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Dynamics and controls of CO_2 and CH_4 emissions in the wetland of a montane permafrost region, northeast China

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HIGHLIGHTS

- Soil temperature controls the seasonal CO_2/CH_4 emissions from permafrost marshes.
- The sensitivity of CO_2 flux to soil temperature has a high spatially variability.
- There are different controls on the gas emissions at different spatial scales.

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ABSTRACT

To quantify the fluxes and examine the controls on greenhouse gas emissions from the permafrost marshes where the fate of the large quantity of soil organic carbon remains poorly understood, we measured carbon dioxide (CO_2) and methane (CH_4) emissions in the northern region of the Great Xing'an Mountains, northeast China, in the thawing seasons of 2011 and 2012. The mean CO_2 and CH_4 fluxes from the marshes were estimated at 403.47 and 0.14 mg m^{-2} h^{-1} on average during the two years. Soil temperature was determined as the primary control on the seasonal greenhouse gas emissions during the growing period. The Q_{10} values, calculated from the exponential regression between soil temperature and CO_2 emissions, suggest that the sensitivity of CO_2 flux to climate warming has a high spatially variability in the study area. Absorption of atmospheric CH_4 was seasonally detected at the sites with lower water table, which confirms the potential of the natural marshes as CH_4 sink when water table goes down due to climate change. When viewed from the ecosystem scale, the mean annual water table level and aboveground primary production were deemed as the dominant influencing factors for the mean annual fluxes, which suggests that there were different controls on the gas emissions at different spatial scales. Therefore, the primary controls of the CO_2 and CH_4 emissions at different spatial scales need to be surveyed in more detail when focusing on the future alteration of greenhouse gas emissions from permafrost marshes due to climate warming.

1. Introduction

Permafrost soils have acted as sinks for atmospheric carbon (C) since at least the late Pleistocene, and there is global concern that they may become an important source of greenhouse gases as a result of climate changes (Smith et al., 2004; Reyes et al., 2010). Greenhouse gas emissions from permafrost wetlands have always been very important for predicting the biospheric feedbacks between terrestrial ecosystems and global changes (Petrescu et al., 2010). Recent climate warming has produced significant changes in permafrost thawing and wetland degradation, and there is likely a much higher potential for greenhouse gas release from the wetlands than expected (Song et al., 2014; Kim, 2015).

Recent work has shown that the outcomes of permafrost thaw would induce changes in hydrological processes, soil thermal regimes, and plant assemblages (Harden et al., 2012; Jorgenson et al., 2013). These changes in turn alter the availability of stored C to microbial metabolism, and the balance of subsequent CO_2 and CH_4

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fluxes (O'Donnell et al., 2011). The alterations in hydrology and thermal regime in permafrost wetlands will substantially change the river flood extent and water table level across the different landforms. The water table, which determines the depth of the oxic/anoxic boundary and redox level within wetland soil, can have important effects on the production of CO_2 and CH_4 (Dinsmore et al., 2009). CH_4 emissions from wetlands can be stimulated under strictly anaerobic conditions resulting from long-term soil saturation (Song et al., 2014), whereas rising water tables decrease CO_2 emissions (Blodau et al., 2004). Jungkunst and Fiedler (2007) concluded that CO_2 fluxes had been reduced 10–20% and 30–60% with rising water tables in tropical and temperate wetlands, respectively, whereas the reduction amounted to over 60% in boreal wetlands. This finding indicates that there would probably be a major flux change of the greenhouse gases in boreal wetlands under conditions of climate warming and disturbed hydrological regime.

Hydrological and temperature conditions have been extensively incorporated into ecological models aiming to predict future fluxes of the greenhouse gases in the permafrost region (Zhang et al., 2012; Johnston et al., 2014). However, net CH_4 emissions, determined by the balance between CH_4 production and removal through oxidation, are also closely related to a broad range of other environmental variables, such as vegetation composition—particularly the presence or absence of sedges (Ström et al., 2005); plant productivity as indicated by CO_2 fluxes (Öquist and Svensson, 2002); and active layer thickness (van Huissteden et al., 2005). Therefore, the reported high spatial and temporal variability of CH_4 fluxes in permafrost regions was likely the combined effect of biological and physical variables (Olefeldt et al., 2013). As different environmental variables dominate at different temporal and spatial scales, the relationships between the variables with CH_4 fluxes, as well as CO_2 fluxes, in different permafrost regions and ecosystems need to be surveyed in more detail.

The northern region of the Great Xing'an Mountains in northeast China is located in the southern margin of the continuous permafrost zone in Eurasia. This area has 8.245×10^5 hm^2 of natural wetlands and is an important reservoir of soil carbon. The mean annual temperature has increased by 0.3 °C per 10 years on average during the last 50 years, and the active layer thickness has increased 20–40 cm from the 1970s to 2000 (Jin et al., 2000). However, there has been very limited research on the greenhouse gas fluxes from the wetland so far, and the emission fluxes are potentially urgently needed to evaluate the feedbacks of the wetland and predict possible changes in the fluxes in the future. Consequently, this study will examine the emissions of CO_2 and CH_4 in the permafrost wetlands in the northern region of the Great Xing'an Mountains, and we initially determined the key factors that affect the emissions of the gases and established the basis for predicting the future flux in this area.

2. Materials and methods

2.1. Site description

The Kandu River is located in the discontinuous permafrost in the northern parts of the Great Xing'an Mountains. The annual average temperature in the region is approximately −2.0 °C, and the average annual precipitation amounts to 400 mm. Marshes are distributed extensively across the flat river valleys where the river channel meanders through. The marsh surface is covered by organic soil with an organic carbon content in the range of 20–40%. The growing season lasts from May until early October, and the vegetation is typical of herbaceous species dominated by *Carex meyeriana*, which is a typical vascular plant in the study area. The maximum thaw depth of the active layer in the marshes is approximately 80–100 cm, which occurs mostly in late August.

