

Permafrost Distribution Drives Soil Organic Matter Stability in a Subarctic Palsa Peatland

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ABSTRACT

Palsa peatlands, permafrost-affected peatlands characteristic of the outer margin of the discontinuous permafrost zone, form unique ecosystems in northern-boreal and arctic regions, but are now degrading throughout their distributional range due to climate warming. Permafrost thaw and the degradation of palsa mounds are likely to affect the biogeochemical stability of soil organic matter (that is, SOM resistance to microbial decomposition), which may change the net C source/sink character of palsa peatland ecosystems. In this study, we have assessed both biological and chemical proxies for SOM stability, and we have investigated SOM bulk chemistry with mid-infrared spectroscopy, in surface peat of three distinct peatland features in a palsa peatland in northern Norway. Our results show that the stability of SOM in surface peat as determined by both biological and chemical proxies is consistently higher in the permafrost-associated palsa mounds than in the surrounding internal lawns and bog hummocks. Our results also suggest

that differences in SOM bulk chemistry is a main factor explaining the present SOM stability in surface peat of palsa peatlands, with selective preservation of recalcitrant and highly oxidized SOM components in the active layer of palsa mounds during intense aerobic decomposition over time, whereas SOM in the wetter areas of the peatland remains stabilized mainly by anaerobic conditions. The continued degradation of palsa mounds and the expansion of wetter peat areas are likely to modify the bulk SOM chemistry of palsa peatlands, but the effect on the future net C source/sink character of palsa peatlands will largely depend on moisture conditions and oxygen availability in peat.

Key words: palsa peatland; discontinuous permafrost; soil organic matter; potential carbon mineralisation; chemical composition; climate change; infrared spectroscopy.

INTRODUCTION

Soils of tundra and boreal ecosystems contain large carbon (C) stocks, often as an organic layer of peat that covers the underlying mineral soil (Shaver and others 2006). These ecosystems are generally characterized by low productivity, but due to low soil temperatures combined with anaerobic

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conditions, huge amounts of organic matter (OM) accumulate as peat (Gorham 1991; Scanlon and Moore 2000; Shaver and others 2006). Northern soils store an estimated 1400–1850 Pg of organic C, out of which peatlands account for an estimated 200–450 Pg (McGuire and others 2009). These soils also contain large amounts of organic nitrogen (N; Shaver and others 2006). Northern peatlands are currently experiencing substantial warming (Camill 2005) with associated changes in permafrost distribution and modifications of their biogeochemical C and N cycles, but their future as a net source or sink for greenhouse gases (for example, CO₂, CH₄, N₂O) is still unclear (Billings and others 1982; Scanlon and Moore 2000; Schuur and others 2008; Repo and others 2009; Grosse and others 2011; Schmidt and others 2011).

Palsa peatlands form unique ecosystems in northern-boreal and arctic regions, characteristic of the outer margin of the discontinuous permafrost zone (Fronzek and others 2006). Palsas are peat-covered mounds with a frozen core protruding above the surface of the surrounding peatland. The permanently frozen core is covered by a relatively dry peat layer that thaws during the warm season, the so-called active layer. Peatland areas with palsas are heterogeneous ecosystems with various permafrost regimes (permafrost, degraded permafrost, no permafrost) found in a mosaic within the same mire (Seppala 1986). Field observations and model simulations suggest a strong dependence of palsa distribution on climate (Fronzek and others 2006), long-lasting air temperature below 0°C, thin snow cover, and low summer precipitation being the main requirements for their formation (Seppala 2011). Even small increases in temperature (1°C) and precipitation (10%) resulted in considerable simulated losses of areas suitable for palsa development (Fronzek and others 2006), in agreement with the widespread degradation of palsa mounds observed by Zuidhoff and Kolstrup (2000) and Johansson and others (Johansson and others 2006) in northern Sweden during the last decades. It is expected that most permafrost-associated palsa mounds will disappear within a few decades at the most marginal sites throughout the discontinuous permafrost zone, with palsa mounds being progressively replaced by wetter peat areas (Hofgaard 2003).

Degradation of palsa mounds alters peatland hydrology, thermal regime and plant species communities (Turetsky and others 2002). All these factors are expected to affect the net C budget of palsa peatlands ecosystems, which have received considerable attention in the past decade (for example, Turetsky and others 2002; Nykanen and others

2003; Johansson and others 2006; Backstrand and others 2008, 2010; Jackowicz-Korczynski and others 2010; Christensen and others 2012; Olefeldt and others 2012). Main findings from these studies anticipate a decrease in C emissions from palsa peatland ecosystems due to increased productivity and CO₂ uptake, but with an increased radiative forcing on climate due to the expansion of CH₄ emitting wetter peat areas. This pattern is further enhanced as the dry palsa mounds (source of CO₂ through aerobic oxidation of soil organic matter (SOM)) are progressively replaced by wetter peat areas (sink of CO₂, source of CH₄ through anaerobic reduction of SOM). However, large uncertainties remain with regard to climatic and hydrological changes, the response of vegetation communities, and associated C fluxes (Backstrand and others 2010; Bosiö and others 2012).

Permafrost thaw and the degradation of palsa mounds are likely to affect the biogeochemical stability of SOM (that is, SOM resistance to microbial decomposition), which may change the net C source/sink character of palsa peatland ecosystems. Few studies have investigated the composition and stability of SOM in palsa peatlands, most of them being conducted in northern America (for example, Turetsky 2004; Turetsky and others 2007; but see also the study of Alewell and others 2011 in northern Sweden). All these studies underlined the importance of spatial patterns of permafrost in controlling SOM turnover in northern palsa peatlands.

The first objective of this study was to investigate SOM stability of the three main peatland features created by small-scale variations in permafrost (that is, palsa mounds with permafrost, internal lawns representing localised permafrost degradation, bog hummocks without permafrost) in a palsa peatland in northern Norway, using both biological (cumulative CO₂ respiration as a proportion of initial soil organic carbon (SOC); Plante and others 2011) and chemical proxies (water soluble and hot-water extractable C and N and acid hydrolysis) for SOM stability. The second objective was to analyze the relationship between the stability of SOM and its bulk chemistry as assessed by mid-infrared spectroscopy (MIR; Baes and Bloom 1989; Artz and others 2008).

