AGU ADVANCING EARTH AND SPACE SCIENCE

JGR Biogeosciences

RESEARCH ARTICLE
10.1029/2020JG006181

Lignin Preservation and Microbial Carbohydrate Metabolism in Permafrost Soils

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Abstract Permafrost-affected soils in the northern circumpolar region store more than 1,000 Pg soil organic carbon (OC), and are strongly vulnerable to climatic warming. However, the extent to which changing soil environmental conditions with permafrost thaw affects different compounds of soil organic matter (OM) is poorly understood. Here, we assessed the fate of lignin and non-cellulosic carbohydrates in density fractionated soils (light fraction, LF vs. heavy fraction, HF) from three permafrost regions with decreasing continentality, expanding from east to west of northern Siberia (Cherskiy, Logata, Tazovskiy, respectively). In soils at the Tazovskiy site with thicker active layers, the LF showed smaller OC-normalized contents of lignin-derived phenols and plant-derived sugars and a decrease of these compounds with soil depth, while a constant or even increasing trend was observed in soils with shallower active layers (Cherskiy and Logata). Also in the HF, soils at the Tazovskiy site had smaller contents of OC-normalized lignin-derived phenols and plant-derived sugars along with more pronounced indicators of oxidative lignin decomposition and production of microbial-derived sugars. Active layer deepening, thus, likely favors the decomposition of lignin and plant-derived sugars, that is, lignocelluloses, by increasing water drainage and aeration. Our study suggests that climate-induced degradation of permafrost soils may promote carbon losses from lignin and associated polysaccharides by abolishing context-specific preservation mechanisms. However, relations of OC-based lignin-derived phenols and sugars in the HF with mineralogical properties suggest that future OM transformation and carbon losses will be modulated in addition by reactive soil minerals.

Plain Language Summary Permafrost thawing and subsequent decomposition of large parts of the soil organic carbon (OC) currently stored in the northern circumpolar permafrost region are projected to cause a positive feedback on global warming. To understand the potential consequences of climate change for organic matter (OM) decomposition in permafrost soils, we determined the concentration and degree of decomposition of two dominating constituents of soil OM, lignin and non-cellulosic carbohydrates by using CuO oxidation and TFA hydrolysis, respectively, in density fractionated soils covering a longitudinal gradient of northern Siberia (from east to west: Cherskiy; Logata; Tazovskiy). We found a stronger degradation of lignin and neutral sugars at Tazovskiy with its shallower active layer, probably due to better aeration, as compared to the other sites. Our study, hence, suggests that climate-induced degradation of permafrost soils will promote lignin and carbohydrate transformation and carbon loss. In addition, larger contents of clay and Fe and Al oxides at the Cherskiy site with appear to favor accumulation of lignin and neutral sugars, likely suggesting the extent of OM transformation is further modulated by soil mineralogical properties.

Key Points:

- The deepening of active layer favors the decomposition of lignin and plant-derived sugars in permafrost soils
- Soil clay and mineral phases appear to favor accumulation of lignin and neutral sugars in permafrost soils
- Magnitude of climate-induced degradation of lignin and carbohydrates will depend on soil texture and mineralogical properties

Supporting Information:

Supporting Information may be found in the online version of this article.

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Citation:
Dao, T. T., Mikutta, R., Sauheitl, L., Gentsch, N., Shibistova, O., Wild, B., et al. (2022). Lignin preservation and microbial carbohydrate metabolism in permafrost soils. *Journal of Geophysical Research: Biogeosciences*, *127*, e2020JG006181. https://doi.org/10.1029/2020JG006181

Received 27 FEB 2021
Accepted 11 OCT 2021

1. Introduction

Arctic soils store about 1,035 Pg of organic carbon (OC, Hugelius et al., 2014), which is currently protected from microbial decomposition as consequence of low temperature, poor drainage, and frequent anoxic conditions (Hobbie et al., 2000; Ping et al., 2015), as well as cryoturbation caused by seasonal freeze-thaw processes (reviewed by Ping et al., 2015). Most atmosphere circulation models predict amplified Arctic warming by the late 21st century and beyond (IPCC, 2019) that is expected to stimulate permafrost thaw and deepening of the seasonally thawed active layer (Anisimov et al., 1999; Mueller et al., 2015; Nelson et al., 2001; Prater et al., 2020; Schuur et al., 2008). The deepening of the active layer will increase oxygen availability (Lawrence et al., 2015; St Jaques & Sauchyn, 2009), promoting plant rooting as well as the downward transport of water, nutrients, and microorganisms into the subsoils (Schuur and Mack, 2018). These patterns may accelerate soil organic matter (OM) decomposition in deep soil layers and increase carbon losses to the atmosphere (Fontaine et al., 2007; Gocke et al., 2010; Schuur et al., 2015; Wild et al., 2016).

Understanding the potential consequences of climate change for OM decomposition in permafrost soils and predicting the response of global carbon budgets requires knowledge on the behavior of individual OM constituents, and their interaction with the mineral matrix under different environmental conditions (Koven et al., 2015; Ping et al., 2015). This study focuses on two most predominant compounds of soil OM, lignin (as more stable plant biomacromolecule) and carbohydrates (as more labile plant and microbial-derived molecules). Lignin is a high-molecular-weight phenolic biopolymer that constitutes up to 30% of dry wood mass (Higuchi, 1981). It is not susceptible to hydrolytic attack but is readily degradable by oxidative enzymes (Kirk and Farrell, 1987). Thus oxygen availability is an important factor for lignin degradation. For instance, temperate soils typically exhibit a decrease of OC-normalized lignin concentrations with depth as result of progressive lignin degradation (Dignac et al., 2002; Feng & Simpson, 2011; Rumpel et al., 2004). Conversely, lignin appeared to be selectively preserved in deeper horizons of peat (Bambalov, 2007; Bourdon et al., 2000) and permafrost soils (Dao et al., 2018; Gundelwein et al., 2007), where the oxygen availability is low as result of high soil moisture. Furthermore, lignin phenols in association with minerals are considered to be protected against microbial decomposition, regardless of oxygen availability (Eusterhues et al., 2014; Hall et al., 2016; Riedel et al., 2013).

Noncellulosic carbohydrates (e.g., hemicelluloses) in soils consist of relatively short, mainly branched heteropolymers, which originate from plant tissues and are also synthesized during microbial neoformation (reviewed by Gunina and Kuzyakov, 2015). Plant-derived carbohydrates are to some extent chemically bound to lignin through cinnamic acid ester linkages and form the so-called lignocelluloses (Decker et al., 2008; Fengel & Wegener, 1984). In consequence, plant-derived carbohydrate degradation can be constrained by slow lignin degradation (Benner et al., 1984). Carbohydrates, especially of microbial origin, can also be stabilized in soils by sorption to soil minerals (Derrien et al., 2006). Fine soil particles, thus, often show higher ratios of microbial sugars to plant-derived sugars than coarser particles, for example, in arable soils (Kiem and Kögel-Knabner, 2003), peat bogs (Comont et al., 2006), and also in permafrost soils (Dao et al., 2018). The extent of carbohydrate alteration (i.e., microbial degradation of plant-derived carbohydrates and synthesis of microbial ones) generally increases with soil depth in temperate (Guggenberger et al., 1994) and tropical (Nacro et al., 2005) soils, whereas such a pattern was not observed in northeastern Siberian permafrost soils (Dao et al., 2018).

The protection of soil OM by forming associations with soil minerals is well known for temperate and tropical soils (Kleber et al., 2015; Kögel-Knabner et al., 2008). Recently, this process has also been considered as key control in the stabilization of OM in permafrost soils and its temperature response (Gentsch et al., 2018; Patzner et al., 2020; Prater et al., 2020). Soil density fractionation into light and heavy fractions (LF *vs*. HF) yields distinct soil OM pools that differ in structure and function (Lavallee et al., 2019), that is, non or partly decomposed plant residues *vs*. microbially transformed organic molecules stabilized against fast microbial decomposition by associations with minerals such as iron (Fe) and aluminum (Al) oxides or clay minerals (Golchin et al., 1994, 1995; Herold et al., 2014; Kögel-Knabner et al., 2008). Prater et al. (2020) underlined that with deepening of the active layer in permafrost soils the large and rather undecomposed OM pool becomes accessible to microorganisms, while OM occluded in aggregates or associated with clay-sized minerals may be less mobilized. However, thawing along with formation of water-logging and reducing conditions could also unlock carbon associated with metastable Fe phases due to the activity of Fe(III)-reducing bacteria (Patzner et al., 2020).

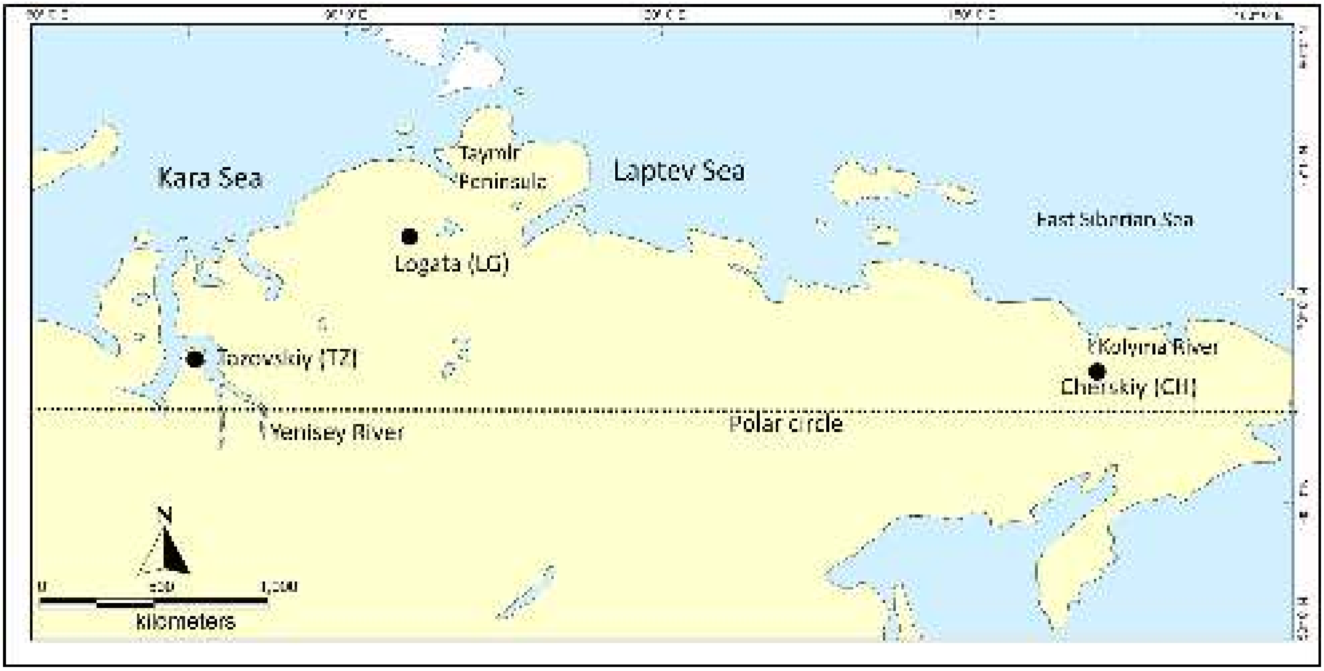

Figure 1. Study area and location of sites.