2.2. Design of field study

Field observation was carried out in the middle reaches of the Kandu River, where the width of the flat valley exceeds 1.0 km. Across the valley, the landform slope is only about 2/1000 from the valley boundary to the river channel in the centre. Three observation sites were selected along the cross profile of the valley according to the distance to the river channel and the hydrological conditions. The first site was located 60 m away from the river channel (N 51.132°, E 125.137°) , where the floods could easily reach. Namely, it was a flood-affected, intermittently inundated marsh site (FM). The second site was located at approximately 150 m away from the river channel (N 51.136°, E 125.143°) , where the floods of normal grade could not reach, and the elevation was approximately 10 cm higher than the first site. The second site was not a flood-affected marsh site (NFM). The third site was located approximately 240 m away from the river channel (N 51.137°, E 125.144°) , and had the highest elevation of the three sites where no flood could reach. At the third site, the vegetation community was partly invaded by white birch, a common forest species usually occurring in degraded marshes or meadows in Eurasian permafrost. Thus, the third site represented a non-flooded, degraded marsh landscape with forest invasion (NFMF). In each of the three sites, the dominant wetland vegetation is *Carex meyerian*.

2.3. Chamber measurements

During the growing season of 2011 and 2012, gas emission measurements by the static chamber method were performed from mid-May to mid-October. There were four replicated plots at each site, and an opaque chamber (50 × 50 × 50 cm) made of stainless steel, as well as a 50 × 50 × 20 cm steel base permanently installed, was used for head-space sampling at each plot. The chambers were shaded with Styrofoam to minimize temperature changes within the system and were equipped with two battery-operated fans to keep the air mixed. Gas emission measurements were made at intervals of approximately 10 days, and gas was sampled during the time of 9:00–11:00 at each measurement day. Before sampling, the chambers were placed into the collars of the bases with water to prevent leakage, and the vegetation was included within the chambers. Gas sampling lasted half an hour, and four gas samples were collected at 10-min intervals. The gas samples were stored in syringes for less than 12 h before being measured using a gas chromatograph (Agilent 7890A, Agilent Company, USA). Then, the gradient of the time-series of gas concentrations during the sampling was used to calculate the gas fluxes. Sample sets were rejected unless they yielded a linear regression with an R^2 greater than 0.85. Average flux values and standard deviations were calculated from the four replicates for each observation in each site.

2.4. Auxiliary measurements

In each site, air temperature was measured with a portable digital thermometer (JM624, Jinming Instrument CO., China). At each plot, soil temperature at depths of 0, 5, 10, 15, 20 and 30 cm was measured using precise geothermometers (Accuracy: 0.2 °C) during the entire observation period. The water table position relative to the soil surface was obtained by steel rulers with an accuracy of 0.1 cm, which were fixed near the plots. The thaw depth of the active layer was measured with a steel rod. The aboveground plant biomass measurement was determined in mid-August. The plants (0.5 × 0.5 m) were cut at the ground surface near the plots and then taken back to the laboratory. All of the samples (in triplicate) were oven-dried to a constant mass at 80 °C, and weighed (Wang et al., 2011). Additionally, continuous meteorological data of air temperature and precipitation were obtained from an automatic weather station (Campbell Series, USA) located near the FM site.

2.5. Statistical analyses

The mean and the standard deviation of the gas fluxes at the three sites were statistically analysed with the Statistical Program for Social Sciences (SPSS 16.0). The relationship between environmental factors and gas fluxes was examined by a two-tailed Pearson correlation and regression analysis, and a one-way Analysis of Variance (ANOVA) was run to test for differences in mean fluxes, as well as environmental factors, between the three sites ($\alpha = 0.05$). The temperature coefficients (Q_{10}), which were commonly used to express the soil temperature sensitivity of ecosystem respiration, for the three sites were calculated as follows (Maier and Kress, 2000):

$$\mathrm{FLUX}_{CO_2} = \alpha \exp(\beta T) \quad (1)$$

$$Q_{10} = \exp(10\beta) \quad (2)$$

where FLUX_{CO_2} and T were CO_2 flux and soil temperature for the measurements during the study period, respectively, and α and β were fitting parameters. In this study, Q_{10} was calculated with the soil temperature in different soil depth to compare the soil temperature sensitivity in different depth and to determine the representative Q_{10} value for each site.

3. Results

3.1. Environmental conditions

Great seasonal variations in air temperature and precipitation were observed in the study area (Fig. 1). No significant difference in the average temperature was detected between the two years. The precipitation in the growing season of 2011, 287.5 mm in total, was much higher than that in 2012 (224.3 mm). However, no significant differences were detected between the total precipitation, as well as the mean temperature, for each study period and the mean value for the years from 1985 to 2010 ($P > 0.05$). Significant differences in thaw depth and water table level among the three sites was detected for both of the years ($P < 0.05$). The NFMF site exhibited the minimum thaw depth and the lowest average water table level, whereas FM showed the opposite trend. For the two years, the average water table levels were −9.96, −16.98 and −22.76 cm for the FM, NFM and NFMF sites, respectively. At FM, the water table level often rose beyond the ground surface due to floods, and the maximum level reached 18 cm aboveground on 25th July, 2012.

3.2. Seasonal variation of CO_2 and CH_4 emissions

There were clear seasonal variations in the CO_2 emissions at the three sites during the growing seasons, and peak CO_2 emissions emerged generally in the summer months (Fig. 2). There was no significant difference in the mean CO_2 emission rates between the three sites in 2011 ($P > 0.05$), whereas the emission rate at FM was significantly higher than that at the other two sites in 2012 ($P < 0.05$). The average CH_4 emission at FM site was significantly higher than those of the other two sites in both years ($P < 0.05$). In 2012, clear seasonal variation was not detected at NFM or NFMF as it was in 2011. The CH_4 emissions at the two sites were sustained at a level lower than 0.1 mg m^{-2} h^{-1} throughout the growing season of 2012, and the absorption of atmospheric CH_4 by the wetland was

