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Multi-proxy study of soil organic matter dynamics in permafrost peat deposits reveal vulnerability to climate change in the European Russian Arctic

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Abstract

Soil organic carbon (SOC) in permafrost terrain is vulnerable to climate change. Perennially frozen peat deposits store large amounts of SOC, but we know little about its chemical composition and lability. We used plant macrofossil and biomarker analyses to reconstruct the Holocene paleovegetation and paleoenvironmental changes in two peat plateau profiles from the European Russian Arctic. Peat plateaus are the main stores of permafrost soil C in the region, but during most of the Holocene peats developed as permafrost-free rich fens with woody vegetation, sedges and mosses. Around 2200 cal BP, permafrost aggraded at the site resulting in frost heave and a drastic reduction in peat accumulation under the drier uplifted surface conditions. The permafrost dynamics (aggradation, frost-heave and thaw) ushered changes in plant assemblages and carbon accumulation, and consequently in the biomarker trends too.

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Detailed biomarker analyses indicate abundant neutral lipids, which follow the general pattern: n -alkanols $>$ sterols $\geq$ n -alkanes $\geq$ triterpenols. The lignin monomers are not as abundant as the lipids and increase with depth. The selected aliphatic and phenolic compounds are source specific, and they have different degrees of lability, which is useful for tracing the impact of permafrost dynamics (peat accumulation and/or decay associated with thawing). However, common interpretation of biomarker patterns, and perceived hydrological and climate changes, must be applied carefully in permafrost regions. The increased proportion (selective preservation) of n -alkanes and lignin is a robust indicator of cumulative decomposition trajectories, which is mirrored by functional compounds (e.g. n -alkanol, triterpenol, and sterol concentrations) showing opposite trends. The distribution of these compounds follows first order decay kinetics, and concurs with the downcore diagenetic changes. In particular, some of the biomarker ratios (e.g. stanol/sterol and higher plant alkane index) seem promising for tracing SOC decomposition despite changes in botanical imprint, and sites spanning across different soil types and locations. Carbon accumulation rate calculated at these sites varies from 18.1 to 31.1 gC m⁻² yr⁻¹, and it is evident selective preservation, molecular complexity of organic compounds, and freezing conditions enhance the long-term stability of SOC. Further, our results suggest permafrost dynamics strongly impact the more undecomposed SOC that could be rapidly remobilized through ongoing thermokarst expansion.

Key words: permafrost; peat deposits; biomarkers; plant macrofossils; Holocene; carbon storage; lability

1. Introduction

Soils in northern high latitude regions store large amounts of organic carbon (C) because permafrost and anoxic conditions from water logging reduce decomposition rates

(Davidson and Janssens, 2006). Recent estimates of these huge soil organic carbon (SOC) pools in the permafrost region are ~ 1024 PgC ($\text{Pg} = \text{g} \times 10^{15}$) in the upper 3 m, with an additional 241 PgC stored in the deltaic deposits and 407 PgC in deep (>3 m) Yedoma deposits (Tarnocai et al., 2009). Because of a warming Arctic climate, there is increased evidence of permafrost thaw (Romanovsky et al., 2010), which may enhance decomposition of SOC stored in soils, and shift them from being net carbon sinks to sources (White et al., 2002). In situ long-term studies have shown that soil warming and permafrost thaw lead to elevated rates of carbon respiration (Dorrepaal et al., 2009; Schuur et al., 2008, 2009). The magnitude and impact of remobilization of carbon pools on climate forcings therefore depend on the extent and rate of thaw in periglacial landscapes, as well as the potential lability of the thawed-out SOC.

Regional inventories from discontinuous permafrost terrain in the European Russian Arctic have identified permafrost peatlands (particularly peat plateaus, which rise above the surrounding landscape due to high ground ice content) as especially sensitive to carbon remobilization because they hold large stocks of relatively undecomposed SOC (Hugelius and Kuhry, 2009; Hugelius et al., 2011; 2012). These peat plateaus store the largest amount of SOC in the area ($\approx 65\%$ of all landscape carbon), and are particularly vulnerable to remobilization through thermokarst formation (Hugelius and Kuhry, 2009; Hugelius et al., 2011, 2012). The area is currently experiencing permafrost warming and thaw (Oberman, 2008) and, hence, it is of great interest for assessing climate change impacts.

As part of an ongoing investigation at the Seida site (Fig. 1), we have previously characterized decomposition of bulk SOC at the landscape level (Hugelius et al., 2012). In this study, we describe molecular characteristics of SOC stored in the peat plateaus. We analyzed two ^{14}C -dated peat profiles for plant macrofossils and various geochemical proxies. Plant macrofossil analyses are used to ascertain the botanical origin of SOC, as well as to

reconstruct Holocene peatland succession at the two investigated sites. To assess SOC lability, we use an array of geochemical analyses involving total organic carbon (TOC), C/N ratios, stable carbon isotopes, and specific biomarkers. The data provide information about the: 1) major components of SOC and their botanical origin, 2) proportion of chemically labile vs. potentially ‘refractory’ fractions, and 3) preservation of SOC affected by depth/age in relation to permafrost history and changes in the active layer depth. The selected aliphatic (*n*-alkanes, alkanols, sterols, and triterpenols) and phenolic compounds (lignin) and their ratios in particular are useful for tracing the impact of permafrost thawing on carbon storage despite changes in botanical composition. Moreover, the general pattern of peat accumulation overlain with local variations in botanical and geochemical composition, and regional permafrost history converge to explain the current vulnerability of SOC in this area that can be further extended to other permafrost regions in Eurasia and North America.

2. Study area

Peat profiles were collected July-August 2008 from a peat plateau-thermokarst complex located near the village of Seida, west of the Ural Mountains (Fig. 1). The mean annual temperature and precipitation are $-6.1\text{ }^{\circ}\text{C}$ and 538 mm (Vorkuta climate station, 75 km northeast of Seida, period 1961–1990), respectively. The area is underlain by undulating glaciofluvial sandy loam of uncertain age (Oberman and Mahzhitova, 2003), and was last glaciated during the Late Saalian (160–140 ka).

Seida is located in a region of Massive Island Permafrost (20–50%) with mean annual ground temperatures in permafrost terrain of $-0.5\text{ }^{\circ}\text{C}$ to $-2.0\text{ }^{\circ}\text{C}$ (Popova et al., 2009). Permafrost-free ground occurs in uplands and along river/stream valleys. The peatlands vary considerably in their vegetation as well as their water content and soil chemistry, which are largely due to the variability in surface hydrological regimes. The present-day peat plateaus

are an important landscape feature, and form part of a mosaic of permafrost bogs, fens, and thermokarst lakes. The raised peat plateaus have a dry surface dominated by dwarf shrubs (*Vaccinium* spp., *Empetrum hermaphroditum*, *Betula nana*), mosses (*Sphagnum* spp.) and lichens, but bare peat patches also occur. Peat thickness varies and reaches up to > 4 m; upper frost tables are at 45-50 cm (August 2008).

