



## Fate of carbohydrates and lignin in north-east Siberian permafrost soils



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### ABSTRACT

Permafrost soils preserve huge amounts of organic carbon (OC) prone to decomposition under changing climatic conditions. However, knowledge on the composition of soil organic matter (OM) and its transformation and vulnerability to decomposition in these soils is scarce. We determined neutral sugars and lignin-derived phenols, released by trifluoroacetic acid (TFA) and CuO oxidation, respectively, within plants and soil density fractions from the active layer and the upper permafrost layer at three different tundra types (shrubby grass, shrubby tussock, shrubby lichen) in the Northeast Siberian Arctic. The heavy fraction (HF;  $> 1.6 \text{ g mL}^{-1}$ ) was characterized by a larger enrichment of microbial sugars (hexoses vs. pentoses) and more pronounced lignin degradation (acids vs. aldehydes) as compared to the light fraction (LF;  $< 1.6 \text{ g mL}^{-1}$ ), showing the transformation from plant residue-dominated particulate OM to a largely microbial imprint in mineral-associated OM. In contrast to temperate and tropical soils, total neutral sugar contents and galactose plus mannose to arabinose plus xylose ratios (GM/AX) decreased in the HF with soil depth, which may indicate a process of effective recycling of microbial biomass rather than utilizing old plant materials. At the same time, lignin-derived phenols increased and the degree of oxidative decomposition of lignin decreased with soil depth, suggesting a selective preservation of lignin presumably due to anaerobiosis. As large parts of the plant-derived pentoses are incorporated in lignocelluloses and thereby protected against rapid decomposition, this might also explain the relative enrichment of pentoses with soil depth. Hence, our results show a relatively large contribution of plant-derived OM, particularly in the buried topsoil and subsoil, which is stabilized by the current soil environmental conditions but may become available to decomposers if permafrost degradation promotes soil drainage and improves the soil oxygen supply.

### 1. Introduction

Arctic permafrost-affected soils store around 1300 Gt carbon (Hugelius et al., 2014), which accounts for approximately 50% of the global soil organic carbon (OC) pool. Organic matter (OM) in permafrost soils has been protected from microbial decomposition by the

climatic conditions at high-latitudes, i.e., by being perennially frozen in the permafrost exposed to seasonally frozen conditions in the active layer as well as by the frequent soil water saturation (Chapin et al., 1980; Schuur et al., 2008). However, increasing temperatures and changing precipitation pattern will likely promote permafrost loss, changes in plant productivity, species composition and plant-soil C

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allocation, and soil organic matter (SOM) decomposition, which likely facilitate either directly or indirectly further carbon release to the atmosphere and a possible positive feedback to global warming (Schuur et al., 2011; Runyan and D'Odorico, 2012; Gentsch et al., 2015b; Wild et al., 2016).

The chemical composition and accumulation of OM in different soil horizons of a particular ecosystem reveals the state of OM decomposition, which is an integral result of both biotic and abiotic soil conditions. Carbohydrates entering the soil system with plant rhizodeposits, roots and aboveground litter as well as products of microbial and faunal metabolism represent a major energy source for heterotrophic soil microbial communities (Cheshire, 1979; Murayama, 1984; Gunina and Kuzyakov, 2015). Plant-derived carbohydrates in soils are represented by relatively greater proportions of pentoses (e.g., arabinose and xylose), whereas sugars of microbial origin are relatively richer in hexoses (e.g., galactose and mannose) and deoxysugars (e.g., fucose and rhamnose) (Murayama, 1984; Oades, 1984). While plant-derived sugars are reported to decompose rapidly in soil (Martin and Haider, 1986), microbially synthesized sugars can contribute to older SOM fractions when stabilized physically or chemically (Tsutsuki and Kuwatsuka, 1989; Guggenberger et al., 1994; Rumpel et al., 2010) or upon their continuous recycling by microorganisms (Sauheitl et al., 2005; Derrien et al., 2006).

Unlike carbohydrates, lignin is exclusively derived from plants. This aromatic biopolymer contains resistant C bonds, e.g., C-O-C and C-C between the monomeric phenylpropanoid units, and is intimately associated with celluloses and hemicelluloses, i.e., lignocelluloses. The degradation of lignin is primarily driven by fungi. White-rot fungi are most efficient in lignin degradation and mineralization (Haider and Trojanowski, 1980; Arora and Sharma, 2010) while brown-rot fungi preferentially degrade celluloses and hemicelluloses, and modify lignin only to a limited extent (Highley and Illman, 1991). In addition to fungi, three groups of bacteria *actinomycetes*, *α-proteobacteria*, and *γ-proteobacteria* (Zimmermann, 1990; Bugg et al., 2011) are also partly involved in lignocellulose degradation. As most microbial lignolytic enzymes, e.g., peroxidases and laccases, are mainly active under presence of oxygen, complete lignin degradation is basically restricted to aerobic soil conditions (Kirk and Farrell, 1987; Bugg et al., 2011). Due to its biochemical resistance and limited abundance of ligninolytic degraders in soils, lignin has been considered in the literature to be slowly degradable in soils and to represent the slower C-cycling fraction of plant litter (Haider et al., 1975; Stevenson, 1994). However, the rate of lignin decomposition in soil is still under debate. For example, Kiem and Kögel-Knabner (2003) used CuO oxidation to determine soil lignin contents and composition in fertilized land vs. bare fallow, and found no evidence for long-term stabilization of lignin in soil. Furthermore, compound-specific isotope analysis of lignin phenols derived from CuO oxidation indicated that lignin turnover can be as fast or even faster than that of bulk SOM (Dignac et al., 2005; Heim and Schmidt, 2007) or bulk litter (Sanaullah et al., 2010; Klotzbücher et al., 2011).