Despite of the high vulnerability of OM in permafrost soils to climatic change, several studies used fractionation approaches to investigate the distribution and composition of OM pools in permafrost-affected soils (Dao et al., 2018; Diochon et al., 2013; Gentsch, Mikutta, Shibistova, et al., 2015; Höfle et al., 2013; Mueller et al., 2015; Xu et al., 2009). Nevertheless, most of them used spectroscopic and isotopic techniques, which provided an overview of the total but not on the more detailed molecular OM composition. In order to delineate the possible consequences of active layer deepening on OM composition, we analyzed the molecular composition and microbial transformation of lignin and carbohydrates in the density fractionated soils (LF vs. HF) along a longitudinal gradient in northern Siberia. We hypothesized that permafrost soils in the western part of northern Siberia with a warmer climate and deeper active layer show a higher degree of lignin and carbohydrate transformation than regions of colder climate and shallower active layer, particularly in the subsoil horizons. We expected that these differences are more pronounced in the LF than in the HF, as the latter is more protected by association with minerals. We further assumed that differences in the mineral composition among sites also affect the composition and transformation of lignin and carbohydrates in the HF, as the presence of reactive mineral phases may control the formation of mineral-associated OM in the active layer.

2. Materials and Methods

2.1. Site Description, Plant, and Soil Sampling

Samples were collected from three sites in northern Siberia along a longitudinal gradient, from Cherskiy in the Kolyma region in the east to Logata on the Taymyr peninsula, in the center, to Tazovskiy in the Siberian Plain in the west (Figure 1). According to WorldClim database (Hijmans et al., 2005), the mean annual temperature (MAT) and mean annual precipitation (MAP) were relatively similar at Cherskiy (−12.7°C; 160 mm) and Logata (−13.5°C; 270 mm), but higher at Tazovskiy (−8.2°C; 454 mm, Table 1). The continentality index (K) was calculated after Gorczynski (Blüthgen & Weischet, 1980), based on the annual temperature amplitude (difference of highest and lowest mean monthly temperature) and the latitude, and Werchojansk (east Siberia) being considered to represent 100% continentality. Continental indexes of Cherskiy 67.8, Logata 60.8, and Tazovskiy 56.5, respectively, demonstrate decreasing degree of continentality from the east to the west Siberian sampling sites, which potentially affects active layer thickness (May and Gerya, 2021). However, active layer thickness was similar for Cherskiy and Logata (30–85 cm vs. 30–70 cm, respectively), while a deeper active layer was observed for Tazovskiy (100–150 cm, Table 1). All sites are in regions with continuous permafrost and comprise forest-tundra

Table 1
Characterization of Sampling Sites (Data for Cherskiy are From Dao et al., 2018 and Those for Logata and Tazovskiy From Gentsch, Mikutta, Alves, et al., 2015)

Site	Coordinates	MAT (°C)	MAP (mm)	Continentality index	Vegetation type	Soil type	Active layer (cm)	Dominant plant species
Cherskiy	68°45′N, 161°20′E	−12.7	160	68	Shrubby grass tundra	Ruptic-Histic Aquiturbel	30–70	*Betula exilis, Salix sphenophylla, Carex lugens, Calamagrostis holmii, Aulacomnium turgidum*
					Shrubby tussock tundra	Ruptic-Histic Aquiturbel	35–60	*Eriophorum vaginatum, Carex lugens, Betula exilis, Salix pulchra, Aulacomnium turgidum*
					Shrubby lichen tundra	Typic Aquiturbel	60–85	*Betula exilis, Vaccinium uligonosum, Flavocetraria nivalis, Flavocetraria cucullata*
Logata	73°25′N, 98°16′E	−13.5	270	61	Dryas tundra	Typic Aquiturbel	35–70	*Dryas punctata, Rhytidium rugosum, Hylocomium splendens*
					Grassy moss tundra	Typic Aquiturbel	30–65	*Betula nana, Carex arctisibirica, Hylocomium splendens, Tomentypnum nitens*
Tazovskiy	67°16′N, 78°50′E	−8.2	454	57	Shrubby lichen tundra	Typic Aquiturbel	100–120	*Empetrumnigrum, Ledum palustre, Betulanana, Cladonia rangiferina,Cladonia stellaris*
					Forest tundra	Typic Aquiturbel	130–150	*Larix sibirica, Ledum palustre, Betula nana, Vaccinium uligonosum, Cladonia rangiferina, Cladonia stellaris*

Note. Mean annual temperature (MAT) and mean annual precipitation (MAP) were derived from the WorldClim database (Hijmans et al., 2005); soil description follows the USDA Soil Taxonomy (Soil Survey Staff, 2014). Active layer depth was determined at the time of sampling.

and tundra biomes with different plant associations (Table 1). Soils were predominantly classified as Aquiturbels (Gentsch, Mikutta, Alves, et al., 2015) according to USDA Soil Taxonomy (Soil Survey Staff, 2014). Strong reducing conditions were however only observed close to the permafrost surface, as indicated by color hues between 5G and 10BG and low Munsell color values (≤4) and chroma (2). Redoximorphic soil features were less prominent at Tazovskiy with its deeper active layer than at the other two sites.

Sampling was done at the end of summer in 2010 (Cherskiy), 2011 (Logata), and 2012 (Tazovskiy), respectively, ensuring maximum annual thawing depth at the date of sampling. At each study site, three (Cherskiy) or two (Logata, Tazovskiy) tundra vegetation types were identified, and dominating plants of the main tundra vegetation types collected. For each vegetation type, we excavated three soil profiles as replicates. Soil profiles were dug as 5 × 1 m trenches down to the permafrost surface to obtain a representative cross section through micro-topographic features (hummocks, patterned ground) and irregular cryoturbation pattern. Because of hummocks and irregular cryoturbation patterns, soil horizons were heterogeneously distributed. We collected all diagnostic horizons including cryoturbated topsoil materials at various positions within the soil profile but at comparable depth. For that, about 20 subsamples per diagnostic horizon were sampled at random and bulked. We additionally sampled the upper part of the permafrost in three replicates using a steel corer, to a maximum depth of 30 cm from the permafrost table.

Following Gentsch, Mikutta, Alves, et al. (2015), the active layer horizons were categorized into organic topsoil (O), mineral topsoil (A/AB), buried topsoil, that is, topsoil material that was buried in deeper horizons by cryoturbation (Ojj/Ajj), mineral subsoil (BCg/Cg), and the upper part of the permafrost layer (Cff). Directly after sampling, living roots and visible soil fauna were removed and soil samples were dried at 50°C and ground in the laboratory before further analyses. Data from Cherskiy were previously published by Dao et al. (2018).

2.2. Density Fractionation, Organic Carbon, and Total Nitrogen, Soil Texture, and Soil Mineralogy

The separation of particulate and mineral-associated OM was achieved by density separation, knowing that this physical separation method is operationally defined (Cerli et al., 2012). Soil density fractions were obtained by separation of a light fraction (LF; <1.6 g mL^{-1}) from a heavy fraction (HF; >1.6 g mL^{-1}) using a sodium polytungstate solution as described in Gentsch, Mikutta, Alves, et al. (2015), Gentsch, Mikutta, Shibistova, et al. (2015). Organic carbon and total nitrogen (TN) contents and the $\delta^{13}C$ value of OM in the organic topsoil, LF, and HF were measured in duplicates (Gentsch, Mikutta, Alves, et al., 2015; Gentsch, Mikutta, Shibistova, et al., 2015) using an Elementar IsoPrime 100 IRMS (IsoPrime Ltd.) coupled to an Elementar Vario Isotope cube EA C/N analyzer (Elementar Analysensysteme GmbH) after removing traces of carbonates by acid fumigation (Harris et al., 2001).

Contents of pedogenic Fe and Al in bulk soils were determined using extractions with 0.2 M ammonium oxalate and sodium dithionite-citrate-bicarbonate (McKeague and Day, 1966). Oxalate-extractable Fe (Fe_o) and Al (Al_o) represent poorly crystalline oxide phases and organic complexes, while dithionite-extractable Fe (Fe_d) includes Fe-organic complexes, poorly crystalline as well as crystalline Fe oxides (Cornell & Schwertmann, 2003). The extraction solutions were analyzed for Fe and Al by inductively coupled plasma optical emission spectroscopy (ICP-OES; Varian 725-ES, Palo Alto). More details are reported in Gentsch, Mikutta, Alves, et al. (2015). The data are presented in Table 2.

2.3. Lignin Analysis

Concentrations of lignin-derived phenols and their degree of oxidative alteration in soil were determined using alkaline CuO oxidation following the method of Hedges and Ertel (1982) with modifications of Amelung et al. (1999). Lignin-derived phenols were released by oxidation with CuO in the presence of $Fe(NH_4)_2(SO_4)_2.6H_2O$, glucose and 2 M NaOH at 170°C for 3 hr. The lignin-derived monomers were purified using a conditioned C_{18} column (Bakerbond) and converted to trimethylsilyl (TMS) derivatives by reaction with (N, O-bis-trimethylsilyl)-trifluoroacetamide (BSTFA) in pyridine. Thereafter, derivatized-lignin monomers were identified and quantified using gas chromatography-mass spectrometry (Varian 450-GC with ion trap 220MS, Palo Alto). Ethylvanillin and phenylacetic acid were used as internal and recovery standard, respectively. Analyzed lignin-derived phenols were vanillin, acetovanillone, vanillic acid, syringaldehyde, acetosyringone, syringic acid, ferulic acid, and *p*-coumaric acid. Vanillyl (V) and syringyl (S) units were calculated as the sum of their aldehyde, ketone and carboxylic acid forms, and cinnamyl units (C) are the sum of ferulic acid and *p*-coumaric acid. The acid to aldehyde ratios of vanillyl $(Ac/Al)_V$ and syringyl units $(Ac/Al)_S$, were used to assess the degree of lignin alteration (Hedges and Ertel, 1982). The concentration of lignin-derived C was defined as the sum of C in the eight lignin-derived phenols normalized to the OC content (g kg^{-1} OC). The lignin-derived phenol contents of bulk soils were calculated by combining the values of two density fraction, based on the efficiency of fractionation (Gentsch, Mikutta, Alves, et al., 2015). The lignin stock was reported based on the directly measured lignin-derived phenols (VSC) per square meter soil (kg m^{-2}), using the bulk density values reported in Gentsch, Mikutta, Alves, et al. (2015).

2.4. Carbohydrate Analysis

Neutral sugars were analyzed following the method of Amelung et al. (1996) with modifications of Rumpel and Dignac (2006), Eder et al. (2010), and Dao et al. (2018) for purification and derivatization steps. After hydrolysis with 4 M trifluoroacetic acid (TFA) at 105°C for 4 hr, neutral sugars were derivatized using $NaBH_4$ solution (20 mg L^{-1}) and acetic anhydrite. Derivatized compounds were extracted with dichloromethane before injection into a gas chromatograph equipped with a flame ionization detector (Agilent 7890A, Palo Alto, USA). Myo-inositol and D-allose were used as internal and recovery standard, respectively. Analyzed neutral sugars were rhamnose, fucose, arabinose, ribose, xylose, mannose, galactose and glucose. While the pentoses arabinose (A) and xylose (X) are mainly of plant origin, the hexoses galactose (G) and mannose (M) and the deoxyhexoses rhamnose (R) and fucose (F) are largely formed by microbial biomass (Murayama, 1984; Oades, 1984) and some lower plant groups, for example, lichens and mosses (Olafsdottir and Ingólfsdottir, 2001). The ratios of GM/AX and RF/AX are, hence, widely used to trace the origin of carbohydrates in soils (Murayama, 1984).

