Response of Methane and Nitrous Oxide Emissions from Peatlands to Permafrost Thawing in Xiaoxing’an Mountains, Northeast China

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Abstract: Permafrost thawing may lead to the release of carbon and nitrogen in high-latitude regions of the Northern Hemisphere, mainly in the form of greenhouse gases. Our research aims to reveal the effects of permafrost thawing on CH4 and N2O emissions from peatlands in Xiaoxing’an Mountains, Northeast China. During four growing seasons (2011–2014), in situ CH4 and N2O emissions were monitored from peatland under permafrost no-thawing, mild-thawing, and severe-thawing conditions in the middle of the Xiaoxing’an Mountains by a static-chamber method. Average CH4 emissions in the severe-thawing site were 55-fold higher than those in the no-thawing site. The seasonal variation of CH4 emission became more aggravated with the intensification of permafrost thawing, in which the emission peaks became larger and the absorption decreased to zero. The increased CH4 emissions were caused by the expansion of the thawing layer and the subsequent increases in soil temperature, water table, and shifts of plant communities. However, N2O emissions did not change with thawing. Permafrost thawing increased CH4 emissions but did not impact N2O emissions in peatlands in the Xiaoxing’an Mountains. Increased CH4 emissions from peatlands in this region may amplify global warming.

Keywords: CH4 emission; N2O emission; peatland; permafrost thawing

1. Introduction

Permafrost underlies 23.9% of the exposed land area of the Northern Hemisphere [1], which stores about 50% of the earth’s soil organic carbon (SOC) [2,3]. In most regions, the thawing permafrost is driven by global warming, and the thawing area and speed may increase during the 21st century [4]. The thawing process may release vast amounts of carbon (C) and nitrogen (N), mainly as CO2, CH4 and N2O, from the frozen soil [5–8]. CO2, CH4 and N2O are the three main greenhouse gases that contribute to 87.5% of global warming [9]. Therefore, it is important to pay more attention to the impact of permafrost thawing on greenhouse gas (GHG) emissions. Previous research [10] shows that C absorption by plants increased more than carbon loss induced by heterotrophic respiration after permafrost thawing, which strengthened the C sink. This should cause a negative feedback to diminish global warming. However, given the higher global warming potentials (GWP) of CH4 and N2O, when CH4 and N2O are converted to CO2 (GWP900), increasing emissions of CH4 and N2O might partially or completely offset the enhanced C sink [10,11].

CH4 is produced by methanogenic archaea during soil organic matter degradation under anaerobic conditions [12]. N2O is produced in soils mainly by two microbial processes:
aerobic nitrification and anaerobic denitrification [13]. Global warming affects several environmental factors in wetlands, mainly including the depth of the permafrost active layer [14,15], soil temperature [16], and water table level [17]. These factors also control CH$_4$ and N$_2$O production and emission from wetlands in permafrost regions [5,18,19]. One model has projected that CH$_4$ emissions will increase by 25–30% when soil active layers are deepened by 30–50% in permafrost in Russia [20]. Positive correlations were found between the soil active layer and CH$_4$ emissions in permafrost regions [21,22]. Deepened active layers increased nitrogen availability [23], which could increase the substrates of nitrifying and denitrifying bacteria and further enhance N$_2$O emissions [24]. Temperature is also one of the most important environmental factors affecting the bacteria active layer. Rising soil temperatures induced by permafrost thawing would enhance the activity of methanogens and nitrifying and denitrifying bacteria, further enhancing CH$_4$ and N$_2$O production and emissions [18,25]. Increased N$_2$O emission due to thawing has been found by a lab-incubation experiment [25], but the in situ evidence in wetlands is still insufficient [26,27].

Besides the effects of deepened soil active layers, changes in hydrological conditions caused by permafrost thawing also affect CH$_4$ and N$_2$O emissions from wetlands. Permafrost thawing leads to increased formation of thermokarst lakes and ponds in continuous and discontinuous permafrost regions [28,29], which also increased flooding events in some locations [17]. High water level will increase the thickness of soil anaerobic layer, thus promoting methane production and emission [30]. However, higher water levels may inhibit nitrification and decrease N$_2$O production and emissions in this way [31]. Pärn et al. [32] found a bell-shaped regression curve between N$_2$O emissions and soil volumetric water content; the N$_2$O emission peaked at around 50% soil moisture. Viru et al. [33] studied four disturbed peatlands and found that N$_2$O emission was the highest when the water level was 30 to 40 cm below soil surface. These results indicate that medium soil moisture was the optimal level for microbial activity in the soil matrix, and favored N$_2$O production and emission. Therefore, if permafrost thawing leads to the increase in soil saturation, N$_2$O emission from wetlands may be inhibited. The composition and growth of wetland plant communities may also change with water levels and soil nitrogen availability during permafrost thawing [10,34,35]. Changed vegetation compositions of plant species not only provides different substrates for associated microbes with CH$_4$ and N$_2$O, but also have different gas transmission capacities, thus also altering CH$_4$ and N$_2$O emission [36,37].