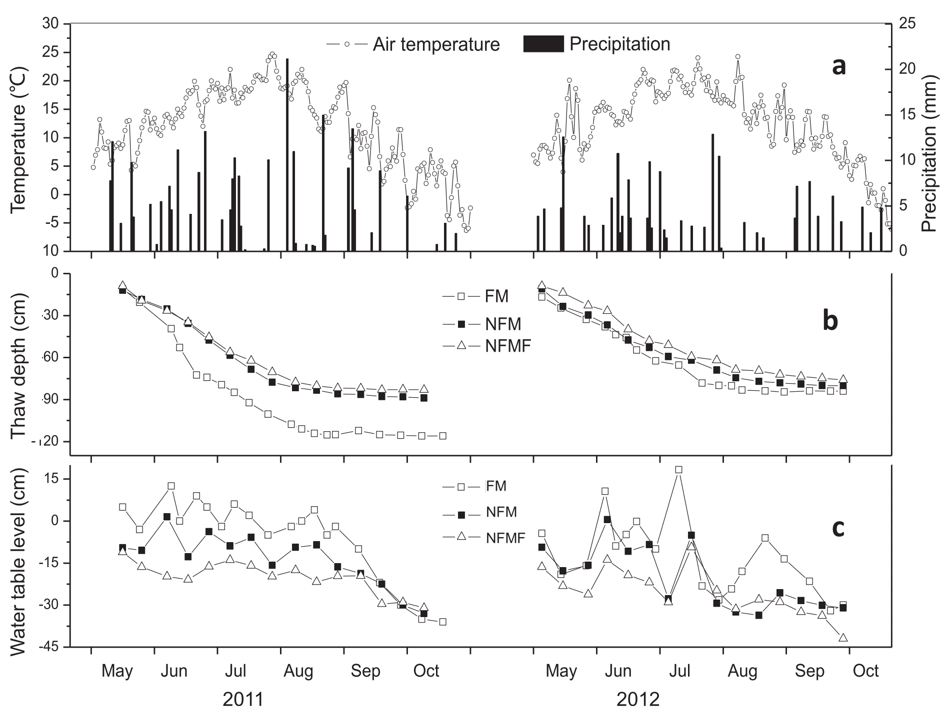

Fig. 1. Seasonal patterns of (a) air temperature and precipitation in the study area, (b) thaw depth, and (c) water table level at the three sites during the growing seasons of 2011 and 2012.

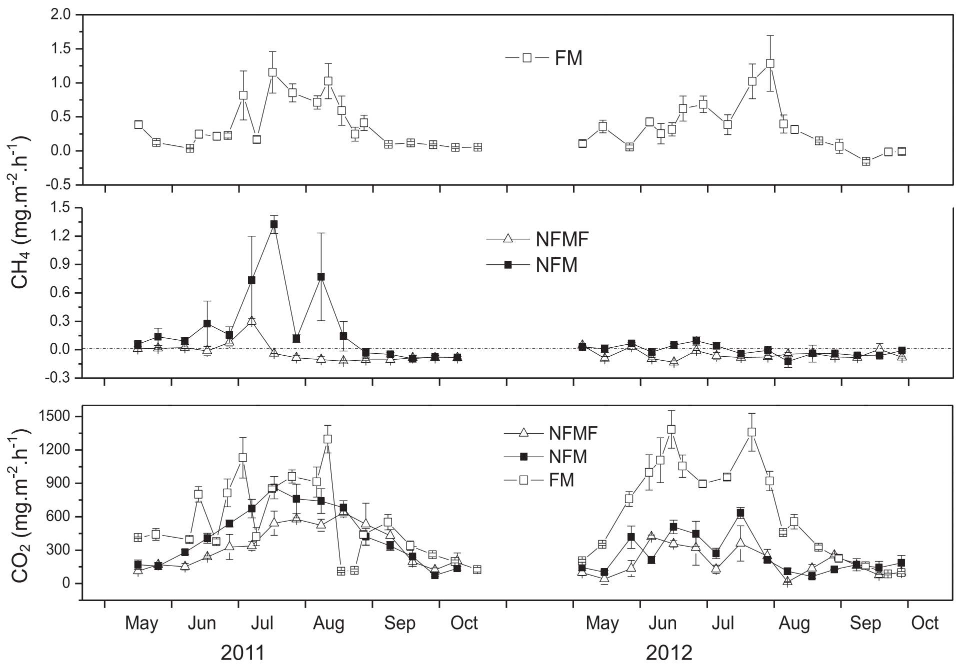

Fig. 2. Variations in CH_4 and CO_2 emissions at the three sites during the growing seasons of 2011 and 2012.

clearly observed in most days of the study period (Table 1). In the view of the mean annual emissions of CO_2 and CH_4, the values declined gradually from the FM to the NFMF site. The CO_2 and CH_4 fluxes were estimated at 403.47 and 0.14 mg m^{-2} h^{-1} on average for the three sites during the two years.

For all of the sites, temperature was an important environment variable influencing CO_2 emissions, as the air and soil temperature at each depth were significantly positively related to the fluxes (Table 2). The CH_4 emissions were closely related to the soil temperature at FM and NFM, and they showed strong linkage to thaw depth at NFMF. Therefore, soil temperature was the main controlling factor affecting both CO_2 and CH_4 fluxes at FM and NFM, as well as the CO_2 emissions at NFMF. Water table level seemed to have no universal effect on the seasonal dynamics of CH_4 and CO_2 fluxes.

Exponential regression equations were very suitable to quantify the relationship between CO_2 fluxes and soil temperature for all of the sites (Table 3). The Q_{10} values of the soil temperature varied according to both the soil depth and the observation site. At FM and NFM, there was a similar trend in the Q_{10} values along the soil profile, with the maximum Q_{10} occurring at the 20 cm depth. At NFMF, Q_{10} exhibited a gradual increase from the surface to the lower soil layer, with the largest spatial variation.

3.3. Relationship between CO_2 and CH_4 emissions

At the FM and NFM sites, the CH_4 emission rates were positively related to the CO_2 emissions during the two growing seasons (Fig. 3). However, according to the difference in the slopes of the regression equations between the two years, there was a great inter-annual variation in the linkage between the CH_4 and CO_2 emissions, especially at the NFM site. In contrast, no significant relationship between the gases was detected at the NFMF site, and the CH_4 emissions roughly showed a declining trend with the rise of the CO_2 emissions.

3.4. Spatial relationships of CO_2 and CH_4 emissions

The three observation sites were distributed across the valley according to gradually changing hydrological regimes. Taking the three sites as an observation profile, the influences of various environmental factors on the mean annual gas fluxes for the three sites were evaluated in Fig. 4. The mean emissions of both CH_4 and CO_2 had positive linear relationships with the mean water table and the dry weight of the sedge family vegetation, which represented a negative relationship with the surface soil temperature. Simultaneously, there was no clear relationship between the mean emissions and the maximum thaw depth.