3. Methodology

3.1 Peat sampling

The SE8 and SE9 profiles were sampled from cleaned exposures at thermally eroding margins of thermokarst depressions. Gross peat stratigraphy was described in the field. The peat soils were classified as Folic Fibric Cryosols (IUSS Working Group WRB, 2007; Hugelius et al., 2012). In the upper seasonally thawed-out sections, samples were cut out at 1-5 cm (SE8) or 10 cm (SE9) intervals. Samples from permafrost were extracted using stainless steel pipes that were hammered into the ground at 5-10 cm increments. Coring was pursued until we reached the peat-mineral soil contact (410 cm in SE8 and 330 cm in SE9). Samples were packed and transported in plastic bags, and later stored at -18 °C.

3.2 Radiocarbon dating

For radiocarbon (^{14}C) analysis of bulk SOC, roots were removed under a microscope. The samples were treated with 8% HCl for dissolution of carbonates, and combusted in quartz tubes with CuO and Ag wool at 900 °C (Goslar et al., 2004). The ^{14}C concentration was measured at the Poznań Radiocarbon Laboratory (Poland) using accelerator mass spectrometry. The 1- σ error in results were calibrated by OxCal v4.1.6 (Bronk Ramsey, 2010) and IntCal09 calibration curve (Reimer et al., 2009), and expressed in (median) calendar years before present (cal BP; BP = AD 1950).

3.3 Plant macrofossil analyses

Plant macrofossils were analyzed after deflocculating samples of known volume (5-20 cm³) with 5% KOH and sieving (150 µm mesh) to remove fine detritus; remains were identified under a stereo binocular (25-40x magnification) using reference literature (Hallingbäck and Holmåsén, 1982; Mossberg and Stenberg, 2003). *Sphagnum* species were identified by their leaf morphology (Lange, 1982; Laine et al., 2009) under microscope (100-400x magnification). Selected species of macrofossils were presented as volume percentages of the total macrofossil assemblage (< 1% was marked by +), or as counts recalculated to a fixed volume of 4 cm³ (seeds, leaves, needles, bracts, and sterigmata; 1-5 counts was marked with +, 5-10 counts with ++, and >10 with +++).

3.4 *Elemental and isotopic analyses*

Dry bulk density was measured before geochemical analyses were performed. Elemental (Total Organic Carbon (TOC) and C/N ratio) and stable carbon isotope analyses were performed in decarbonated samples (Hedges and Stern, 1984) using a Carlo Erba Elemental Analyzer NC2500 attached to a Finnigan MAT Delta Plus mass spectrometer. The standard deviations for C and N analyses were 0.15% and 0.09%, respectively. C/N values were reported as weight ratios. Carbon isotopes were reported in the conventional delta (δ) notation vs. Vienna PeeDee Belemnite (V-PDB). The machine analytical precision for carbon isotope was ± 0.18‰; deviation between duplicate samples was < ± 0.1‰.

3.5 *Biomarker analyses*

About 3 to 5 g of freeze-dried sample was extracted with a mixture of CH₂Cl₂ and CH₃OH (9:1 v/v) in an automated solvent extractor (Dionex ASE 300; three cycles at 1000 psi and 100 °C). The total lipid extract was saponified with methanolic 0.5N KOH, and separated into fractions by column chromatography using deactivated silica gel (Wakeham et al., 2002). The *n*-alkanes were eluted using hexane. Further elution was done with 5 ml each of solvent mixtures (5% ethyl acetate: 95% hexane; 10% ethyl acetate: 90% hexane; 15%

ethyl acetate: 85% hexane and 20% ethyl acetate: 80% hexane) to separate *n*-alkanols, sterols and triterpenols. At the end, ~20 ml of the extract was recovered and evaporated to ~1 ml. The extracts were derivitized with 100 μ l N,O-bis(trimethylsilyl) trifluoroacetamide (BSTFA) and 100 μ l pyridine, and heated at 70 °C for 2 hrs. The extracts were injected in pulsed splitless mode into an Agilent 6890 GC interfaced with a 5973 MS with a DB5-MS column (30 m x 0.25 mm i.d. x 0.25 μ m film). The GC oven was started at 35 °C held isothermally for 1 min, and increased to 130 °C at 20 °C min⁻¹, the temperature was further increased to 320 °C at 6 °C min⁻¹ and held isothermally for 15 min. The MS was operated at 70 eV under full-scan mode (*m/z* 50-500), and the run-time was 57.42 min. The compounds were identified based on retention time and fragmentation patterns (NIST library and Lipid library, 2011) in standards (S-4066 from Chiron and sterols and triterpenols from Sigma Aldrich). Recovery of deuterated hexatriacontane added prior to extraction ranged from 75-85%. Internal standards (deuterated tetracosane and androstane) were used for quantification; detection limits were at ng/mg dry weight and sample reproducibility was $\pm$ 20%. The concentrations were normalized to TOC (ng/mg TOC) to compensate for shifts in bulk accumulation, and to express the enrichment or depletion of biomarkers relative to TOC.

Lignin phenols were isolated from humic acid fractions (Swift, 1996) that were previously isolated using the IHSS method (Hugelius et al., 2012). The alkaline CuO oxidation method was used to extract lignin by mixing < 200 mg sample with 330 mg of CuO in stainless steel Monel reaction vessels (Filley et al., 2008). The vessels were purged and 2N NaOH added in a N₂-filled glove box. Samples were placed in a rotating carousel and heated to 150 °C for 3 hrs. After cooling, 50 μ l of ethyl vanillin was added (recovery standard). The vessels were centrifuged, their contents decanted, and the residue rinsed with 2N NaOH. Samples were acidified to pH 1 with 6M HCl, and extracted with freshly distilled diethyl ether. The extract was reduced to dryness under a steady stream of N₂, and spiked with

methyl 3,4-dimethoxybenzoate (recovery standard). The extract was re-dissolved in pyridine, derivitized with BSTFA, and heated at 70 °C for 25 minutes. Samples were analyzed on an Agilent 5971 GCMS using an RTx-5MS capillary column. The oven was programmed from 100 °C to 270 °C at 4 °C/min and held isothermally for 16 min (run time 58.5 min). The GCMS was run at 70 eV over the range of m/z 45-400. Trimethylsilyl ether derivatives of lignin monomers were identified from their mass spectra and quantified relative to ethyl vanillin response.