MATERIALS AND METHODS

Study Area

Peat samples were collected from the palsa peatland *Böttemyra* in Øvre Neiden, Finnmark County, Norway (N69°41'05", E29°11'45") in September 2010. *Böttemyra* covers an area of approximately

1.5 km², and is located at the transition between north-boreal and low-arctic vegetation zones (Moen 1999). Here, the palsa mounds date back to the seventeenth century, whereas the ombrotrophic peat they originate from started to develop some 4,000 years ago (Hofgaard 2003). Silt-rich sediments lay under the peat. Mean annual air temperature is -0.7°C (Aune 1993), with an average annual precipitation of 455 mm (1961–1990; Førland 1993). For this area, the annual temperature is predicted to increase $1.5\text{--}3.0^{\circ}\text{C}$ and the annual precipitation is predicted to increase by 1–15% within a 50-year period due to climate change (Hanssen-Bauer and others 2009).

Peat Sampling and Sample Pre-treatment

Three distinct peatland features created by small-scale variations in permafrost were sampled, that is, palsa mounds with permafrost, internal lawns representing localized permafrost degradation, and bog hummocks with no surface permafrost. The peatland features were identified based on the dominant vegetation cover and variations in topography and moisture conditions (that is, degree of submergence);

1. Palsa mounds with permafrost. Covered by drained peat and sparse vegetation dominated by larger patches of barren peat, lichens and low prostrate shrubs (for example, *Betula nana* L., *Ledum palustre* L., *Vaccinium uliginosum* L., *Empetrum hermaphroditum* Hagerup). The depth of the active layer varied between 70 cm and greater than 1 m for the sampled palsas.
2. Internal lawns representing localized permafrost degradation. Identified as wet peat, partly or completely submerged, with a high contribution of *Sphagnum* mosses (*Sphagnum* sect. *Cuspidata*), *Eriophorum augustifolium* Honck. and *Carex rostrata* Stokes.
3. Bog hummocks with no surface permafrost. Vegetation cover dominated by *Sphagnum* mosses (*Sphagnum* sect. *Acutifolia*), cloudberry (*Rubus chamaemorus* L.) and vertical shrubs (for example, *Betula nana* L., *Vaccinium uliginosum* L., *Ledum palustre* L.). Comparatively drier than the internal lawns.

Samples were collected from ten distinct palsa mounds, with the concurrent sampling of adjacent internal lawns and bog hummocks, giving a total of ten field replicates (composite of ten subsamples each) for each peatland feature. The bog hummocks and the palsa mounds were sampled in the

upper 5 cm using a cylindrical auger (5 cm diameter). The internal lawns were sampled between 5 and 15 cm using a spade (different sampling depth due to wet conditions). Green, living plant material was excluded from all samples. Headspace was removed from each sample bag, and samples were stored in the dark at 4°C until analyzed.

Sample pre-treatment and homogenization were carried out on field moist samples. The internal lawn samples were drained to field capacity, whereas palsa mound and bog hummock samples were kept at field moisture. As the palsa peat was more decomposed, and therefore easy to sieve, these samples were sieved to less than 4 mm. The internal lawn and bog hummock samples were cut by knife to less than 1 cm. Visible roots were removed by hand sorting, removing as many fine roots as possible. A subsample was taken out for chemical analyses and dried at 35°C for more than 5 days. A further subsample (0.5–2 g) was then taken for determination of dry weight (105°C overnight) and loss on ignition (550°C for 3 h).

Basic Chemical Analyses

Soil pH was measured in water 1:2.5 (v/v) with a combined Orion pH electrode (SA 720, Allometrics, Inc., Baton Rouge, LA). Total C and N were determined by dry combustion using a Leco CHN 1000 analyzer (Leco Corporation, MI, USA).

Biological Proxies for Soil Organic Matter Stability

Potential C mineralization of the palsa mound, internal lawn and bog hummock samples was assessed in a 90-day laboratory incubation experiment. Field moist samples (ten field replicates of each peat type), equivalent to 3–5 g dry weight, were weighed into 850-ml sealed glass jars. The sample amounts varied depending on sample density and moisture content to ensure oxygen diffusion throughout the sample material and limit possibilities for anaerobic conditions to occur. A small vial containing 5.0 ml 1 M sodium hydroxide (NaOH) was placed in each jar. Samples were incubated in the dark at 15°C . The NaOH traps were replaced and the samples were aerated at 3–10 days intervals during the incubation. The trapped CO_2 was liberated and quantified by mixing the NaOH samples with 3 M H_2SO_4 in a gas-liquid separator coupled to a LI-820 CO_2 Gas Analyzer (LI-COR Biosciences, Lincoln, Nebraska, USA). The samples showed no sign of drying out during the incubation.

To determine whether moisture content could be a limiting factor for SOM mineralization in the palsa peat, a separate set of the ten palsa field replicate samples was incubated for 31 days under similar conditions but with higher moisture content. Field moist samples in amounts equivalent to what was used in the first experiment were weighed into 850-ml glass jars and distilled water was gently added to each sample. This addition of water increased mean moisture content (% of wet weight) from 69 to 80%, which is more comparable to moisture content in the bog hummock peat. During the 31-day incubation, the NaOH traps were replaced at corresponding intervals as in the first experiment.

Chemical Proxies for Soil Organic Matter Stability

Cold- and hot-water extractions were performed on field moist samples according to the procedure described by Ghani and others (2003). Water soluble C (C_{WS}) and hot-water extractable C (C_{HW}) were measured on a TOC-V CPN total organic C analyzer (Shimadzu, Japan), whereas water soluble N (N_{WS}) and hot-water extractable N (N_{HW}) were measured by flow injection analysis on a FIA star 5010 Analyzer (Tecator, Sweden).

Total carbohydrates in the hot-water extracts were determined by the phenol-sulphuric acid procedure as described by Safarik and Santruckova (1992). Acid hydrolysis was performed on the dried (35°C) soil residues after hot-water extraction by a modified method of Leavitt and others (1996). Samples were hydrolyzed with 25 ml 6 M HCl (1:50, soil to acid, w/v) at 95°C for 18 h, and thereafter filtered on a GF/F (0.45 μm) glass-fibre filter. The non-hydrolyzable fraction was kept on the filter, washed with hot distilled water to remove any chlorine residue, and dried at 105°C before determination of total C and weight loss. The non-hydrolyzable C fraction (% C_{RES}) was calculated as the proportion of the initial total C content remaining on the filter (Paul and others 2006).