4. Discussion

4.1. CH_4 emissions and environmental variables

Soil temperature and water table level have long been known as important variables influencing greenhouse gas emissions in high-

Table 1
Characteristics of CO_2 and CH_4 emissions at the three sites during the two growing seasons.

Sites	Variables	Average value (mg m^{-2} h^{-1})	Range of variables (mg m^{-2} h^{-1})	Percentage of negative values in 2011	Percentage of negative values in 2012
FM	CO_2	604.42	85.24–1384.59	0%	0%
	CH_4	0.36	−0.15–1.28	0%	17%
NFM	CO_2	340.89	63.85–861.65	0%	0%
	CH_4	0.11	−0.12–1.32	25%	60%
NFMF	CO_2	265.12	15.10–638.23	0%	0%
	CH_4	−0.04	−0.13–0.30	67%	80%

Table 2
Relationships between environmental factors and the emissions of CO_2 and CH_4.

Environmental factor		FM		NFM		NFMF	
		CH_4	CO_2	CH_4	CO_2	CH_4	CO_2
Thaw depth	Pearson	0.117	−0.198	0.161	−0.028	0.502**	0.077
	Sig. (2-tailed)	0.485	0.233	0.334	0.866	0.001	0.646
Water level	Pearson	0.162	0.293	0.201	0.333*	−0.116	0.245
	Sig. (2-tailed)	0.330	0.074	0.226	0.041	0.487	0.138
$T_{Chamber}$	Pearson	0.598**	0.677**	0.395*	0.623**	0.227	0.528**
	Sig. (2-tailed)	0.000	0.000	0.019	0.000	0.182	0.001
$T_{Soil\text{-}0\ cm}$	Pearson	0.646**	0.697**	0.462**	0.682**	0.142	0.584**
	Sig. (2-tailed)	0.000	0.000	0.004	0.000	0.403	0.000
$T_{Soil\text{-}5\ cm}$	Pearson	0.700**	0.663**	0.357*	0.599**	0.284	0.650**
	Sig. (2-tailed)	0.000	0.000	0.022	0.000	0.088	0.000
$T_{Soil\text{-}10\ cm}$	Pearson	0.710**	0.670**	0.383*	0.582**	0.257	0.664**
	Sig. (2-tailed)	0.000	0.000	0.019	0.000	0.125	0.000
$T_{Soil\text{-}20\ cm}$	Pearson	0.738**	0.558**	0.382*	0.568**	0.186	0.622**
	Sig. (2-tailed)	0.000	0.000	0.020	0.000	0.269	0.000
$T_{Soil\text{-}30\ cm}$	Pearson	0.719**	0.470**	0.353*	0.515**	0.068	0.660**
	Sig. (2-tailed)	0.000	0.004	0.035	0.002	0.687	0.000
$T_{Soil\text{-}40\ cm}$	Pearson	0.689**	0.458**	0.323*	0.501**	0.051	0.603**
	Sig. (2-tailed)	0.000	0.005	0.041	0.004	0.717	0.000

"**" indicates $p < 0.01$; "*" indicates $p < 0.05$.

Table 3
Regression equations between soil temperature and the CO_2 emissions at the three sites.

Soil temperature	FM		NFM		NFMF	
	Equation Q_{10}	R^2, Sig.	Equation Q_{10}	R^2, Sig.	Equation Q_{10}	R^2, Sig.
$T_{0\ cm}$	y = 182.56exp(0.07T)	0.375	y = 84.07exp(0.061T)	0.493	y = 83.61exp(0.053T)	0.259
	2.01	0.000**	1.84	0.000**	1.70	0.004**
$T_{5\ cm}$	y = 229.96exp(0.082T)	0.365	y = 109.34exp(0.062T)	0.268	y = 90.24exp(0.074T)	0.220
	2.27	0.000**	1.86	0.003**	2.10	0.009**
$T_{10\ cm}$	y = 218.98exp(0.096T)	0.367	y = 121.67exp(0.073T)	0.230	y = 86.69exp(0.087T)	0.232
	2.61	0.000**	2.08	0.008**	2.39	0.007**
$T_{20\ cm}$	y = 268.21exp(0.095T)	0.244	y = 168.99exp(0.071T)	0.171	y = 82.24exp(0.106T)	0.258
	2.59	0.002**	2.03	0.023*	2.89	0.004**
$T_{30\ cm}$	y = 335.92exp(0.081T)	0.152	y = 220.79exp(0.046T)	0.052	y = 84.64exp(0.111T)	0.255
	2.25	0.019*	–	0.252	3.03	0.004**
$T_{40\ cm}$	y = 436.11exp(0.045T)	0.033	y = 234.15exp(0.021T)	0.024	y = 91.73exp(0.109T)	0.232
	–	0.306	–	0.405	2.97	0.007**

"**" indicates $p < 0.01$; "*" indicates $p < 0.05$.

latitude ecosystems (Song et al., 2009; Treat et al., 2014). Olefeldt et al. (2013) emphasized that the two variables were the main controls on CH_4 emissions in the permafrost region, and their effects were interactive and exhibited different predominance according to ecosystem characteristics. Temperature was the primary control of organic matter decomposition and mineralization, which provide the substrates for the growth of methanogens. Sachs et al. (2010) identified surface temperature as a good predictor of CH_4 flux in permafrost. Our study also confirmed that soil temperature was the main control on the seasonal dynamics of CH_4 emissions at the two sites with relatively high water table level. In contrast, there was no clear relationship between water table level and CH_4 emissions for the three sites with different hydrological regimes. These results suggested that soil temperature rather than water table level could explain the seasonal variation in CH_4 emissions in the study area. This is consistent with the dominant temperature effect shown by other reports (Hargreaves and Fowler, 1998; Mu et al., 2009).

