PEATLANDS

The Effects of Hydrological Management on Methane Emissions from Southeastern Shrub Bogs of the USA

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Abstract

Peatlands are responsible for the majority of methane (CH₄) emission from wetlands globally. Hydrological changes induced by climatic and anthropogenic disturbance may substantially alter CH_4 emission in peatlands. Here we measured CH_4 emission monthly for 1.5 years in natural, drained and restored shrub bogs in North Carolina, USA. Methane emissions from all sites were consistently low (< 0.05 mg CH₄ m⁻² h⁻¹). We occasionally detected markedly higher CH₄ emissions (> 1 mg CH₄ m⁻² h⁻¹) at sites where the water level remained close to the ground surface for 2–3 months, suggesting that surface litter mostly, not deep peat, contributes to CH4 emission. We verified this inference by incubating 2-cm sections of peat sliced from intact soil cores for 6 months. Only the saturated surface litter emitted CH4, which indicated a 5-cm threshold of ground water level for CH4 emission in our shrub bogs. During a wet year, water levels in the wet sites (natural and restored) remained at least 5 cm below soil surface for about 90 % of the days. We thus demonstrate the CH₄ emission is negligible from these shrub bogs. This study also indicates that restoration through a non-inundated rewetting would not stimulate CH₄ emission in drained/degraded low-latitude shrub bogs, such as pocosins.

Keywords Flux \cdot Low latitude \cdot CH₄ \cdot Optimal water level \cdot Peatland \cdot Rewetting \cdot Shrub bog \cdot Pocosin

Introduction

Methane, as the most abundant greenhouse gas after $CO₂$, is responsible for a large amount of anthropogenically-mediated warming due to its high global warming potential (IPCC 2006). Methanogens produce CH₄ efficiently under strictly anaerobic conditions. Only fully or partially saturated wetlands could emit substantial amounts of $CH₄$ that accounts for the largest natural source of atmospheric $CH₄$ (Bridgham et al. [2013\)](#page-7-0). Peatlands, a type of wetland characterized by highly organic soils, store about one third of global soil carbon (Limpens et al. [2008;](#page-8-0) Joosten [2010](#page-7-0)). A comprehensive synthesis including 19,000 instantaneous measurements mostly from boreal, temperate, and subtropical peatlands reported

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that the mean CH_4 emission from these peatlands was about 4.0 mg m⁻² h⁻¹ ranging from − 0.8 to 238.4 mg m⁻² h⁻¹ (Turetsky et al. 2014). Based on the mean CH₄ emission, the near-natural peatlands $(> 3$ million $km²)$ worldwide could release about 105 Tg CH₄ yr⁻¹, which represents two thirds of CH4 emitted from global wetlands (Bridgham et al. [2013\)](#page-7-0).

Although temperature, water table, and vegetation have been identified as the primary controls on $CH₄$ emission, the high spatiotemporal variations by several orders of magnitude (Bridgham et al. [2013;](#page-7-0) Turetsky et al. [2014\)](#page-8-0) raise uncertainty in predicting $CH₄$ emission from peatlands. More interestingly, among the 19,000 measurements, the highest $CH₄$ emissions (238.4 mg m⁻² h⁻¹) occurred in bogs under optimal water levels around 25 cm below peat surface (Turetsky et al. [2014\)](#page-8-0), which indicates that bogs with low concentrations of inorganic alternative electron acceptors like NO_3^- , Mn (III,V), Fe(III) and SO_4^2 ⁻ actually could have a more important contribution to global atmospheric $CH₄$ if the hydrology shifts toward more methanogen-prone conditions. Recent studies also found that humic substances in peat can serve as organic alternative electron acceptors, constraining CH₄ production (Keller et al. [2009;](#page-7-0) Klupfel et al. [2014\)](#page-7-0). The role of humic substances could partially explain why highly recalcitrant

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deep peat plays only a minor role in $CH₄$ production in many studies (Chanton et al. [1995](#page-7-0); Charman et al. [1999](#page-7-0); Couwenberg [2009;](#page-7-0) Strack and Zuback [2013\)](#page-8-0), making the development of peatland CH4 emission factors even more complicated. Most of the bog data from Turetsky et al. ([2014](#page-8-0)) were collected from boreal regions, where Sphagnum mosses dominate. Given low phenolics and humic substance in fresh Sphagnum (Wang et al. [2015](#page-8-0)), we deduce a possible reason for the maximum CH_4 emission occurred in the upper surfaces of groundwater at around 25 cm (Turetsky et al. [2014\)](#page-8-0). Living and marginally decomposed Sphagnum mosses provide sufficient fresh carbon to anoxic layers just below 25-cm layers for the anaerobically active methanogens, but are not yet limited by the organic electron acceptor—dissolved humic substance (Keller et al. [2009;](#page-7-0) Klupfel et al. [2014\)](#page-7-0) transported from the highly humified catotelm.

