



Wetland plant development overrides nitrogen effects on initial methane emissions after peat rewetting

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ABSTRACT

Growing productive wetland species on rewetted peatland (paludiculture) is a promising solution to offset carbon loss from drained peatlands. The inlet of nitrogen (N) rich surface water, a proposed method to improve productivity of vegetation, may affect methane (CH₄) emissions. This study aims to compare initial CH₄ emissions from newly rewetted peat with different types of vegetation and N loading simulating diffuse N inlet. Diffusive CH₄ emissions were measured in peat mesocosms during one growing season. Peat cores were either planted with *Typha latifolia* or *Phragmites australis* or they were left bare. Mesocosms received 0, 50, 150 or 450 kg ha⁻¹ year⁻¹ N. Plants affected CH₄ emissions from rewetted peat soil, leading to stable fluxes over time of 133 mg m⁻² day⁻¹ CH₄ at 20 °C. Biomass harvesting lead to a 153% increase of CH₄ emissions. With increasing N load, CH₄ emissions from mesocosms with *Typha* and *Phragmites* decreased up to a load of 150 kg ha⁻¹ N, but this was only significant for the *Phragmites* treatment. Emissions of unvegetated mesocosms increased with increasing N load but not significantly. In conclusion, our mesocosm study suggests that vegetation can reduce or prevent an increase in CH₄ emissions from rewetted peatlands compared to only rewetting, possibly due to an increased oxygenation of the sediments by macrophyte roots preventing excessive CH₄ formation, while added N does not provoke great changes in emissions at N concentrations up to 150 kg ha⁻¹.

1. Introduction

Rewetted peatlands are a net sink for carbon dioxide (CO₂), storing an estimated 400 kg ha⁻¹ year⁻¹ CO₂ (Günther et al., 2020). Their anoxic sediments lead to diminished nitrous oxide (N₂O) emissions but also to increased methane (CH₄) emissions, which are estimated at 250 kg ha⁻¹ year⁻¹ for rewetted peatlands (Günther et al., 2020; Tiemeyer et al., 2020). As CH₄ is 27 times more potent as a greenhouse gas than CO₂ on a 100-year time horizon, rewetted peat shows an initial net warming effect due to an initial spike in CH₄ emissions (Günther et al., 2020; IPCC et al., 2021). Paludiculture, the cultivation of crops on rewetted peatlands, can reduce many of the issues caused by drainage practices and is therefore currently seen as a promising solution to reduce greenhouse gas emissions whilst maintaining an agricultural,

productive system (e.g., Abel et al., 2013). Nonetheless, much remains unknown on how CH₄ emissions are affected when drained peatland is rewetted under different paludiculture practices, i.e. combined effects of aquatic nitrogen (N) and various wetland species (Kirschke et al., 2013).

Vegetation effects on CH₄ emissions from peatlands are dependent on the species selected (e.g., Noyce and Megonigal, 2021). *Typha* spp. and *Phragmites* spp. are prominent among 184 target species in paludiculture, natural wetlands and restoration projects. They are highly suitable for cultivation in wet environments due to their high productivity and various flooding adaptations (Abel et al., 2013), such as oxygen transport through aerenchyma to the anoxic root zone (radial oxygen loss or ROL; Matsui and Tsuchiya, 2006; Gong et al., 2020). This, however, directly and indirectly influences the GHG emissions from peatlands (Fig. 1). ROL facilitates CH₄ oxidation and diminishes

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methanogenesis, reducing emissions up to 17% (Jespersen et al., 1998; Dullo et al., 2017). Aerenchyma also enables transport of CH_4 up to the atmosphere, a process known as “shunt effect”, bypassing oxic layers and therefore CH_4 oxidation, potentially leading to increased emissions (Couwenberg and Fritz, 2012; Minke et al., 2016). The net effect of wetland species on CH_4 emissions remains under debate (Whiting and Chanton, 1993; Laanbroek, 2010; Turner et al., 2020).

To ensure vegetation productivity while making use of the nutrient filtering capacity of paludiculture, the inlet of N rich surface water, resulting from agricultural runoff, has been proposed (Vroom et al., 2022). However, N loading could affect CH_4 emissions from vegetated peat by boosting primary production, in turn reinforcing the shunt effect and ROL (Fig. 1; Juutinen et al., 2018). Indirectly, the increase in ROL could frustrate CH_4 production and emission due to increased redox potential, an oxic rhizosphere and eventually CH_4 oxidation (Fig. 1; Gong et al., 2020). Bodelier (2011) reports a threshold around $100 \text{ kg ha}^{-1} \text{ yr}^{-1} \text{ N}$, where CH_4 oxidation is stimulated at lower N concentrations and inhibited at higher concentrations. Other studies additionally highlight the complex interaction between plant coverage, N-form, N-concentration, experimental duration and N-uptake dynamics across different plant types and its consequences for microbial turnover of both CH_4 and soil N (Nykänen et al., 2002; Gong et al., 2020). At higher N loads, several processes affect the balance between methane production and methane oxidation: (1) NH_4^+ can stimulate nitrate (NO_3^-) reducing bacteria thereby indirectly decreasing rates of anaerobic CH_4 oxidation, (2) NH_4^+ is energetically preferred over CH_4 by CH_4 oxidizing bacteria thereby decreasing rates of anaerobic CH_4 oxidation, and (3) increased NO_3^- -concentrations maintain an increased redox potential, which stimulates CH_4 oxidation and decreases CH_4 production rates (Fig. 1; Bodelier and Laanbroek, 2004; Laanbroek, 2010; Bodelier, 2011; Zhu et al., 2012). This added N effect is exacerbated by the carbon fueling effect, as increased biomass production results in increased carbon substrate for methanogenesis.