3.6 Specific biomarkers and their ratios

Neutral lipids and lignin monomers are frequently used to calculate diagnostic ratios, which are then related to SOC sources, diagenesis and paleoenvironmental conditions. These compounds can also be used to trace microbial activity, which in turn, has been related to climatic conditions (Xie et al., 2004; Andersson et al., 2011). Presence of specific biomarkers, their diagnostic ratios, and the inferences that can be derived based on these ratios are briefly discussed below.

n-Alkanes: Contribution from cuticular waxes of vascular plants is supported by enhanced inputs of Σn -C_{25,27,29} alkanes. Peat-forming vegetation is associated with saturated *n*-alkanes maximizing at *n*-C₂₃ or C₂₅ for *Sphagnum* and *n*-C₂₅₋₃₁ for vascular plants (Ficken et al., 2000; Pancost et al., 2002; Vonk and Gustafsson, 2010). *n*-Alkanes are used to calculate the Carbon Preference Index (CPI_{alkanes}). Higher plants have a strong odd/even predominance and high CPI_{alkane} values (> 5), whereas bacteria and algae have a weak odd/even predominance and CPI_{alkane} values of ~1 (Cranwell et al., 1987).

$$\text{CPI}_{\text{alkane}} = \frac{\Sigma(\text{C}_{21}\text{-C}_{29})_{\text{odd}} + \Sigma(\text{C}_{23}\text{-C}_{31})_{\text{odd}}}{2\Sigma(\text{C}_{22}\text{-C}_{30})_{\text{even}}} \quad (1)$$

P_{aq} index: This proxy is based on the abundance of mid-chain *n*-C₂₃ and C₂₅ alkanes in submerged and floating macrophytes, and their paucity in algae or land plants (Ficken et al.,

2000). We modified the original equation to include the n -C₂₇ alkane and exclude the n -C₃₁ alkane (which was absent in many SE8 samples).

$$P_{aq} = \frac{C_{23} + C_{25}}{C_{23} + C_{25} + C_{27} + C_{29}} \quad (2)$$

P_{wax} index: This proxy developed by Zheng et al. (2007) evaluates the relative contribution of waxy hydrocarbons from macrophytes and higher plants. Higher P_{wax} values suggest a stronger input from vascular plants.

$$P_{wax} = \frac{C_{25} + C_{27} + C_{29}}{C_{23} + C_{25} + C_{27} + C_{29}} \quad (3)$$

n -C₂₃/C₂₉ and n -C₂₅/(n -C₂₅+C₂₉) alkane ratios: *Sphagnum* typically produces n -C₂₃ and C₂₅-alkanes, whereas vascular plants have n -C₂₉ (Pancost et al., 2002; Vonk and Gustafsson, 2010). The ratio of these n -alkanes provides a relative estimate of major sources of SOC in peat deposits. Vonk and Gustafsson (2010) preferred the latter ratio because it shows least variation between *Sphagnum* spp., and samples from different latitudinal settings.

n -Alkanols: Land plants contain high proportions of n -C₂₂₋₃₀ alkanols and are dominated by the even chain moieties (Rieley et al., 1991; Zheng et al., 2007). CPI value of alkanols has a strong even predominance (Rieley et al., 1991), and has been related to climate change (Zheng et al., 2007; Zhou et al., 2010; Andersson and Meyers, 2012).

$$CPI_{alkanol} = \frac{\Sigma(C_{20}-C_{26})_{even} + \Sigma(C_{22}-C_{28})_{even}}{2\Sigma(C_{21}-C_{29})_{odd}} \quad (4)$$

Higher Plant Alkane (HPA) index: This ratio was introduced by Poynter and Eglinton (1990) to provide a quantitative measure of degradation of saturated vs. functional compounds. Since n -alkanes are preserved preferentially compared to n -alkanols, a decrease in HPA index indicates increased decomposition.

$$HPA = \frac{(C_{24} + C_{26} + C_{28})_{alkanol}}{(C_{24} + C_{26} + C_{28})_{alkanol} + (C_{25} + C_{27} + C_{29})_{alkane}} \quad (5)$$

Σ Stanol/ Σ sterol ratio: Presence of sterols such as β -sitosterol, stigmasterol, campesterol, and brassicasterol indicate input from higher plants and mosses (Rieley et al., 1991; Lehtonen and Ketola 1993). Stanols are the saturated counterparts of their respective Δ^5 -sterols produced through microbial hydrogenation. Hence, increase in the stanol/sterol ratio (e.g., sitostanol/ β -sitosterol) is associated with enhanced degradation.

Lignin ratios: Lignin monomers are divided into V - vanillyl (vanillic acid, vanillin, and acetovanillone), S - syringyl (syringic acid, syringaldehyde, and acetosyringone), C - cinnamyl (p-coumaric acid and ferulic acid), and P – (hydroxyphenyl 4-hydroxybenzaldehyde, 4-hydroxyacetophenone, and 3,4-dihydroxybenzoic acid) groups. In anaerobic and perennially water-logged environments, lignin macromolecules are relatively ‘recalcitrant’ (Williams et al., 1998). The S and C monomers are, however, more susceptible to decay than V, and consequently, S/V and C/V ratios decrease with greater decomposition (Zeigler et al., 1986; Zacccone et al., 2008). Similarly, the ratios of vanillic acid to vanillin and syringic acid to syringaldehyde ($Ac/Al_{v,s}$) indicate fungal decay because acid monomers tend to increase relative to aldehydes during decomposition (Ertel and Hedges, 1984).

4. Results and discussion

4.1 Holocene peatland inception, vegetation succession and permafrost dynamics

Detailed macrofossil analyses are available for the entire SE9 profile and for the upper 90 cm of the SE8 profile. For the lower part of profile SE8 (410-90 cm) only gross stratigraphic descriptions are available. Radiocarbon dates for the SE9 and SE8 profiles are presented in Table 1 and Figure 2, the latter showing the calibrated age-depth models. Radiocarbon dating and macrofossil evidences suggest similar development at both sites. The most complete reconstruction of peatland development and associated permafrost/hydrological changes can be made from the SE9 profile (Fig. 3). The presence of

wood and spruce remains at the base of this deposit indicates that this site formed through paludification (lateral expansion of peat deposit) of upland forests ca. 7600 cal BP. At this time, regional climatic conditions were warmer and the Arctic treeline was located north of Seida (Kultti et al., 2004). For most of its existence (until 2200 cal BP), the SE9 site developed as a permafrost-free fen with woody vegetation (particularly birch), sedges, and brown mosses. Radiocarbon dating provides evidence of a stratigraphic hiatus between 2200 and 990 cal BP. From 990 cal BP onwards, the peatland is dominated by mosses, including *S. riparium* - a collapse scar fen species (Zoltai 1993; Oksanen et al., 2001). From this we infer that at ca. 2200 cal BP permafrost aggraded resulting in frost heave, and a drastic reduction in peat accumulation under drier conditions of the uplifted peat surface. Permafrost aggradation around this period has also been reported from the nearby Rogovaya (Oksanen et al., 2001) and Lek-Vorkuta (Andersson et al., 2011) sites, where stratigraphic evidence of the early permafrost stage is preserved in the form of dry bog assemblages. At SE9, peat ceased to accumulate and was wind abraded exposing the older underlying fen peat. Consistent with this, old fen peat is currently exposed in many palsas and peat plateaus across the circumpolar north (Zoltai 1995; Oksanen et al., 2003). At about 990 cal BP, the permafrost at SE9 degraded, resulting in the formation of a collapse scar fen. More recently, the permafrost re-aggraded resulting in the formation of the extant dry peat plateau surface with *Dicranum* moss and dwarf shrubs. In SE8, fen peat dominates throughout most of the profile, and macrofossils in the upper 90 cm of the sequence (Fig. 4) points to an abrupt change from a sedge-brown moss peat towards *S. riparium* dominated interval starting ca. 820 cal BP. We interpret this shift in vegetation as due to permafrost aggradation, which is followed by degradation and the formation of a collapse scar fen. The extant peat plateau bog, dominated by *S. Section Acutifolia* and dwarf shrubs, developed in sub-recent times.

