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Asymmetric responses of soil heterotrophic respiration to rising and decreasing temperatures

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ABSTRACT

Periodic changes in temperature commonly occur diurnally and seasonally. However, the response of soil heterotrophic respiration to rising and decreasing temperatures during these periods remains poorly understood; thus the feedback between climate change and carbon (C) cycling requires further investigation. In this study, soils from three grasslands in the Qinghai-Tibet Plateau were incubated separately at rising (from 5 °C to 31 °C) and decreasing (from 31 °C to 5 °C) temperatures modes over 161 days, to explore how soil heterotrophic respiration rates (R_S) respond to different temperature changes. The parameters of R_S and temperature sensitivity (Q_{10}) were used for the analyses. In addition, microbial biomass C (MBC), microbial biomass nitrogen (N) (MBN), dissolved organic C (DOC), and other soil properties were measured. The results indicated a pronounced hysteresis of R_S for both rising and decreasing temperatures. Furthermore, the hysteresis loops differed in the different sites. R_S values were significantly higher for rising temperature (2.71 μg C g^{-1} d^{-1}) versus decreasing temperature (1.75 μg C g^{-1} d^{-1}) in all three alpine grasslands. The Q_{10} values were significantly higher for decreasing temperature (2.42) versus increasing temperature (1.55), with these differences being observed over the 161-d incubation period. Furthermore, soil microbes (specifically, MBC and MBC/MBN) explained 46–77% of the total variation in Q_{10}, followed by substrate and other properties. Our results provide experimental evidence for the asymmetric responses of soil heterotrophic respiration to rising and decreasing temperatures. In addition, the microbial effect was primarily associated with soil heterotrophic respiration, suggesting strong asymmetric responses to rising and decreasing temperatures that require investigation in future studies.

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1. Introduction

In response to increasing CO_2 concentrations in the atmosphere, the global mean temperature is predicted to increase 2–7 °C by the end of the 21st century (Allison et al., 2011). Temperature modifies the amount of carbon (C) stored in soils by influencing soil heterotrophic respiration rates (R_S) and the global C balance (Davidson and Janssens, 2006). Most studies have investigated how temperature affects R_S in relation to rising temperature, with it being assumed the same effects occur with decreasing temperature (Xia et al., 2009; Peng et al., 2013). Thus, it is necessary to test this assumption by better characterizing the responses of R_S to changing temperature under both rising and decreasing temperatures.

In nature, periodic changes in temperature are common. For example, soil temperature typically rises during the daytime and decreases at night, representing a dynamic diurnal pattern (Fig. 1A). In addition, larger temperature changes occur over greater time scales such as over seasons and years (Fig. 1B). Temperature sensitivity (Q_{10}) is a useful index to describe the proportional change in R_S with a 10 °C increase in temperature (Lloyd and Taylor,

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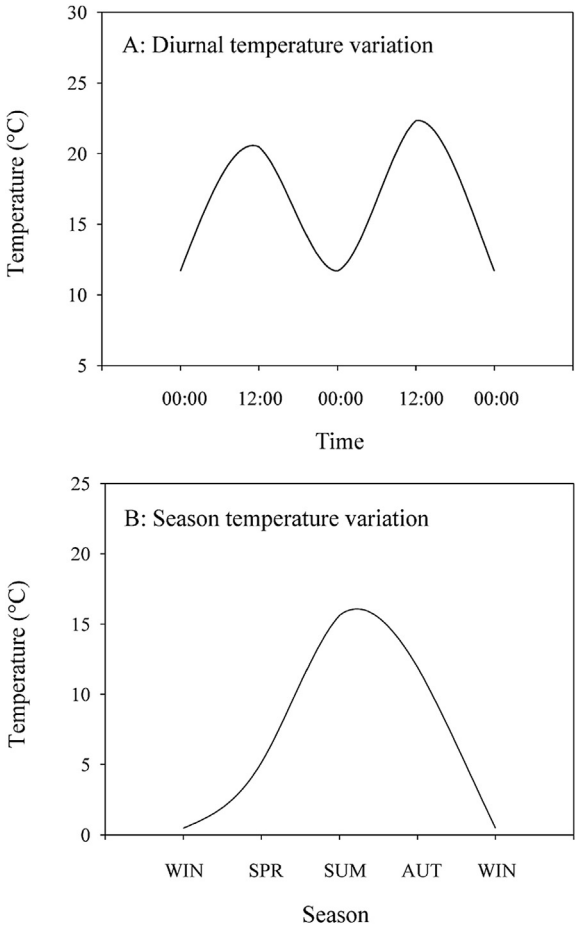

Fig. 1. Diurnal (A) and seasonal (B) variation in temperature in natural ecosystems.