With a mesocosm experiment, we aim to elucidate the effect of growing and harvesting productive wetland species in combination with additional N loading on net CH_4 emissions from peat soil directly after rewetting, when peak emissions are found (Günther et al., 2020). Specifically, we studied how CH_4 emissions are affected by *Typha latifolia* (broadleaf cattail) and *Phragmites australis* (common reed), where we hypothesize that their presence leads to increased CH_4 emissions as a function of biomass, due to a dominant shunt effect. In addition, we expect that biomass harvesting leads to a further increase in CH_4

emissions, as the plants need to rebuild their structure requiring rapid production, leading to an increased amount of photosynthates exuded by roots. For the effect of additional N loading, we hypothesize that CH_4 emissions increase with an increase of N-loading at low N conditions due to increased plant growth. At higher N concentrations, we expect further increased CH_4 emissions because CH_4 oxidation will be inhibited due to toxic compounds produced by denitrifying bacteria and because the shunt effect is expected to be dependent on vegetation biomass. In addition, we expect higher plant biomass of *T. latifolia* compared to *P. australis* with increasing N loads, since NH_4^+ can be toxic to *P. australis* (Tylová et al., 2008; Vroom et al., 2022). This may further magnify plant-mediated CH_4 emission in *T. latifolia* (plant species – N load interaction).

2. Methods

2.1. Mesocosms

The experiment was performed in the greenhouse facility at the Radboud University, The Netherlands, following the same experimental setup as Vroom et al. (2022). Peat cores were collected at two sites in the Netherlands using PVC pipes with a diameter of 15 cm and a length of 30 cm. The sod of each core was cut (5 cm) in order to remove the part of the soil with high labile carbon, which is common practice in paludiculture soil preparation as it is known to reduce CH_4 emissions (e.g., Harpenslager et al., 2015; Huth et al., 2020). The first site is a drained agricultural peat meadow in Zegveld ($52^\circ 08' \text{N}$, $4^\circ 50' \text{E}$), which has an average peat depth of 6 m and a soil pH of 5.6. This site is intensively managed with cattle grazing, liming and historic fertilization. Peat from this site will from now on be referred to as intensively managed, neutral soil (abbreviated as IN). The second site is a former agricultural peat meadow in Bûtefjild ($53^\circ 15' \text{N}$, $5^\circ 57' \text{E}$), which has an average peat depth of 1.5 m and a soil pH of 4.4. The relatively lower soil pH is the result of ceased liming 20 years ago. This site had been extensively managed with regular grazing of sheep, occasional mowing, but no artificial fertilization. Peat from this site will from now on be referred to as extensively managed, acid soil (abbreviated as EA). In total, 58 soil cores were taken, 46 from IN and 12 from EA.

The pipes with peat, from now on referred to as mesocosms, were placed in a water bath cooled to 14°C with an effective sediment temperature of $18\text{--}20^\circ \text{C}$ during the course of the experiment. The water temperature was kept constant at 14°C by a cryostat, and constant

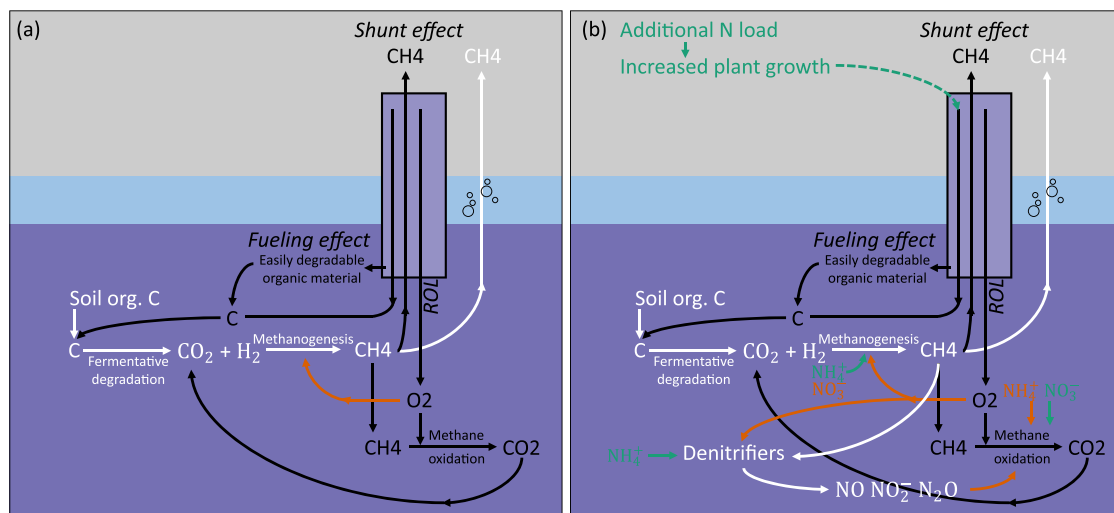


Fig. 1. Overview of methane (CH_4) production, oxidation and emission pathways (a) and the effects that additional N load may have of these mechanisms (b). White arrows identify mechanisms in rewetted, unvegetated peat. Black arrows identify mechanisms in rewetted, vegetated peat. Green arrows identify stimulating and red arrows identify inhibiting effects from nitrogen (N) on the carbon cycle that ultimately results to CO_2 and CH_4 emission. ROL stands for Radial Oxygen Loss. Chemical compounds: organic carbon (C), carbon dioxide (CO_2), hydrogen (H_2), ammonium (NH_4^+), nitrate (NO_3^-), nitric oxide (NO) and nitrous oxide (N_2O).