Although there was no significant statistical relationship between seasonal CH_4 fluxes and water table level, there was clear evidence that the lower mean water table would stimulate the absorption of atmospheric CH_4 by the wetland ecosystem in the study area. At the NFM and NFMF sites, the negative values for CH_4 fluxes were only observed in the autumn of 2011 and in the whole growing season of 2012, which indicated a clear promotion of the oxidation absorption of atmospheric CH_4. Studies had found that the drawdown of water table level would lead to the oxidation of atmospheric CH_4 in natural ecosystems such as boreal forest and wetland (Yu et al., 2014; Zhu et al., 2014). Our study confirmed the ability of natural permafrost wetland to absorb atmospheric CH_4 where the water table was at a low level for a certain period. This was very true at the NFMF site, where the invasion of white birch had been observed due to the long-term low water table condition. The gradual transformation from wetland to forest would ultimately alter the direction of CH_4 fluxes if the low water level was sustained.

Plants also play an important role in CH_4 emission from wetlands, especially vascular plants. Vascular plants not only provide available organic exudations for CH_4 production (Ström et al., 2012), but also provide a channel from the anaerobic zone to the atmosphere, thereby decreasing CH_4 oxidation in the oxic layer and enhancing CH_4 emission (Whiting and Chanton, 1992). Studies had indicated that biomass was an important predictor for CH_4 emission across both successional wetland gradient (Klinger et al., 1994) and disparate wetlands (Whiting and Chanton, 1993). In our study, the significant effect of plants on the CH_4 emissions from the marshes was also confirmed by the strong relationship between mean CH_4 flux and aboveground biomass across the observation

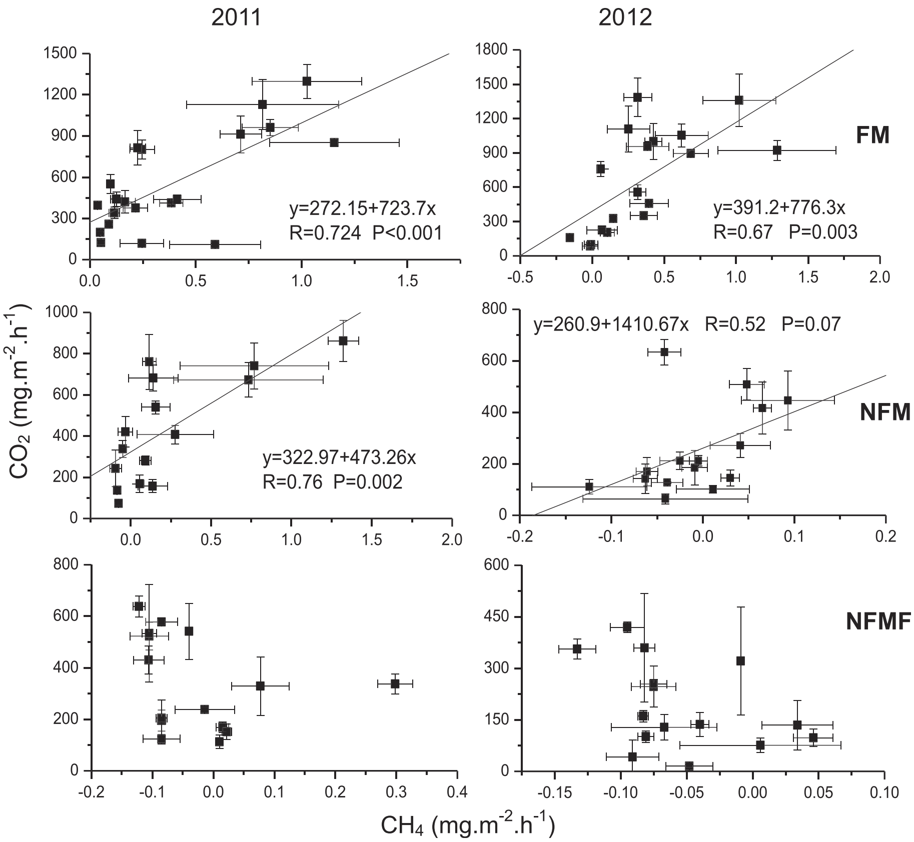

Fig. 3. Relationships between CO_2 and CH_4 emissions at the three sites during the two growing seasons.

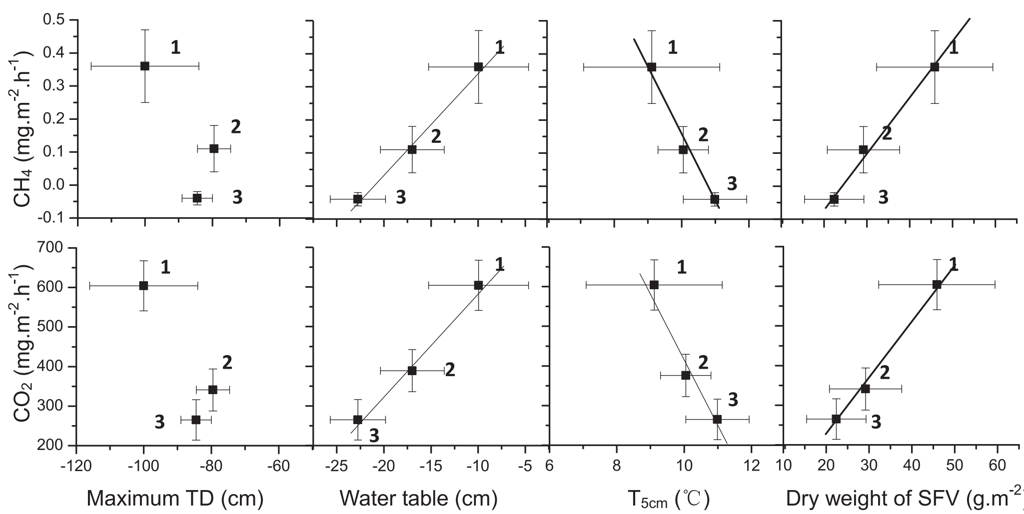

Fig. 4. Relationships between the mean values of the maximum thaw depth (TD), water table, soil temperature at 5 cm depth (T_{5cm}), dry weight of sedge family vegetation (SFV), and the average gas emissions during the two growing seasons. Numbers 1, 2 and 3 indicate the FM, NFM and NFMF sites, respectively.

profile, although no direct observation of the plant transport was conducted (Fig. 4).

