Two-way analysis of variance (ANOVA) was used to analyze the differences in R_{20} , Q_{10} , R^2 (the goodness of the fitted exponential equation to the experimental data, which was calculated sensitivity of R_s to temperature) among different forest soil samples and incubation times. The correlations between R_{20} , Q_{10} , microbial,

Table 3. Correlations Between Soil Microbial Respiration Rate at 20°C (R_{20}) and Temperature Sensitivity (Q_{10}) Related to Soil Substrate, Microbial, and Chemical Properties

Properties	R_{20}		Q_{10}		
	R^2	P	R^2	P	
Substrate	DOC ^a	0.16	<0.05	0.06	0.19
	DON	0.02	0.71	0.12	0.18
Microbe	MBC	0.03	0.33	0.005	0.71
	MBC/DOC	0.04	0.53	0.01	0.57
	MBN	0.51	<0.001	0.08	0.13
	MBN/DON	0.02	0.46	0.16	<0.05
Chemistry	pH	0.22	<0.05	0.39	<0.01
	ORP	0.11	0.59	0.28	0.01
	COND	0.24	<0.01	0.07	0.34

^aDOC, MBC, DON, MBN, ORP, and COND are abbreviations for soil organic carbon, microbial biomass carbon, dissolved organic nitrogen, microbial biomass nitrogen, oxidation reduction potential, and conductivity, respectively.

substrate, and chemical properties were analyzed using regression analysis. Structural equation modeling (SEM) was used to explicitly evaluate the causal relationships among multiple interacting variables and to determine the relative roles of microbial, substrate, and chemical properties in influencing R_{20} and Q_{10} . The SEM was conducted using the procedure of Amos 17 for Windows. Statistical analysis was conducted using SPSS 18.0 for Windows (SPSS Inc., Chicago, IL, USA). The significance level was set at $P=0.05$ level.

3. Results

3.1. Changes in R_{20} Along the Transect

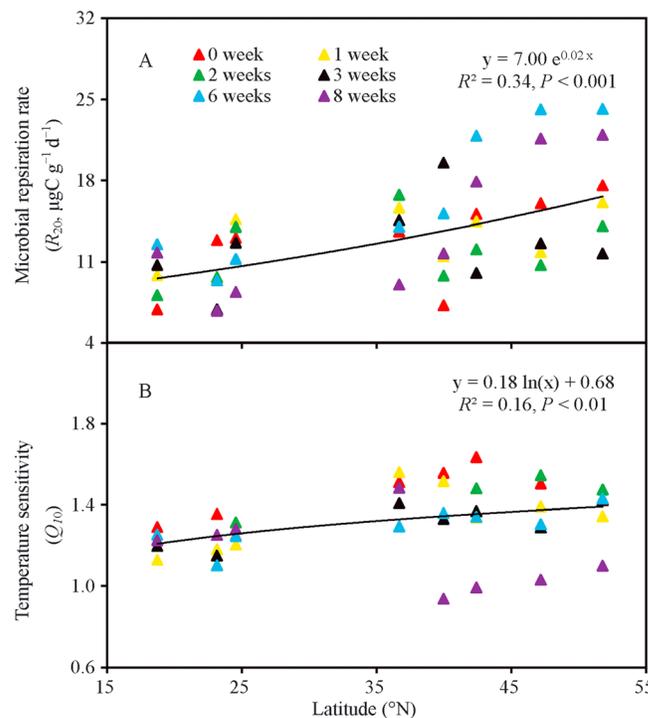


Figure 3. Changes in soil (a) microbial respiration rates at 20°C (R_{20} , $\mu\text{gC g}^{-1} \text{d}^{-1}$) and (b) temperature sensitivity (Q_{10}) of six-time incubations with latitude. Six different colors represents six different incubation times. The regression curve was used to depict the relationship between mean R_{20} or Q_{10} and latitude irrespective of incubation time.