Soil Organic Matter Bulk Chemistry

Spectral characterization of the 30 finely ground peat samples was performed by diamond attenuated total reflectance (ATR) spectroscopy using a Nicolet iS10 FT-IR spectrometer (Thermo Fisher Scientific Inc., Madison, WI, USA). All the 30 samples were analyzed in five replicates over the spectral range 4,000–500 cm^{-1} , with spectral resolution of 4 cm^{-1} and 16 scans per replicate. All spectra were corrected

for atmospheric interferences (H_2O and CO_2) and variations in the depth of penetration that occurs with the ATR technique. Spectral data were further processed and analyzed using R software version 2.14.0 (R Development Core Team 2011), with the following R packages: hyperSpec (Beleites and Sergio 2011), ptw (Bloemberg and others 2010), and StreamMetabolism (Sefick 2009). Four waveband regions were chosen for further characterization and peak ratio comparisons among peat types; (1) the saturated (SAT) region 2,985–2,820 cm^{-1} corresponding to alkyl C (CH_2 , CH_3 , and CH), (2) the unsaturated (UNSAT) region 1,800–1,525 cm^{-1} corresponding to C=O and aromatic C=C bonds, (3) the polysaccharide (POLY) region 1,185–915 cm^{-1} corresponding to O-Alkyl C, and (4) the aromatic CH (AROCH) region 855–740 cm^{-1} (Smith 1999; see Figure 1 for an illustration of Gaussian curve-fitting and integration of spectral regions). Six different peak ratios, slightly adapted from the following references, were computed:

1. Hydrophobicity index (Capriel and others 1995), $\text{HI} = \text{SAT}/\text{SOC}$ (g kg^{-1}).
2. Reticulation index (Ibarra and others 1996), $\text{RI} = \text{CH}_3/\text{CH}_2$.
3. Aromaticity index (Dick and others 2011), $\text{AI} = \text{C}=\text{C}/\text{SOC}$ (g kg^{-1}).
4. Maturation index (Ibarra and others 1996), $\text{MI} = \text{C}=\text{C}/\text{UNSAT}$.
5. Condensation index (Guo and Bustin 1998), $\text{CI} = \text{AROCH}/\text{C}=\text{C}$, and
6. Polysaccharide index, $\text{PI} = \text{POLY}/\text{SOC}$ (g kg^{-1}).

The aromaticity index (AI) is commonly calculated as the proportion of aromatic C=C to aliphatic CH functional groups (Dick and others 2011). We have, however, chosen to calculate AI as the absorbance of aromatic C=C relative to SOC, to avoid this index being mainly dominated by the aliphatic CH signal. Absorbance in the 1,200–900 cm^{-1} region is mainly ascribed to polysaccharides (Bornemann and others 2010) and Si–O (Nguyen and others 1991). The polysaccharide index, as derived from the sample absorbance in the 1,185–915 cm^{-1} region relative to total SOC, is here included as the contribution of silicates to these bands is considered negligible for our peat samples.

Statistical Analyses

Statistical analyses were performed using Minitab 16.1.1 Statistical Software (Minitab Inc., USA) and R software version 2.14.0 (R Development Core Team 2011) with the package ade4 (Chessel and others

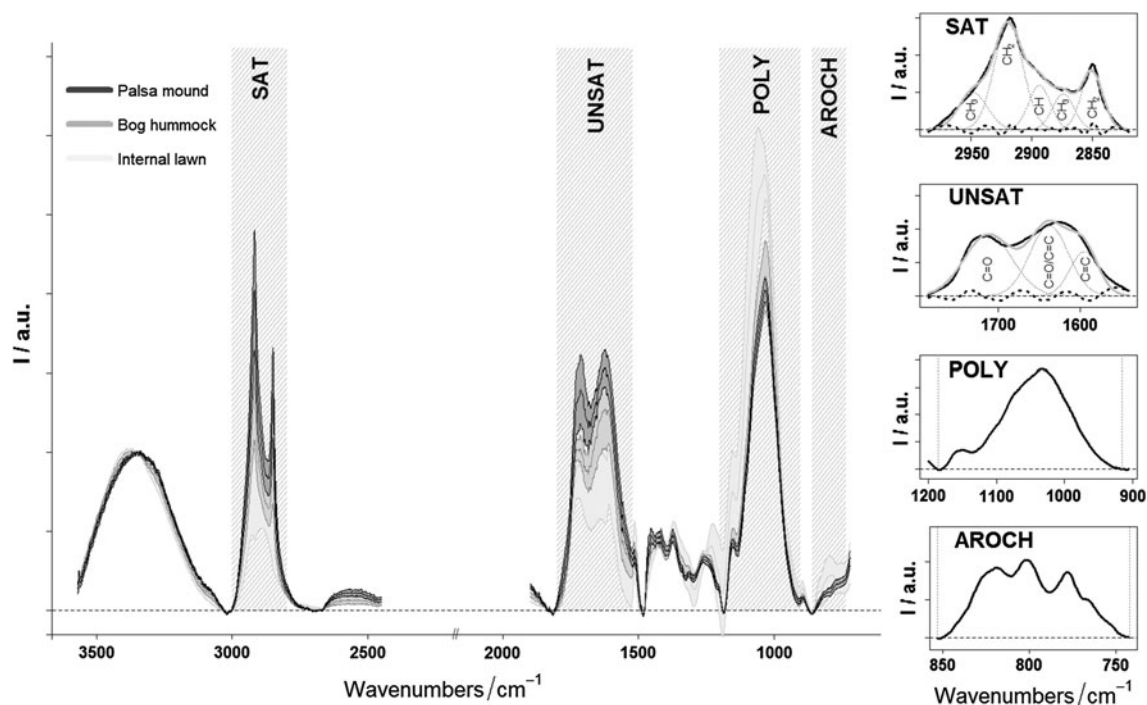


Figure 1. Baseline corrected and normalized ($3,350\text{ cm}^{-1}$; OH H_2O band) MIR spectra of palsa mound, internal lawn and bog hummock replicate samples (*left panel*). The region of diamond and CO_2 interference ($2,450\text{--}1,900\text{ cm}^{-1}$) is excluded. The MIR waveband regions selected for characterization of peat samples and peak ratio calculations were: (1) the saturated (SAT) region $2,985\text{--}2,820\text{ cm}^{-1}$, (2) the unsaturated (UNSAT) region $1,800\text{--}1,525\text{ cm}^{-1}$, (3) the polysaccharide (POLY) region $1,185\text{--}915\text{ cm}^{-1}$, and (4) the aromatic CH (AROCH) region $855\text{--}740\text{ cm}^{-1}$. The *right panel* shows the fitted Gaussian curves within the SAT and UNSAT regions and the structural assignment of the respective absorption bands (according to Smith 1999). Total absorbance in the POLY and AROCH regions were computed by integrating the respective spectral ranges.