4.2. CO_2 emissions and environmental variables

Most often, soil temperature is the dominant environmental control on wetland CO_2 fluxes in permafrost regions (Mu et al., 2009; Miao, 2014). Activity of microorganisms is generally temperature-dependent in permafrost region. It was a clearly evident in our study that there were strong positive relationships between CO_2 emissions and the soil temperature at each depth at all sites. Our study also indicated that near-surface soil temperatures were better predictors of CO_2 fluxes than deeper soil temperatures (Table 3). This may be attributed to the organic-mineral structure of the covered soil, which was extensively distributed in the permafrost regions in north Eurasia. The soil total carbon and nitrogen contents usually decreased with depth in this study area, which indicated more active decomposition and exchange of matter and energy in the surface soil layer (Deppe et al., 2010). Additionally, the active growing fine roots of sedge were most abundant in the surface (5–20 cm depth) (Crow and Wieder, 2005), which also means more respiration. Therefore, the CO_2 production from the surface soil layer was the main contributor to the CO_2 flux and was not constrained by the carbon source quantity and nutrient conditions, which led to soil temperature being the main constraint in the study area due to the thermal energy required for CO_2 production.

Q_{10} was commonly used to quantify the temperature sensitivity of ecosystem respiration (Kirschbaum, 2006). The variation of Q_{10} depended on both soil depth and observation position in our study. The Q_{10} values for the FM and NFM sites fell within the considerable range for boreal wetlands reported in previous research (Zhu et al., 2015), whereas the values for NFMF varied in a broader range. Although there was a lack of standardization of the depth at which soil temperature was measured in the early studies, the Q_{10} value at the upper soil layer was deemed as the representative value for wetland ecosystems. Our results demonstrate the importance of information on the depth of the soil temperature measurement when estimating Q_{10} values for current terrestrial ecosystem models. However, the regression fitting Q_{10} to an exponential equation has incorporated the functions of all of the variables including water table level and vegetation, besides of temperature. The clear differences in the Q_{10} values between the three sites suggested that there was substantial spatial variation influenced by varied environmental conditions. Hence, further studies should pay more attention to the temperature sensitivity under controlled conditions.

4.3. Relationship between CH_4 and CO_2 emissions

During the growing seasons, significant positive correlations between CH_4 and CO_2 emissions were detected at FM and NFM. As both of the gas fluxes had strong linkage with soil temperature at the two sites, the relationship was predictable. However, soil temperature may not be the direct bridge connecting the two gases. The measured CO_2 emission, namely ecosystem respiration, was an important indicator of carbon utilization strength in the primary production processes. Whiting and Chanton (1993) demonstrated a strong linear correlation between net ecosystem production and CH_4 fluxes in a range of wetlands across wide latitudes, suggesting that ecosystem production was a master variable integrating many factors that control CH_4 emissions in vegetated wetlands. Hence, the relationship between CH_4 and CO_2 fluxes likely reflected a production-driven stimulation of methanogenesis by increased root exudation. However, Updegraff et al. (2001) suggested that the relationship was constrained by site-specific dynamics of the wetland community and the water table level. This finding was confirmed by our discovery of the non-relationship at the NFMF site, which experienced vegetation invasion and lower water table levels.

4.4. Major controls at different spatial scales

The major controls of greenhouse gas fluxes were usually different at the laboratory, field site, ecosystem and regional scales, which was due to the spatial interactions between the environmental variables (Zhang et al., 2012; Olefeldt et al., 2013). Our results also showed a clear difference in the controls on the gas fluxes between the individual field sites and the set of field observations as a whole. As for the individual field sites, the seasonal variations of the CO_2 and CH_4 fluxes were mostly positively related to soil temperature and generally had no relation to water table level (Table 2). However, in the set of field observations as a whole, the mean annual values were significantly positively correlated to mean water table ($P < 0.05$) and negatively correlated to soil temperature ($P < 0.05$) (Fig. 4). Higher water table, resulted from summer floods, had been confirmed as having important ecological functions for wetlands, such as transporting necessary nutrients and stimulating the growth of vegetation and microbial communities (Davidson et al., 2012). Therefore, the rise of water table level would stimulate the mean fluxes of the two gases for the whole wetland ecosystem in the study area. The higher aboveground primary production in FM compared to that in NFM and NFMF illustrates the importance of the floods. Furthermore, the significant positive relationship between the primary production and the mean annual fluxes showed clearly the significant effect of biomass on the fluxes in the scale of successional marsh gradient. The relationship provides an important tool for refining regional scale carbon source estimates using satellite-derived indices of net primary production, and is useful as inputs for biogeochemical models

Table 4
CO_2 emissions in the wetlands with frozen soil across northeast China.

Frozen soil type	MAT (°C)	MT-GP (°C)	Lattitude	Wetland type	Mean flux ($mg\ m^{-2}\ h^{-1}$)	Relationship with soil temperature	Measuring period	Reference
Continuous permafrost	−3.5	12.5 12.2	52°56′	Herbaceous peatland	343.75 366.25	Positive/Exponential	May–October, 2011 May–October, 2012	Miao, 2014
Discontinuous permafrost	−2.0	11.5 11.6	51°08′	Herbaceous marsh	440.45 366.91	Positive/Exponential	May–October, 2011 May–October, 2012	This study
Sporadic permafrost	−1.0	14.8	48°07′	Herbaceous marsh	487.89	Positive/linear	Jun–October, 2007	Mu et al., 2009
Sporadic permafrost	−1.0	14.1	48°07′	Herbaceous marsh	498.88	Positive/linear	May–October, 2009	Zhang, 2011
Seasonal frozen soil	1.9	15.8 16.0 16.2 16.9	47°29′	Herbaceous gley marsh	478.1 503.1 455.0 486.2	Positive/Exponential	May–September, 2002 May–September, 2003 May–September, 2004 May–September, 2005	Song et al., 2009
Seasonal frozen soil	1.9	16.2 16.9	47°29′	Herbaceous gley marsh	508.6 467.1	Positive/Exponential	April–October, 2004 April–October, 2005	Liu et al., 2007
Seasonal frozen soil	2.0	16.8 16.9	47°29′	Herbaceous peatland	1024.4 587.8	Positive/Exponential	May–October, 2012 April–October, 2013	Zhu et al., 2015

MAT is the mean annual air temperature, and MT-MP is the mean air temperature during the measuring periods.

of trace gas to understand the mechanism that regulate emission (Whiting and Chanton, 1993).

