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Regulation of soil organic matter decomposition in permafrost-affected Siberian tundra soils - Impact of oxygen availability, freezing and thawing, temperature, and labile organic matter

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ABSTRACT

The large amounts of soil organic matter (SOM) in permafrost-affected soils are prone to increased microbial decomposition in a warming climate. The environmental parameters regulating the production of carbon dioxide (CO_2) and methane (CH_4), however, are insufficiently understood to confidently predict the feedback of thawing permafrost to global warming. Therefore, the effects of oxygen availability, freezing and thawing, temperature, and labile organic matter (OM) additions on greenhouse gas production were studied in northeast Siberian polygonal tundra soils, including the seasonally thawed active layer and upper perennially frozen permafrost. Soils were incubated at constant temperatures of 1 °C, 4 °C, or 8 °C for up to 150 days. CO_2 production in surface layers was three times higher than in the deeper soil. Under anaerobic conditions, SOM decomposition was 2–6 times lower than under aerobic conditions and more CO_2 than CH_4 was produced. CH_4 contributed less than 2% to anaerobic decomposition in thawed permafrost but more than 20% in the active layer. A freeze-thaw cycle caused a short-lived pulse of CO_2 production directly after re-thawing. Q_{10} values, calculated via the equal-carbon method, increased with soil depth from 3.4 ± 1.6 in surface layers to 6.1 ± 2.8 in the permafrost. The addition of plant-derived labile OM (^{13}C-labelled *Carex aquatilis* leaves) resulted in an increase in SOM decomposition only in permafrost (positive priming). The current results indicate that the decomposition of permafrost SOM will be more strongly influenced by rising temperatures and the availability of labile OM than active layer material. The obtained data can be used to inform process-based models to improve simulations of greenhouse gas production potentials from thawing permafrost landscapes.

1. Introduction

Soils and sediments in permafrost regions have accumulated about 1300 Pg of soil organic carbon (SOC), of which about 800 Pg are perennially frozen (Hugelius et al., 2014) and are therefore not part of the active carbon (C) cycle. Hence, permafrost landscapes have been a sink for atmospheric C over thousands of years. Only in the seasonally thawed active layer do soil microorganisms actively decompose soil organic matter (SOM), producing carbon dioxide (CO_2) and methane (CH_4), which may be released back to the atmosphere. In a warmer Arctic, an additional 150–440 Pg of SOC could thaw by 2050 due to permafrost degradation and active layer deepening (Harden et al., 2012). Although it is expected that warming-induced environmental changes will result in higher greenhouse gas fluxes between soils and the atmosphere (Koven et al., 2011; Schneider von Deimling et al., 2012), the factors regulating SOM decomposition in the active layer and thawing permafrost are insufficiently understood.

SOM turnover in permafrost-affected soils is governed by a complex interplay between several environmental parameters such as temperature, moisture, oxygen and nutrient availability, and other soil forming factors, e.g. parent material, SOM quality, and cryoturbation (Hobbie et al., 2000). In addition to low decomposition rates due to low temperatures, impermeable permafrost in the ground impedes water drainage, creating large wetland ecosystems (Lehner and Döll, 2004). In water-logged soils,

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anaerobic conditions and the lack of electron acceptors further inhibit anaerobic decomposition processes. Although SOM decomposition is substantially slowed down under anaerobic conditions, the absence of oxygen also favors the production of CH_4, which has a 28–34 times higher warming potential than CO_2 on a century timescale (Myhre et al., 2013). Methanogenesis may principally constitute an important source of greenhouse gases, although the majority of currently available laboratory incubation studies suggest that greenhouse gas production in permafrost-affected soils is dominated by CO_2 (Schädel et al., 2016; Treat et al., 2015).

Temperature is a main driver of microbial processes and higher temperatures increase SOM decomposition rates (Davidson and Janssens, 2006). Old C incorporated in permafrost could be particularly sensitive to temperature changes (Knorr et al., 2005). Temperature may also indirectly influence SOC dynamics. Shifts in plant community structures, higher air temperatures, and rising atmospheric CO_2 concentrations can lead to higher plant net primary production and above-ground uptake of CO_2 (Ainsworth and Long, 2004). Part of this additional C will be transferred into soils, e.g. as plant litter or root exudates (Jastrow et al., 2005). In addition, higher temperatures and associated increases in active layer depths will lead to larger rooting depths and higher C inputs (Jorgenson et al., 2010). This may have contrasting effects on SOC storage. On the one hand, SOM is decomposed more slowly in deeper soil layers and relatively undecomposed material is eventually incorporated into permafrost (Palmtag et al., 2015). On the other hand, the input of fresh and labile OM from the surface may stimulate microbial activity and enhance the decomposition of older SOM through positive priming (Fontaine et al., 2007). Consequently, higher SOM decomposition rates will result in a loss of SOC. Considerable C losses can also be caused by freeze-thaw cycles, which cause short bursts of greenhouse gas production (Matzner and Borken, 2008).

To better understand the effect of different environmental parameters on SOM decomposition in thawing permafrost environments, the current study quantifies the effect of oxygen, freezing and thawing, temperature, as well as the availability of labile OM on CO_2 and CH_4 production in Siberian tundra soils. The multitude of these factors, their interconnections, as well as differences in the response of the active layer and the permafrost to warming-induced environmental changes are still underrepresented in the literature. Therefore, mineral soil samples from the active layer and shallow permafrost were incubated for up to 150 days, which reflects about one thaw period. We hypothesized that (i) SOM in the active layer is decomposed more quickly than in thawed permafrost, (ii) the absence of oxygen reduces the production of greenhouse gases, (iii) freeze-thaw cycles increase the microbial decomposition of SOM, (iv) temperature sensitivity is higher in permafrost than in the active layer, and (v) the addition of labile OM increases the decomposition of autochthonous SOM in the whole soil profile. The obtained data can be used to inform process-based models to improve simulations of greenhouse gas production potentials from thawing permafrost.