The developmental histories at SE9 and SE8 peat deposits permit us to qualitatively reconstruct the decomposition trajectories of SOC. SOC in the upland forests prior to paludification, were exposed to rapid carbon cycling/degradation and leaching under aerobic conditions. Subsequently, fen peat accumulated in a permafrost-free environment for ca. 5000 years. During this time, peat was briefly exposed to relatively rapid aerobic decomposition in the upper (aerated) acrotelm before being incorporated into the deeper (water-saturated) catotelm, where SOC was exposed to slower anaerobic decay. Permafrost aggraded around 2200 cal BP, which inhibited SOC decomposition below the active layer. The associated uplift and drainage due to frost heave led to dry aerated conditions in the active layer during the warm season where the fen peat deposits that accumulated prior to permafrost aggradation were exposed to more intensive aerobic degradation. During subsequent permafrost degradation and collapse scar formation, the entire deposit became exposed to renewed (but mostly slow anaerobic) decomposition. In sub-recent times permafrost re-aggraded, inhibiting decay in deeper layers, but exposing the upper dry peat to more intensive aerobic decomposition. Below, we discuss these changes in SOC related to permafrost development and the impact of thawing based on various bulk and molecular geochemical characteristics preserved in the Seida peat plateaus.

4.2 Elemental and stable isotope trends

Specific details of the dry bulk density (DBD), TOC, C/N ratio, and stable carbon isotope trends associated with soil C storage and humification at Seida have been discussed by Hugelius et al. (2012). The DBD sharply increases at the peat/mineral contact in both profiles (Figs. 5 and 6). TOC concentrations are ca. 2-3% in the mineral soil at the base of peat deposits, but increase sharply and vary between 40 and 50% in the overlying peat. These high values of >40% TOC are typical in peat deposits from North America and Siberia (Tarnocai et al., 2009; Gorham et al., 2012; Hugelius et al., 2012). C/N ratios range from 15-

25 in the top peat plateau, the deeper fen peats, and the underlying mineral sub-soil. The C/N ratios are higher (25-50) in the *Sphagnum* dominated collapse fens just below the peat plateau deposits, which can partly be ascribed to the originally high C/N ratios in the living tissues of these mosses (Kuhry and Vitt, 1996). The overall high C/N ratio suggests that N is not limiting, and that SOC is susceptible to further decomposition (Dai et al., 2002; Pedersen et al., 2011).

The $\delta^{13}\text{C}$ values follow very similar patterns as the C/N. The average isotopic value of -27.3‰ in the deeper fen deposits are consistent with vascular plant input. In contrast, the *Sphagnum* dominated intervals show $\delta^{13}\text{C}$ increases of ~4‰, which reflect the botanical origin. More negative $\delta^{13}\text{C}$ values are found in the very top of the peat plateau deposits, particularly at SE8. Andersson et al. (2012) report very similar C/N and $\delta^{13}\text{C}$ values in the nearby Lek-Vorkuta peat plateau deposits. While C/N and $\delta^{13}\text{C}$ values are influenced by vegetation (Loisel et al., 2009), SOC preservation also plays a role in the observed C/N and $\delta^{13}\text{C}$ trends (Kuhry and Vitt, 1996; Kaislahti Tillman et al., 2010). The interpretation of low SOC degradation in the deeper fen deposits is consistent with the C/N ratios, humification (Hugelius et al., 2012) and biomarker data (see below), which show limited changes in these peat layers. It seems that this SOC has been protected from degradation by the anaerobic catotelm during early and mid-Holocene periods, and by sub-zero temperatures since permafrost aggradation. Similarly, other studies report that under permafrost conditions perennially frozen peat deposits undergo limited decomposition (Vardy et al., 2000; Sannel and Kuhry, 2009).

4.3 Biomarker trends

Northern peatlands generally show an autogenic fen to bog succession related to progressive peat accumulation (Kuhry and Turunen, 2006). In peat plateaus affected by periglacial dynamics, local processes and changes in permafrost aggradation or thaw are

important controls on plant assemblages (Oksanen et al., 2003; Kuhry, 2008). Hence, recent studies emphasize the need to consider changing botanical constituents and diagenesis under peculiar climatic and environmental conditions experienced by permafrost peat deposits, which influence SOC composition and preservation (Turetsky et al., 2007; Andersson et al., 2011; Andersson and Meyers, 2012).

While interpreting biomarker trends in permafrost peat deposits there are two important caveats. First, while regional patterns in peatland succession and permafrost dynamics have been linked to climate (Kuhry and Turunen, 2006; Turetsky et al., 2007), specific changes in plant assemblages (and consequently their biomarker trends) are not necessarily transferrable to other peat deposits. For example, if a wet fen aggrades permafrost, the surface will be uplifted due to segregation of ground ice, and the vegetation will shift to a dry species assemblage. This observed shift in species assemblages would not necessarily reflect change in regional precipitation. Consistent with this idea, Anderson et al. (2011) found that while *n*-alkanes helped reconstructing SOC sources and paleoenvironmental conditions, they misled interpretation of past precipitation trends. Second, it is cautioned that biomarker trends in peat deposits mainly provide a ‘qualitative record’ of paleovegetation and climatic shifts, and their absolute values do not accurately record the magnitude of these changes.

4.3.1 Saturated lipids

n-Alkanes: Previous studies suggest that *n*-alkane accumulation and preservation in temperate and boreal raised peat bogs respond strongly to climatic changes (Zheng et al., 2007; Xie et al., 2010; Zhou et al., 2010). Thus, changes in precipitation affect plant assemblages that contribute towards lipids and peat formation. The chain-length distribution of *n*-alkanes in Seida range from C₂₁₋₂₉, and has a maximum at the C₂₇ and/or C₂₉ positions representative of epicuticular waxes in higher vascular plants (Eglinton and Hamilton, 1967;

Rieley et al., 1991; Ficken et al., 2000). The overall low amounts of short-chain homologues ($n\text{-C}_{17}\text{-C}_{20}$) indicate minor contributions of n -alkanes from algae and bacteria (Cranwell et al., 1987). In general, $n\text{-C}_{27}$ and C_{29} alkanes are dominant below 70 cm, whereas $n\text{-C}_{23}$ and C_{25} alkanes are abundant (although not necessarily dominant) in the upper sections, particularly in *Sphagnum* dominated layers (Figs. 5 and 6). The $n\text{-C}_{23}$ alkane, and to a lesser degree $n\text{-C}_{25}$, are relatively uncommon in terrestrial settings (Eglinton and Hamilton, 1967), but in general they are more abundant in *Sphagnum* (Nott et al., 2000; Baas et al., 2000).

