Importance of lichen and moss litters to soil carbon storage in black spruce forests on permafrost

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Abstract

Aims

Climate warming is predicted to increase permafrost degradation and soil carbon (C) loss, while changes in microrelief and vegetation cover can also influence soil C storage at local scale. Black spruce forests develop lichen/moss-covered organic mounds on permafrost. Recalcitrance of lichen and moss litters, as well as cold climate, is hypothesized to increase C storage in hummocky soils.

Methods

We compared the decomposition rates of lichen and moss litters, spruce root litter, and cellulose at hummocky clayey soils, non-hummocky clayey soils, and non-hummocky sandy soils in northwest Canadian subarctic.

Results

Lichen/moss-covered hummocky clayey soils display greater C stocks than non-hummocky clayey and sandy soils. Lichen and moss litters decomposed more slowly than did spruce root litter and cellulose. Recalcitrant litter inputs of lichen and moss contribute to greater C stocks of hummocky clayey soils, compared to non-hummocky clayey and sandy soils. Lower temperature dependency of lichen and moss litter decomposition, compared to vascular plant litter, suggests stronger resistance of lichen and moss litters to decomposition.

Conclusion

Permafrost degradation by climate warming would reduce hummocky microrelief covered by lichen and moss, major contributors to soil C, and decrease the high potential for C storage of black spruce forests on permafrost.

Introduction

In northern circumpolar regions, huge amounts of carbon (C) have accumulated as soil organic matter (SOM). Soil C stocks in these regions account for 30–40 % of global soil C (Ping et al., 2015), and 70 % of the soil C in the northern soil C pool is affected by permafrost (Tarnocai et al., 2009). Climate warming is predicted to increase active layer thickness and SOM decomposition, which risks inducing a feedback loop of CO₂ emission from permafrost and climate warming (Schuur et al., 2009; Koven et al., 2011). In addition to global climatic controls, soil C gain/loss is also dependent on local factors such as landscape and vegetation (Turetsky et al., 2007). Understanding both global and local factors regulating SOM

decomposition and accumulation on permafrost is crucial for predicting the responses of arctic ecosystem C cycles to future climate change.

The “drunken” black spruce forest with leaning trees on hummocky microrelief is one of the dominant ecosystems on permafrost in northeast Canada (Zoltai, 1975; Fig. 1a). Hummocky microrelief composing of mounds (1 to 3 m in diameter) and troughs are generated through the ice wedge formation and freeze-thaw cycles over thousands of years, but accumulation of lichen and moss debris also promotes mound development in fire-forest regeneration cycles (i.e., several hundreds of years) (Fig. 1bc; Kokelj et al., 2007; Walker et al., 2008; Fujii et al., 2020a). In spite of low productivity of aboveground tree biomass (Tei et al., 2017), black spruce forest exhibits the huge belowground C stocks on permafrost (Tarnocai et al., 2009; Fujii et al., 2019). However, it remains unclear what processes drive high SOM accumulation on permafrost.

Soil C storage results from the balance of organic matter inputs and decomposition (Camill et al., 2011). Organic matter decomposition is limited by the cold climate on permafrost, anaerobic soil conditions (low oxygen availability) imposed by the impermeable permafrost table, and recalcitrance of litters (Hobbie et al., 2000; Davidson and Janssens, 2006; Bragazza et al., 2009; Ping et al., 2015). In hummocky microrelief, lichens and mosses, which grow in dry mounds and wet troughs respectively, can supply more diverse C sources, compared to the wetter tundra with non-hummocky microrelief, where vascular plants [birch (*Betula glandulosa* L.) and Poaceae grass (*Calamagrostis canadensis* L.)] are dominant. Lichen and moss litters are resistant to microbial attack due to their antibacterial compounds and the recalcitrant cell structure (Lang et al., 2009; Turetsky et al., 2008; Hagemann and Moroni, 2015). Despite the lower litter production rates compared to vascular plants, the lower decomposability of litter from lichens and mosses on hummocky microrelief is hypothesized to slow organic matter decomposition and increase soil C storage (Moore et al., 2007; Camill et al., 2011).