water levels were maintained by replacing evaporated water with demineralized water three times a week (ThermoFlex 1400, Thermo Fisher Scientific, Waltham, MA, USA). Mesocosms were placed in plastic bags that were open at the top to separate the mesocosms from the water bath. After five days of stabilization, N addition started (see below). To prevent K limitation, each mesocosm received 222 kg ha⁻¹ K by adding 5 mL 1 M KCl solution twice during the experiment. To rewet the soils, demineralized water was added to the mesocosms to create and maintain a surface water level up to 5 cm, depending on shoot length. Water tables were maintained 3–4 times per week.

Conditions at the greenhouse were kept similar to outside conditions throughout the length of the experiment, with an average relative humidity of 42.3% and average daytime temperature of 21.7 °C, 22.4 °C and 23.8 °C in March, April and May, respectively. Natural daylight was allowed into the greenhouse for 16 h per day with a minimum of 186 W m⁻², during dark day time conditions this was ensured by artificial grow lights.

2.2. Vegetation

The mesocosm experiment started on March, 8th 2016 and ran for three months. 10 weeks before the start of the experiment, *Typha latifolia* (from now on referred to as *Typha*) was raised from seeds that were collected alongside nutrient-rich ditches at EA. For *Phragmites australis* (from now on referred to as *Phragmites*), plants were grown from small rhizomes, which were grown in the greenhouse from seeds collected at EA. For the control treatment, the mesocosms were covered by a black canvas to prevent algae or plant growth. Non-viable plants were replaced by new ones during the first two weeks of the experiment. In each mesocosm designated to a vegetation treatment with plants, five *Typha* seedlings of 15–25 cm or five *Phragmites* plants were allocated after which all shoots were cut to a length of 5 cm above the peat to ensure comparable starting conditions. During the experiment, the shoot length of all plants in each mesocosm was measured every three to eight days. These lengths were averaged over separate shoots, resulting in one average height per mesocosm. At day 91 of the experiment, all above-ground plant biomass was harvested and 5 cores were taken per mesocosm using a soil corer with a diameter of 1 cm reaching the entire depth of the core (25 cm). Each core was thoroughly rinsed to retain the roots. All material was dried at 70 °C for 96 h and weighed.

2.3. Nitrogen loading

Four nitrogen (N) treatments were applied: 0, 50, 150 and 450 kg ha⁻¹ N. N was added to the surface water as a combination of ammonium nitrate (NH₄NO₃) and ammonium chloride (NH₄Cl) in a molar ratio of 1:1.5, as if N rich irrigation water was let in. The 0 kg ha⁻¹ N treatment acted as the control. The 50 kg ha⁻¹ N treatment was based on N concentrations found in surface waters close to EA (5 mg per liter). The 150 kg ha⁻¹ N treatment resembled a situation in which this surface water has a one-month retention time in the system. The 450 kg ha⁻¹ N treatment simulated an extreme situation similar to the N loads of constructed wetlands and corresponding removal rates (Land et al., 2016). One week after planting, N loads were added weekly for twelve weeks accumulating to 50, 150 and 450 kg ha⁻¹ N, respectively. This method mimicked the diffuse inlet of N from N rich surface water resulting from agricultural runoff or from N being released from N rich topsoil that is submerged.

2.4. Experimental design

The effect of vegetation type and soil type on short term CH₄ emissions was studied with a factorial design with three vegetation treatments (control, *Typha*, *Phragmites*) on both soil types (IN, EA) and a natural range of N concentrations (50 kg ha⁻¹ N). The effect of N loading and vegetation type on CH₄ emissions were only studied for the

IN soil using a factorial design with four N treatments (0, 50, 150, 450 kg ha⁻¹ N) and three vegetation treatments (control, *Typha*, *Phragmites*). This resulted in a fractional factorial design, with two soil types, three treatments for vegetation and four N loads. All treatments had four replicates except for the following treatments on IN soil: control with 0, 150 and 450 kg ha⁻¹ N had 2, 3 and 3 replicates, respectively, *Typha* with 0 kg ha⁻¹ N had 3 replicates and *Phragmites* with 150 kg ha⁻¹ N had 3 replicates (Appendix 1). This resulted in a total of 54 mesocosms (Appendix 1).

2.5. Chemical analyses

Both in IN and EA, peat cores with a length of 30 cm and 15 cm in diameter were taken at four sublocations. These were used to characterize the chemical composition of the soil. Each sample was homogenized. Salt extractions were done as described by Vroom et al. (2018) in order to determine loosely absorbed P and K. In addition, subsamples of fresh soil were dried at 70 °C for 48 h to determine the bulk density.

Surface water (day 0, 8, 36, 64, and 81) and pore water (day 2, 21, 41, 63, and 80) samples were taken at five times during the experiment. These were analysed following the approach described by Vroom et al. (2022) to determine NH₄⁺, NO₃⁻ and O₂ from surface water and total dissolved NH₄⁺, NO₃⁻, Fe and S from pore water.

