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Responses of ecosystem respiration to short-term experimental warming in the alpine meadow ecosystem of a permafrost site on the Qinghai–Tibetan Plateau

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ABSTRACT

As the largest high-altitude permafrost region in the world, the Qinghai–Tibetan Plateau (QTP) has experienced pronounced warming, which may exert a profound effect on ecosystem's CO_2 emissions due to the large amounts of organic carbon in the permafrost soil. In this study, response of ecosystem respiration to short-term experimental warming was investigated in the alpine meadow ecosystem of a permafrost site on the QTP during the 2012 growing season. The results showed that cumulative growing season ecosystem CO_2 emissions were 277.09 and 325.33 g C m^{-2} for the control and warming plots, respectively. Thus, a 2.18 °C increase in ground surface temperature and a 0.62 °C increase in soil temperature prompted a 17.41% increase in the ecosystem's CO_2 emissions. The relationships between temporal variations in ecosystem respiration and soil temperature can be described through exponential equation. Soil temperature accounted for 50 and 64% of the variations in ecosystem respiration on a diurnal scale, and 71 and 84% of the variations in ecosystem respiration on a seasonal scale in the control and warming plots, respectively. Moreover, the temperature sensitivity (i.e. apparent Q_{10} values) of the ecosystem respiration rates was significantly higher in the warming plots than in the control plots. Our results indicate that the effect of warming promoted CO_2 emissions of the alpine meadow ecosystem at a permafrost site on the QTP, and that soil temperature is the key factor controlling ecosystems' CO_2 emissions. In addition, while ecosystem respiration provides positive feedback on the rise in temperature through an increase in temperature sensitivity under warming conditions, at least in the short term, this feedback may be partially offset by an increase in above- and belowground biomass caused by warming.

1. Introduction

Carbon store in permafrost soil is about 1700 Pg in high-latitude and -altitude regions, accounting for approximately 50% of the estimated global belowground organic carbon pool (Wang et al., 2002; Tarnocai et al., 2009). Prevailing low temperatures and permanently low turnover rates result in large soil organic carbon (SOC) stocks in permafrost soils, providing great potential for ecosystem CO_2 emission under warming conditions (Dörfer et al., 2013). After photosynthesis, ecosystem respiration is one of the largest and most important fluxes of carbon in terrestrial ecosystems (Hicks Pries et al., 2013), exerting dominant control over atmospheric CO_2 levels and feedback to climate change. Small imbalances in CO_2 uptake via photosynthesis and CO_2 release by ecosystem respiration can lead to significant interannual variation in atmospheric CO_2 (Cox et al., 2000; Grogan and Jonasson, 2005; Bond-Lamberty and Thomson, 2010; Warren and Taranto, 2011). Experimental warming is an ideal tool for directly testing an ecosystem's carbon dynamics in relation to climate change to gain a better understanding of ecosystem respiration's response to a rise in temperature.

Ecosystem respiration consists mainly of above-ground vegetation, root and microbial respiration. Therefore, influence of biological and abiotic factors on vegetation productivity, SOC and microbial activity such as soil temperature, water content and substrate supply affects ecosystem respiration rates (Davidson et al., 2006b). However, soil or ecosystem respiration rates are mainly dependent on changes in mean annual temperature caused by global climate warming (Raich and Schlesinger, 1992). Great efforts have been made to investigate response of soil or ecosystem respiration to climate warming among different ecosystems, based on field observations (Oechel et al., 2000; Vogel et al., 2009; Belshe et al., 2013) and manipulative warming experiments (Welker et al., 2004; Oberbauer et al., 2007; Dorrepaal et al., 2009; Natali et al., 2014). Several potential mechanisms may account for regulation of climate warming to soil or ecosystem respiration. First, rise in temperature strongly influences vegetation's phenological process (Yu et al., 2010; Zhang et al., 2011) and permafrost degradation (Yang et al., 2010), which can significantly contribute to variations in soil or ecosystem respiration and its temperature sensitivity (Fu et al., 2002; Yuste et al., 2004) and ecosystem carbon release when permafrost is thawing (Hicks Pries et al., 2013; Köhler et al.,

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2014). Second, climate warming alters vegetation photosynthesis, leading to changes in the net carbon exchange between gross photosynthetic uptake and respiratory losses (Janssens et al., 2001), along with above- and belowground biomass allocation (Yang et al., 2009) because root respiration and heterotrophic respiration are constrained by the allocation of photosynthates to the roots (Moore et al., 2002; Gregory, 2006). Finally, climate warming may alter quantity and quality of plant litter entering belowground system, which may in turn affect soil microbial activity controlling decomposition of plant litter and soil organic matter (Luo et al., 2010). Recently, Lin et al. (2011) and Lu et al. (2013) examined responses of ecosystem carbon dynamics to experimental warming in alpine grassland ecosystem of non-permafrost region on the QTP. However, the potential mechanisms of climate change regulating ecosystem respiration of alpine grassland ecosystems are still unknown, particularly in permafrost regions.

The QTP is a particularly sensitive area in terms of the potential effects of global climate change. Approximately 60% of the QTP is covered by alpine grassland with about 50% of the alpine grassland underlain by permafrost (Zhao et al., 2000). The QTP has experienced pronounced climatic warming over past decades, and the region is predicted to experience “much greater than average” increases in surface temperatures in the future (IPCC, 2013). Permafrost on the QTP has degraded and is expected to continue degrading in the future, which will cause soil drought and warming in alpine grassland ecosystems (Cheng and Wu, 2007; Wu and Zhang, 2010). These processes lead to substantial changes in soil nutrient availability (Wang et al., 2008), species composition and even alpine grassland degradation (Yang et al., 2010). Numerous field observations have been conducted through “space for time” studies, i.e. setting up quadrats in different types of permafrost zones and comparing vegetation and soil characteristics. However, permafrost degradation effects may be confounded by variation in land use and microtopography that coincide with permafrost thaw. Therefore, a controlled warming experiment is expected to provide improved evaluations of response of ecosystem carbon dynamics to permafrost warming in high-altitude ecosystems.