2. Material and methods

2.1. Study site

The study site of Samoylov Island (72° 22′ N, 126° 30’ E) is located in the Lena River Delta, northeast Siberia. The Lena River Delta lies within the zone of continuous permafrost and consists of three main geomorphological units (terraces) and the active floodplains (Schwamborn et al., 2002). Samoylov Island is part of the youngest first terrace, which developed during the Holocene. The elevated river terrace is characterized by ice wedge polygons with low-lying polygon centers and elevated polygon rims. The dominating vascular plant species is *Carex aquatilis*, with a total coverage of 25% in polygon centers (Kutzbach et al., 2004). Below ground, *C. aquatilis* forms a dense mat of coarse perennial roots and fine roots can be found down to the permafrost table (Kutzbach et al., 2004). Main soil types (IUSS Working Group WRB, 2014) on the river terrace include Histic Cryosols in polygon centers and Turbic Cryosols in elevated polygon rims (Pfeiffer et al., 2002).

The study site is characterized by an arctic climate with a mean annual (1981–2010) temperature of −12.8 °C and mean annual precipitation of 322 mm (WMO station 218240, Federal Service for Hydrometeorology and Environmental Monitoring of Russia, http://www.meteorf.ru). The ground remains completely frozen from November until June. In the active layer, temperatures above freezing during the summer months enable microbial decomposition of SOM. The mean duration of thaw is 129 ± 10 days and the mean maximum thaw depth of polygon centers is 51 ± 5 cm, with a maximum recorded thaw depth of 61 cm in wet polygons (Boike et al., 2013).

2.2. Soil sampling and analysis

Three different low-centered polygons (Table 1) were sampled on the river terrace. Soil cores were obtained using a portable SIPRE-corer (Jon's Machine Shop, Fairbanks, AK, USA) with a STIHL BT 121 engine (STIHL, Waiblingen, Germany). Coring was conducted in April 2011 (Polygons 1 and 2) and May 2013 (Polygon 3) while the entire soil profile was still frozen. Cores were recovered to depths of 82 cm, 86 cm, and 92 cm.

Frozen soil cores were divided into four soil layers: (i) the surface active layer (0–11 cm) including relatively undecomposed plant material, (ii) the bottom active layer (11–41 cm), both thawing every year, (iii) the transition zone (41–60 cm), which only thaws in some years, and (iv) permafrost (>60 cm), presumably not thawed for several decades to centuries. Cores were further

Table 1
Sample overview, treatments, and soil properties.

Depth (cm)	Layer[a]	Treatment[b]	SOC (mg g^{-1})	C/N	pH	$\delta^{13}C_{SOC}$ (‰ VPDB)
Polygon 1, 72° 22.5 N, 126° 29.3 E						
0–11	sAL	Ae, An, FT	146	27.5	5.63	−28.7
11–22	bAL	Ae, An	100	36.4	5.91	−27.9
22–32	bAL	Ae, An, FT	41	25.0	6.40	−27.5
32–42	bAL	Ae, An	81	29.3	6.66	−26.3
42–51	TZ	Ae, An	59	27.4	6.44	−26.4
51–60	TZ	Ae, An	67	31.9	6.31	−26.3
60–68	Pf	Ae, An	65	30.7	6.13	−26.9
68–77	Pf	Ae, An	73	29.0	6.15	−26.0
77–86	Pf	Ae, An, FT	101	29.0	6.21	−26.5
Polygon 2, 72° 22.3 N, 126° 29.9 E						
0–11	sAL	Ae, An, FT	137	31.5	6.28	−28.1
11–22	bAL	Ae, An	99	29.6	5.36	−27.3
22–32	bAL	Ae, An, FT	87	28.6	5.50	−27.4
32–42	bAL	Ae, An	106	28.2	5.69	−26.4
42–51	TZ	Ae, An	177	32.7	5.64	−25.3
51–60	TZ	Ae, An	107	31.4	5.62	−26.0
60–67	Pf	Ae, An	55	23.4	5.61	−26.6
67–74	Pf	Ae, An	137	31.8	5.41	−26.5
74–82	Pf	Ae, An, FT	84	20.5	5.37	−26.1
Polygon 3, 72° 22.5 N, 126° 29.4 E						
0–10	sAL	Ae, T, P	110	40.3	6.02	−27.4
20–30	bAL	Ae, T, P	52	23.6	6.53	−25.4
70–80	Pf	Ae, T, P	115	21.3	6.45	−26.3

[a] sAL = surface active layer, bAL = bottom active layer, TZ = transition zone, Pf = permafrost.
[b] Ae = aerobic, An = anaerobic, FT = freeze-thaw, T = temperature, P = priming.

subdivided into depth increments of approximately 10 cm, resulting in a total of nine subsamples per core: one from the surface active layer, three from the bottom active layer, two from the transition zone, and three from the permafrost. Due to the limited amount of soil collected, not all the experiments could be performed on each sample. Samples from Polygons 1 and 2 were used for aerobic and anaerobic incubations, as well as a freeze-thaw experiment, while samples from Polygon 3 were used for studying temperature sensitivity and priming (Table 1).

Soil water contents were calculated as the weight difference between wet and dried (105 °C) samples. pH values were measured in a suspension of 5 g thawed soil in 12.5 ml distilled water (CG820, Schott AG, Mainz, Germany). For soil chemical analyses, bulk soil samples were dried at 70 °C and milled. Total C and nitrogen (N) contents were measured with an element analyzer (VarioMAX cube, Elementar Analysensysteme GmbH, Hanau, Germany), while SOC contents were measured with a liquiTOC *II* coupled to a solids module (Elementar Analysensysteme GmbH, Hanau, Germany). The $\delta^{13}C$ values of SOC ($\delta^{13}C_{SOC}$) were measured with an isotope-ratio mass spectrometer (Delta V, Thermo Scientific, Dreieich, Germany) coupled to an elemental analyzer (Flash 2000, Thermo Scientific, Dreieich, Germany) after samples were treated with phosphoric acid to release inorganic C.

Soil classification was done according to the World Reference Base for Soil Resources (IUSS Working Group WRB, 2014). All investigated soil layers are mineral soils and were classified as Reductaquic Cryosol (Hyperhumic), with intermediate to high SOC contents (4.1–18.7%, Table 1), a wide range in SOC to N (C/N) ratios (21–40), and strongly acidic to neutral pH values (5.4–6.7). $\delta^{13}C_{SOC}$ ranged between −28.7 ‰VPDB and −25.3 ‰VPDB. Generally, SOC contents were highest in the surface layers and decreased with depth, while $\delta^{13}C_{SOC}$ values were lowest in the surface layers and highest in the deeper layers.

