Soil Biology and Biochemistry 121 (2018) 35–42

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

The optimum temperature of soil microbial respiration: Patterns and controls

Yuan Liu[a,b], Nianpeng He[a,b,c,*], Xuefa Wen[a,b], Li Xu[a], Xiaomin Sun[a,b], Guirui Yu[a,b], Liyin Liang[d], Louis A. Schipper[d]

[a] Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China
[b] College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100049, China
[c] Institute of Grassland Science, Northeast Normal University and Key Laboratory of Vegetation Ecology, Ministry of Education, Changchun 130024, China
[d] School of Science, University of Waikato, Private Bag 3105, Hamilton, New Zealand

ARTICLE INFO

Keywords:
Soil respiration
Optimum temperature
Adaption
Substrate
Microbe
Forest

ABSTRACT

The temperature response of soil microbial respiration (R_h) is of significance, with the optimum temperature of R_h being the key parameter for accurately modeling how it responds to temperature change under climate warming scenarios. However, knowledge about T_{opt} in natural ecosystems remains limited, especially at large scales, which increases the uncertainty of climate projections. Here, we collected 25 soils from tropical to cold-temperate forests in the northern hemisphere to quantify regional variation in T_{opt} and the controls underlying this variation. R_h was measured at high frequency using a novel system under the mode, with temperature gradually increasing from 5 to 50 °C. The results showed that T_{opt} ranged from 38.5 to 46.0 °C (mean: 42.4 °C). Of note, this study is the first to demonstrate that T_{opt} is far higher than the assumed value used in models (35 °C), varying greatly across different climatic zones and increasing with latitude from tropical to cold-temperate forest soils. To some extent, our results supported the substrate supply hypothesis, and contrast with the climate adaption hypothesis. In addition, climate, nutrient, and soil microorganisms jointly regulate regional variation in T_{opt}, together explaining 53% of variation in T_{opt}. The higher T_{opt} in northern regions indicated that these regions have a greater potential to release more CO_2 from soil, which might lead to a positive feedback to global warming. In conclusion, process-based models should incorporate the high variability of T_{opt} across regions to improve predictions of the carbon dynamics of terrestrial ecosystems under climate warming scenarios.

1. Introduction

The temperature response of soil microbial respiration (R_h) is of broad concern and is a major source of uncertainty in climate projections (Friedlingstein et al., 2006; Kirschbaum, 1995, 2006). In the past several decades, most studies have focused on the temperature response of R_h within normal temperature ranges (e.g., under 35 °C), generally finding an exponential increase of R_h to increasing temperature (Hamdi et al., 2013; Kirschbaum, 2010; Llord and Taylor, 1994). Few studies have tried to explore the response of R_h above 35 °C (Richardson et al., 2012). In general, the optimum temperature of R_h (T_{opt}) is defined as the temperature at which the maximum rate of R_h occurs, based on enzyme catalyzed biochemical reactions (Fig. 1) (Daniel and Danson, 2010). Yet, T_{opt} might change with differences in soil substrate availability or soil enzyme activity (Richardson et al., 2012; Schipper et al., 2014). As a physiological parameter, T_{opt} might reflect the long-term adaption of the soil microbial community to the climate and environment (Rinnan et al., 2009). T_{opt} is also a key parameter for modeling the temperature response of R_h to climate warming (Ise and Moorcroft, 2006; Parton et al., 1987).

Theoretically, there should be a T_{opt} threshold at which a biochemical reaction reaches a maximum rate over a wide temperature range (Fang and Moncrieff, 2001). T_{opt} might depend on the climate regime due to the physiological adaption of soil microbes to specific habitats. The climate adaption hypothesis states that climate-oriented acclimation or adaption of soil microbes determines the temperature response of R_h (Koepf, 1953); thus, T_{opt} should be positively correlated with external temperature. From an evolutionary perspective, natural selection should generate an adaptive fit of enzyme kinetics to their thermal environment (Allison et al., 2010; Bradford, 2013). Therefore, soil microbes that survive in warmer environments have a higher T_{opt} than those that survive in cooler environments (Angilletta, 2009;

* Corresponding author. Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China.
E-mail address: henp@igsnrr.ac.cn (N. He).

https://doi.org/10.1016/j.soilbio.2018.02.019
Received 10 November 2017; Received in revised form 22 February 2018; Accepted 24 February 2018

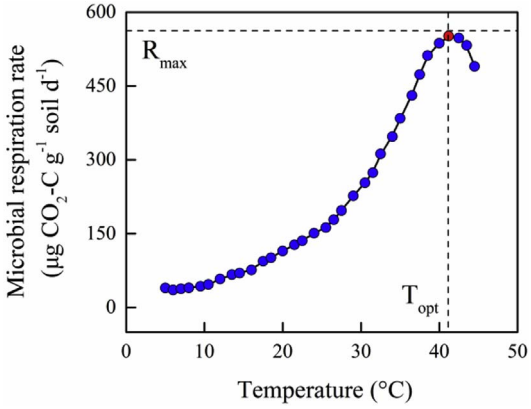

Fig. 1. An example of the temperature response curve for soil microbial respiration rate (R_h) from Shennon (SN) site. The optimum temperature of R_h (T_{opt}) was defined as the temperature at which the maximum rate of soil respiration (R_{max}) occurred (red point). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Richardson et al., 2012). In contrast, other studies have shown that substrate availability, to a large extent, directly influenced the temperature response of R_h (Agren and Wetterstedt, 2007; Fissore et al., 2013). At lower substrate supply, limited enzyme activity results in apparent insensitivity to warming, while the diffusion rate of substrate to microbes might limit the maximum rate of R_h at optimum temperatures (Fissore et al., 2013). Consequently, the substrate supply hypothesis assumes that T_{opt} is the greatest in soils with richer SOM, because SOM content is a proxy of substrate availability, to some extent (Richardson et al., 2012).

A few studies conducted at single sites have recorded distinct T_{opt} through measuring soil respiration rates. For example, Parker et al. (1983) observed a T_{opt} near 41 °C in desert soil in New Mexico (USA). Balser and Firestone (2005) reported a T_{opt} of approximately 30 °C for the Taiga and temperate ecosystems, and 37 °C for the tropical ecosystems. In addition, along a semi-arid elevation gradient, Richardson et al. (2012) found that T_{opt} consistently exceeds 35 °C at all sampling sites. Previous studies have shown that T_{opt} varies among different soils and regions; however, because it is difficult to obtain information about T_{opt} at large scales, most of the models, such as CENTURY (Ise and Moorcroft, 2006; Parton et al., 1987), tend to set the T_{opt} as a unique value (35 °C) when simulating the temperature-response of soil respiration. Therefore, it is important to delineate the regional variation in T_{opt}, along with the factors that regulate this variation, to reduce the uncertainty of model predictions.