The synthesis by Turetsky et al. [\(2014\)](#page-8-0) brings up questions whether broadly-distributed lower-latitude peatlands emit comparable $CH₄$ as these subtropical bogs typically experience a seasonal lowering of groundwater often well below the ground surface and are under warmer temperatures (Wang et al. 2015). While the response of CH₄ emission to water level in these low-latitude wooded peatlands might differ from boreal Sphagnum peatlands because of the lower water levels, higher phenolics, and higher humic substances in the low-latitude peatlands (Wang et al. [2015](#page-8-0); Hodgkins et al. [2018\)](#page-7-0). In terms of restoring degraded low-latitude peatlands and expanded wooded plants in current boreal Sphagnum peatlands due to climate change, a key question that needs to be resolved is what is the optimum water level or hydrological manipulation to mitigate $CH₄$ emission from these peatlands. To address the question, we monitored $CH₄$ emission and associated environmental parameters in natural, restored, and drained sites in a low-latitude shrub bog (pocosin) from August 2011 to January 2013. In addition, we randomly measured $CH₄$ emission from selected shallow ditches and their riparian areas to identify potential hotspots in the shrub bog.

Methods

Site Description

Pocosins are naturally-occurring freshwater evergreen shrub bogs and are found along the southeastern coastal plain from Virginia to Florida in the USA (Richardson [2012\)](#page-8-0). Natural pocosins covered over 900,000 hectares in North Carolina alone before the 1970s, after which, about 70 % of pocosins were ditched and drained for farming or forestry (Richardson [1991](#page-8-0)). In the 1990s, the Pocosin Lakes National Wildlife Refuge (PLNWR) administration started blocking the drainage canals to restore water levels. Our study sites are located in

the PLNWR in the east coast of North Carolina, USA. The site is dominated by dense broadleaf evergreen shrubs (< 2 m high) with peat depths of $1 \sim 3$ m. The mean annual temperature is 16.8 °C, and precipitation is about 1230 mm. Because of high evapotranspiration, the groundwater levels rarely rise above the ground surface and often stay > 20 cm below the ground surface (Wang et al. [2015](#page-8-0)).

We established this study in 5 blocks (1600 \times 900 m each) with different hydrologic regimes—natural, drained, and restored (rewetting) as treatments (Fig. [1](#page-2-0)). Each treatment had been in place for > 20 years. The natural site (RF T2) is close to Pungo Lake and has been rarely disturbed, with water levels of $0 \sim$ − 60 cm (negative values of water level indicate water levels were below ground surface and hereinafter) in winter and often \lt - 100 cm in summer. It is covered by mature trees, including loblolly bay [Gordonia lasianthus (L.) Ellis], pond pine (Pinus serotina Michx.), and swamp bay [Persea palustris (Raf.) Sarg.]. For the restored sites (B7, C2T2, and D11), the water level is about $-20 \sim -30$ cm, where native shrubs dominate, including inkberry [Ilex glabra (L.) A. Gray], large gallberry [Ilex coriacea (Pursh) Chapm.], honeycup [Zenobia pulverulenta (W. Bartram ex. Willd.) Pollard], fetterbush lyonia [Lyonia lucida (Lam.) K. Koch] and laurel greenbrier (Smilax laurifolia L.) with some smaller trees of pond pine, and loblolly bay. The drained sites (C14T1, C14T2 and C14T3,) have the lowest water levels, mostly below − 50 cm depth and lower than − 150 cm in summer. The ground cover is occupied by western brakenfern [Pteridium aquilinum (L.) Kuhn] with scattered woody shrubs like winged sumac (Rhus copallinum L.), wax myrtle [Morella cerifera (L.) Small] and titi (Cyrilla racemiflora L.).

