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Removing 10 cm of degraded peat mitigates unwanted effects of peatland rewetting: a mesocosm study

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Abstract Topsoil removal (TSR) is a management option performed before rewetting drained agricultural peatlands to reduce greenhouse gas (GHG) emissions and remove nutrients. Currently, its common practice to remove 30 to 60 cm of topsoil, which is labor-intensive, costly, and highly disruptive. However, optimal TSR depth for mitigating carbon emissions from rewetted peat soils has neither been determined nor linked to soil biogeochemical factors driving carbon emissions. We performed two mesocosm experiments to address this. In experiment 1, we removed the topsoil of two contrasting drained peat soils before rewetting (i.e., extensively managed, acid peat *and* intensively managed, near-neutral peat) with a 5 cm interval up to 25 cm TSR. In experiment 2, we combined TSR with the presence and absence of *Typha latifolia* on intensively managed, near-neutral peat soil. The experiments ran for 22 and three months, respectively, in which we measured carbon dioxide (CO_2) and methane (CH_4) emissions and porewater chemistry. Our experiments reveal that (i) 5 cm TSR greatly reduced CH_4 and CO_2 emissions irrespective of peat nutrient status during the 22-month experiment, and (ii) the presence of *T. latifolia* further reduced CH_4 emissions during the 3-month experiment. Specifically, CH_4 emissions

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were six to 10-times lower with 5 cm TSR compared to 0 cm TSR. Peak CH_4 emissions occurred after three months with 0 cm TSR and strongly decreased thereafter. Random forest analyses highlighted that variation in CH_4 emissions could mainly be explained by cumulative root biomass and porewater alkalinity. Furthermore, 5 cm TSR reduced porewater values of pH, alkalinity, CH_4, and ammonium. The effectiveness of TSR in preventing the build-up of phosphorus, iron, and sulfur in porewater was site-specific. Our results show that only 5 to 10 cm TSR may already effectively prevent the adverse effects of rewetting former agriculturally peatlands by reducing undesirable CH_4 emissions and avoiding nutrient release. Further, we argue that target setting and site-specific assessments are crucial to optimize the amount of TSR to reduce carbon emissions while minimizing disturbance and costs.

Keywords Greenhouse gas emissions · Paludiculture · Climate mitigation · Topsoil removal · *Typha* · Nutrients

Introduction

Although peatlands cover only 3% of the global land area, they store 30% of global soil carbon (Yu 2012; Leifeld and Menichetti 2018; Chaudhary et al. 2020). Historical drainage for agriculture or peat extraction has turned large areas of peatlands into carbon sources, accounting for 5% of the global anthropogenic carbon dioxide (CO_2) emissions (Cobb et al. 2017; Chaudhary et al. 2020; IPCC 2021). To mitigate carbon emissions from peatlands and restore their function as carbon sinks worldwide, peatland rewetting is proposed as an important measure (IPCC 2021; Evans et al. 2021; Temmink et al. 2022). While increasing water levels in drained peatlands reduces CO_2 emissions, it is known to stimulate methane (CH_4) emissions (Evans et al. 2021). In the long-term, however, rewetting degraded peat benefits the climate despite CH_4 emissions (Günther et al. 2020).

In natural peat soils, a high-water table leads to anoxic conditions due to continued oxygen (O_2) consumption and near-absent O_2 intrusion (Laanbroek 1990; Rydin and Jeglum 2013; Conrad 2020). Rewetting of peat results in rapid depletion of O_2 availability and initiates the reduction of alternative electron acceptors, preferentially in the sequence of nitrate, manganese, ferric iron, and sulfate before CH_4 production starts (Glaser and Chanton 2009; Rydin and Jeglum 2013; Conrad 2020). CH_4 production is mainly substrate-limited (Segers 1998; Drake et al. 2009), and pathways of CH_4 production in peatlands are primarily the reduction of acetate (more than 70%) and CO_2 (Smolders et al. 2002; Artz 2009). Therefore, CH_4 production is suppressed as long as concentrations of methanogenic substrates (e.g., H_2, acetate) are limited by the presence of alternative electron acceptors (Estop-Aragonés and Blodau 2012; Conrad 2020). Rewetting often leads to a shift from drainage-based CO_2-emissions to CH_4-dominated emissions (Wilson et al. 2016a; Renou-Wilson et al. 2019; McNicol et al. 2020).

Topsoil removal (TSR) has recently been shown as an effective measure to reduce greenhouse gas (GHG) emissions prior to rewetting drained and agriculturally used peatlands (Harpenslager et al. 2015; Huth et al. 2020). TSR affects GHG emissions through two main pathways. First, the high labile carbon content in the topsoil (e.g., shoots, roots, and humic soil) is largely removed with TSR, which prevents the rapid decomposition of the peat and subsequent release of CO_2 (aerobic) or CH_4 (anaerobic) to the atmosphere (Segers 1998; Drake et al. 2009; Conrad 2020). Second, TSR removes high nutrient concentrations in the topsoil that have accumulated during agricultural use, which reduces CH_4 emissions by limiting production and favoring oxidation, both directly and indirectly via microbial activity (Schrier-Uijl et al. 2011; Medvedeff et al. 2014; Nijman et al. 2022). However, the nutrient concentrations at different depths and, thus, the amount of topsoil to be removed are still difficult to predict. As such, the application of TSR strongly depends on the land-use history (e.g., type of agriculture, fertilization) and would be most suitable on agriculturally used peat rather than on peat extraction sites. The latter is an extreme form of TSR from natural peatlands in which large amounts of peat are removed, resulting in a high carbon footprint and environmental impacts (Graf and Rochefort 2016). For post-extraction peatlands, the active restoration technique applied in Canada – moss layer transfer – reduces carbon emissions and the time needed for the rewetted peatland to become a carbon sink (Graf and Rochefort 2016; Nugent et al. 2019).

Since it is currently unknown which layers still include labile carbon and higher nutrient concentrations, the standard practice of TSR for peatland restoration or paludiculture (i.e., the cultivation of crops on wet or rewetted peatlands), is to remove 30 to 60 cm (Allison and Ausden 2004; Harpenslager et al. 2015; Gaudig et al. 2017; Huth et al. 2020). Most of the material can be used to fill in ditches, thereby preventing CH_4 point sources (Cooper et al. 2014; Köhn et al. 2021). In the case of paludiculture, the removed topsoil is frequently applied next to the field to raise the soil level, allowing heavy mowing machinery to work around the waterlogged fields (e.g., Gaudig et al. 2017). Besides causing a substantial alteration to the environment, TSR is a costly practice and may thus put a large constraint on the applicability of this technique to restore peatlands on a large scale (Klimkowska et al. 2010; Zak et al. 2018; Convention on Wetlands 2021). Therefore, more understanding is needed for optimal removal depths to minimize environmental impacts and reduce costs. Moreover, factors controlling CH_4 emissions in peatlands are not fully known (Fenner et al. 2011), such as the role of vegetation (Yavitt and Knapp 1998; Fritz et al. 2011; Agethen et al. 2018). For instance, *Typha* has been reported to reduce CH_4 emissions due to increased oxidation in the root zone, but also to increase CH_4 emission via direct transportation to the atmosphere by roots (i.e., the shunt effect) and the provision of labile organic substrate (Lawrence et al. 2017; Vroom et al. 2018). The discrepancy based on vascular plants may come from varying transport mechanisms and growth stages (Vroom et al. 2022a) or the duration of the experiment and, thus, the amount of lateral carbon input (Geurts and Fritz 2018).

To unravel the contribution of different soil layers and the presence of vascular plants to GHG emissions, we performed two mesocosm experiments where we rewetted agricultural-used drained peat. In the first experiment, we removed topsoil from 5 cm up to 25 cm. The second experiment focused on the effect of vegetation coupled with TSR on GHG fluxes. We selected *Typha latifolia* as model species, as it is a common wetland and paludiculture species. With these experiments, we aimed to address the following research questions for agriculturally used and formerly drained peat:

1. What is the mitigation potential of minimal TSR (i.e., compared to the standard practice) and the presence of *T. latifolia* on the GHG emission of rewetted peat?
2. How is the nutrient availability of rewetted peat affected by minimal TSR and the presence of *T. latifolia*?
3. What are the main drivers of CH_4 emissions from rewetted peat?