2.6. Gas measurements

Methane (CH₄) fluxes were measured four times during the experiment. The first measurements (day 42) were done after the second pulse of applied N loading, whereas the other three measurements (day 69, 89 and 98) were done after the third pulse. We also measured N₂O on day 88 of the experiment. All measurements were carried out between 8 AM and 4 PM as described below, and the order was randomized to account for diurnal variability. Soil temperature at 5 cm depth was recorded regularly.

Gas measurements were carried out similarly to Vroom et al. (2018). A dark PVC chamber (15 cm inner diameter), equipped with a temperature logger (HOBO, Onset Computer Corporation, Bourne, MA, USA) and a battery-driven fan was sealed to each mesocosm consecutively. The chamber was linked to a greenhouse gas analyser through fine plastic tubing (0.4 cm inner diameter) via two gas-tight ports in a closed loop. When measuring CH₄ we used a Los Gatos Greenhouse Gas Analyzer (GGA-24EP, Los Gatos Research, Mountain View, CA, USA), and when measuring N₂O we used a Picarro G2508 Greenhouse Gas Analyzer (Picarro Inc., Santa Clara, CA, USA). Measurements usually lasted 180 seconds and included only diffusive fluxes: measurements were repeated if ebullition was observed. CH₄ and N₂O fluxes (mg m⁻² d⁻¹) were calculated according to Almeida et al. (2016).

2.7. Statistical analyses

We used repeated measures three-way ANOVAs to determine differences in CH₄ emission over time (3 levels) and between vegetation treatments (3 levels) and soil types (2 levels), with all three factors used as fixed effects and the mesocosm ID was used as random effect to indicate the repeated measures. A similar repeated measures ANOVA was performed to test the effect of biomass removal on CH₄ emissions, here with only 2 levels for the fixed effect time (before and after harvest). To test the effect of nitrogen loading on CH₄ emissions for IN soil, we used a two-way ANOVA with N load (4 levels) and vegetation treatment (3 levels) as independent variables. In addition, we only included emission data from the last measurements on these mesocosms (day 69 of the experiment) presumably showing the full effect of additional N load on CH₄ emissions.

We determined the relationship between CH₄ emissions and plant length using a linear model, where soil type, vegetation treatment, time and plant length were included as independent variables. Soil

differences in bulk density, P and K were determined using a two-way ANOVA, with location and sub-location included as independent variables. Last, we performed four three-way ANOVAs, with aboveground biomass production, belowground biomass production, N_2O fluxes and dissolved O_2 in surface water as the dependent variables per ANOVA, and vegetation treatment, N load and soil type as the independent variables for all ANOVAs.

Prior to all analyses, CH_4 emission fluxes were filtered, where we only included positive fluxes with an R^2 larger than 0.5. We also did a log10 transformation on the emission values in order to meet the assumptions of tests on outliers, normal distributions and sphericity. For all performed ANOVAs, when independent variables proved significant ($p < 0.05$) or marginally significant ($p < 0.1$), paired samples t-tests with Bonferroni correction were performed. For all analyses involving repeated measures, the results regarding time are based on within repeated measures results while other results (e.g. on vegetation treatment, N load, or soil) are based on between repeated measures results. All analyses were done in R (R Core Team, 2016) using the *rstatix* (Kassambara, 2020a) and *ggpubr* (Kassambara, 2020b) package.

3. Results

Soil characteristics at the start of the experiment differed between the two locations (Appendix 2). IN showed significantly higher P (1577 g m^{-2} ; $F(1,61) = 173.24$, $p < 0.001$), K (1989 g m^{-2} ; $F(1,61) = 684.88$, $p < 0.001$) and bulk density (783 g L^{-1} ; $F(1,61) = 49.24$, $p < 0.001$) compared to EA (899 g m^{-2} P, 366 g m^{-2} K, bulk density 704 g L^{-1}). Methane emissions from IN and EA with a loading of 50 kg ha^{-1} N ranged from 4 to $2014 \text{ mg m}^{-2} \text{ day}^{-1} CH_4$ and 1 to $160 \text{ mg m}^{-2} \text{ day}^{-1} CH_4$, respectively. Although the average IN methane emissions released almost four times as much CH_4 ($109 \pm 339 \text{ mg m}^{-2} \text{ day}^{-1} CH_4$; mean \pm sd) than EA ($28 \pm 37 \text{ mg m}^{-2} \text{ day}^{-1} CH_4$), soil type and its interaction with vegetation type were only marginally significant factors ($F(1,15) = 3.13$, $p = 0.10$ and $F(2,15) = 2.76$, $p = 0.10$; Fig. 2).

At the end of one growing season (on day 89 of the experiment), unvegetated peat emitted $425 \pm 785 \text{ mg m}^{-2} \text{ day}^{-1} CH_4$ (averaged over both soil types with 50 kg ha^{-1} N), whereas both *Typha* and *Phragmites* treatments (from now on referred to as the vegetated treatment) on average emitted $23 \pm 23 \text{ mg m}^{-2} \text{ day}^{-1} CH_4$ (averaged over both soil types). Contrasting to our hypothesis, CH_4 emissions did not differ between the three vegetation treatments at a N load of 50 kg ha^{-1} N, $F(2,15) = 0.28$, $p = 0.76$ (Fig. 2). The course of CH_4 emissions over time did differ between vegetation treatments, $F(4,33) = 4.53$, $p < 0.01$: in the absence of vegetation on IN soil, emissions increased significantly from $33 \pm 18 \text{ mg m}^{-2} \text{ day}^{-1} CH_4$ at day 42, to $50 \pm 43 \text{ mg m}^{-2} \text{ day}^{-1} CH_4$ at day 69, to $828 \pm 1028 \text{ mg m}^{-2} \text{ day}^{-1} CH_4$ at day 89 (Fig. 2; Appendix 3), while for all other soil type and vegetation type combinations CH_4 emissions did not change significantly over time.