Most research about the effects of permafrost thawing on greenhouse gas emissions has focused on Arctic and subarctic regions [5,15,17,38]. Few studies have focused on the southern global permafrost boundary [11]. The Xing’an Mountains are the second largest permafrost region in China, after the Qinghai–Tibetan Plateau, having a permafrost area of $0.38 \times 10^6$ km$^2$ [39]. This area is also the main wetland distribution region in China [40]. Northeast China’s permafrost region lies at the southern margin of Eurasian permafrost, where mean annual air temperature is about 0 ± 1.0 °C [41]. Thinner permafrost layers and higher soil temperature made the region more sensitive to climate warming. Jin et al. [41] predicted that permafrost areas would decline to an estimated 35% of that amounts in the 1970s and 1980s if air temperature increases 1.0 to 1.5 °C during the next 40–50 years. Some studies have reported GHG emissions in this region [42–47]. Among these studies, Miao et al. [42,43] and Cui et al. [44] discussed the relationship between GHG emissions and active layer depth in one peatland site. Liu et al. [45] studied but did not find a relationship between the active layer depth and GHG emissions. The other research did not measure the active layer depth of wetlands, although their research sites were on the permafrost region [46,47]. None of these studies focused on the change of GHG emissions on the permafrost thawing gradient. Few studies about the influence and mechanisms of permafrost thawing on wetland CH$_4$ and N$_2$O emissions inhibits the understanding of how wetlands in high latitude regions respond and feed back to global warming.

In this paper, field CH$_4$ and N$_2$O emissions from peatlands were observed under different permafrost thawing conditions in the Xiaoxing’an Mountains during the 2011–
2014 growing seasons. The objectives were to test the effects of permafrost thawing on CH$_4$ and N$_2$O emissions in peatlands, and to identify the crucial environmental factors regulating CH$_4$ and N$_2$O emissions during permafrost thawing. We hypothesized that: (1) permafrost thawing will increase the release of CH$_4$ and N$_2$O from peatlands in this region; and (2) increased CH$_4$ and N$_2$O release are driven by both biotic and abiotic factors.

2. Materials and Methods

2.1. Site Description

The study area was located in the middle of the Xiaoxing’an Mountains, Northeast China (48°03′53″–48°17′11″ N, 128°30′36″–128°45′00″ E; 260–500 m a.s.l.), which is at the southern margin of Eurasian permafrost. The region is located in a temperate climate zone, with a mean annual temperature of 0.4 °C and mean annual precipitation of about 630 mm. Wetlands have developed in this area because of the low, flat valleys and permafrost which prevents water from penetrating underground. Peat has accumulated due to the cold and hydrologic conditions.

Three peatlands with no-thawing, mild-thawing, and severe-thawing permafrost conditions were selected in this study. The depths of the soil active layers were 60–90 cm (no-thawing), 110–140 cm (mild-thawing), and 140–170 cm (severe-thawing) during the years 2011–2014.

The dominant plant in the permafrost no-thawing peatland was *Larix gmelinii*, with a mean height of 5.0 m and canopy cover of 40%. Trees were typically short because low nutrient levels and low temperatures in peat limited the tree growth. The region’s inhabitants call them “old little trees”. The dominant shrub species was *Ledum palustre* var. *angustum*, followed by *Vaccinium uliginosum*. High shrubs grow up to 0.5 m, but short shrubs are only 0.2 m in height. Herbs were scattered among the species of *Calamagrostis angustifolia* and *Eriophorum vaginatum*. The ground layer was covered by moss (mainly *Sphagnum* spp.) with a high coverage of 80%.

The dominant plant in the permafrost mild-thawing peatland was also *L. gmelinii*, with a mean height of 8.0 m and canopy cover of 50%. The high shrub species was *Betula ovalifolia*, which could grow up to 1.5 m. Short shrub species included *L. palustre* var. *angustum* and *V. uliginosum*, with mean height of about 0.4–0.5 m. The dominant herbs included *Carex schmidtii* and *E. vaginatum*. The ground was covered by *Sphagnum cymbifolium*, *S. magellanicum* and *Polytrichum juniperinum*.

No trees existed in the permafrost severe-thawing peatland due to the increased flooding conditions after permafrost thawing. The dominant plant was *Carex schmidtii*. Also present were *C. angustifolia*, *Sanguisorba parviflora*, *Equisetum heleocharis*, *Caltha palustris*, *Iris laevigata*, etc. The mean vegetation height was 0.5 m.