Our hypotheses are: (1) we expect higher CH_4 emission in the 0 cm TSR treatment due to the higher availability of labile carbon and nutrients. In addition, we expect higher CH_4 emissions in the presence of *T. latifolia* due to the increased transportation of CH_4 from the soil to the atmosphere (shunt effect). (2) We expect reduced nutrient concentrations with TSR due to direct nutrient removal. In addition, we expect lower nutrient concentrations with the presence of *T. latifolia* due to plant uptake. (3) We expect the labile carbon to be the biggest driver of CH_4 emissions from rewetted peat soils by limiting or supporting methanogenesis.

Materials and methods

Sampling

At two sites in the Netherlands, 72 peat soil cores with a depth of 30 cm were taken using 15 cm diameter PVC-pipes (Vroom et al. 2022b). The first site is an extensively managed agricultural peat meadow in Bûtefjild (coordinates: 53°15’N, 5°57’E), which has acid peat, and it will be referred to as EA (i.e., extensively managed and acid peat) (Table 1); 24 cores were extracted from this site. The second site is a drained, intensively managed agricultural peat meadow in Zegveld (coordinates: 52°08’N, 4°50’E), which has near-neutral peat, and it will be referred to as IN (i.e., intensively managed and near-neutral peat) (Table 1); 48 cores were extracted from this site. We sampled these contrasting sites to assess the site and history influence on GHG fluxes and nutrient removal (i.e., different agricultural history, nutrient availability, and pH). These cores were used for two separate experiments. For experiment 1, both peat types were investigated, while for

Table 1 Soil characteristics of the collected peat types averaged over the entire depth (0–30 cm). Values represent average ± standard error ($n = 4$). Source: Vroom et al. (2022b), atmospheric deposition from TNO (2020)

Peat type	Intensively managed, near-neutral soil (IN)	Extensively managed, acid soil (EA)
Location	Zegveld	Bûtefjild
Composition	Fen	Bog
Agricultural history	Actively fertilized, grazed by cattle, limed	Artificial fertilization and liming ceased 1995, grazed by sheep and grass-cutting occasionally
Atmospheric nitrogen deposition (kg N ha^{-1} yr^{-1})	24–30	18–24
Peat depth (m)	6	1.5
H_2O-pH	5.57 ± 0.05	4.36 ± 0.24
C:N (g g^{-1})	11.16 ± 0.14	18.15 ± 0.88
C (%)	20.2 ± 0.8	19.9 ± 2.9
Organic matter (%)	44.5 ± 1.8	48.6 ± 5.7
Wet bulk density (g L^{-1})	790 ± 16.5	948 ± 22.5
Dry bulk density (g L^{-1})	314 ± 12.4	448 ± 29.3
Total nitrogen (mmol L^{-1})	405 ± 10.9	348 ± 38.7
Total potassium (mmol L^{-1})	20.3 ± 1.64	5.04 ± 0.52
Total phosphorus (mmol L^{-1})	20.4 ± 1.3	15.4 ± 1.3

experiment 2, only IN peat was used due to logistical constraits.

Experiment 1: topsoil removal every 5 cm

In the first experiment, we investigated the effects of TSR on GHG emissions and nutrient availability by removing the topsoil of the collected peat cores at 5 cm intervals up to 25 cm, resulting in six different TSR depths (Fig. 1 A). In the 0 cm TSR, only the aboveground grass biomass was removed. The experiment was performed using four replicates distributed randomly in a dark climate chamber of the Radboud University in the Netherlands with an air temperature of 15 °C and relative humidity of 70%. The peat cores were placed in slightly larger cylinders and inundated with 5 cm of demineralized water (average ± standard deviation of pH: 6.5 ± 0.1). The water level was kept constant throughout the experiment by the regular addition of demineralized water. In total, we used 48 cores for this experiment (four replicates for each of the twelve TSR-site combinations). The experiment ran for 22 months, from March 2016 until December 2017.

Experiment 2: interaction between topsoil removal and presence of *T. latifolia*

In the second experiment, we investigated the effects of TSR coupled with the presence of *T. latifolia*, a typical paludiculture and wetland species, on CH_4 emissions and nutrient availability. Only IN soil was used due to logistical constraints to use multiple soils, since the vegetated experiment required more space. We created three TSR depths (0, 5, and 15 cm) in the presence and absence of *T. latifolia* (Fig. 1B). In contrast to experiment 1, in the 0 cm TSR the aboveground grass biomass was not trimmed back. The cores were placed in a temperature-controlled water bath at 14 °C in the Radboud University greenhouse facilities after they were closed at the bottom with a PVC cap and placed in a plastic bag (open at the top). The temperature was slightly lower than in the previous experiment because the water needed extra cooling to compensate for incoming radiation and higher air temperature in the greenhouse. Each core was inundated up to the peat surface using rainwater. For each TSR treatment, five cores were planted with three *T. latifolia* seedlings (±5 cm each) (on day 0; total $n = 15$). Seedlings were raised in the greenhouse from seeds collected at Deurnese Peel

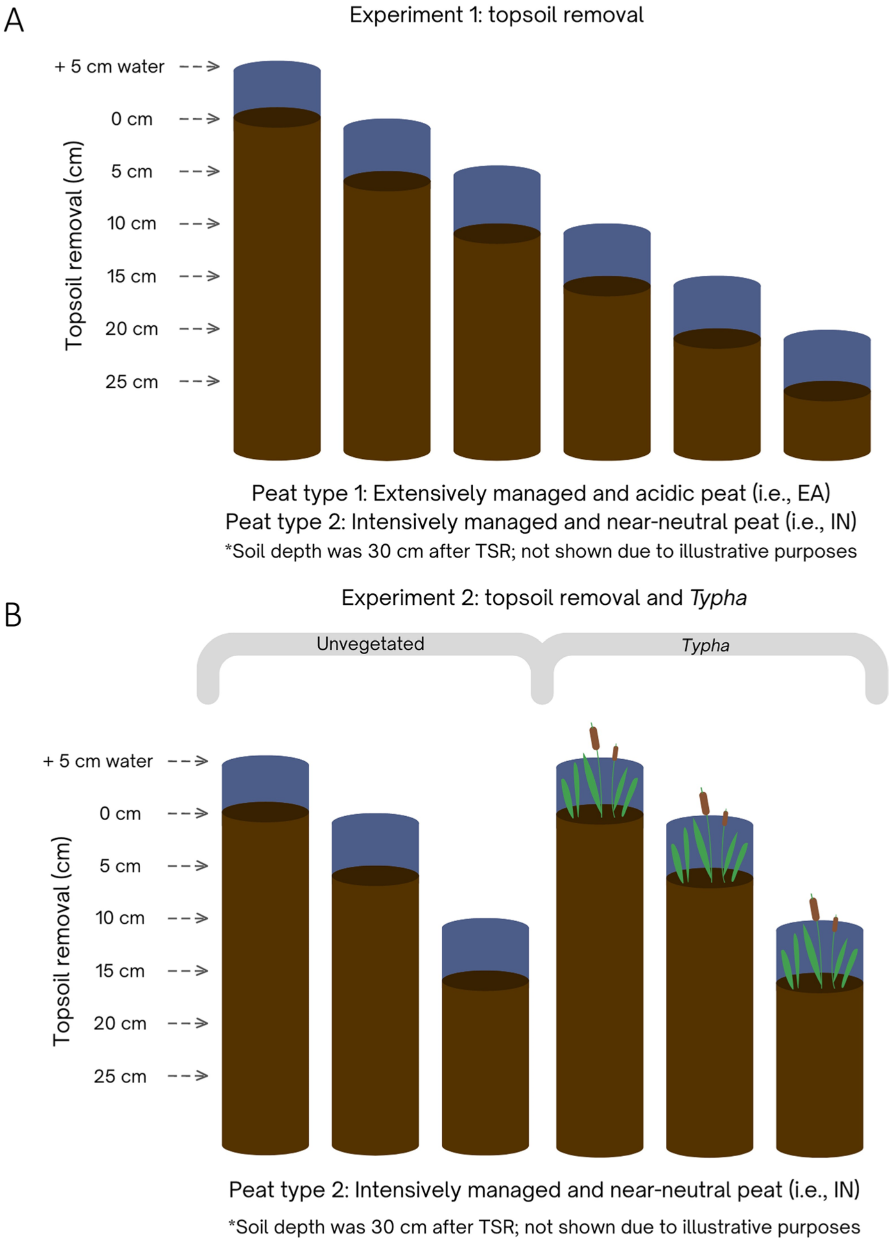


Fig. 1 Overview of the experimental setup of experiments 1 (**A**) and 2 (**B**). The soil depth of all cores was 30 cm after topsoil removal (TSR).

in the Netherlands (coordinates: 51°25’N, 5°52’E). Three cores per TSR treatment were not vegetated and served as controls (total $n = 9$). The unvegetated cores were covered by a polypropylene ground cover mesh to avoid algae growth. For brevity, the treatments with *T. latifolia* are called ‘*Typha*’, and unvegetated controls are called ‘unvegetated’, hereafter. Twelve days after planting the seedlings, the water table in all cores was raised to 5 cm above the peat surface and kept steady throughout the experiment by the regular addition of rainwater. This experiment was supplied with rainwater instead of demineralized water because it was not available in sufficient amounts at the greenhouse (i.e., to water the plants). In total, there were 24 cores for this experiment (five *Typha* replicates and three control replicates for each of the three TSR treatments). The experiment ran for three months, from April to June 2018.