CH_4 emissions increased after plants were harvested at day 98 of the experiment ($F(2,14) = 34.70$, $p < 0.001$; Fig. 3, Appendix 4). Soil type affected emissions marginally, with overall higher emissions from IN ($F(1,16) = 4.48$, $p = 0.05$; Fig. 3, Appendix 4). For all vegetated mesocosms from both soil types, CH_4 emissions increased on average with 153% after harvesting, which translates to $36 \text{ mg m}^{-2} \text{ day}^{-1} CH_4$. This increase was significant for all treatments except for *Phragmites* on IN peat, which showed only a marginally significant difference ($t(3) = -2.908$, $p < 0.1$). The treatment without vegetation did not show an increase in CH_4 emission for the same period (Appendix 4). Regarding the hypothesized relation between CH_4 emissions and plant morphology, CH_4 emissions were not related to dry weight for *Typha* nor for *Phragmites* ($F(1,14) = 0.06$, $p = 0.81$; Appendix 5), but CH_4 emissions were negatively related to plant length for both species ($F(2,16) = 7.632$, $p < 0.01$; Appendix 5).

Considering multiple levels of N loading (0, 50 150 and 450 kg ha^{-1} N) the type of vegetation affected CH_4 emissions, $F(2,30) = 10.88$, $p < 0.001$: *Typha* had lower emissions ($29 \pm 49 \text{ mg m}^{-2} \text{ day}^{-1} CH_4$)

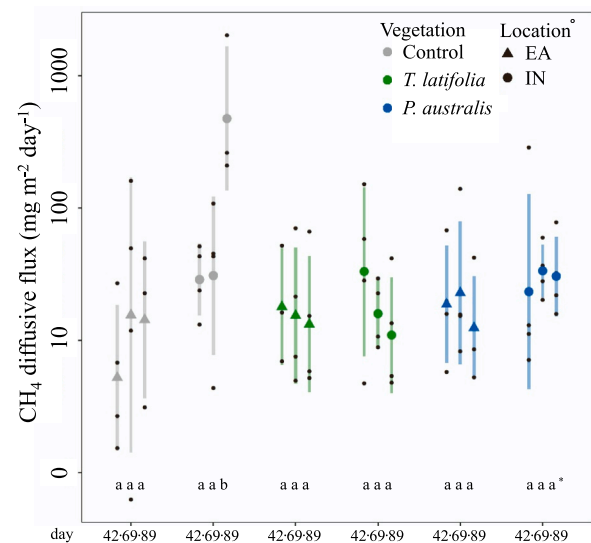


Fig. 2. Methane (CH_4) emissions (with logarithmic transformation) over time (day 42, day 69, day 89) of two soil types (EA, IN) and three vegetation treatments (Control (bare peat), *Typha*, *Phragmites*) with a N load of 50 kg ha^{-1} N. Black dots represent different mesocosms (replicates), colored symbols identify the mean emission of these replicates per vegetation-soil treatment combination, and colored vertical lines represent the standard deviation of those replicates. The three consecutive bars per treatment represent the three different time steps, where from left to right they represent CH_4 emissions on day 42, 69 and 89 of the experiment. Significant differences are indicated with symbols: * when $p < 0.05$ and ° when $p < 0.10$. Letters indicate differences between measurements within the same treatment. Please note that fluxes with an $R^2 < 0.5$ were removed, possibly resulting in fewer datapoints per soil-vegetation-time combination shown in this figure compared to the indication in Appendix 1.

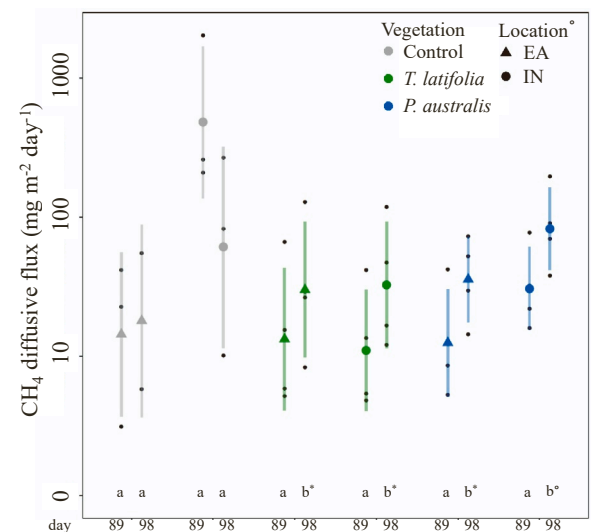


Fig. 3. Shoot biomass harvesting effects on methane (CH_4) emissions on a logarithmic scale over time of two soil types (EA, IN) and three vegetation treatments (Control (bare peat), *Typha*, *Phragmites*) with a N load of 50 kg ha^{-1} N. Points represent different mesocosms (replicates), colored symbols identify the mean emission of similar treatments, and colored vertical lines represent the standard deviation. The two consecutive bars per treatment represent the two different time steps, where the left and the right represent CH_4 emissions on day 89 and 98 of the experiment, respectively. The vertical dashed line represents the harvesting event on day 91. Significant differences are indicated with symbols: * when $p < 0.05$ and ° when $p < 0.10$. Letters indicate differences between measurements within the same treatment.