Traditionally, due to the limitation in the method of measurement, it has been difficult to acquire T_{opt} due to limited measurements of R_h. In practice, soils were usually incubated at several constant temperatures (often 3–6 constant temperatures), and T_{opt} was derived from the temperature response curve of R_h, which reduces the comparability of different studies. Consequently, it remains unclear how T_{opt} varies among different ecosystems, along with the underlying controls that drive it at large scales. This information gap impedes our understanding of the carbon cycle in terrestrial ecosystems and its response to climate warming.

In this study, we selected 25 forest soils along a thermal gradient in the northern hemisphere to investigate regional variation in T_{opt} and its influencing factors. In the laboratory, soils were incubated from 5 to 50 °C, and R_h was measured at high frequency using a novel measuring system to improve T_{opt} estimates. Our main objectives were to (1) explore regional variation in T_{opt} among different ecosystems and regions, and (2) investigate the underlying controls of T_{opt} at a large scale (climate adaption hypothesis *vs.* substrate supply hypothesis). Our results are expected to provide new insights on how to improve the optimization of T_{opt} in climate change models.

2. Materials and methods

2.1. Study area and sampling of soils

The study area encompassed different forest ecosystems along a thermal gradient spanning cold-temperate, mid-temperate, warm-temperate, subtropical, and tropical forests from north to south in eastern China (108° 51′ 26″–123° 01′ 12″ W, 8° 44′ 18″–51° 46′ 48″ N) (Liu et al., 2017). These forests provide an ideal natural laboratory to explore the pattern and underlying controls of T_{opt} (climate adaption assumption *vs.* substrate supply assumption), as the climate, soil types and microbial properties vary greatly among different ecosystems (Tables S1–S3). In practice, 25 typical forests were selected, where mean annual temperature (MAT) and mean annual precipitation (MAP) ranged from −5.36–23.15 °C and 473.0–2265.8 mm, respectively. The vegetation covered five major forest types in the northern hemisphere, which were designated as evergreen broadleaf forests, deciduous broadleaf forests, broadleaf and needleleaf mixed forests, evergreen needleleaf forests, and deciduous needleleaf forests (He et al., 2018; Zhao et al., 2016).

During the summers (July and August) of 2013 and 2015, we collected soils from 25 forests (Fig. 2). At each site, we randomly established four plots (30 m × 40 m). After removing the surface litter, we collected 30–40 topsoil samples (0–10 cm) in each plot by using a 5-cm-diameter soil auger. Soil samples were then combined as a composite sample in each plot to reduce soil heterogeneity. To examine the substrate supply hypothesis from a vertical gradient, in addition to the latitudinal gradient, we also collected the corresponding subsoil (10–30 cm) from three sites [Mohe (MH), Liangshui (LS), and Huinan (HN)]. All soil samples were sieved (2 mm diameter), with roots and visible organic debris being removed manually. These homogenized samples were divided into two subsamples. One subsample was maintained at −20 °C until the start of the incubation experiment and microbial measurements. Another subsample was air-dried and processed to measure physical and chemical properties.

2.2. Laboratory incubation and determination of the microbial respiration rate

For each site, the homogenized soil subsample kept at −20 °C (30 g, dry weight) was placed in 150 mL polyethylene plastic bottles, and adjusted to 60% of water holding capacity (WHC) by adding deionized water (four replicates for each site). All sample bottles were sealed with preservative films, into which several small holes were punched for ventilation. Then, the bottles were pre-incubated at 25 °C for 7 days, to avoid any pulse effect on microbial activities (Liu et al., 2017). Water loss in these bottles was measured and corrected for weight at intervals of 2–3 days. After pre-incubation, all samples were placed in a varying temperature incubator (JYL-253, Jiayu, Shanghai, China), in which incubation temperature gradually increasing from 5 to 50 °C for the first 12 h, and then gradually decreasing from 50 °C to 5 °C over the second 12 h, allowing soil microbes to adapt to the varying temperature.

After one-day of adaption, the soil microbial respiration rate (R_h) was measured under the varying temperature (5–50 °C) with an automatic sampling and analysis system (Liu et al., 2017). The Automatic Temperature Control Soil Flux System (LI-7100; Pre-Eco, Beijing, China) was a new system, the design of which was modified from He et al. (2013). This system enabled us to increase the incubation temperature step-by-step over a given time (Julabo, Seelbach, Ortenau, Germany), in parallel with measuring the R_h rate at a high frequency. In brief, soil samples were placed in a 16-hole electric water bath controlled by an automatic temperature regulator, which was connected to a Li-COR CO_2 analyzer (Li-7100, LI-COR, Lincoln, NE, USA) that records CO_2 concentration every second. During measurements, the temperature of the water bath was gradually increased from 5 to 50 °C within 12 h, and the R_h of each sample was synchronously calculated over 75 s.

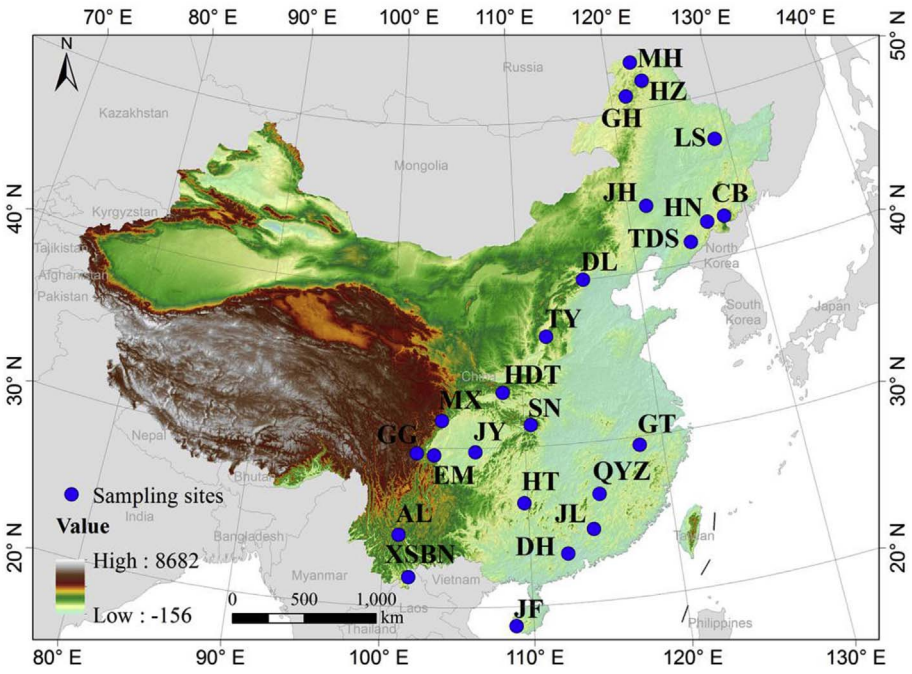

Fig. 2. Spatial distribution of the sampling sites across different forest types in eastern China. Mohe (MH), Huzhong (HZ), Genhe (GH), Liangshui (LS), Jiaohe (JH), Changbai Mountain (CB), Huinan (HN), Tudingzi Mountain (TDS), Dongling Mountain (DL), Huoditang (HDT), Taiyue Mountain (TY), Maoxian (MX), Shennonjia (SN), Jinyun Mountain (JY), Gongga Mountain (GG), Ermei Mountain (EM), Gutian Mountain (GT), Qianyanzhou (QYZ), Jiulian Mountain (JL), Huitong (HT), Ailao Mountain (AL), Dinghu Mountain (DH), Xishuangbanna (XSBN), Jianfenglin (JF).

