



Carbon release from *Sphagnum* peat during thawing in a montane area in China



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HIGHLIGHTS

- The C released quickly during thawing in the peat and permafrost soils.
- The CO₂ emission was higher during thawing in the sphagnum moss layer.
- The CH₄ emissions showed different trend to the CO₂ emissions during thawing.
- The Q₁₀ values of peat and permafrost soil were increased across the freezing point of water.
- The changes of soil substrates and environments during thawing could affect the type of greenhouse gas.

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ABSTRACT

Soil thawing may affect the turnover of soil organic carbon (C) and the release of C to the atmosphere. Little is known about C release during thawing in the Great Hing'an Mountains, China. Through the incubations, we studied the emissions of CO₂ and CH₄ during thawing from the *Sphagnum* moss layer to the permafrost layer under aerobic and anaerobic conditions. Carbon was released quickly during thawing under different conditions. The *Sphagnum* moss layer produced more CO₂ than the other layers. However, there was little CH₄ release during thawing in the *Sphagnum* moss layer and burst of CH₄ emissions in the peat and permafrost soils. These bursts include stored CH₄ in the frozen samples and productions from microbial activity. The temperature sensitivity during thawing decreased across the freezing point in the *Sphagnum* moss layer, did not change greatly in the root layer, and increased greatly in the peat and permafrost layers. Changes in soil substrates and enzyme activities may affect C release during thawing.

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1. Introduction

Boreal peatland ecosystems cover about 3% of the earth's surface and store approximately one-third of the total terrestrial C pool (Gorham, 1991; Tarnocai et al., 2009). Peat is partially decomposed plant material that accumulates where plant production exceeds organic matter losses through heterotrophic respiration, leaching or dissolved export, fire combustion or other disturbance-related losses and it represents the balance between CO₂ fixation by net primary production and carbon releases throughout the entire peat column (Turetsky, 2004). *Sphagnum* mosses are usually dominant

in the peatland ecosystems and decompose very slowly (Dorrepaal et al., 2005; Wieder and Vitt, 2006). *Sphagnum* mosses and peat soils provide good thermal for the underlying permafrost and contribute to permafrost stability (Turetsky, 2004; Wieder and Vitt, 2006). However, climate models predict that climate change will be most intense at high latitudes (IPCC, 2007). Increased air and soil temperatures could contribute to permafrost thawing in the high latitude ecosystems and expose a large pool of stable C stored in permafrost to microbial decomposition (Davidson and Janssens, 2006; Schuur et al., 2008).

Increases in CO₂ and CH₄ emissions following soil thawing have been shown to affect total annual gas budgets (Papen and Butterbach-Bahl, 1999; Song et al., 2006). Microbial activity essentially stops once the soil is frozen (Schaefer et al., 2011). During thawing, the sudden flush of water and nutrients may induce changes in microbial activity, with organisms shifting rapidly (Schimel and Clein, 1996). The general

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mechanisms that explain the increased C emission after thawing include release of C from microbial biomass, death of roots, and changes in soil structure (Matzner and Borken, 2008). However, the mechanisms that control C releases during thawing events are not fully understood (Kim et al., 2012). Future climate change is likely to alter the thawing events. Soil thawing raises the questions about the fate of C cycling in peatland ecosystems.

Peatland environments are generally highly heterogenous, which creates large uncertainties in understanding the resulting effects of dynamic processes such as permafrost thawing (Bäckstrand et al., 2010). Permafrost thawing could also affect the soil moisture and result in different soil environments (Wickland et al., 2006). The organic carbon in the permafrost might be relatively labile since it is not protected from decomposition by physical protection or humification mechanisms (Fan et al., 2008). There are still knowledge gap regarding the extent to which permafrost-protected C is available for microbial metabolism once soils thaw (Warldrop et al., 2010). Laboratory study may reflect the climate effects on permafrost soils under aerobic and anaerobic conditions. The results should help parameterize and validate ecosystem and climate models of C release from permafrost thawing (Lee et al., 2011).

