

University of Groningen

Species-dependent methane emissions in a Dutch peatland during paludiculture establishment

Vroom, Renske J.E.; Gremmen, Thomas M.; van Huissteden, Jacobus; Smolders, Alfons J.P.; Kosten, Sarian; Fritz, Christian; van de Riet, Bas P.; van Huissteden, Corine; van den Berg, Merit

Published in:
 Mires and Peat

DOI:
 [10.19189/MaP.2023.OMB.Sc.2422120](https://doi.org/10.19189/MaP.2023.OMB.Sc.2422120)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
 Publisher's PDF, also known as Version of record

Publication date:
 2024

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Vroom, R. J. E., Gremmen, T. M., van Huissteden, J., Smolders, A. J. P., Kosten, S., Fritz, C., van de Riet, B. P., van Huissteden, C., & van den Berg, M. (2024). Species-dependent methane emissions in a Dutch peatland during paludiculture establishment. *Mires and Peat*, 31, Article 13.
 <https://doi.org/10.19189/MaP.2023.OMB.Sc.2422120>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Species-dependent methane emissions in a Dutch peatland during paludiculture establishment

Renske J.E. Vroom^{1,2}, Thomas M. Gremmen³, Jacobus van Huissteden⁴,
Alfons J.P. Smolders^{1,3}, Sarian Kosten¹, Christian Fritz^{1,5}, Bas P. van de Riet^{1,3},
Corine van Huissteden⁶, Merit van den Berg⁶

¹ Department of Ecology, Radboud University, Nijmegen, The Netherlands

² Institute of Botany and Landscape Ecology, Greifswald University, partner in the Greifswald Mire Centre, Germany

³ B-WARE Research Centre, Nijmegen, The Netherlands

⁴ VOF Kytalyk Carbon Cycle Research, Epse, The Netherlands

⁵ Integrated Research on Energy, Environment and Society, University of Groningen, Groningen, The Netherlands

⁶ Department of Earth Sciences, Faculty of Science, Vrije Universiteit Amsterdam, Amsterdam, The Netherlands

SUMMARY

Paludiculture (crop cultivation on wet peatlands) is an effective means to reduce carbon emissions and nutrient losses from formerly drained peatlands. However, methane (CH₄) emissions and associated pathways may vary substantially between paludicultures, depending on the cultivated paludicrop. Whereas many studies have investigated diffusive CH₄ emissions from paludicrops, large uncertainties exist in relation to the importance of CH₄ ebullition, species-specific differences and seasonal dynamics. In this study we aimed to quantify CH₄ emissions from stands of three paludicrop species, namely *Typha latifolia*, *Typha angustifolia* and *Azolla filiculoides*. CH₄ diffusive fluxes - including plant-mediated emissions - and ebullitive fluxes were studied year-round on a rewetted former agricultural peatland in The Netherlands. Additionally, we tested the effect of irrigation strategy (water table depth) and nutrient loading on CH₄ emissions from stands of both *Typha* species. Diffusive CH₄ emissions were lowest from *A. filiculoides* stands (average 15.4 ± 6.6 mg m⁻² d⁻¹), followed by open water (36.4 ± 6.0 mg m⁻² d⁻¹). Substantially higher diffusive emissions were measured for both *Typha* species, with the highest emissions in *T. latifolia* (187.0 ± 29.4 mg m⁻² d⁻¹). Ebullitive fluxes were generally low (<100 mg m⁻² d⁻¹), but the highest ebullitive fluxes occurred in the *A. filiculoides* stand, contributing 79 % on average to its total CH₄ emissions. A water table just below the peat surface substantially reduced *Typha* CH₄ emissions, but also led to lower biomass production, compared to a flooded (+20 cm) water table. Nutrient loading increased biomass production and did not affect diffusive CH₄ emissions. Our results underline that species choice substantially affects paludiculture carbon dynamics in the first phase after establishment. Quantifying both diffusive and ebullitive fluxes is of paramount importance in adequately assessing paludiculture CH₄ fluxes.

KEY WORDS: *Azolla*, greenhouse gases, nutrient loading, *Typha*, water table depth