2004). Pairwise comparisons of medians were performed by non-parametric Kruskal–Wallis ($P < 0.05$) followed by Mann–Whitney tests, with $P < 0.05/3$ for each single test to give an overall test level of $P < 0.05$. A principal component analysis (PCA) of the standardized (centred and scaled) infrared peak ratios and potential C mineralization was performed to investigate the correlations between the composition and the stability of SOM.

RESULTS

General Peat Properties and Chemical Analyses

All the investigated samples displayed high OM and total C contents, and low pH (Table 1). Total C and pH differed significantly among peat types ($n = 10$, $P < 0.01$). Moisture content, being a highly temporal property, also differed significantly among

Table 1. General Characteristics of Palsa Mound, Internal Lawn and Bog Hummock Peat Samples

	Palsa mound	Internal lawn	Bog hummock
Moisture content (% of wet weight)	68.8 ± 1.0^c	93.0 ± 1.0^a	83.0 ± 2.2^b
Loss on ignition (% w/w)	98.5 ± 0.1^a	95.9 ± 1.0^b	97.9 ± 0.1^b
Volume weight (g cm^{-3})	0.15 ± 0.01^a	0.07 ± 0.02^b	0.09 ± 0.01^b
pH (1:2.5, v/v)	3.8 ± 0.0^c	4.3 ± 0.0^a	4.0 ± 0.0^b
Total C (%)	54.0 ± 0.2^a	46.8 ± 0.6^c	50.6 ± 0.6^b
Total N (%)	1.3 ± 0.0^a	1.0 ± 0.2^a	1.1 ± 0.1^a
C/N	42.7 ± 1.5^a	57.2 ± 7.4^a	47.9 ± 3.2^a

Different superscript letters within the same analysis (row) indicate significant differences between peat types (Mann–Whitney comparison of medians, with $P < 0.05/3$ for each single test).

Values are mean \pm standard error of ten field replicates.

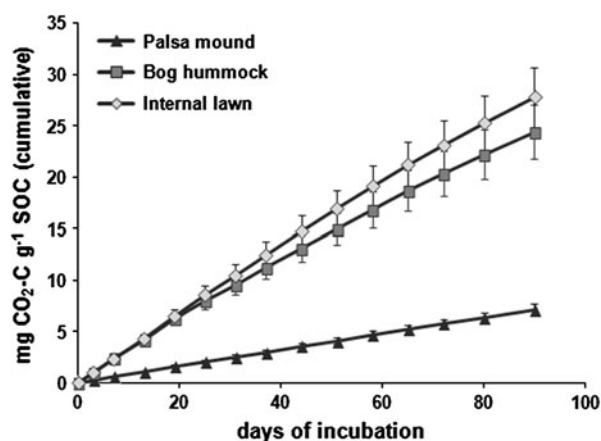


Figure 2. Cumulative C mineralization during 90 days of incubation (15°C) for the palsa mound, internal lawn and bog hummock peat ($\text{mg CO}_2\text{-C g}^{-1}\text{ SOC day}^{-1}$). Error bars indicate standard error of the mean.

peat types ($n = 10$, $P < 0.01$), with the lowest moisture content in the palsa peat and highest in the internal lawn peat.

Biological Proxies for Soil Organic Matter Stability

Cumulative CO_2 respiration was significantly higher in internal lawn and bog hummock than in palsa peat throughout the 3-month incubation (Figure 2; $n = 10$, $P < 0.001$). The proportion of SOC respired as $\text{CO}_2\text{-C}$ after 90 days of incubation was $2.8 \pm 0.3\%$ in the internal lawn peat, $2.4 \pm 0.3\%$ in the bog hummock peat, and only $0.7 \pm 0.0\%$ in the palsa peat. The increase in mean moisture content from 69 to 80% did not significantly alter the measured respiration in the palsa peat, with cumulative CO_2 respiration of $0.25 \pm 0.02\%$ and $0.28 \pm 0.02\%$, respectively, after 31 days of incubation.

Chemical Proxies for Soil Organic Matter Stability

Water soluble C (C_{WS}) differed significantly among peat types ($n = 10$, $P < 0.01$; Table 2). Hot-water extractable C (C_{HW}) was lower in internal lawn than in palsa and bog hummock peat ($n = 10$, $P < 0.05$). Water soluble N (N_{WS}) was significantly

Table 2. Chemical Proxies for SOM Stability Derived from Cold- and Hot-Water Extractions and Acid Hydrolysis

	Palsa mound	Internal lawn	Bog hummock
C_{WS} ($\text{mg C g}^{-1}\text{ SOC}$)	$0.5 \pm 0.1^{\text{c}}$	$1.5 \pm 0.1^{\text{a}}$	$0.9 \pm 0.1^{\text{b}}$
C_{HW} ($\text{mg C g}^{-1}\text{ SOC}$)	$50.5 \pm 1.3^{\text{a}}$	$38.1 \pm 3.3^{\text{b}}$	$54.9 \pm 2.4^{\text{a}}$
N_{WS} ($\mu\text{g N g}^{-1}\text{ dry weight}$)	$11 \pm 3^{\text{b}}$	$29 \pm 6^{\text{a}}$	$12 \pm 2^{\text{b}}$
N_{HW} ($\mu\text{g N g}^{-1}\text{ dry weight}$)	$838 \pm 28^{\text{a}}$	$709 \pm 55^{\text{a}}$	$1020 \pm 81^{\text{a}}$
C_{CARB} (%)	$25.6 \pm 0.8^{\text{c}}$	$41.2 \pm 2.7^{\text{b}}$	$51.1 \pm 1.6^{\text{a}}$
C_{RES} (%) ¹	$56.8 \pm 1.7^{\text{a}}$	$41.9 \pm 2.8^{\text{b}}$	$54.7 \pm 3.3^{\text{ab}}$

Different superscript letters within the same analysis (row) indicate significant differences between peat types (Mann–Whitney comparison of medians, with $P < 0.05/3$ for each single test).