Measurements

CH_4 and CO_2 fluxes were measured six times during experiment 1 (months 1, 2, 3, 10, 19, and 22) and three times during experiment 2 (months 1, 2, and 3). Gas measurements were carried out using a dark PVC chamber (15 cm inner diameter), which was connected to a Los Gatos Greenhouse Gas Analyzer (GGA-24EP, Los Gatos Research, Mountain View, CA, USA) for experiment 1 and to an Ultraportable Greenhouse Gas Analyzer (UGGA-30EP, Los Gatos Research, Mountain View, CA, USA) for experiment 2. For experiment 2, the chambers enclosed the plants. A battery-driven fan allowed constant airflow in the chamber. The measurements lasted for 180 s and were repeated if ebullition was observed (i.e., in case of an abrupt increase in gas concentration). The air temperature was logged using a HOBO logger (Onset Computer Corporation, Bourne, MA, USA). CH_4 and CO_2 fluxes (mg m^{-2} d^{-1}) were calculated following Almeida et al. (2016):

$$F = \frac{V}{A} * slope * \frac{P * F1 * F2}{R * T}$$

where F is CH_4 or CO_2 flux (mg m^{-2} d^{-1}); V is chamber volume (m^3); A is chamber surface area (m^2); slope is the slope of the relationship between CH_4 or CO_2 and time (ppm s^{-1}); P is atmospheric pressure (kPa); F1 is the molecular weight (CO_2: 44 and CH_4: 16 g $mole^{-1}$); F2 is the conversion factor of seconds to days; R is the gas constant (8.3144 J K^{-1} mol^{-1}); and T is the temperature in Kelvin (K).

CH_4 in the porewater from the upper 10 cm of peat was sampled twice during experiment 1 (months 2 and 3), and three times during experiment 2 (months 1, 2, and 3). The porewater CH_4 was collected using rhizon samplers (Rhizosphere Research Products, Wageningen, The Netherlands) attached with a needle to a pre-vacuumed 12 mL exetainer (Labco, Lampeter, UK) containing 1 mL of hydrochloric acid (0.1 M) to stop the biological activity. The samples were, then, analysed by equilibrating with the headspace of ambient air immediately after sampling and measuring the gas phase on an HP 5890 gas chromatograph equipped with a Porapak Q column (80/100 mesh), and a flame ionization detector (GC-FID, Hewlett Packard, Palo Alto, CA, USA). Concentrations were calculated using Henry's law (Sander 2015).

Porewater chemical composition from the upper 10 cm of peat was determined from samples taken four times during experiment 1 (months 1, 2, 3, and 10) and three times during experiment 2 (months 1, 2, and 3) using the same rhizon samplers attached to a syringe under vacuum mentioned above. The samples were analysed following the approach described by Vroom et al. (2022b) to determine pH, alkalinity, ammonium (NH_4^+), phosphorus (P), iron (Fe), and sulfur (S). The pH and alkalinity were determined using Ag/AgCl electrode (Orion Research, Beverly, MA, USA) and a TIM 840 Titration Manager (Radiometer Analytical SAS, Villeurbanne, France). NH_4^+ was determined by colorimetric methods (Auto Analyser III, Bran and Luebbe GmbH, Norderstedt, Germany). P, Fe, and S were determined using inductively coupled plasma emission spectrometry (ICP-OES, IRIS Intrepid II, Thermo Electron Corporation, Franklin, MA, USA).

For experiment 1, root samples were washed from additional cores that were not rewetted ($n=4$). The 15 cm diameter cores were sliced every 5 cm to a depth of 30 cm. The samples were thoroughly rinsed to retain the roots (living and dead), after which the material was weighed, dried at 70 °C for 96 h, and weighed again.

Statistical analyses

All GHG emissions were checked for extreme outliers, as these are most likely caused by CH_4 bubbles that we have not visually detected during the measurement. As mentioned in the measurements, we focus only on diffusive fluxes, which is why we removed one extreme outlier ($n=1$). GHG emissions were log-transformed before all analyses. To enable the inclusion of extremely low CH_4 fluxes (± 1 mg m^{-2} day^{-1}), these were set to 0 after the transformation. We did not filter fluxes based on their fit (R^2). Negative fluxes (< -1 mg m^{-2} day^{-1}; $n=7$ for CH_4 from experiment 1, $n=0$ for CH_4 from experiment 2, and $n=15$ for CO_2 from experiment 2) were removed from all analyses, since this study focused on emissions only.

The effect of TSR depths and the effect of *Typha* on GHG emissions (Research Question 1) of rewetted peat soils were assessed using three-way repeated-measures ANOVAs. For experiment 1, differences in CH_4 and CO_2 emissions were separately assessed using TSR treatment, peat type (EA vs. IN), time (the month into the experiment), and their interactions as independent variables. When statistical significance was not shown between peat types, both sites were combined in the results (text and graphs). The results were kept separated in the supporting information. We also averaged emission data over time, as this describes the overall treatment emission better. For experiment 2, differences in CH_4 emission were assessed using TSR treatment, plant presence, time (the month into the experiment), and their interactions as independent variables. Since the response variables were not normally distributed according to the Shapiro-Wilk normality test, differences between individual treatments that proved significant in the ANOVA were tested using the non-parametric Wilcox paired samples post-hoc tests with Bonferroni correction of *p* values.

The effect of TSR depths and the effect of *Typha* growth on nutrient availability (Research Question 2) of rewetted peat soils were assessed using three-way repeated-measures ANOVAs. For experiment 1, differences in the grass and root biomass, porewater CH_4 concentrations, and porewater nutrient concentrations were separately assessed using TSR treatment, peat type (EA vs. IN), time (the month into the experiment), and their interactions as independent variables. For experiment 2, differences in porewater CH_4 concentrations and nutrient concentrations were assessed using TSR treatment, plant presence, time (the month into the experiment), and their interactions as independent variables. To test for differences between individual treatments that proved significant in the ANOVA, we used pairwise t-tests for porewater alkalinity, pH, P, and Fe and the non-parametric Wilcox paired samples test for porewater CH_4, NH_4^+, and S because these variables were not normally distributed. All post-hoc tests were performed with Bonferroni correction of *p* values.

We performed two random forest analyses for both experiments to determine the main drivers of the mitigation potential for CH_4 emissions (Research Question 3). For experiment 1, measurements over months 1, 3, and 10 were used as they had complete measurements. The CH_4 fluxes were the dependent variable, and CO_2 flux, cumulative CO_2, cumulative root biomass, time (the month into the experiment), soil type, and porewater results (alkalinity, pH, NH_4^+, Fe, S, and P) were used as independent variables. For experiment 2, CH_4 emissions were also used as the dependent variable, and time (the month into the experiment), vegetation treatment, and porewater results (alkalinity, pH, NH_4^+, Fe, S, and P) as independent variables. Porewater CH_4 concentration was not included in the random forest because it was not measured during the whole experiment 1 due to logistical constraints. Therefore, the relation between porewater CH_4 concentrations and CH_4 fluxes were tested separately using linear regression.

The statistical analyses were conducted in R (R core team, 2016), where the random forest analysis was performed using the 'RandomForest' package (Liaw and Wiener 2002). Graphs were created using JPM (JMP 2021).