Field Measurements

A static chamber technique was used to measure $CH₄$ emission monthly from August 2011 to January 2013. We initially set up triplicate plots for each treatment. Black bears repeatedly destroyed on site equipment at two of the natural site plots; therefore, only one plot was kept there. The static chamber contains two parts, an anchored bottom soil collar and a matched and portable top chamber. In May 2011, we permanently installed triplicate soil collars (28-cm diameter, 13-cm height) at each plot. Each collar is fashioned with a circular groove (2 cm wide by 1.5 cm deep) on the upper rim to receive the corresponding upper chamber. When the soil collar was submerged in > 5 cm standing water, the upper chamber was modified to act as a floating buoy. Plants (aboveground) inside the collar were removed. A temperature probe and a battery-driven fan for air mixing were installed inside the upper chamber (28-cm diameter, 21-cm height). At each plot, we recorded water levels every 30 min by an automated datalogger (Solinst Levelogger model 3001) since 2010.

Fig. 1 Sampling sites in the Pocosin Lakes National Wildlife Refuge on the southeastern coastal plains of the USA (image from Google Earth)

When collecting gas samples, we placed the lower edge of the top chamber into the water-filled groove to create a good seal. Four gas samples were taken at 10–15 min interval, depending on season, from the headspace through polytetrafluoroethylene tubes into 100 mL gas sampling bags (multilayer polymer with aluminum foil) by syringe. Simultaneously, air temperature, soil temperature, and soil moisture (0–5 cm) were recorded, and the surface soil (0–5 cm) was collected for physicochemical analyses at each gas sampling (see details later). Methane concentrations were determined within 3 d after sampling by a gas chromatograph (GC, Varian 450, California, USA) equipped with a flame ionization detector with a methanizer. The analytical accuracy was maintained by calibrating the GC against two standard gas mixtures in every 8 samples. The concentration of the $CH₄$ standard was 2 ppm. The $CH₄$ emission rate was calculated from the linear change of its concentrations in the chamber as a function of time, base area, chamber volume, and the molar volume of $CH₄$ at air temperature inside of chamber. Emissions with an r^2 < 0.8 in a linear regression of concentration change over time were considered erroneous and excluded. Based on the gas sampling interval and our GC sensitivity, the lowest reliable $CH₄$ emission rate were about $0.01-0.03$ mg CH₄ m⁻² h⁻¹. About 76 and 42 % of emission rates were higher than 0.01 and 0.03 mg CH₄ m⁻² h⁻¹, respectively.

Microcosm Experiment

As we observed clear differences in $CH₄$ emissions across replicate collars located only 2–3 m apart during the 2 to 3 month flooding period in some natural and restored sites, the variations of water levels near the soil surface seemed to contribute to the emission patterns. We collected three soil cores (30–45 cm deep) from the natural and restored sites, including RFT2 at the north of Pungo Lake, C2T2, and Pungo East at the east edge of Pungo Lake. Pungo East, dominated by shrubs, is also a natural site without major disturbance for $>$ 30 years, more like the restored C2T2 than the natural RFT2 in terms of vegetation. Each soil core was sliced into 2-cm Sec. (54 in total) on site and transported back to our lab and stored in a cold room at 4 °C. About 8–10 g fresh soil (\sim 2.5 g dry soil) from each section was placed in a 60-mL vial with a silicone stopper. A 20 mL DI water was then added to a fully saturated condition at a water level about 2–3 cm above the soil surface, similar to the field conditions when we observed high CH₄ emissions. We used Parafilm M® Laboratory film, which is air permeable but water-resistant, to seal the top during the non-sampling period. Hence, the incubation with oxygen presence in the headspace could, to a large extent, mimic the field surface-saturation conditions. After a oneweek equilibration, we collected gas samples with a syringe from the vial headspace at the beginning and end of 48-hour sealed incubation. Gas samples were analyzed by a GC (Varian 450, California, USA) for CH₄ concentration. The $CH₄$ emission was calculated based on the elevated $CH₄$ concentration, time, air volume and temperature (25 °C) in the vial and the dry weight of peat soil. We took samples twice a week initially, then progressed to weekly, and finally biweekly after the third month. We did not detect any $CH₄$ emission until the end of the third month.

