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Comparing microbial carbon sequestration and priming in the subsoil versus topsoil of a Qinghai-Tibetan alpine grassland

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ABSTRACT

Subsoils of alpine grasslands on the Qinghai-Tibetan Plateau represent a tremendous yet poorly investigated reservoir of soil organic carbon (SOC) on a global “hotspot” of warming. Compared with the temperature sensitivity of SOC decomposition, microbial anabolism of new carbon and priming of native SOC remain poorly constrained under warming-enhanced labile carbon input in these subsoils. Here we employed an innovative approach to investigate the sequestration of freshly added carbon in microbial necromass versus SOC priming in the top- (0–10 cm) and subsoils (30–40 cm) from a field experiment that simulated varied warming scenarios in an alpine grassland on the Qinghai-Tibetan Plateau. The ^{13}C composition of microbial necromass-derived amino sugars was analyzed in tandem with respired CO_2 and dissolved SOC components (including dissolved lignin) in an 86-day laboratory incubation with ^{13}C-labeled glucose. A higher fraction of freshly added carbon was respired while a smaller proportion was stabilized as amino sugars in the subsoil relative to the topsoil, leading to a much lower microbial carbon accumulation efficiency at depth. Meanwhile, a higher relative priming effect was observed in the subsoil (47± 14%) compared to the topsoil (14± 4%), suggesting a higher vulnerability to substrate-induced SOC loss at depth, although such changes may be associated with higher glucose addition rate (relative to SOC) in the subsoil. Furthermore, enhanced winter warming significantly reduced degradable SOC (assessed by SOC mineralization and dissolved lignin content) in the subsoil and potentially intensified nitrogen limitation under labile carbon additions, which further decreased microbial carbon accumulation (in the form of amino sugars) in the subsoil without affecting the topsoil. These results collectively indicate a limited microbial carbon sequestration potential and a higher vulnerability to warming-induced substrate changes in the subsoil of this alpine grassland, which warrants better understanding to predict soil carbon responses to climate warming on the Qinghai-Tibetan Plateau.

1. Introduction

The Qinghai-Tibetan Plateau is the highest plateau in the world, comprising an area of more than 2.4 million km^2 with an average altitude exceeding 4000 m a.s.l. (above sea level). More than 60% of the plateau's surface is covered by alpine grasslands (including meadows and steppe), whose soils store 33.5 Pg organic carbon (OC) in the top 0–75 cm, equivalent to 23.4% of soil organic carbon (SOC) stock in China (Wang et al., 2002). In the past 50 years, the plateau has experienced rapid climate warming with an average temperature increase of 0.2 °C per decade, especially in winter (Chen et al., 2013). This warming trend has further intensified since 2000 (Yao et al., 2007). With prolonged growing season and enhanced plant growth (Shen et al., 2015), warming is reported to induce a significant increase in net primary production (NPP) on the Qinghai-Tibetan Plateau (Wang et al., 2012), increasing plant OC input into soils. Meanwhile, SOC stock in the top 30 cm of alpine grasslands on the plateau has not changed from 1980 to 2004 (Yang et al., 2009), suggesting that increased carbon input may be counteracted by accelerated decomposition (Davidson and Janssens, 2006). Yet it remains to be investigated what

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mechanisms inhibit the build-up of SOC with increased NPP and whether SOC composition (or stability) has shifted under enhanced soil carbon cycling in order to better predict soil carbon response to climate warming on the Qinghai-Tibetan Plateau.

Climate warming may alter SOC cycling via at least two mechanisms: (i) enhancing microbial decomposition of soil organic matter (SOM) through accelerating enzymatic reaction at higher temperatures (Davidson and Janssens, 2006), and/or (ii) inducing "priming effect" (PE) on SOC through increased labile carbon supply to soil microbes (Fontaine et al., 2004; Hopkins et al., 2014) under enhanced plant growth or belowground allocations with warming (Xu et al., 2014; Walker et al., 2016). While the former has been extensively studied and recognized in soils (Allison and Treseder, 2008), SOC dynamics altered by warming-induced PE remain relatively poorly understood (Reinsch et al., 2013). As NPP increases with warming, plant inputs into the soil increase in the form of litter and root exudates, including carbohydrates, organic acids, and amino acids (Fontaine et al., 2004; Wild et al., 2014). These energy-rich and readily degradable compounds rapidly fuel catabolic and anabolic activities of soil microbes (Gunina and Kuzyakov, 2015), leading to potential shifts in microbial community composition (Hopkins et al., 2014) and increased (positive PE) or decreased (negative PE) decomposition of native SOC (Blagodatskaya and Kuzyakov, 2008; Kuzyakov, 2010).