In the Mackenzie upland area, different geological substrates from glaciofluvial sands and a mixture of fluvial clayey sediments and fine-grained glacial till provides the wide variation in permafrost table depths and hummocky microrelief (Fig. 1d). Clayey soils could develop the larger hummocks, compared to sandy soils, due to the higher ice contents and shallower permafrost table (Tarnocai and Smith, 1993). The differences in microrelief and soil texture provide the variation in litter inputs and soil conditions affecting litter decomposition rates. These effects of clayey texture, as well as sorption of SOM onto clays, limit microbial activity and thus, increase soil C stocks (Bauhus and Pare, 1998; Hayakawa et al., 2018). Comparing litter production and decomposition rates between hummocky and non-hummocky soils and between clayey and sandy soils enables an analysis of the effects of hummocky microrelief and vegetation covers on soil C storage. We hypothesized the development of lichen/moss-covered mounds leads to greater C stocks in clayey soils with hummocky microrelief, compared to clayey or sandy soils with non-hummocky microrelief.

Field incubation of standard substrates (i.e., litter bag or cellulose test) is a useful approach for analyzing the contribution of (micro)climatic and litter-quality factors to litter turnover and soil organic C (SOC)

storage (Moore, 1984; Hayakawa et al., 2014). To test the aforementioned hypotheses, we conducted a 4-year field incubation of lichen, moss, and spruce root litters in black spruce forests on permafrost. Then, we attempted to reconstruct the accumulation of organic C in the soils with/without hummocky microrelief, using litter production and decomposition rates.

Materials And Methods

Experimental sites

We investigated 16 black spruce forest sites in the Mackenzie upland area between Inuvik and Tsiigehtchic in the Northwest Territories, Canada (68°15' N, 133°16' W; Fig. S1) (Fujii et al., 2020a). The upland area around the Mackenzie Delta is underlain by continuous permafrost that has developed during ice ages with no coverage by Laurentide Glacier. Inuvik has an arctic climate; the mean annual air temperature is -8.8°C . Annual precipitation is 248 mm y^{-1} , of which snow accounts for 131 mm y^{-1} . The sampling sites were located at upland and foothill locations (Fig. S1b). Most of the soil on the uplands is derived from clayey sediments (a mixture of glacial till and fluvial sediment), whereas some foothill soil is derived from sandy sediments (glaciofluvial or aeolian origin) (Fig. S1). The clayey soil is derived from a mixture of fine-grained glacial till (27–37% clay, 22–30% sand), and the sandy soil is derived from glaciofluvial sands (8–12% clay, 73–75% sand) (Table 1; Fujii et al., 2019). The soil layer that thaws to the permafrost table in August (termed the active layer thickness) tends to be deeper in the sandy soil (mean $\pm$ SE, $73 \pm 46\text{ cm}$) than in the clayey soil (mean $\pm$ SE, $43 \pm 7\text{ cm}$) (Fujii et al., 2019). The clayey soil is classified as Glacic Aquorthel due to the presence of ice wedge and redox morphological feature within the profile, whereas the sandy soil is classified as Spodic Psammorthel or Typic Psammorthel due to the weak feature of podzolization and sandy texture (Soil Survey Staff, 2014).

Hummocky microrelief is dominant (80%) type of terrain in Inuvik along regional climatic gradient, where coverage of hummocky microrelief changes from $< 5\%$ of terrain in south (Fort Simpson) to 95% (Tuktoyaktuk) towards north (Tarnocai and Zoltai, 1978). Both the clayey soil and sandy soil sites were divided into two groups: sites with strongly developed hummocky microrelief ($> 20\text{ cm}$ elevation gap between mound and trough) and those with non-hummocky microrelief, respectively. At the clayey soil sites with hummocky microrelief, the soil surface is covered by mounds bearing lichens (*Cladonia mitis* L. and *Cladonia stellaris* L.) and mosses (*Pleurozium schreberi* L., *Hylocomium splendens* L., and *Sphagnum fuscum* L.). The vegetation is dominated by black spruce, with understory plants including *Rosa acicularis* L., Labrador tea (*Rhododendron groenlandicum* L.), and lingonberry (*Vaccinium vitis-idaea* L.). The vegetation on the sandy soil with hummocky microrelief comprises black spruce, white spruce (*Picea glauca* L.), and birch (*Betula papyrifera* L.). At the clayey soil sites and sandy soil sites with non-hummocky microrelief, birch (*Betula glandulosa* L.) and grass (*Calamagrostis canadensis* L.), as well as black spruce, are dominant.