During measurements, each sample bottle was sealed with preservative films to prevent water loss. Soil water loss was less than 3% WHC during the measurements. Overall, each soil sample was measured 37 times over the 12 h measuring period. In parallel, soil temperature in each incubation bottle was synchronously monitored every minute with a button thermometer (DS, 1922L; Maxim Integrated, Dallas, TX, USA) (Liu et al., 2017), and the actual soil temperature was used in this study. R_h was calculated from the slope of CO_2 concentration and specific transformation factors using Eqn. (1):

$$R_h = \frac{C \times V \times \alpha \times \beta}{22.4 \times m} \quad (1)$$

where R_h is the rate of soil microbial respiration (μg CO_2-C g^{-1} soil day^{-1}); C is the slope of CO_2 concentration; V is the volume of the incubation bottle and gas tube; m is soil dry weight; α is the relative atomic mass of C; β is the transformation coefficient of time; and 22.4 is the standard gas volume (L mol^{-1}).

The optimum temperature of R_h (T_{opt}) was defined as the temperature at which R_h reached a maximum rate. When the temperature was higher than this point, R_h tended to decline (Fig. 1) (Daniel et al., 2008; Richardson et al., 2012).

2.3. Soil and microbial analyses

Soil pH, soil oxidation–reduction potential (ORP), and soil electrical conductivity (EC) of air-dried soils in a 1:2.5 (v/v) soil/water ratio were measured using an Ultrameter-2 pH meter (Myron L. Company, Carlsbad, CA, USA). Soil texture was measured using a particle analyzer (Mastersizer, 2000, Malvern, Worcestershire, England) after removing organic matter and carbonates by using 30% hydrogen peroxide and 30% hydrochloric acid, respectively. Soil total nitrogen (TN) concentrations were measured using an elemental analyzer (Vario EL III, Elementar, Germany). SOC was analyzed using the H_2SO_4–$K_2Cr_2O_7$ oxidation method (Nelson and Sommers, 1982).

Soil subsamples kept at −20 °C were used to measure the soil microbial composition, which was characterized by using phospholipid fatty acid (PLFA) analysis, following the method described by Bååth and Anderson (2003) to obtain fungal, bacterial, and actinomycete content (Frostegård et al., 1993). In practice, we used the number and abundance of all fatty acids to calculate fatty acid diversity (Simpson index, SIDI), which was defined as:

$$SIDI = 1 - \sum_{i=1}^{N} p_i \times lnp_i \quad (2)$$

where N is the number of fatty acids, and p_i is the proportional abundance of the *i*th type (Balser and Firestone, 2005).

2.4. Climate data

Mean annual temperature (MAT), maximum annual temperature (CT_{max}), minimum annual temperature (CT_{min}), climate temperate variation (CT_{var}, defined as the difference between CT_{max} and CT_{min}), and mean annual precipitation (MAP) were obtained from long-term monitoring data (1951–2010) recorded by 722 meteorological stations throughout China (http://cdc.cma.gov.cn). These data were first interpolated using kriging methods applied to latitude, longitude, and altitude. Then, the MAT, CT_{max}, CT_{min}, CT_{var}, and MAP values for each site were extracted using the tool "Extract Multi Values to Points" in ArcMap software, based on the corresponding latitude and longitude (Wen and He, 2016).

2.5. Statistical analyses

Before the analyses, variables that did not meet the assumption of parametric statistical tests (normality and homoscedasticity of errors) were log-transformed. Data normality was tested with a Shapiro–Wilk test. Differences in T_{opt} between the topsoil and subsoil, and among different climatic regions were tested with independent-samples T-test ($P < 0.05$). Regression analysis was used to examine the latitudinal pattern of T_{opt}. Correlation analyses were conducted to examine how T_{opt} was correlated with climate, soil physio-chemical, and microbial properties.

We further built a structural equation model (SEM) to evaluate the direct and indirect factors regulating T_{opt}, and to evaluate how these factors contribute to the standardized total effect (direct effect plus indirect effect). Predicted causal relationships between variables were based on prior knowledge of how soil and climate properties affect T_{opt}. Because the variables of climate, soil nutrients, and soil environment groups were closely correlated, a principal components analysis (PCA)

was performed to create a multivariate index representing each group (Wang et al., 2017). Within each group, only variables that were significantly correlated with T_{opt} were included in the PCA. The first principal components (PC1), which explained 56–87% of the total variance for each group, was subsequently used in the SEM analysis. In the SEM analysis, the data were fitted to the model using the maximum likelihood estimation method. The adequacy of the model was determined by the χ^2 -test, goodness of fit (GIF) index, and root mean squared error of approximation (RMSEA) index. Favorable model fits were suggested by no significant difference when using the χ^2-test ($P > 0.05$), high GIF (> 0.9), and low RMSEA (< 0.08) (Liu et al., 2017). The SEM analysis was conducted using Amos 21.0 (Amos Development Corporation, Chicago, IL). The figures for variable correlation and ternary graphics were produced with OriginPro 9.0 (OriginLab Corporation, Massachusetts, USA). All other statistical analyses were conducted in SPSS 13.0 (SPSS, Chicago, IL, USA).

3. Results

3.1. Changes of optimum temperature (T_{opt}) from site to region to biome

Through continuously measuring soil microbial respiration rates (R_h) with increasing temperature from 5 to 50 °C, we observed that all soils showed a clear temperature-response curve of R_h (Fig. S1), and the optimum temperature of R_h (T_{opt}) was clearly defined. The values of T_{opt} in the 25 forest soils ranged from 38.5 to 46.0 °C (mean: 42.4 °C) (Fig. S2). T_{opt} was significantly different among different soils ($P < 0.05$). Interestingly, T_{opt} exhibited a significantly positive latitudinal pattern (Fig. 3a), which was significantly higher in cold-temperate regions compared with tropical regions (Fig. 3b). Furthermore, our results showed that the values of T_{opt} were all significantly higher in the topsoil compared to the subsoil in three additional boreal forest soils (Fig. S3).

3.2. Linking variation of T_{opt} to climate, soil, and microbial properties

The values of T_{opt} were correlated with climate variables (MAT, MAP, CT_{var}, and CT_{min}), soil nutrients (SOC and TN), soil environmental parameters (pH, ORP), and soil microbial properties (total, fungal, actinomycete, and bacterial PLFAs), as well as the diversity of PLFAs (Table S4). Specifically, T_{opt} was significantly negatively correlated with MAT, MAP, and CT_{min} (Fig. 4abd), while significantly positively correlated with CT_{var} (Fig. 4c). Both of the assessed soil nutrients (SOC and TN) were positively correlated with T_{opt} (Fig. S4 ab). In comparison, soil environmental variables exhibited opposing effects on T_{opt}, with pH having a positive effect, while ORP had a negative effect (Fig. S4 cd). In addition, T_{opt} was positively correlated with three main PLFA components (fungi, bacteria, and actinomycetes) and total PLFAs (Fig. S5).

