



Environmental controls on soil respiration in alpine meadow along a large altitudinal gradient on the central Tibetan Plateau



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ABSTRACT

Little is known about how environmental factors modify spatiotemporal variations of soil respiration (R_s) and its temperature sensitivity (Q_{10}) in alpine grasslands on the Tibetan Plateau (TP). We conducted an altitudinal experiment across lower and upper limits of alpine meadows on the central TP. Soil respiration and related environmental factors were observed at each of 7 altitudes (from 4400 m to 5200 m) during the growing seasons of 2012 and 2013. Soil temperature (ST) rather than soil moisture (SM) was the major abiotic factor controlling seasonal variation of R_s in alpine grasslands across the seven altitudes. In addition to ST and SM, plant biomass is also an important factor controlling seasonal trends of R_s . The seasonal mean R_s increased with increasing altitude up to 4950 m, and then decreased above 4950 m. Below-ground biomass (BGB), ST and SM have direct effects on R_s , and the altitudinal trends of R_s can be well-predicted from these three variables ($R^2 = 0.65$). The Q_{10} values of seasonal R_s generally increased with increasing altitude. Alpine meadows generally have higher Q_{10} values comparing with steppe meadows. Along the altitude gradient, Q_{10} was negatively correlated with ST, but positively correlated with SM, AGB, BGB and SOC. The results suggested that future climate warming would enhance R_s rates more dramatically in high-altitudes grasslands, and changes in vegetation structure under climate change might have a large impact on R_s in these alpine grasslands.

1. Introduction

Soil respiration (R_s) is a major carbon flux from terrestrial ecosystems to the atmosphere (Luo et al., 2001; Davidson et al., 2006), and even small perturbations to the global R_s flux can have the potential to significantly alter patterns of both carbon cycling and climate (Cox et al., 2000; Davidson and Janssens, 2006; Piao et al., 2009). Soil respiration is a composite flux of autotrophic root respiration and heterotrophic microbial respiration, interacting with both abiotic and biotic factors. The temporal and spatial variation of R_s is complex and is controlled by different environmental factors, such as temperature, water available, substrate available, climate conditions and even human disturbance (Raich and Tufekciogul, 2000; Wan and Luo, 2003; Cao et al., 2004; Davidson and Janssens, 2006; Geng et al., 2012). A better understanding of how R_s respond to environmental factors is essential to improve C cycle models and forecast possible response of ecosystem C cycling to future climate change.

Temperature is considered as major factor controlling R_s (Lloyd and Taylor, 1994; Saito et al., 2009). However, the dependence of R_s on soil

temperature may be much less when respiratory substrate or soil water becomes limiting factor (Davidson et al., 1998; Wohlfahrt et al., 2008; Wagle and Kakani, 2014). Especially in arid ecosystems, precipitation and soil moisture are considered to be critical to determining seasonal changes of plant growth and R_s (Jia et al., 2014), which usually also confound the relation of R_s with soil temperature (Qi and Xu, 2001; Wagle and Kakani, 2014; Jiang et al., 2015). Q_{10} is a common indicator of temperature sensitivity of R_s , which is an important ecological parameter in ecosystem carbon cycle models. Increasing evidences reveal that Q_{10} is no longer a reflection of temperature sensitivity, but an integration of several confounding ecosystem processes (Janssens and Pilegaard, 2003; Davidson and Janssens, 2006). In the field study, a large number of studies show that the variation of Q_{10} value is largely regulated by both biotic and abiotic factors (Xu and Qi, 2001a; Janssens and Pilegaard, 2003; Peng et al., 2009; Xu et al., 2015), and these environmental factors are spatially heterogeneous. The Q_{10} values resulted from field measurements were not a constant value, but varied with geographic locations. However, how these environmental factors controlling the spatial variability of Q_{10} are still poorly understood

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(Hirota et al., 2009; Moriyama et al., 2013).

Grasslands occupy extensive areas in terrestrial ecosystems, and considerable attention has been given to carbon cycles in grassland ecosystems due to their potential importance in the global carbon budget and climate change (Adams et al., 1990; Cao et al., 2004; Wang and Fang, 2009). Among these ecosystems, alpine grasslands, which contain enormous stores of carbon belowground, are assumed to release through soil respiration under warming condition (Yang et al., 2008; Piao et al., 2012). Especially on the Tibetan Plateau (TP), where the climatic has become warmer and wetter, and alpine grassland ecosystems will experience more rapid changes in temperature and precipitation than ecosystems at lower elevations (Yang et al., 2014; Pepin et al., 2015; Bosch et al., 2017). Given that temperature and precipitation are key drivers of ecosystem biogeochemical processes, the increase in temperature and precipitation on TP will likely have direct implications for Rs (Rustad et al., 2001; Saito et al., 2009). However, despite large number of manipulative experiments on the response of Rs to changing temperature in alpine grasslands, no consensus has been reached (Kato et al., 2004; Saito et al., 2009; Zhu et al., 2015). Additionally, how the high-altitude ecosystems response to the future climate warming is still uncertain. In mountains areas, altitudinal gradients are generally correlated with climate gradients and changes on vegetation communities over short geographic distances, which are considered well suited to study the long-term effects of climate and vegetation impact on ecosystem processes (Rodeghiero and Cescatti, 2005; Raich et al., 2006; Zimmermann et al., 2010). Thus, knowledge on how environmental factors governing Rs along the altitudinal gradient is necessary to predict the response of alpine grasslands to future climate change.

