

The optimum temperature of soil microbial respiration: Patterns and controls

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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 CO₂ 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; Lord 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;

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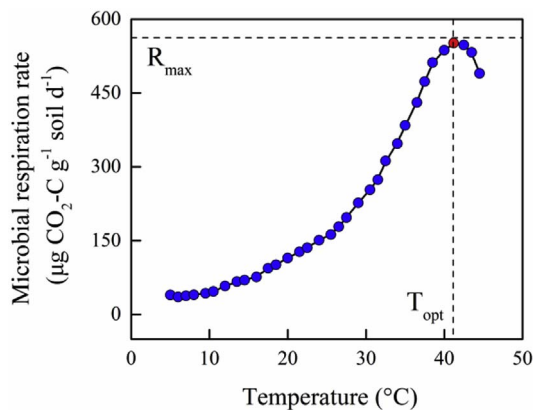


Fig. 1. An example of the temperature response curve for soil microbial respiration rate (R_h) from Shannon (SN) site. The optimum temperature of R_h (T_{opt}) was defined as the temperature at which the maximum rate of soil respiration (R_{max}) occurred (red point). (For interpretation of the references 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 CO₂ analyzer (Li-7100, LI-COR, Lincoln, NE, USA) that records CO₂ 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.

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