Quantification of soil carbon stocks

To study the local variation in SOC storage, we quantified the SOC stocks in nine profiles at sites with hummocky microrelief and seven profiles at sites with non-hummocky microrelief. The organic horizons were sampled with three replicate 30 × 30-cm quadrates. After lichens, mosses, and live woody roots were removed, the organic horizon samples were oven-dried (48 h, 70°C) and individually weighed. For the mineral soil horizons (< 200 g C kg⁻¹), bulk density (g cm⁻³) was measured using a 0.1-L core in three replications. The mineral soil horizons [0 cm (beneath the organic horizon) to 30 cm] were collected to the depth of the permafrost table. Soil samples were air-dried and crushed to pass through a 2-mm sieve. Total C and nitrogen (N) concentrations in the soil was determined using a CN analyzer (Sumigraph NC-22; Sumika Chemical Analysis Service, Tokyo, Japan).

The SOC stocks in each soil horizon were calculated by multiplying the soil C concentration, bulk density, and individual depth as follows:

$$\text{Soil C stock (kg C m}^{-2}\text{)} = \text{Soil C concentration (g C kg}^{-1}\text{)} \times \text{Soil horizon depth (m)} \times \text{Bulk density (Mg m}^{-3}\text{)} \quad (\text{Eq. 1})$$

The SOC stocks at each site were calculated by summing the organic horizon C stocks and the mineral soil C stocks to the mineral soil depth of 30 cm. A mineral soil depth of 30 cm was set in our study to compare the C stocks among soils with different active layer thicknesses without increasing the uncertainty by extrapolation.

Measurement of litter and cellulose decomposition rates under field conditions

To examine whether litter decomposition rates depend simply on litter quality or whether they are also affected by the soil environments, the decomposition rates of four standard substrates (cellulose filter paper, lichen litter, moss litter, and fine root litter of black spruce) were conducted at the selected sites [hummocky clayey soil sites (*N* = 3), non-hummocky clayey soil sites (*N* = 3), and non-hummocky sandy soil sites (*N* = 3)]. Because there was no significant difference in C stocks between hummocky and non-hummocky microrelief, as discussed later (Fig. 2), litter bag tests were not conducted in the sandy soil sites with hummocky microrelief due to limitation imposed by logistics. Because cellulose is a major constituent of plant materials [10–87%; from Berg and McClaugherty (2003)], decomposition rates of cellulose filter paper (Advantec no. 6, 55-mm diameter) were used as a rough indicator of the soil microbial activities involved in litter decomposition (Hayakawa et al., 2014). Lichen (*Cladonia stellaris*) litter, moss (*Sphagnum fuscum*) litter, and spruce fine roots (diameter < 2 mm; length, 10 mm) collected from the surface mineral soil were used for litter bag tests after oven drying at 70°C for 48 h. The Klason lignin concentrations in the litter samples were determined by digestion with sulfuric acid (Allen et al., 1974). Total C and N concentrations in the litter samples were determined using a CN analyzer. The phosphorus (P) concentrations in the litter samples were determined using inductively coupled plasma atomic emission spectrometry (SPS1500; Seiko Instruments, Inc., Chiba, Japan) after nitric–sulfuric acid wet digestion (Knight, 1980).

Substrates were buried at depths of 5 cm at the non-hummocky clayey soil sites and the non-hummocky sandy soil sites. At the hummocky clayey soil sites with thick organic horizons, substrates were buried at depths of 5 cm (surface organic horizon), 20 cm (subsurface organic horizon), and 30 cm (5 cm depth from the boundary between organic and mineral soil) to compare decomposition rates between depths. All substrates were packed in nylon mesh bags (65 × 65 mm, mesh pore size of 100 µm) to keep insects and worms out. At each site ($N = 3$), five mesh bags of litter or cellulose filter paper ($N = 5$) were collected at 1, 2, and 4 years after burial. The substrate remaining in the mesh bag was dried (70°C, 48 h) and weighed after soil particles had been carefully removed. The remaining weight of each substrate was calculated on an ash-free basis by subtracting the weight of the soil adhering to the substrate, which was estimated by dry combustion (600°C, 4 h).