At both sites, Σn -alkane concentrations including the long-chained hydrocarbons ($n\text{-}\Sigma\text{C}_{25,27,29}$) increase sharply above the peat and mineral-soil interface. From the peat-mineral contacts at the bottom to ca. 150 cm (in SE9) and ca. 120 cm (in SE8) n -alkane concentrations do not vary. Above these depths, n -alkane concentrations show a decrease and also indicate more variability (as in SE9). The difference is most likely caused by preferential preservation following long-term decomposition. The lack of any clear trends in the deeper fen deposits suggest limited decomposition due to anaerobic conditions in wet fen environments, and in the late Holocene, sub-zero temperatures in permafrost. This interpretation fits well with the previous (lack of) trends described for C/N and $\delta^{13}\text{C}$ enrichment (Hugelius et al., 2012) and diagenesis. However, the SOC sources in these peats also needs to be considered. The (near) surface peat layers consist mostly of *Sphagnum*; these mosses produce lipids, but their net output is low and the lipid monomers degrade rapidly (Pancost et al., 2002). Although other studies suggest that mosses decompose more slowly than vascular plants (Turetsky 2004), ongoing studies have not adequately characterized non-vascular plant decomposition in peat deposits. The observed variability in Σn -alkane in the upper 100 cm of the SE9 profile, however, does not correspond to any obvious plant assemblage shift. Likewise, changes in upper peat stratigraphy at SE8 deposit are barely reflected. The increased proportion of n -alkanes seems, therefore, quite a robust indicator of

cumulative decay in SOC, which is mirrored by the *n*-alkanol and HPA index showing opposite trends (see below; Figs. 5 and 6).

In general, high CPI_{alkane} values are reportedly associated with well-preserved SOC (Xie et al., 2004; Nierop and Jansen, 2009). In Seida, the CPI_{alkane} displays high values (> 5) and has a distinct odd-over-even carbon number predominance indicating the abundance of vascular plants (Cranwell et al., 1987). The CPI_{alkane} values in SE8 are very high (> 20) compared to SE9. Although unusual, high CPI_{alkane} values (> 18) occur in the Lek-Vorkuta peat plateau deposits where they are attributed to better preservation of SOC (Andersson and Meyers, 2012). Likewise, high CPI_{alkane} values occur in ombotrophic peat bogs and they have been related to reduced SOC degradation (Xie et al., 2004). The low CPI_{alkane} value near the peat and mineral-soil interface in both sites is most likely due to diagenesis occurring prior to peat formation, and the onset of anoxic conditions at these sites. In SE9, immediately above the mineral-soil interface and upto ca. 150 cm, the CPI_{alkane} values remain generally constant implying conditions under which microbial degradation most likely slowed down. The interpretation that anaerobic and cold conditions during past fen stages, and sub-zero temperatures during permafrost stages have slowed decomposition is further supported by humification trends (Hugelius et al., 2012), which show a very gradual increase implying limited degradation. In the upper ca. 150 cm of the SE9 profile, there is an up-core decreasing trend and more variability in CPI_{alkane} values, which is similar to the Σn -alkane trend. This implies that conditions favoring microbial degradation (which decreases CPI_{alkane}) have affected the upper parts in SE9. Consistent with this, a decrease in CPI_{alkane} value in peat deposits has been related to temperature-sensitive microbial alteration (Zhou et al., 2005; Zheng et al., 2007). The present peat plateau at SE9 is dominated by dwarf shrubs and *Dicranum* moss suggesting drier conditions. This trend is caused by aerobic conditions in the active layer following permafrost aggradation and uplift, which affected the underlying top

fen deposits resulting in unusually high $\text{CPI}_{\text{alkane}}$ values in the 50-90 cm interval. In SE9, our interpretation of the macrofossil and ^{14}C dating evidence suggests initial late Holocene permafrost aggradation occurring at a time corresponding to peat layers presently at 35 cm depth. The active layer depth at that time would have extended deeper, corresponding with intervals where $\text{CPI}_{\text{alkane}}$ trends suggest increased decomposition. A decreasing trend in $\text{CPI}_{\text{alkane}}$ is absent at the SE8 site, although *n*-alkane concentration shows a sharp decline.

The P_{aq} ratio is generally high (> 0.5) and, according to previous studies, this would imply input from submerged and floating macrophytes under wet conditions (Ficken et al., 2000; Mead et al., 2005). This interpretation has been applied to raised peat bogs to reconstruct paleoenvironmental conditions (Xie et al., 2004; Zhou et al., 2005, 2010; Zheng et al., 2007). However, this can be misleading because *Sphagnum* and other (brown) mosses, which affect this ratio can grow either under wet fen or dry bog conditions (Blackford, 2000; Loisel et al., 2009). These mosses can have a significant input of *n*-C₂₅ alkane (Vonk and Gustafsson, 2010), and hence the P_{aq} ratio can become biased. Because Seida peat deposits are a mixture of mosses and vascular plants in varying proportions, this makes interpretation of paleohydrological conditions at this site using the P_{aq} ratio contentious.

High values of the P_{wax} ratio suggest greater input from vascular plants, which in temperate bogs has been used to infer colder and drier conditions (Zheng et al., 2007). In general, relatively high (> 0.70) P_{wax} values occur in most of the Seida peat sequences signifying the dominance of vascular plants. The P_{wax} based interpretation of SOC sources is consistent with the $\text{CPI}_{\text{alkane}}$ and $\Sigma n\text{-C}_{25,27,29}$ trends signifying dominance of higher plants. Similarly, macrofossil analyses and field based core descriptions indicate that between 310 and 35 cm in SE9, and between 400 and 65 cm in SE8, these peats are dominated by vascular plants. Peat plateaus are typically dominated by dwarf shrubs, and it is typical of them to yield high P_{wax} (> 0.80) and generally low P_{aq} (< 0.5) values (Zheng et al., 2007; Andersson

et al., 2011), which are in this case representative of drier conditions due to frost heave. Even though this ratio shows variability in both profiles, there are no obvious trends with depth. The lowest P_{aq} and highest P_{wax} values occur in the top peat layer of SE9 corresponding to the peat plateau stage. In contrast, P_{aq} and P_{wax} values show little variation in the upper part of the SE8 profile.

There are other *n*-alkane ratios which have been related to SOC sources and water table conditions. High values (> 7) of C_{23}/C_{29} ratio coincide with intervals where *Sphagnum* is dominant in SE9 (40-10 cm, *S. Sect. Cuspidata*) and SE8 (65-35 cm, *S. Sect. Cuspidata*; 4-0 cm, *S. Sect. Acutifolia*). However, high values also occur in some of the underlying fen intervals. A clear trend with depth is absent in SE9, but overall values of the C_{23}/C_{29} ratio increase up-core in SE8. Similar to the C_{23}/C_{29} ratios, there is no strong correspondence between the $C_{25}/(C_{25}+C_{29})$ ratios and the macrofossil data or depth, implying the lack of sensitivity of these proxies to reconstruct paleoenvironmental changes in Seida peat deposits.