Soil Chemistry

Deionized-water extraction was used to determine dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC) by a total C analyzer (Shimadzu 5000 A, Kyoto, Japan), whereas soluble phenolics were determined by following the Folin–Ciocalteu procedure (Lowe [1993](#page-8-0)). Inorganic nitrogen $(NH_4^+$ –N and $[NO_3^- + NO_2^-]$ –N) extracted with 2 M KCl was analyzed colorimetrically on a flow–injection analyzer (Lachat QuikChem 8000, Wisconsin, USA). A combustion CN analyzer (ThermoQuest Flash EA1112, Milan, Italy) was used to measure total carbon and total nitrogen in soil.

Statistical Analysis

A Shapiro-Wilk normality test was run first for CH_4 emission at each site. The NPAR1WAY procedure performs nonparametric tests to compare the difference in CH_4 emission among sites. Pearson's correlation was employed to detect the association between environmental factors and $CH₄$ emission using the mean CH₄ emissions from triplicated plots at each site. Standard error was calculated for means and error bars. Unless otherwise noted, significant difference was set at a probability of 0.05. All analyses were conducted with SAS 9.4 software (SAS Institute Inc., Cary, NC, USA).

Results

The soil physicochemical parameters have been described in detail previously (Supplementary Table 3 in Wang et al. [2015\)](#page-8-0). Briefly, the soil in the natural site ($pH = 3.3$) was more acidic than that in other sites (pH: $4 \sim 5$). The soils in all sites contained similar soil carbon (53–56 %). The drained sites showed much higher N content of nitrate plus nitrite, about twice as much as that in the natural and restored sites. The annual precipitation in 2011 was 1150 mm, and the year of 2012 was a little wetter (1205 mm) with 70 % of its annual precipitation in the growing season. The mean air temperatures in 2011 and 2012 were similar. The mean water levels in 2012 was -25 ± 17 cm at the natural site (RFT2). Mean water levels were $-16 \pm 7, -38 \pm 10$, and -55 ± 14 cm at the restored sites (B7, C2T2, and D11T1, respectively) and $-68 \pm 8, -70 \pm 10$ and -84 ± 11 cm at the drained sites (C14T1, C14T2 and C14T3, respectively). As the synthesis study (Turetsky et al. [2014](#page-8-0)) showed the optimal water level

for CH_4 emission in northern bogs is about 25 cm below ground surface. To compare with their study we counted the total days of water levels at $-20 \sim -30$ cm, > -5 cm and $> -$ 10 cm in 2012 (Table 1). There were 34, 113 and 80 days in 2012 at RFT2, B7 and C2T2, respectively, when water levels stayed within $-20 \sim -30$ cm. We observed water levels above − 5 cm for 44 days, and above − 10 cm for 76 days at the natural site (RFT2). The water levels in the drained sites (C14T1, C14T2, C14T3) were nearly always below -50 cm.

Methane emissions and their temporal variations at each site are presented in Figs. [2](#page-4-0) and [3A](#page-4-0). The median emission at the natural site (RFT2) was 0.128 mg CH₄ m[−] $2 h^{-1}$, which was much higher than at the restored sites (0.024, 0.018 and 0.015 mg CH4 m[−] ² h[−] ¹ at B7, C2T2 and D11T1, respectively) and the drained sites (0.005, 0.005 and 0.008 mg CH4 m[−] ² h[−] ¹ at C14T1, C14T2 and C14T3, respectively). Generally, the mean emissions at each site were about 10 times higher than the median. The emissions of $CH₄$ from the drained pocosin were always small, often below the detection limit and negative $(CH₄$ oxidation was higher than its production) at times. In the whole observation period, we only detected high emission (> 1 mg CH₄ m^{$-$ 2} h^{$-$ 1}) at RFT2 and B7 two months after the summer storm that happened in late June 2012 (Fig. [3](#page-4-0)A and B), in which the emissions reached 5.8 mg CH₄ m[−] 2 h^{− 1} at B7 and 45.6 mg CH₄ m[−] ² h^{− 1} at RFT2 in September and November, respectively. However, during the peak emission period we observed exceptional high spatial variation of $CH₄$ emission within the triplicate plots that were only 2–3 m apart at the same site (Fig. [3](#page-4-0)A). We dug a small hole next to each chamber to measure the water level temporally below the ground surface or measured the standing water depth by a ruler at sites RFT2 and B7, and we found an exponential increase of $CH₄$ emission with water levels when the water level rose above -5 cm (Fig. [4](#page-5-0)A and B) and the emission reached its maximum when the water level was close to the ground surface. We also examined what other physicochemical parameters might affect the emission by running Pearson's correlation using all data