The decomposition rate constant k (yr^{-1}) for litter and cellulose decomposition was obtained using the following equation:

$$R_t = R_i e^{-kt}, \quad (\text{Eq. 2})$$

where R_t is the remaining proportion of the substrate (%), R_i is the initial proportion of the substrate (i.e., 100%), k is the decomposition rate constant (yr^{-1}), and t is the time (yr) since conversion. The remaining fraction of substrate (lichen litter, moss litter, root litter, or cellulose filter paper) relative to the initial weight of the substrates was plotted against time (yr) and fitted to a single exponential decay function (Sparrow et al., 1992).

Monitoring temperature and volumetric water content in soil

Along with the field incubation study, volumetric water contents in the soil were measured using amplitude domain reflectometry probes (Theta probe, ML2x, Delta-T Devices, Cambridge, UK) at depths of 5 cm (surface organic horizon), 20 cm (subsurface organic horizon), and 30 cm (mineral soil, 5 cm depth from the boundary between the organic and mineral soil horizons) at the hummocky clayey soil sites and at depths of 5 cm at the non-hummocky clayey soil sites and sandy soil sites. The soil temperature at each depth was also measured using temperature loggers (SL type, Thermochron, Baulkham Hills, Australia).

Litterfall, lichen, moss, and fine root production

Litterfall was collected using circular litter traps (diameter, 30 cm) at the selected sites (hummocky clayey soil sites [$N = 3$], non-hummocky clayey soil sites [$N = 3$], and non-hummocky sandy soil sites [$N = 3$]). The organic layers and fine roots (diameter < 2 mm) were collected in 30 cm × 30 cm quadrats in three replicates. Fine root biomass in the mineral soil (0–30 cm) was estimated by collecting roots at 5-cm depth intervals in 0.1-L (volume) cores in five replicates. The roots were rinsed in distilled water to remove soil materials.

To estimate root litter input, the annual production of fine roots was measured using the root mesh method (Fujii et al., 2020b) in five replicates. A net sheet (width 20 cm × depth 20 cm) with 2-mm openings was inserted vertically into the mineral soil to a depth of 20 cm. After 1 year of incubation, a soil block (width 20 cm × depth 20 cm × thickness 2 cm) containing the net sheet was collected to measure the biomass of the fine roots that had grown through the net sheet. Annual production rates of lichen and moss litters were estimated by harvesting the biomass produced after the fires recorded in 1968 at Inuvik. By neglecting caribou grazing of lichen based on the observed density in the region near Tsiigehtchic (Carruthers et al., 1986), we assumed that annual biomass production was equal to the litter input.

Reconstructing organic matter accumulation

Using the annual litter inputs and decomposition rate constants of Eq. 2, we calculated the sum of the remaining mass after 200 years. Based on previous observations (Zoltai and Pettapiece, 1973), we assumed that 50% of the unburned organic matter was lost by the fire in each 200-year fire-regeneration cycle and that the remaining organic matter was preserved as recalcitrant or inert fraction, such as charred materials, found in the permafrost-affected soils (Kane et al., 2007; Guggenberger et al., 2008). We estimated soil C stocks in a mound that had formed over a period of 9000 years, assuming that mound formation took place after deglaciation (9000 years ago) (Tarnocai and Zoltai, 1978; Tarnocai et al., 1993). To identify the contributions of lichen, moss, and spruce-root inputs to soil C stocks, we estimated soil C stocks under three scenarios: (1) lichen, moss, and spruce-root inputs, (2) moss and spruce-root litter inputs, and (3) only spruce-root litter inputs at each site.