Peat depths in most of this region were about 0.5–1 m but reached 3 m in some areas. According to the results from a peatland in the same area located about 50 km away from our research sites, the peat ages from 60 to 217 cm depth were 1310–5116 years BP (Lin et al., 2004) [48]. Chemical characteristics of the soil in the study peatlands are shown in Table 1.

| Soil Characteristics | No-Thawing Site | Mild-Thawing Site | Severe-Thawing Site |
|----------------------|-----------------|-------------------|---------------------|
|                      | 0–20 cm         | 20–40 cm          | 0–20 cm             | 20–40 cm          | 0–20 cm             | 20–40 cm          |
| pH                   | 4.75 ± 0.05     | 4.89 ± 0.02       | 4.72 ± 0.02         | 5.00 ± 0.06       | 4.74 ± 0.13         | 4.79 ± 0.15       |
| SOC/gkg$^{-1}$       | 238.91 ± 3.57   | 290.96 ± 64.76    | 213.15 ± 15.62      | 192.92 ± 12.85    | 182.61 ± 3.89       | 168.49 ± 4.04     |
| TN/gkg$^{-1}$        | 13.33 ± 0.41    | 13.28 ± 0.42      | 13.37 ± 0.04        | 13.66 ± 0.34      | 12.48 ± 1.40        | 12.18 ± 0.26      |
| C/N                  | 17.92           | 21.91             | 15.94               | 14.12             | 14.63               | 13.83             |

Data are mean ± SE (n = 3).
2.2. CH₄ and N₂O Flux Measurements

Triplicate plots in the no-thawing site and quadruplicate plots in the mild-thawing and severe-thawing sites were established in 2011. CH₄ and N₂O fluxes, soil temperatures, and water table levels were measured simultaneously three or four times per month during the growing season (May–early October) from 2011 to 2014.

We used static chambers to collect gas samples between 08:00 a.m. and 11:00 a.m. (GMT + 8 h). We did not observe the diurnal variations of the studied sites. However, due to the results from Sanjiang Plain, GHG flux at 09:00 a.m. was almost equal to the daily mean flux [49]. Therefore, we collected gas samplings between 08:00–11:00 a.m. to reduce the error between the sampling time flux and the daily average flux. Stainless-steel chambers (0.7 m in height and 0.25 m² in area) were equipped with rubber stoppers for headspace sampling and a fan for mixing air during the measurements. Four gas samples were drawn from a port on top of the chamber at 0, 10, 20 and 30 min using a 50 mL syringe. Samples were injected into pre-evacuated packs and analyzed within a week on a gas chromatograph (GC, Angelent 7890). CH₄ and N₂O concentration analyses were according to Song et al. [49]. The gas fluxes were calculated by the following equation:

\[ F = \frac{dc}{dt} \cdot \frac{M}{V_0} \cdot \frac{P}{P_0} \cdot \frac{T_0}{T} \cdot H \]

where \( F \) is the gas flux; \( \frac{dc}{dt} \) is the slope of gas concentration changing with time; \( M \) is the molar mass of each gas; \( P \) is the atmosphere pressure of the chamber; \( T \) is the absolute temperature inside the chamber; \( V_0, P_0, \) and \( T_0 \) are the gas molar volume, atmospheric pressure, and absolute air temperature under standard conditions, respectively; and \( H \) is the height of chamber. Data were accepted when \( r^2 \) of the linear regression between gas concentrations and time was ≥0.90 for CH₄ or ≥0.80 for N₂O.

2.3. Environmental Factors and Plant Biomass

We recorded air temperature inside the chamber and soil temperature at 10 cm with digital thermometers (JM624, China) when collecting gas samples. Water table position relative to the soil surface was measured by digging a small well near the chambers at each peatland. Soil thaw depth was measured with a steel rod with scales on it. We harvested herbs in each site to gain the aboveground biomass in mid-July every year. Three 1 m × 1 m plots were selected randomly in each site, and herbs were cut at the peat surface in each plot and weighed immediately. The plants were subsequently sampled and taken to the laboratory, where they were oven-dried to a constant mass at 80 °C. The dry biomass was calculated by multiplying the fresh weight of the plants by the dry/wet ratio of the sample.

2.4. Data Analysis

One-way ANOVA (Duncan comparison) was employed to test the difference of CH₄ or N₂O fluxes among sites with different thawing stages. Regression analysis was performed to test which environmental factors regulate CH₄ or N₂O fluxes. Significance of the test was set at a probability of 0.05. All error bars were standard errors of the mean. The statistical analysis was performed by SPSS version 18.0 software (SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Variations of Environmental Factors

The highest temperatures and the highest precipitation appeared in July or August (Figure 1). Mean temperatures and precipitation during all four growing seasons (May to October) from 2011 to 2014 were above the 50-year average for years 1961–2010. Mean temperatures were 0.7 °C, 1.0 °C, 1.4 °C, and 0.3 °C higher, and precipitation amounts were 45.3 mm, 128.3 mm, 91.8 mm, and 116.9 mm more than the average. The highest yearly mean temperature was recorded in 2013, and the highest precipitation in 2012.
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Figure 1. Monthly air temperature (A) and precipitation (B) from May to October 2011–2014.