In the Great Hing'an Mountains in China, low temperatures, a short growing season, partial water-saturation, and permafrost limit decomposition of organic matters resulting in an accumulation of organic matter in soils (Wang et al., 2010). However, the permafrost boundary has moved northward with a deeper active layer and the total permafrost area has shrunk remarkably since the 1970s in this montane area (Jin et al., 2007). Such changes may influence the C cycle in local permafrost peatlands. To improve our understanding of the present and future C dynamics in permafrost peatland ecosystems, we collected samples from the continuous permafrost peatlands in the Great Hing'an Mountains, China. The objective of this study was to quantify CH₄ and CO₂ release during thawing under aerobic and anaerobic conditions and to compare the C emissions from the *Sphagnum* moss layer with the permafrost layer during thawing. We hypothesized that the stored CH₄ in the frozen samples would affect the calculation of the CH₄ emission from the microbial production during thawing and that permafrost soils could have high potential decomposability after thawing compared with the active layer.

2. Materials and methods

2.1. Study area

The sampling sites (52°55'–53°10'N, 122°46'–122°16'E) were near the town of Mohe County, which located in the continuous permafrost zone of the Great Hing'an Mountains, northeastern China. Permafrost in this region is an integral part of Eurasian continuous permafrost. The mean annual air temperature is –5.5 °C and the annual precipitation from 1961 to 2000 was 400 mm (Jin et al., 2007). The peatland is poor fen in this region and distributed in the wide valleys, which dominated by *Ledum palustre*, *Vaccinium uliginosum*, *Sphagnum* spp., and *Larix gmelini* Rupr. The thickness of the active layer ranges from 50 to 70 cm above the permafrost layer (Wang et al., 2010; Miao et al., 2012).

Table 1

Substrate quality of the samples used in the incubation study.

Depth (cm)	TOC (g kg ⁻¹)	TN (g kg ⁻¹)	C/N ratio	pH	Water content (%)	CH ₄ content (μmol g ⁻¹)
0–10	431.70 ± 40.71	10.80 ± 0.04	36.68 ± 3.96	5.57 ± 0.24	1575.00 ± 275.00	6.40 ± 1.67
10–20	488.63 ± 28.16	19.03 ± 0.04	24.50 ± 0.81	5.30 ± 0.33	992.05 ± 17.05	19.32 ± 4.34
20–30	407.97 ± 4.31	17.11 ± 0.07	22.70 ± 1.78	5.38 ± 0.40	407.97 ± 4.31	29.69 ± 2.65
40–50	234.57 ± 6.62	9.24 ± 0.03	23.25 ± 2.65	5.52 ± 0.20	246.68 ± 5.17	661.73 ± 68.14
80–90	126.23 ± 1.80	5.55 ± 0.01	19.49 ± 0.62	5.74 ± 0.51	103.07 ± 1.01	236.41 ± 6.00

Values are the means ± 1 SE (n = 3).

2.2. Soil sampling and preparation

We collected samples from *Sphagnum* hummock in December 2010 while the soils were totally frozen. The samples included the *Sphagnum* spp., shrub root, peat, and permafrost soil, which were wrapped in aluminum foil with 10 cm using a band. The 0–10 cm layer was the *Sphagnum* moss layer, which included frozen living *Sphagnum* moss. The 10–20 cm layer was the root layer, which included the shrub roots. The 20–30 and 40–50 cm layers were the peat layer, which could thaw during the summer months. The 80–90 cm layer was the permafrost soil layer, which had frozen over 2 years (Table 1). Then the samples were split along their axis with saw for incubation experiments. Some small pieces (approximately 10 g) of the different layers were taken for analyzing the CH₄ concentration in the frozen samples. The other samples were taken to the Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences and stored at –20 °C. In the laboratory, some samples of each layer were thawed at 4 °C, and then dried for analysis of the soil properties.