Statistical analyses

All data are expressed as the mean ± standard error (SE), using combined SEs from three to six replicates (Taylor, 1997). The significance of differences in rate constant, k , for litter and cellulose decomposition among sites and substrate types was tested using the F -test and the Tukey method modified for comparing regression slopes (Zar, 1999). Two-way analysis of variance was used to evaluate statistical differences in mean soil carbon stocks by the main effects of microrelief (hummocky vs. non-hummocky) and soil type (clayey sediment vs. glaciofluvial sand) as well as their interaction. Pearson's correlation coefficients were calculated to examine the relationships between the rate constants and soil properties. All statistical analyses were performed using SigmaPlot 12.3 software (Systat Software, San Jose, CA, USA), with the significance level set at $P < 0.05$ (unless otherwise stated).

Results

Soil properties and carbon stocks

The organic horizon thickness varied from 2 cm to 30 cm, and proportionally, the organic horizon C stocks varied from 0.7 to 9.6 kg C m⁻² among the 16 soil profiles (Table S1). Two-way analysis of variance indicated a significant interaction between microrelief (hummocky vs non-hummocky) and soil type (clayey vs sandy) regarding soil C stocks (Fig. 2). For the clayey soil, organic horizon C stocks at the

hummocky sites were significantly greater than those at the non-hummocky sites (Fig. 2). However, there was no significant difference in mineral soil C stocks between hummocky and non-hummocky microrelief sites with clayey soil (Fig. 2). For the clayey soils, the difference in total C stocks between hummocky and non-hummocky microrelief sites was calculated to be $5.6 \pm 3.0 \text{ kg C m}^{-2}$ (Fig. 2). For the sandy soil, mineral soil C stocks at hummocky sites were significantly greater than those at non-hummocky sites (Fig. 2). There was no significant difference in organic horizon C stocks between hummocky and non-hummocky microrelief sites in the sandy soil sites (Fig. 2).

Soil temperature and water dynamics

The cumulative soil temperature (degree days), which was calculated by summing the average daily soil temperatures above 0°C in 1 year, was higher at the 5-cm depth from the surface in the non-hummocky sandy soil (1263 degree days) than in the non-hummocky clayey soil (1075 degree days) and hummocky clayey soil (605 degree days). At the hummocky clayey soil sites, soil temperature decreased with depth (Fig. S2). The cumulative soil temperature increased at the sites with increasing distance from the permafrost table in the growing season.

Volumetric water contents fluctuated widely throughout the year, although the pattern of seasonal fluctuation was similar between years (Fig. S3). The water contents that exceeded the maximum water holding capacity in the hummocky clayey soil (0.1, 0.4, and 0.5 L L^{-1} at depths of 5, 10, and 30 cm, respectively) indicated that the soil was affected by water flooding (Fig. S3). There were two occurrences of soil water flooding each year, and then soil water was frozen in winter at all sites and all horizons (Fig. S3). The first peak of water flooding in spring (April to May) indicated that the melting of snow caused flooding over the surface soil. The second peak of flooding observed at depths of 10 and 30 cm in May and June corresponded with water saturation from permafrost thaw due to the presence of a shallow and impermeable permafrost table (Fig. S3). The seasonal flooding events were also observed in the non-hummocky clayey soil with a relatively shallow permafrost table (mean $\pm$ SE, $39 \pm 5 \text{ cm}$) (Fig. S3). By contrast, the second peak of flooding caused by permafrost thawing was not observed in the non-hummocky sandy soil site with a deeper permafrost table (Fig. S3).

Decomposition rates of lichen, moss, and root litters and cellulose paper

Lichen and moss litters exhibit the lower lignin concentration and lignin/N or P ratios, compared to the spruce root litters, while lichen litter has much lower P and lignin concentrations than moss litter (Table 2). The litter bag tests showed that the rates of mass loss differed markedly among substrates and locations (Fig. 3). The coefficient of determination (R^2) for curve fitting to Eq. 2 ranged from 0.80 to 0.98, and the decomposition rate constants (k) were significant ($P < 0.05$; Table 3). Decomposition rate as represented by the k value was ranked in the following order: cellulose > spruce root litter > moss and lichen litters (Table 3). The k values of spruce root or moss litter decomposition were positively correlated with those of cellulose decomposition, but not with those of lichen litter decomposition (Table 3). There

were no correlations between k values and litter chemical properties (litter lignin/N, litter C/N, and litter N or P) at each site (Tables 2 and 3). The k values of decomposition of moss and spruce root litters and cellulose were positively correlated with cumulative soil temperature, but this was not the case for lichen litter (Fig. 4). Significant differences in the slopes of the regression equations suggest that the responses of substrate decomposition to increases in soil temperature differed among substrates (Fig. 4). The substrate decomposition rate constants responded to increases in soil temperature in the following order: cellulose > spruce root litter > moss litter (Fig. 4).