2.5. Statistics

One-way ANOVA, followed by Tukey's HSD post-hoc test, was used to test for significant differences in lignin-derived phenol and neutral sugar contents between sites and between horizons at a significance level of $p < 0.05$. All variables were tested for normal distribution and log transformed if necessary. The effect of soil properties and pedogenic minerals on lignin and sugar patterns was examined using Pearson correlation. Non-metric multidimensional scaling (NMDS) was used to visualize the variation of lignin and neutral sugar contribution between sites and soil horizons. The ellipses show 95% confidence intervals, axes are arbitrary and scaled in units of Euclidean distance (Oksanen et al., 2016). Permutational multivariate analysis of variance using distance

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10.1029/2020JG006181

Table 2

Basic Characteristics Related to Organic Matter in Bulk Soils, the Light Fraction (LF) and Heavy Fraction (HF) Along With pH, Soil Texture, and Iron (Fe) and Aluminum (Al) Contents Originating From Pedogenic Metal Oxide Phases Within the Soil Profiles (n = 3) of Each Sampling Site (Data are From Gentsch, Mikutta, Alves, et al., 2015)

	Bulk soil									LF			HF		
Soil horizon	OC ($g\ kg^{-1}$ OC)	C/N	$\delta^{13}C$ (‰)	pH	Clay (%)	Silt (%)	Fe_o ($g\ kg^{-1}$ dw)	Fe_d ($g\ kg^{-1}$ dw)	Al_o ($g\ kg^{-1}$ dw)	OC (%)	C/N	$\delta^{13}C$ (‰)	OC (%)	C/N	$\delta^{13}C$ (‰)
Organic topsoil															
Cherskiy	239 ± 70	24.0 ± 5.7	−28.3 ± 0.6	5.1 ± 0.3			n.d.	n.d.	n.d.						
Logata	195 ± 66	22.9 ± 5.3	−28.4 ± 0.8	5.7 ± 0.6			n.d.	n.d.	n.d.						
Tazovskiy	236 ± 69	33.2 ± 6.3	−26.6 ± 0.5	4.8 ± 0.6			n.d.	n.d.	n.d.						
Mineral topsoil															
Cherskiy	34 ± 35	14.4 ± 3.2	−26.8 ± 0.6	5.6 ± 0.3	19.3 ± 4.3	73.2 ± 3.8	6.3 ± 2.0	11.9 ± 1.6	1.6 ± 0.6	34.4 ± 8.9	34.5 ± 10.2	−28.6 ± 1.1	1.7 ± 1.3	12.1 ± 2.6	−26.6 ± 0.4
Logata	70 ± 20	16.0 ± 1.7	−27.9 ± 0.6	5.5 ± 0.3	22.7 ± 10.0	48.7 ± 14.7	4.0 ± 1.6	5.9 ± 1.7	0.8 ± 0.3	33.6 ± 3.8	26.7 ± 5.3	−29.1 ± 0.3	5.6 ± 1.7	15.0 ± 1.7	−27.7 ± 0.6
Tazovskiy	3.5 ± 2.5	16.9 ± 3.8	−25.8 ± 0.3	5.3 ± 0.4	26.8 ± 9.3	66.6 ± 7.0	3.8 ± 0.9	5.6 ± 0.7	1.8 ± 0.7	36.3 ± 5.2	40.1 ± 3.3	−27.4 ± 0.3	2.7 ± 1.9	14.1 ± 3.1	−26.9 ± 2.4
Burried topsoil															
Cherskiy	101 ± 56	16.1 ± 2.1	−27.5 ± 0.5	5.8 ± 0.5	28.7 ± 8.4	66.7 ± 7.4	10.5 ± 6.0	12.9 ± 5.0	2.6 ± 0.6	36.6 ± 2.3	25.7 ± 2.3	−27.9 ± 0.5	7.8 ± 4.3	13.7 ± 2.5	−26.6 ± 0.5
Logata	84 ± 33	17.0 ± 3.6	−27.4 ± 0.4	6.4 ± 0.4	25.7 ± 5.8	62.3 ± 6.4	5.1 ± 2.8	6.8 ± 2.6	0.8 ± 0.2	32.4 ± 2.3	22.2 ± 4.2	−28.2 ± 0.4	5.8 ± 1.4	15.0 ± 1.4	−27.0 ± 0.4
Tazovskiy	42 ± 48	16.1 ± 4.5	−25.8 ± 0.8	5,9 ± 0.6	28.9 ± 9.8	64.5 ± 7.0	4.7 ± 1.6	6.2 ± 1.1	1.9 ± 1.1	39.8 ± 5.0	36.7 ± 6.6	−26.9 ± 0.6	3.0 ± 3.3	13.0 ± 3.7	−26.1 ± 1.5
Mineral subsoil															
Cherskiy	13 ± 5	11.5 ± 1.9	−26.3 ± 0.9	6.1 ± 0.6	17.0 ± 2.9	76.1 ± 4.5	6.3 ± 2.7	10.5 ± 2.2	1.2 ± 0.2	40.5 ± 3.7	32.9 ± 6.9	−27.7 ± 0.7	0.9 ± 0.4	9.4 ± 2.6	−26.1 ± 0.7
Logata	18 ± 7	13.9 ± 2.8	−26.3 ± 0.9	6.7 ± 0.6	29.1 ± 4.9	67.3 ± 7.0	5.3 ± 1.2	8.4 ± 1.2	0.9 ± 0.2	34.6 ± 2.6	26.8 ± 2.4	−27.6 ± 0.9	1.6 ± 0.7	11.4 ± 0.7	−26.4 ± 1.0
Tazovskiy	3 ± 1	9.0 ± 3.2	−24.1 ± 1.1	6.6 ± 0.5	19.1 ± 7.2	74.2 ± 7.5	2.8 ± 0.7	4.7 ± 1.0	0.9 ± 0.3	26.7 ± 11.1	34.7 ± 9.3	−26.0 ± 0.8	0.3 ± 0.1	6.4 ± 2.4	−24.7 ± 1.0
Permafrost															
Cherskiy	20 ± 21	11.7 ± 4.5	−26.5 ± 0.9	7,1 ± 0.2	16.7 ± 4.8	78.5 ± 7.7	7.0 ± 2.3	9.7 ± 2.6	1.1 ± 0.3	39.7 ± 2.0	25.5 ± 8.1	−27.5 ± 0.7	1.1 ± 1.0	8.2 ± 4.0	−26.1 ± 0.6
Logata	15 ± 17	12.2 ± 2.5	−24.6 ± 1.2	6,9 ± 0.5	24.8 ± 0.8	74.9 ± 0.8	4.3 ± 0.8	8.5 ± 2.5	0.6 ± 0.1	39.1 ± 4.2	29.2 ± 2.1	−26.3 ± 1.0	1.0 ± 0.6	10.6 ± 0.6	−24.4 ± 1.3
Tazovskiy	2 ± 1	7.3 ± 2.0	−23.7 ± 0.7	7,3 ± 0.2	13.4 ± 7.7	60.9 ± 13.5	2.4 ± 0.7	4.5 ± 1.6	0.6 ± 0.1	20.4 ± 10.5	29.4 ± 4.4	−25.5 ± 0.4	0.1 ± 0.0	4.8 ± 0.5	−24.6 ± 0.9

Note. Values are mean ± SD, n.d.: not determined. Feo, Alo: Oxalate-extractable Fe and Al, Fed: dithionite-extractable Fe.

Table 3
Total OC-Normalized Lignin-Derived Phenol and Neutral Sugar Carbon Contents of Dominant Plant Species at Each Sampling Site

	Total lignin-derived phenol (g C kg^{-1} OC)				Total neutral sugar (g C kg^{-1} OC)			
Plant species	Cherskiy	Logata	Tazovskiy	All	Cherskiy	Logata	Tazovskiy	All
Dwarf shrub	21.1 ± 10.0	22.0 ± 8.0	20.3 ± 3.1	20.9 ± 7.3	88.7 ± 10.6	127.4 ± 24.0	100.6 ± 11.5	94.6 ± 12.1
Graminoid	38.5 ± 10.0	38.0 ± 4.8	n.d	36.0 ± 4.5	165.5 ± 7.7	211.8 ± 29.8	n.d	176.4 ± 21.0
Lichen	0.7	n.d	0.6 ± 0.4	0.7 ± 0.4	276.0	n.d	411.0 ± 130.4	316.4 ± 37.7
Moss	8.2	5.2	n.d	6.7 ± 2.1	183.0	266.8	n.d	224.9 ± 59.2

Note. Values are mean ± SD, n.d.: not determined due to no appearance. Mean values without SD are not replicated.

matrices (ADONIS) and post hoc-ADONIS (pairwise-ADONIS) in the vegan package of *R* were used to test for significant differences of sugar and lignin composition within sites and horizons (Anderson, 2001; McArdle & Anderson, 2001). The effect of soil properties and mineral phases on NMDS ordination was examined using environmental fitting tests in the envfit function in vegan, and the significance of vectors was tested with 999 permutations. For statistical analyses, calculations, and plots we used *R* version 3.2.2 (R Core Team, 2015) and Sigma Plot 10 (Systat Software).

3. Results

3.1. Lignin and Carbohydrate Compositions of Arctic Plants

The contribution of lignin-derived phenols to OC, as assessed by the CuO oxidation method, accounted for 36.02 ± 4.53 g C kg^{-1} OC (mean ± SD) in arctic graminoids, 20.94 ± 7.28 g C kg^{-1} OC in dwarf shrubs, and 2.84 ± 2.77 g C kg^{-1} OC in lichen/moss (Table 3). The averaged OC-normalized contents of lignin-derived phenols of plant tissues were slightly higher in shrubby grass tundra and shrubby tussock tundra than tundra types with smaller lichen/moss contents (Table 4). The OC-normalized of neutral sugar contents were highest in lichen and mosses with 261,7 ± 57,4 g C kg^{-1} OC, followed by graminoids (176,4 ± 21.0 g C kg^{-1} OC), and dwarf shrubs (94.6 ± 12.1 g C kg^{-1} OC; Table 3). The averaged neutral sugar contents of plant tissues were higher in shrubby lichen and moss tundra than other tundra types (Table 4). Overall, dwarf shrubs and graminoids showed higher percentages of arabinose and xylose and smaller percentages of mannose and galactose compared to lichens and mosses, and all plants were characterized by small fucose and negligible ribose contents (Table S1 in Supporting Information S1).

3.2. Lignin and Carbohydrate Contents and Stocks in Bulk Soils

The OC-normalized lignin-derived phenol contents of the organic topsoils were smaller in shrubby lichen tundra compared with other tundra types at Cherskiy, and in grassy moss tundra compared to dryas tundra at Logata, while they were similar between tundra types at Tazovskiy, following the lignin contents of the parent plant materials (Table 4). In comparison of all tundra types at each site, the lignin-derived phenol contents in bulk soils ranged from 5.5 ± 2.9 to 41.9 ± 33.2 g C kg^{-1} OC and tended to be largest in Cherskiy followed by Logata and Tazovskiy, and did not show a clear trend with soil depth (Table 5). On a soil mass basis, lignin-derived phenol contents ranged from 1.7 ± 1.3 to 24.2 ± 20.5 g kg^{-1} dry weight (dw, Table 5), which translates to stock values in the entire examined soil profiles ranging from 0.11 ± 0.06 to 0.56 ± 0.22 kg lignin-derived phenol m^{-2} (Table 6). Cherskiy and Logata tended to show the largest stocks of lignin-derived phenols in the mineral subsoils and permafrost layers, followed by the organic topsoils and the mineral and buried topsoils (Table 6). In contrast, Tazovskiy showed the largest stocks of lignin-derived phenols in the organic topsoil compared to deeper horizons (Table 6). Integrated over all soil horizons, soils from Cherskiy and Logata stored more lignin-derived phenols than those from Tazovskiy.