CH₄ concentrations in frozen samples were obtained by thawing small frozen subsamples of material in saturated NaCl solution, following the method described by Wagner et al. (2007) (Table 1). We took about 10 g samples in glass jars and sealed them tightly with black rubber stoppers in the field. There were also four blank samples. Then the thawed samples were shaken by hand and CH₄ concentrations were analyzed by gas chromatography (Agilent 7890, Agilent Co., Santa Clara, CA, USA).

2.3. Incubation experiment

In the laboratory, about 40–50 g of frozen samples were placed in 500 ml glass vials and sealed with rubber stoppers. Three vials were incubated under aerobic conditions and three vials were incubated under anaerobic conditions. All vials were incubated in the dark. Anaerobic incubations were conducted by flushing with N₂ for 15–20 min at a time to ensure that O₂ was removed. At each measured time, the samples were also flushed with N₂ for 15–20 min to remove the cumulative gases. During the 48-day incubation, we measured the concentrations of CO₂ and CH₄ emissions from –10 °C to 10 °C. The C emission rates were measured when the soils were at –10 °C (on day 3), and after the soils had been warmed to 0 °C (on day 3). The soils were then incubated at 10 °C for the rest of the incubation period.

At each measurement time, 20 ml of headspace was collected and the CO₂ and CH₄ concentration measured by gas chromatography (Agilent 7890). Once the sampling of a vial was completed, vials under aerobic conditions were flushed with ambient air and resealed for the next measurement.

2.4. Soil characteristics techniques

Soil moisture content was determined gravimetrically by drying the soil at 105 °C for 48 h and measuring the weight changes before and after drying. The C contents were measured with a Multi N/C 2100 Analyzer (containing an HT 1500 Solid Module, Analytik Jena, Germany). Total N concentration was analyzed by the Kjeldahl

digestion method using a Behr S5 analyzer (Behr Labor–Technic GmbH, Düsseldorf, Germany). Sample pH was measured using oven-dried (60 °C) soil samples. The samples were diluted 1:5 using deionized water and stabilized, and the pH measurements taken using an Orion pH meter (PHS-25, Shanghai, China).

After incubation, soil dissolved organic carbon (DOC) was determined by the method of Jones and Willett (2006). About 10 g samples were extracted with 50 ml of distilled water for 30 min on a shaker at approximately 230 rpm and centrifuged for 20 min at 8000 rpm. The supernatant was filtered through a 0.45 µm filter into separate vials for C analysis. The extracts were measured by using the Multi N/C 2100 Analyzer. Soil microbial biomass carbon (MBC) was determined by chloroform fumigation (Vance et al., 1987) on all soils at all treatment temperatures after the 48-day incubation. After the incubation experiment, the soil was carefully mixed and DOC from 10 g soil was extracted with 0.05 M K₂SO₄ in a 1:4 ratio. Another 10 g of soil was firstly fumigated with chloroform for 24 h and then extracted in the same way. The extracts were frozen until analyses for total C concentrations on the Multi N/C 2100 Analyzer.

Enzyme activity potentials were assayed on all samples after the aerobic and anaerobic incubations. The enzymes assayed were amylase, invertase, and cellulase, which were determined by the modified methods described by Guan (1986) and Rahmansyah and Sudiana (2010). Assays were conducted on 0.5 g samples with acetate–phosphate buffer (pH 5.5). The substrates were carboxymethylated cellulose for cellulase, starch solution for amylase, and sucrose for invertase. The cellulase activity was incubated for 72 h, while the amylase and invertase activity were incubated for 24 h. Enzyme activity was measured colorimetrically at 508 nm (U-2800, Japan) and expressed as mg glucose g soil⁻¹ d⁻¹.