4.3.2 Functional lipids

n-Alkanols: The distribution of these compounds range from C_{14-28} with a strong even/odd predominance. The alkanols show bimodal distributions maximizing at C_{16} and C_{22} or C_{28} monomers, and are characteristic of organic matter derived from microorganisms and higher plants, respectively (Zheng et al., 2007; Andersson and Meyers, 2012). The Σn -alkanol trend shows an inverse relationship to that of Σn -alkanes (Figs. 5 and 6), both in terms of its abundance and carbon chain length. Because alkanols are functional compounds, their degradation rates are much higher compared to *n*-alkanes (Poynter and Eglinton, 1990; Meyers and Ishiwatari, 1993). In both peat profiles, *n*-alkanol concentrations increase up-core, suggesting rapid degradation in the upper intervals, where aerobic conditions prevail.

The $CPI_{alkanol}$ values show high variability and an absence of clear relation to either botanical imprint or depth. Increase in $CPI_{alkanol}$ has been associated with formation of

secondary products during SOC degradation (Simoneit and Mazurek, 2007). Acidic conditions in peat deposits may enhance ester hydrolysis, and consequently, increase the availability of free alcohols (Ficken et al., 1998). Hence, there is very little resemblance between the distributions of *n*-alkanols and those predicted based on macrofossils. Slightly elevated average CPI_{alkanol} values in the middle and lower SE8 and SE9 deposits can be indicative of a higher degree of cumulative decay. Zheng et al. (2007) related the low (≤ 5) CPI_{alkanol} values to warming, and the high (≥ 10) values to cooling trends. In contrast, an opposite pattern is observed at Seida, where relatively low values (< 10) correspond to the colder late Holocene, whereas the higher values (> 10) occur during the warmer early and mid-Holocene periods. Hence, caution should be exercised in explaining biomarker trends in peat deposits in terms of regional climatic changes particularly in areas affected by permafrost activity.

In both the SE8 and SE9 profiles, the HPA index and Σn -alkanol trends show remarkably similarity. The ratio has maximum values of around 0.8 at the top, and then decreases to < 0.4 in the deeper fen deposits. The trend is consistent with the fact that both alkanols and alkanes would decrease with increase in degradation (particularly aerobic decomposition). However, functional compounds undergo greater degradation, which would decrease the HPA index. In addition to tracing early diagenetic changes in sediments, this index has been also related to climate change. Schmidt et al. (2011b) correlated the high TOC and HPA index in lake sediments to warmer and wetter conditions. However, caution is needed when interpreting the trend in Seida because high HPA index correlates with cold and locally dry surface conditions (peat plateau stage).

Sterols and triterpenols: Presence of these compounds indicate SOC input from higher plants and mosses in peat deposits (Lehtonen and Ketola, 1993; Pancost et al., 2002; Ortiz et al., 2010; Andersson and Meyers, 2012). At both sites, C_{29} sterols as a group

dominate over C₂₈ sterols (β -sitosterol (C₂₉) > stigmasterol (C₂₉) $\geq$ campesterol (C₂₈) > brassicasterol (C₂₈)). However, campesterol is sometimes the second most abundant sterol present. The results are in good agreement with previous studies of sterols in peat deposits (Baas et al., 2000; Pancost et al., 2002; Xie et al., 2004; Andersson and Meyers, 2012). β -sitosterol and stigmasterol are diagnostic of *Sphagnum*, but are typically absent (or present in low concentrations) in other bog-forming plants. Indeed, the highest abundance of β -sitosterol and stigmasterol (not shown) is found in the *Sphagnum*-rich interval between 65-35 cm in SE8, but minor maxima do occur in the deeper fen deposits in SE9 where *Sphagnum* macrofossils are not present implying either that *Sphagnum* was present in these peat stages, but macrofossils were not preserved, or that there may be additional sources of these compounds.

The Σ sterol and Σ triterpenol compounds follow the *n*-alkanol trend; the concentrations are low at the bottom and increase rapidly above 100 cm. The low concentration of these compounds is associated with the high degradation rate of functional compounds (Poynter and Eglinton, 1990; Meyers and Ishiwatari, 1993). Degradation of these compounds in the very early stages when SOC accumulates leaves very little to be preserved to contribute significantly towards the organic matter pool in peat deposits. This is despite the fact that sterols and triterpenols are more abundant compared to other organic compounds, implying they are good substrates for supporting microbial activity, which limits their physical or chemical stabilization in peat deposits. In particular, microbial degradation of peat results in production of stanols by reducing their corresponding diagnostic stenols (Δ^5 -sterols; Lehtonen and Ketola, 1993). In line with other biomarker proxies, the Σ stanol/ Σ sterol and Σ sitostanol/ Σ sitosterol ratios increase with depth (particularly in SE8), indicating increased microbial decomposition. The stanol/sterol ratio for other pairs (stigmastanol-stigmasterol, campestanol-campesterol, and brassicastanol-brassicasterol) in these deposits shows similar

trends (not shown) implying that these sterol pairs are robust indicators of SOC decomposition.

4.3.3 Phenolic components

Lignin: Phenolic compounds contribute towards the formation of humic substances and can be used as diagnostic paleoenvironmental tracers (Turetsky et al., 2000; Filley et al., 2001; Tareq et al., 2006; Zacccone et al., 2008). Although few samples were analyzed in this study, the total lignin content (Σ_{VSC}) shows a positive increase with depth. The trend is similar to those reported from Canadian peatlands (Turetsky et al., 2000; 2007). The elevated levels of methoxyphenols (S and V monomers and their ratios $S/V > 0.5$ and $C/V \neq 0$) indicate that higher plant matter is an important component of lignin (Ertel and Hedges, 1984) in these peat deposits. In general, *Sphagnum* lacks lignin (Turetsky et al., 2000; 2007), but contains other phenolic compounds (e.g., P monomers), which can be extracted by the CuO method (Williams et al., 1998).

This lignin trends suggest both selective preservation and dominant woody tissue input in the deeper peat layers. The basal peat/mineral soil boundary shows low concentrations of lignin like other biomarker trends, and is probably a result of diagenesis. The overall low concentration of lignin in surface samples indicates the botanical imprint (dominance of *Sphagna*) and presence of more labile compounds such as *n*-alkanols, triterpenols, and sterols in SOC. However, microbial decomposition rapidly decreases in anoxic soil environments, and SOC degradation is increasingly replaced by those of polysaccharides and other functional moieties. Thus, better preservation of lignin leads to their overall increase in the catotelm. The lignin phenol (S/V, C/V) ratios exhibit large changes with depth (Fig. 7), and demonstrate better preservation of less labile forms of lignin (C and S monomers), which is consistent with accumulation of lignin (Σ_{VSC}). Decrease in these ratios at the peat/mineral interfaces is most likely due to diagenetic changes related to

enhanced microbial decomposition prior to peat formation. These compounds have different reactivities, and previous studies indicate preferential degradation of C and S over V monomers (Zeigler et al., 1986). This is also supported by increase in proxies for lignin oxidation ratios ($Ad/Ald_{v,s}$; Opsahl and Benner, 1995; Zaccone et al., 2008).