The OC-normalized neutral sugar contents of the organic topsoils were similar between tundra types at Logata and Tazovskiy, while they showed a higher value in shrubby lichen tundra compared with other tundra types at Cherskiy, which likewise followed the contents of the parent plant materials (Table 4). Considering all tundra types at each site, the neutral sugar contents of OM in bulk soils ranged from 50.0 ± 24.3 to 177 ± 51.0 g C kg^{-1} OC

Table 4
Total OC-Normalized Lignin-Derived Phenol and Neutral Sugar Carbon Contents of Representative Plant Species at Each Tundra Type

	Cherskiy				Logata			Tazovskiy		
	Shrubby grass tundra	Shrubby tussock tundra	Shrubby lichen tundra	All	Dryas tundra	Grassy moss tundra	All	Shrubby lichen tundra	Forest tundra	All
C/N	31.3 ± 3.6	33.7 ± 7.2	34.1 ± 30.5	34.3 ± 28.5	49.8 ± 6.2	35.8 ± 12.6	37.7 ± 15.3	49.6 ± 42.3	35.8 ± 48.25	58.2 ± 40.9
δ^{13}C (‰)	−28.4 ± 6.1	−28.8 ± 5.0	−29.6 ± 2.9	−28.6 ± 1.7	−30.1 ± 1.0	−29.1 ± 1.1	−29.5 ± 1.2	−28.8 ± 2.0	−28.4 ± 1.2	−26.6 ± 2.2
VSC (g C kg^{-1} OC)	37.5 ± 11.0	35.9 ± 9.9	27.2 ± 18.2	34.0 ± 15.0	15.8 ± 4.7	43.3 ± 15.2	39.3 ± 13.0	27.6 ± 8.2	30.1 ± 9.6	27.6 ± 9.1
Neutral sugar (g C kg^{-1} OC)	110.8 ± 44.0	113.1 ± 47.4	158.1 ± 91.9	142.8 ± 52.7	193.0 ± 104.3	188.7 ± 71.3	174.8 ± 54.5	128.3 ± 84.9	143.6 ± 99.9	110.2 ± 146.1

Note. Values are mean ± SD.

with only clear difference between organic topsoil of Cherskiy and Tazovskiy was observed, and tended to decrease with soil depth at all sites (Table 5). On a soil mass basis, neutral sugar contents ranged from 15.3 ± 11.0 to 111.5 ± 61.0 g kg^{-1} dw (Table 5). There were no differences between organic topsoil horizons, but in the mineral topsoil contents were highest at Cherskiy followed by that at Tazovskiy and Logata. Expressed as stock values, soils contained from 2.4 ± 0.6 to 5.5 ± 1.5 kg neutral sugar m^{-2} for the total examined depth (Table 6). In general, at all three sites, organic topsoil and mineral subsoils stored more neutral sugars than the mineral topsoil and buried topsoil horizons, while at Cherskiy and Logata also permafrost horizons comprised large stocks of neutral sugars (Table 6).

3.3. Lignin in Soil Density Fractions

For the LF, OC as well as soil dw-normalized contents of lignin-derived phenols tended to increase toward the permafrost layer at Cherskiy and Logata (Figure 2a, Figure S1a and Table S2 in Supporting Information S1), but no clear trend was observed for the $(Ac/Al)_V$ and $(Ac/Al)_S$ ratios (Figures 2b and 2c, Table S2 in Supporting Information S1). In contrast, at Tazovskiy the LF showed a significantly decreasing OC and soil dw-normalized lignin-derived phenol contents (Figure 2a, Figure S1 and Table S2 in Supporting Information S1) and increasing $(Ac/Al)_V$ ratios with soil depth, including the buried topsoils (Figure 2b, Table S2 in Supporting Information S1).

Although a similar lignin-derived phenol content was observed for organic topsoils at all three sites, over all mineral soil horizons the LF showed smaller OC- and soil dw-normalized lignin-derived phenol contents and higher $(Ac/Al)_V$ ratios at Tazovskiy than at Logata and Cherskiy ($p < 0.0001$, Figures 2a and 2b; Figure S1a in Supporting Information S1). The NMDS and subsequent pairwise-ADONIS showed distinct clusters of individual lignin-derived phenols relating to OC and soil dw as well across sites (Figures 3a and 3b; Table S3 in Supporting Information S1). Also here, Tazovskiy tended to show a smaller abundance of lignin-derived phenols in the LF than the two other sites.

The HF contained less lignin-derived phenols normalized to OC than the LF, and no clear trend was observed for $(Ac/Al)_V$ und $(Ac/Al)_S$ ratios (Figure 2). For the HF, the contribution of lignin-derived phenols tended to increase toward the permafrost layer at the Cherskiy but to decrease at Logata and Tazovskiy (Figure 2d, Figure S1b and Table S2 in Supporting Information S1). The $(Ac/Al)_V$ and $(Ac/Al)_S$ ratios of the HF tended to increase with soil depth at the Cherskiy and Logata sites, whereas no trend was observed for Tazovskiy (Figures 2e and 2f; Table S2 in Supporting Information S1). However, the ANOVA followed by Tukey's HSD showed no significant differences in lignin-derived phenol contents as well as $(Ac/Al)_V$ and $(Ac/Al)_S$ ratios between soil horizons at all sites (Table S2 in Supporting Information S1), except for contents of lignin-derived phenols between Ojj/Ajj and deeper horizons at the Cherskiy site. Comparing the HF between sites, Tazovskiy had smaller amounts of OC-based lignin-derived phenols than Logata and Cherskiy (Figure 2d). The NMDS and subsequent pairwise-ADONIS showed distinct clusters of individual lignin-derived phenols as related to OC and soil dw as well across sites (Figures 4a and 4b, Table S3 in Supporting Information S1). Confirming the ANOVA results, Tazovskiy tended to show the smallest abundance of lignin-derived phenols in the HF, which increased over Logata to Cherskiy.

3.4. Carbohydrates in Soil Density Fractions

For the LF, the contents of OC and soil dw-normalized total neutral sugars decreased from organic topsoils to mineral subsoils at Tazovskiy (Figure 5a, Figure S2a and Table S2 in Supporting Information S1). A similar, but less pronounced pattern was observed at Logata, whereas concentrations were relatively constant at Cherskiy. Comparing the LF between sites, OC- and soil dw-normalized neutral sugar contents were larger at Tazovskiy than at the other sites ($p < 0.001$) in organic topsoil horizons, while they were smaller in the mineral subsoils and buried topsoils ($p < 0.01$; Figure 5a; Figure S2a in Supporting Information S1). Like for lignin, the NMDS and subsequent pairwise-ADONIS showed distinct clusters of individual neutral sugars related to OC and soil dw as well across sites (Figures 3c and 3d, Table S3 in Supporting Information S1). Cherskiy tended to show a higher abundance of arabinose and xylose, while Logata and Tazovskiy soils showed a higher abundance of mannose, rhamnose, and fucose (Figures 3c

Table 5
Lignin-Derived Phenol and Neutral Sugar Contents Normalized to OC and Dry Weight (dw) in Bulk Soils

	Lignin-derived phenols		Neutral sugars	
Site/horizon	g C kg^{-1} OC	g kg^{-1} dw	g C kg^{-1} OC	g kg^{-1} dw
Cherskiy				
O	16.4 ± 3.6	6.2 ± 1.9	85.0 ± 20.8	54.3 ± 25.6
A/AB	25.1 ± 11.5	13.0 ± 7.1	109.6 ± 27.2	79.6 ± 28.2
Ojj/Ajj	10.1 ± 5.5	4.2 ± 3.5	56.1 ± 11.5	31.7 ± 13.9
BCg/Cg	18.6 ± 13.2	9.0 ± 7.8	55.0 ± 21.2	40.1 ± 36.8
Cff	41.9 ± 33.2	24.2 ± 20.5	60.9 ± 34.6	45.3 ± 35.8
Logata				
O	14.9 ± 5.4	4.4 ± 1.1	148.3 ± 10.4	75.8 ± 29.2
A/AB	10.0 ± 3.4	1.7 ± 1.3	86.4 ± 15.0	21.6 ± 8.4
Ojj/Ajj	9.6 ± 2.9	2.2 ± 2.0	59.4 ± 10.4	19.2 ± 8.5
BCg/Cg	12.3 ± 5.4	4.2 ± 2.6	67.6 ± 8.6	25.0 ± 15.5
Cff	27.4	n.d.	n.d.	n.d.
Tazovskiy				
O	13.0 ± 0.9	4.9 ± 1.8	177.8 ± 51.0	111.5 ± 61.0
A/AB	10.6 ± 7.4	5.2 ± 4.2	89.5 ± 29.3	42.4 ± 23.9
Ojj/Ajj	5.5 ± 2.9	2.3 ± 2.3	50.0 ± 24.3	15.3 ± 11.0
BCg/Cg	11.8 ± 5.8	6.7 ± 4.7	55.2 ± 27.5	40.8 ± 27.5
Cff	n.d.	n.d.	40.5	1.8

Note. Values are mean ± *S*; n.d.: not determined due to lack of samples.

and 3d). The GM/AX ratios in the organic topsoils and the LF of other genetic horizons were larger at Tazovskiy for the whole soil profiles than at the other sites (Figure 5d).

The HF had higher OC-normalized neutral sugars contents and higher GM/AX ratios than the LF (Figure 2). For the HF, all sites showed a decrease of OC- and soil dw-normalized total neutral sugar contents with soil depth (Table S2 in Supporting Information S1). The GM/AX ratios also decreased with soil depth at Cherskiy and Tazovskiy while no clear trend was observed for Logata (Figures 5e and 5h). Comparing the HF between sites, no significant difference in neutral sugars contents related to OC was observed, but Tazovskiy and Logata showed higher GM/AX ratios than Cherskiy (Figure 5h). The NMDS and subsequent pairwise-ADONIS revealed distinct clusters of individual OC-based neutral sugars between the three sites, while no significant difference in soil dw-based neutral sugars was observed between Cherskiy and Tazovskiy (Figures 4c and 4d, Table S3 in Supporting Information S1).

3.5. Lignin and Carbohydrate Contents Related to Soil Properties

For the LF of all sites, OC- and soil dw-normalized lignin-derived phenol contents were positively correlated with pH while neutral sugar contents exhibited a negative correlation (Table 7). Further, the lignin-derived phenols and neutral sugar contents on basis of OC and soil dw were negatively correlated with active layer thickness while a positive correlation was observed for $(Ac/Al)_V$ and GM/AX ratios. Environmental vector fitting on NMDS of LF showed a strong significant relationship between the distribution of lignin phenols and neutral sugars with active layer thickness (Figure 3, Table S4 in Supporting Information S1). It also revealed a significant relation with pH, C/N, and $\delta^{13}C$, but in poorer significance compared to active layer thickness.

For the HF of all sites, pH shows a negative correlation with soil dw-based lignin-derived phenols, and a positive one with $(Ac/Al)_V$ and $(Ac/Al)_S$ ratios (Table 7). At the same time, pH was negatively correlated with OC- and soil dw-normalized neutral sugar contents and with the GM/AX ratio. Lignin derived-phenol contents on basis of OC and soil dw decreased with increasing active layer depth, while no such correlation was observed for

Table 6
Stocks of Lignin-Derived Phenols and Neutral Sugars in Organic Topsoil (O) Horizons and the Light Fraction (LF), Heavy Fraction (HF), and the Bulk Soil for Different Sampling Sites and Soil Horizons (0–100 cm)