2.5. Statistical analyses

Q₁₀ values were calculated to reflect the potential decomposability of soil organic carbon during thawing, which were calculated as the CO₂ emission rates at –10 °C divided by the rates at 0 °C and the rates at 0 °C divided by the rates at 10 °C. Cumulative gas production was calculated for all samples. We used analysis of variance (ANOVA) to test differences in the physicochemical variables of samples between the different layers. Statistical analyses were performed using the OriginPro 8.0 software package.

3. Results

3.1. Carbon emissions during thawing

At –10 °C, the rates of CO₂ emissions were very low for all frozen samples under aerobic and anaerobic conditions (Fig. 1). For samples thawed at 0 °C and 10 °C, these rates increased greatly and the amounts of CO₂ emissions were higher under aerobic conditions than those under anaerobic conditions. The rates in the 0–10 cm layer were higher than those in the other layers in the thawed samples.

The rates of CH₄ emissions showed different trend to the rates of CO₂ emissions for the different layers. The rates of CH₄ emissions in the *Sphagnum* moss layer were very lower under both aerobic and anaerobic conditions, even below 0 under aerobic conditions during the incubation period. On the first day of thawing in the incubation conducted at 10 °C, CH₄ emission rates showed sharp peaks under aerobic and anaerobic conditions in the root and soil layers (Fig. 2). However, the rates of CH₄ emissions were very low under aerobic conditions for the rest of the incubation period. The average percentages of the first day CH₄ emissions in the root and soil layers were about 40% under aerobic conditions and about 25% under

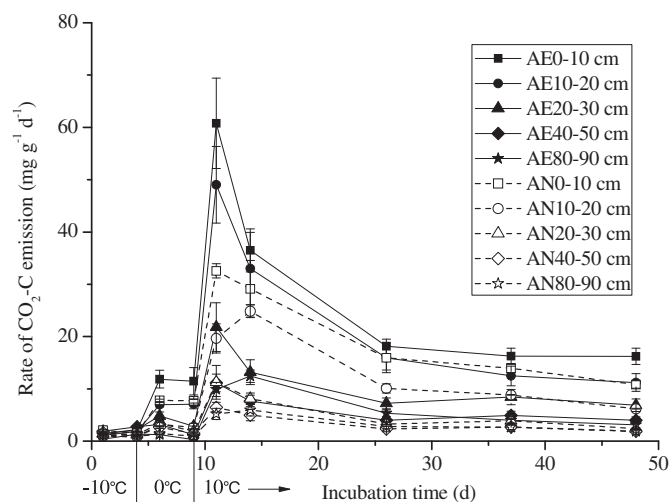


Fig. 1. CO₂ emission rates under aerobic and anaerobic conditions during a 48-day incubation (AE: aerobic condition; AN: anaerobic condition). Values are means ± 1 SE (n = 3).

anaerobic conditions. The stored CH₄ could be released during thawing and influence the estimation of CH₄ emissions by microbial production. However, these percentages in the *Sphagnum* moss layer were only 16.7% under aerobic conditions layer and 2.3% under anaerobic conditions.

3.2. Temperature sensitivity of organic carbon decomposition

Q₁₀ values were calculated by using the ratio of average CO₂ emission rates for 3 days (Table 2). Calculated Q₁₀ values in the *Sphagnum* moss layer were higher at –10 °C to 0 °C than those at 0–10 °C under aerobic and anaerobic conditions. The Q₁₀ values increased during thawing across the freezing point in peat layers under aerobic and anaerobic conditions. In the permafrost soil layer, the Q₁₀ values were much higher at 0–10 °C under aerobic conditions. During thawing of permafrost, the permafrost soils could have a higher potential for decomposition under aerobic conditions compared with the active layer.

