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Temperature sensitivity of organic matter decomposition of permafrost-region soils during laboratory incubations

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ABSTRACT

Permafrost soils contain more than 1300 Pg of carbon (C), twice the amount of C in the atmosphere. Temperatures in higher latitudes are increasing, inducing permafrost thaw and subsequent microbial decomposition of previously frozen C, which will most likely feed back to climate warming through release of the greenhouse gases CO_2 and CH_4. Understanding the temperature sensitivity (Q_{10}) and dynamics of soil organic matter (SOM) decomposition under warming is essential to predict the future state of the climate system. Alaskan tundra soils from the discontinuous permafrost zone were exposed to *in situ* experimental warming for two consecutive winters, increasing soil temperature by 2.3 °C down to 40 cm in the soil profile. Soils obtained at three depths (0–15, 15–25 and 45–55 cm) from the experimental warming site were incubated under aerobic conditions at 15 °C and 25 °C over 365 days in the laboratory. Carbon fluxes were measured periodically and dynamics of SOM decomposition, C pool sizes, and decay rates were estimated. Q_{10} was estimated using both a short-term temperature manipulation ($Q_{10\text{-ST}}$) performed at 14, 100 and 280 days of incubation and via the equal C method ($Q_{10\text{-EC}}$, ratio of time taken for a soil to respire a given amount of C), calculated continuously. At the same time points, functional diversities of the soil microbial communities were monitored for all incubation samples using a microbial functional gene array, GeoChip 5.0. Each array contains over 80,000 probes targeting microbial functional genes involved in biogeochemical cycling of major nutrients, remediation strategies, pathogenicity and other important environmental functions. Of these, over 20,000 probes target genes involved in the degradation of varying C substrates and can be used to quantify the relative gene abundances and functional gene diversities related to soil organic matter turnover. The slow decomposing C pool (C_S), which represented close to 95% of total C in the top 25 cm soils, had a higher Q_{10} than the fast decomposing C pool (C_F) and also dominated the total amount of C released by the end of the incubation. Overall, C_S had temperature sensitivities of $Q_{10\text{-ST}} = 2.55 \pm 0.03$ and $Q_{10\text{-EC}} = 2.19 \pm 0.13$, while the C_F had a temperature sensitivity of $Q_{10\text{-EC}} = 1.16 \pm 0.30$. In contrast to the 15 °C incubations, the 25 °C microbial communities showed reduced diversities of C-degradation functional genes in the early stage of the incubations. However, as the incubations continued the 25 °C communities more closely paralleled the 15 °C communities with respect to the detection of microbial genes utilized in the degradation of labile to recalcitrant C substrates. Two winter seasons of experimental warming did not affect the dynamics and temperature sensitivity of SOM decomposition or the microbial C-degradation

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genes during incubation. However, under the projected sustained warming attributable to climate change, we might expect increased contribution of C_S to organic matter decomposition. Because of the higher Q_{10} and the large pool size of C_S, increased soil organic matter release under warmer temperatures will contribute towards accelerating climate change.

1. Introduction

Permafrost zone soils contain approximately 1330–1580 Pg of organic C, which is twice the amount of atmospheric C (Schuur et al., 2008; Tarnocai et al., 2009; Hugelius et al., 2014; Schuur et al., 2015). Though they cover less than 15% of global soil area, permafrost zone soils store about one-third of total global soil C to 3 m depth (Schuur et al., 2015). Temperatures in high latitude regions are increasing faster than in the rest of the world (Hassol, 2004; Fyfe et al., 2013) and future climate projections indicate a potential increase between 7 and 8 °C by the end of the 21st century (Trenberth et al., 2007; IPCC, 2013). Sustained warming thaws permafrost (Romanovsky et al., 2010; Smith et al., 2010; Koven et al., 2013), leading to a thicker seasonal active layer that exposes a large pool of previously frozen organic C to microbial decomposition (Harden et al., 2012). The release of CO_2 and CH_4 from this newly thawed C by increased microbial activity could add significant quantities of C to the atmosphere. Recent efforts to model permafrost C in response to warming project a shift from a C sink to a source in the arctic and sub-arctic regions by the end of the 21st century, leading to a positive feedback to a warming climate (Koven et al., 2011; Schaefer et al., 2011, 2014).