	O Horizon and LF			HF			Bulk soil		
	Lignin-derived phenols (kg m^{-2})								
Horizon	Cherskiy	Logata	Tazovskiy	Cherskiy	Logata	Tazovskiy	Cherskiy	Logata	Tazovskiy
O	0.11 ± 0.12	0.05 ± 0.03	0.08 ± 0.06				0.11 ± 0.12	0.05 ± 0.03	0.08 ± 0.06
A/AB	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.04 ± 0.02	0.01 ± 0.01	0.02 ± 0.02	0.05 ± 0.03	0.01 ± 0.01
Ojj/Ajj	0.03 ± 0.00	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.00	0.02 ± 0.01	0.02 ± 0.01	0.05 ± 0.005	0.04 ± 0.02	0.02 ± 0.01
BCg/Cg	0.02 ± 0.01	0.05 ± 0.02	0.01 ± 0.00	0.11 ± 0.06	0.13 ± 0.07	0.02 ± 0.01	0.17 ± 0.007	0.18 ± 0.07	0.02 ± 0.01
Cff	0.06 ± 0.05	0.04 ± 0.03	n.d.	0.11 ± 0.07	0.04 ± 0.03	n.d.	0.21 ± 0.15	0.10	n.d.
Total	0.22 ± 0.19	0.10 ± 0.02	0.09 ± 0.03	0.28 ± 0.12	0.20 ± 0.06	0.03 ± 0.01	0.56 ± 0.22	0.35 ± 0.08	0.11 ± 0.06
	Neutral sugars (kg m^{-2})								
	Cherskiy	Logata	Tazovskiy	Cherskiy	Logata	Tazovskiy	Cherskiy	Logata	Tazovskiy
O	1.16 ± 1.08	1.02 ± 0.77	1.23 ± 0.82				1.16 ± 1.08	1.02 ± 0.77	1.23 ± 0.82
A/AB	0.04 ± 0.03	0.09 ± 0.08	0.05 ± 0.08	0.11 ± 0.1	0.54 ± 0.29	0.24 ± 0.28	0.17 ± 0.21	0.63 ± 0.36	0.30 ± 0.36
Ojj/Ajj	0.20 ± 0.10	0.09 ± 0.07	0.02 ± 0.04	0.39 ± 0.1	0.36 ± 0.18	0.48 ± 0.38	0.62 ± 0.06	0.46 ± 0.23	0.50 ± 0.41
BCg/Cg	0.10 ± 0.04	0.27 ± 0.08	0.02 ± 0.02	0.64 ± 0.44	1.85 ± 0.64	0.47 ± 0.17	0.75 ± 0.21	1.75 ± 1.02	0.48 ± 0.14
Cff	0.19 ± 0.14	0.32 ± 0.55	n.d.	0.71 ± 0.62	1.45 ± 1.09	n.d.	1.02 ± 0.77	3.75	n.d.
Total	1.52 ± 1.05	2.80 ± 0.84	1.18 ± 0.21	1.80 ± 0.88	4.76 ± 1.76	1.25 ± 0.29	3.72 ± 0.89	5.50 ± 1.52	2.35 ± 0.58

Note. Values are mean ± SD; n.d.: not determined due to the large active layer thickness in the western Siberian soils, where no permafrost appeared within the examined soil depth.

oxidative indicators of lignin degradation. Neutral sugar contents did not show a clear correlation with active layer thickness, whereas GM/AX showed a positive one (Table 7). The soil dw-based lignin-derived phenol and neutral sugar contents were also positively correlated with clay, Fe_d, Fe_o, and Al_o contents but negatively with silt contents. The $(Ac/Al)_V$ and $(Ac/Al)_S$ ratios showed only a positive correlation with silt contents. In contrast, GM/AX ratios were positively correlated with clay contents but negatively correlated with silt contents as well as with Fe_d and Fe_o contents.

Environmental vector fitting for HF revealed that pH, active layer thickness, contents of clay as well as of Fe_d, Fe_o, and Al_o were significantly correlated with both lignin-derived phenol and neutral sugar patterns. However, the effect of mineral contents was stronger than that of pH on lignin patterns, while the opposite was observed for the neutral sugar patterns (Figure 4, Table S4 in Supporting Information S1).

4. Discussion

4.1. Lignin and Carbohydrate Contents in Permafrost Environments Versus Other Ecosystems

The arctic graminoids showed generally smaller CuO oxidation lignin contents than those in peatlands (Bourdon et al., 2000), in grasslands (Otto and Simpson, 2006), in forest (Prietzel et al., 2013) and in mangrove soils (Opsahl and Benner, 1995, Table 8). The lignin-derived phenol contents of dwarf shrubs were also smaller than those of pine needles (Kuo et al., 2008; Opsahl & Benner, 1995; Otto & Simpson, 2006), while the observed lignin phenol contents of lichen and mosses were higher than those reported in the study of Zavarzina et al. (2015) (Table 8). The observed OC-normalized lignin-derived phenol contents of organic topsoil horizons, ranging from 12 to 19 g C kg^{-1} OC, were smaller than in the surface layer of peatlands (Bourdon et al., 2000) and organic topsoil of grasslands (Otto & Simpson, 2006), and either smaller or comparable to lignin concentrations reported for organic layers of forest soils (Rumpel et al., 2002; Spielvogel et al., 2007), while being higher than report of Feng and Simpson (2007) for grassland. In the studied permafrost soils, the OC-normalized contents of lignin-derived phenols declined in the organic topsoil relative to the parent plants, mirroring the degradation of lignin in the organic surface layer of tundra soils. The OC-based lignin-derived phenol contents in bulk soil showed no clear

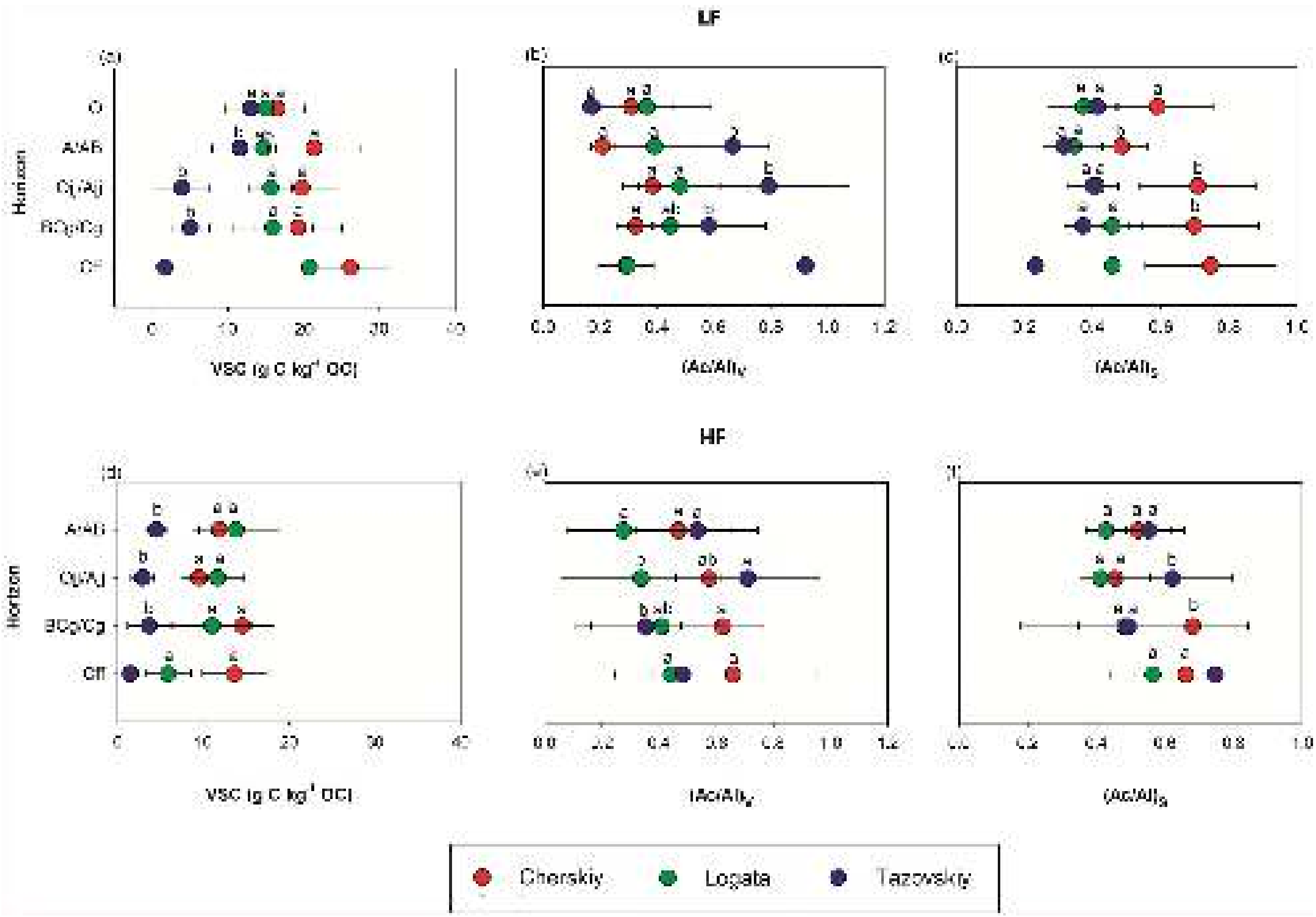

Figure 2. Contents of lignin-derived phenols (VSC) along with $(Ac/Al)_V$ and $(Ac/Al)_S$ ratios in organic topsoil (O) horizons and the light fraction, LF (a–c) and heavy fraction, HF (d–f) of mineral soil horizons. Error bars represent standard deviations. The different letters indicate significant differences between sites for each horizon. Since the present study followed several other investigations (e.g., Gentsch, Mikutta, Alves, et al., 2015; Gentsch, Mikutta, Shibistova, et al., 2015), the amount of available material did not allow replicate analyses for both fractions of the permafrost Cff horizon from the Tazovskiy site.

trend with soil depth (Table 5), being consistent with peat soils (Williams et al., 1998), whereas in many studies of grasslands and forests the contents decreased from the topsoil to deeper horizons (Feng & Simpson, 2007; Rumpel et al., 2002; Wiesmeier et al., 2009). As a consequence, OC-normalized lignin contents in permafrost subsoils were larger than those in subsoils of the temperate zones by factors of 2–7 (Feng & Simpson, 2007; Rumpel et al., 2002), while they were smaller than in subsoil horizons of peat (Bourdon et al., 2000, Table 8). We, hence, suggest that lignin decomposition in the bulk mineral subsoils of permafrost-affected soils appears to be restrained.

The arctic graminoids and dwarf shrubs showed lower TFA-hydrolyzable sugar contents than those of Alpine (Prietzel et al., 2013) and of mangrove soils (Opsahl and Benner, 1999). These contents of moss and lichen, in contrast, were higher than reported for peatbog (Comont et al., 2006, Table 8). The OC-normalized content of neutral sugars in the organic topsoils of the studied permafrost soils was generally larger than that of Alpine soils (Prietzel et al., 2013), and of temperate forest soils (Spielvogel et al., 2007), but smaller than the upper section of a peat core (Comont et al., 2006). The observed decrease of neutral sugar contents with soil depth in the study soils was in line with the observation of a peat core (Comont et al., 2006) and temperate soils (Navarrete and Tsutsuki, 2008; Spielvogel et al., 2007). Hence, in contrast to the decomposition of lignin, the transformation of carbohydrates in bulk soils appears to be similar in permafrost compared to temperate soils.