3.3. Contribution of climate and soil properties on T_{opt} at a large scale

SEM analysis showed that climate, soil nutrients, and soil microbial properties had direct effects on T_{opt}, while the soil environment exerted indirect effects. Together, these variables explained 53% of the variance in T_{opt} (Fig. 5a). Specifically, both climate (including MAT, MAP, CT_{var}, and CT_{min}) and soil nutrients (SOC and TN) had direct negative effects on T_{opt}, whereas soil microbial properties had direct positive effects on T_{opt}. Taking the direct and indirect effects together, climate and soil microbial properties were the two most important predictors shaping regional variation in T_{opt} (Fig. 5b). Furthermore, the ternary graph indicated that soils with abundant substrate supply, low climate history, and higher soil microorganisms should have higher T_{opt} (Fig. 6).

4. Discussion

4.1. Variation in T_{opt} at different scales

Within 5–50 °C, the soil microbial respiration rate (R_h) of all 25 forest soils first increased and then decreased, gradually, with temperature increasing when the optimum temperature was exceeded (T_{opt}, Fig. S1). This decline in R_h rate above T_{opt} has been previously attributed to the fact that higher temperatures make proteins overly flexible, reducing substrate affinity by disrupting the active site and, ultimately, leading to the denaturation of critical enzymes (Balser and Wixon, 2009; Knies and Kingsolver, 2010). However, enzyme denaturation is not an appropriate explanation in soil systems because enzyme denaturation generally occurs at temperatures that are higher than those commonly observed in soils. For example, a typical enzyme from *Bacillus subtilis* has an unfolding (denaturation) temperature of 59 °C (Daniel et al., 2007). Besides, the optimum temperature of the enzyme related to carbon decomposition (e.g., α-glucosidase and β-glucosidase) even reaches 70 °C (Daniel et al., 2007). Recently, a new theory proposed by Hobbs et al. (2013) called the macromolecular rate theory (MMRT) provided a reasonable explanation for this observed decline in R_h, to some extent. This theory suggest that the decline of R_h should be a consequence of changes in the heat capacity ($\Delta CP^{\ddagger}$) of the enzyme without needing to invoke enzyme denaturation at modest temperatures. Furthermore, several laboratory experimental studies demonstrated that MMRT fits the response of soil respiration to changing temperature well (Robinson et al., 2017; Schipper et al., 2014).

In this study, T_{opt} varied significantly among different ecosystems, ranging from 38.5 to 46.0 °C, with an average of 42.4 °C, which was far higher than the assumed value used in models (35 °C) (Ise and Moorcroft, 2006). Supporting previous studies, the T_{opt} in our study differed among different climate regions (Balser and Wixon, 2009;

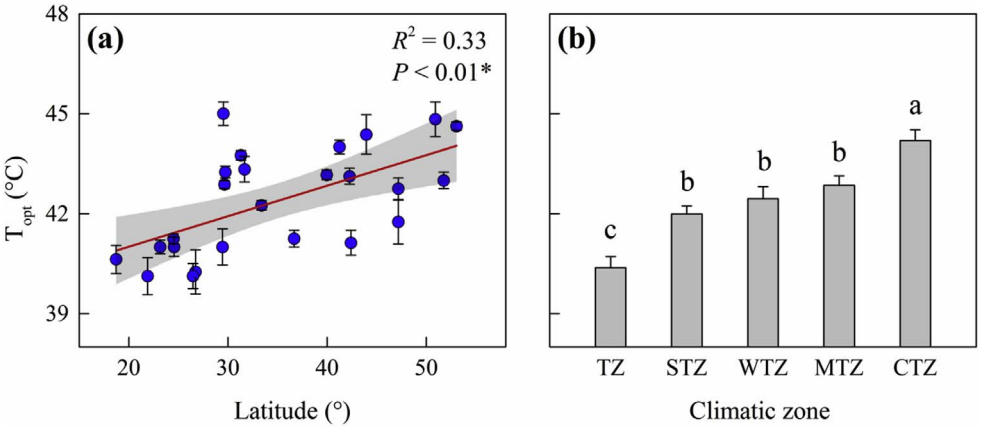

Fig. 3. Latitudinal patterns of the optimum temperature of soil microbial respiration (T_{opt}) (a) and their variation among different climatic zones (b). Shaded areas indicate the 95% confidence interval and vertical bars denote SE. TZ, tropical forests; STZ, sub-tropical forests; WTZ, warm-temperate forests; MTZ, mid-temperate forests; CTZ, cold-temperate forests.

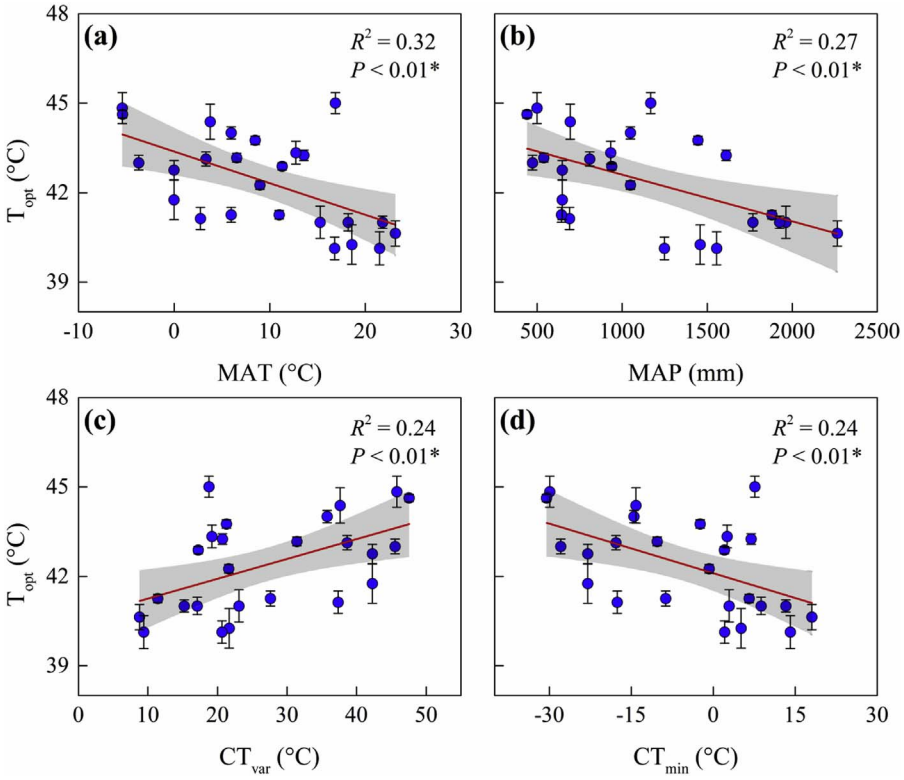

Fig. 4. Correlations between the optimum temperature of soil microbial respiration (T_{opt}) and climate factors (including MAT, MAP, CT_{var}, and CT_{min}). The red lines are fitted using linear regression. Shaded areas indicate the 95% confidence interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

