



Input of easily available organic C and N stimulates microbial decomposition of soil organic matter in arctic permafrost soil



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ABSTRACT

Rising temperatures in the Arctic can affect soil organic matter (SOM) decomposition directly and indirectly, by increasing plant primary production and thus the allocation of plant-derived organic compounds into the soil. Such compounds, for example root exudates or decaying fine roots, are easily available for microorganisms, and can alter the decomposition of older SOM (“priming effect”). We here report on a SOM priming experiment in the active layer of a permafrost soil from the central Siberian Arctic, comparing responses of organic topsoil, mineral subsoil, and cryoturbated subsoil material (i.e., poorly decomposed topsoil material subducted into the subsoil by freeze–thaw processes) to additions of ¹³C-labeled glucose, cellulose, a mixture of amino acids, and protein (added at levels corresponding to approximately 1% of soil organic carbon). SOM decomposition in the topsoil was barely affected by higher availability of organic compounds, whereas SOM decomposition in both subsoil horizons responded strongly. In the mineral subsoil, SOM decomposition increased by a factor of two to three after any substrate addition (glucose, cellulose, amino acids, protein), suggesting that the microbial decomposer community was limited in energy to break down more complex components of SOM. In the cryoturbated horizon, SOM decomposition increased by a factor of two after addition of amino acids or protein, but was not significantly affected by glucose or cellulose, indicating nitrogen rather than energy limitation. Since the stimulation of SOM decomposition in cryoturbated material was not connected to microbial growth or to a change in microbial community composition, the additional nitrogen was likely invested in the production of extracellular enzymes required for SOM decomposition. Our findings provide a first mechanistic understanding of priming in permafrost soils and suggest that an increase in the availability of organic carbon or nitrogen, e.g., by increased plant productivity, can change the decomposition of SOM stored in deeper layers of permafrost soils, with possible repercussions on the global climate.

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1. Introduction

Soil organic matter (SOM) decomposition rates in permafrost soils are expected to increase with rising temperatures in the Arctic (Hartley et al., 2008; Conant et al., 2011). In addition to the direct temperature effect, warming might also indirectly affect SOM decomposition, mediated by an increase in plant net primary production. Higher plant productivity is accompanied by an increased input of plant-derived C into the soil (as root litter or root exudates), and can thus increase soil C stocks, as observed for a mineral subsoil in the Alaskan tundra (Sistla et al., 2013). In contrast, higher productivity was found to reduce soil C stocks in a sub-arctic system, offsetting the increase in above- and belowground plant biomass, and, consequently, leading to a net loss of C from the ecosystem (Hartley et al., 2012).

Plants supply the soil microbial community with a range of organic compounds that can be either immediately taken up by microorganisms (e.g., sugars, amino acids and organic acids from root exudation), or that can be easily decomposed (e.g., cellulose and protein from root litter). These organic compounds can stimulate the soil microbial community to decompose more SOM (“priming effect”; Bingeman et al., 1953), (i) by promoting microbial groups that target complex compounds of SOM (Fontaine et al., 2003), (ii) by providing the energy to break down these compounds (Blagodatskaya and Kuzyakov, 2008), or (iii) by providing C for microbial growth, thus increasing microbial N demand and facilitating N mining, i.e., the microbial breakdown of SOM to get access to N (Craine et al., 2007; Dijkstra et al., 2013).

The latter two mechanisms might be of particular importance in arctic soils. Microbial activity in arctic soils is considered N limited (Sistla et al., 2012), suggesting that an increased allocation of plant C to the soil might strongly stimulate N mining. Additionally, microbial activity in subsoil horizons in general is considered energy limited (Fontaine et al., 2007), as the subsoil is poorly rooted, and supply of plant-derived compounds from root exudation and root litter is scarce. With 80% of arctic SOM located below 30 cm (Tarnocai et al., 2009), a large amount of SOM might be protected from decomposition by energy limitation of microbial decomposers, and might thus be particularly susceptible to an increased input of plant-derived compounds. So far, it is unknown how SOM decomposition in different horizons of arctic permafrost soils will respond to an increased input of plant-derived organic compounds, and what mechanisms might be involved.