Results

Research question 1: mitigation potential of TSR and the presence of Typha on the GHG emission

Experiment 1: topsoil removal every 5 cm

CH_4 emissions differed over time and with different amounts of TSR, but not between peat types (Fig. 2A; Tables S1 and S2). The highest CH_4 emissions were found in the 0 cm TSR treatments (average ± standard deviation: 395 ± 758 mg CH_4 m^{-2} day^{-1}; two peat types were aggregated), and the emissions were 6-times lower with 5 cm TSR (67 ± 186 mg CH_4 m^{-2} day^{-1}). CH_4 emissions further decreased to 23 ± 67 mg CH_4 m^{-2} day^{-1} at 10 cm TSR, 23 ± 122 mg CH_4 m^{-2} day^{-1} at 15 cm TSR, and less than 1 mg CH_4 m^{-2} day^{-1} at 20 and 25 cm TSR (Fig. 2 A). Emissions peaked after three months for the 0, 5, and 10 cm TSR and gradually declined afterward (Fig. 2 A).

CO_2 emissions differed between TSR treatments and over time, but not between peat types (Fig. 2B; Table S3). The highest CO_2 emissions were found in the treatments with 0 cm TSR (average ± standard deviation: 6496 ± 9243 mg CO_2 m^{-2} day^{-1}; two peat types were aggregated). CO_2 emissions decreased with an increase in TSR: 2655 ± 3798 mg CO_2 m^{-2} day^{-1} with 5 cm, 1967 ± 2468 mg CO_2 m^{-2} day^{-1} with 10 cm, 1309 ± 1685 mg CO_2 m^{-2} day^{-1} with 15 cm, 1423 ± 2469 mg CO_2 m^{-2} day^{-1} with 20 cm, and 617 ± 885 mg CO_2 m^{-2} day^{-1} with 25 cm. Despite water-logged conditions, TSR treatments caused CO_2 emissions to differ by a factor of 10.

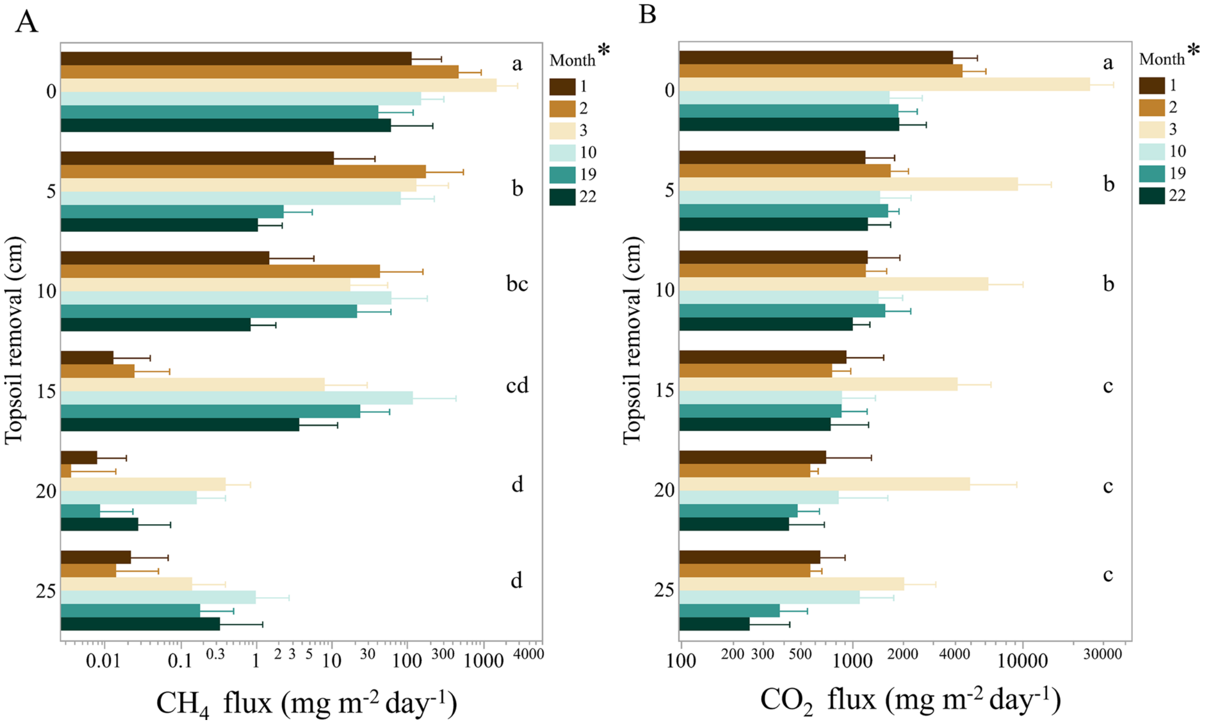


Fig. 2 Data from experiment 1. Emissions of (**A**) methane (CH_4; mg m^{-2} day^{-1}) and (**B**) carbon dioxide (CO_2; mg m^{-2} day^{-1}) under water-logged conditions per topsoil removal treatment over time. The two peat types were aggregated because they were not significantly different. Bars represent the average and standard deviation ($n = 8$ for each TSR treatment). Colors indicate the time of measurement (months into the experiment). Significant differences between TSR treatments are indicated with the letters, and the * indicates the significant difference in time (Tables S1 to S3). The result separated by peat type is available in the supporting information (Fig. S1). Note: the x-axes are presented on a logarithmic scale

Experiment 2: interaction between topsoil removal and presence of Typha

CH_4 emissions differed over time, with different amounts of TSR and with the presence or absence of *Typha* (Fig. 3; Tables S4 and S5). The lowering effect of TSR on CH_4 emissions remained when *Typha* was present. Vegetated mesocosms in combination with TSR revealed the lowest CH_4 emissions (Fig. 3). In the presence of *Typha*, 5 cm TSR significantly reduced CH_4 emissions by ~20 times, from 115 ± 113 mg CH_4 m^{-2} day^{-1} at 0 cm TSR to 6 ± 10 mg CH_4 m^{-2} day^{-1} at 5 cm TSR (Fig. 3; $p < 0.001$). In unvegetated treatments, 5 cm TSR significantly reduced CH_4 emissions by more than 8 times, from 523 ± 276 mg CH_4 m^{-2} day^{-1} at 0 cm TSR to 64 ± 137 mg CH_4 m^{-2} day^{-1} at 5 cm TSR (Fig. 3; $p < 0.001$). There was no further significant decrease in emissions from 5 to 15 cm TSR. CH_4 emissions appeared to increase over time, except for mesocosms with *Typha* at 0 cm TSR where emissions appeared to decrease. However, none of these differences were significant (Tables S4 and S5). *Typha* attained a maximum height of 100 ± 15 cm after three months, with a biomass of 37 ± 8 g dry weight per mesocosm.

Research question 2: effects of TSR and the presence of Typha on nutrient availability

Experiment 1: topsoil removal every 5 cm

Grass and root biomass, our proxy for easily decomposable carbon, differed per TSR treatment and per peat type ($p = 0.004$; Fig. 4, Table S6). Overall, values were higher in the 0 cm TSR treatments and on IN peat (Fig. 4, Table S6).

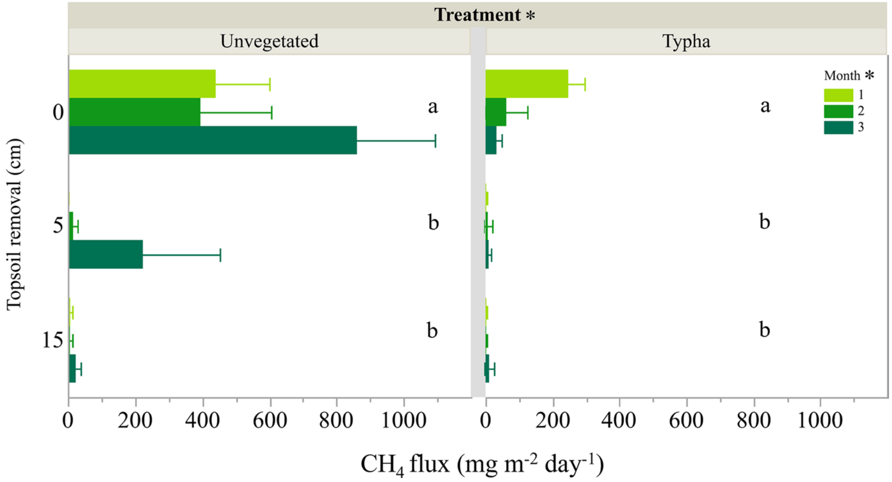


Fig. 3 Data from experiment 2, where only one peat type (IN) was used. Methane (CH_4) emissions (mg m^{-2} day^{-1}) per topsoil removal treatment. Distinctions have been made over time (months into the experiment, indicated by color) and between treatments (i.e., unvegetated and *Typha*). Bars represent the average and standard deviation ($n=5$ for each TSR treatment with *Typha*, $n=3$ for each unvegetated TSR treatment). Significant differences between TSR treatments per vegetation are indicated with the letters, and the * indicates the significant difference in time (Tables S4 and S5). Note: CH_4 fluxes are not shown on a logarithmic scale