Litter inputs of lichen, moss, and spruce-root litters

The annual fine root production was 42–73% of the total litter production by vascular plants (aboveground litterfall + fine root production) (Table 4). The annual biomass production of moss ($15.0\text{--}19.5\text{ g C m}^{-2}\text{ yr}^{-1}$) was greater than that of lichen ($3.2\text{--}9.2\text{ g C m}^{-2}\text{ yr}^{-1}$) at all sites (Table 4). When we estimated the sum of remaining mass derived from spruce litter, lichen litter, and moss litter over 200 years using litter decomposition rate constants (Table 3) and litter inputs (Table 4), the remaining mass of moss-derived C was largest after 200 years (Fig. 5a; Table 4). Despite lower litter inputs of lichens and mosses, their contribution to soil C was estimated to be greater than that of spruce root litter in the hummocky clayey soil (Fig. 5a). In contrast, the contribution of lichen and spruce root litters to soil C stocks was greater in the non-hummocky sandy soil than that of moss litter (Fig. 5b). The reconstructed C stock in the clayey soil with hummocky microrelief was greater than that in the non-hummocky clayey soil and sandy soil (Fig. 5).

Discussion

Effects of microclimate and substrate type on litter decomposition rates

The slower mass loss rates of lichen and moss litters compared to spruce root litter or cellulose filters at each location (Fig. 3; Table 3) suggest that substrate quality affects litter turnover in the permafrost-affected soils. Although litter C/N or lignin/N ratios and N, P or lignin concentrations are well-known to regulate litter decomposability in boreal forests (Moore et al., 1999; Moore et al., 2007), decomposition rate constants cannot be explained by these parameters in our study (Tables 2 and 3). Litters of lichen and moss contain substantial amounts of antibacterial compounds (e.g., phenolics) and have recalcitrant cell structure (Lang et al., 2009; Turetsky et al., 2008). These litter traits could also increase resistance to microbial attack and reduce decomposition rates in our study (Table 3). The slower decomposition rates of moss litters than vascular plant litters have been confirmed across boreal peatlands (Bragazza et al., 2009), but our study expands the applicability of this finding to the colder permafrost-affected soils (Table 3; Fig. 4). Especially, *Sphagnum fuscum* and *Pleurozium schreberi* litters found in the hummocky clayey soils tend to exhibit lowest decomposability among moss litters (Camill et al., 2001). The slow lichen litter decomposition in our study (Figs. 2 and 3) is also consistent with the

results in the Canadian subarctic woodland (Moore, 1984). Note that the use of single litter species for standard substrates in our study risks ignoring synergistic and antagonistic effects of mixing litters that occur in the field condition (Paloizzi and Lindo, 2017). Despite methodological limitation of litter bag over/underestimating litter decomposition, litter type was found to be a key factor affecting litter turnover in our study.

The variation in decomposition rates of standard substrates (cellulose and litters) among five locations (Fig. 3) suggests that decomposition rates are not only simply dependent on litter types but also affected by environmental conditions. The key soil properties can be C and N concentrations, microbial biomass, soil temperature and moisture, oxygen availability, texture, and pH (Bauhus and Pare, 1998; Hayakawa et al., 2014; Fujii et al., 2020b). Especially, microbial decomposition activity in the clayey soils could be lower than the sandier soils (Bauhus and Pare, 1998). In our study, however, only soil temperature was extracted as a key property limiting decomposition (Fig. 4). Although water availability from high water table can increase decomposition rates in some temperate peatlands (Belyea, 1996), summer flooding on shallow permafrost could limit oxygen supply in the clayey soil sites (Fig. S3). This leads to relatively low microbial biomass-C (Table 1) and the lower decomposition activities of cellulose, moss, and root litters (Table 3; Fig. 4). On the other hand, the higher temperature and drainage of the non-hummocky sandy soil (Figs. S2 and S3; Farouki, 1981) are favorable for decomposition of spruce root litter and cellulose filter, but not for the lichen and moss litters (Fig. 4). The litter types and soil temperature were extracted as key factors regulating decomposition rates at local scale.