Among the observed years, the seasonal variations in the thawing depth, water table levels, and soil temperature at 10 cm depths were similar (Figure 2). The active layers peaked at the end of the growing season (Figure 2A). The soil temperatures peaked in July or August (Figure 2B). The water tables dropped to the lowest level of the year during the short drought period from June to July (Figure 2C). During the four investigated years, the maximum active layers were 65.2–90.0 cm, 110.8–138.0 cm, and 141–165.2 cm in the no-thawing, mild-thawing, and severe-thawing sites, respectively (Figure 3A). Seasonal mean water tables were −11.2 cm, −6.9 m, and 14.0 cm in no-thawing, mild-thawing, and severe-thawing sites, respectively (Figure 3B). Seasonal mean soil temperatures at a depth of 10 cm were 5.9 °C, 7.3 °C, and 10.5 °C in the no-thawing, mild-thawing, and severe-thawing sites, respectively (Figure 3C). Dominant plants shifted from trees/shrubs to herbs because of the permafrost thawing. The herb aboveground biomasses were 23.5, 111.0, and 445.2 gm$^{-2}$ in permafrost no-thawing, mild-thawing, and severe-thawing sites, respectively (Figure 3D).
Figure 2. Seasonal variation of soil thaw depth (A), water table level (B) and soil temperature (C) in different sampling sites.

Figure 3. Differences in soil thaw depth (A), water table level (B), soil temperature (C) and herb biomass (D) among sampling years and sites. Data are means ± SE. For water table level and soil temperature, \( n = 18 \) in 2011, \( n = 16 \) in 2012, and \( n = 17 \) in 2013 and 2014. For soil thaw depth, \( n = 10 \) in each year. For herb biomass, \( n = 3 \) in each year. Different lowercase letters indicate the significant differences among sites in the same year or the mean of the four years. Different capital letters indicate the significant differences in the same site between different years.
3.2. Seasonal Variations of CH$_4$ Fluxes

In the no-thawing site in years 2011–2013 and in the mild-thawing site from 2011 to 2012, CH$_4$ fluxes were low (≤0.5 mg m$^{-2}$ h$^{-1}$) and did not vary seasonally. In the other years, CH$_4$ flux peaks appeared in summer, and the fluxes ranged from −0.68 to 2.60 mg CH$_4$ m$^{-2}$ h$^{-1}$ in the no-thawing site and from −0.59 to 6.88 mg CH$_4$ m$^{-2}$ h$^{-1}$ in the mild-thawing site, respectively (Figure 4A, B). Negative values indicate that peatlands absorb CH$_4$ from the atmosphere.

Noticeable seasonal variations of CH$_4$ fluxes ranged from 0.35 to 46.63 mg CH$_4$ m$^{-2}$ h$^{-1}$ (Figure 4C) in the severe-thawing site. The CH$_4$ fluxes were always ≤1 mg CH$_4$ m$^{-2}$ h$^{-1}$ in spring before the soil active layer thawed. The fluxes peaked mostly in July and August, and occasionally in early September (e.g., September 3, 2011).

CH$_4$ fluxes were positively related to soil temperatures and soil thawing depths ($p < 0.05$, Table 2) but not water tables ($p > 0.05$) in the no-thawing site. No relationship was found between CH$_4$ fluxes and any environmental factors in the mild-thawing site ($p > 0.05$). CH$_4$ fluxes were exponentially correlated with soil temperatures in the severe-thawing site ($p > 0.01$, Table 2). A quadratic relationship was found between CH$_4$ fluxes and soil thawing depths ($p < 0.01$, Table 2), with no relationship between CH$_4$ fluxes and water tables ($p > 0.05$).

![Figure 4](image-url). Seasonal variation of CH$_4$ fluxes in no-thawing (A), mild-thawing (B) and severe-thawing (C) sites. Data are means ± SE. $n = 3$ for the no-thawing site, $n = 4$ for the mild-thawing and severe-thawing sites.
significant differences in the same site between different years.

Among sites in the same year or the mean of the four years. Different capital letters indicate the significant differences between mild- and no-thawing sites (mild-thawing and no-thawing sites) from the severe-thawing site were always significantly higher than from the mild-thawing and severe-thawing sites, respectively (Figure 5). The mean CH$_4$ fluxes over the four growing seasons were 0.12 $\pm$ 0.06 mg CH$_4$ m$^{-2}$ h$^{-1}$, 0.38 $\pm$ 0.12 mg CH$_4$ m$^{-2}$ h$^{-1}$ and 6.58 $\pm$ 1.09 mg CH$_4$ m$^{-2}$ h$^{-1}$ in the no-thawing, mild-thawing, and severe-thawing sites, respectively (Figure 5). The mean CH$_4$ fluxes from the severe-thawing site were always significantly higher than from the mild-thawing and no-thawing sites ($p < 0.001$). However, no significant difference was found between mild- and no-thawing sites ($p > 0.05$).