Values are mean \pm standard error of ten field replicates.

C_{WS} = water soluble C; C_{HW} = hot-water extractable C; N_{WS} = water soluble N; N_{HW} = hot-water extractable N; C_{CARB} = % carbohydrate C of C_{HW} ; C_{RES} = % residual C after acid hydrolysis.

¹ $n = 7$, 5, and 3 for the palsa, internal lawn and bog hummock peat, respectively, due to difficulties in recovering the entire residue after the hydrolysis procedure for some samples.

Table 3. Peak Ratios Derived from Selected Waveband Regions of MIR Spectra

	Palsa mound	Internal lawn	Bog hummock
Hydrophobicity index (HI)	$0.21 \pm 0.01^{\text{a}}$	$0.14 \pm 0.02^{\text{b}}$	$0.16 \pm 0.01^{\text{b}}$
Reticulation index (RI)	$0.39 \pm 0.01^{\text{b}}$	$0.63 \pm 0.05^{\text{a}}$	$0.46 \pm 0.01^{\text{a}}$
Aromaticity index (AI)	$0.118 \pm 0.003^{\text{a}}$	$0.103 \pm 0.008^{\text{a}}$	$0.111 \pm 0.004^{\text{a}}$
Maturation index (MI)	$0.35 \pm 0.01^{\text{b}}$	$0.37 \pm 0.01^{\text{ab}}$	$0.39 \pm 0.01^{\text{a}}$
Condensation index (CI)	$0.04 \pm 0.00^{\text{c}}$	$0.17 \pm 0.02^{\text{a}}$	$0.07 \pm 0.01^{\text{b}}$
Polysaccharide index (PI)	$0.39 \pm 0.01^{\text{b}}$	$0.63 \pm 0.01^{\text{a}}$	$0.45 \pm 0.02^{\text{b}}$

Different superscript letters within the same analysis (row) indicate significant differences between peat types (Mann–Whitney comparison of medians, with $P < 0.05/3$ for each single test).

Values are mean \pm standard error of ten field replicates.

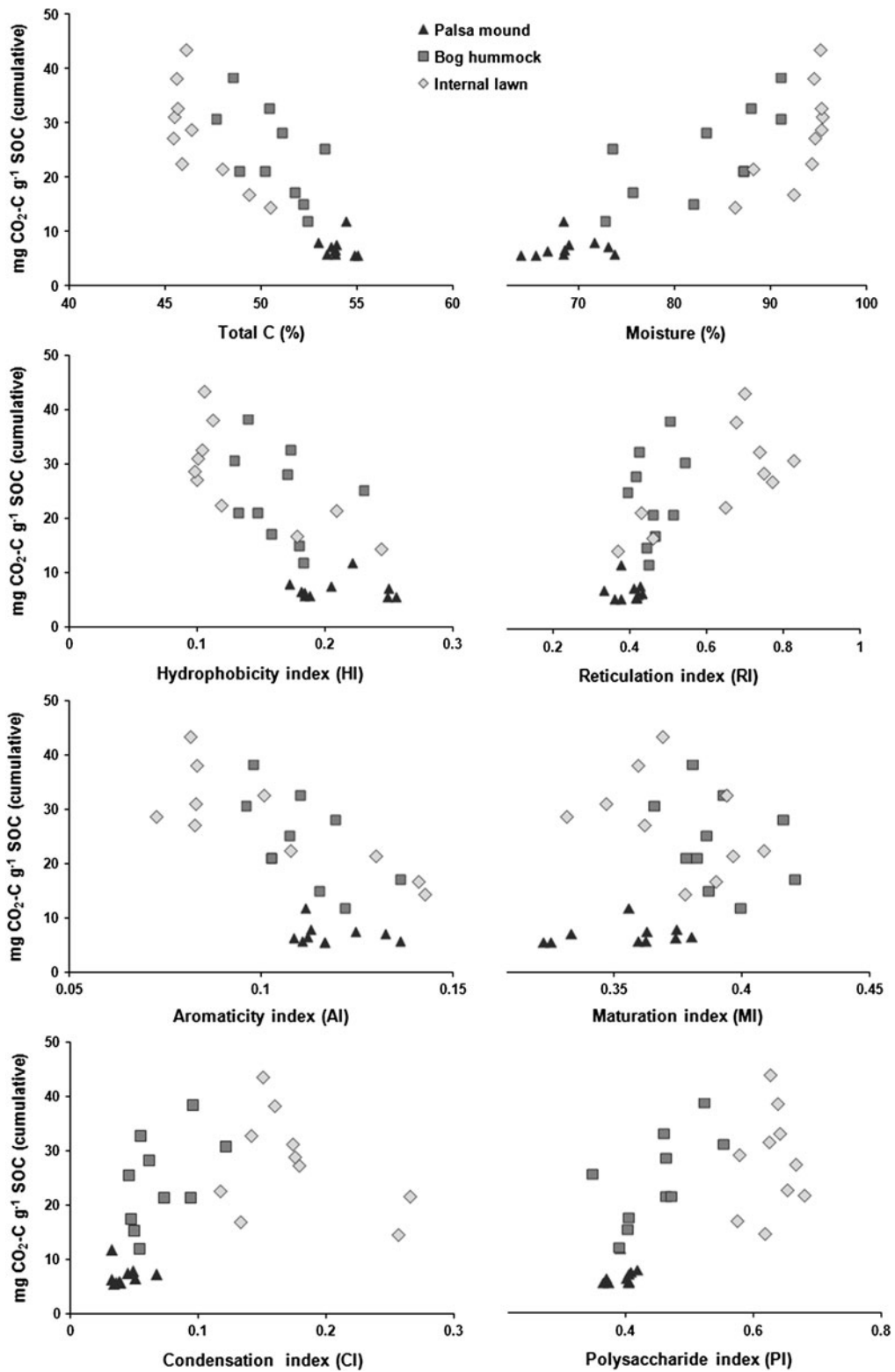


Figure 3. Plots of cumulative C mineralization (mg CO₂-C g⁻¹ SOC) against total C (%), moisture (%), hydrophobicity index (HI), reticulation index (RI), aromaticity index (AI), maturation index (MI), condensation index (CI), and polysaccharide index (PI) for palsa mound, internal lawn and bog hummock peat samples.