compared to unvegetated peat ($191 \pm 212 \text{ mg m}^{-2} \text{ day}^{-1} \text{ CH}_4$) and *Phragmites* ($83 \pm 103 \text{ mg m}^{-2} \text{ day}^{-1} \text{ CH}_4$). The addition of different levels of N affected plant treatments marginally different, $F(6,30) = 2.38$, $p = 0.05$. Specifically, *Phragmites* showed a decrease in emissions between 0 and $150 \text{ kg ha}^{-1} \text{ N}$ (Fig. 4; Appendix 6).

Nitrogen loading also affected the emission of nitrous oxide on day 83 (the only day when nitrous oxide was measured, Appendix 7). For each vegetation treatment, the highest emissions were found at $450 \text{ kg ha}^{-1} \text{ N}$. This N effect increasing nitrous oxide emissions was in turn reduced by wetland plants that also reduced nitrogen concentrations in pore water and surface water (Appendix 8). Additionally, N increased aboveground biomass, but this was only significant for *Phragmites* (Appendix 9). Belowground biomass also increased marginally significantly for *Phragmites* for a N load of $50\text{--}150 \text{ kg ha}^{-1} \text{ N}$ (Appendix 10). Furthermore, ammonium in pore water and surface water was lower for both vegetated treatments compared to the bare, unvegetated treatment (Appendix 8). Iron (Fe) concentrations in the mesocosms with *Typha* appear lower compared to *Phragmites*, which is again lower compared to bare, unvegetated peat (Appendix 8). Sulphate remained present in the porewater during the course of the experiment (Appendix 8). Ammonium concentration in pore water and surface water also increased with increasing additional N load for the unvegetated treatment, and only appeared higher at $450 \text{ kg ha}^{-1} \text{ N}$ for vegetated treatments (Appendix 8). Overall, with an additional N load of $450 \text{ kg ha}^{-1} \text{ N}$, the ammonium and nitrate concentration in the pore water and surface water was much higher compared to the other N load treatments (Appendix 8).

4. Discussion

Rewetting drained peatlands has been proposed as a climate mitigating method. However, the effects of vegetation and additional N on methane (CH_4) emissions are varying between different studies (e.g., Bhullar et al., 2014; Noyce and Megonigal, 2021). To improve our understanding of these two factors, we specifically tested the effect of

growing and harvesting productive wetland species, the effect of additional N loading, and their interaction on net CH_4 emission from newly rewetted peat soil for a period of three months. Mean CH_4 emissions from this current mesocosm study ($133 \text{ mg m}^{-2} \text{ day}^{-1} \text{ CH}_4$) are similar to field fluxes from rewetted peatlands in temperate climates (Günther et al., 2020; Tiemeyer et al., 2020) when extrapolating fluxes assuming an Arrhenius-type temperature relationship with a Q10 of 2. Compared to unvegetated peat, the presence of *Typha* and *Phragmites* resulted in persistent low CH_4 emissions while plant harvesting increased CH_4 emissions. With increasing N load, CH_4 emissions from bare, unvegetated mesocosms did not change while emissions from vegetated mesocosms decreased, but this was only significant for *Phragmites* and up to a N load of 150 kg ha^{-1} .

4.1. Stabilization of low CH_4 emissions from vegetated peat

The general understanding of rewetted peat soil is that the presence of graminoids increases CH_4 release into the atmosphere (e.g., Couwenberg and Fritz, 2012), due to the shunt effect of aerenchyma tissue that provide a faster plant-mediated transport of CH_4 from the sediment (Jørgensen et al., 2012; Wang et al., 2013). Contrastingly, our study results showed CH_4 emissions to be constant when peat was vegetated, while CH_4 emissions of bare soil seemed to increase over time, though not significantly. This may be a result of our method, as we focused on diffusion and not ebullition, possibly leading to a substantial underestimation of the total CH_4 emissions, especially for the bare, unvegetated peat after rewetting. Additionally, this study only looked at vegetation growing for three months, after which the emissions may change due to plant biomass dependency of this process: more shoots increase the shunt effect consequently increasing CH_4 emission (Whiting and Chanton, 1993; Couwenberg and Fritz, 2012), although there are studies that report no effect or even a negative effect of plant biomass on CH_4 emissions (Bhullar et al., 2014, 2013; Koelbener et al., 2010; Korrensalo et al., 2022). In addition, plant material will result in litter deposition in the water (fueling effect), which increases the amount of degradable organic matter sourcing methanogenesis (Ström et al., 2005).

