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Effects of warming on the degradation and production of low-molecular-weight labile organic carbon in an Arctic tundra soil

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ABSTRACT

The fate of soil organic carbon (SOC) stored in the Arctic permafrost is a key concern as temperatures continue to rise in the northern hemisphere. Studies and conceptual models suggest that degradation of SOC is affected by its composition, but it is unclear exactly which SOC fractions are vulnerable to rapid breakdown and what mechanisms may be controlling SOC degradation upon permafrost thaw. Here, we examine the dynamic consumption and production of labile SOC in an anoxic incubation experiment using soil samples from the active layer at the Barrow Environmental Observatory, Barrow, Alaska, USA. Free-reducing sugars, alcohols, and low-molecular-weight (LMW) organic acids were analyzed during incubation at either −2 or 8 °C for up to 240 days. Results show that degradation of simple sugar and alcohol in SOC largely accounts for the initial rapid release of CO_2 and CH_4 through anaerobic fermentation, whereas the fermentation products, acetate and formate, are subsequently utilized as primary substrates for methanogenesis. Iron(III) reduction is correlated with acetate production and methanogenesis, suggesting its important role as an electron acceptor in SOC respiration in tundra environment. These observations are further supported in a glucose addition experiment, in which rapid CO_2 and CH_4 production occurred concurrently with rapid production and consumption of labile organics such as acetate. However, addition of tannic acid, as a more complex organic substrate, showed little influence on the overall production of CO_2 and CH_4 and organic acids. Together our study shows that LMW labile SOC controls the initial rapid release of green-house gases upon warming of permafrost soils. We present a conceptual framework for the labile SOC transformations and their relations to fermentation, iron reduction and methanogenesis, thereby providing the basis for improved model prediction of climate feedbacks in the Arctic.

1. Introduction

Arctic soils represent a large organic carbon pool, and it is estimated that approximately half of terrestrial soil organic carbon (SOC) is associated with permafrost in high-latitude ecosystems (Schuur et al., 2008; Tarnocai et al., 2009; Hugelius et al., 2014). Climate warming is expected to increase permafrost thaw, both in depth and duration, that could trigger substantially increased degradation of frozen soil organic matter and the release of CH_4 and CO_2 to the atmosphere (Schuur et al., 2009, 2015; McCalley et al., 2014; Koven et al., 2015; Tveit et al., 2015). The effect of thawing permafrost is inevitably associated with increased microbial activity and SOC decomposition (Lipson et al., 2012, 2013), yet it remains largely unknown what and how fast SOC degrades in water-saturated tundra soil under warming. Numerous field and laboratory short-term studies have observed an initial rapid release of CO_2 and CH_4 upon warming, followed by declines in carbon loss rates over time (Waldrop et al., 2010; Lee et al., 2012; Roy Chowdhury et al., 2015; Schuur et al., 2015; Treat et al., 2015), as more labile carbon pools are preferentially degraded (Drake et al., 2015). Conceptual models suggested that this initial, rapid degradation is related to, among other factors, the potential of SOC to decompose (i.e., decomposability) (Schuur et al., 2015), but it is not clear at the molecular level what specific types of SOC are susceptible to rapid breakdown upon thaw. This lack of mechanistic understanding of the biogeochemistry of SOC limits our ability to build process-based

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models in predicting carbon cycling and future climate change in the Arctic (Riley et al., 2011; Graham et al., 2012; Tang and Riley, 2015). It highlights the need for long-term detailed studies of SOC compositional changes, particularly the production and consumption of labile SOC in relation to CH_4 and CO_2 dynamics (Treat et al., 2015) and the degradation rates of permafrost-associated SOC.

We hypothesized that SOC degradation rates are correlated to its composition, i.e., certain types of SOC are more labile and susceptible to rapid breakdown than the other C pools (Hernández and Hobbie, 2010; Pare and Bedard-Haughn, 2013; Jagadamma et al., 2014; Wild et al., 2014; Drake et al., 2015), resulting in initial rapid release of CO_2 and CH_4 upon warming. To test this hypothesis, we monitored the production and consumption of low-molecular-weight (LMW) labile organic compounds such as reducing sugars, ethanol, and acetate during anaerobic incubations with both active-layer organic and mineral soils from a continuous permafrost field site on the Coastal Plain of Alaska. Additionally, we separately studied degradation of glucose, as a simple carbohydrate, and tannic acid, as a more complex polyphenolic compound, during the incubation. Based on previous studies (Lipson et al., 2010, 2013; Herndon et al., 2015a,b), we also examined the role of ferric ion, serving as an important electron acceptor, in SOC respiration and methanogenesis. Using a suite of analytical techniques, we characterized specific labile organic compounds, including C_1–C_4 organic acids, alcohols, and reducing sugars, in the organic and mineral soil layers during incubations at either −2 or 8 °C to mimic the near-freezing and maximum thaw conditions at the Barrow field site in Alaska, USA (Roy Chowdhury et al., 2015). Our study specifically addresses the effect of thaw on transformations of labile SOC and the dynamic changes in C flow through fermentation intermediates to CH_4 and CO_2 emissions.