INTRODUCTION

Peat soils form the world's densest terrestrial carbon stock, storing 450 Gt C on only 3 % of the global land area (Joosten 2009, Joosten *et al.* 2016). Peatland drainage for agriculture and peat extraction has resulted in severe degradation of 10 % of peatlands globally, and 50 % of peatlands in the European Union (EU) (Joosten 2009, Tanneberger *et al.* 2017). Drainage boosts aerobic organic matter breakdown and turns peatlands from a weak carbon (C) sink into a strong C source (Frolking *et al.* 2011, Tiemeyer *et al.* 2016). In the EU alone, drained peatlands cause 25 % of agricultural greenhouse gas (GHG)

emissions while comprising only 3 % of the agricultural land area (Tanneberger *et al.* 2022). Rewetting drained peatlands is thus essential to mitigate global climate change and attain the goals of the Paris agreement (Günther *et al.* 2020, Tanneberger *et al.* 2021). To smooth the transition from agricultural land to fully restored natural peatland, the cultivation of wetland plants on rewetted peat, i.e. paludiculture, is a promising solution (Wichtmann *et al.* 2016). Wetland plant (i.e. paludicrop) cultivation provides an alternative income for farmers from the production of e.g. horticultural substrate, building and insulation materials or nutrition (Georgiev *et al.* 2014, Gaudig

et al. 2018, Pijlman *et al.* 2019). Simultaneously, the presence of vegetation can speed up the recovery of ecosystem services such as carbon and nutrient sequestration, water retention and habitat provision (Muster *et al.* 2015, Temmink *et al.* 2017, Vroom *et al.* 2022a).

A concern in paludiculture is the potential occurrence of elevated methane (CH₄) emissions after rewetting, which may (partly) offset the newly created CO₂ sink (Hemes *et al.* 2018, Günther *et al.* 2020, Antonijević *et al.* 2023). CH₄ has a 27 times higher global warming potential than CO₂ over a 100-year time horizon (Canadell *et al.* 2021) and is formed when anoxia returns to peat soils after inundation, leading to elevated emissions. Rewetted peatlands will have a lower warming effect than drained peatlands in the long term, as organic matter decomposition rates are substantially lower and CH₄ has a much shorter residence time in the atmosphere than CO₂ (Frolking *et al.* 2001, Günther *et al.* 2020). However, minimising paludiculture CH₄ emissions by making informed management decisions could at the same time boost carbon storage and increase stakeholder support for the implementation of paludiculture.

Paludicrops can affect CH₄ emissions in myriad ways. For a complete overview, see Bodmer *et al.* (2021), Vroom *et al.* (2022b) and Bastviken *et al.* (2023). Briefly, plants can enhance CH₄ production by organic matter provision (root exudates and decaying plants) and by CH₄ transport from sediment to the atmosphere through aerenchyma. In addition, plants can enhance CH₄ production by trapping organic matter, reducing oxygen (O₂) diffusion into the water, and by epiphytic and endophytic CH₄ production. In turn, CH₄ oxidation is promoted by root zone oxygenation (which also reduces CH₄ production), CH₄ ebullition retention by roots or other biomass, and epiphytic and endophytic methanotrophy (Bodmer *et al.* 2021, Bastviken *et al.* 2023). The net vegetation effect depends on plant growth form (emergent/floating/submerged), mode of CH₄ transport (diffusion/pressurised flow), growth stage, and physical condition (e.g. herbivore damage or harvesting), among other factors (Dinsmore *et al.* 2009, van den Berg *et al.* 2020, Vroom *et al.* 2022b).

As a perennial emergent macrophyte that can spread rapidly using rhizomes, *Typha* (cattail) is a paludicrop genus with high production and utilisation potential, particularly in eutrophic systems. *Typha* biomass can be used for a range of purposes such as building material, biodegradable packaging, fodder and biogas (Pijlman *et al.* 2019, Martens *et al.* 2021, Haldan *et al.* 2022). Native species in Europe include *Typha latifolia* (broadleaf cattail) and *Typha*

angustifolia (narrowleaf cattail), which are widespread in wetlands and shallow waters. To aerate their roots, *Typha* spp. have a high proportion of aerenchyma in their tissues, with air spaces composing >50 % of the internal leaf volume (Pazourek 1977). Furthermore, they are capable of pressurised gas transport, resulting in high radial oxygen loss (ROL) but also potentially high CH₄ transport from anoxic sediments to the atmosphere (“chimney effect”) (Sebacher *et al.* 1985). Previous research has shown that *Typha* spp. can either increase (McInerney & Helton 2016) or decrease (Jespersen *et al.* 1998, Vroom *et al.* 2018, Antonijević *et al.* 2023) CH₄ emissions compared to an open water situation. Additionally, CH₄ venting through plant biomass could decrease the sediment CH₄ stock, resulting in reduced ebullitive emissions (Van Der Nat *et al.* 1998, van den Berg *et al.* 2020). However, the importance of ebullition as a CH₄ emission pathway in *Typha* and in paludiculture has rarely been studied (van den Berg *et al.* 2024).