Decreases in S/V and C/V and corresponding increases in $Ac/Al_{v,s}$ ratios at the surface in both profiles imply intensive decay, which contradicts some other biomarker evidence representing less degraded SOC near the surface. Changes in lignin ratios are however influenced by other processes besides SOC decomposition. Thus, selective input of different plant types and their tissues can lead to different lignin ratios (Filley et al., 2008). For example, shifts in plant community to low input carbon tissues (woody plant parts) can raise Λ_{VSC} and lower C/V and Ac/Al ratios. In contrast, greater input of carbon rich material (leaves), that are low in total lignin, and have higher Ac/Al ratio, can raise C/V, but lower the Λ_{VSC} yield. In addition, the type of fungal community in soil impacts Ac/Al ratios; brown rot fungi decrease the ratio, whereas white rot fungi increase the ratio. Although aldehydes are converted to acids during fungal decay, the oxidized products are more soluble. Because these ecosystems are open, oxidized materials once they have cleaved from soil matrix, will eventually leach away. This will affect the Ac/Al ratios, and they will decrease despite enhanced decay. Hence, in these profiles, where C/V and S/V ratios and Λ_{VSC} increase, whereas $Ac/Al_{v,s}$ decrease, simultaneously, the easiest conclusion is lower fungal decomposition with depth.

4.4 SOC accumulation, lability and carbon remobilization

Integrative multi-proxy studies of SOC decomposition in periglacial landscapes are very limited. Available information from permafrost sites indicate that SOC is relatively undecomposed and post-thaw remobilization of this large carbon pool can happen possibly within decadal timescales (Schurr et al., 2008, 2009). Hence, knowledge regarding the fate of

labile vs. recalcitrant SOC fractions is important for establishing the sensitivity of peat deposits to climate warming. How and on what time scale the SOC pools are affected is variable, and involves large uncertainties in our estimates (Tarnocai et al., 2009; Schurr et al., 2008, 2009; Hugelius et al., 2011; Gorham et al., 2012).

There is macrofossil evidence for occurrence of local permafrost thaw and subsidence in Seida. Concurrent with this, elevated concentrations of functional compounds in surface sediments followed by their steady decline in these high latitude soils imply that SOC is most susceptible to degradation under oxic conditions and increase in temperature. In this connection, knowledge regarding actual turnover rates of organic compounds would be highly useful, and such experiments have been conducted in bulk SOC (and on rare occasions in lignin and *n*-alkanes) from non-permafrost sites using stable carbon isotopes (see Amelung et al., 2008). Such information for Seida would be helpful in coupling the results with temperature change to have a better estimate of SOC remobilized from thawing.

As a preliminary assessment of what is happening to the SOC pool in terms of its storage capacity and decomposition, we calculated the: 1) carbon accumulation rate (CAR; $\text{gC m}^{-2} \text{ yr}^{-1}$ based on TOC, dry bulk density, and sedimentation rate), and 2) diagenetic alteration at both sites. The peat plateaus show the same trend i.e., CAR is high when peat starts to deposit ~7000 cal BP and is associated with elevated waterlogging, precipitation, and high primary productivity (Figs. 5 and 6). CAR declines gradually before reaching the hiatus ~950-2200 cal BP, and thereafter CAR increases slowly. In SE8, the average value of CAR is $18.1 \text{ gC m}^{-2} \text{ yr}^{-1}$, whereas in SE9 CAR is $31.1 \text{ gC m}^{-2} \text{ yr}^{-1}$. The average value of Holocene CAR for the northern hemisphere peat deposits are estimated as ~17.2 to $18.6 \text{ g m}^{-2} \text{ yr}^{-1}$ (O'Donnell et al. 2011; Gorham et al, 2012, Yu et al., 2012), and is comparable to our estimate at SE8.

We applied the first order G model reaction kinetics, which estimates degradation constants (Berner, 1980). We extend this idea to estimate the degradation constant of bulk organic matter and different compound classes using the equation:

$$G_t = G_0 \cdot e^{-kt} \quad (5)$$

where G_0 and G_t are the concentration of specific compounds at the time of deposition and at a specific depth; t is the time elapsed after deposition corresponding to that depth; apparent rate constant k is estimated from the linear regression of lipid biomarker concentration versus time t . Negative value of the degradation constant (Table 2) indicates a logarithmic decline in TOC and biomarker concentration in the peat plateaus. The data indicate TOC (in SE8), lignin, and n -alkanes do not follow the logarithmic decline in concentration. In SE8 the degradation constants follow the trend n -alkanol > sterol = triterpenol, whereas in SE9 the trend is triterpenol > sterol > n -alkanol. Although both sites are not far apart, they indicate certain level of heterogeneity in carbon dynamics in terms of decomposition, preservation, and storage capacity.

Schmidt et al. (2011a) suggested that various physicochemical conditions and ongoing biological processes in the soil zone reduce the probability (and rate) of SOC decomposition. Further, the authors suggested that ‘recalcitrance’ of SOC based on their molecular complexity is probably less relevant. While this may be correct and geochemical evidence supports this idea, particularly in low latitude regions (Marschner et al., 2008; Schmidt et al., 2011a), SOC stabilization in permafrost is a more complex process. Our results confirm that anaerobic water-logged conditions and permafrost aggradation in Seida played a crucial role i.e., initially towards the formation of these deposits, and subsequently, their preservation. The biomarker profiles indicate that SOC of different molecular complexity and ‘recalcitrance’ react differently. Thus, functional compounds degrade more rapidly (> 90% mineralized within the top 20-30 cm). In contrast, n -alkane and lignin

monomers in deeper peat layers persist following their incorporation into the anoxic catotelm, and they are less degraded. When exposed due to frost heave and drying out of the active layer following local permafrost aggradation, the organic compounds in these layers can however, undergo renewed aerobic degradation. Consistent with our study, SOC characterization from the Alaskan Arctic indicate high concentrations of O-alkyl compounds (alcohols, carbohydrates, and unsaturated compounds) in early stages of decomposition (Pedersen et al., 2012). Likewise, a similar trend has been indicated in boreal peat deposits from Canada (Turetsky et al., 2000; 2007). These authors indicate that loss of hydrolysable compounds in SOC at the surface is compensated by increasing aromaticity (phenolic compounds) with depth.