The temperature sensitivity in the *Sphagnum* moss layer showed a decreasing trend during thawing across the freezing point under aerobic and anaerobic conditions. The Q₁₀ values in the root layer increased across the freezing point under aerobic conditions, but

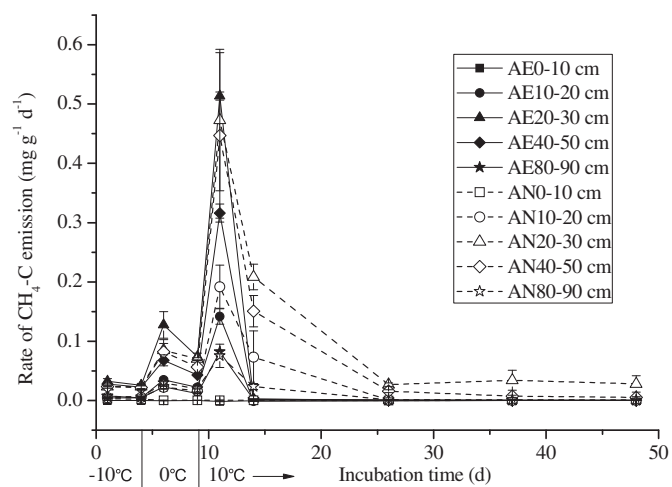


Fig. 2. CH₄ emission rates under aerobic and anaerobic conditions during a 48-day incubation (AE: aerobic condition; AN: anaerobic condition). Values are means ± 1 SE (n = 3).

Table 2
Calculated Q_{10} values of CO_2 emissions under aerobic and anaerobic conditions.

Depth (cm)	Q_{10} values under aerobic conditions		Q_{10} values under anaerobic conditions	
	–10 °C to 0 °C	0–10 °C	–10 °C to 0 °C	0–10 °C
0–10	6.86 ± 0.78	4.19 ± 0.20	5.41 ± 0.48	3.24 ± 0.06
10–20	5.18 ± 0.24	5.71 ± 0.30	3.75 ± 0.22	3.48 ± 0.29
20–30	2.27 ± 0.22	4.93 ± 0.34	1.60 ± 0.16	3.83 ± 0.26
40–50	1.96 ± 0.13	5.15 ± 0.69	1.56 ± 0.08	2.89 ± 0.19
80–90	1.93 ± 0.43	29.21 ± 1.62	1.18 ± 0.11	5.24 ± 0.41

Values are means ± 1 SE ($n = 3$).

did not change greatly under anaerobic conditions. In the peat layer, the Q_{10} values increased across the freezing point under aerobic conditions more than under anaerobic conditions. The values were increased greatly in the permafrost layer under aerobic conditions. When peat and permafrost thaw, the decomposition of organic carbon could be more sensitive in the aerobic environment.

3.3. Soil characteristics after thawing

DOC concentrations decreased with depth under aerobic and anaerobic conditions (Fig. 3a). In the *Sphagnum* moss and root layers, the DOC concentrations were higher under anaerobic than under aerobic conditions. However, these concentrations did not change greatly in the peat and permafrost layer under different conditions. The MBC concentrations were higher in the *Sphagnum* moss and root layers than in the peat and permafrost layers (Fig. 3b). These concentrations in the *Sphagnum* moss and root layers were higher under