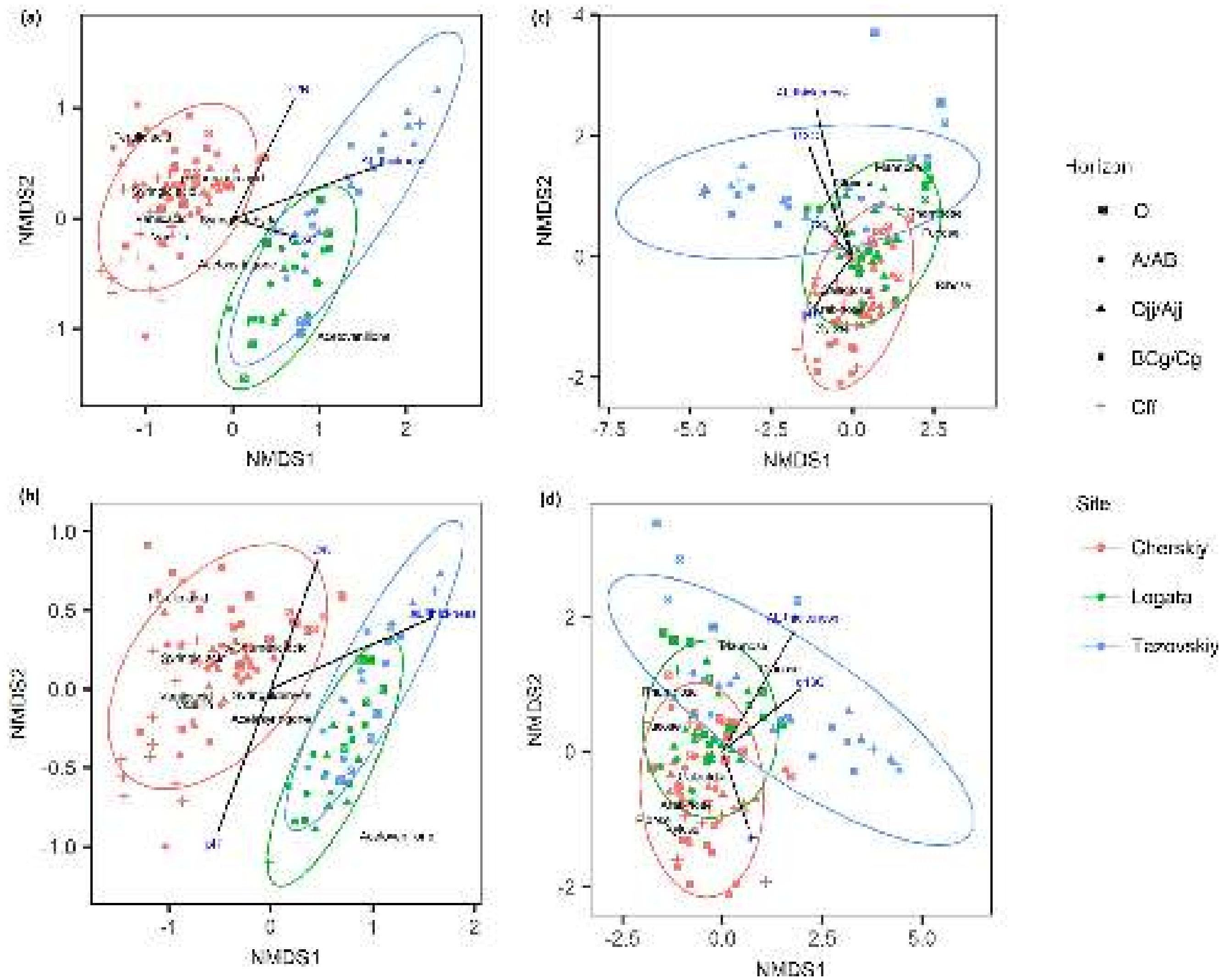

Figure 3. Nonmetric multidimensional scaling analysis (NMDS) plots of contents of individual lignin-derived phenols and neutral sugars on basis of OC (g C kg^{-1} OC) (a, c) and of soil dw (g kg^{-1} dw) (b, d) from individual soil samples over all sites for organic topsoil (O) horizons and the light fraction. The significant fitting vectors refer to the correlations between active layer (AL) thickness, soil pH, C/N, and δ^{13}C of the LF, and contents of individual lignin-derived phenols. Arrow lengths refer to the strength of correlation. The data were log-transformed to reduce stress values.

4.2. Decomposition Pathways in Functional Organic Matter Fractions

4.2.1. Lignin and Neutral Sugars in Light Fraction Materials

In combination of all tundra types there was no significant difference in OC-normalized lignin contents in plants and organic horizons between sites (Table 4, Figure 2). This suggests that the source of lignin entering the mineral soil was not a factor explaining the difference in lignin content and degradation along soil profiles between sites. The LF in mineral soils derives from plant residues and root detritus, and more LF is generally present in topsoils, as they receive more aboveground litter and represent the main rooting zone with higher belowground litter inputs than in deeper soil horizons (Gentsch, Mikutta, Alves, et al., 2015). However, also cryoturbation may cause the translocation of LF material to the deeper mineral soil. At the colder sites Cherskiy and Logata with their shallow active layer, the contributions of lignin-derived phenols and plant-derived sugars to LF fraction (on both, OC and soil dw basis) were constant or even increased with soil depth. At the same time, the ratios of $(Ac/Al)_V$ and $(Ac/Al)_S$ were constant or even decreased in all mineral soil horizons. These findings indicate that lignin-derived phenols and neutral sugars in the LF in the subsoils of these two sites are hardly degraded, which is supported by relatively constant values of C/N and δ^{13}C in this fraction with depth (Table 2). The retarded

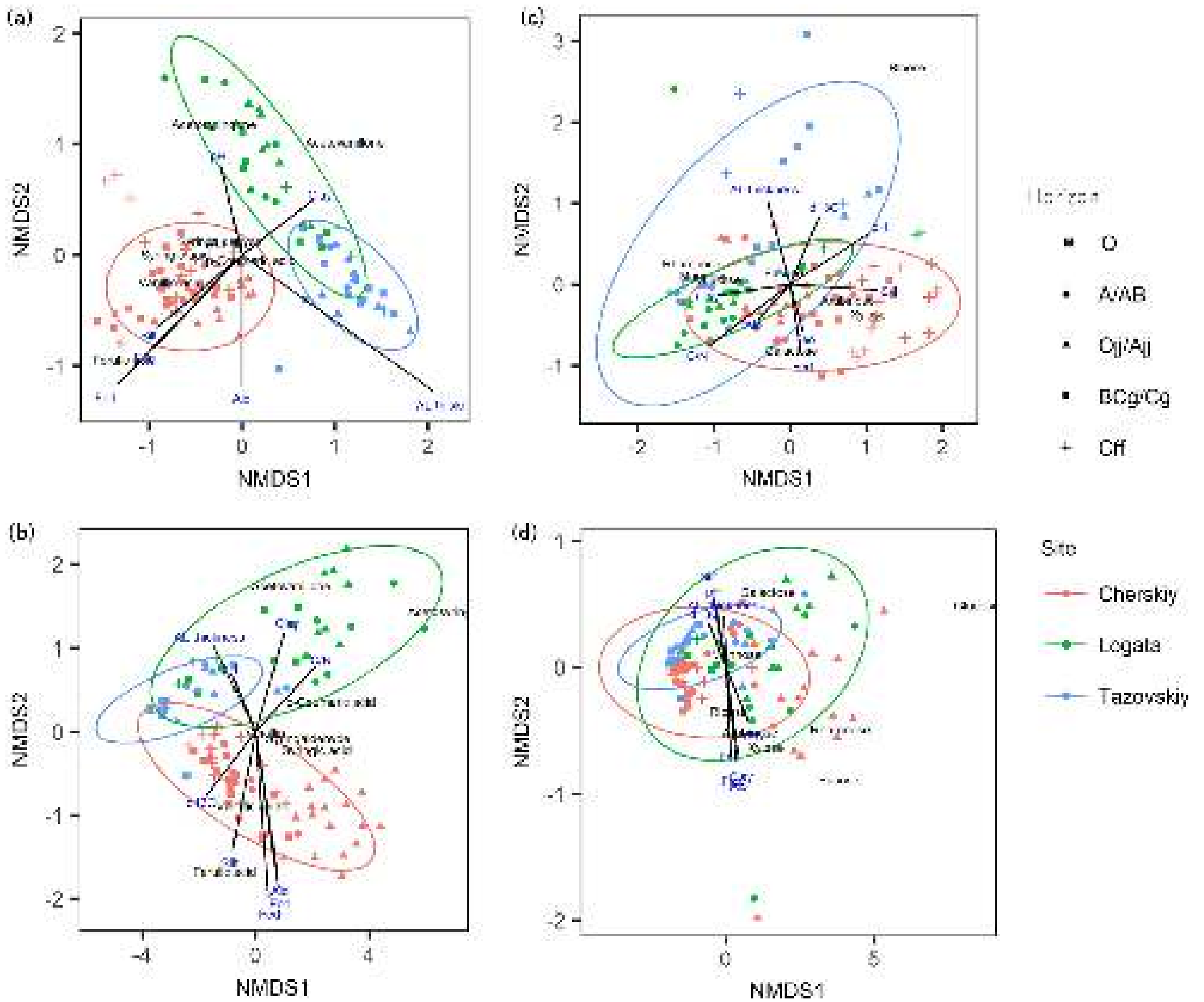

Figure 4. Nonmetric multidimensional scaling analysis (NMDS) plots of contents of individual lignin-derived phenols and neutral sugars on basis of OC (g C kg^{-1} OC) (a, c) and of soil dw (g kg^{-1} dw) (b, d) from individual soil samples over all sites for the heavy fraction. The significant fitting vectors refer to the correlations between active layer (AL) thickness, C/N, and δ^{13}C of the HF, pH, contents of oxalate-extractable Fe and Al (Fe_o, Al_o), and dithionite-extractable Fe (Fe_d) (g kg^{-1} dw). Arrow lengths refer to the strength of correlation. The data were log-transformed to reduce stress values.

degradation is additionally supported by high ^{14}C ages of LF material at the Cherskiy site, ranging from 3,060 to 8,560 years (Gentsch, Mikutta, Shibistova, et al., 2015), while LF material from temperate forest soils is usually much younger, for example, 60–100 years at Spanish Pyrenees (Leifeld et al., 2015).

In contrast, the western site Tazovskiy with a deeper active layer exhibited decreasing contents of lignin-derived phenols and plant-neutral sugars from topsoil to deeper horizons, including the buried topsoil. These results suggest that the LF material becomes progressively altered with soil depth (Otto and Simpson, 2005; Rumpel et al., 2002), which for lignin is also reflected by increasing $(Ac/Al)_V$ ratios and for sugars by generally higher GM/AX ratios. The more advanced decomposition of LF-lignin and neutral sugars at Tazovskiy as compared to Logata and Cherskiy is also in line with generally higher δ^{13}C values in the LF of Tazovskiy soils (Table 2). Given the comparable δ^{13}C values of source plants of all sites (Table 3), the higher δ^{13}C values in the LF of Tazovskiy than Cherskiy and Logata reflect the preferential respiratory loss of the isotopically light carbon during microbial decomposition of soil OM (Wang et al., 1996). This pattern was also supported by decreasing C/N ratios with soil depth at Tazovskiy but not at Cherskiy and Logata (Table 2).