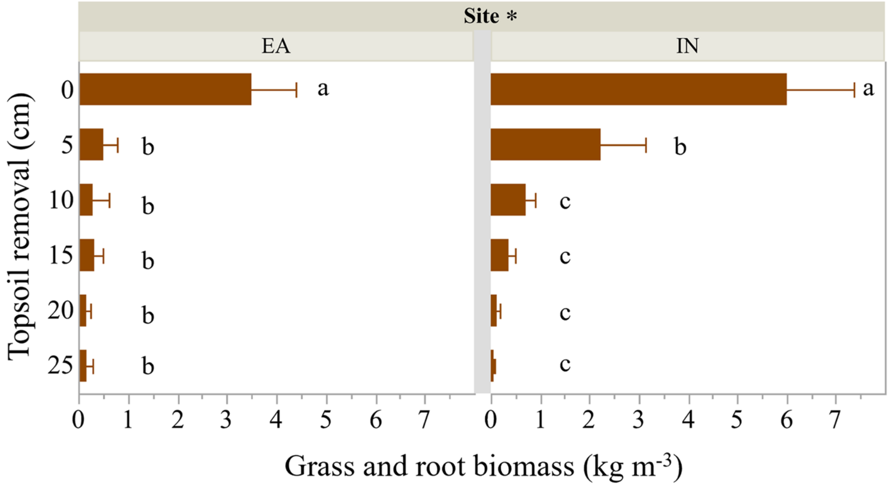


Fig. 4 Data from experiment 1. Grass and root biomass per volume (kg dry weight m^{-3}) per topsoil removal treatment in the extensively managed, acid peat (EA) and in the intensively managed, near-neutral peat (IN). Bars represent the average and standard deviation ($n=4$ per TSR and peat type). The 0 cm TSR treatment contained both aboveground biomass (leaf and shoot biomass) and belowground biomass (grass roots). Significant differences between TSR treatments per peat type are indicated with the letters, and the * indicates the significant difference in sites (Tables S6)

Considering the results without interactions (i.e., only location, depth, or time), there was a difference between peat types for porewater pH, alkalinity, P (Fig. 5), and NH_4^+ (Fig. S2), but not porewater CH_4 (Fig. 5), Fe and S concentrations (Fig. S2, Table S7). TSR affected porewater values of CH_4, pH, alkalinity, NH_4^+, Fe, and S, except for P concentrations (Fig. 5, Fig. S2, Table S7). Moreover, porewater values of pH, alkalinity, P, NH_4^+, Fe, and

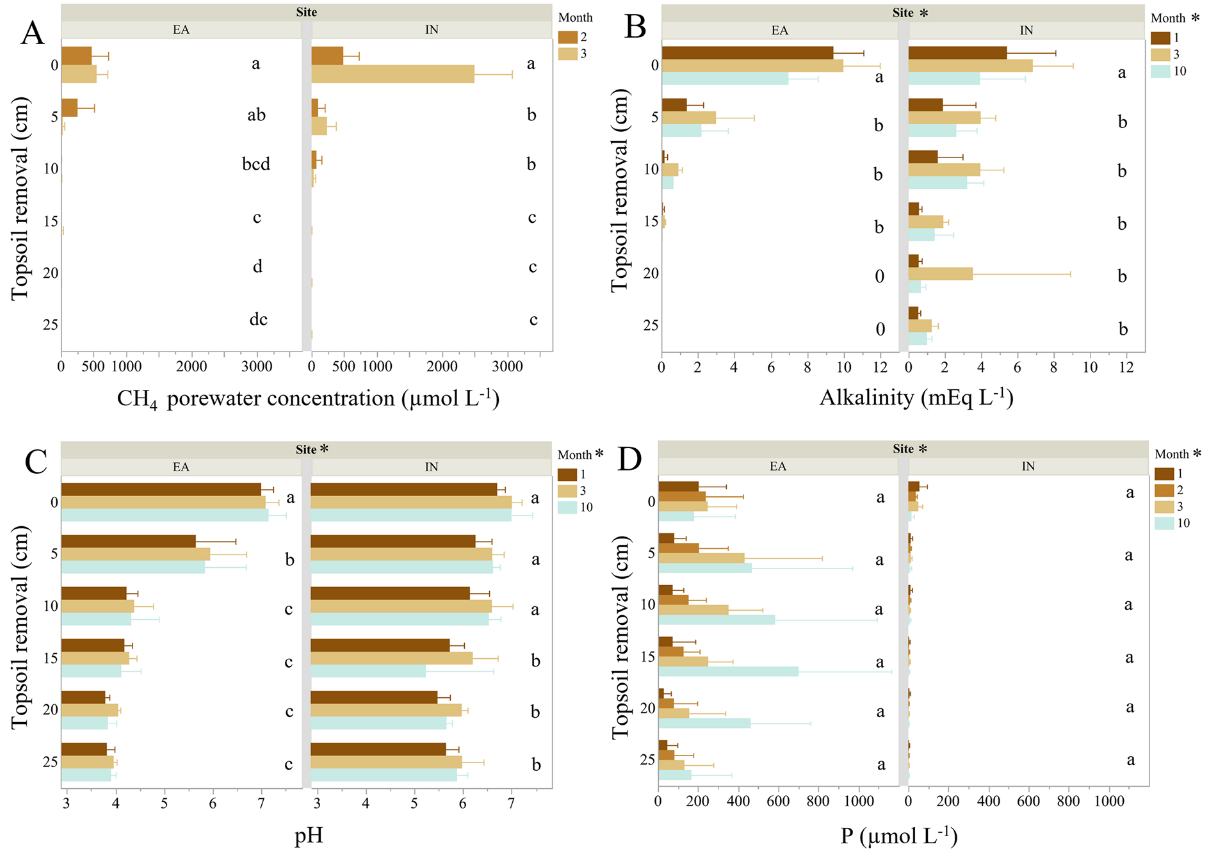


Fig. 5 Data from experiment 1. Porewater chemistry results of (A) methane (CH_4; µmol L^{-1}), (B) alkalinity (mEq L^{-1}), (C) pH, and (D) phosphorus (P; µmol L^{-1}) per topsoil removal treatment over time and per peat type. EA = extensively managed, acid peat. IN = intensively managed, near-neutral peat. Bars represent the average and standard deviation (*n* = 4 for each TSR and peat type). Colors indicate the time of measurement (months into the experiment). Significant differences between TSR treatments are indicated with the letters, and the * indicates the significant difference in time and sites (Tables S7)

S changed over time, except for CH_4 concentrations (Fig. 5, Fig. S2, Table S7).

CH_4 porewater concentrations declined with increasing TSR (Fig. 5 A, Table S7). The highest CH_4 concentrations were found in the treatments with 0 cm TSR (EA = 665 ± 500 µmol L^{-1}; IN = 1624 ± 1218 µmol L^{-1}). The 5 cm TSR treatment lowered CH_4 porewater by 2 and 12-times (EA = 223 ± 312 µmol L^{-1}; IN = 135 ± 236 µmol L^{-1}). The decrease in pH with increasing TSR was more pronounced on EA peat, which lines up with the alkalinity being lower in EA at increased TSR compared to IN (Fig. 5B and C, Table S7). Concentrations of P (only for EA) and Fe (for EA and IN) accumulated over time, showing higher concentrations in month 10 (Fig. 5D, Fig. S2B, Table S7). Contrary to the other elements where concentrations decreased with increased TSR, the concentrations of S species (oxidized, reduced, and elemental sulfur) increased overall (Fig. S2C, Table S7).