Mechanisms governing the direction of PE are still unclear (Georgiou et al., 2015) but nutrient availability has been suggested to play a decisive role. Under high nutrient availabilities, microbes switch from SOM decomposition to labile OC utilization, leading to negative priming ("preferential substrate utilization" hypothesis; Blagodatskaya et al., 2007). On the opposite, under low nutrient availabilities soil microbes utilize labile OC to synthesize extracellular enzymes for the acquisition of nutrients from SOM, thereby leading to positive priming ("microbial nutrient mining" hypothesis; Craine et al., 2007). Given that nitrogen (N) mineralization rates are restricted by low temperatures in alpine grasslands, plants and microbes may compete strongly for inorganic N (Xu et al., 2006). It is hence worth investigating whether warming induces positive priming of native SOC on the Qinghai-Tibetan Plateau and how it affects SOC quality as well as quantity. Furthermore, subsoils (>30 cm) in the first meter store more than 47% of SOC on the Qinghai-Tibetan Plateau (Yang et al., 2009) and have distinct abiotic (e.g., soil texture, reactive minerals and permafrost distribution) and biotic (e.g., microbial biomass and diversity) properties from the topsoil (Ollivier et al., 2013). The response of subsoil OC to warming and labile carbon addition can be different from that of topsoil (Fierer et al., 2003a; Wild et al., 2014) and will be pivotal in predicting the change of SOC storage under climate warming.

In contrast to priming, microbial anabolism may increase SOC content in the form of microbial residues (mainly necromass) and represents a not-yet-fully-investigated fate of fresh carbon added into soils (Liang et al., 2011). Microbial cell wall components such as amino sugars are an important part of microbial residue or necromass (Engelking et al., 2007; He et al., 2011). The most important amino sugars in soils include glucosamine mainly derived from fungal cell walls, galactosamine, and muramic acid exclusive to bacteria (Zhang and Amelung, 1996). These compounds are relatively stable in soils and are hence used as a time-integrated measure of microbial carbon not subject to rapid fluctuations (Liang and Balser, 2012). Due to the slow turnover of microbial necromass (Liang et al., 2011), it is difficult to investigate amino sugar dynamics in the short term. However, coupled with intensive isotopic labeling, these compounds may be utilized to probe microbial sequestration of newly added carbon in soils (He et al., 2011), which may counteract positive priming of SOC.

Here we conduct a ^{13}C-labeled priming experiment on the topsoil (0–10 cm) and subsoil (30–40 cm) from a field warming study on an alpine grassland of Qinghai-Tibetan Plateau. Our approach serves two purposes. First, with the amendment of ^{13}C-labeled glucose, we attempt to simulate labile carbon increase resulting from warming-induced plant growth and to assess the response of microbial anabolism to freshly added carbon (assessed by novel δ^{13}C measurement of individual amino sugars) and degradation of native SOC (via respiration in the form of CO_2). Second, we examine SOC mineralization in the priming experiment to evaluate changes in the degradability or quality of SOM collected from different field warming treatments. We hypothesize that labile carbon input stimulates both microbial carbon accumulation and native SOC decomposition, which in turn diminishes easily degradable substrates in the soil and decreases SOC degradability (or quality) under warming. These effects may be particularly pronounced in the subsoil that is relatively depleted of energy-rich OC and are hence worthy of comparison with the topsoil in terms of predicting SOC responses to warming.

2. Materials and methods

2.1. Study site and soil sampling

The field warming experiment is located at the Haibei Alpine Grassland Ecosystem Research Station (101°19′E, 37°36′N, mean elevation of 3215 m a.s.l.), which lies on the northeastern Qinghai-Tibetan Plateau. The region has a continental monsoon climate with a mean annual temperature of −1.2 °C and a mean annual precipitation of 489 mm, 80% of which occurs during the summer monsoon season. Soils at the site are Mat-Gryic Cambisol with a relatively high SOC content (~7% at 0–10 cm), a clay loam texture (Table 1) and a mean pH of 8.01 (measured in 2.5 ml of water per gram of soil). The native plant community is dominated by *Kobresia humilis, Elymus nutans, Stipa aliena* and *Gentiana straminea*.

A multi-factorial field experiment was established at the Haibei Research Station with the aim to investigate effects of warming and altered precipitation on plant communities and soil processes (Fig. 1). The manipulative experiment was a full factorial design, initially including two warming levels [control without warming (CK) and regular whole-year warming (W1)] and three precipitation levels (drought, ambient and wet) in July 2011. Each treatment had six independent and randomly distributed replicates (1.8 m × 2.2 m per plot) on a relatively homogeneous landscape in terms of geomorphology and soil properties. The experiment was expanded subsequently to include an enhanced winter warming (W2) treatment with 5 replicates in January 2012. For this study we focused on CK, W1 and W2 treatments to examine warming effects on the degradability of native SOC.

The W1 and W2 plots were heated by infrared heaters installed 1.6 m above the soil surface while dummy heaters were installed above the CK plots. Heating started immediately after installation and surface soil temperature was monitored continuously at depths of 5 cm, 10 cm and 20 cm. Compared with the CK plots, surface soil temperature increased by an average of 2 °C throughout the year in the W1 plots, and increased by ~3 °C in winter (mid-October to mid-April) and by 0.5~1 °C for the rest of the year in the W2 plots. On an annual average basis, W1 and W2 treatments represented similar degree of warming but varied scenarios of seasonality. As the Tibetan Plateau is experiencing stronger warming trend in the winter (Chen et al., 2013), W2 treatment represents a more likely seasonality of future warming and likely has a stronger influence on the freeze-thaw cycles or seasonal permafrost dynamics in the soil.

In August 2013, after ~2 years of W1 treatment, we selected three plots in each of the CK, W1 and W2 treatments and collected three soil cores (diameter of 3 cm) up to the depth of 70 cm from