higher in the internal lawn compared to the palsa mound and bog hummock peat ($n = 10$, $P < 0.05$). The proportion of carbohydrate C (C_{CARB}) in the hot-water extracts differed significantly among peat types ($n = 10$, $P < 0.01$). The residue on acid hydrolysis (C_{RES}) was significantly higher in the palsa as compared to the internal lawn peat ($n = 7$ and 5 , $P < 0.01$).

Soil Organic Matter Bulk Chemistry

The computed peak ratios based on mid-infrared (MIR) spectra revealed significant differences among peat types in the relative contribution of OM functional groups (Table 3; Figure 3). The palsa peat showed significantly higher hydrophobicity (HI) and lower reticulation (RI) index compared to both the internal lawn and bog hummock peat ($n = 10$, $P < 0.01$). The maturation index (MI) decreased significantly from bog hummock to palsa peat types ($n = 10$, $P < 0.001$), with intermediate values for the internal lawn peat. Conversely, SOM of all peat types had a similar aromaticity. Only the degree of condensation of aromatic rings (CI) and polysaccharide index (PI) revealed significant differences between the internal lawn and bog hummock peat, both indexes being significantly higher in the internal lawn compared to both the palsa and bog hummock peat ($n = 10$, $P < 0.001$; Table 3; Figure 3).

The PCA of infrared peak ratios and potential C mineralization illustrated the differences in SOM bulk chemistry and stability among peat types, with a clear ordination of the 30 samples according to peat type on the PC1 and PC2 factorial map, which represented 79% of total variance (Figure 4). Peat samples from palsa mounds showed a very homogeneous signature, whereas an increased variation among samples was observed from the bog hummock to the internal lawn peat type on both PC1 and PC2. PC1 represented 60% of total variance and was mainly associated with potential C mineralization, PI and RI (positively), and with HI and AI (negatively). PC2 represented 19% of total variance and was mainly associated with MI and AI (negatively). Palsa peat samples showed negative PC1 scores and positive PC2 scores, whereas an increase in PC1 scores and either positive or negative scores on PC2 were observed for samples from bog hummock and internal lawn peat types. Potential CO_2 mineralization showed a strong positive correlation with PI and RI, and strong negative correlation with HI and AI (Figure 4).

DISCUSSION

Biological and Chemical Proxies for SOM Stability

Having the lowest potential C mineralization, peat from the permafrost-associated palsa mounds showed the highest SOM biological stability compared to the bog hummocks and the internal lawns (degraded permafrost). There was no significant difference in potential CO_2 production between internal lawn and bog hummock, which both displayed a CO_2 production rate more than 3 times higher than that of palsa peat. These results are in agreement with the observations of Turetsky (2004) in palsa peatlands in Canada. She noted a significantly higher potential C mineralization of internal lawns and bog peat compared to peat from permafrost mounds in short-term (days) laboratory incubations. However, Turetsky (2004) also found a higher potential C mineralization for internal lawns than for the bog peat, which was not the case in our study. Overall, the lower biological stability assessed for the internal lawn and bog hummock peat with the 90-day incubation suggests that both internal lawns and bog hummocks contain considerable amounts of labile C compared to palsa peat (see below). Such contrasted patterns for SOM stability in palsa peatlands suggest that a C stabilization mechanism other than for example, prolonged low temperature or anaerobic conditions (see Torn and others 2009) is active in permafrost-associated palsa mounds. This should only be selective preservation of recalcitrant OM (for example, lignin or phenolic compounds) during intense aerobic decomposition over time because other C stabilization mechanisms such as physical protection in soil microaggregates and mineral association (von Lutzow and others 2006; Torn and others 2009) are unlikely in surface peat samples.

Despite the variability induced by experimental setups, our results are within the range of aerobic CO_2 production rates in northern peatlands reported by, for example, Moore and Dalva (1997), Scanlon and Moore (2000), and Turetsky (2004). All these incubations were of relatively short duration (2–12 days) compared to our 90-day incubation. Incubations of longer duration are more suited for detecting shifts in microbial communities and SOM pools during decomposition, and less prone to artefacts linked with initial sampling and transport disturbances (Turetsky 2004). In 80-week aerobic laboratory incubations at 15°C , Updegraff and others (1995) found that approximately 8% of SOC was mineralized to $\text{CO}_2\text{-C}$ in

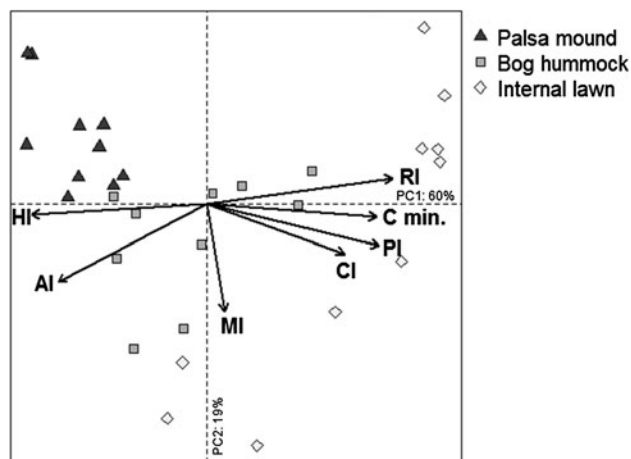


Figure 4. Principal component analysis of mid-infrared peak ratios and potential C mineralization. The first two components, PC1 and PC2, explain 60 and 19 % of total variance, respectively. *HI* hydrophobicity index, *RI* reticulation index, *AI* aromaticity index, *MI* maturation index, *CI* condensation index, *PI* polysaccharide index, and *C min.* cumulative C mineralization.