2.3. Incubation and gas measurements

Frozen samples were slowly thawed from −18 °C to 4 °C over 48–60 h in a refrigerator. Samples for anaerobic incubations were prepared in a N_2 atmosphere in a glove box. All samples were homogenized and large roots were removed. Approximately 20–50 g thawed soil was weighed into glass bottles. All bottles were sealed with rubber stoppers to prevent gas exchange with the ambient air and to keep water content constant. 10–30 ml of N_2-flushed, CO_2-free distilled water was added to anaerobic samples to saturate them and displace any residual oxygen in the pore space. The headspace of anaerobic samples was exchanged with N_2. The headspace of aerobic samples was exchanged with synthetic air (20% oxygen, 80% N_2).

The concentrations of CO_2 and CH_4 inside the headspace of each bottle were measured repeatedly via gas chromatography (GC 7890, Agilent Technologies, Santa Clara, CA, USA). The gas chromatograph was equipped with a nickel catalyst to reduce CO_2 to CH_4 and a flame ionizing detector (FID). Gases were separated on a PorapakQ column with helium as carrier gas. If the concentration of CO_2 in the headspace of aerobic incubations approached 3%, the headspace was again exchanged with synthetic air.

The amount of gas was calculated from the gas concentration, headspace volume, incubation temperature, and pressure inside the bottle using the ideal gas law. The amount of dissolved gas was calculated from the gas concentration in the headspace, pressure inside the bottle, water content, and gas solubility in water. Solubility for CO_2 and CH_4 was calculated after Carroll et al. (1991) and Yamamoto et al. (1976), respectively. To account for the dissociation of carbonic acid in water, the amounts of dissolved C species were calculated using dissociation constants from Millero et al. (2007). Gas production rates were calculated by a linear fit of produced gas and incubation time using four consecutive measurements.

2.4. Influence of soil depth and oxygen availability

To examine the influence of soil depth and oxygen availability on SOM decomposition, samples from Polygons 1 and 2 were used. Samples were prepared in three aliquots for either aerobic or anaerobic incubations and incubated at a constant temperature of 4 °C for 150 days. Concentrations of CO_2 and CH_4 were measured every second to third day during the first four weeks of incubation, then once a week for a further eight weeks, and finally every two weeks until the end of the incubation experiment.

2.5. Freeze-thaw cycle

For a freeze-thaw experiment, samples from the surface active layer, the bottom active layer, and the permafrost of Polygon 1 (aerobic) and Polygon 2 (anaerobic) were used. Samples were prepared in six aliquots and incubated for 30 days at 4 °C. After 30 days, all aerobic and anaerobic samples were flushed with synthetic air or N_2, respectively. Three aliquots of each sample were incubated for another 30 days at 4 °C. The other three aliquots were refrozen inside the incubation bottle to −18 °C. After seven days at this temperature, samples were re-thawed and incubated at 4 °C for another 30 days. Gas concentrations were measured every second day. During the 7-day re-freezing period, gas concentrations in the headspace of refrozen bottles remained constant. Thus, both treatments were incubated for a total of 60 days at 4 °C, with a break of seven days at −18 °C for the freeze-thaw treatment. The relative freeze-thaw effect (FT%) was calculated as

$$FT\% = \frac{(FTc - c)}{c} \times 100\,\% \quad (1)$$

where *FTc* and *c* are the amounts of C decomposed to either CO_2 or CH_4 in freeze-thaw and control samples, respectively.

2.6. Temperature sensitivity

The temperature sensitivity of SOM decomposition was examined using surface active layer, bottom active layer, and permafrost samples from Polygon 3. Samples were prepared in four aliquots and aerobically incubated for 150 days at 1 °C, 4 °C, or 8 °C. To assess the temperature response and to calculate Q_{10} values, the equal-C method was applied. Unlike the traditional approach to Q_{10} values, where decomposition rates at different temperatures over a fixed incubation period are compared (equal-time), this approach compares the time needed to decompose the same amount of SOC, thereby excluding temperature-induced differences in the depletion of the labile SOM pool (Conant et al., 2008; Rey and Jarvis, 2006). Furthermore, the equal-C method has been found to accurately estimate the temperature sensitivity of the labile SOM pool (Liang et al., 2015), which is captured in the 150-day incubation period. In the current study, a target amount of 5 mg CO_2-C g^{-1} SOC was chosen, because this was the lowest expected amount of SOC to be decomposed within the 150-day incubation period. The temperature response of SOM decomposition was determined by fitting the data to an Arrhenius type equation

$$\ln(t) = m \times T^{-1} + b \quad (2)$$

where t is the day of incubation when 5 mg CO_2-C g^{-1} SOC were produced in each sample, T is the incubation temperature (K), and

m and b are the slope and intercept of the linear regression line, respectively. Q_{10} values were then calculated as the ratio between the theoretical incubation days at 0 °C and at 10 °C derived from Equation (2).

2.7. Labile organic matter addition and priming effect

To examine the influence of labile OM availability on SOM decomposition, surface active layer, bottom active layer, and permafrost samples from Polygon 3 were amended with ^{13}C-labelled OM from leaves of *Carex aquatilis*, which is the dominant vascular plant species in polygon centers at the study site. The plants were grown under a ^{13}C-CO_2 enriched atmosphere on Samoylov Island and the leaves harvested after about three weeks. The δ^{13}C-value of the labelled OM ($\delta^{13}C_{Carex}$) was 744‰ VPDB. Samples were prepared in four aliquots, individually amended with the *Carex* material at a rate of 1.3% of the initial SOC content and aerobically incubated at 1 °C, 4 °C, or 8 °C for 150 days.

The concentration of CO_2 was measured every week. The isotopic signature of CO_2 produced in amended samples was also measured weekly by isotope-ratio mass spectroscopy (Finnigan Delta Plus, Thermo Scientific, Dreieich, Germany) coupled to a gas chromatograph (6890, Agilent Technologies, Santa Clara, CA, USA). To differentiate between SOM-derived and *Carex*-derived CO_2, a mixing model was used

$$f_{SOM} = \frac{\left(\delta^{13}C_{CO_2} - \delta^{13}C_{Carex}\right)}{\left(\delta^{13}C_{SOC} - \delta^{13}C_{Carex}\right)} \quad (3)$$

and

$$f_{Carex} = 1 - f_{SOM} \quad (4)$$

where f_{SOM} and f_{Carex} are the fractions of SOM-derived and *Carex*-derived CO_2, $\delta^{13}C_{Carex}$ and $\delta^{13}C_{SOC}$ are δ^{13}C values of the added *Carex* material and of SOC (Table 1), and $\delta^{13}C_{CO_2}$ are the measured isotopic signatures of CO_2 inside each bottle. The same samples were also incubated for the temperature sensitivity experiment without *Carex* addition and thus served as a control group for quantifying the priming effect. In control samples, all CO_2 is SOM-derived. The relative priming effect (PE%) was then calculated as

$$PE\% = \frac{(aSOM\ CO_2 - cSOM\ CO_2)}{(cSOM\ CO_2)} \times 100\ \% \quad (5)$$

where $aSOM\ CO_2$ and $cSOM\ CO_2$ are the amounts of SOM-derived CO_2 in amended and control samples, respectively.