Table 1 Total days in 2012 under specific water levels (cm) in the natural (RFT2), restored (B7, C2T2 and D11T1) and drained (C14T1, C14T2 and C14T3) pocosin sites

Water levels RFT2 B7 C2T2 D11T1 C14T1 C14T2 C14T3					
$-20 \sim -30$ 34 113 80 3 0					
>10	76		92 0 0 0		
>–5	44	$12 \quad 0 \quad 0$		Ω	

Fig. 2 Methane emission from the natural (RFT2), restored (B7, C2T2 and D11T1) and drained (C14T1, C14T2 and C14T3) sites in pocosins. All measurements at triplicated plots are included in this box chart. Same letters above the box indicates nonsignificant differences of $CH₄$ emission among sites, $CI =$ confidence interval

regardless of treatments. These parameters included soil and air temperatures, soil moisture (0–5 cm), ammonium, nitrate + nitrite, soluble phenolics, DOC, soil total nitrogen and carbon. Other than water level $(r = 0.311,$ $p = 0.001$, only soil moisture $(r = 0.566, p < 0.0001)$

Fig. 3 Temporal variations of CH₄ emission (A, mean \pm 1 SD, $n = 3$) and water level (**B**) in 7 sites in pocosins. The dash line at water level of − 5 cm, is identified as a threshold of $CH₄$ emission in the shrub bogs

was significantly related to $CH₄$ emissions, which actually was partially controlled by the water level $(r =$ 0.202, $p = 0.04$).

As methanogens require strictly anaerobic conditions, we expected even higher $CH₄$ emission in locations with higher standing water. However, in the shallow flooded ditch in the pocosin the CH₄ emissions were low, only about 0.05 mg CH₄ $m^{-2} h^{-1}$ on the same day in November 2012 when we observed the peak emission at RFT2. In October 2019, we tested CH4 emissions on the edge of a small shallow ditch in pocosins. Again, the highest emission reached 128 mg CH₄ m⁻² h⁻¹ with the water level close to the ground surface, while only 1 m away from this hotspot the higher elevation (about 30 cm above) plot emitted CH₄ only at a rate of 2.7 mg CH₄ m⁻² h[−] $\frac{1}{\cdot}$. Collectively, these findings suggest that only the surface soil layer, after months of saturation, significantly contributed to po- \cos in CH₄ emissions. This assumption is verified by our incubation experiment (Fig. [5\)](#page-5-0). In this experiment, we did not find any CH4 emission within the first three months although the water levels were always about 2–3 cm above the soil surface. In the fourth month high $CH₄$ emissions occurred only in the surface soil [(0–4 cm) in RFT2 and Pungo East and (0- 6 cm) in C2T2], and sharply dropped to almost undetectable below 4–6 cm, hence, we suggest the-water level threshold for $CH₄$ emissions in pocosins is about 5 cm below the peat surface. Based on the bulk density of 0.03 g cm^{$-$ 3} (Richardson [2003](#page-8-0)), the potential

Fig. 4 Spatial variation of CH4 emission caused by microtopography-induced water level differences at B7 restored (A) and RFT2 natural (B). The same symbol in each figure represents the emissions from the triplicate soil collars located only 2–3 m apart at one site

 $CH₄$ emission at 25 °C from the top 5-cm soil in RFT2 natural site was 0.104 mg CH₄ m⁻² h⁻¹.

Discussion

Optimal Water Levels, Potential Hotspot and Hot Periods for $CH₄$ Emission in Shrub Bogs

Our study shows that water levels play an overarching role in controlling $CH₄$ emission in pocosin shrub bogs. When water level was below $a - 5$ cm threshold, the CH₄ emission was low and could be ignored. We did not observe any relationships between CH_4 emission and soil or air temperature

Fig. 5 Methane emission along soil depths at 2 cm intervals of soil cores in pocosin after 4 months of lab incubation under a saturated condition

although the soil temperature varied in from 2 to 30 °C. Low-latitude peatlands differ from boreal peatlands, where temperature is more of a limiting factor than in pocosins. Also, the soil temperature tended to be higher when water levels were lower in pocosins; thus, it is difficult to determine the full temperature effect.