Sphagnum-derived surface peat. In our experiment, only a very slight decrease in potential CO₂ production was observed at the end of the incubation period for the internal lawn and bog hummock samples (Figure 2), indicating that a longer incubation period would have been necessary to detect any significant shift in SOM pools during decomposition.

Chemical proxies for SOM stability supported the results of the laboratory incubations. Acid hydrolysis preferentially removes labile O-alkyl components, primarily originating from polysaccharides, with the residue being enriched in more resistant aromatic and aliphatic C components (Kögel-Knabner and others 2008). Therefore, higher C_{RES} and C concentration in palsa compared to bog hummock and internal lawn peat suggest a higher content of more recalcitrant compounds rich in C, which could explain the low proportion of SOC respired as CO₂ in the palsa peat compared to the internal lawn and bog hummock peat. The palsa peat also showed a significantly lower content of carbohydrate C in the hot-water extracts (C_{CARB}), indicating a lower contribution of labile C compounds for this peat type compared to the internal lawn and bog hummock peat. These results are similar to the observations of Turetsky (2004) and Turetsky and others (2007) who found higher acid insoluble material in surface peat of permafrost features than in the peat from the surrounding unfrozen bogs. However, these two studies also reported a high content of hot-water soluble carbohydrates in the peat from the permafrost features, with the lowest content observed in the

internal lawn peat samples (Turetsky 2004; Turetsky and others 2007), which contrasts with our findings. These contrasting results could be explained by the denser and different vegetation cover on the permafrost features in the studies of Turetsky and colleagues compared to that of our palsa mounds or different extraction procedures before determination of hot-water soluble carbohydrates. The time span since permafrost formation/degradation (that is, age of palsa mounds and internal lawns) is an additional factor assumed to influence the content of labile C compounds in surface peat of these peatland features.

Links Between Soil Organic Matter Stability and Bulk Chemistry

We used mid-infrared spectroscopy (MIR) to assess SOM bulk chemistry and the relative enrichment or depletion of certain OM functional groups between and/or within the different peat types of the palsa peatland. The MIR peak ratios revealed strong differences in SOM bulk chemistry of palsa peat compared to the two other peat types and suggest a strong influence of substrate quality on the higher biogeochemical stability of the palsa peat. SOM bulk chemistry of the palsa peat was very homogeneous and appeared to be closer to the one of the bog hummock peat than to the one of the peat from internal lawns (degraded permafrost), as shown by the PCA of mid-infrared peak ratios and potential C mineralization (Figure 4). This same pattern was shown by Turetsky and others (Turetsky and others 2007) based on factor analysis of pyrolysis mass

spectra. Furthermore, Turetsky and others (2007) found an increase in holocellulose content and cellulosic and hemicellulosic pyrolysis markers in bog and internal lawns, and a greater amount of phenolic pyrolysis markers in the permafrost-associated peat in their study of Canadian peatlands. Our results from a Norwegian palsa peatland support their findings, as mid-infrared peak ratios showed a relative increase in the polysaccharide index (PI) in the bog hummock and the internal lawns compared to the palsa peat, and a relatively higher aromaticity index (AI) in the palsa peat compared to the bog hummock and the internal lawn peat (although not significant, Table 3; Figure 3; but note the highly negative PC1 loading of AI, and the highly positive PC1 loading of PI on the PCA, Figure 4). The high positive correlation between the MIR-derived polysaccharide index (PI) and potential C mineralization (Figure 4) supports the link between O-alkyl C content and SOM biogeochemical stability recently shown by Leifeld and colleagues in temperate peatlands in Switzerland (Leifeld and others 2012). Overall, our study illustrates the reliability of the fast and cheap ATR-MIR spectroscopic approach for assessing SOM bulk chemistry in peat samples, as was also demonstrated by Artz and others (2008) and Cécillon and others (2012). This approach further provided additional meaningful information regarding SOM hydrophobicity (HI), reticulation (RI), condensation of aromatic rings (CI), and maturation (MI). The high HI and relatively low RI in the palsa peat indicate a high contribution of aliphatic functional groups (Capriel and others 1995), predominantly of longer chain lengths (Ibarra and others 1996). With increasing hydrophobicity, SOM surface wettability is reduced with subsequent reduced accessibility of SOM for microorganisms (von Lutzow and others 2006). The predominance of longer aliphatic chain lengths could indicate a large proportion of plant-derived fatty acids, and a lower proportion derived from microbial activity (Rennert and others 2011). The higher CI in the internal lawn compared to the palsa peat could result from the higher input of *Sphagnum*-derived material rich in phenols (Alewell and others 2011), and a possible high degree of condensation (Guo and Bustin 1998) of polyphenolic compounds. Polyphenols are often water soluble and can form highly resistant complexes with proteins, which may dramatically slow the rates of C oxidation (Brady and Weil 2002). This could further imply that the amount of water soluble C (C_{WS}) and hot-water extractable C (C_{HW}) are not necessarily good measures for labile C in

Sphagnum-dominated peat soils. Turetsky and others (2007) also observed a strong contribution of phenolic pyrolysis markers in peat from internal lawns. For the maturation index (MI), the palsa peat showed the lowest values, whereas the bog hummock peat showed the highest values. MI values were intermediate in the internal lawns (Figure 3). Thus, the MI index could reflect the O_2 status of each peat type, with lower values indicating aerobic SOM decomposition in surface palsa peat (that is, increase in C=O relative to C=C) and higher values indicating anaerobic SOM decomposition in the bog hummocks. The intermediate values in the internal lawns may be explained by a highly variable O_2 status among the sampled internal lawns, but more likely by a larger variation in aromatic C=C content for the internal lawns (that is, highly variable AI index; Figure 3). This is even better illustrated in the PCA of mid-infrared peak ratios and potential C mineralization (Figure 4), with positive PC2 scores for palsa peat, negative or close to zero PC2 scores for bog hummock peat and highly variable PC2 scores for the internal lawn peat, where higher PC2 scores denote an increase in bulk C oxidation state (that is, increase in C=O relative to C=C).