Temperature significantly influenced R_s , with the relationship being well depicted by exponential equations (Figure 2). At the same time, when compared the R^2 estimates from Figure 2 by one-way ANOVA, we found no significant difference among incubation times (Table 2). Forest type and incubation time had a significant impact on R_{20} ($P < 0.001$ for forest type; $P < 0.001$ for incubation time), with a significant interaction ($P < 0.001$; Table 3). R_{20} increased logarithmically with increase in latitudes ($R^2 = 0.34$, $P < 0.001$; Figure 3a). Furthermore, the observed R_{20} significantly decreased with forest type in the following order: temperate forest ($15.08 \mu\text{gC g}^{-1} \text{d}^{-1}$) > subtropical forest ($10.76 \mu\text{gC g}^{-1} \text{d}^{-1}$) > tropical forest ($9.97 \mu\text{gC g}^{-1} \text{d}^{-1}$). R_{20} differed significantly among different soil types, in the following order: black soil > cinnamon soil > brown soil > red soil (data not shown). When R_{20} was calculated based on MBC, R_{20} ($\mu\text{g g}_{\text{MBC}}^{-1} \text{d}^{-1}$) also significantly increased with latitude (Figure S3).

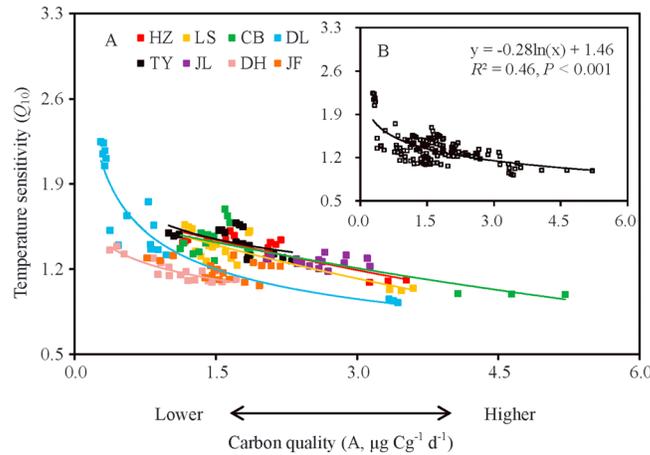


Figure 4. Relationship between temperature sensitivity (Q_{10}) and carbon quality (A). (a) The different sampling locations with each point being a different incubation time. And just significant fitted curve was displayed. (b) All the data of Q_{10} and carbon quality without regard for sampling locations.

was significant in higher latitudes and weakened with increasing latitudes except the sample site DH (Figure 4a). Without considering sample sites, Q_{10} (across incubation times) was significantly negatively correlated with A ($R^2 = 0.46, P < 0.001$; Figure 4b).

3.3. Dominant Factors Affecting R_{20} and Q_{10}

Regression analysis revealed that R_{20} was significantly correlated with MBN ($P < 0.001$), DOC ($P < 0.05$), COND ($P < 0.01$), and pH ($P < 0.05$; Table 3). However, when all the factors were classified into microbial characteristics, soil chemical properties, and substrate properties by using SEM, all three factors could explain 47% variation of R_{20} (Figure 5a); the decisive factors were microbial characteristics ($R = 0.46, R$: correlation coefficient, when a correlation coefficient is positive this indicates a positive relationship between R_{20} or Q_{10})