2.8. Statistics

Data were tested for normal distribution (Shapiro-Wilk test) and homogeneity (Levene's test). One-way ANOVA followed by Tukey's honest significant difference test were used to analyze the effect of soil depth and incubation temperature, while the Student's t-test was used to test for the effect of freezing and thawing as well as substrate addition on SOM decomposition. Unless otherwise noted, a significance level of $P < 0.05$ was used. Propagation of error theory was used to estimate uncertainties for freeze-thaw effects, Q_{10} values, and priming effects. Pearson's correlation was used to characterize the relationship between soil properties and SOM decomposition. All statistical analyses were performed using MATLAB® (MATLAB and Statistics Toolbox Release, 2014b; The MathWorks Inc. Natick, MA, USA).

3. Results

3.1. Effect of depth and oxygen availability

The patterns of SOM decomposition were similar in both of the investigated polygons (Fig. 1) and production after 150 days of incubation correlated significantly with SOC content, total N, and $\delta^{13}C_{SOC}$ (Supplementary Table S1). In the surface active layer, between 30.2 and 32.3 mg CO_2-C g^{-1} SOC were aerobically produced after 150 days, which was significantly more ($P < 0.001$) than in deeper layers (Fig. 1a). Total C production in the bottom active layer, transition zone, and permafrost ranged between 3.5 and 9.4 mg CO_2-C g^{-1} SOC, but did not differ significantly between layers. Anaerobically, less SOM was decomposed to either CO_2 or CH_4 (Fig. 1b and c) than under aerobic conditions, but the general pattern of decreasing SOM decomposition with increasing soil depth persisted. Anaerobic CO_2 production in the surface active layer ranged between 6.9 and 9.4 mg CO_2-C g^{-1} SOC, which was again significantly more ($P < 0.001$) than in deeper layers, where production ranged between 1.2 and 3.0 mg CO_2-C g^{-1} SOC. Anaerobic CH_4 production was highest in the surface active layer of Polygon 1 (3.9 ± 0.6 mg CH_4-C g^{-1} SOC) but comparatively low in Polygon 2 (0.5 ± 0.1 mg CH_4-C g^{-1} SOC). Methanogenesis gradually decreased with depth and was an order of magnitude smaller in the transition zone and permafrost (0.01–0.03 mg CH_4-C g^{-1} SOC) than in the bottom active layer (1.7–0.2 mg CH_4-C g^{-1} SOC). Overall, the contribution of CH_4 to anaerobic decomposition was low, but showed strong differences with depth (Supplementary Figure S1). In the surface and bottom active layer the contribution of CH_4 steadily increased over the incubation period and accounted for 7–34% (mean 21 ± 9%) of the total anaerobic C production after 150 incubation days. In the permafrost, the contribution was generally less than 2%. However, while aerobic and anaerobic CO_2 production rates were highest during the initial incubation (0–30 days) and decreased by more than 40–80% towards the end of the incubation, CH_4 production rates were lowest in the beginning of the incubation and increased by up to 525% towards the end of the incubation period. No maximum CH_4 production rates were reached within the 150-day incubation period.

3.2. Effect of freezing and thawing

Both aerobic and anaerobic CO_2 production rates in the surface active layer, the bottom active layer, and the permafrost were highest at the beginning of the incubations and declined sharply within the first seven to ten days (Fig. 2). Production rates in the control and the freeze-thaw replicates did not differ significantly at the end of the first 30-day period. During the 7-day freezing period at −18 °C the concentration of CO_2 and CH_4 inside the headspace of freeze-thaw samples did not increase. While aerobic and anaerobic CO_2 production rates in the control samples remained constant between 30 and 60 days of incubations, CO_2 production rates in the freeze-thaw samples of the surface and bottom active layer increased after re-thawing and remained significantly higher for up to 14 days after re-thawing. By the end of the 60-day incubation period at 4 °C, rates between freeze-thaw and the control group were again not significantly different. After 60 days at 4 °C, freeze-thaw samples from the surface active layer had produced 23.3 ± 6.7% more CO_2 aerobically ($P < 0.01$) and 28.0± 10% more CO_2 anaerobically ($P < 0.001$). The bottom active layer produced 24.7 ± 5.5% more CO_2 aerobically and 20.4 ± 4.5% more CO_2 anaerobically ($P < 0.01$) (Fig. 3). Within the permafrost, CO_2 production rates only increased in anaerobic samples for about three days after re-thawing (Fig. 2f) but the cumulative amount of aerobically as well as anaerobically produced CO_2 after 60 days did

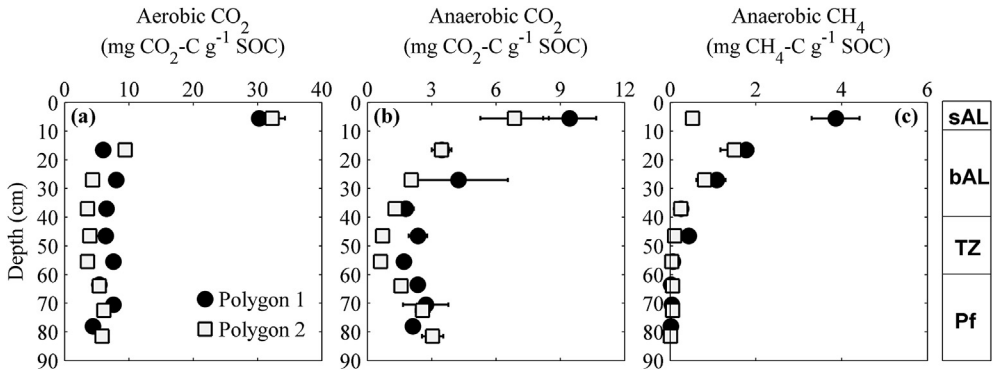

Fig. 1. Depth profiles of total aerobic CO_2 (a), anaerobic CO_2 (b), and anaerobic CH_4 (c) after 150 incubation days at 4 °C for Polygons 1 and 2 in the surface active layer (sAL), bottom active layer (bAL), transition zone (TZ), and permafrost (Pf). Data are mean values ($n = 3$) and error bars represent one standard deviation.