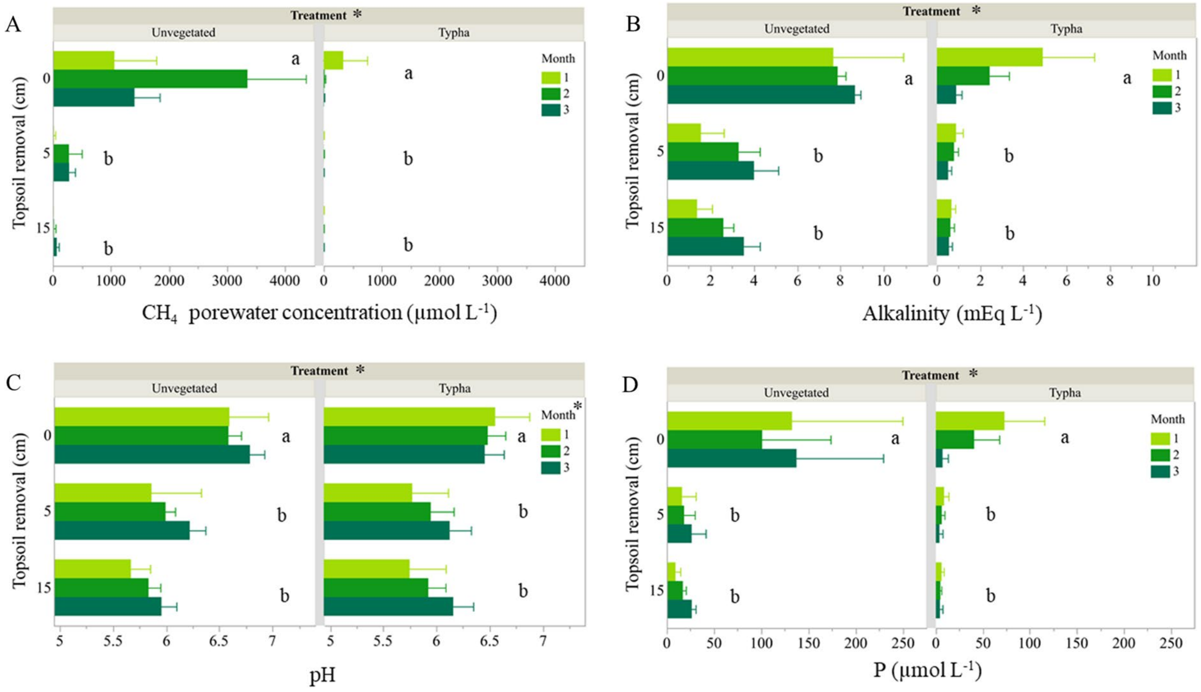


Fig. 6 Data from experiment 2, where only one peat type (IN) was used. Porewater chemistry results of (**A**) methane concentration (CH_4; μmol L^{-1}), (**B**) alkalinity (mEq L^{-1}), (**C**) pH, and (**D**) phosphorus concentration (P; μmol L^{-1}) per topsoil removal treatment. Distinctions have been made over time (months into the experiment, indicated by color) and between treatments (i.e., unvegetated and *Typha*). Bars represent the average and standard deviation ($n=5$ for each TSR treatment with *Typha*, $n=3$ for each unvegetated TSR treatment). Significant differences between TSR treatments per vegetation treatment are indicated with the letters, and the * indicates the significant difference in vegetation treatment and time (Tables S8)

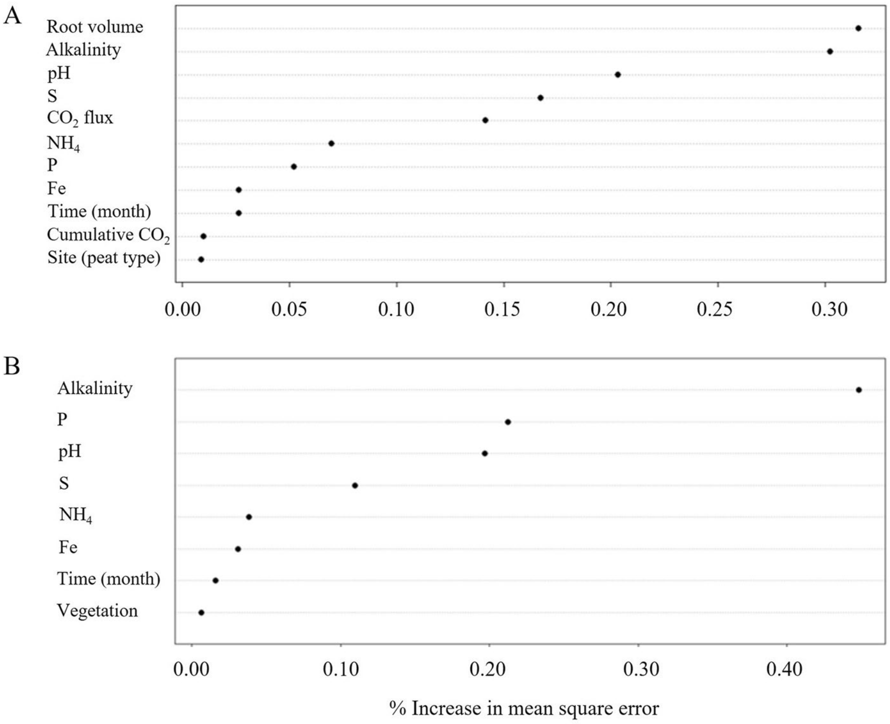
Experiment 2: interaction between topsoil removal and presence of Typha

Peat porewater chemistry was also affected by the presence of plants. Overall, porewater CH_4 concentrations were about 15 times lower in *Typha* treatments (48 ± 47 μmol L^{-1}) than in unvegetated treatments (729 ± 386 μmol L^{-1}; $p<0.001$; Fig. 6 A). CH_4 concentrations were higher in the 0 cm TSR treatments than 5 or 15 cm, with or without *Typha* (Fig. 6 A). The addition of *Typha* and the different TSR treatments altered pH, alkalinity, P, NH_4^+, and Fe values, but not S concentrations (Fig. 6, Fig. S3, Table S8). Only pH, NH_4^+, Fe, and S values changed over time (Fig. 6, Fig. S3, Table S8). We observed decreased porewater NH_4^+, P, and Fe concentrations in the *Typha* treatments (Fig. 6, Fig. S3, Table S8). The effect of TSR, independent of the presence of *Typha*, was observed for NH_4^+ and P, with higher concentrations in the treatments with 0 cm TSR. In unvegetated treatments, TSR had a positive effect on Fe concentrations ($p<0.001$) (Fig. S3B), while in both *Typha* and unvegetated treatments, S concentrations increased with increasing TSR ($p<0.001$) (Fig. S3C).

Research question 3: main drivers of CH_4 emissions

For experiment 1, the random forest analysis showed that cumulative root biomass and porewater alkalinity were the most important determinants of CH_4 emissions (Fig. 7 A). For experiment 2, porewater alkalinity, P concentration and pH mostly explained CH_4 emissions (Fig. 7B). Furthermore, porewater CH_4 concentration showed a positive correlation with CH_4 flux for experiment 1 (Fig. S4; EA: $R^2=0.293$, $p<0.0001$; IN: $R^2=0.402$, $p<0.0001$) and experiment 2 (Fig. S4; *Typha*: $R^2=0.64$, $p<0.0001$; unvegetated: $R^2=0.16$, $p=0.0157$).

Fig. 7 Data from experiments 1 and 2. Importance of different variables in predicting CH_4 emissions in the Random Forest analysis for experiment 1 (**A**): MSE = 0.28, $R^2 = 0.75$, and experiment 2 (**B**): MSE = 11,381, $R^2 = 0.75$. Cumulative root volume was not included for experiment 2 due to a lack of data. For experiment 1, we included measurements from months 1, 3, and 10 only since not all predictors were measured at other times



Discussion

We show in an experiment with detailed peat slicing (i.e., every 5 cm) that TSR has a strong effect on the availability of nutrients, (labile) carbon, and minerals, and the consequent emission of CH_4 and CO_2 from shallow rewetted, formerly drained agricultural peat. Specifically, the highest CH_4 emissions occurred after three months with 0 cm TSR. Surprisingly, 5 cm TSR and 10 cm TSR largely reduced these high GHG emissions post-rewetting. Moreover, with increasing amounts of TSR, there was no additional significant reduction in GHG emissions. Furthermore, climate benefits from shallow TSR prevailed in mesocosms planted with *Typha*, a wetland plant associated with high CH_4 emissions in wetlands. However, we stress that our vegetation experiment only lasted for three months when roots potentially allow for minimal oxidation of submerged peat, while root exudates and easily degradable plant litter of *Typha* can potentially boost CH_4 production and thus emissions over time. Optimal TSR depth with the goal of reducing nutrient availability requires the removal of at least 5 cm, while the inclusion of plants reduces the depth of peat that should be removed. Optimal TSR depth depends on the goal of rewetting the peatland, thus, a clear goal setting is vital to determine optimal TSR depth. Nevertheless, our results suggest that the standard 30–60 cm of TSR before shallow rewetting is not always necessary to gain climate benefits nor for nutrient reduction.