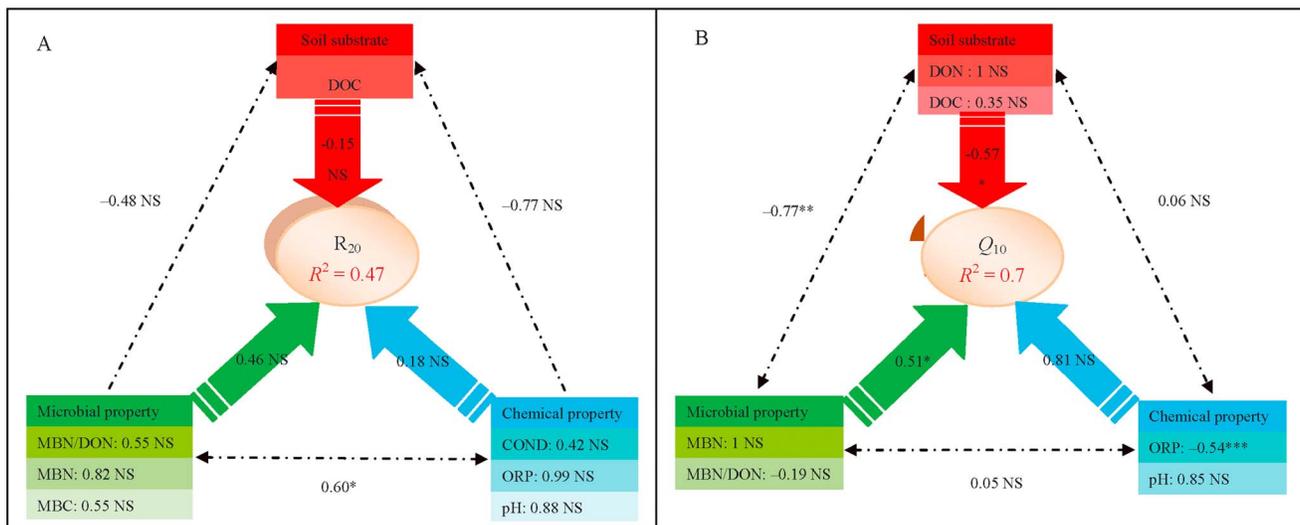


Figure 5. The effects of substrate, microbial, and chemical properties on (a) soil microbial respiration rate (R_{20}) and (b) temperature sensitivity (Q_{10}) were estimated using structural equation models. NS represents no significant difference; *, **, and *** represent significant differences at $P < 0.05, P < 0.01,$ and $P < 0.001,$ respectively. DOC, dissolved organic carbon; DON, dissolved organic nitrogen; MBN/DON, ratio of microbial biomass nitrogen to dissolved organic nitrogen; MBN, microbial biomass nitrogen; MBC, microbial biomass carbon; COND, electrical conductivity; ORP, oxidation-reduction potential.

and an environmental factor, e.g., substrate property, microbial property, chemistry property. When a correlation coefficient is negative this indicates a negative relationship between the two), soil chemical properties ($R=0.18$), and substrate properties ($R=-0.15$). Similar to R_{20} , Q_{10} values were significantly correlated with MBN/DON ($P < 0.05$), ORP ($P = 0.01$), and pH ($P < 0.01$; Table 3). The three factors could explain 70% variation of Q_{10} (Figure 5b) and primarily driven by substrate ($R = -0.57$, $P = 0.039$) and microbial ($R = -0.51$, $P = 0.049$) properties.

4. Discussion

4.1. Q_{10} Increased in Forest Soils With Increasing Latitude

The Q_{10} values increased logarithmically with increasing latitude, and the maximum and minimum Q_{10} values were observed in the temperate and tropical zones, respectively. The significant positive correlation between Q_{10} and latitude suggests that the temperature sensitivity of soil microbial respiration might decline under continued global warming; further, the temperature sensitivity of soil microbial respiration is greater in cold, high-latitude ecosystems than in warm, temperate areas, supporting previous findings [Peng et al., 2009; Piao et al., 2003]. It was important to speculate a temperature dependence of microbial carbon use efficiency, which implied that microbial carbon use efficiency decreased with increasing temperature, although we did not measure the data of microbial growth rates, exudation rates or their carbon use efficiency. A theoretical framework [Gillooly et al., 2001] and an empirical data [Tucker et al., 2013] have been developed to explain the temperature dependence of microbial carbon use efficiency although the temperature dependence is not always measurable [Dijkstra et al., 2011]. Hagerty et al. [2014], using metabolic tracer probing to determine microbial growth efficiency, found that microbial turnover accelerates with warming and determines the response of microbial respiration to temperature change as the principles of enzyme kinetics. Some studies provided some plausible explanations for the increasing Q_{10} with decreasing temperature. For example, Wang et al. [2013] conducted an incubation experiment along the elevation gradient in the Wuyi Mountains, China, and showed that Q_{10} linearly increased with elevation. Based on China FLUX data and Q_{10} data in public literatures, Zheng et al. [2009] found that ecosystems in colder regions have potentially relatively higher Q_{10} values. Other studies also provided experimental evidences for the similar results [German et al., 2011; Gershenson et al., 2009; Wang et al., 2013; Whitby and Michael, 2013; Xu et al., 2013]. Taken together, these findings suggest that soils from low native temperatures have a greater potential to release C in response to climate warming.