The biomarker trends from detailed characterization of SOC in Seida imply that ‘selective preservation’ indeed plays a role in SOC stabilization, and further enhances it due to the molecular complexity of organic compounds. We also infer that while permafrost is not the key environmental factor controlling SOC decomposition, its presence/absence has a strong impact on undecomposed SOC and its long-term storage and remobilization. Moreover, while active layer deepening leads to increased aerobic decay of upper peat layers (which this study shows historic evidence of), thermokarst can result in rapid remobilization of the entire peat deposit. Future work should continue to focus on the key factors that influence the geochemical composition and fate of SOC. Without a better understanding of both issues, our estimates of SOC stocks and their potential decomposition in permafrost regions will be incomplete.

5. Conclusions

Peatland succession is largely mediated through local autogenic processes and, in the case of permafrost peat deposits, periglacial dynamics play a significant role in influencing

the bulk and molecular geochemical characteristics of peat deposits. We have investigated in detail macrofossil and biomarker trends in permafrost peat plateaus, and related their distribution to variable sources/inputs of SOC, preservation, and diagenetic changes associated with shifts in ground temperature and/ hydrologic conditions. Although spatial extent of SOC characterization in this study is restricted to just two sites, peat plateaus are dominant landform features and they store large amounts of carbon. This detailed study and its implications can therefore be useful to infer more accurately the impact of thawing on SOC degradation and lability not only in the investigated peat deposits, but possibly also in peat deposits of other permafrost regions.

The macrofossil and biomarker records indicate a coherent picture of Holocene paleoenvironmental changes in Seida. These peats developed as permafrost-free fens with woody plants, sedges and brown mosses. Around 2200 cal BP, permafrost aggraded resulting in frost heave and reduction in peat accumulation under drier conditions. The biomarker trends indicate SOC preserved in the peat deposits have undergone limited degradation under anoxic fen conditions or since permafrost aggraded. Biomarker concentrations are low at the mineral-soil interface, but increase up-core. The neutral lipid concentrations follow the trend: n -alkanols $>$ sterols $\geq$ n -alkanes $\geq$ triterpenols. The lignin monomers are not as abundant as the lipids and increase with depth. The functional compounds are dominant near the peat surface (upper 30 cm), but indicate a steep (logarithmic) decline coinciding with increase in n -alkanes and lignin. The increase of n -alkanes is a robust indicator for cumulative decay, and some of the biomarker ratios, notably stanol/sterol and HPA index seem promising for tracing SOC decomposition across soil layers with different botanical imprint. These qualities confirm that biomarker ratios can be useful for understanding environmental applications spanning across different locations, soil types and age.

The biomarker trends emphasize that molecular complexity, anoxia in the waterlogged catotelm, and permafrost conditions all played an important role in preservation of SOC in these peat deposits. Permafrost aggradation and uplift of waterlogged fen peats enhanced SOC decomposition in the active layer as previously anoxic catotelm peat became exposed to aerobic degradation. This interplay of a long-term regional trend of Holocene peatland development and local scale changes related to permafrost dynamics can complicate interpretation of biomarkers trends, demonstrating that inferences from temperate/boreal peat bogs cannot always be directly transferred to permafrost peatlands. However, the study shows that multi-proxy studies combining macrofossil evidence with biomarkers remain powerful tools for explaining past shifts in species assemblages and environmental changes. The bulk geochemical parameters and biomarker data conclude that SOC in the permafrost peat plateaus of the Seida area is relatively undecomposed, and if exposed to thawed conditions, rapid decay could occur. The same fate can be expected of the large SOC pool in the European Russian Arctic (and in other permafrost regions), which has undergone little decomposition, and can therefore be expected to be potentially labile. Deepening of the active layer is expected to progress relatively slowly due to the insulating properties of dry peat, but nevertheless these ice-rich peat plateaus are highly vulnerable to thermokarst processes. As the relatively undecomposed SOC is remobilized from frozen peat plateaus, the fate of this material depends largely on the environmental conditions in the resulting thermokarst lakes or fen deposits.

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CAPTIONS

Fig. 1. Sampling locations (SE9 and SE8) and land cover pattern in Seida northern European Russian Arctic (from Hugelius et al., 2012). Molecular characteristics have been detailed for only these two sites, the focus of this study.

Fig. 2. Age-depth models of Seida peat profiles SE8 and SE9 are based on median values in calendar years before present (cal BP) $\pm 1\sigma$, calibrated by OxCal v4.1.6 (Bronk Ramsey 2010) and IntCal09 calibration curve (Reimer et al., 2009).

Fig. 3. Gross stratigraphy of the Seida peat profile SE9 with median ages marked to the left, and macrofossil analysis presented as volume percentages for selected taxa rescaled to a standard volume of 4 cm³ (1-5 counts was marked with +, 5-10 counts with ++ and >10 with +++).

Fig. 4. Gross stratigraphy of the Seida peat profile SE8 (upper part) with median ages marked to the left (more humified peat marked by a tighter component key), and macrofossil analysis presented as volume percentages for selected taxa rescaled to a standard volume of 5 cm³ (less than 1% of the total sum marked by +).

Fig. 5. Geochemical proxies analyzed in a peat plateau (core SE9) under permafrost in Seida. Alternating gray panels indicate shifts in the gross stratigraphy.

Fig. 6. Geochemical proxies analyzed in a peat plateau (core SE8) under permafrost in Seida. Alternating gray panels indicate shifts in the gross stratigraphy.

Fig. 7. S/V and C/V lignin ratio with depth in the peat plateaus.

Table 1. Chronology of Seida peat deposit (cores SE9 and SE8) with corresponding calibrated ages (cal BP).

Table 2. First order reaction kinetics traces change in SOC and degradation constants (negative value indicates logarithmic decline in concentration).

Fig. 1.

Fig. 2

Fig. 4

Fig. 5.

Fig. 6

Fig. 7.

Table 1

Profile	Depth (cm)	Poznan Lab No.	Material type	¹⁴ C-age (yr BP)	Calibrated age (cal BP)*
SE9	27-35	Poz-28244	Bulk peat	935 ± 30	852
SE9	40-50	Poz-36630	Bulk peat	2225 ± 35	2231
SE9	154-164	Poz-28245	Bulk peat	4835 ± 35	5584
SE9	331-336	Poz-28246	Bulk peat	6200 ± 50	7094
SE8	10-11	Poz-28006	Sphagnum	185 ± 30	179
SE8	20-21	Poz-32068	Sphagnum	295 ± 25	388
SE8	65-66	Poz-28007	Sphagnum	895 ± 30	819
SE8	185-190	Poz-28241	Bulk peat	5290 ± 40	6077
SE8	405-408	Poz-28242	Bulk peat	6790 ± 40	7634

* Median of highest 68.2% probability interval in the calibration

Table 2.

	SE8 Plateau	SE 9 Plateau
TOC	0.0000047	-0.000026
Σn -Alkane	0.00014	0.00031
Σn -Alkanols	-0.0003	-0.00027
Σ Sterols	-0.0001	-0.00069
Σ Triterpenols	-0.0001	-0.00081
Λ (P,V,S,C)	0.00021	0.00022