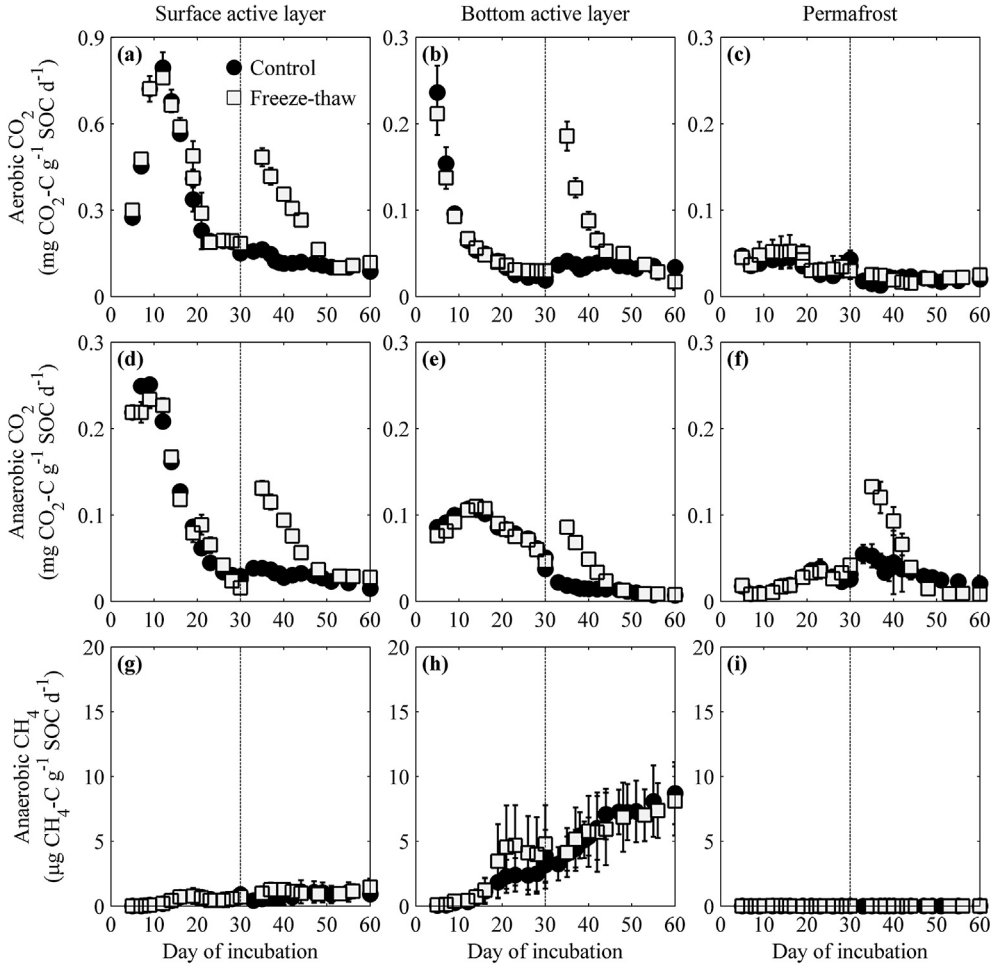

Fig. 2. Gas production rates for aerobic CO_2 (a, b, c), anaerobic CO_2 (d, e, f), and anaerobic CH_4 (g, h, i) for the surface active layer (a, d, g), bottom active layer (b, e, h), and permafrost (c, g, i) for the control and the freeze-thaw groups. Data are mean values ($n = 3$) and error bars represent one standard deviation. The vertical line separates the two 30-day incubation periods at 4 °C pre- and post-refreezing for the freeze-thaw group. Note the different scales and units for CO_2 and CH_4.

not differ significantly between the two treatments (Fig. 3b). Methanogenesis only occurred in surface and bottom active layer samples and rates increased with time (Fig. 2g and h). Neither the CH_4 production rates nor the amount of CH_4 produced after 60 days differed significantly between control and freeze-thaw replicates (Fig. 3c). No CH_4 was produced in any permafrost samples.

3.3. Temperature sensitivity

Higher temperatures significantly ($P < 0.001$) increased CO_2 production at all depths (Fig. 4). The temperature sensitivity, however, increased with soil depth. As expected, decomposition was most rapid in the surface active layer, where it took 6.0 ± 0.5

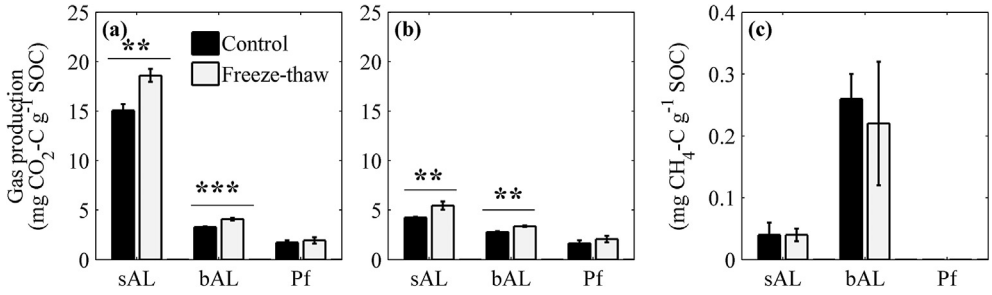

Fig. 3. Total C production for the control and freeze-thaw treatment for aerobic CO_2 (a), anaerobic CO_2 (b), and anaerobic CH_4 (c) after 60 incubation days at 4 °C in the surface active layer (sAL), bottom active layer (bAL), permafrost (Pf). Data are mean values ($n = 3$) and error bars represent one standard deviation. Significant differences in the production are indicated (**P < 0.01; ***P < 0.001). Note the different scale in (c).