In this study, Q_{10} values ranged from 1.2 to 1.6 for the NSTEMC soils under periodic incubation temperatures. These values are slightly lower on average than those previously reported (e.g., Hopkins et al. [2012] $Q_{10} = 1.5-1.9$ and $Q_{10} = 2.9-3.1$ for two different North American temperate forests; Zimmermann and Bird [2012] $Q_{10} = 1.43-1.58$ for short-term incubation and $Q_{10} = 2.02-2.21$ for long-term (1 year) incubation). This difference may owe to the different incubation temperature conditions. As mentioned above, most incubation experiments have been conducted at a constant incubation temperature. Zhu and Cheng [2011], who incubated two soils (a farm soil and grassland soil) under two temperature regimes (constant versus diurnally varying), found that Q_{10} values under constant temperature regime were consistently and significantly higher than those under diurnally varying temperature regime. The varying temperature regime should be paid certain attention when compared Q_{10} from different researches.

4.2. CQT Hypothesis in Forest Soils at a Large Spatial Scale

The Q_{10} values showed significant negative correlation with C quality in forest soils; this provided experimental support for the CQT hypothesis. Xu et al. [2012], who incubated samples with changing temperature (low-high-low at $\pm 5^{\circ}\text{C}$), also found that soils with lower C quality had higher Q_{10} , as have others [Hartley and Ineson, 2008; Liski et al., 1999]. In this study, greater variation of C quality (A) with prolonged incubation time was found at higher latitude than at lower latitude. Briones et al. [2014] used ^{14}C isotope technology and found higher Q_{10} values than those reported here in boreal forests possibly due to the positive controlling effects of substrate availability on Q_{10} in long-term incubation experiments. Additionally, this difference might be due to the lower C quality in the soils used in this study before incubation as well as the shorter preincubation time, leading to poor initial soil condition in this study. With the prolongation of incubation, the formation rates of labile SOM exceeded the soil microbial respiration rate. While our findings as well as those of many others support the CQT hypothesis, many studies also show contradictory

evidence (e.g., *Lefevre et al.* [2014] used bare fallow soils with different treatments and found that the Q_{10} values were higher in soils with stable C than in those with labile C). Because of the large amount of contradictory findings, the CQT hypothesis still requires further testing. As proposed by *Wagai et al.* [2013], some issues for better understanding the CQT hypothesis need to be addressed in the future by (1) providing a better definition of "C quality" based on the actual molecular structure of organic compounds in soil; (2) distinguishing the active or microbial accessible fraction from bulk SOM; and (3) simultaneously assessing the temperature effect on easily soluble C pools and microbial biomass C in addition to microbial respiration.