The TP hosts the highest and largest alpine grassland ecosystems worldwide. During recent decades, the TP has experienced a more rapid warming than other regions in the world (Yang et al., 2014; Pepin et al., 2015). How the TP's alpine grasslands response to future climate change has attracted extensive concern and large number of manipulative experiments was conducted to solve the puzzles (Kato et al., 2004; Lin et al., 2011; Jiang et al., 2013; Lu et al., 2013; Peng et al., 2014; Chen et al., 2017). Most of these observations were mainly confined within one site, except for Geng et al. (2012), whose study suggested that belowground biomass and soil moisture well explained the spatial variability of Rs in Tibetan alpine grasslands. Bosch et al. (2016) compared the ability of six regression models in predicting Rs and suggested that regression model based on precipitation performs best in calculating Rs on the TP. However, few reports have addressed on altitudinal variation of Rs and Q_{10} and their controlling factors on the TP. To fill this gap, we conducted an altitudinal experiment across lower and upper limits of alpine meadows (4400–5200 m) along the south-facing slope of Nyaiqentanglha Mountains on the central TP. Seasonal Rs and related environmental factors were observed at each of 7 altitudes during the growing season of 2012 and 2013. In this study, we used opaque chamber-based CO_2 efflux (measured by Li-Cor 8100) to explore altitudinal variation of Rs and their driving factors. We aim (1) to test altitudinal changes of Rs and Q_{10} in alpine grasslands and (2) to clarify the relationships of Rs and Q_{10} with environmental factors during the growing season.

2. Materials and methods

2.1. Study site

This study was conducted along the south-facing slope of the Nyaiqentanglha Mountains (30°30'–30°32'N, 91°03'E), which was located in the zonal ecotone between alpine *Stipa* steppe and alpine *Kobresia* meadow on the central TP (Fig. 1). According to the meteorological observation at Damxung station, the mean air temperature for the year was 1.7 °C and the annual precipitation was 479 mm. The mean air temperature was 2.7 °C and 2.4 °C, and the annual

precipitation was 338.7 mm and 365.4 mm in 2012 and 2013, respectively. The vegetation types changed from the steppe-meadow dominated by *S. capillacea* at 4400–4500 m, to the alpine meadow dominated by *K. pygmaea* at 4650–5200 m. Other coexisting species mainly included *A. tapete*, *Arenaria lancangensis*, *Potentilla nivea*, *Carex atrofusca* etc. Soils in this region are poorly developed, and soil profile differentiation is relatively weak and the soil layer is thin. The soil types changed from alpine steppe soil at 4400–4500 m to alpine meadow soil at 4650–5200 m. Detailed information about soil properties can be found in Ohtsuka et al. (2008). Pasture for domestic yaks and sheep is the main land-use type in this region. The stock rate would be higher at lower altitudes because the most severely degraded grasslands were found at 4300–4500 m. In August 2005, seven HOBO weather stations (Onset Inc., Bourne, MA) were set up at 4400 m, 4500 m, 4650 m, 4800 m, 4950 m, 5100 and 5200 m along the slope. Air temperature (1.5 m aboveground) and precipitation were recorded at 30-min intervals. Seven 20 × 20 m plots were set nearby the HOBO weather stations at each of the 7 altitudes. Detailed information is found in Zhao et al. (2016a).

2.2. Field sampling and measurements of respiration

The CO_2 efflux without aboveground vegetation measured in dark chamber was considered as soil respiration (Rs). During the growing seasons (June to September) of 2012 and 2013, diurnal variation (08:00–18:00, local time) of Rs at 2–3 h intervals was measured once a month using the opaque chamber of Li-8100 103 automatic soil CO_2 flux system (LI-COR Biosciences, Lincoln, NE, USA). The sampling frequency of Re measurements for each month during the growing season was low because of difficulty in the field campaign at high altitudes. Given that the altitudinal measurements were made under similar weather conditions of sunny days, the sampling procedure would be fine for a comparison along altitudes at a certain point in time. At beginning of measurement, five chloride collars (diameter: 20 cm; height: 5 cm) were inserted 3 cm into the soil for measurement of respiration at each of the 7 altitudes. All the collars were installed at least 24 h prior to the measurements in order to reduce disturbance. Before Rs measurement, the plants within those collars were clipped to the ground level and collected in the envelopes, and the dry matter weight was calculated to reflect dynamics of aboveground biomass during growing season. To determine the differences in soil temperature (ST) and moisture (SM) across altitudes, ST and SM at 5 cm were measured simultaneously with Rs using a digital temperature sensor (Type E, OMEGA Engineering, Inc., Stamford, CT, USA) and a Time Domain Reflectometer with a handheld push probe (Type ML2x, Delta-T Devices Ltd., Burwell, Cambridge, United Kingdom) attached to the Li-8100 system.

2.3. Measurements of plant biomass and soil organic carbon

We set up five quadrats (0.5 × 0.5 m) at each of the 7 altitudes. In total, 35 quadrats were sampled at seven altitudes from 4400 to 5200 m. The maximum above-ground biomass (AGB) was harvested in each quadrat in mid-August of 2012 and 2013, which was dried in an oven at 65 °C for 48 h. At the same time, below-ground biomass (BGB) was measured by collecting five soil cores (diameter: 5.0 cm; depth: 30 cm) in each quadrat. BGB samples were washed off the soil by a 2-mm sieve and dried at 65 °C for 48 h. We collected top soil samples (0–10 cm in depth) with a soil auger (diameter: 3.0 cm) from each quadrat in mid-August of 2012 and 2013. After removal of any visible roots, soil samples were air-dried at room temperature and sieved for measuring soil organic carbon (SOC) (Nelson and Sommers, 1982). Briefly, 0.5 g of sieved soil samples were digested with 5 ml of 1 N $K_2Cr_2O_7$ standard solution, and then mixed with 10 ml of concentrated H_2SO_4 at 180 °C for 5 min with an oil bath furnace, followed by titration of the digests with standardized $FeSO_4$ (Shang et al., 2012; Chen

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