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The effect of warming on the vulnerability of subducted organic carbon in arctic soils

Petr Čapek [a, *], Kateřina Diáková [a], Jan-Erik Dickopp [b], Jiří Bárta [a], Birgit Wild [c, d, e], Jörg Schnecker [c, d, f], Ricardo Jorge Eloy Alves [d, g], Stefanie Aiglsdorfer [g], Georg Guggenberger [h], Norman Gentsch [h], Gustaf Hugelius [j], Nikolaj Lashchinsky [k], Antje Gittel [l, m], Christa Schleper [d, g, k], Robert Mikutta [h, i], Juri Palmtag [j], Olga Shibistova [h, n], Tim Urich [d, g, o], Andreas Richter [c, d], Hana Šantrůčková [a, **]

[a] University of South Bohemia, Department of Ecosystems Biology, Branišovská 31, České Budějovice, Czech Republic
[b] Institute of Systematic Botany and Ecology, University of Ulm, Albert-Einstein-Allee 11, D-89081 Ulm, Germany
[c] University of Vienna, Department of Microbiology and Ecosystem Research, Division of Terrestrial Ecosystem Research, Althanstrasse 14, 1090 Vienna, Austria
[d] Austrian Polar Research Institute, Althanstrasse 14, 1090 Vienna, Austria
[e] University of Gothenburg, Department of Earth Sciences, Guldhedsgatan 5A, 40530 Gothenburg, Sweden
[f] University of New Hampshire, Department of Natural Resources & the Environment, Durham, NH 03824, USA
[g] University of Vienna, Department of Ecogenomics and Systems Biology, Division of Archaea Biology and Ecogenomics, Vienna, Austria
[h] Leibniz Universität Hannover, Institute of Soil Science, Herrenhäuser Strasse 2, 30419 Hannover, Germany
[i] Martin-Luther-University Halle-Wittenberg, Soil Sciences, 06120 Halle, Germany
[j] University of Stockholm, Department of Physical Geography, 10691 Stockholm, Sweden
[k] Central Siberian Botanical Garden, Siberian Branch of the Russian Academy of Sciences, St. Zolotodolinskaya 101, 630090 Novosibirsk, Russian Federation
[l] University of Bergen, Department of Biology, Centre for Geobiology, Thormohlensgate 53B, 5020 Bergen, Norway
[m] Center for Geomicrobiology, Department of Bioscience, Ny Munkegade 114, 8000 Aarhus C, Denmark
[n] VN Sukachev, Institute of Forest, Siberian Branch of the Russian Academy of Sciences, Akademgorodok, 660036 Krasnoyarsk, Russian Federation
[o] University of Greifswald, Institute for Microbiology, 17489 Greifswald, Germany

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ABSTRACT

Arctic permafrost soils contain large stocks of organic carbon (OC). Extensive cryogenic processes in these soils cause subduction of a significant part of OC-rich topsoil down into mineral soil through the process of cryoturbation. Currently, one-fourth of total permafrost OC is stored in subducted organic horizons. Predicted climate change is believed to reduce the amount of OC in permafrost soils as rising temperatures will increase decomposition of OC by soil microorganisms. To estimate the sensitivity of OC decomposition to soil temperature and oxygen levels we performed a 4-month incubation experiment in which we manipulated temperature (4–20 °C) and oxygen level of topsoil organic, subducted organic and mineral soil horizons. Carbon loss (C_{LOSS}) was monitored and its potential biotic and abiotic drivers, including concentrations of available nutrients, microbial activity, biomass and stoichiometry, and extracellular oxidative and hydrolytic enzyme pools, were measured. We found that independently of the incubation temperature, C_{LOSS} from subducted organic and mineral soil horizons was one to two orders of magnitude lower than in the organic topsoil horizon, both under aerobic and anaerobic conditions. This corresponds to the microbial biomass being lower by one to two orders of magnitude. We argue that enzymatic degradation of autochthonous subducted OC does not provide sufficient amounts of carbon and nutrients to sustain greater microbial biomass. The resident microbial biomass relies on allochthonous fluxes of nutrients, enzymes and carbon from the OC-rich topsoil. This results in a "negative priming effect", which protects autochthonous subducted OC from decomposition at present. The vulnerability of subducted organic carbon in cryoturbated arctic soils under future climate conditions will largely depend on the amount of allochthonous carbon and nutrient fluxes from the topsoil.

* Corresponding author. Tel.: +420 387772347; fax: +420 387 772 368.
** Corresponding author. Tel.: +420 387772361; fax: +420 387 772 368.
E-mail addresses: petacapek@gmail.com (P. Čapek), hana.santruckova@prf.jcu.cz (H. Šantrůčková).

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1. Introduction

Soils in permafrost areas contain an estimated ~1300 ± 200 Pg of organic carbon (OC), of which ~500 Pg resides in non-permafrost soils or in deeper taliks or is seasonally thawed (i.e. in the "active layer"), while ~800 Pg is perennially frozen (Hugelius et al., 2014). Much of this OC is predicted to be vulnerable to extensive decomposition under warming climate conditions of the northern circumpolar region (Davidson and Janssens, 2006; Zimov et al., 2006; Schuur et al., 2008, 2009). Several studies in the arctic have already shown increasing carbon loss from upper top and permanently frozen soil horizons under higher temperatures (Oechel et al., 1993; Schuur et al., 2009; Schädel et al., 2014). As well as rising temperatures, recent model scenarios predict an increase of precipitation and the occurrence of more numerous anaerobic sites, which can lead to methane production and release of additional carbon from permafrost-affected soils (Olefeldt et al., 2013). Therefore, both aerobic and anaerobic carbon transformation processes need to be included in predictions of OC vulnerability to decomposition.