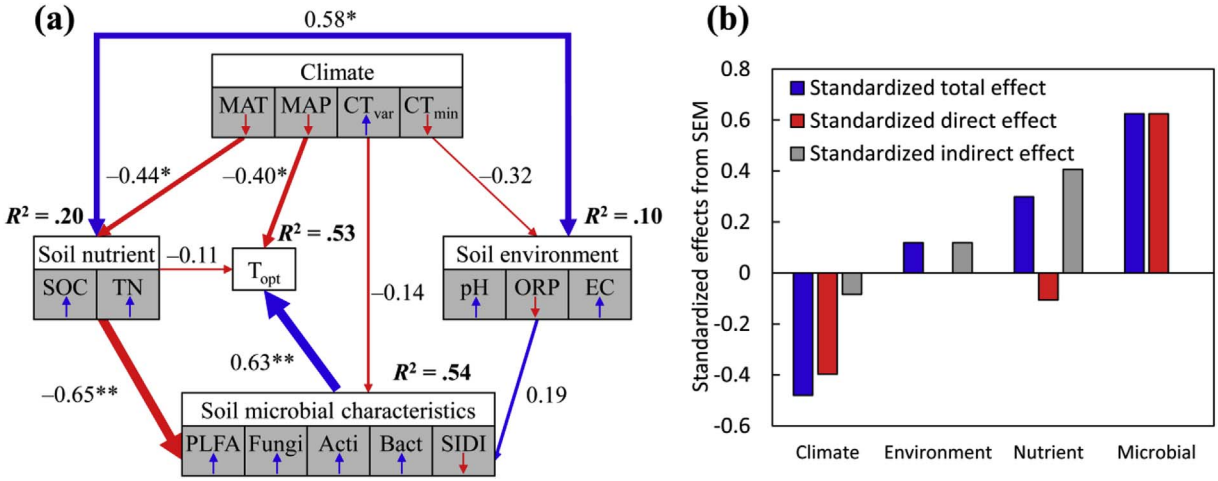

Fig. 5. Structure equation modeling exploring the direct and indirect effects of soil microbial respiration (T_{opt}) on optimum temperature in forest soils. In panel (a), the double-headed arrows represent covariance between related variables; single-headed arrows indicate the hypothesized direction of causation; blue and red arrows indicate positive and negative relationships, respectively. Arrow width is proportional to the strength of the relationship. Double-layer rectangles represent the first component from the PCA conducted for soil nutrient, climate, soil environment, and soil microbial characteristics. The blue "↑" and red "↓" symbols indicate a positive or negative relationship between the variables and T_{opt}, respectively. The numbers adjacent to the arrows are standardized path coefficients. The proportion of variance explained (R^2) appears alongside each response variable in the model. Goodness-of-fit statistics for the model are: $\chi^2 = 0.12$, $P = 0.73$, GFI = 0.998, RMSEA < 0.001, AIC = 28.12, BIC = 42.744. *$p < 0.05$, **$p < 0.01$. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Richardson et al., 2012), soil types (Pietikainen et al., 2005; Šantruckova et al., 2003), and ecosystem types (Šantruckova et al., 2003). Furthermore, the T_{opt} data reported here were comparable to other results of a laboratory study in California, where T_{opt} ranged from 42.3 to 44.8 °C along a semi-arid elevation gradient (Richardson et al., 2012). Previous studies of diverse soils showed that the T_{opt} of soil respiration is often above ambient temperatures (Balser and Wixon, 2009; Richardson et al., 2012), exceeding 40 °C (Parker et al., 1983; Pietikainen et al., 2005). In addition, Holland et al. (2000) did not detect a maximum respiration rate, even at 55 °C. In general, when combing our results with those from previous studies, we found that T_{opt} exhibits great regional variation among different climate regions and ecosystems.

4.2. *T_{opt} significantly increases with increasing latitude*

Our results showed that T_{opt} increased linearly with increasing latitude, and was higher in cold-temperate ecosystems compared with tropical ecosystems. This study is the first to report the increasing latitudinal patterns of T_{opt}; consequently, it was not possible to verify or compare our results directly with previous studies, because these studies were mainly conducted at different sites and with different

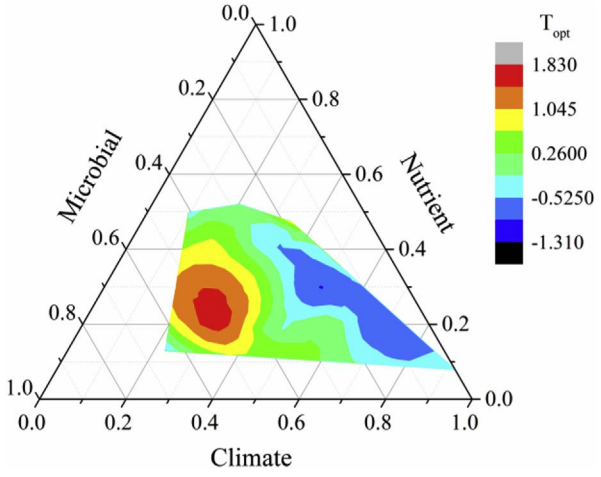

Fig. 6. Ternary graph showing the influence of climate, microbial, and nutrients on the optimum temperature of soil microbial respiration (T_{opt}).

methods. This latitudinal increase in T_{opt} might be attributed to differences in climate and soil chemical and microbial properties along the latitudinal gradient (Table S4). First, T_{opt} was negatively correlated with MAT, contrasting with the climate adaption hypothesis, which suggests that the adaption of soil microbes to ambient temperature cannot explain the latitudinal increase in T_{opt} (Koepf, 1953; Richardson et al., 2012). The temperature response of microbes is influenced by multiple factors, such as initial temperature, moisture, and substrate availability (Angilletta, 2009; Davidson and Janssens, 2006; Rousk and Baath, 2011). At low temperature conditions, soil microbial enzymes are dominated by temperature. Thus, when the limitation of enzymes is gradually removed with increasing temperature, other factors like moisture content or substrate concentration might become dominant. Under such conditions, soil microbes probably adjust, which masks the effect of temperature. In contrast to MAT, T_{opt} was positively correlated with CT_{var} (variation in temperature). Thus, T_{opt} might occur at a temperature that far exceeds MAT. However, the highest temperature over a given year might be the most important in determining T_{opt} (Table S4). For example, Fenner et al. (2005) reported that the thermal optimum of many carbon-cycling processes shifts seasonally and coincides with the highest ambient soil temperature, suggesting that microbial community is adapted to the prevailing external temperature. If the temperature is higher than T_{opt}, even for a short period, dominant soil microbes might be replaced by others with higher T_{opt} (Barcenas-Moreno et al., 2009; Rousk and Baath, 2011). Thus, higher CT_{var} at higher latitudes might be favorable for soil microbes with higher T_{opt}, which is significantly greater than the ambient temperature.