### Table 2. Correlations between CH$_4$ flux and environmental factors.

| Site                | Equation                                      | Variable   | $df$ | $R^2$  | $p$  |
|---------------------|-----------------------------------------------|------------|------|--------|------|
| No-thawing site     | $F_s = -0.173 + 0.048T$                        | Soil       | 67   | 0.074  | <0.05|
|                     | $F_s = 0.237 + 0.007TD$                       | Thaw depth | 67   | 0.083  | <0.05|
| Severe thawing site | $F_s = 0.82 \times 10^{0.159T}$              | Soil       | 67   | 0.407  | <0.01|
|                     | $F_s = -3.172 + 0.26TD - 0.001TD^2$           | Thaw depth | 67   | 0.142  | <0.01|

$F_s$ indicates single CH$_4$ flux. Soil temperatures were measured at 10 cm depth.

#### 3.3. Annual and Spatial Variations of CH$_4$ Fluxes

CH$_4$ fluxes increased with thawing, as well as soil temperature, water table and aboveground biomass of herbs (Figures 3 and 5). In the no-thawing and mild-thawing sites, mean CH$_4$ fluxes were significantly higher in 2011 than in other years (Figure 5, $p < 0.05$), while in the severe-thawing site mean CH$_4$ fluxes were significantly higher in 2011 (Figure 5, $p < 0.001$). Interannual variations of CH$_4$ fluxes were in accordance with the variations of maximum thawing depth ($R^2 = 0.442 - 0.619, p = 0.213 - 0.335$, Figure 6) but not with the variations in air temperature, water table depth, and other environmental factors.

Mean CH$_4$ fluxes over the four growing seasons were 0.12 $\pm$ 0.06 mg CH$_4$ m$^{-2}$ h$^{-1}$, 0.38 $\pm$ 0.12 mg CH$_4$ m$^{-2}$ h$^{-1}$ and 6.58 $\pm$ 1.09 mg CH$_4$ m$^{-2}$ h$^{-1}$ in the no-thawing, mild-thawing, and severe-thawing sites, respectively (Figure 5). The mean CH$_4$ fluxes from the severe-thawing site were always significantly higher than from the mild-thawing and no-thawing sites ($p < 0.001$). However, no significant difference was found between mild- and no-thawing sites ($p > 0.05$).

![Figure 5. Mean CH$_4$ fluxes in different years and sampling sites. Data are means $\pm$ SE. $n = 18$ in 2011, $n = 16$ in 2012, $n = 17$ in 2013 and 2014. Different lowercase letters indicate the significant differences among sites in the same year or the mean of the four years. Different capital letters indicate the significant differences in the same site between different years.](image-url)
3.4. Seasonal Variations of N$_2$O Fluxes

Obvious seasonal variations of N$_2$O fluxes were observed in all four growing seasons, except in the no-thawing and severe-thawing sites in 2013 and in the mild-thawing site in 2013 and 2014. High N$_2$O flux peaks with no more than 200 $\mu$g m$^{-2}$ h$^{-1}$ appeared in 2011 in all the three study sites, and those with low N$_2$O flux peaks of about 20 $\mu$g m$^{-2}$ h$^{-1}$ appeared in 2013 (Figure 7). Flux peaks could appear in any month from June to September, and more than two peaks were observed at most sites and in most years. N$_2$O absorptions were observed in all three study sites under different permafrost thawing conditions. The rates ranged from $-24.1$ to $151.8$ $\mu$g N$_2$O m$^{-2}$ h$^{-1}$, from $-51.7$ to $78.7$ $\mu$g N$_2$O m$^{-2}$ h$^{-1}$, and from $-41.1$ to $199.9$ $\mu$g N$_2$O m$^{-2}$ h$^{-1}$ in the no-thawing, mild-thawing, and severe-thawing sites, respectively (Figure 7). N$_2$O fluxes were always low in years with little seasonal variations.
Figure 7. Seasonal variation of N$_2$O fluxes in no-thawing (A), mild-thawing (B) and severe-thawing (C) sites. Data are means ± SE. $n$ = 3 for the no-thawing site, $n$ = 4 for the mild-thawing and severe-thawing sites.

N$_2$O fluxes increased with soil temperatures ($p < 0.05$) in the severe-thawing site but decreased with water levels ($p < 0.01$) in the no-thawing site (Table 3). No significant correlations were found between N$_2$O fluxes and environmental factors in the mild-thawing site.

Table 3. Correlations between N$_2$O flux and environmental factors.

| Site             | Equation       | Variable         | df  | $R^2$   | $p$    |
|------------------|----------------|------------------|-----|---------|--------|
| No-thawing site  | $F_s = 10.087 - 1.227x$ | Water table     | 67  | 0.058   | <0.05  |
| Severe thawing site | $F_s = -4.682 + 3.430x$ | Soil temperature | 67  | 0.098   | <0.05  |

$F_s$ indicates single N$_2$O flux. Soil temperatures were measured at 10 cm depth.