Table 4 shows the regional variations in the CO_2 fluxes in the wetlands with frozen soils across northeast China according to the published literature. There was an approximate increase in the CO_2 fluxes with the mean air temperature from continuous permafrost to seasonal frozen soil area, but no significant relationship was detected by statistical analysis in the view of the whole region. This result hints that permafrost degradation due to climate warming would greatly stimulate CO_2 emission from the wetlands in northeast China. This result also suggested that temperature alone cannot adequately explain the regional variation of CO_2 fluxes in the wetlands, although there were significant positive relationships between the flux and soil temperatures at each study site. It was reasonable that other parameters, such as precipitation and biomass, were also needed to predict the regional fluxes in the context of global climate warming.

5. Conclusions

Emissions of CO_2 and CH_4 from the permafrost wetland in the Great Xing'an Mountains, northeast China, were recorded during two years of study. There were clear and uniform seasonal variations in the CO_2 emissions for all of the measuring sites with different hydrological and soil temperature conditions, whereas the seasonal CH_4 emissions varied depended on the different sites. At each measuring site, soil temperature was determined as the main control on the seasonal gas emissions during the thawing season, and the mean annual water table level and primary production were confirmed as the dominant influencing factors for the mean annual fluxes when viewed from the ecosystem scale. The CO_2 and CH_4 fluxes were estimated at 403.47 and 0.14 mg m^{-2} h^{-1}, respectively, on average during the two years; these values were in the normal range of fluxes from wetlands in the frozen soil region across northeast China. Our study indicated a large emission potential, as well as a substantial spatial variability, of CO_2 and CH_4 fluxes in the study area. The exact hydrological and soil temperature regimes in a warmer climate are urgently needed to evaluate future changes in the fluxes in the permafrost wetlands of northeast China.

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References

Blodau, C., Basiliko, N., Moore, T.R., 2004. Carbon turnover in peatland mesocosms exposed to different water table levels. Biogeochemistry 67, 331–351.

Crow, S.E., Wieder, R.K., 2005. Sources of CO_2 emission from a northern peatland: root respiration, exudation and decomposition. Ecology 86 (7), 1825–1834.

Davidson, T.A., Mackay, A.W., Wolski, P., Mazebedi, R., Murray-Hudson, M., Todd, M., 2012. Seasonal and spatial hydrological variability drives aquatic biodiversity in a flood-pulsed, sub-tropical wetland. Freshw. Biol. 57 (6), 1253–1265.

Deppe, M., Knorr, K.H., McKnight, D.M., Blodau, C., 2010. Effects of short-term drying and irrigation on CO_2 and CH_4 production and emission from mesocosms of a northern bog and an alpine fen. Biogeochemistry 100, 89–103.

Dinsmore, K.J., Skiba, U.M., Billett, M.F., Rees, R.M., 2009. Effect of water table on greenhouse gas emissions from peatland mesocosms. Plant Soil 318, 229–242.

Harden, J.W., Koven, C.D., Ping, C.L., Hugelius, G., McGuire, A.D., Camill, P., Jorgenson, T., Kuhry, P., Michaelson, G.J., O'Donnell, J.A., Schuur, E.A.G., Tarnocai, C., Johnson, K., Grosse, G., 2012. Field information links permafrost carbon to physical vulnerabilities of thawing. Geophys. Res. Lett. 39, 1–6.

Hargreaves, K.J., Fowler, D., 1998. Quantifying the effects of water table and soil temperature on the emission of methane from peat wetland at the field scale. Atmos. Environ. 32 (19), 3275–3282.

Jin, H.J., Li, S.X., Cheng, G.D., Wang, S.L., Li, X., 2000. Permafrost and climatic change in China. Glob. Planet. Change 26, 387–404.

Johnston, C.E., Ewing, S.A., Harden, J.W., Varner, R.K., Wickland, K.P., Koch, J.C., Fuller, C.C., Manies, K., Jorgenson, M.T., 2014. Effect of permafrost thaw on CO_2 and CH_4 exchange in a western Alaska peatland chronossequence. Environ. Res. Lett. 9 http://dx.doi.org/10.1088/1748-9326/9/8/085004.

Jorgenson, M.T., Harden, J., Kanevskiy, M., O'Donnell, J., Wickland, K., Ewing, S., Manies, K., Zhuang, Q.L., Shur, Y., Striegl, R., Koch, J., 2013. Reorganization of vegetation, hydrology and soil carbon after permafrost degradation across heterogeneous boreal landscapes. Environ. Res. Lett. 8, 1–13.

Jungkunst, H.F., Fiedler, S., 2007. Latitudinal differentiated water table control of carbon dioxide, methane and nitrous oxide fluxes from hydromorphic soils: feedbacks to climate change. Glob. Change Biol. 13, 2668–2683.

Kim, Y., 2015. Effect of thaw depth on fluxes of CO_2 and CH_4 in manipulated Arctic coastal tundra of Barrow, Alaska. Sci. Total Environ. 505, 385–389.

Kirschbaum, M.U.F., 2006. The temperature dependence of organic matter decomposition – still a topic of debate. Soil Biol. Biochem. 38 (9), 2510–2518.

Klinger, L.F., Zimmerman, P.R., Greenberg, J.P., Heidt, L.E., Guenther, A.B., 1994. Carbon trace gas fluxes along a successional gradient in the Hudson Bay lowland. J. Geophys. Res. 99, 1469–1494.

Liu, D.Y., Song, C.C., Wang, Y.Y., Zhao, Z.C., 2007. Influence of plants on CO_2 and CH_4 emission in wetland ecosystem. Acta Bot. Boreal. Occident Sin. 27 (11), 2306–2313 (in Chinese).

Maier, C.A., Kress, L.W., 2000. Soil CO_2 evolution and root respiration in 11 year-old loblolly pine (Pinus taeda) plantations as affected by moisture and nutrient availability. Can. J. For. Res. 30 (3), 347–359.