Permafrost soils are extensively affected by cryogenic processes (repeated freeze and thaw cycles of the active layer), which result in subduction of carbon rich topsoil organic horizons deeper into the soil profile (Bockheim and Tarnocai, 1998). The amount of OC in subducted organic horizons can make up 90% of total OC in the first meter of soil (Bockheim, 2007), and in total it represents approximately one-fourth of all OC currently stored in permafrost soils (Harden et al., 2012). Recent data indicates lower OC quality and distinctly different microbial community composition and enzyme activities of subducted organic horizons in comparison with topsoil organic horizons (Harden et al., 2012; Gittel et al., 2014; Schnecker et al., 2014; Gentsch et al., 2015a, 2015b), which presumably is the cause of the retarded decomposition of subducted OC previously observed (Kaiser et al., 2007; Wild et al., 2014). As a result, the age of organic C in cryoturbated organic pockets could reach several thousand years (Bockheim, 2007; Kaiser et al., 2007; Hugelius et al., 2014; Palmtag et al., 2015). Although the effects of temperature and oxygen level on the rate of OC decomposition are generally well studied and many investigations have documented significant positive effects of both, specific studies on subducted OC are still scarce (Schädel et al., 2014).

Without a direct manipulation study, the vulnerability of subducted OC decomposition to warming is currently impossible to predict from these findings. The effect of temperature on OC decomposition is not uniform across published studies because it is confounded by other factors such as oxygen level, OC quality, nutrients, microbial physiology and enzymatic performance (e.g. Giardina and Ryan, 2000; Brown et al., 2004; Hyvonen et al., 2005; Conant et al., 2008; Allen and Gillooly, 2009; Allison et al., 2010; Davidson et al., 2012; Steinweg et al., 2013). Because of such multifactorial control, no general mechanism of the temperature effect on OC decomposition has become widely accepted (Reichstein et al., 2005; Agren and Wetterstedt, 2007; Allison et al., 2010; Sierra, 2012). According to kinetic theory, the temperature sensitivity of OC decomposition is a function of OC quality (Knorr et al., 2005; Davidson and Janssens, 2006; Conant et al., 2008). The lower the OC quality, the higher is the temperature sensitivity as the decomposition of low quality OC requires more energy. According to metabolic theory, the temperature sensitivity of OC decomposition is determined by the temperature sensitivity of heterotrophic microbial metabolism and thus is independent of OC quality per se (Allen et al., 2005; Yvon-Durocher et al., 2012). Variability in temperature sensitivity of OC decomposition depends entirely on changes in the amount and physiology of microbial biomass, which might be induced by a multitude of different factors (for example, OC quality change). When estimating the effects of temperature and other abiotic or biotic factors on OC decomposition, it is necessary to include not only the effect of OC quality but also effects on microbial activity.

The main objective of the present study was to estimate the temperature sensitivity of OC decomposition in a subducted organic horizon under aerobic and anaerobic conditions and identify key factors determining this sensitivity. We hypothesize that the observed distinctly different composition of microbial communities, low OC quality and inadequate enzymatic activities in the subducted organic horizon pose the barrier for OC utilization by microbial biomass. We expect the increase of OC depolymerization by extracellular enzymes leading to an increase of carbon and nutrient supply to microbial biomass and its increase at higher temperatures. This will result in higher temperature sensitivity of OC decomposition in comparison with regular soil horizons. We further expect slower decomposition of subducted OC and lower temperature sensitivity under anaerobic conditions. To test these hypotheses we set up a 4-month incubation experiment, in which we manipulated the temperature and oxygen level of subducted organic, upper organic and lower mineral horizons. We determined soil carbon loss and the potential biotic and abiotic drivers of OC decomposition, including concentrations of available nutrients, microbial activity and its biomass and stoichiometry, and extracellular oxidative and hydrolytic enzyme pools.

2. Materials and methods

2.1. Soil sampling and preparation

Soil samples for the incubation experiment were collected from a shrubby moss tundra site on the Taymir peninsula, Russia (72°29.57′N, 101°38.62′E). This area is within a continuous permafrost zone. Active layer depth at the sampling site reached 65–90 cm in August 2011. Vegetation was dominated by *Cassiope tetragona*, *Carex arctisibirica* and *Aulacomnium turgidum*. The soil was classified as fine loamy to coarse loamy Typic Aquiturbel according to the US Soil Taxonomy (Soil Survey Staff, 1999) or as Turbic Cryosol according to the World Reference Base for Soil Resources (IUSS Working Group WRB, 2007). Bulk samples from three different horizons within the active layer were collected: topsoil organic material from an OA horizon at the surface (further referred to as O horizon), subducted organic material from an Ajj horizon, and mineral subsoil material from the BCg horizon, the latter two from a depth of 50–70 cm. The mineral subsoil material sampled did not include cryoturbated organic material. Living roots were removed from bulk samples after sampling and soil material was kept at 4 °C until processing. Bulk soil material was homogenized before the start of the laboratory incubation and assessed for basic chemical, physical and microbial characteristics (Table 1).

2.2. Incubation setup

A 19 week-long incubation experiment was performed for each soil horizon (O, Ajj and BCg) at three different temperatures (4, 12 and 20 °C) and three moisture levels (50, 80 and 100% of water holding capacity; WHC) in four replicates. The two lower moisture treatments (50 and 80% WHC) used aerobic conditions, whereas the 100% WHC treatment used anaerobic conditions. Aerobic treatments were regularly flushed with moist air to maintain the oxygen concentration at the atmospheric level and to avoid oxygen limitation. For the anaerobic treatment, the headspaces of the incubation bottles were maintained anoxic by filling them with a He/CO_2 mixture (5% CO_2, 95% He). A CO_2 concentration of 5% was chosen to correspond with CO_2 concentrations commonly detected