As expected, the optimal water levels for increasing $CH₄$ emissions in the pocosin shrub bogs are much higher, i.e., close to the ground surface, which differs from the Sphagnum peatlands where it is at about -25 cm (Turetsky et al. [2014](#page-8-0)). The acrotelm of Sphagnum-dominated boreal peatlands consists of substantial living, or marginally decomposed mosses, that are generally thicker (> 25 cm) than in wooded peatlands. These living Sphagnum mosses maintain high soil moisture and release fresh carbon in abundance, which is the primary substrate for methanogenic Archaea (Segers [1998](#page-8-0); Lai [2009\)](#page-7-0). However, this substrate contains little humic substance (Hodgkins et al. [2018](#page-7-0)) that can act as alternative electron acceptors to constrain $CH₄$ production (Keller et al. [2009](#page-7-0); Klupfel et al. [2014](#page-7-0)). Although the old recalcitrant peat in our deeper layers is saturated, the lower fresh carbon and higher humic substance result in very low rates of CH₄ production, a finding supported by our incubation experiment (Fig. 5) and also consistent with other studies (Chanton et al. [1995;](#page-7-0) Charman et al. [1999;](#page-7-0) Clymo and Bryant [2008\)](#page-7-0). In addition, the water level of -25 cm in northern Sphagnum peatlands could be a sweet-spot layer of anoxia for methanogens with plenty of fresh carbon and lower humic substances. For example, Bogs at Mer Bleue in Canada, carbohydrate content in the surface layer (0 \sim - 25 cm) was about twice as high as that in deeper layers (below -25 cm) and it showed a sharp decrease at depths of round $-25 \sim -$

30 cm (Hodgkins et al. [2018](#page-7-0)). However, compared to Sphagnum peatlands, the fresh litter layer in our shrub peatlands is much thinner, and in pocosins soil color turns to dark black below − $3 \sim$ − 5 cm with a sharp decrease in carbohydrate content (Hodgkins et al. [2018](#page-7-0)), which indicates that the humification increases from the surface to soils below − 5 cm. Higher peat humics content in deeper soil might be the reason why we only detected high $CH₄$ emission when the water level rose above − 5 cm. Importantly, the water levels of > − 5 cm in our wettest site appeared in less than 15 % of the days in a wet year, thus the Archaea might be dormant most of the time. After a heavy storm, methanogens also take a long time to regain a fully active metabolism to break their dormancy while the saturation partially suppresses methanotrophs (Taubner et al. [2015\)](#page-8-0). Our laboratory incubation experiment with oxygen present in the headspace differed from a fullyanaerobic incubation but was close to the field conditions. Thus, the results in the incubation were in line with our field observations, that is, it took 2–3 months for the saturated surface layer to emit CH_4 at a high rate. As we sampled monthly, we may have missed the peak event while still showing exceptional burst after the heavy storm in 2012, which did not happen in a drier 2011 after a light storm. Detailed sampling research is needed to determine the dormancy time of methanogens in pocosins that have high phenolic content. The high emissions we observed follow the range that was reported in peatlands globally (Turetsky et al. [2014](#page-8-0)). Therefore, the surface saturated sites are potential hotspots of CH4 emission in the shrub bogs, while only occurring after months of saturation.

Roles of Plants in $CH₄$ Emission in Peatlands

In this study, the CH_4 emissions from the natural sites were much higher than those in the restored site even when the surface litter in both sites was under saturated conditions (Fig. [4](#page-5-0)). The field observation was reaffirmed in the incubation experiment (Fig. [5](#page-5-0)) in which we had mimicked the surface-saturation field conditions only. The incubated vials allowed oxygen in the headspace which means the CH_4 emission we observed represent a difference between CH_4 production and oxidation. Therefore, the different on site $CH₄$ emissions between the natural and restored sites likely stemmed from distinct substrates for methanogens, rather than from the time we took measurements, i.e., whether we caught the right moments. Phenolics have shown to constrain $CH₄$ emission (Miao et al. [2012](#page-8-0); Ye et al. [2012;](#page-8-0) Ward et al. [2013](#page-8-0)). Compared to high-phenolic shrubs (Wang et al. [2015](#page-8-0)), we noticed that the mature trees at the natural sites contained less phenolics, and thus allowed for methanogen more accessible to fresh carbon. Also, in comparison with the potential emission in the incubation, we found that the highest on site emissions were over 400 times higher, likely caused by diminishing

fresh carbon availability in the absence of living plants during laboratory incubation. Hence the quality of fresh litter or exudates from the living plants may play important roles in regulating $CH₄$ emission when the water level is optimum. Finally, as noted earlier, the natural site has existed next to Pungo Lake for thousands of years and thus the hydrologic flooding conditions have greatly influenced the plant and microbial communities at this site. This suggests the pocosin soil near the lake may be a hotspot for CH₄ emissions compared to the domed peatlands found away from the lakes.