To verify ecosystem respiration's response to climate warming and investigate the dominant controlling factors affecting ecosystem CO_2 emission, we conducted a whole growing season manipulative warming experiment in an alpine meadow at a permafrost site in a semi-arid basin on the north-east edge of the QTP. At least in the short term, we hypothesized that: (1) soil warming would promote ecosystem CO_2 emission on a diurnal, monthly and seasonal scale during the growing seasons; (2) soil temperature and soil moisture would be the dominant controlling factors of ecosystem CO_2 emission in alpine meadow ecosystem underlain by permafrost; and (3) experimental warming would decrease temperature coefficient (Q_{10}) of alpine meadow ecosystem respiration rates.

2. Materials and methods

2.1. Site description

The studies were conducted in the permanent plots at Suli Alpine Meadow Ecosystem Observation and Experiment Station (98°18′33.2″ E, 38°25′13.5″ N, 3887 m a.s.l.), located in the southeast portion of Suli country, the northeast edge of the QTP, China. The area has a typical continental climate mainly controlled by westerly winds. The mean annual precipitation is 200–400 mm, about 90% of which falls from May to September (Qin et al., 2014). The mean annual temperature is −4.0 °C, with the minimum and maximum temperatures ranging from −22.7 °C in January to 10.0 °C in July. Soils in the study site are classified as “felty” with a pH of 8.56. Soil particle proportion is 30.96% silt and fine, 57.52% fine sand and 10.68% coarse sand, and soil bulk density is 1.41 g cm^{-3} within a 0–40 cm depth of the soil layer. The dominant species are *Kobresia capillifolia* and *Carex moorcroftii*. The permafrost type at our experiment site is transition and the active layer depth is 2.78 ± 1.03 m (Chen et al., 2012). The detailed information about the classification of different permafrost types can be found in Yi et al. (2011).

2.2. Controlled warming experiment

We applied a paired design with two treatments replicated three times. Six 3 × 3 m^2 plots were arranged in a 2 × 3 matrix. The distance between any two adjacent plots was 2 m. One of the two plots in each row (i.e., a replication) was assigned to the control or warming treatment group, respectively. In each plot, two quadrats (1 × 1 m^2) were set up. One quadrat was used for ecosystem respiration measurement and another for vegetation and soil sampling. Two open-top chambers (OTCs) (45 cm high, 85 cm wide at the top and 105 cm wide at the bottom) were evenly placed in each warming plot. All of the selected plots were expected to be less in spatial heterogeneity by calculating the fractional vegetation cover (FVC) (Fig. 1). The OTCs were installed on May 12, 2012 and the observations were initiated beginning May 18, 2012.

2.3. Ecosystem respiration measurement

Ecosystem respiration rates were measured using the LICOR-8150 Automated Soil CO_2 Flux System equipped with four LICOR-8100-104 long-term chambers (LICOR, Inc., Lincoln, NE, USA). To measure ecosystem respiration, polyvinyl chloride collars with a 20 cm inner diameter and a 12 cm height were inserted into soil with 3–4 cm exposed to the air. All of the collars were installed at least 24 h before the first measurement to reduce disturbance-induced ecosystem CO_2 effluxes. Over the 2012 growing season, ecosystem respiration rates were measured every 7–15 days from May 18 to September 3 depending on weather conditions. A round-the-clock measurement protocol was carried out and ecosystem respiration rates were measured every half hour. The rotation measurements of ecosystem respiration were made alternately in a Control 1–Control 2–Control 3–Control 1–Control 2–Control 3...... , Warming 1–Warming 2–Warming 3–Warming 1–Warming 2–Warming 3...... sequence for the control and warming plots, respectively. Therefore, 3 days at least was needed to complete one rotation measurements of ecosystem respiration. Ground surface temperature, soil temperature at a 5 cm depth and soil moisture at a 10 cm depth were measured continuously in the control and warming plots. Soil temperature and moisture measurements were conducted within 0–10 cm of surface soil because the majority of belowground biomass and soil organic matter are stored in the upper 10 cm of soil, and ecosystem respiration is more highly correlated with a 5 cm depth soil temperature than with a 10 cm depth soil

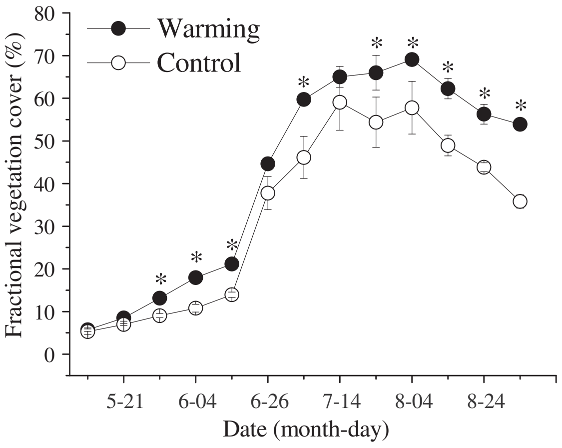

Fig. 1. Fractional vegetation cover in the control and warming plots in an alpine meadow during the period of the experiment. *Significant difference between warming and control at 0.05 level. Vertical bars indicate the standard error of the measurement mean (n = 3).