T_{opt} was positively correlated with SOM content, supporting the substrate supply hypothesis, which indicates that T_{opt} is correlated with substrate concentration (Richardson et al., 2012). Substrate availability is an important factor controlling the temperature response of R_h (Erhagen et al., 2015; Fissore et al., 2013; Gershenson et al., 2009). Agren and Wetterstedt (2007) proposed three different mechanisms to explain the temperature response of SOM decomposition: (a) the rate at which decomposers take up substrate at their surface; (b) the rate at which substrate diffuses up to the surface of the decomposer; and (c) the rate at which substrate is made available to the environment. At low substrate concentrations, the diffusion rate of the soil substrate to microbes might limit the maximum rate at optimal temperatures, which might result from the physical and physiological adjustment of the microbial community (Cheng et al., 1996). In this study, soil substrate availability increased significantly with increasing latitude (Table S4), which might explain the higher T_{opt} at higher latitudes (Richardson et al., 2012). Furthermore, the T_{opt} of the topsoil was significantly higher than that of the subsoil (Fig. S3), supporting the substrate supply hypothesis, to some extent (Fig. 7), which suggested that soils with the greatest substrate availability have the greatest T_{opt}.

Soil microbes were the dominant factors controlling spatial variation in T_{opt}, whereas the soil environment (pH, ORP, and EC) directly influenced T_{opt} through regulating soil microbial composition (Fig. 5, Table S4). Because soil microbes are responsible for the decomposition reaction, the abundance of microbes in soil reflected the extent to

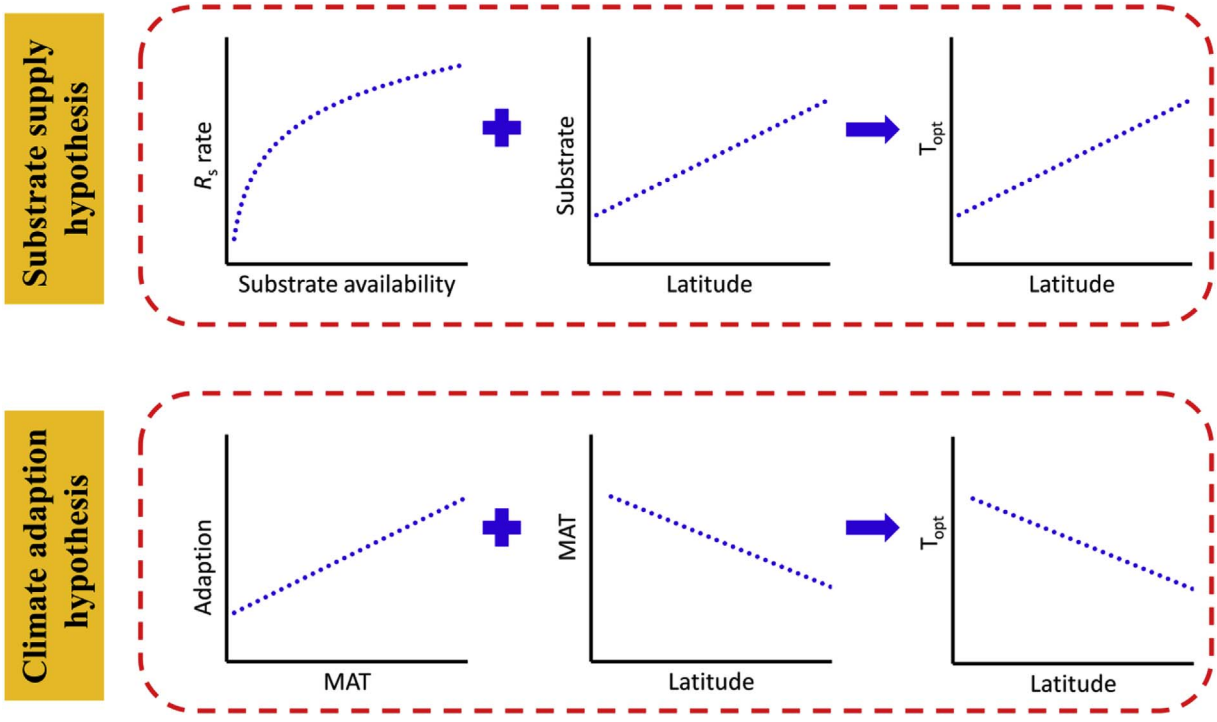

Fig. 7. Conceptual frame of substrate supply hypothesis and climate adaption hypothesis that regulate regional variation in the optimum temperature of soil microbial respiration (T_{opt}) in forests at a large scale. MAT, mean annual temperature.

which they have adapted to the environment. When the soil substrate did not influence temperature response, soils containing a greater abundant microbes would be more responsible for this response, resulting in higher T_{opt}. Furthermore, any soil that contains a diverse microbial species is likely to contain species that are adapted to slightly different temperature ranges and, hence, specific T_{opt}. Therefore, soils with abundant microbes are likely to adapt the local environment, due to the presence of diverse microbes and the function of isoenzymes (Schipper et al., 2014). Soil environmental factors, such as soil pH, ORP, and EC, are important in altering the activity and structure of the microbial community, directly influencing T_{opt}. Higher soil pH is generally favorable for bacteria growth, but limits the growth of fungal communities (Rousk and Baath, 2011). Some studies have shown that, compared to fungi, bacteria have a higher optimal temperature (Barcenas-Moreno et al., 2009; Ley and Schmidt, 2002; Pietikainen et al., 2005). Therefore, we inferred that increased pH leads to a higher T_{opt} by indirectly altering microbial community composition at a large scale. ORP is the result of a redox reaction of oxides, characterizing the relative strength of oxidation and reduction, and is an important indicator for regulating soil biochemical processes (Ascar et al., 2008). Therefore, changes in ORP and EC might alter soil microbial composition and activity, and indirectly influences the spatial patterns of T_{opt} (Ascar et al., 2008; Li et al., 2017).

4.3. Implications of T_{opt} and its relevance to model predications

T_{opt} in high latitude ecosystems (cold-temperature forests) reached temperatures as high as 46 °C, and was significantly higher than the ambient temperature of these systems (including maximum temperature). Thus, soils in higher latitude regions might have a greater potential to release more CO_2 under global warming scenarios (Fig. 7). This suggestion is possible, when considering that these high latitude regions will experience scenarios with greater warming amplitude than other regions (IPCC, 2013). The higher T_{opt} combined with a higher warming expectation might accelerate the release of CO_2, leading to a positive feedback to global warming. Due to the large stock of the C pool and high average temperature, soils in low latitude/tropical region are more likely to be affected by increasing temperature. First, tropical region store more than 315×10^{15} g C, which is equal to 23% of global soil C (Jenkinson et al., 1991). Consequently, even small changes of soil respiration in response to increasing temperature will cause a significant feedback to global warming. Second, soil surface temperature is predicted to increase by about 1.4 °C–5.8 °C in the twenty-first century (IPCC, 2013). Soil temperature in tropical regions frequently exceeds 35 °C (Richardson et al., 2012), and with the soil temperature of many warm drylands and forests reaching 40 °C due to land use change. These values are marginally close to the lower limit of T_{opt} observed in this study. Thus, soil respiration in these regions might decline and adapt to climate warming after temperature exceeds T_{opt}, generating a negative feedback to climate warming.