Implications for Peatland Restoration and Unravelling of CH₄ Emission Puzzle

Rewetting drained or degraded peatlands as a climate-mitigation measure can effectively reduce aerobic $CO₂$ emission. However, addressing $CH₄$ emission after rewetting is still a challenge. Our research, together with other studies (Turetsky et al. [2014](#page-8-0)), suggests that the varied water-level threshold for $CH₄$ emission in peatlands might be the reason why $CH₄$ emission responses to rewetting differ among types of wetland and among samples within the same wetland. Only when the water levels exceed a depth threshold do the methanogens become active and/or more $CH₄$ is produced by methanogens than consumed by methanotrophs. In our shrub bogs the threshold is about -5 cm, and we also observed the soil moisture ($0 \sim -5$ cm) significantly impacted the emissions, which is consistent with the observations in the Great Dismal Swamp (Gutenberg et al. [2019\)](#page-7-0). The pocosin site in the Great Dismal Swamp, with comparable plant communities to our natural site, emitted CH₄ as high as 75 mg CH₄ m^{−2} h^{−1} when water level stayed above − 5 cm. Thus water level thresholds for CH_4 emissions likely are controlled by the downward infiltration of fresh carbon/substrate that are affected by plant community, root depth, root exudates and the upward moving of dissolved humic substance (Blodau and Deppe [2012](#page-7-0)) as an alternative electron acceptor when water level rises. More studies are needed to detect the water-level thresholds in different peatlands, to determine the optimal water level for CH4 abatement, which can be site-specific. We suggest that the future restoration and hydrological management in peatlands should keep the water level below the threshold for CH_4 emission. Otherwise, the higher CH_4 emission after rewetting (Mahmood and Strack [2011](#page-8-0); Strack et al. [2014;](#page-8-0) Knox et al. [2015](#page-7-0); Christen et al. [2016](#page-7-0)) may balance out the reduced CO_2 emission as the radiative forcing of CH_4 is about 32–45 times more than $CO₂$ in a century on a mass basis (Neubauer and Megonigal [2015\)](#page-8-0). Alternatively, as only the saturated litter layer produces substantial $CH₄$ (Fig. [5\)](#page-5-0), the top litter layer above the threshold could be removed prior rewetting to reduce CH_4 emission at the beginning of rewetting. Removal of surface litter has been shown to reduce CH4 emissions by factors of 30–400 in a temperate rewetted

bog (Huth et al. 2020), and over 1000 times from rewetting former agricultural peatlands (Harpenslager et al. 2015).

The exceptionally high spatiotemporal variations, by several orders of magnitude, seriously limit the predictability of CH_4 emission from peatlands. Our studies suggest that the threshold of water level and the time lag of $CH₄$ production after rewetting or storm might be two keys to more precisely predicting and managing CH4 emission in peatlands. Only when the water levels are above the water-level threshold for a period of time can methanogens be fully reactivated from their dormancy, and the peatlands start emitting $CH₄$. Therefore, after the site-specific or peatland type-specific threshold of water level and the time lag for methanogens are identified, the rainfall amount, intensity, duration, and frequency, can be used to develop water management practices to determine whether and when the peatlands become $CH₄$ sources. Once the water level and time lag requirements are met, the magnitude of CH_4 emissions could be further explained by temperature, soil moisture, and substrate quality associated with plant communities, as well as organic and inorganic electron acceptors (Bridgham et al. 2013).

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Authors' Contributions HW and CJR designed and set up the field experiment. HW and MH collected and analyzed soil/gas samples, HW design and conduct the lab incubation. NF monitored water level in field. HW was a major contributor in writing the manuscript. All authors read and approved the final manuscript.

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Data Availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Code Availability Not applicable.

Declarations

Conflicts of Interest/Competing Interests The authors have no conflicts of interest.

Ethics Approval Not applicable.

Consent to Participate Not applicable.

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