3.5. Annual and Spatial Variations of N$_2$O fluxes

Mean N$_2$O fluxes from the no-thawing site were significantly higher in 2011 than 2013 and 2014 (Figure 8, $p > 0.05$). Mean N$_2$O fluxes from the mild-thawing site were significantly higher in 2012 than 2013 ($p < 0.05$), and both years were not significantly different from 2011 and 2014 (Figure 8, $p > 0.05$). In the severe-thawing site, the highest N$_2$O fluxes happened in 2011 (Figure 8, $p < 0.05$).

Mean N$_2$O fluxes from the severe-thawing site in 2011 and 2012 or over the entire four years were significantly higher than from the mild-thawing site ($p < 0.01$). No significant differences were found among the three sites in the years 2013 and 2014 ($p > 0.05$). Additionally, no significant differences were found between the no-thawing site and the
other two sites in each and over the entire four years ($p > 0.05$). Mean $\text{N}_2\text{O}$ fluxes for the four growing seasons were $22.9 \pm 3.6 \mu\text{g N}_2\text{O m}^{-2} \text{h}^{-1}$, $13.9 \pm 2.9 \mu\text{g N}_2\text{O m}^{-2} \text{h}^{-1}$ and $30.2 \pm 5.2 \mu\text{g N}_2\text{O m}^{-2} \text{h}^{-1}$ in the no-thawing, mild-thawing, and severe-thawing sites, respectively (Figure 8). Mean $\text{N}_2\text{O}$ fluxes for the entire four-year period were higher in the severe-thawing than the mild-thawing site (Figure 8, $p < 0.05$).

![Figure 8. Mean $\text{N}_2\text{O}$ fluxes in different years and sampling sites. Data are means ± SE. $n = 18$ in 2011, $n = 16$ in 2012, $n = 17$ in 2013 and 2014. Different lowercase letters indicate the significant differences among sites in the same year or the mean of the four years. Different capital letters indicate the significant differences in the same site between different years.](image)

### 4. Discussion

#### 4.1. Permafrost Thawing Increased $\text{CH}_4$ Fluxes

4.1.1. Effects of Thawing on Seasonal Variations of $\text{CH}_4$ Fluxes

Our results showed that with permafrost thawing, seasonal variations of $\text{CH}_4$ flux from peatlands became more noticeable, emission peaks became higher, and $\text{CH}_4$ absorption frequency decreased or disappeared (Figure 4). This was in accordance with the results from peatlands in permafrost regions in northern Europe [50], Alaska [6,8,51], and Canada [52]. These responses are related to the increased soil inundation with permafrost thawing inducing a thicker anaerobic layer in peat, along with increased soil temperature, which enhanced $\text{CH}_4$ production and emission.

There were significant correlations between $\text{CH}_4$ fluxes and soil temperatures in the severe-thawing sites (Table 2). Temperature is one of the key factors in controlling $\text{CH}_4$ emissions from wetlands [46,53]. High temperatures stimulate methanogenic bacteria activities and further accelerate $\text{CH}_4$ production and emission. This has been demonstrated by previous studies [45,54,55]. The quadratic relationship between $\text{CH}_4$ fluxes and soil thawing depths ($p < 0.01$, Table 2) in the severe-thawing site might be affected by soil temperature. Soil temperatures were highest in the middle of the growing season, resulting in higher $\text{CH}_4$ emission rates in this period rather than at the end of the growing season, when the soil thaw depths were highest.

There were weak or no significant relationships ($p > 0.05$) between $\text{CH}_4$ emissions and soil temperatures, soil thawing depth, or water tables in the no-thawing or mild-thawing sites (Table 2). This is because $\text{CH}_4$ emissions were low in these two sites. Previous studies also showed that there were no significant relationships between $\text{CH}_4$ emissions and environmental factors when $\text{CH}_4$ fluxes were low enough to fluctuate near zero [46,53].

The water table is one of the most important factors controlling $\text{CH}_4$ fluxes from wetlands. However, according to our previous results in the same region, the relationship was obvious between water table level and spatial variation of $\text{CH}_4$ fluxes rather than seasonal variation of $\text{CH}_4$ fluxes. This is because there was a time lag between the variations...
of water table and the \( \text{CH}_4 \) fluxes from wetlands. \( \text{CH}_4 \) fluxes may not change until some time (from hours to weeks) after the water table has changed [46]. The time lag effect of the water table on \( \text{CH}_4 \) production and emission led to no correlation between seasonal variation of \( \text{CH}_4 \) fluxes and the water table in all the three studied sites.