Soil organic matter is composed of a continuum of C compounds. For simplicity, it is often conceptualized as fast, slow, or passively decomposing C pools (Trumbore, 1997; Amundson, 2001; Schädel et al., 2014). In permafrost zone soils, the fast C pool, with turnover times of a few days to weeks at laboratory temperatures (Schädel et al., 2014), represents less than 10% of total soil C, while the majority belongs to the slow C pool, with turnover times from years to decades (Knoblauch et al., 2013; Schädel et al., 2014) Since slow C is a large proportion of total soil C and has a long residence time, it will dominate the long term response of permafrost soil C decomposition to warming (Schuur et al., 2007; Sistla et al., 2013, 2014).

Soil organic matter decomposition in arctic and subarctic ecosystems undergoing permafrost thaw is controlled by a complex of biophysical interactions including soil temperature, soil moisture, physical and chemical protection, C quality, changes in microbial biomass and microbial communities, and the dominant plant community composition (Hirsch et al., 2002; Wickland and Neff, 2008; Karhu et al., 2010; Waldrop et al., 2010; O'Donnell et al., 2011; Schmidt et al., 2011; Hugelius et al., 2012; Sistla et al., 2013, 2014). Changes in the biophysical factors that control SOM decomposition will likely be reflected most rapidly in the abundance and structure of the microbial communities as they adapt to their new physical and chemical environment (Deslippe et al., 2011; Rinnan et al., 2011; Sistla et al., 2013, 2014). Functional adaptations of microbial communities to seasonal environmental changes have been documented in alpine and arctic tundra soils; winter microbial biomass is fungus dominated, while growing season microbial biomass is bacteria dominated (Schadt et al., 2003; Wallenstein et al., 2007; Buckeridge et al., 2013). New dominant microbial communities and the C substrates they decompose may have different temperature sensitivities, and small changes could have a significant effect on the C balance of permafrost soils (Davidson and Janssens, 2006; Fan et al., 2008).

Field warming experiments often show an initial burst of respiration after the application of the warming manipulation associated with consumption of the fast C pool, followed by a decline in C release rates as slow C increasingly dominates respiration (Kirschbaum, 1995, 2004; Melillo et al., 2002; Eliasson et al., 2005; Knorr et al., 2005; Hartley et al., 2007, 2009; Streit et al., 2014). In these field warming experiments, microbes can acclimate to warming by adjusting their metabolism to the new temperature regime, thus reducing their respiration rate at a given temperature and improving their carbon use efficiency (CUE) (Luo et al., 2001; Barcenas-Moreno et al., 2009). Microbial communities may also shift in composition as a new C balance is established perhaps reflecting the changes in the environment as well as in C availability. Experimental field warming in arctic and low arctic ecosystems have been shown to shift microbial communities toward dominance of fungi over bacteria leading towards increased use of more recalcitrant slow decomposing C and change in the plant–microbial associations that accompany shifts in plant community composition and productivity (Deslippe and Simard, 2011; Deslippe et al., 2011, 2012; Natali et al., 2011; Natali et al., 2012; Sistla et al., 2013, 2014).

Accurate measurements of the turnover rates and temperature sensitivity of fast and slow C decomposition are difficult in field conditions. Field studies measure only the apparent temperature sensitivity because of environmental constraints and the confounding effects of different C pools' contribution to total respiration (Davidson and Janssens, 2006; Kirschbaum, 2013). Laboratory soil incubations are a valuable means for estimating the long-term potential for C release from thawing permafrost soils because environmental constraints over SOM decomposition can be carefully controlled (Holland et al., 2000; Reichstein et al., 2000; Dutta et al., 2006). Continuous C loss measurements from long-term incubation experiments provide information on potential C release, kinetics of soil organic matter decomposition, separation of different C pools comprising the SOM, their decay rates and temperature sensitivities, and the composition and abundance of associated microbial populations (Dutta et al., 2006; Karhu et al., 2010; Lavoie et al., 2011).

While many connections between microbial community compositions and ecosystem functions have been made, it has been recently suggested that ecosystem processes may be more dependent on the abundance and diversity of related functional genes rather than the phylogenetic structures of communities (Philippot et al., 2013; Paula et al., 2014). The utilization of the GeoChip functional gene array provides a platform in which a variety of important functional genes, including critical genes for C-turnover, can be detected even when present at low abundances. The sensitivity of the GeoChip arrays was reported previously over half of probes producing positive signal with 10 or fewer pg of DNA template (He, 2007). It is also specific as probe design accounts for minimal-to-no cross-hybridization of sequences with less than 90% similarity and was designated a quantitative tool in which R^2 values averaged 0.93 for signal intensity and DNA concentration correlations (Liebich et al., 2006; Wu et al., 2006; Zhou et al., 2010, 2012). These arrays allowed for comparison of samples throughout the