Effects of hummocky microrelief on soil carbon storage

We found greater C stocks in the hummocky clayey soils with than the clayey soils and sandy soils with non-hummocky microrelief (Fig. 2). The reconstructed soil C stocks suggested that lichen-derived C (2.4 kg C m^{-2} ; Fig. 5a) contributed to the difference in C stock between the clayey soils with hummocky and non-hummocky microrelief (4.1 kg C m^{-2} ; Fig. 2). In addition, the lower decomposability of moss litter in hummocky clayey soil resulted in the greater C stocks than in non-hummocky clayey soil (Table 3; Fig. 5). Due to the incomplete dataset, we could take the data of aboveground and coarse root litter inputs and decomposition into account (Fig. S4). Assuming that aboveground litterfall decomposes at a similar rate as spruce root litter, the inclusion of aboveground litterfall-derived C into the C stocks accounts for the discrepancy between the measured and estimated C stocks (Table 4; Fig. 5). The higher decomposability of moss litter and lower inputs of lichen litter in the non-hummocky clayey soil, compared to the hummocky clayey soil (Table 4), result in the smaller C stocks in the non-hummocky clayey soil (Fig. 5b). Similarly, a higher decomposability of litter leads to smaller C stocks in the non-hummocky sandy soil, compared to the hummocky clayey soil (Fig. 5c). The difference in litter decomposability could explain one of reasons why soil C stocks can vary at the local scale, depending on soil texture and microrelief (Fig. 2).

We reconstructed SOM accumulation over 9000 years using litter decomposition rates (Fig. 5), assuming 50% mass loss by the fires (Zoltai and Pettapiece, 1973) without considering historical and recent climate

changes. Note that soil C stabilization should also be affected by SOM–clay interactions, sorption of dissolved organic matter from litter, translocation of surface organic matter into deeper soil by freeze–thaw cycles (Ping et al., 2015), decomposition of old SOM deposited after fires, and fluctuation of permafrost table depth caused by the insulation effect of organic matter accumulation (Kokelj et al., 2007). The use of decomposition rates of single lichen or moss species for total lichen or moss inputs also increases uncertainties in reconstructed soil C stocks (Palozzi and Lindo, 2017). However, despite the several assumptions made for reconstructing soil C stocks, the estimated C stocks were close to the measured C stocks (Fig. 5). This implies that litter turnover and accumulation of undecomposed litter or burned materials have strong influences on C storage in permafrost-affected soils. In our study, organic matter accumulated after the fire in the deeper soil is not counted as the active fraction for microbial decomposition, because (i) the organic matters remaining after the fire are highly recalcitrant due to their lower decomposition rate constants [$0.0002\text{--}0.017\text{ year}^{-1}$ from O'Donnell et al. (2011)] than fresh litters ($0.07\text{--}0.48\text{ year}^{-1}$; Table 3) and (ii) organic matter in the deeper soil on shallow permafrost table is protected from microbial decomposition due to summer flooding and cold microclimate (Hobbie et al., 2000; Davidson and Janssens, 2006). The minor contribution of the old SOM to CO_2 production in permafrost-affected soils is close to the roles of inert or passive fraction of the existing soil C modelling [Roth C model (Coleman and Jenkinson, 1996) or Century C model (Skjemstad et al., 2004), respectively]. However, the additional data of reliable rate constants of the old SOM fractions on permafrost table would improve the precision of the reconstructed C stocks.