As CH_4 emissions for increased plant biomass are reasoned to result from increased root exudates and an increased shunt effect, increased ROL is a likely possibility that could explain the lack of effect of plant biomass on CH_4 emissions (Jørgensen et al., 2012). This was also suggested by Bhullar et al. (2013), who found that plant productivity positively correlated to microbial respiration and negatively to CH_4 production. To test the specific role of ROL, in-situ quantification is required but this is costly and could not be performed in this experiment. Instead, we used water oxygen levels in the surface water and the fate of iron and sulphate in the pore water of as an indicator of ROL. We found elevated oxygen levels compared to bare soils, likely due to the presence of adventitious roots in the surface water, but no direct relationship between root biomass and surface water oxygen levels nor between vegetation treatment and surface water oxygen levels was found (Appendix 11). The balance between the rhizosphere oxygenation effect (triggered by ROL) and transport effects might have shifted during the course of the experiment before harvesting. The first emission measurements were performed when plant root biomass was small, assuming a more-or-less constant root:shoot biomass ratio over the course of the experiment. In case plant-mediated transport would have been the main route for CH_4 release, higher emissions would have been observed in treatments with higher biomass, found in treatments with a N load of 150 and $450 \text{ kg ha}^{-1} \text{ N}$. In addition, CH_4 production could still be suppressed by small, but effective ROL. Nonetheless, given our results, the effect of increased oxygen loss in the anoxic peat layers, thereby reducing methanogenesis and promoting CH_4 oxidation, is dominant over the presumed increase in CH_4 production due to the increase of carbon root exudates. This hypothesis of the dominance of ROL effects over methanogenesis fueled by plant-released carbon and the shunt effect, is additionally supported by the increased CH_4 release we

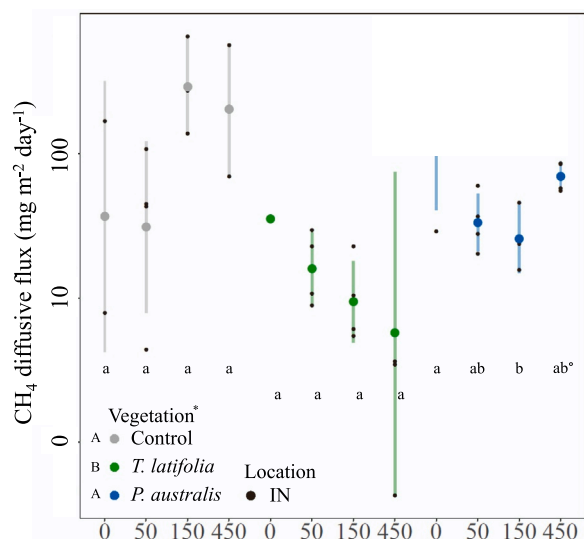


Fig. 4. Methane (CH_4) emissions on a logarithmic scale over four different N loads (0, 50, 150 and $450 \text{ kg ha}^{-1} \text{ N}$) at day 69 of one soil type (IN) and three vegetation treatments (Control (bare peat), *Typha*, *Phragmites*). Points represent different mesocosms (replicates), colored symbols identify the mean emission of similar treatments, and colored vertical lines represent the standard deviation. Significant differences are indicated with symbols: * when $p < 0.05$ and ° when $p < 0.10$. Letters indicate differences between measurements within the same treatment (lowercase) or between species (uppercase). Note that the symbol for *Typha* at N = 0 is the average of three measurements that have very similar CH_4 emissions.

found after harvesting the aboveground biomass and by the overall high concentrations of oxidized redox species such as nitrate and sulphate (Appendix 9, 10).

Theoretically, cutting plants will directly reduce the oxygen transport into the root zone leading to decreased CH₄ oxidation and thus increased emissions (Brix et al., 1992; Minke et al., 2016). But, simultaneously, harvesting biomass directly reduces the labile carbon pool leading to decreased emissions (Hahn-Schöfl et al., 2011). Since effects of biomass harvesting on CH₄ emissions at a short-term and long-term effects have been found and not found (Günther et al., 2015; Johnson et al., 2021), further research is required to get a more comprehensive understanding of the harvest of productive wetland species. This is a fundamental step when converting agricultural peatlands into paludiculture systems is thought to reduce GHG emissions, where harvested carbon should not be forgotten in the carbon balance.

There are three other reasons for finding constant CH₄ emissions on vegetated peat while the opposite was hypothesized. First, the plants were still young resulting in less established root systems and small shunt effects. Second, extrapolations from planted mesocosms to field conditions may require some modulation given the container walls influencing rooting patterns, and with that oxidation of deeper peat layers and full mixing of added nitrogen into the peat. Third, the mesocosms were rewetted with rainwater free of relevant concentrations of organic or inorganic carbon. Our findings need further testing in environments that are exposed to high organic carbon inputs as carbon loading may stimulate CH₄ release in both peatland mesocosms (Wang et al., 2013; Harpenslager et al., 2015; Zak et al., 2017; Huth et al., 2020) and constructed wetlands (Wang et al., 2013). In addition, an experiment with extended temporal replication in addition to mesocosm replicates could improve interpretability of our findings and link emissions to more specific biological and/or biochemical mechanisms in order to improve long-term carbon balance models (Xu et al., 2016).

4.2. Variable effects of nitrogen loading on CH₄ emissions

The general understanding of 'higher productivity, higher CH₄ emissions' could also be interpreted in terms of higher N load available to plants, for example in rice-planted wetlands (Banger et al., 2012; Liu and Greaver, 2009). As expected, we found an increase in plant biomass with increased N loading (Appendix 8, 9). For N₂O we also found an increasing effect of N loading on N₂O emissions. These results should not be extrapolated as they are limited to one measurement campaign only, although few measurements may be sufficient to draw a solid conclusion (Hahn-Schöfl et al., 2011) and our results reproduce well the results of Vroom et al. (2018). Unexpectedly, we did not find the pronounced nitrogen effect of increasing CH₄ emissions that other studies have found before (e.g., Vroom et al., 2018; Wu et al., 2022). However, we have not tested the effect of additional carbon or additional organic N, and since water levels in paludiculture fields are often maintained using effluent water which is high in both N and C, this may be of great concern and further research should be done.