As a physiological index of the soil microbial community, T_{opt} might reflect the long-term adaption of microbes to the local climate and environment (Rinnan et al., 2009), which is a key parameter in modeling the temperature response of R_h to climate warming (Ise and Moorcroft, 2006; Parton et al., 1987). In this study, we observed increasing latitudinal patterns of T_{opt}, and found that T_{opt} differed among different ecosystems and climatic regions. These findings provided new insights towards optimizing models in the future. To date, most of the models using T_{opt} have simply set it as a unique value as 35 °C, to simulate the temperature-response of soil respiration (Ise and Moorcroft, 2006; Parton et al., 1987). Our findings provide actual values for T_{opt} under different conditions (Tuomi et al., 2008), which could help to reduce the uncertainty in current climate projections.

5. Conclusions

To sum up, this study is the first to focus on the temperature response of R_h from 5 to 50 °C at a large scale. In addition, this study demonstrates the spatial patterns of T_{opt} and the controls that underlie this variation. The greater variation of T_{opt} (from 38.5 °C to 46.0 °C) at the site, regional, and biome scales suggests it is not appropriate to use a unique value of T_{opt} in many process-based models of soil carbon dynamics. Thus, our findings provide baseline values to optimize T_{opt} in different environments and ecosystems. Our findings support the substrate supply hypothesis, which suggests that soils with abundant substrate should have higher T_{opt}. The greater regional variation of T_{opt} was mainly explained by climate, soil microbes, and their interactions with the soil environment. The latitudinal pattern of T_{opt} reflected the trade-off of microbes between abundant resources and favorable environmental conditions. Furthermore, the higher T_{opt} in higher latitudinal regions indicated that these regions have a greater potential to release CO_2 from the soil, and might have a positive feedback to global warming. Alternatively, soils in low latitude region are more likely to adapt to increasing temperature and might act as a negative feedback to climate warming. In conclusion, process-based models should incorporate the high variability of T_{opt} across regions to improve predictions of the carbon dynamic of terrestrial ecosystems under climate warming scenarios.

Conflicts of interest

There are no conflicts of interest to declare.

Acknowledgements

This work was supported by the Natural Science Foundation of China (31770655 and 41571130043), the National Key R&D Program of China (2016YFC0500202), and the program of Youth Innovation Research Team Project (LENOM2016Q0005). The original data are available from the corresponding author upon request (henp@igsnrr.ac.cn). We thank the comments from the professor of Institute of Botany, CAS (Xingguo Han).

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2018.02.019.

References

Agren, G.I., Wetterstedt, J.A.M., 2007. What determines the temperature response of soil organic matter decomposition? Soil Biology and Biochemistry 39, 1794–1798.
Allison, S.D., Wallenstein, M.D., Bradford, M.A., 2010. Soil-carbon response to warming dependent on microbial physiology. Nature Geoscience 3, 336–340.
Angilletta, M.J., 2009. Thermal Coadaptation, Thermal Adaptation: a Theoretical and Empirical Synthesis. Oxford University Press, pp. 181–198.
Ascar, L., Ahumada, I., Richter, P., 2008. Influence of redox potential (Eh) on the availability of arsenic species in soils and soils amended with biosolid. Chemosphere 72, 1548–1552.
Bååth, E., Anderson, T.H., 2003. Comparison of soil fungal/bacterial ratios in a pH gradient using physiological and PLFA-based techniques. Soil Biology and Biochemistry 35, 955–963.
Balser, T.C., Firestone, M.K., 2005. Linking microbial community composition and soil processes in a California annual grassland and mixed-conifer forest. Biogeochemistry 73, 395–415.
Balser, T.C., Wixon, D.L., 2009. Investigating biological control over soil carbon temperature sensitivity. Global Change Biology 15, 2935–2949.
Barcenas-Moreno, G., Gomez-BrandoN, M., Rousk, J., Baath, E., 2009. Adaptation of soil microbial communities to temperature: comparison of fungi and bacteria in a laboratory experiment. Global Change Biology 15, 2950–2957.
Bradford, M.A., 2013. Thermal adaptation of decomposer communities in warming soils. Frontiers in Microbiology 4, 333.
Cheng, W., Zhang, Q., Coleman, D.C., Carroll, C.R., Hoffman, C.A., 1996. Is available carbon limiting microbial respiration. Soil Biology and Biochemistry 28, 1283–1288.
Daniel, R.M., Danson, M.J., 2010. A new understanding of how temperature affects the