The fate of carbohydrates and lignin has been investigated intensively in temperate soils (Kögel et al., 1988; Guggenberger et al., 1994; Spielvogel et al., 2007), tropical soils (Guggenberger et al., 1995; Möller et al., 2002), tropical wetlands (Tareq et al., 2004), and tropical

and European peat soils (Bourdon et al., 2000; Bambalov, 2007). However, the understanding of OM transformation in permafrost soils is still scarce. Gundelwein et al. (2007) determined acid insoluble lignin, i.e., Klason lignin, of a few permafrost soil samples from central Siberia and suggested a restrained degradation of lignin in the lower parts of the active layer in permafrost soils. Höfle et al. (2013) applied <sup>13</sup>C-NMR spectroscopy and lipid analysis of permafrost soils and reported that the chemical composition and inherent decomposability of organic substances play a more important role in OM stabilization than the formation of mineral-organic association, which contrasts findings for temperate soils (Marschner et al., 2008). Likewise, Gentsch et al. (2015b) used <sup>13</sup>C-NMR and X-ray photoelectron spectroscopy to show a progressive alteration of OM composition with increasing soil depth. However, these spectroscopic techniques only provide an overview of the total OM composition, and lipid analysis might reflect the origin of OM rather than its degradation state.

To characterize the detailed composition and transformation of OM in permafrost soils and its potential vulnerability to climate warming, we investigated the carbohydrate and lignin signatures of plants and soil samples from the active layer (seasonal thawing) and the upper permafrost layer in north-eastern Siberia by using chemolytic methods. Since on landscape level, tundra vegetation is highly heterogeneous (Fletcher et al., 2010), we included three tundra types (shrubby grass, shrubby tussock, shrubby lichen) in our study to examine their impact to SOM quality and transformation. As the majority of OM in permafrost soils resides in mineral-organic associations (Gentsch et al., 2015a), which is considered relatively stable against biodegradation (Torn et al., 1997; Kalbitz et al., 2005; Mikutta et al., 2006), we applied density fractionation to separate the light fraction (LF; < 1.6 g mL<sup>-1</sup>), containing mainly particulate OM (POM), from the heavy fraction (HF; > 1.6 g mL<sup>-1</sup>), comprising mostly mineral-associated OM (MOM). We hypothesized that (i) lignin decomposition is restrained in deeper soil horizons because of the low temperature and frequent anoxic conditions and (ii) plant-derived carbohydrates decline with soil depth, as they represent an easily available carbon and energy source also under anoxic conditions. Hence, permafrost-affected soils with their unfavorable environmental conditions for microbial decomposition may be relatively enriched in lignin-derived components, particularly at larger soil depth.

## 2. Materials and methods

### 2.1. Soil and vegetation samples

The study was carried out at three different tundra types (shrubby grass, shrubby tussock and shrubby lichen) along the lower Kolyma river near the settlement Cherskiy, Russia (Table 1), within the zone of continuous permafrost (Brown et al., 1998). According to WorldClim database, the mean annual precipitation is 160 mm and the mean annual temperature is -12.7 °C (Hijmans et al., 2005). All soils in the study area were classified as Gelisols with intensive cryoturbation. Three 5-m wide soil profiles per each tundra type were excavated and soil horizons from active layer and the upper permafrost (up to 45 cm depth below the permafrost table) were sampled at the end of summer

**Table 1**  
Sampling sites, vegetation and soil classification (Gentsch et al., 2015b).

Tundra type	Latitude	Longitude	Dominant plants	Active layer depth	Soil classification and texture
Shrubby grass tundra	N69° 26' 15.5"	E161° 42' 36.4"	<i>Betula exilis</i> , <i>Salix sphenophylla</i> , <i>Carex lugens</i> , <i>Calamagrostis holmii</i> , <i>Aulacomnium turgidum</i>	30–70	Ruptic-Histic Aquiturbel, fine silty
Shrubby tussock tundra	N69° 26' 46.0"	E161° 45' 5.5"	<i>Eriophorum vaginatum</i> , <i>Carex lugens</i> , <i>Betula exilis</i> , <i>Salix pulchra</i> , <i>Aulacomnium turgidum</i>	35–60	Ruptic-Histic Aquiturbel, clayey to fine silty
Shrubby lichen tundra	N68° 44' 51.9"	E161° 35' 40.5"	<i>Betula exilis</i> , <i>Vaccinium uliginosum</i> , <i>Flavocetraria nivalis</i> , <i>Flavocetraria cucullata</i>	35–90	Ruptic-Histic Aquiturbel, fine silty to loam-skeletal

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