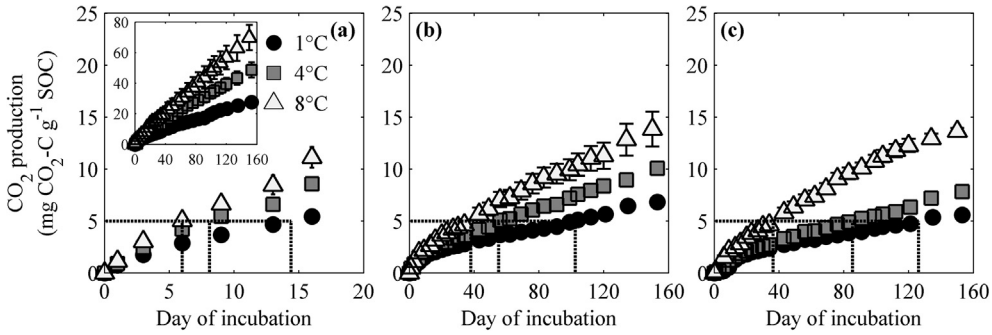

Fig. 4. Cumulative aerobic CO_2 production in the surface active layer (a), bottom active layer (b), and permafrost (c) for the three temperature treatments. Data are mean values ($n = 4$) and error bars represent one standard deviation. The dashed lines indicate the day of incubation, when 5 mg CO_2-C g^{-1} SOC were produced, which was used to calculate Q_{10} values. The inset in panel (a) shows the complete time series for the surface active layer.

days, 8.1 ± 0.9 days, and 14.4 ± 1.2 days to decompose the amount of 5 mg CO_2-C g^{-1}SOC at 8 °C, 4 °C, and 1 °C. Decomposition in the bottom active layer and permafrost was significantly ($P < 0.001$) slower. In the bottom active layer, it took 37.9 ± 4.9 days (8 °C), 55.2 ± 0.6 days (4 °C), and 102.5 ± 4.8 days (1 °C) to decompose the same amount. In permafrost, it took 36.3 ± 4.8 days (8 °C), 85.4 ± 12.1 days (4 °C), and 126.2 ± 6.3 days (1 °C). The resulting Q_{10} values (Table 2), increased from 3.4 ± 1.6 in the surface active layer and 4.1 ± 1.7 in the bottom active layer to 6.1 ± 2.8 in permafrost.

3.4. Effect of labile OM on decomposition

The addition of relatively labile OM significantly ($P < 0.01$) increased total CO_2 production at all depths and temperatures, except in surface active layer soils incubated at 1 °C and 4 °C (Fig. 5). The amount of additional CO_2 varied with depth and temperature. Cumulative CO_2 production in the surface active layer increased by 13–18% compared to the control incubations. In deeper soil layers the increase in CO_2 production ranged between 28 and 39% in the bottom active layer and 46–71% in the permafrost. However, partitioning the amount of CO_2 in *Carex*-amended samples into SOM-derived and *Carex*-derived CO_2 revealed that most of the additional CO_2 came from the amendment. A significant ($P < 0.01$) increase in SOM-derived CO_2 (positive priming) was only evident in permafrost samples. At 1 °C and 4 °C, SOM-derived CO_2 increased by 15.6 ± 7.2% and 14.6 ± 7.8%, respectively.

Table 2
Linear regression coefficients (± one standard deviation) from fitting data to Equation (2) and resulting Q_{10} values for the surface active layer (sAL), bottom active layer (bAL), and permafrost (Pf).

	sAL	bAL	Pf
Slope	9399 ± 3692	10849 ± 3211	13966 ± 3864
Intercept	−31.7 ± 13.3	−35.0 ± 11.6	−46.0 ± 13.9
R^2	0.89	0.93	0.94
Q_{10}	3.4 ± 1.6	4.1 ± 1.7	6.1 ± 2.8

4. Discussion

4.1. Soil organic matter decomposability

The potential positive feedback between climate warming and greenhouse gas release from thawing permafrost is a topic of intensive scientific debate (Koven et al., 2011; Schuur et al., 2015; Zimov et al., 2006). Environmental conditions in the seasonally thawed active layer and perennially frozen permafrost are substantially different and may therefore respond differently to warming-induced environmental changes (Gillespie et al., 2014). We hypothesized that older SOM currently stored in permafrost is less easily decomposable than SOM stored in the active layer. As OM is incorporated into soils, easily decomposable C compounds are mineralized and lost to the atmosphere. Consequently, fewer, but more stable C compounds, such as aromatic ring structures (von Lützow et al., 2008), remain within soils. An increase in the stable OM fraction within deeper permafrost soils in Siberia, Alaska, and Greenland has been shown in a study by Schädel et al. (2014). Schädel et al. (2014) further report, that the labile pool size of permafrost-affected soils is typically < 5% of SOC and that there is no difference between organic, shallow (< 1 m) and deeper mineral soils. The labile pool of deeper permafrost (0.5–4.5 m) on Samoylov Island comprises about 2% of SOC (Knoblauch et al., 2013). In the current study, we did not separate C pools because longer incubations (> 1 year) are needed for reliable estimates (Knoblauch et al., 2013). We only observed significantly higher decomposability

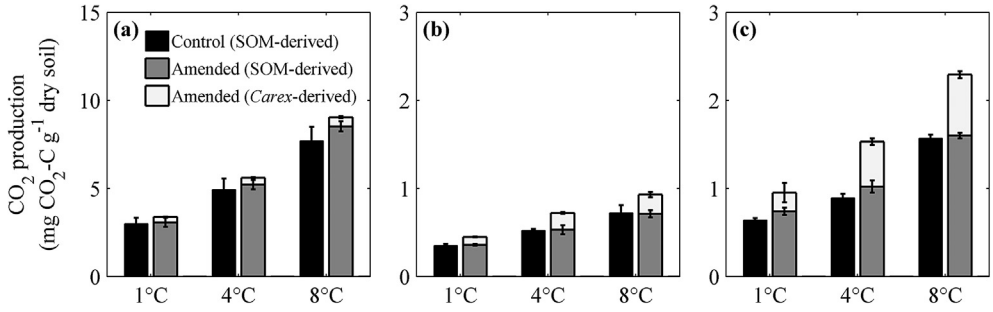

Fig. 5. CO_2 production and source partitioning into SOM- and *Carex*-derived CO_2 in control and amended samples after 150 incubation days at different temperatures in surface active layer (a), bottom active layer (b), and permafrost (c). Data are mean values ($n = 4$) and error bars represent one standard deviation. Note the different scale in (a).

of SOM in the surface active layer, while CO_2 production in soil layers below did not differ significantly from those in the permafrost. This suggests that labile C from root exudates and plant litter, which is incorporated at the soil surface where microbial abundance and diversity are also highest (Liebner et al., 2008), dominates SOM turnover. Thus, most of the labile pool is decomposed in near-surface layers within one thaw period and less decomposable compounds from vascular plants and mosses are the source of deeper SOM.