The seasonal mean \( \text{CH}_4 \) emission increasing with thawing depth in this study is in line with previous reports. For example, in Siberia, when permafrost active layers deepened from 29.8 cm to 50.8 cm, mean \( \text{CH}_4 \) fluxes increased six-fold [56]. \( \text{CH}_4 \) fluxes from Alaskan peatlands with active permafrost depths more than 2.2 m were 15–28-fold higher than those from peatlands, where the permafrost active layer was only 0.4 m [51]. \( \text{CH}_4 \) fluxes from discontinuous permafrost regions in western Canada increased by 30-fold with permafrost thawing [57]. Similarly, in our sites, the severe thawing increased the emission by 55-fold, which confirms part of our first hypothesis that permafrost thawing will increase the release of \( \text{CH}_4 \) from peatlands in this region. This indicates that the frozen soil organic carbon may be more sensitive to global warming in the southern permafrost margin of Eurasia. Methane contributes 18.3% to global warming, only lower than \( \text{CO}_2 \) [9]. Therefore, increased \( \text{CH}_4 \) emissions caused by permafrost thawing in this region will provide a positive feedback to global warming.

The permafrost active layer deepened with thawing in our study peatlands. Thawing permafrost provides more organic substrates and more suitable temperatures for methanogens [3], or increases the abundance of methanogens [58,59]. Thus, \( \text{CH}_4 \) production and emission rates increased. Furthermore, water levels rose with permafrost thawing, and vegetation types changed from trees and shrubs to herbs. Anaerobic conditions were the basis of \( \text{CH}_4 \) production [12]. Herbs can provide more organic substrates for \( \text{CH}_4 \) production [60,61] and provide a pathway for \( \text{CH}_4 \) release which bypasses the oxic zone [62]. Therefore, the differences of \( \text{CH}_4 \) emissions from peatlands under different permafrost thawing conditions were driven by the combined effects of permafrost active layer depth, water table levels and vegetation types, which is consist with our second hypothesis that increased \( \text{CH}_4 \) release is driven by both biotic and abiotic factors.

4.1.2. Effects of Thawing on Annual Variations of \( \text{CH}_4 \) Fluxes

There are few studies reporting the controls of interannual variations of \( \text{CH}_4 \) emissions from peatlands. Huttunen et al. [63] found that interannual variation of \( \text{CH}_4 \) emissions from ten minerotrophic peatlands was controlled by interannual variation of rain amounts. Results from a fen in New Hampshire and a bog in south Canada suggested that significant interannual differences of \( \text{CH}_4 \) fluxes were driven by water table levels and air and peat temperatures [64,65]. In this study, we did not find significant relationships (\( p > 0.05 \)) between annual mean \( \text{CH}_4 \) fluxes and mean soil temperatures, water tables, or herb above-ground biomass because there were smaller interannual changes of these environmental factors or herb biomass. We found that annual mean \( \text{CH}_4 \) fluxes were in accordance with the annual maximum thawing depth of the permafrost active layer in all three thawing or no-thawing sites, although without significant correlations between the emission and thawing depth (Figure 6). Miao et al. [42] found that seasonal \( \text{CH}_4 \) fluxes were correlated to the thaw depth in the same permafrost region in northeast China. However, they only observed less than two years of \( \text{CH}_4 \) fluxes and lacked interannual variations. Shigubara et al. [66] found that soil thawing depth can partly explain the interannual variations of \( \text{CH}_4 \) flux in northeastern Siberia. Our results also showed that interannual variation of \( \text{CH}_4 \) fluxes may be controlled by the differences of maximum permafrost active layer thawing depths; however, more years of data are needed to confirm this conclusion.

4.2. No Effects of Permafrost Thawing on \( \text{N}_2\text{O} \) Fluxes

The similar seasonal \( \text{N}_2\text{O} \) flux and \( \text{N}_2\text{O} \) flux peaks among sites indicated that permafrost thawing did not change the seasonal \( \text{N}_2\text{O} \) flux in our investigated peatland.

Seasonal variations of \( \text{N}_2\text{O} \) fluxes from the no-thawing site were weak and negatively correlated to water table levels (\( p < 0.05 \)) and did not correlate to permafrost thawing depth
or peat temperature (Table 3). This indicated that high water table levels may inhibit N\textsubscript{2}O emissions in this site. Viru et al. [33] studied four disturbed peatlands and found that N\textsubscript{2}O emission was the highest when the water level was 30 to 40 cm below soil surface. Pärn et al. [32] found that N\textsubscript{2}O emissions from organic soils peaked at around 50% soil moisture and then decreased with the increase in soil moisture, which was accordance with our results. Similar results have also been found in other permafrost or seasonal frost regions [67,68]. In severe inundation conditions, wetlands might also change from a N\textsubscript{2}O source to a N\textsubscript{2}O sink [69].

No significant correlations were found between N\textsubscript{2}O fluxes and any observed environmental factors in the mild-thawing site (\(p > 0.05\)). This might be because some environmental factors were not included in our investigation, such as peat nitrogen availability [23,70], or because the low flux rates induced non-relationships between N\textsubscript{2}O fluxes and the environmental factors [71].