The mitigation potential of minimal TSR and Typha presence on GHG emissions

We show that a mere 5 to 10 cm of TSR can largely reduce CH_4 and CO_2 emissions from shallow flooded and rewetted, formerly drained agricultural peatlands. On average, for the two peat types used in this study, we show that 5 cm of TSR reduces CH_4 emissions by 1.9 tons of CH_4 ha^{-1} yr^{-1} and an additional 5 cm of TSR reduces emissions only further by 0.2 tons of CH_4 ha^{-1} yr^{-1}. However, this does not include the carbon being released from the removed peat. Although TSR is already known to reduce GHG emissions, previous studies applied at least 25 cm of TSR (Harpenslager et al. 2015; Zak et al. 2018; Huth et al. 2020). Therefore, our results suggest that the standard practice of removing 30 to 60 cm of peat (Allison and Ausden 2004; Huth et al. 2020) exceeds what would be required from a climate change mitigation perspective. Rewetting alone reduced CO_2 emissions, which agrees with previous studies (Wilson et al. 2016b; Günther et al. 2020; Huth et al. 2022). However, the rewetting of drained peatlands is found to favor CH_4 fluxes at the beginning (Wilson et al. 2009; Evans et al. 2021), while CH_4 emissions decrease in the long-term (Günther et al. 2020). This prior increase can be explained by the lag in CH_4 production resulting from the availability of alternative electron acceptors and the time required for the growth of methanogenic archaea and other anaerobic microorganisms (Hahn-Schöfl et al. 2011; Conrad 2020). In this study, CH_4 emissions rose for three months, followed by a marked lowering in treatments where TSR was small or absent, which is likely to be the result of labile carbon depletion.

Besides the impact of TSR directly on the local environment and indirectly on costs, the removed peat needs to be considered in the carbon balance of rewetted peat soils. Huth et al. (2022) found that TSR is a sustainable option for climate mitigation in nutrient-rich temperate bogs even when the carbon losses of worst or best-case topsoil decomposition scenarios were considered. According to the radiative forcing model applied in that study, rewetting coupled with TSR reduced the radiative forcing of GHG emissions compared to intensive grasslands (Huth et al. 2022). However, the time needed for the peatland to experience climate benefits increased with larger TSR depths (Huth et al. 2022). This agrees with our findings that 5 cm TSR already greatly improves climate mitigation, even without considering the larger amounts of carbon emitted from the increased amount of removed peat and the translocation thereof.

Even though wetland vegetation is known to enhance CH_4 emissions by the shunt effect, transporting CH_4 from the soil to the atmosphere (Fritz et al. 2011; Agethen et al. 2018; Huth et al. 2020), our data show that climate gains by TSR are not offset by the presence of *Typha* in the first phase after rewetting. In our study, the presence of *Typha* decreased CH_4 emissions to the atmosphere, most likely due to rhizosphere oxidation. Similar results were found in other short-term mesocosm experiments for *Typha* (Vroom et al. 2018, Boonman et al. 2022) and for a broad range of wetland plants (Kao-Kniffin et al. 2010). However, over time, higher CH_4 in situ emissions in peatlands in the presence of *Typha* are observed (Wilson et al. 2009). This may be explained by the effect of the growth stage on radial oxygen loss, as some species showed higher radial oxygen loss in young root tissues compared to old ones (Manzur et al. 2014). Contrastingly, some studies showed that the methane-oxidizing bacteria population size increased with the plant age (Vishwakarma and Kumar Dubey 2007). Therefore, young plants, such as those used in our study, could support CH_4 oxidation by radial oxygen loss, but the methane-oxidizing bacteria population may still be underdeveloped. If so, the main explanation for the observed CH_4 emission reduction may be the suppressing effect of oxygen on methanogenesis (Segers 1998). As such, future studies focusing on different plant growth stages may lead to a better understanding of the role of vegetation in CH_4 production and oxidation over time. Overall, we suggest that *Typha* can be planted directly after rewetting but should be harvested or removed before the onset of decay and thereby removing material to fuel methanogenesis.

Effect of minimal TSR and Typha presence on nutrient availability

In restoration projects of formerly drained and agriculturally used peatlands, TSR is also a promising practice to reduce internal eutrophication and pollution downstream by reducing, for example, P mobilization (Allison and Ausden 2004; Harpenslager et al. 2015; Zak et al. 2017; Zak et al. 2018). This reduction in nutrient availability can even be achieved with the minimal TSR approach, as we found that porewater NH_4^+ and Fe concentrations reduced significantly with 5 cm TSR. The presence of *Typha* further decreased the porewater concentrations of NH_4^+ and Fe. Although we did not find a clear reduction in porewater P concentration with minimal TSR, the presence of *Typha* did lower P mobilization. Peat type also had an influence on the effect of minimal TSR: near-neutral peat lowered P mobilization compared to the more acid peat type, but Fe concentrations only reduced on near-neutral peat with more than 15 cm TSR.

This suggests that, depending on peat pH, more or less TSR might be required and that nutrient-specific goals will be needed to reduce efforts on TSR while simultaneously reducing internal eutrophication and nutrient leaching. This is especially relevant for S,

Table 2 Summary of relevant CH_4 flux mechanisms. The table was limited to the elements investigated in the present study

Category	Element(s) involved	Mechanism	Proof	Supporting refs
CH_4-production stimulating	pH	Optimal production at pH 6.0 to 7.0	Similar trend to CH_4 flux (i.e., pH decreased with increasing TSR)	1, 2, 3
	Alkalinity	Stimulates mineralization	Similar trend to CH_4 flux (i.e., alkalinity decreased with increasing TSR)	4, 5, 6
	Labile C	Substrate for methanogenesis	Similar trend to CH_4 flux (i.e., labile C decreased with increasing TSR)	2, 6, 7, 8, 9
	NH_4^+	Increases mineralization of labile carbon and limits CH_4 oxidation by binding to receptors of methanotrophs	Similar trend to CH_4 flux (i.e., NH_4^+reduced with increasing TSR)	10, 11, 12, 13
	Fe^{3+}	Increased mobilization results in organic matter breakdown	Increasing concentrations over the first three months as the CH_4 fluxes	14
CH_4-production limiting	SO_4^{2-}	Competitive advantage SO_4^{2-} over CO_2 reducers and sulfide toxicity	Opposite trend to CH_4 flux (i.e., S increased with increasing TSR)	15, 16, 17, 18, 19
CH_4-consuming	SO_4^{2-} and Fe^{3+}	Enables anaerobic CH_4 oxidation	Different trends compared to CH_4 flux (i.e., S increased with increasing TSR, and Fe concentrations were not affected as CH_4 by TSR)	20, 21, 22, 23, 24
Ambiguous	P	Stimulates microbial growth (producers and oxidizers)	P concentrations were not affected as CH_4 by TSR.	25, 26, 27

References 1 Williams and Crawford 1984; 2 Smolders et al. 2002; 3 Ye et al. 2011; 4 Roelofs 1991; 5 Smolders et al. 2006; 6 Harpenslager et al. 2015; 7 Segers 1998; 8 Conrad 1999; 9 Conrad 2007; 10 O'Neill and Wilkinson 1977; 11 King and Schnell 1994; 12 Bodelier and Laanbroek 2004; 13 Currey et al. 2010; 14 Emsens et al. 2016; 15 Maillacheruvu et al. 1993; 16 Gauci et al. 2004; 17 Gauci et al. 2005; 18 Blodau et al. 2007; 19 De Jong et al. 2020; 20 Smemo and Yavitt 2007; 21 Zhu et al. 2012; 22 Wegener et al. 2015; 23 Ettwig et al. 2016; 24 Cai et al. 2018; 25 Schrier-Uijl et al. 2011; 26 Medvedeff et al. 2014; 27 Nijman et al. 2022

since we found that porewater S concentrations only increased with minimal TSR, while peat type and vegetation had no influence. Our results further suggest that vegetation growth for a short period of time after shallow rewetting may be a solution to limit nutrient availability on near-neutral peat, which is in line with earlier findings on near-neutral and acid peat (Vroom et al. 2022b).