Miao, Y.Q., 2014. Net Ecosystem Carbon Fluxes of Peatland in the Continuous Permafrost Zone, Great Hinggan Mountains. Dissertation. University of Chinese Academy of Sciences, p. 120 (in Chinese).

Mu, C.C., Shi, L.Y., Sun, X.X., 2009. Fluxes and controls of CO_2, CH_4 and N_2O in a marsh wetland of Xiaoxing'an Mountains, Northeastern China. Chin. J. Plant Ecol. 33 (3), 617–623 (in Chinese).

O'Donnell, J.A., Jorgenson, M.T., Harden, J.W., McGuire, A.D., Kanevskiy, M.Z., Wickland, K.P., O'Donnell, J.A., 2011. The effects of permafrost thaw on soil hydrologic, thermal, and carbon dynamics in an Alaskan Peatland. Ecosystems 15, 213–219.

Olefeldt, D., Turetsky, M.R., Crill, P.M., David Mcguire, A., 2013. Environmental and physical controls on northern terrestrial methane emissions across permafrost zones. Glob. Change Biol. 19, 589–603.

Öquist, M.G., Svensson, B.H., 2002. Vascular plants as regulators of methane emissions from a subarctic mire ecosystem. J. Geophys. Res. Atmos. 107, 4580. http://dx.doi.org/10.1029/2001JD001030.

Petrescu, A.M.R., van Beek, L.P.H., van Huissteden, J., Prigent, C., Sachs, T., Corradi, C.A.R., Parmentier, F.J.W., Dolman, A.J., 2010. Modelling regional to global CH_4 emissions of boreal and arctic wetlands. Glob. Biogeochem. Cycles 24, GB4009. http://dx.doi.org/10.1029/2009GB003610.

Reyes, A.V., Froese, D.G., Jensen, B.J.L., 2010. Permafrost response to last interglacial warming: field evidence from non-glaciated Yukon and Alaska. Quat. Sci. Rev. 29, 3256–3274.

Sachs, T., Giebels, M., Boike, J., Kutzbach, L., 2010. Environmental controls on CH_4 emission from polygonal tundra on the microsite scale in the Lena river delta, Siberia. Glob. Change Biol. 16, 3096–3110.

Smith, L.C., MacDonald, G.M., Velichko, A.A., Beilman, D.W., Borisova, O.K., Frey, K.E., Kremenetski, K.V., Sheng, Y., 2004. Siberian peatlands a net carbon sink and global methane source since the early Holocene. Science 303, 353–356.

Song, C.C., Wang, X.W., Miao, Y.Q., Wang, J.Y., Mao, R., Song, Y.Y., 2014. Effect of permafrost thaw on carbon emissions under aerobic and anaerobic environments in the Great Hing'an Mountains, China. Sci. Total Environ. 487, 604–610.

Song, C.C., Xu, X.F., Tian, H.Q., Wang, Y.Y., 2009. Ecosystem-atmosphere exchange of CH_4 and N_2O and ecosystem respiration in wetlands in the Sanjiang Plain, Northeastern China. Glob. Change Biol. 15, 692–705.

Ström, L., Mastepanov, M., Christensen, T.R., 2005. Species-specific effects of vascular plants on carbon turnover and methane emissions from wetlands. Biogeochemistry 75, 65–82.

Ström, L., Tagesson, T., Mastepanov, M., Christensen, T.R., 2012. Presence of Eriophorum scheuchzeri enhances substrate availability and methane emission in an Arctic wetland. Soil Biol. Biochem. 45, 61–70.

Treat, C.C., Wollheim, W.M., Varner, R.K., Grandy, A.S., Talbot, J., Frolking, S., 2014. Temperature and peat type control CO_2 and CH_4 production in Alaskan permafrost peats. Glob. Change Biol. 20, 2674–2686.

Updegraff, K., Bridgham, S.D., Pastor, J., Weishampel, P., Harth, C., 2001. Response of CO_2 and CH_4 emissions from peatlands to warming and water table manipulation. Ecol. Appl. 11 (2), 311–326.

van Huissteden, J., Maximov, T.C., Dolman, A.J., 2005. High methane flux from an arctic floodplain (Indigirka lowlands, eastern Siberia). J. Geophys. Res. Biogeosci. 110, G02002. http://dx.doi.org/10.1029/2005JG000010.

Wang, B., Lu, S.W., Li, H.J., 2011. Long-term Field Observation Methods of Forest Ecosystem. China Standard Press, Beijing, pp. 85–86.

Whiting, G.J., Chanton, J.P., 1992. Plant-dependent CH_4 emission in a subarctic Canadian fen. Glob. Biogeochem. Cycles 6, 225–231.

Whiting, G.J., Chanton, J.P., 1993. Primary production control of methane emission from wetlands. Nature 364, 794–795.

Yu, D.P., Wang, X.Y., Yin, Y., Zhan, J.Y., Lewis, B.J., Tian, J., Bao, Y., Zhou, W.M., Zhou, L., Dai, L.M., 2014. Estimates of forest biomass carbon storage in Liaoning Province of northeast China: a review and assessment. Plos One 9 (2), e89572. http://dx.doi.org/10.1371/journal.pone.0089572.

Zhang, B.W., 2011. Effects of Fire Disturbance on Greenhouse Gas Emissions from Marsh, Shrub Swamp, Broadleaved Forest Swamp in Xiaoxing'an Mountains. Dissertation for Master Degree. Northeast Forestry University of China (in Chinese).

Zhang, Y., Sachs, T., Li, C.S., Bioke, J., 2012. Upscaling methane fluxes from closed chambers to eddy covariance based on a permafrost biogeochemistry intergrated model. Glob. Change Biol. 18, 1428–1440.

Zhu, X.Y., Song, C.C., Guo, Y.D., Sun, X.X., Zhang, X.H., Miao, Y.Q., 2014. Methane emissions from temperate herbaceous peatland in the Sanjiang plain of northeast China. Atmos. Environ. 92, 478–483.

Zhu, X.Y., Song, C.C., Swarzenski, C.M., Guo, Y.D., Zhang, X.H., Wang, J.Y., 2015. Ecosystem-atmosphere exchange of CO_2 in a temperate herbaceous peatland in the Sanjiang plain of northeast China. Ecol. Eng. 75, 16–23.