Under anaerobic conditions, 2–6 times less CO_2 was produced than under aerobic conditions. Schädel et al. (2016) reported on average a 3.4 lower C release under anaerobic than aerobic conditions for different high latitude ecosystems (tundra, boreal forests, and northern peatlands) and found this pattern to be independent of active layer or permafrost material as well as incubation temperature. CH_4 production in the current study was only observed after a lag phase of several days (surface active layer) to weeks (bottom active layer) to months (permafrost) and at a much lower rate than CO_2 production, most likely due to the overall low abundance of methanogenic microbes in permafrost (Treat et al., 2014; Waldrop et al., 2010). However, under *in situ* conditions, soil microbial communities will develop depending on the environmental conditions, and increased CH_4 production under anaerobic conditions can be expected. In the current study, CH_4 production in the surface active layer was high in Polygon 1, but low in Polygon 2, which can be explained by differences in the water table. While the entire active layer of Polygon 1 is water-saturated under *in situ* conditions, the water table depth in Polygon 2 is 9–12 cm below the soil surface.

The late onset of CH_4 production has been observed in several anaerobic incubation studies (Knoblauch et al., 2013; Lee et al., 2012; Lipson et al., 2012; Treat et al., 2014; Waldrop et al., 2010). The length of the lag time varies strongly between studies and has been discussed in detail by Treat et al. (2015). For studies with incubation temperatures < 10 °C, a mean lag time of 341 ± 65 days until maximum CH_4 production rates were observed has been reported (Treat et al., 2015). In the current study, no maximum CH_4 production rates were reached within the 150-day incubation period, which makes longer-term projections of CH_4 production difficult. But increasing CH_4 production rates even at the end of the incubations suggest that anaerobic decomposition could become more important in the long-term, especially considering that increased CH_4 production is accompanied by increasing anaerobic CO_2 production as well (Knoblauch et al., 2013). Current evidence suggests that CO_2 production dominates in permafrost-affected soils (Schädel et al., 2016; Treat et al., 2015), but most of the anaerobic incubation studies are shorter than the lag time of methanogenesis and the importance of CH_4 production on time scales beyond several years remains unclear.

4.2. Freezing and thawing

Seasonal freezing and thawing characterizes the active layer. We hypothesized that freeze-thaw cycles increase the microbial decomposition of SOM and result in short-lived bursts of greenhouse gases after thawing (Herrmann and Witter, 2002; Schimel and Clein, 1996). There are several explanations for the increase in CO_2 production after freeze-thaw cycles. In non-permafrost soils, the increase in decomposition has been related to the death of up to 50% of microorganisms and the release of easily decomposable C compounds from lysis (Soulides and Allison, 1961). Herrmann and Witter (2002) estimated that about 65% of the CO_2-flush after a freeze-thaw cycle was due to microbial necromass. However, soil microorganisms in arctic soils are well adapted to low temperatures and prolonged freezing (Morozova and Wagner, 2007). Some studies have shown that moderate frost events (−5 °C) had no effect on microbial biomass in tundra soils (Grogan et al., 2004; Lipson and Monson, 1998), while others reported a decrease in microbial biomass C after repeated moderate freeze-thaw cycles (Larsen et al., 2002; Schimel and Clein, 1996). In the current study, a lower freezing temperature of −18 °C was applied, which is close to the average soil temperature during the coldest month (−24.4 °C at 20 cm depth in February) at the study site (Boike et al., 2013). An increase in decomposition after one freeze-thaw cycle has only been observed in the active layer, while in the permafrost, the pronounced peaks in decomposition rates were absent after the initial thawing and only weak after samples were subjected to a freeze-thaw cycle. The immediate start and continuous production of CO_2 after thawing, however, indicate that the microorganisms of the northeast Siberian tundra survive the very low temperatures. Therefore, it seems unlikely that microbial necromass and lysis are solely responsible for the burst in greenhouse gas production after thawing. If microbes would not survive frost events, we would expect the largest cell death and thus a large peak in permafrost samples, which were frozen for the longest time.

Another possible explanation for the increase in decomposition rates after thawing is the destruction of soil aggregates and exposure of previously physically protected labile substrate to microbial decomposition (van Bochove et al., 2000). In experiments with repeated freeze-thaw cycles, the size of the C flush often decreased with each freezing event, which has been connected to the depletion of labile SOM, which is most susceptible to freeze-thaw cycles (Feng et al., 2007; Herrmann and Witter, 2002). However, under *in situ* conditions, the additional input of fresh OM during each vegetation period would supply every year labile substrate to be physically broken down by frost action, resulting in a flush of CO_2 right at the beginning of each thaw period. Although the current data do not allow to identify the source of the CO_2 flush

after thawing, they demonstrate the importance of freeze-thaw dynamics for SOM decomposition, which should be considered for estimates of long-term greenhouse gas production in thawing permafrost-affected soils. However, an effect of freeze-thaw cycles on CH_4 production could not be shown. Rising CH_4 production rates during the incubations indicate that methanogenic communities were not substrate limited, which might explain why additional substrate availability through a freeze-thaw cycle did not increase CH_4 production.

4.3. Temperature sensitivity

Temperature is a main driver of microbial soil processes. We hypothesized that less decomposable permafrost SOM is more sensitive to temperature than more decomposable active layer material. This is consistent with the third component of kinetic theory and has been shown across a range of ecosystems (Davidson and Janssens, 2006). In permafrost-affected soils, the slowly decomposing C pool has also been shown to have a higher temperature sensitivity (equal-C $Q_{10} = 2.19$) than the fast (1.16) decomposing C pool (Bracho et al., 2016). For different tundra ecosystems, a mean Q_{10} of 3.4 has been reported (Hamdi et al., 2013). Q_{10} values in the current study were slightly higher (3.4–6.1) but we used lower temperature range (1–8 °C) than most other studies from tundra soils (> 10 °C). This lower temperature range might be one reason for the generally higher Q_{10} values in the current study. According to the second component of kinetic theory, temperature sensitivities exponentially increase with decreasing temperatures. C pools in soils in colder regions therefore respond stronger to increasing temperatures than those in temperate environments (Hamdi et al., 2013).