2. Materials and methods

2.1. Soil sampling and processing

Frozen soil cores were collected in April 2012 (average temperature, −15 °C) from trough areas of a high-center polygon (N 71°16.757′ W 156°36.274) at the Barrow Environmental Observatory (BEO) in northern Alaska, as described previously (Roy Chowdhury et al., 2015; Herndon et al., 2015a,b). A coring auger (manufactured by Jon's Machine Shop in Fairbanks, AK) mounted on a sled was used to collect ~1 m length soil cores in clear PVC liners (3″ diameter × 36″ length) that were sterilized with ethanol prior to use. Soil cores were kept frozen during shipment and stored at −20 °C till the day of processing inside an anoxic glove chamber under a N_2 atmosphere (Coy, Grass Lake, MI). Soil cores were placed on frozen blue ice packs to minimize thaw and a power oscillating tool with sterilized cutting blades was used to section, then homogenize the soil cores in autoclaved containers. Different soil layers were identified by both moist soil Munsell color and the soil chemistry analysis (Table S1). The organic-rich (8–20 cm below ground surface) and the mineral-rich (22–45 cm below surface) soils in the active layer were separated for the incubation study. The very top of the organic layer consisting of plant materials and the bottom ice wedge layer were excluded from the incubation.

2.2. Soil microcosm incubations

The thawed and homogenized wet soil subsamples (150 ± 0.5 g) were then transferred into autoclaved and N_2-purged glass bottles (600 mL, VWR International) in the anoxic chamber. They were subsequently sealed tightly with thick butyl rubber stoppers and capped. Soil samples were taken and analyzed at selected time intervals from once a week for the first two months of incubation and then once every two weeks after 60 days. The headspace was evacuated (with a vacuum pump) and flushed at least three times with N_2 after each sampling event to remove residual CO_2 and CH_4 for subsequent measurements of the CO_2 and CH_4 production. Net CO_2 and CH_4 production was calculated by subtracting any remaining CO_2 and CH_4 in solution after N_2 purging. All samples were incubated in the dark at two temperatures (−2 °C and 8 °C). Three replicates per temperature per soil layer in separate bottles were incubated for up to 240 days under anoxic conditions.

At the later stage of the microcosm experiments, glucose and tannic acid were added to soil incubations at 8 °C to study their effects on SOC anaerobic respiration and transformations. Dissolved D-(+)-glucose (Sigma Aldrich) in water (0.1 M) was added on day 144 when the degradation or production of CO_2 and CH_4 reached a steady state. Only a small volume (<1 mL) was introduced to the soil, well mixed using a spatula, to minimize effects on the soil water content and soil chemistry. The total amounts of glucose added to the organic and mineral soils were 6.0 ± 1.0 and 0.5 ± 0.1 μmol of glucose-C g^{-1} dwt. soil (dry weight of soil), respectively, comparable to the amounts of reducing sugars in the initial soils. The reducing sugar concentrations were then monitored periodically, along with CO_2 and CH_4 production, organic acids, alcohols, and Fe concentrations, as described above. Tannic acids (JT Baker) were added on day 188 after observing that the production of CO_2 and CH_4 (or organic acids) reached a new steady state. Similar to the glucose addition on day 144, only a small amount of tannic acid was added, equivalent to 5 and 0.5 μmol of tannic acid g^{-1} dwt. soil to the organic and mineral layer soils, respectively.

2.3. Analytical techniques

Headspace CO_2 and CH_4 were analyzed with a gas chromatograph (GC) equipped with a methanizer and a flame ionization detector (SRI 8610C, SRI Instruments, Torrance, CA) with He as the carrier gas. A gas-tight syringe was used first to mix the gas by drawing and pumping the headspace gas several times in each sealed incubation bottle, and then to take a 0.5 mL of headspace gas sample and immediately injected into the GC for analysis. Calibration with gas standards (99.99%; Scotty Specialty Gas Calibration Standards, Sigma Aldrich) was performed prior to the sample analysis. Gas production rates (μmol g^{-1} dwt. soil day^{-1}) were estimated by the change of gas concentrations between every two adjacent measured time points during incubation. The dissolved gas concentrations were calculated using Henry's law after correcting for temperature and soil pH. Subsamples (n = 3) of the organic and mineral soils were taken for the determination of water content, soil pH, total C and N using similar methods as described previously (Roy Chowdhury et al., 2015).

Aliquots of wet soil samples (1–2 g from the 600-mL incubation) were taken at pre-determined time intervals and subsequently equilibrated with either 10 mM NH_4HCO_3 (pH ~ 7.3) or 0.1 M KCl (pH ~ 5.0) solution. The NH_4HCO_3 extraction (6 h) was used for determining soluble soil organic matter compositions, whereas the KCl extraction (2 h) was used to determine exchangeable and dissolved inorganic species including Fe(II), Fe(III), major anions and cations. Samples were centrifuged for 15 min at 6500 × *g*, and the supernatants were collected and subsequently filtered through 0.45-μm membrane filters before analysis. Exchangeable Fe(II) concentrations from filtered KCl extract samples were quantified using the HACH (Loveland, Colorado) Ferrous method 8146 (1,10-phenanthroline) on a HACH DR 900 colorimeter, whereas the total dissolved iron concentrations were determined using the HACH FerroVer method 8008. Samples were diluted as necessary, and the colorimeter was calibrated with