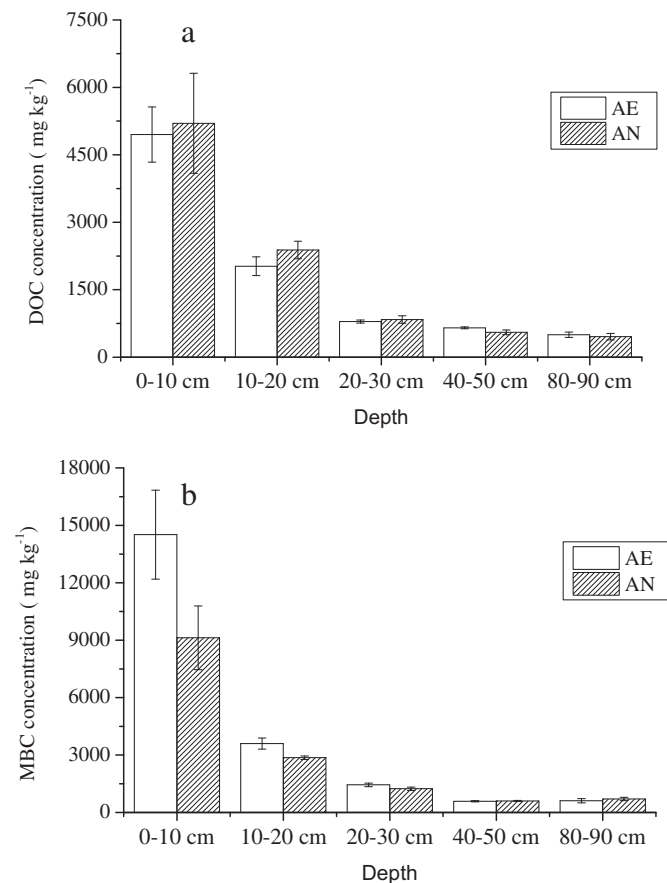


Fig. 3. Soil dissolved organic carbon (DOC) (a) and soil microbial biomass carbon (MBC) concentrations (b) of the samples (AE: aerobic condition; AN: anaerobic condition). Values are means ± 1 SE ($n = 3$).

aerobic conditions than those under anaerobic conditions. However, the MBC concentrations did not change greatly in the peat and permafrost layers under the different conditions.

Enzyme activity potentials showed a decreasing trend with depth under the different conditions (Fig. 4). Enzyme activities in the *Sphagnum* moss and root layers were higher under aerobic conditions. Amylase activities in the peat and permafrost layers were also higher under aerobic conditions, but the invertase activities in the peat layer were lower. The cellulose activities did not change greatly in the peat and permafrost layers under different conditions.

4. Discussion

4.1. CO_2 emissions during thawing

During thawing, trapped organic C may become more accessible for microbial degradation (Osterkamp, 2007) and previously frozen organic carbon may be released to the atmosphere (Mastepanov et al., 2008). Increased CO_2 emissions after thawing have been observed in marsh (Song et al., 2006), bog (Panikov and Dedysch, 2000), taiga and tundra (Schimel and Clein, 1996). The *Sphagnum* moss layer released more C than the other layers in our study. The rate of CO_2 release from *Sphagnum* litter from the 2.5–5 cm depth layer was nearly twice as high as that from organic material from the 10–12.5 cm depth layer under aerobic conditions in Sweden (Hogg, 1993). The high CO_2 emissions in the *Sphagnum* moss layer suggest the presence of more fresh carbon substrates in this layer than in the other sampled layers.

Although there are many studies, the mechanisms and impacts of thawing on C emissions are still unclear (Henry, 2007; Kim et al.,