Main drivers of CH_4 emissions

TSR may directly affect factors known to drive CH_4 emissions, e.g., substrate availability (labile carbon), pH, alkalinity, porewater (micro)nutrients, and redox potential. These mechanisms can be categorized as CH_4-production stimulating (e.g., pH and alkalinity), CH_4-production limiting (e.g., SO_4^{2-}), or CH_4 consuming (e.g., anaerobic CH_4 oxidation) (Table 1).

Porewater alkalinity was strongly associated with CH_4 emissions in both experiments and to a lesser extent porewater pH. Minimal TSR decreased both porewater alkalinity and pH. Studies performed in peatlands indicate the suppression of CH_4 production in acid conditions (Williams and Crawford 1984; Smolders et al. 2002; Ye et al. 2011) and report an optimal pH for methanogenesis between pH 6.0 and pH 7.0 (Williams and Crawford 1984; Blodau 2002; Nilsson and Öquist 2009). Therefore, the drop in pH due to TSR may have affected CH_4 fluxes, but it is unlikely to be the dominant factor in the 10 cm TSR treatment (large emission reduction without a substantial drop in pH). Acid and poorly buffered conditions may also favour peat accumulation, meaning that low alkalinity values, usually observed in less reactive systems, may hamper mineralization (Roelofs 1991; Smolders et al. 2006). This is supported by the simulated CH_4

production when bicarbonate is added to a system (Harpenslager et al. 2015). After inundation, alkalinity (bicarbonate) is generated internally due to the anaerobic mineralization of labile organic matter (van der Heide et al. 2010). Since porewater elements and nutrients seemed to be only loosely associated with CH_4 emissions, it is suggested that substrate availability seemed to be the dominant controller of methanogenic activity in our study.

We found that cumulative root biomass, used here as a proxy for easily decomposable or labile carbon, was also highly associated with CH_4 emissions. Although root biomass data were not available for experiment 2, we assume that the rooting depth of grasses remained similar over the course of two years in the same paddock sampled for experiment 1. Similarly, Pypker et al. (2013) found that increased plant productivity observed in summer favored CH_4 production due to the enhanced input of labile carbon. The top layer of the peat, which is typically oxic, receives most of the labile carbon (Artz 2009; Hahn-Schöfl et al. 2011; Hahn et al. 2015). Especially decaying aboveground and belowground biomass have been associated with peak CH_4 emissions (Hahn-Schöfl et al. 2011; Sibiya and Muzenda 2014; Franz et al. 2015). A similar result was found by Helfter et al. (2022), where the higher green vegetation and aboveground biomass during the summer resulted in higher CH_4 emissions. Noteworthy, Girkin et al. (2018) showed that the composition of root exudates can be more important as regulators of CO_2 and CH_4 production than their input rate. In addition, when roots decay (i.e., loss of labile carbon), a rapid turnover to more recalcitrant compounds occurs (Artz 2009; Glaser and Chanton 2009; Hahn-Schöfl et al. 2011). Accordingly, we argue that the reduction of CH_4 emissions observed with TSR is mainly related to the removal of labile carbon from the system. The substrate argument is further supported by the initial increase followed by a decrease in GHG emissions over time when less than 15 cm of topsoil was removed. Similarly, the highest CO_2 emissions arise with 5 cm TSR suggesting high carbon turnover. In top layers, methanogenic and heterotrophic microorganisms could use the large carbon pool, whereas deeper TSR would result in a cut-off from the labile carbon resulting in suppression of CH_4 emissions (Segers 1998). The CH_4 emissions observed in the treatments with deeper TSR are probably related to very low substrate availability limiting methanogen activity deeper in the profile (Yrjälä et al. 2011; Urbanová and Bárta 2016).

Although low amounts of CH_4 are still being emitted after almost two years, we expect that high emissions would occur if a new pool of fresh carbon enters the system, e.g., as a consequence of plant or algae growth (Hahn-Schöfl et al. 2011; Harpenslager et al. 2015). That could be an important reason to remove the nutrient-rich layer rather than only the top 5 cm, resulting in largely lower productivity and, consequently, biomass production and labile organic matter. However, we also showed that 5 cm TSR reduced nutrient concentrations in IN peat, and therefore, we argue that an assessment of labile carbon in the top peat layer prior to peat treatment (i.e., TSR and rewetting) can save resources and reduce environmental impacts. This assessment can make use of porewater CH_4 concentrations since it showed positive correlations with CH_4 emissions on both peat types and with and without the presence of *Typha*. In addition, both CH_4 emissions and CH_4 porewater were similarly affected by TSR. This suggests that the effects we observe on emissions are likely the result of increased CH_4 production. In turn, differences in the transport mechanism and CH_4 oxidation in the water layer are less likely to explain the TSR effect (Table 2).

Challenges for scaling up TSR for peatland rewetting

It is important to highlight that in our experiment, the water table was kept constant above the peat surface to generate anoxic conditions and mimicked extended summer flooding. In the field, not all rewetted peatlands will experience prolonged and continuous summer flooding due to the lack of irrigation infrastructure or water availability (Liu et al. 2020; Oestmann et al. 2022). In that light, water levels in field conditions may lead to different GHG emission dynamics (Koebsch et al. 2020), because water table fluctuations may affect oxidation and reduction processes by either stimulating CH_4 production or oxidation (Estop-Aragonés and Blodau 2012; Koebsch et al. 2020). Active water table management to maintain shallow submergence would be ideal for reducing carbon emissions (Evans et al. 2021). At the same time, however, using carbon and/or nutrient-rich irrigation water may also affect emissions and thus require further study prior to large-scale upscaling of TSR.

Moreover, we studied two sites from the Netherlands, which are characterized by high rainfall, high atmospheric N deposition, and S concentrations in the peat (Table 1). This historic and environmental context may influence carbon dynamics by affecting mineralization rates, microbial competition, and anaerobic CH_4 oxidation (Keller et al. 2005; Smemo and Yavitt 2007; Zhu et al. 2012; De Jong et al. 2020). As such, sites located in other regions with different environmental factors and microbial communities could lead to other results and warrant further study. To overcome the historic and environmental dependency, a field investigation may aid in decision-making for optimal TSR depths by quantifying levels of labile carbon and nutrients in a depth profile. Finally, the interrelated effects of pH and alkalinity on CH_4 production and carbon turnover (CO_2 vs. HCO_3^- depending on pH and total inorganic carbon) warrant further investigation, especially in degraded peat soils with a history of liming and oxic peat decomposition.

Conclusions and implications for peatland management

The present study clearly showed that (i) there is a large variation in GHG emissions depending on TSR and time since shallow flooding; (ii) 5 to 10 cm TSR may be sufficient to greatly reduce GHG emissions upon rewetting; (iii) these climate benefits are not offset by introducing wetland vegetation (i.e., *Typha*), which actually further reduce emissions in the first period after rewetting and bypasses CH_4 emission peaks three months after rewetting; and (iv) 5 cm TSR may not be enough to reduce nutrient availability. Our results indicate that costs can be reduced by minimizing TSR prior to peatland rewetting (e.g., transport, labor, machines), when reducing GHG emissions and minimizing soil subsidence is the main goal. Topsoil should largely be recycled on-site (e.g., by infilling ditches). In this light, current standard TSR practices of 30–60 cm are not required from a climate perspective but will, in many cases, be necessary from a nutrient perspective (Van Diggelen et al. 2020). As GHG emission after rewetting is largely driven by labile carbon, we suggest rapid rewetting after TSR to prevent the establishment of vegetation that enriches the topsoil with easily decomposable carbon. Moreover, before determining TSR depth, clear targets need to be set for the site, targeting climate, nutrients, or both. Further research may develop a tool to easily predict optimal TSR depth to reduce GHG emissions for all types of peatlands (e.g., differing in nutrient/mineral status) in temperate and boreal climates.

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Author contributions CF, RJEV, JJMG, and AJPS participated in the conception and design of the study. RJEV, JJMG, STJW, and CF participated in the sampling and experiments. GRQ, CCFB, and RJEV analyzed the data. GRQ and CCFB prepared the figures. GRQ, CCFB, RJEV, RJMT, and CF, wrote the first draft of the manuscript. All authors contributed to the interpretation of the data, revised the manuscript critically for important intellectual content, and approved the version of the manuscript to be published.

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Declarations

Competing interest The authors have no relevant financial or non-financial interests to disclose.

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