It should be noted that a number of factors other than SOM chemical composition also could contribute to explain the higher biogeochemical stability of the palsa peat, such as for example, microbial community structure, microbial biomass relative to substrate availability, pH, and moisture conditions. All our samples were incubated at field moisture content, which differed significantly among peat types, and across peat types there is an apparent positive relationship between cumulative C mineralization and moisture content (Figure 3). However, a significant effect of increased moisture content on palsa CO_2 production is unlikely, as demonstrated by our separate incubation experiment where palsa samples were incubated at 80% moisture. Also, within palsa and internal lawn peat types there is only a weak or no relationship between cumulative C mineralisation and moisture content (Figure 3).

As we did not perform a separate anaerobic incubation experiment, we cannot exclude the possibility that SOM decomposition in the bog hummock and internal lawn peat is also limited by the supply of labile C compounds. To better elucidate the relative importance of the different stabilisation mechanisms, further research should include a moisture gradient from dry to submerged (anaerobic) conditions to explore to what extent decomposition is limited by oxygen availability.

Relevance of SOM Stability for the C Budget of Palsa Peatlands in a Changing Environment

Using biological and chemical proxies for SOM stability, we showed that the presence of permafrost drives the stability of surface SOM in a palsa peatland in northern Norway. The frost heave associated with permafrost aggradation in palsa mounds resulted in profound aerobic decomposition of the upper dry palsa peat that has stabilized SOM over time. Indeed, the stability of surface peat was consistently higher in the permafrost-associated palsa mounds than in the surrounding internal lawns and bog hummocks. Our results also pointed out the differences in SOM bulk chemistry as a main factor explaining SOM stability in this palsa peatland, with selective preservation of recalcitrant and highly oxidized SOM components in the palsa mounds (well drained, aerobic conditions), whereas SOM in the wetter areas of the peatland remains stabilized mainly by anaerobic conditions (partly or completely submerged). These results on SOM stability in a Norwegian palsa peatland are strongly supported by the results of Turetsky (2004) and Turetsky and others (2007) from palsa peatlands in Canada. Therefore, we argue that the spatial pattern of permafrost in palsa peatlands is generating a similar spatial pattern for SOM biogeochemical stability and C oxidation state in these ecosystems.

Results from in-situ greenhouse gas measurements and rates of peat accumulation in palsa peatlands have shown that the spatial patterns of permafrost are also associated with strong differences in the net C sink/source character of palsa mounds, internal lawns and bog hummock areas (for example, Turetsky and others 2002; Turetsky and others 2007; Backstrand and others 2008; Backstrand and others 2010). These differences are mainly linked to differences in the vegetation, productivity and O₂ status of the respective peatland features. Overall, permafrost-associated palsa mounds are considered a net C source (through aerobic CO₂ emissions), whereas the wetter peat areas are considered a small net C sink (through moderate anaerobic CH₄ emissions and a high net peat accumulation rate).

The ongoing degradation of palsa mounds was clearly visible in our study area in northern Norway. The ongoing degradation of palsas is characterized by the presence of the internal lawns, where larger fragments at the edges of adjacent palsa mounds break off and fall into the internal lawns. Palsas may also collapse as a result of thawing of the inner

frozen core (Seppala 1986). The continued degradation and collapse of palsa mounds may be considered a source of stable and oxidized C into the surrounding peatland, but this is unlikely to significantly modify the overall stability of SOM and C oxidation state because the amount of palsa-mound C is small as compared to the total peatland C stock. On the other hand, recent results from Alewell and others (2011) showed that the $\delta^{13}\text{C}$ isotope depth profile of the internal lawn peat significantly differed between a palsa peatland showing no degradation of palsa mounds (steady decomposition under anaerobic conditions, higher contribution of recalcitrant compounds depleted in ¹³C), and a palsa peatland showing clearly visible degradation of palsa mounds in northern Sweden. They attributed this difference in the $\delta^{13}\text{C}$ isotope depth profiles mainly to inputs of oxidized C from the degrading palsa mounds in the latter.

It is difficult to predict how these “inputs” of relatively more stable C and the expansion of internal lawn and bog hummock areas will alter the future net C sink/source status of palsa peatlands. Changes in the net C sink/source character of palsa peatlands will largely depend on the degree of water saturation and peat oxidation status, especially in the internal lawns and surrounding bog hummocks which should dominate these peatlands after the collapse of most palsa mounds. A recent study suggested that the effect on climate of permafrost C thawing under aerobic conditions may be greater than a similar amount of permafrost C thawing under anaerobic conditions when both produced CO₂ and CH₄ are scaled according to their warming potential (Lee and others 2012). It is, however, difficult to predict hydrological changes in high-latitude systems such as palsa peatlands following permafrost thaw (Schoor and others 2008), and there are still large uncertainties related to moisture controls on C exchange in *Sphagnum*-dominated peatlands (Strack and others 2009). Even if a dominance of anaerobic conditions is likely in degraded palsa peatlands, there may also be a reverse process of drying as the mass of water will move over larger areas when permafrost thaw and palsas disappear (Bosiö and others 2012), that may create aerobic conditions for SOM decomposition in degraded palsa peatlands.

CONCLUSIONS

This study emphasized the spatial patterns of permafrost as a main driver for SOM biogeochemical stability in a subarctic palsa peatland in northern Norway. The observed differences in SOM biogeochemical stability (as determined by both biological

and chemical proxies) were largely explained by SOM bulk chemistry, with an enhanced aerobic decomposition in permafrost-associated palsa mounds leading to selective preservation of recalcitrant and oxidized C in these permafrost features. Contrary, SOM in the wetter areas of the peatland remains stabilized mainly by anaerobic conditions (partly or completely submerged).

With the continued degradation and collapse of permafrost-associated palsa mounds, these will become a source of relatively more stable and oxidized C into the surrounding peatlands. However, these inputs are small compared to the total peatland C stock, and we therefore expect the expansion of internal lawn and bog hummock areas to have a larger impact on the bulk SOM chemistry of surface peat in palsa peatlands. Both the internal lawn and bog hummock peat contain considerable amounts of labile C currently stabilized by anaerobic conditions, indicating that the future net C source/sink character of palsa peatlands will depend on moisture conditions and oxygen availability in peat. Large uncertainties remain with regard to the future O₂ status of SOM decomposition in northern peatlands, and further studies are needed to provide insights into the future role of the discontinuous permafrost zone in the global C cycle and potential feedback to global warming.

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