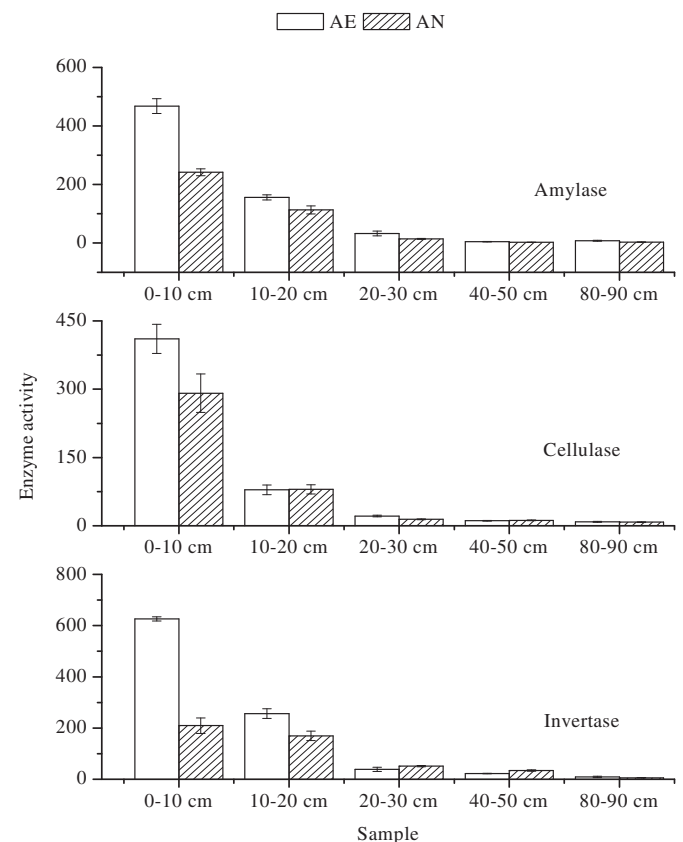


Fig. 4. Potential enzyme activities for all samples under different conditions. Enzyme activities are expressed as mg glucose g soil⁻¹ d⁻¹ (AE: aerobic condition; AN: anaerobic condition). Values are means ± 1 SE ($n = 3$).

2012). Changes in microbial biomass and populations, root turnover and soil structure might explain increased C emissions after thawing (Matzner and Borken, 2008). The decomposition of permafrost soils under different environmental conditions could affect the type of greenhouse gas released (Lee et al., 2011). Under aerobic conditions, permafrost thawing will result in increased decomposition of soil organic matter and increase CO₂ release to the atmosphere (Wickland et al., 2006; Lee et al., 2011).

4.2. CH₄ emissions during thawing

At the onset of the freezing process in the upper *Sphagnum* moss layer in autumn, a frozen layer overlies unfrozen soil, and a temperature gradient is established between the sub-zero air and the unfrozen soil. There is still CH₄ production when the active layer is gradually freezing, so CH₄ that had accumulated in deeper layers is probably squeezed out through the frost action (Mastepanov et al., 2008). This study showed that, during thawing, this stored CH₄ could be released quickly. CH₄ also can be stored in soils with freezing and consequently released to the atmosphere during thawing in tundra (Mastepanov et al., 2008). Thawing of previously frozen peat and increases in the thickness of the active layer could influence estimation of CH₄ emissions during the growing season. Miao et al. (2012) found CH₄ emission rates in the permafrost peatland were not controlled by the water table and strongly controlled by the active layer depth in our study region.

The mechanisms of CH₄ emissions during thawing are complex because they involve the response of both methanogenesis and methanotrophy to changes in availability of substrates, the soil environment, particularly soil moisture, and the availability of electron donors and acceptors that determine the redox status (Kim et al., 2012). In our study, there were more CH₄ emissions in the peat and permafrost soils under anaerobic conditions during thawing. The estimated CH₄ emissions in our study represented the potential C release and a proportion of the CH₄ may be consumed by methanotrophs in the soil. About 90% of the CH₄ produced in peat can be consumed by methanotrophs in the soil (Whalen, 2005). CH₄ emissions in the *Sphagnum* moss layer were very low during thawing under aerobic and anaerobic conditions in our study. *Sphagnum* mosses may host a large community of methanotrophs and play a role in controlling CH₄ oxidation (Larmola et al., 2010).

4.3. Potential decomposition during thawing

The Q_{10} values decreased across the freezing point of water in the *Sphagnum* moss layer, did not change greatly in the root layer, and increased greatly in the peat and permafrost layers. The different layers showed differences in potential decomposability. The unique chemical structures of *Sphagnum* species could influence the C emissions during thawing. The peat and permafrost soils had high potential decomposability during thawing in our study. These Q_{10} values during thawing were higher than the values in *Sphagnum* peat (3.1) (Dioumaeva et al., 2003). The permafrost C is more intrinsically labile than C in surface soils and could have high potential decomposability during thawing (Warldrop et al., 2010).