1994). Previous studies have demonstrated that Q_{10} values vary greatly at different temperatures and in different ecosystems, ranging from nearly 1 to over 12 (Hamdi et al., 2013; Liu et al., 2015). Usually, higher Q_{10} values are detected under colder temperatures versus warmer temperatures (Kirschbaum, 1995).

Multiple hypotheses have been developed to explain the observed variability in Q_{10}. First, the C quality-temperature hypothesis predicts that Q_{10} is controlled by enzyme kinetics and should decrease as the quality of C in soil organic matter (SOM) increases (Bosatta and Ågren, 1999). C quality varies among different ecosystems (Craine et al., 2010a; Bosatta and Ågren, 1999), or even within the same ecosystems, depending on the season (Niu et al., 2011), soil depth (Rovira and Vallejo, 2002), and the different stages of SOM decomposition (early or late stages). Experimental evidence supports the C quality hypothesis by demonstrating that the decomposition of lower quality C substrates is more sensitive to changes in temperature than the decomposition of higher C quality substrates (Fierer et al., 2005). Alternatively, varying Q_{10} might be derived from the physiological adjustments of microbes (Bradford et al., 2008). Microbes inhabiting colder regions may be more sensitive to increasing temperature than those in warm regions, resulting in a higher Q_{10} (Karhu et al., 2014). Some studies have shown that the adaptation of soil microbes changes differently when temperature increases or decreases (Fenner et al., 2005; Bradford et al., 2008). Moreover, abiotic soil properties, such as oxidation-reduction potential (ORP), pH (Min et al., 2014), and the substrate used for microbial metabolism (Blagodatskaya et al., 2014), might influence R_S, because these soil properties regulate microbial activity directly or indirectly. Microbial adaptation when the temperature rises or decreases might generate a hysteresis phenomenon. Hysteresis occurs when an increase in a given independent variable, x, does not cause the same magnitude of response in a dependent variable, y, compared with when variable x decreases by the same amount (Zeppel et al., 2004). Hysteretic temperature responses have been reported for R_S, however, the mechanisms remain unclear (Vargas and Allen, 2008; Phillips et al., 2011).

Traditional methods used to quantify Q_{10} are performed at a single constant incubation temperature (Wagai et al., 2013; Quan et al., 2014) or by placing multiple soil samples at different constant temperatures along a temperature gradient (Weedon et al., 2013; Xue et al., 2015). Unfortunately, these methods produce limited data to calculate Q_{10}, and might influence the accuracy of Q_{10}, to some extent. More importantly, soils incubated at a constant temperature might consume more substrate at higher temperatures compared to lower temperatures, leading to large differences in substrate supply (or C quality), which influence Q_{10} estimates, especially for long-term incubation experiments. These disadvantages of traditional incubation experiments must be overcome in future studies.

Here we designed a novel soil incubation experiment under rising (from 5 °C to 31 °C) and decreasing (from 31 °C to 5 °C) temperature regimes, to simulate periodic changes in temperature during daytime and night-time. Using an equipment with continuous measurement, we evaluated R_S (recorded approximately every 20-min) at intervals of 0, 7, 14, 21, 28, 49, 77, 105, 133, and 161 days, and calculated the corresponding Q_{10}. We used three alpine soils from the Qinghai-Tibet grasslands to investigate hysteretic responses of R_S and Q_{10} under rising and decreasing temperatures, and to explore the influence of soil microbes and soil substrate quality.

2. Materials and methods

2.1. Study sites

The experimental plots were selected from three main grassland types distributed widely across the Qinghai-Tibet Plateau. These grassland types were designated as alpine meadow, alpine steppe, and alpine desert (Fig. S1). The mean annual temperature at these sites ranged from −0.2 °C to 3.1 °C; and the mean annual precipitation ranged from 150.0 mm to 641.0 mm (Table 1). Detailed information on the three plots was primarily derived from a previous publication (Li et al., 2015) and is presented in Table 1.

2.2. Field sampling

Field sampling was conducted in August 2013. In each plot, nine sampling quadrats (0.5 m × 0.5 m) were established at about 10 m intervals along three random transects in each selected grassland type. The community structure and aboveground biomass were investigated in each quadrat. Subsequently, surface litter was removed and soil samples (approximately 5 kg) were randomly collected using a soil sampler (10 cm in diameter) from the surface soil (0–20 cm) in each quadrat. The samples were passed through a 2-mm sieve and all visible plant material was manually removed. Homogenized soil samples from the same depth were mixed and divided into two subsamples. Then, approximately 100 g of each soil sample was air-dried to analyze soil properties [e.g., C, nitrogen (N), and pH]. Approximately 5 kg fresh soil was immediately packed in labeled polyethylene bags and stored in a portable refrigerator (4 °C). The soil was then transported to the laboratory for subsequent incubation experiments.

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