Estimations of temperature sensitivity are dependent on methods and assumptions (Liang et al., 2015). Dutta et al. (2006) reported a range of equal-time Q_{10} values of 1.7–2.9 for different permafrost soils but found that rates between temperatures treatments (5–15 °C) did not differ after 200 incubation days, possibly due to the differential depletion of labile SOM at different temperatures. This suggests that SOM quality is more important than temperature and that SOM decomposition at temperatures close to freezing might not respond strongly to small temperature changes until more favorable conditions are established (Schädel et al., 2014). A similar effect was observed in the current study, where decomposition of low quality permafrost SOM was similar at 1 °C and 4 °C but much higher at 8 °C (Fig. 4c).

Although laboratory results cannot be directly transferred to *in situ* conditions, they do highlight the importance of temperature effects on slow decomposing low quality C pools (Bracho et al., 2016; Schädel et al., 2016). In addition to SOM quality, temperature sensitivity has been shown to negatively correlate with SOC content (Balogh et al., 2011). Especially in forest and grassland ecosystems, lower Q_{10} values have been observed in soils with high amounts of SOC (Hamdi et al., 2013). Organic soils generally show higher greenhouse gas production than mineral soils (Schädel et al., 2014), but greenhouse gas production in mineral soils, which are more wide spread in the permafrost region and contain together a larger fraction of the permafrost SOC stock (Hugelius et al., 2014), may respond more strongly to warming. However, a recent study (Čapek et al., 2015) reported that Q_{10} values of organic surface layers, cryoturbated, and non-cryoturbated mineral soils were not significantly different from each other.

4.4. Effect of labile organic matter

The addition of labile plant-derived OM increased overall CO_2 production in all samples. We hypothesized that the addition of *Carex* material would increase the decomposition of autochthonous SOM in the whole soil profile. A significant increase in SOM-derived CO_2 (positive priming effect), however, was only observed in permafrost samples. This suggests that soil microorganisms living in deeper soil layers with older, more degraded SOM as substrate were energy limited (Fontaine et al., 2007) and that microbial activity can be stimulated by additional substrate and nutrients. The size of the priming effect depends on both the frequency of labile OM inputs as well as the quality of the added material (Fan et al., 2013). For sub-arctic ecosystems, Hartley et al. (2010) reported that decomposition in surface soils did not respond to C additions, but did respond to N and phosphorous additions. Similarly, a strong priming effect was observed for active layer soils (Wild et al., 2014) as well as permafrost (Wild et al., 2016) after the addition of amino acids and proteins. De Baets et al. (2016) reported that N additions had an inhibitory effect on decomposition and that microbial activity in deeper soil layers is rather C than N limited. In the current study, we used structural C from *Carex,* which is the dominate vascular plant species at the study site, and observed small but significant priming effects in permafrost. At low temperatures in particular, labile OM inputs provide the necessary energy for microbial activity to also decompose more stable SOM (Garcia-Pausas and Paterson, 2011).

4.5. Contribution of thawing permafrost SOM to total C release

Permafrost-affected soils are an important component in regional and global C cycles but have so far been underrepresented in climate models. Higher greenhouse gas production from these soils can be expected due to the combined effect of higher soil temperatures in the active layer and successive permafrost thaw. In the current study, aerobic CO_2 production after 150 days in different soil layers at different temperatures was measured. The data can be used for estimating the effect of thawing permafrost on total SOM decomposition under rising temperatures. The current mean active layer depth at the study site is 50 cm (Boike et al., 2013). Assuming a mean soil temperature of 4 °C for the surface active layer (0–10 cm) and 1 °C for the bottom active layer (10–50 cm), the surface active layer could potentially produce 4.5 g C kg^{-1} and the bottom active layer 0.5 g C kg^{-1} within one thaw period of 150 days. To get absolute production, potential production is multiplied with the dry bulk density (300 kg m^{-3} for the surface active layer and 500 kg m^{-3} for the bottom active layer, Zubrzycki et al. (2013)) and the respective layer thickness. This results in a contribution of 135 g C m^{-2} from the surface active layer and 100 g C m^{-2} from the bottom active layer and a total of 235 g C m^{-2}. No SOM decomposition is assumed in the currently frozen permafrost layer below 50 cm. In a future warmer Arctic, the active layer may deepen to 100 cm in northeast Siberia until 2100 (Koven et al., 2011). Assuming a future mean soil temperature of 8 °C in the surface active layer, 4 °C in the bottom active layer, and 1 °C in the newly thawed permafrost, potential production would increase to 6.5 g C kg^{-1}, 1.0 g C kg^{-1}, and 0.5 g C kg^{-1} in the respective soil layers. This would result in absolute productions of 195 g C m^{-2}, 200 g C m^{-2}, and 225 g C m^{-2} in these three soil layers (with a dry bulk density of 900 kg m^{-3} for newly thawed permafrost, Zubrzycki et al. (2013)) and a total of 620 g C m^{-2}. Hence, under this scenario the newly thawed permafrost would account for 36% of total SOM decomposition. The contribution of permafrost SOM may even increase, if fresh surface SOM mixes with former permafrost OM, e.g. by higher rooting depths or cryoturbation, causing a positive priming of permafrost SOM decomposition.

5. Conclusion

The current study highlights the importance of different environmental parameters for SOM decomposition in permafrost-affected tundra soils. Although decomposability was generally lower in deeper soil layers than in near-surface layer, permafrost SOM was more sensitive to temperature and responded stronger to labile OM additions than active layer material. The additional C release from successively thawing permafrost may therefore contribute substantially to future greenhouse gas production in tundra soils. Longer and deeper thaw, higher soil temperatures, and the translocation of labile OM from the surface into deeper soil layers could accelerate the decomposition of a previously frozen and therefore stable C pool. However, the amount of C released, and whether C will be released as CO_2 or as CH_4 will largely depend on *in situ* thaw and hydrological conditions. Reliable projections of circumpolar greenhouse gas production in thawing permafrost need improved projections of future landscape hydrology to quantify SOM decomposition in water-saturated or non-saturated soils. Further, studies should focus on anaerobic SOM decomposition, its sensitivity to temperature, and labile organic matter input. In particular, the long-term formation of CH_4 from thawing permafrost is one of the least understood processes. Furthermore, studies including repeated freeze-thaw cycles are needed to evaluate, if the observed effect diminishes over time.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2017.03.001.

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