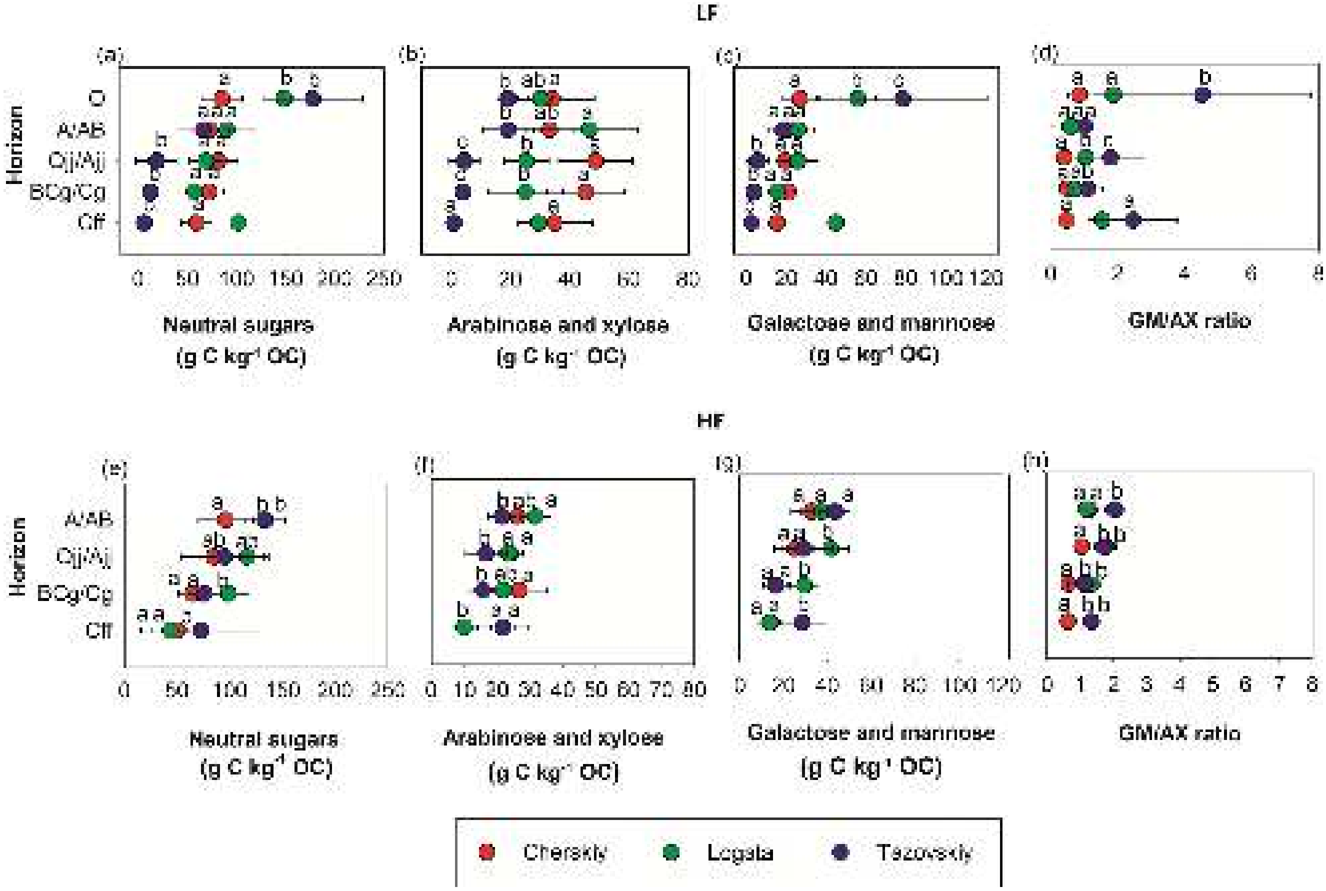

Figure 5. Contents of total neutral sugars, primarily plant-derived sugars arabinose plus xylose, and primarily microbially derived sugars galactose plus mannose along with GM/AX ratios within soil profiles of all sampling sites in the organic topsoil (O) horizons and the light fraction, LF (a–d), and heavy fraction, HF (e–h) of mineral soil horizons. Error bars represent the standard deviation. The different letters indicate significant differences between sites for each horizon. GM/AX stands for (galactose + mannose)/(arabinose + xylose). Since the present study followed several other investigations (e.g., Gentsch, Mikutta, Alves, et al., 2015; Gentsch, Mikutta, Shibistova, et al., 2015) the amount of available material did not allow replicate analyses of the LF from the Cff horizon of the LogataG site.

The concurrent transformation patterns of lignin and neutral sugars with soil depth hint to their presence as lignocellulose (Seelenfreund et al., 1990), with ongoing decomposition causing the parallel alteration of both structural components. At Cherskiy and Logata, such impregnation of saccharides by lignin may protect them from rapid microbial utilization (Moran & Hodson, 1989), while the accelerated lignin decomposition at Tazovskiy also unlocks the plant-derived sugars. This finding was supported by a positive correlation between VSC and AX for LF materials of each site (Figure 6a).

The enhanced LF degradation at the western Tazovskiy site may be caused by higher MAT and probably more available oxygen as a result of the deeper active layer than at Cherskiy and Logata. The deeper active layer at Tazovskiy may increase drainage and enhance oxygen transport into subsoils, as it has been shown for northeast Siberian polygonal tundra soils (Walz et al., 2017). When combining the three sites, we further found significant negative correlations between active layer thickness and lignin and sugar contents, and a positive one with $(Ac/Al)_V$ and GM/AX ratios (Table 7). Also in the NMDS plots active layer thickness showed the greatest effect (expressed by the length of fitting arrows, Figure 3) on the lignin and sugar contents of organic topsoils and LF of the mineral soils (Figure 3). All the data indicate a larger degree of lignin and carbohydrate transformation with increasing active layer thickness, suggesting active layer thickness and the zone of aeration as important control in the turnover of OM in permafrost soils.

Table 7
Pearson Correlation Table Between Lignin-Derived Phenol (VSC) and Neutral Sugar Contents, Lignin Oxidation Indicators, and GM/AX Ratios With Environmental Parameters and Soil Properties (n = 100–120) of All Sites

	LF							HF						
	VSC ($g\ kg^{-1}$ dw)	VSC ($g\ kg^{-1}$ OC)	$(Ac/Al)_V$	$(Ac/Al)_S$	Neutral sugars ($g\ kg^{-1}$ dw)	Neutral sugars ($g\ kg^{-1}$ OC)	GM/AX	VSC ($g\ kg^{-1}$ dw)	VSC ($g\ kg^{-1}$ OC)	$(Ac/Al)_V$	$(Ac/Al)_S$	Neutral sugars ($g\ kg^{-1}$ dw)	Neutral sugars ($g\ kg^{-1}$ OC)	GM/AX
C/N	−0.29*	−0.29	0.20*	−0.28*	0.12	−0.07	0.18*	0.62**	−0.23*	−0.34*	−0.31	0.64**	0.17	0.42**
$\delta^{13}C$	0.18	−0.07	0.22*	0.03	−0.38**	−0.29	0.36**	−0.52**	−0.45**	0.19*	0.14	−0.55**	−0.27*	−0.11
pH	0.41**	0.41	0.04	0.20*	−0.36**	−0.45	−0.2*	−0.34*	0.09	0.26*	0.23*	−0.45**	−0.48	−0.32**
AL thickness	−0.59**	−0.64**	0.49**	−0.44**	−0.32**	−0.22*	0.44**	−0.41**	−0.70**	0.00	0.06	−0.21*	0.12	0.72**
Clay (%)								0.37*	−0.24*	−0.1	−0.25*	0.63**	0.31*	0.37**
Silt (%)								−0.53**	0.17*	0.41**	0.35*	−0.63**	−0.48**	−0.37**
Fe_d ($g\ kg^{-1}$ dw)								0.18	0.26*	0.13	0.03	0.33**	−0.19*	−0.35**
Fe_o ($g\ kg^{-1}$ dw)								0.35*	0.21*	0.10	−0.03	0.48**	−0.21*	−0.32**
Al_o ($g\ kg^{-1}$ dw)								0.31*	−0.18*	0.12	−0.03	0.54**	0.03	0.09

Note. Significance level: $*p < 0.05$, $**p < 0.01$. AL denotes active layer.

4.2.2. Lignin and Neutral Sugars in the Heavy Soil Fraction

The presence of plant and microbial compounds in the HF indicates that formation of mineral-organic associations in permafrost soils occurs via two distinct pathways (Sokol et al., 2019): First, the microbial community processes plant residues and then microbial assimilates become sorbed to minerals (Cotrufo et al., 2015). Second, dissolved OM, either leached from topsoils or liberated in mineral horizons by desorption and microbial processes (Liebmann et al., 2020), is directly sorbed to minerals without preceding microbial assimilation of plant-derived carbon (Mikutta et al., 2019).

As lignin is not favorably used for microbial assimilation, lignin accumulation is best explained by the second pathway. In comparison to HF of other soils, soil dw-based contents of lignin-derived phenols in the topsoil were somewhat smaller than in humid tropical Hawaiian soils (Mikutta et al., 2009) but in the range of New Zealand soils under humid temperate climate (Mikutta et al., 2019). Comparing all study sites, Tazovskiy showed smaller OC- and soil dw-normalized contents of lignin-derived phenols compared to Cherskiy and Logata. In addition, lignin contents in Tazovskiy slightly decreased from mineral topsoil to mineral subsoil, which was in general agreement with some studies of clay- and silt-sized mineral-associated in forest soils (Mikutta et al., 2009; Rumpel et al., 2004, 2012; Vancampenhout et al., 2012). The decrease of lignin contents with depth was explained by preferential sorption of lignin to mineral surfaces when dissolved OM moves down the soil profile (Kaiser et al., 2001; Kaiser & Zech, 2000; reviewed by Angst et al., 2021). In contrast, the OC-normalized lignin contents in the HF of Cherskiy and Logata soils tended to remain unchanged from topsoil to subsoil. We speculate that the comparable lignin content in the subsoil HF could also be explained by sorption processes. In permafrost soils, seasonal thawing creates pulses of melting water, draining faster to larger depth than in nonpermafrost soils (Ostroumov, 2004). However, the shallower active layer at Logata and Cherskiy may impair the fast drainage, thus enhancing the opportunity for dissolved OM interactions with soil minerals.

Unlike lignin, neutral sugars derive not only from plants but also from microbial assimilates. The abundance of neutral sugars in the HF, hence, is due to sorption of both dissolved OM and microbial residues. The contents of mainly plant-derived neutral sugars (i.e., xylose and arabinose) in the HF (10–26 g C kg^{-1} OC) have exceeded those of lignin (3–14 g C kg^{-1} OC), which is consistent with temperate forest soils (Córdova et al., 2018; Guggenberger et al., 1995; Kiem & Kögel-Knabner, 2003). The plant-derived sugar contents were slightly smaller at Tazovskiy than at Cherskiy and Logata, while no difference between the three sites was observed for microbially derived sugars as well as the GM/AX ratios (Figure 5). The HF of permafrost soils contained either a similar proportion of neutral sugars as humid tropical Hawaiian soils (Mikutta et al., 2009) and even a three-fold higher share as soils under deciduous and coniferous stands in the temperate zone (Rumpel et al., 2010), suggesting that neutral sugars might be an integral component of stabilized OM in permafrost soils (Angst et al., 2021).

When normalized to OC, neutral sugar contents of all three sites decreased with soil depth. This trend was consistent to those of temperate forest (Rumpel et al., 2012) and steppe soils (Bischoff et al., 2018), but was in contrast to Spielvogel et al. (2008) who reported an increasing proportion of neutral sugars in the HF of acidic forest soils with depth. Further, the GM/AX ratios of HF in permafrost soils generally decreased from topsoil to deeper horizons, while it increased in forest soils (Rumpel et al., 2010). The lower GM/AX ratios and C/N ratios in the HF of mineral subsoil and permafrost layer than in topsoil and buried topsoil rather

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Table 8
Contents of Lignin-Derived Phenols and Neutral Sugars (g C kg^{-1} OC) of Plants and Soils From Reference Studies

					Graminoid		Dwarf shrub/ woody plant		Lichen/moss		O	A	B/C	Cff	O	A	B/C	Cff
Nr.	Location	Land-use	MAT (°C)	MAP (mm)	VSC	Neutral sugars	VSC	Neutral sugars	VSC	Neutral sugars	VSC				Neutral sugars			
1	Siberia	Permafrost	−12.7to −8.2	57–68	20.9	94.6	36	176.4	0.7–6.7	316.4	15.1	15.9	16.5	24	121.5	94.1	59.5	59.0
2	Canada	Permafrost	−6.8	298								6.9*		1.5				
3	Russia	Artic mountain	0	1,600					0.4–4.4									
4	Madagascar	Peaty marsh	16	1,600	90						50	33.4	20.0–32.0					
5	France	Peatbog	7–8	1,349		48–80				110–176					197	122	90	
6	Canada	Grassland	1.7–3.3	413–452	70		128				33.8							
7	Germany	Forest	6.3–11.0	700–1,250							21.6	13.5	7.0					
8	Alberta	Grassland	1.7–5.0	413–452							3,6	3.2	2.5					
9	USA	Forest	18.3	813	96		90											
10	Austria	Alpine soils	5.5	2,109		257–354		267–444		193					69			
11	Germany	Forest	5.7	1,150–1,300							24	19			88.5	62.3		
12	USA	Mangrove		62.3	60.1	230	60.1	90–275										
13	Brazil	Grassland	14.5	1,800–2000	2.7		5.9				0.9	0.4	0.38					

Note. * value of whole active layer. 1. This study; 2. Bröder et al. (2021); 3. Zavarzina et al. (2015); 4. Bourdon et al. (2000); 5. Comont et al. (2006); 6. Otto and Simpson (2006); 7. Rumpel et al. (2002); 8. Feng and Simpson (2007); 9. Kuo et al. (2008); 10. Prietzel et al. (2013); 11. Spielvogel et al. (2007); 12. Opsahl and Benner (1995), (1999); 13. Wiesmeier et al. (2009). O, organic topsoils; A, mineral topsoils; B/C, mineral subsoils; Cff, permafrost horizons.