N\textsubscript{2}O fluxes were significantly and positively correlated to peat temperature (\(p < 0.01\), Table 3) rather than permafrost thawing depth or water table level (\(p > 0.05\)) in the severe-thawing site. This is because the stable water levels in this site stayed between 10 and 20 cm above soil surface during most of the study period. Therefore, water condition was not the key controlling factor of N\textsubscript{2}O fluxes. With increasing peat temperature, available peat substrate and the active layer of nitrifying and denitrifying bacteria increased and further enhanced N\textsubscript{2}O production and effluxes [31,72]. Single environmental factors can explain no more than 10% of the seasonal N\textsubscript{2}O variations of the three studied sites, indicating that the process of N\textsubscript{2}O production and emission and the control factors are complex. No environmental factors showed enhanced or weakened correlations with N\textsubscript{2}O fluxes on the permafrost thawing gradients.

There were no significant differences of mean annual N\textsubscript{2}O emissions between no-thawing and mild-thawing sites (\(p > 0.05\)) or between the no-thawing and severe-thawing sites (\(p > 0.05\)) in this study. This is not consistent with part of our first hypothesis, that permafrost thawing will increase the release of N\textsubscript{2}O from peatlands in this region. Our results were in accordance with the previous study results in boreal and subarctic areas [73,74]. N\textsubscript{2}O emissions from Alaskan tundra remained at very low levels and did not increase with permafrost thawing [73]. N\textsubscript{2}O emissions did not increase with permafrost thawing in an Alaskan bog, where even zero emissions were found both in permafrost thawing and no-thawing sites [74]. There were also some different results. Permafrost cores collected from Greenland showed N\textsubscript{2}O production rates 20-fold higher after permafrost thawing, drainage, and rewetting [5]. However, how much of this produced N\textsubscript{2}O could be released to the atmosphere remained unknown. The results from the discontinuous permafrost zone in northeast Europe and Russia showed that N\textsubscript{2}O emissions from bare peat or vegetated peat surface were both promoted by permafrost thawing, with a five-fold increase from 0.56 to 2.81 mg N\textsubscript{2}O m\textsuperscript{-2} d\textsuperscript{-1} [26,27]. This is in accordance with Elberling’s lab incubation results [5]. However, we did not find this kind of increasing trend of N\textsubscript{2}O emissions during observation over four growing seasons. One reason is that the increased water table after permafrost thaw inhibited N\textsubscript{2}O emissions from peatland, as mentioned above. Another reason may be due to the changes of plants. Increased herb biomass along the permafrost thawing gradient indicated that plants may absorb more nutrient, consequently inhibiting N\textsubscript{2}O production by competing for NO\textsubscript{3}\textsuperscript{-} with soil microorganisms [27,75]. Due to the inhibition of the water table and plants, N\textsubscript{2}O emission did not increase significantly, although the active layer and soil temperature increased after permafrost thawing.

N\textsubscript{2}O emissions from the severe-thawing site were significantly higher than those from the mild-thawing site. These differences were in accordance with soil temperature, soil thawing depth, water level, and herb aboveground biomass. However, N\textsubscript{2}O emissions from the mild-thawing sites decreased more compared to the no-thawing site, although there were the same changing trends of environmental factors between the mild-thawing and no-thawing sites as between the severe-thawing and mild-thawing sites. Therefore,
there were no gradually increasing trends of N\textsubscript{2}O emissions from sites with permafrost thawing because of the complexity of controlling environmental factors or low emission rates. Because the N\textsubscript{2}O emission from peatland in this region did not increase or decrease significantly with permafrost thawing, there was no significant positive or negative feedback on global warming.

5. Conclusions

Our study shows that with more severe permafrost thawing, seasonal variations of CH\textsubscript{4} emissions from peatlands notably increased, CH\textsubscript{4} emission peaks became higher, CH\textsubscript{4} absorption decreased, and, in some cases, gradually disappeared. Mean seasonal CH\textsubscript{4} emission rates were significantly higher \((p < 0.05)\) from the severe-thawing site than the mild-thawing and no-thawing sites, which confirmed part of our hypothesis that permafrost thawing will increase CH\textsubscript{4} emissions from peatlands in this region. Increasing CH\textsubscript{4} emission was induced by the deeper permafrost active layer and in conjunction with the increases in soil temperature, water table level, and changes of vegetation composition and biomass. As global warming continues, permafrost thawing in these peatlands will become more severe. Severe thawing will release more CH\textsubscript{4} to the atmosphere and further amplify global warming. Due to the inhibition of water table and herb biomass increase, N\textsubscript{2}O emissions showed no changes in either seasonal variations or average seasonal rates, although the active layer and soil temperature increased after permafrost thawing. Therefore, even though global warming continues and permafrost thawing become more severe, N\textsubscript{2}O emissions from the peatlands in this area will not increase and will have little feedback to the global climate.

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