4.3. Soil Microbial Properties Control R_{20}

Microbial communities play a more important role in soil microbial respiration than the substrate and soil chemical properties, even though R_{20} was significantly correlated with DOC, COND, and pH. Some studies have shown that factors such as chemical properties (e.g., pH and ORP) and substrate properties (e.g., SOC and DON) affect R_{20} mainly by regulating microbial activity or community structure [*Boberg et al.*, 2014; *Bradford et al.*, 2008; *Entry*, 2000; *Shen et al.*, 2013; *Wei et al.*, 2014]. Further, significant relationships were found between microbial community properties and soil properties (DOC, DON, COND, ORP, and pH). Thus, we conclude that DOC, DON, COND, ORP, and pH have no direct effects on R_{20} but primarily impact R_{20} by regulating microbial properties. In addition, the tendency of C:N to decrease with latitude along the NESTC could partly explain why R_{20} increased logarithmically with latitude. *Leifeld and von Lutzow* [2014] found that, with declining C:N ratios, respiration rates increased. N may be a limiting factor for soil microbial metabolism (or microbial physiology) since organic soils have a wide range of C:N; however, C:N is inherently intertwined with soil pH, making it difficult to separate their effects. *Min et al.* [2014] used a controlled experiment with different pH treatments and found that pH can induce differential effects on reaction rates and temperature sensitivity of organic C and N liberation, leading to changes in the relative availabilities of C and N for microbial assimilation. Moreover, *Sinsabaugh et al.* [2008] showed that soil pH is strongly related to the recalcitrant fractions of SOM, an observation not seen in this study possibly because labile SOM was considerably higher at the preliminary stage of incubation.

4.4. Substrates and Microbial Content Collectively Control Q_{10}

Substrate (DOC and DON) and microbial properties (MBN and MBN/DON) were both important for explaining the variation of Q_{10} along the NESTC transect. Other studies have also reported that increased substrate availability has a significant positive effect on Q_{10} , and this effect is inversely proportional to the original substrate availability [*Davidson and Janssens*, 2006; *Gershenson et al.*, 2009; *He et al.*, 2013; *Zhou et al.*, 2013]. Changes in microbial community structure and quantity exert important impacts on Q_{10} ; however, adaptation in the high-temperature region might be responsible for the lower sensitivity to temperature and declining effects on Q_{10} [*Malcolm et al.*, 2008; *Rousk et al.*, 2012; *Wei et al.*, 2014]. *Hagerty et al.* [2014] used metabolic tracer probing to determine microbial growth efficiency and found that microbial turnover accelerates with warming and determines the response of microbial respiration to temperature change to some extent. Changes in the availability of C and N in SOM might affect the microbial resource strategies, which in turn might influence the response of soil microbial respiration to temperature [*Weedon et al.*, 2013; *Zhou et al.*, 2013]. In this study, the result that MBN plays a more important role in Q_{10} might be attributed to the lower ratio of soil C:N (approximately 10–20) along the transect.

Kinetic theory and empirical studies have predicted that soils from cooler climates might be more sensitive to projected warming with a bigger increase in decomposition rates than those seen in soils from warmer climates [*Davidson and Janssens*, 2006]. Similarly, we found that both R_{20} and Q_{10} increased with latitude. Therefore, our findings gave an experiment support that soils from cooler zones might decompose faster than soils from warmer zones under projected warming because microbes from the warmer zone might already be acclimated to the warm climate.

5. Conclusions

The new experimental design for incubation experiments presented in this study combines periodic changing incubation temperature with continuous measurement eliminating microbial community adaptation to a specific temperature. This method might improve our ability to more accurately explore the response

of soil microbial respiration to temperature in the future. In addition, the results of this study showed that temperature sensitivity of soil microbial respiration differed significantly among different forest soils and increased logarithmically with increasing latitude, providing experimental support for the hypothesis that the sensitivity of soil microbial respiration to temperature is higher at lower temperatures, which indirectly implied that the carbon use efficiency decreased with increasing temperature. Further, these findings also provide experimental support for the CQT hypothesis; low-quality C has greater sensitivity to temperature. In addition, according to the SEM analysis, the controlling factors (microbial versus substrate properties) were found to be different for the spatial patterns of R_{20} and Q_{10} ; the spatial patterns of R_{20} were mainly controlled by microbial properties, and the spatial patterns of Q_{10} were collectively controlled by microbial and substrate properties. Soil microbial respiration is being altered by global climate change, and the response of SOM decomposition to changes in temperature might be more sensitive in the cold-temperate zone than in the tropical zone. These findings advance our understanding of the driving factors (microbial versus substrate properties) of R_{20} and Q_{10} .

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