Considering the lower end of the additional N load gradient from this study (0–150 kg ha⁻¹ N), we did find a decreasing trend of CH₄ emissions with increasing N load for vegetated mesocosms. A suppressing effect of N on CH₄ emissions has been described for non-wetland soils (Aronson and Helliiker, 2010). Here, nitrogen stimulated plant growth and thereby may have reduced CH₄ emissions as we have found an overall reducing effect of vegetation on CH₄ emission. This indirect effect of biomass may have been exacerbated by high nitrate (NO₃⁻) concentrations increasing the redox potential thereby preventing CH₄ production and stimulating CH₄ oxidation, over the stimulation effect of NH₄⁺ on CH₄ production (Laanbroek, 2010; Bodelier and Laanbroek, 2004; Zhu et al., 2012). We indeed found elevated NO₃⁻ concentrations in all treatments, where unvegetated treatments showed lower NO₃⁻ in the porewater in first 40 days compared to vegetated treatments, which suggests limited diffusion from the surface water or consumption by

reduction processes (Appendix 8). In contrast, for vegetated mesocosms, nitrogen concentrations decreased over time in both pore water and surface water, suggesting that plants take up the nutrient for growth (Appendix 8). Therefore, added nitrogen may no longer influence redox potential while plant growth may increase ROL which may lead to root-mediated oxidation of ammonium and consequently denitrification (Laanbroek, 2010; Veraart et al., 2014). In addition, ROL may reduce CH₄ emissions via lowered production and increased oxidation. This reasoning is further supported by the difference in CH₄ emissions from *Typha* and *Phragmites* to increased N load. We found that *Typha* decreased emissions further than *Phragmites* (where the decrease was not significant). Also root biomass was higher, nitrogen concentration in pore water and surface water was lower, and iron in pore water decreased (where demobilization of oxidized Fe is extra evidence for ROL) in mesocosms with *Typha* compared to mesocosms with *Phragmites* (Appendix 9, 10). This suggests that species composition can modulate responses of rewetted peatlands in terms of CH₄ emissions, as has been suggested by other studies (e.g., Bhullar et al., 2014; Noyce and Megonigal, 2021). To extrapolate mesocosm emissions to field scale emissions, natural colonization of rewetted peatlands by wetland vegetation (e.g., helophytes or submerged macrophytes), as well as the proportion of unvegetated 'open water' parts need to be taken into account.

Under extremely high N load, this study still did not find a significant increase in CH₄ emission, though multiple studies have reported a turnover point where vegetated peat increased CH₄ emissions (Nykänen et al., 2002; Aronson and Helliiker, 2010). As Noyce and Megonigal (2021) suggest, a combination of mechanisms leads to net CH₄ emissions, where they specifically point to the proportion of CH₄ that is oxidized and the amount of carbon that is available for methanogenesis. We found highly increased concentrations of ammonium in both surface and pore water, which may lower the redox potential thereby improving conditions for CH₄ production and inhibiting CH₄ oxidation (Appendix 8). In addition, increased ammonium concentrations (Appendix 8, 11) may lead to competition for oxygen reducing potential rates of methane oxidation (De Visscher et al., 1998), while nitrification products including N₂O might be even limiting CH₄ oxidizing bacteria (Dunfield and Knowles, 1995; Appendix 8). Lund et al. (2009) also found this effect and hinted to the importance of considering N₂O when looking at the effect of N load on GHG emissions, as plants may no longer inhibit CH₄ release and N₂O may become a more prominent GHG emitted from the rewetted peat (Liu et al., 2019; Wu et al., 2022). Furthermore, when CH₄ is converted to CO₂ by oxidation, slightly higher CO₂ emissions can be expected in case the extra CO₂ leaves the plant before taken up by photosynthesis (Raghoebarsing et al., 2005; Faußer et al., 2016).

5. Conclusions

Growing productive wetland species had the ability to stabilize low to intermediate methane emissions from rewetted peat soils compared to merely flooding the soil. Since the shunt effect appeared to be less prominent in this three months experiment than the potential effects of root oxygenation, the prevention of excessive methane formation could even lead to a reduction in CH₄ emissions. This plant effect seemed to be slightly higher for *Phragmites* but the species-specific reduction potential may become more prominent in a different context, e.g. with different carbon and nutrient loadings. Nevertheless, without additional carbon, the increased N loads simulating diffuse N inlet from N rich surface water or released from N rich topsoil after rewetting did not change CH₄ emissions. We even found hints where small to medium increases of N can help decrease CH₄ emissions when plants are present. The risk for higher CH₄ emissions increases at the highest N load (450 kg ha⁻¹ N). To control CH₄ emissions from rewetted peatlands, it is important to promote site management for dense vegetation of flood tolerant wetland species, like *Typha* or *Phragmites*. Additionally, the influx of N rich water with concentrations up to 150 kg ha⁻¹ could promote *Typha* and *Phragmites* growth without adverse climate effects due to CH₄ emissions.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.aquabot.2022.103598](https://doi.org/10.1016/j.aquabot.2022.103598).

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