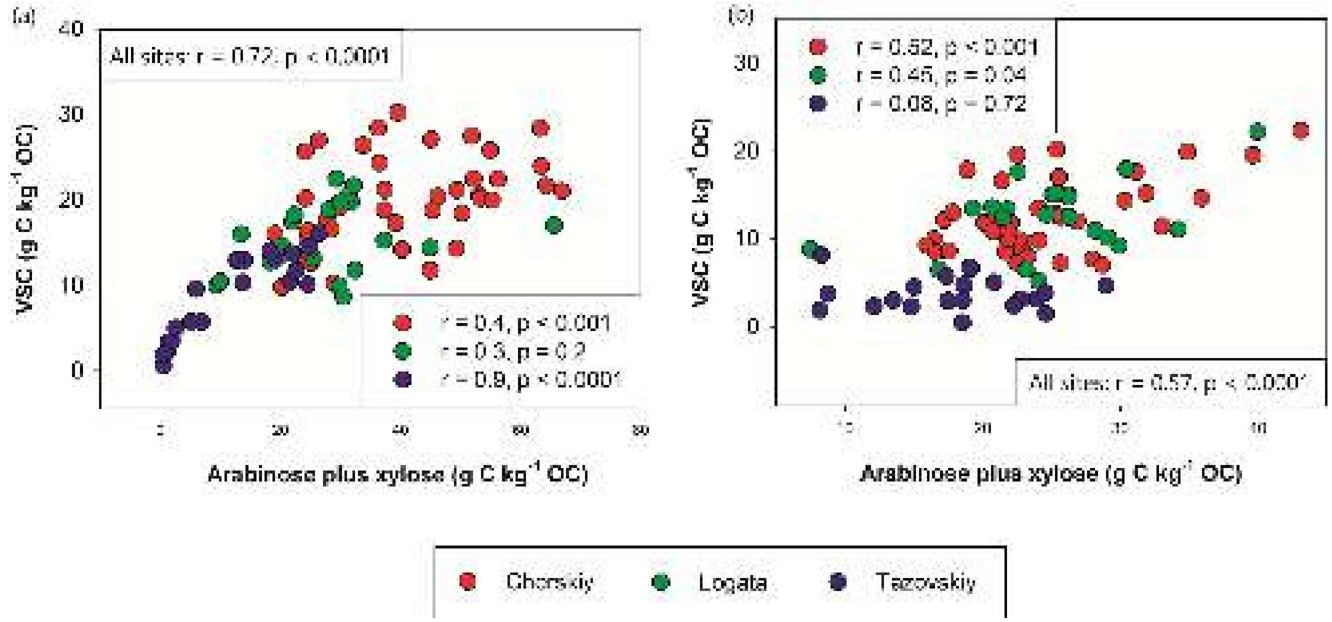

Figure 6. Relationship between total lignin-derived carbon and the sum of arabinose plus xylose carbon in the (a) light fraction (b) and heavy fraction of mineral soil horizons from the three study sites.

suggest a more effective microbial recycling, with preferential use of microbial necromass by microorganisms. Effective recycling of microbial necromass leads to a loss of carbon by respiration whereas N is efficiently recycled, thus also explaining the depth trends in C/N ratios. This finding is supported by the studies at the same soils by Wild et al. (2014) and Čapek et al. (2015), who showed increasing respired substrate-derived carbon and decreasing microbial carbon from mineral topsoil to mineral subsoil horizons.

The relatively larger contribution of lignin moieties and associated plant sugars in the HF of subsoil horizons at Cherskiy and Logata is also likely due to the negative impact of frequently anaerobic conditions on the lignin-degrading microbial community. Although Gittel et al. (2014) showed for the Cherskiy soils that actinobacteria abundance increases with soil depth, actinobacterial lignin degradation activity is apparently lower than fungal activity, due to smaller biomass, lower cell-specific enzyme activities, and absence of hyphae structures (Gittel et al., 2014). Gentsch, Mikutta, Shibistova, et al. (2015) used ^{13}C nuclear magnetic resonance spectroscopy and X-ray photoelectron spectroscopy to demonstrate an increasing proportion of aromatic and aliphatic carbon with soil depth in the HF of the Cherskiy soils, suggesting an enrichment of less oxidized carbon forms of plant and microbial origin in the mostly anaerobic deep active layer of permafrost soils.

4.3. Controls on Lignin and Carbohydrate Transformation in Permafrost Soils

At the western site Tazovskiy, with its quite favorable soil environment, lignin appears to be well decomposable, as has also been shown for temperate soils (von Lützow et al., 2006). In contrast to Tazovskiy, the OC-normalized contents of lignin-derived phenols increased at eastern Cherskiy and middle Logata sites with depth while the degree of oxidative alteration remained at a low level. This indicates that the stage of lignin decomposition is low under the cold and frequently anaerobic conditions in the active layer und the upper permafrost at Cherskiy and Logata. In the absence of oxygen, the decomposition of compounds with a low nominal oxidation state, primarily lipids but also lignin, is strongly restrained since it is thermodynamically ineffective (Boye et al., 2017; Keiluweit et al., 2016). According to Keiluweit et al. (2017), the less efficient anaerobic metabolism selectively preserves otherwise bioavailable reduced organic compounds from decomposition. A shift from anaerobic to aerobic conditions of bulk soils in contrast can increase mineralization rates 10-fold (Keiluweit et al., 2017). Hence, at Cherskiy and Logata lignin in the LF appears to be preserved by a context-specific persistence. As a large part of plant-derived sugars are incorporated in lignocelluloses, this context-specific persistence also protects plant sugars from decomposition in both fractions of Cherskiy and Logata, as supported by a significant, positive regression between OC-normalized VSC and AX in the LF and HF of Cherskiy and Logata (Figure 6b). In contrast, lignocellulose is well decomposed in the much less hydromorphic Tazovskiy soils, possibly additionally facilitated by the higher MAT at this site.

When analyzing the decomposition patterns of lignin and carbohydrates in the HF of the three permafrost sites, not only climatic factors and associated soil physical conditions must be considered, but also soil mineralogy. The HF contained smaller amounts of OC-normalized lignin-derived phenols and neutral sugars of assumed plant origin at Tazovskiy than at Logata and Cherskiy. Concurrently, the degree of oxidative decomposition of the remnant lignin and the relative proportion of microbial sugars were higher at Tazovskiy than at Logata and Cherskiy. At first glance, this observation can be similarly explained as for the LF. The lower soil moisture along with the higher mean annual temperature might have contributed to the more advanced decomposition of plant residues and formation of microbial metabolites (Davidson & Janssens, 2006). However, also the texture and mineralogical composition differed between the sites, which might have an impact not only on OC storage (see Gentsch, Mikutta, Alves, et al., 2015) but also on OM composition. The effect of mineralogical properties was revealed by a positive correlation between soil dw-normalized lignin and neutral sugar contents with clay, Fe_d, Fe_o, and Al_o contents across all sites (Table 7). Hence, differences in the mineralogical composition, with highest contents in pedogenic Fe oxides in Cherskiy, might determine the sorption capacity and thus the accumulation of lignin and neutral sugars in the HF, decreasing in the order Cherskiy > Logata > Tazovskiy. However, we also found indications that biomarker compounds were selectively associated with certain mineral phases. In relation to clay contents, the negative regression of OC-based lignin-derived phenols versus positive regression of neutral sugars in the HF provides evidence for the selective association of neutral sugars with clay minerals. In contrast, the positive regression of lignin-derived phenol contents with Fe contents versus a negative regression of neutral sugars pointed at selective lignin retention by Fe oxides. These findings are in agreement with Kawahigashi et al. (2004), who reported preferentially retained aromatic dissolved OM in the Fe oxide-enriched horizons of central Siberian permafrost soils. Moreover, these patterns were in line with studies of non-permafrost soils that demonstrate the preferential adsorption of OM rich in aromatic moieties and carboxyl groups on Fe oxides (Biber & Stumm, 1994; Gu et al., 1994; Kaiser, 2003; Kaiser &] Zech, 2000; Korshin et al., 1997) and of neutral sugars on clay minerals (Kaiser and Zech, 2000). Recently, Patzner et al. (2020) suggested that permafrost thaw may foster the release Fe and associated carbon due to the activity of Fe(III)-reducing bacteria. Such a process, principally depending on anaerobic conditions, could also partly explain the relatively low Fe_o contents and the more advanced lignin and carbohydrate decomposition at the Tazovskiy site with its larger active layer thickness.

Lignin-derived phenol contents showed no significant relationship to pH when normalized to OC, but a significant negative correlation when expressed by soil dw. This contrasts with the previously observed stimulation of microbial lignin degradation at decreasing soil pH (Thevenot et al., 2010). At the same time, pH was negatively correlated also with neutral sugar contents and GM/AX, indicating a lower contribution of microbially synthesized sugars at higher pH values. Thus, pH might not control microbial lignin and carbohydrate degradation activity, but rather affect the sorption of these substances to mineral phases, since the sorption of anionic compounds is usually greater at lower pH because of the greater protonation and formation of positively charged mineral surfaces (Pierzynski et al., 2005; van Bergen et al., 1997).

5. Conclusions

Density fractionation together with biomarker analysis was used to assess the contents and decomposition of lignin and carbohydrates in permafrost soils in northern Siberia as influenced by climatic conditions and mineral properties. In comparison to many non-permafrost environments, the OC-normalized contents of lignin-derived phenols in bulk soils were smaller, while neutral sugars contents were comparable or even higher. The strongest degradation of lignin and neutral sugars in the LF was observed at Tazovskiy, which may be due to the highest MAT and largest active layer thickness, coinciding with better aeration, as compared to the other sites. These factors might also have contributed to the relatively weak decomposition status of lignin in the HF of soils at Cherskiy and Logata. In addition, the larger contents of Fe and Al oxides likely additionally stabilized lignin-derived phenols associated with the mineral phase at these sites. Our study suggests that the stabilization of lignin and polysaccharides associated with lignin (lignocelluloses) is context-dependent, and climate-induced degradation of permafrost soils, that is, increasing active layer thickness, will promote carbon losses by microbial degradation of lignin and associated polysaccharides. However, the magnitude of future OM losses from permafrost soils will strongly depend on texture and mineralogical properties, either assisting or hampering the turnover of OM in the HF. These findings confirm our initial assumption that, in addition to climatic constraints, soil mineralogy is a decisive factor variegating the transformation of organic matter also in permafrost. Here, generally more knowledge is required about mineralogical soil properties of high-latitude ecosystems, including the transformation of mineral phases under changing environmental conditions.

Data Availability Statement

The data that support the findings of this study are openly available in the EarthChem Library repository at https://doi.org/10.26022/IEDA/112204. Data of soil properties are publicly available at Gentsch, Mikutta, Alves, et al. (2015) (DOI: 10.5194/bgd-12-2697-2015). Neutral and lignin data from Cherskiy site are publicly available at Dao et al. (2018) (DOI: 10.1016/j.soilbio.2017.10.032).

Acknowledgments

Financial support was provided by the German Federal Ministry of Education and Research (03F0616A) within the ERANET EUROPOLAR project CryoCARB. T.T. Dao is grateful for financial support from Vietnamese Education, O. Shibistova acknowledges funding from the National Science Foundation of China and Russian Foundation for Basic Research (NSFC-RFBR joint project No 19-54-53026), and A. Richter, B. Wild and J. Schnecker appreciate the financial support from the Austrian Science Fund (FWF - I370-B17). We thank all members of the CryoCARB project team for their incredible team spirit. We are grateful to the technical staff of the Institute of Soil Science in Hannover for great laboratory assistance. Open access funding enabled and organized by Projekt DEAL.

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