We here report on the susceptibility of different soil horizons from a tundra ecosystem in the central Siberian Arctic to an increased availability of organic compounds. In a priming experiment, we compared organic topsoil and mineral subsoil material, as well as cryoturbated material, i.e., topsoil material that was buried in the subsoil by freeze–thaw processes (Bockheim, 2007; Tarnocai et al., 2009). Cryoturbated organic matter is common in arctic soils, accounting for approximately 400 Gt of C (Harden et al., 2012). Although it is chemically similar to topsoil organic matter (Xu et al., 2009), it shows retarded decomposition as indicated by low respiration rates (Kaiser et al., 2007) and relatively old radiocarbon ages (Kaiser et al., 2007; Xu et al., 2009; Hugelius et al., 2010). We hypothesized that an increased availability of organic compounds would stimulate SOM decomposition in the subsoil (i.e., in mineral subsoil and cryoturbated horizons) by providing energy for microbial decomposers, but less so in the topsoil, where energy is not limiting. Additionally, we tested if priming of SOM decomposition was connected to N mining, by comparing the effect of organic substrates with and without N. We expected that N-containing substrates would result in a weaker priming effect than substrates without N, by reducing the dependence of the microbial

community on SOM as an N source. Finally, we investigated if priming of SOM decomposition was connected to a shift in microbial community composition.

To that end, we analyzed SOM-derived respiration and microbial community composition in soil samples amended with ^{13}C -labeled glucose, cellulose, amino acids, or protein, in comparison with unamended controls. We thus compared substrates containing N to substrates without N, as well as monomeric substrates to polymeric substrates. Since monomeric substrates are immediately available for microorganisms, whereas polymeric substrates need to be broken down by extracellular enzymes before microbial uptake, they might differ in their effect on microbial community composition and function, and thus on SOM decomposition (Fontaine et al., 2003).

2. Material & methods

2.1. Soil sampling

Soils were sampled on the Taymyr peninsula in the central Siberian Arctic ($72^{\circ} 29.57' \text{ N}$, $101^{\circ} 38.62' \text{ E}$), from a shrubby moss tundra (bioclimatic subzone D; CAVM Team, 2003) dominated by *Cassiope tetragona*, *Carex arctisibirica*, *Tomentypnum nitens* and *Aulacomnium turgidum*. The soil was described as a Turbic Cryosol according to the World Reference Base for Soil Resources (IUSS Working Group WRB, 2007) or Typic Aquiturbel according to the US Soil Taxonomy (Soil Survey Staff, 1999), with fine to coarse loamy texture and an active layer depth of around 80 cm at the time of sampling in August 2011. We took samples from three soil horizons in the active layer: We sampled the OA horizon (topsoil material), as well as a buried Ajj (cryoturbated material) and the adjacent BCg horizon (mineral subsoil material), the latter two from a depth of 50–70 cm. Soils were sampled in a 2 m-wide soil profile by pooling samples taken horizontally with a metal soil corer within each horizon. We took care that the mineral subsoil material sampled did not include buried organic material and vice versa. Living roots were carefully removed and samples homogenized by hand directly after sampling. Carbon and nitrogen contents of the individual horizons were 9.4% C and 0.5% N for topsoil material, 4.3% C and 0.2% N for cryoturbated material, and 0.6% C, 0.1% N for mineral subsoil material (determined with a Perkin Elmer 2400 Series II CHNS/O analyzer).

2.2. Incubation experiment

To investigate the effect of increased C availability on SOM decomposition, we amended the soils with ^{13}C -labeled glucose, amino acids, cellulose, or protein. ^{13}C -labeled glucose was purchased from Sigma–Aldrich (U- ^{13}C , 99 at%), ^{13}C -labeled amino acids from Cambridge Isotope Laboratories (algal amino acid mixture, U- ^{13}C , 97–99 at%), ^{13}C -labeled cellulose from Isolife (low degree of polymerization *Cichorium intybus*, U- ^{13}C , >97 at%), and ^{13}C -labeled protein from Sigma–Aldrich (algal crude protein extract, U- ^{13}C , 98 at%). All substrates were mixed with the respective unlabeled compounds to 10 at% ^{13}C before application, and all substrates were applied in dry form.

Aliquots of fresh soil were amended with glucose, amino acids, cellulose or protein of 10 at% ^{13}C , in five replicates of 25 g per treatment, or left unamended as controls (three sets of five 25 g replicates). We adjusted the amount of substrate to the approximate C content of each horizon by adding $554 \mu\text{g C g}^{-1}$ to topsoil material, $138 \mu\text{g C g}^{-1}$ to cryoturbated material and $55 \mu\text{g C g}^{-1}$ to mineral subsoil material. One set of controls was immediately harvested to determine the initial state before the start of the incubation; the remaining samples were filled into microcosms

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