Implications for the impacts of climate change on soil carbon storage

We found that organic matter decomposition is temperature-dependent (Fig. 4). A cold climate or freezing can protect SOM from microbial mineralization (Davidson and Janssens, 2006; Hobbie et al., 2000), allowing the occurrence of the largest C stocks among soil types in permafrost-affected soils (i.e., Gelisols) (Tarnocai et al., 2009). This result suggests that climate change can potentially impact C cycles in permafrost-affected soils. Although litter decomposition is predicted to respond sharply to temperature increase especially in permafrost-affected soils (Kirschbaum, 1995), but the temperature dependency of decomposition varied between substrate types (Fig. 4). Climate warming would have greater effects on decomposition rates of vascular plant litters than on those of lichen and moss litters (Fig. 4). The temperature dependency of lichen and moss litter decomposition is lower, compared to cellulose or vascular plant litters at least in the low temperature range (Fig. 4).

In addition to the direct effect of climate on microbial activity, indirect effects of climate change on litter turnover is predicted to occur through a vegetation shift from black spruce forests to shrub birch tundra (Cornelissen et al., 2001; Fraser et al., 2014). The vegetation shift includes the changes in soil surface environments from lichen/moss-covered hummocky microrelief to Poaceae grass covered non-hummocky microrelief (Fraser et al., 2014). Hummocky microrelief provides dry habitats for lichens and mosses with greater litter recalcitrance than vascular plants (birch and grass) (Table 3; Fig. 4). Permafrost degradation by climate warming would reduce the hummocky microrelief with high potential

for C storage due to loss of lichen and moss litters, major contributors to soil C stocks (Fig. 4; O'Donnell et al., 2011; Fujii et al., 2020a).

Conclusions

Lichen and moss litters are more resistant to microbial attack than spruce root litter. Consistent with this, lichen/moss-covered hummocky clayey soil contain greater C stocks than do non-hummocky sandy soil or clayey soil. The contributions of lichen and moss litters to soil C stocks are greater in the clayey soils with hummocky microrelief than in the non-hummocky soils. The decomposition of lichen and moss litters are also insensitive to temperature increase, compared to higher temperature dependency of vascular plant (spruce root) litter decomposition. A shift from lichen/moss-covered mounds to a vascular plant-dominated community (e.g., shrub birch tundra) could reduce the input of lichen and moss litter, which was the main cause for greater soil C storage in the hummocky microrelief than in the non-hummocky microrelief. The loss of the microrelief by warming-induced permafrost degradation risks reducing the potential for soil C storage of black spruce forests on permafrost.

Declarations

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Author contributions

K.F. and C.H. designed the study. K.F. and C.H. established the field experiment and discussed the results. K.F. wrote the manuscript.

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Tables

Due to technical limitations, table 1 to 4 is only available as a download in the Supplemental Files section.

Supplementary Tables

Table S1 is not available with this version

Figures

Figure 1

Drunken forest and soil hummocks on permafrost layer. a, Drunken forest. b, Hummocky micro-relief. c, Soil mound profile on permafrost layer. d, Theoretical model of hummock formation and organic matter accumulation.

Figure 2

Soil carbon stocks in hummocky and non-hummocky microrelief areas with sandy and clayey sediments. Bars indicate standard errors. * indicates significant differences between groups ($P < 0.05$), n.s. indicates non-significance (ANOVA).

- △ Hummocky clayey soil 5 cm ■ Non-hummocky clayey soil 5 cm
 ○ Hummocky clayey soil 10 cm ○ Non-hummocky sandy soil 5 cm
 ◆ Hummocky clayey soil 30 cm

Figure 3

Remaining proportions of cellulose paper (filter paper) and lichen, moss, and root litters buried in permafrost-affected soils during the field incubation period. Symbols denote experimental data points, and lines represent the fit to a single exponential decay function. Bars indicate standard errors (N = 3).

Figure 4

Relationship between cumulative soil temperature and the substrate decomposition rate constant. Bars indicate standard errors (N = 3).

Figure 5

Accumulation of soil organic matter reconstructed using decomposition rate constants and litter inputs in hummocky clayey soil (a), non-hummocky clayey soil (b), and non-hummocky sandy soil (c). We assumed that 50% of the unburned organic matter was lost by the fires in each 200-year fire-regeneration cycle and that soil formation took place over the 9000 years following deglaciation.

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