The Q_{10} values during thawing were different under aerobic and anaerobic conditions and the permafrost soils have higher potential decomposability under aerobic conditions. Carbon in permafrost soils could be very labile in aerobic environments in Alaska and Siberia (Lee et al., 2011). The chemical recalcitrance of organic matter, microbial population size and oxygen availability could influence the temperature sensitivity of decomposition after thawing (Warldrop et al., 2010). The C emissions measured here represented the potential C release during thawing. However, the active layer depth of permafrost (about 75 cm) increased in 2011 in

our study area (Miao et al., 2012), compared with the depth in 2007 (about 60 cm) (Wang et al., 2010). With expected increases in C emissions as permafrost thaws, the decomposition of peat and permafrost soils around the freezing point has important effects on C emissions in this permafrost peatland.

4.4. Substrate changes under different environments with thawing

Although frozen soils limit microbial activity and the diffusion of substrates and products, there were still C emissions below 0 °C in our study. There is still no evidence that the metabolism of microbes in frozen soils has a minimum temperature (Price and Sowers, 2004). The availability of unfrozen water is believed to be a key determinant control of microbial activity at sub-zero temperatures (Price and Sowers, 2004; Öquist et al., 2009). The main factor controlling soil respiration at –10 °C was the concentration of DOC (Guicharnaud et al., 2010). The permafrost soil had high potential decomposability after thawing and the DOC concentrations were higher in permafrost soils than in the active layer (Warldrop et al., 2010). Composition of microbial community and microbial biomass affect the rate of soil organic C decomposition (Nannipieri et al., 2003). Dörsch et al. (2004) found that the microbial biomass decreased after freezing and quickly recovered after thawing, which indicated the use of microbial necromass by the surviving community. Herrmann and Witter (2002), using ¹⁴C glucose labeling, showed that 65% of the CO₂ flush after thawing was due to decomposition of the microbial necromass.

The enzyme activities were different for all samples under aerobic and anaerobic conditions in our study. In general, higher soil enzyme activities indicate faster breakdown of C bonds, and suppressed enzyme activities result in lower rates of C release (Lee et al., 2011). Anaerobic conditions in peatlands could prevent the activity of the phenol oxidase enzyme and decrease C emissions (Freeman et al., 2001). The enzyme activities are also influenced by the SOC and express complex responses to stress conditions (Chaer et al., 2009). Enzyme activities may exist in soils at –10 and –20 °C (Bremner and Zantua, 1975) and be influenced by the freeze–thaw cycle (Chaer et al., 2009). However, there is still little research about changes in enzyme activities following the freeze–thaw cycle (Yergeau and Kowalchuk, 2008).

5. Conclusions

The Great Hing'an Mountains are the southern edge of Eurasian continuous permafrost and should be very sensitive to climate warming. Through the incubation study, we observed quick release of C during thawing under different conditions and the *Sphagnum* moss layer produced more CO₂ than the other sampled layers. CH₄ emissions during thawing showed different trends to CO₂ emissions for the different layers. There were low CH₄ emissions during thawing of the *Sphagnum* moss layer. However, there were bursts of CH₄ emissions during thawing under different conditions in the peat and permafrost soils. These gases included stored CH₄ in the frozen samples and production from the microbial activity. After thawing, the DOC, MBC, and enzyme activities were also different for all samples under aerobic and anaerobic conditions. These factors could affect the C emissions during thawing.

The observed CO₂ and CH₄ emissions represent the potential C release during thawing under aerobic and anaerobic conditions. The temperature sensitivity during thawing decreased across the freezing point in the *Sphagnum* moss layer, did not change greatly in the root layer, and increased greatly in the peat and permafrost layers. The thawing of frozen soils represents abrupt step changes in soil biophysical conditions, with critical implications for C release. Future climate change is likely to alter thawing events and increase the

permafrost degradation. Lab studies cannot reflect the natural C release during thawing. Future research should focus on measurements of gas fluxes in the field, microbiology and the microbial response to thawing and adaptation to freezing temperatures.

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