catalytic activity of enzymes. Trends in Biochemical Sciences 35, 584–591.
Daniel, R.M., Danson, M.J., Eisenthal, R., Lee, C.K., Peterson, M.E., 2007. New Parameters Controlling the Effect of Temperature on Enzyme Activity.
Daniel, R.M., Danson, M.J., Eisenthal, R., Lee, C.K., Peterson, M.E., 2008. The effect of temperature on enzyme activity: new insights and their implications. Extremophiles 12, 51–59.
Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173.
Erhagen, B., Ilstedt, U., Nilsson, M.B., 2015. Temperature sensitivity of heterotrophic soil CO2 production increases with increasing carbon substrate uptake rate. Soil Biology and Biochemistry 80, 45–52.
Fang, C., Moncrieff, J.B., 2001. The dependence of soil CO2 efflux on temperature. Soil Biology and Biochemistry 33, 155–165.
Fenner, N., Freeman, C., Reynolds, B., 2005. Observations of a seasonally shifting thermal optimum in peatland carbon-cycling processes; implications for the global carbon cycle and soil enzyme methodologies. Soil Biology and Biochemistry 37, 1814–1821.
Fissore, C., Giardina, C.P., Kolka, R.K., 2013. Reduced substrate supply limits the temperature response of soil organic carbon decomposition. Soil Biology and Biochemistry 67, 306–311.
Friedlingstein, P., Cox, P., Betts, R., Bopp, L., Von Bloh, W., Brovkin, V., Cadule, P., Doney, S., Eby, M., Fung, I., 2006. Climate-carbon cycle feedback analysis: results from the C4MIP model intercomparison. Journal of Climate 19, 3337–3353.
Frostegård, Å., Bååth, E., Tunlio, A., 1993. Shifts in the structure of soil microbial communities in limed forests as revealed by phospholipid fatty acid analysis. Soil Biology and Biochemistry 25, 723–730.
Gershenson, A., Bader, N.E., Cheng, W.X., 2009. Effects of substrate availability on the temperature sensitivity of soil organic matter decomposition. Global Change Biology 15, 176–183.
Hamdi, S., Moyano, F., Sall, S., Bernoux, M., Chevallier, T., 2013. Synthesis analysis of the temperature sensitivity of soil respiration from laboratory studies in relation to incubation methods and soil conditions. Soil Biology and Biochemistry 58, 115–126.
He, N.P., Wang, R.M., Gao, Y., Dai, J.Z., Wen, X.F., Yu, G.R., 2013. Changes in the temperature sensitivity of SOM decomposition with grassland succession: implications for soil C sequestration. Ecology and Evolution 3, 5045–5054.
He, N.P., Tian, M., Liu, C.C., Li, M.L., Yang, H., Yu, G.R., Guo, D.L., Smith, M., Yu, Q., Hou, J.H., 2018. Variation in leaf anatomical traits from tropical to cold-temperate forests and linkage to ecosystem functions. Functional Ecology 32, 10–19.
Hobbs, J.K., Jiao, W., Easter, A.D., Parker, E.J., Schipper, L.A., Arcus, V.L., 2013. Change in heat capacity for enzyme catalysis determines temperature dependence of enzyme catalyzed rates. ACS Chemical Biology 8, 2388–2393.
Holland, E.A., Neff, J.C., Townsend, A.R., McKeown, B., 2000. Uncertainties in the temperature sensitivity of decomposition in tropical and subtropical ecosystems: implications for models. Global Biogeochemical Cycles 14, 1137–1151.
IPCC, 2013. Summary for Policymakers, Climate Change 2013: the Physical Scientific Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA., pp. 11–22.
Ise, T., Moorcroft, P.R., 2006. The global-scale temperature and moisture dependencies of soil organic carbon decomposition: an analysis using a mechanistic decomposition model. Biogeochemistry 80, 217–231.
Jenkinson, D.S., Adams, D.E., Wild, A., 1991. Model estimates of CO2 emissions from soil in response to global warming. Nature 351, 304–306.
Kirschbaum, M.U.F., 1995. The temperature-dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. Soil Biology and Biochemistry 27, 753–760.
Kirschbaum, M.U.F., 2006. The temperature dependence of organic-matter decomposition - still a topic of debate. Soil Biology and Biochemistry 38, 2510–2518.
Kirschbaum, M.U., 2010. The temperature dependence of organic matter decomposition: seasonal temperature variations turn a sharp short - term temperature response into a more moderate annually averaged response. Global Change Biology 16, 2117–2129.
Knies, J.L., Kingsolver, J.G., 2010. Erroneous Arrhenius: modified arrhenius model best explains the temperature dependence of ectotherm fitness. The American Naturalist 176, 227–233.
Koepf, H., 1953. Die Temperatur/Zeit–Abhängigkeit der Bodenatmung. Experimentelle Untersuchung unter Verwendung des Ultrarotabsotionsschreibers (URAS). Journal of Plant Nutrition and Soil Science 61, 29–48.
Ley, R.E., Schmidt, S.K., 2002. Fungal and bacterial responses to phenolic compounds and amino acids in high altitude barren soils. Soil Biology and Biochemistry 34, 989–995.
Li, J., He, N., Xu, L., Chai, H., Liu, Y., Wang, D., Wang, L., Wei, X., Xue, J., Wen, X., Sun, X., 2017. Asymmetric responses of soil heterotrophic respiration to rising and decreasing temperatures. Soil Biology and Biochemistry 106, 18–27.
Liu, Y., He, N., Zhu, J., Xu, L., Yu, G., Niu, S., Sun, X., Wen, X., 2017. Regional variation in the temperature sensitivity of soil organic matter decomposition in China's forests and grasslands. Global Change Biology 23, 3393–3402.
Llord, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. Ecology 8, 315–323.
Nelson, D., Sommers, L., 1982. Total Carbon, Organic Carbon, and Organic Matter, Methods of Soil Analysis. American Society of Agronomy and Soil Science Society of American, Madison, WI, pp. 539–579.
Parker, L.W., Miller, J., Steinberger, Y., Whitford, W.G., 1983. Soil respiration in a chihuahuan desert rangeland. Soil Biology and Biochemistry 15, 303–309.
Parton, W.J., Schimel, D.S., Cole, C.V., Ojima, D.S., 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal 51, 1173–1179.
Pietikainen, J., Pettersson, M., Baath, E., 2005. Comparison of temperature effects on soil respiration and bacterial and fungal growth rates. FEMS Microbiology Ecology 52, 49–58.
Richardson, J., Chatterjee, A., Darrel Jenerette, G., 2012. Optimum temperatures for soil respiration along a semi-arid elevation gradient in southern California. Soil Biology and Biochemistry 46, 89–95.
Rinnan, R., Rousk, J., Yergeau, E., Kowalchuk, G.A., Bååth, E., 2009. Temperature adaptation of soil bacterial communities along an Antarctic climate gradient: predicting responses to climate warming. Global Change Biology 15, 2615–2625.
Robinson, J.M., O'Neill, T.A., Ryburn, J., Liang, L.L., Arcus, V.L., Schipper, L.A., 2017. Rapid laboratory measurement of the temperature dependence of soil respiration and application to changes in three diverse soils through the year. Biogeochemistry 133, 101–112.
Rousk, J., Baath, E., 2011. Growth of saprotrophic fungi and bacteria in soil. FEMS Microbiology Ecology 78, 17–30.
Šantruckova, H., Michaek, I.B., Kalaschnikov, Y.N., Rund, M., lhottova, D., Imek, M., Rigoryev, S., Leixner, G., Rneth, A., Chulze, E.-D., Loyd, J., 2003. Microbial characteristics of soils on a latitudinal transect in Siberia. Global Change Biology 9, 1106–1117.
Schipper, L.A., Hobbs, J.K., Rutledge, S., Arcus, V.L., 2014. Thermodynamic theory explains the temperature optima of soil microbial processes and high Q10 values at low temperatures. Global Change Biology 20, 3578–3586.
Tuomi, M., Vanhala, P., Karhu, K., Fritze, H., Liski, J., 2008. Heterotrophic soil respiration—comparison of different models describing its temperature dependence. Ecological Modelling 211, 182–190.
Wang, J., Sun, J., Xia, J., He, N., Li, M., Niu, S., Luo, Y., 2017. Soil and vegetation carbon turnover times from tropical to boreal forests. Functional Ecology 32, 1–12.
Wen, D., He, N., 2016. Forest carbon storage along the north-south transect of eastern China: spatial patterns, allocation, and influencing factors. Ecological Indicators 61, 960–967.
Zhao, N., Yu, G.R., He, N.P., Wang, Q.F., Zhang, X.Y., Wang, R.L., Xu, Z.W., Jiao, C.C., Li, N.N., Jia, Y.L., 2016. Coordinated pattern of multi-element variability in the leaves and roots across Chinese forest biomes. Global Ecology and Biogeography 25, 359–367.