Another high-potential candidate paludicrop is *Azolla* (Abel & Kallweit 2022). *Azolla* is a genus of floating ferns that lives symbiotically with N-fixing cyanobacteria *Nostoc/Anabaena azollae* (Peters & Meeks 1989). Due to this symbiosis, *Azolla* has very high clonal growth rates even in N-depleted conditions (Wagner 1997). *Azolla filiculoides* was introduced to western Europe from North America at the end of the 19th century (Pieterse *et al.* 1977, Sheppard *et al.* 2006). The protein-rich biomass can, for instance, be used for human or animal nutrition or as a biofertiliser (Brouwer *et al.* 2014). Dense floating mats of *Azolla* can reduce light and O₂ concentrations in the underlying surface water (Pinero-Rodríguez *et al.* 2021, Aben *et al.* 2022). Studies on CH₄ emissions from *Azolla* have so far mostly focused on rice paddies, where *Azolla* is commonly used as a biofertiliser (Mandal *et al.* 1999, Kollah *et al.* 2016), and there has been one mesocosm study (Aben *et al.* 2022). Our experiment in a Dutch peatland is the first in which *Azolla* has been tested as a paludicrop in a field setting (van den Berg *et al.* 2024).

We reported previously that a CO₂ sink was effectively restored in this system after rewetting and planting *T. latifolia*, *T. angustifolia* and *A. filiculoides*. However, annual CH₄ emissions were species-dependent and highest for *T. latifolia* (van den Berg *et al.* 2024). The present study aims to provide additional insights on CH₄ emissions from these paludicrop species in the first phase (2–4 years) after rewetting. Specifically, we aim to answer the following research questions: 1) What is the magnitude of CH₄ emissions from paludiculture stands with *A. filiculoides* (hereafter *Azolla*),

T. latifolia and *T. angustifolia*, and what are the seasonal and diel dynamics?; and 2) how do water table (WT; 0 or +20 cm) and nutrient addition (nitrogen and phosphorous) affect water–atmosphere diffusive CH₄ emissions and plant-mediated emissions (further combined and referred to as ‘diffusive emissions’) of *Typha*? We hypothesise that the magnitude and pathways of CH₄ emissions depend on plant species and growth form, with higher diffusive emissions and lower ebullitive emissions in *Typha* spp. than in *Azolla* due to plant-mediated CH₄ transport. We expect higher CH₄ emissions during the day in *Typha* spp. as a result of increased pressurised flow. Lastly, we hypothesise that CH₄ emissions will be lowest with 0 cm WT due to increased O₂ availability, and that nutrients will enhance emissions as a result of increased plant productivity.

METHODS

Study site

The study site was situated in the Zuiderveen (North Holland, The Netherlands, 52° 43.78' N, 04° 73.15' E). This is a formerly drained and extensively managed fen grassland which was fertilised with manure and mowed in summer. The site was partially rewetted and paludiculture experiments were established in 2018 (see also van den Berg *et al.* 2024). First, ~ 20 cm of topsoil was removed to create four 23 × 43 m basins, of which three were included in this study. The fourth basin was not included because a layer of sludge had been added to it, making it incomparable to the others (Figure 1). On the north-east side, the basins were connected to a nearby ditch by small drainage channels, and the water table was regulated with an adjustable weir per individual basin. Each basin also had an overflow outlet which was connected to a second ditch on the south-west side. In one basin (B1) the water table was maintained at the level of the peat surface, whereas in the other two basins (B2, B3) it was set at 20 cm above the peat surface. In B1 and B3 the water table level was logged continuously in dipwells fitted with submerged sensors that measured water pressure (Cera-Diver, Eijkelkamp, Giesbeek, Netherlands), which was recalculated to water table depth by compensating for atmospheric pressure measured with a separate instrument (Baro-Diver, Eijkelkamp, Giesbeek, Netherlands). A wooden boardwalk on poles ran through the centre of each compartment to minimise peat disturbance during sampling. Each basin was split into three compartments (~ 200 m² for *Azolla*, ~ 430 m² for *Typha*) using wooden boards to physically separate the species. One paludicrop

(*Typha latifolia*, *Typha angustifolia* or *Azolla filiculoides*) was introduced to each compartment. Both *Typha* species were introduced in autumn 2018 and spring 2019 by planting shoots (pre-grown in a nursery) at a density of 1 individual m⁻². A floating PVC structure (3 × 3 m) was placed in each *Azolla* compartment to contain the *Azolla* and minimise plant loss by wind. *Azolla* cultivated in the greenhouse facilities of Radboud University was introduced in March 2020 by placing 950 g m⁻² fresh weight (FW) into the floating structures. *Azolla* covered the water surface at 90–100 % from May to August, after which it declined due to an infestation with the *Azolla* weevil (*Stenopelmus rufinasus*). After infestation, *Lemna* spp. gradually took over, and no *Azolla* remained in December 2020. Bulrush wainscot (*Nonagria typhae*) larvae affected both *Typha* species in spring 2020 and 2021, being more prominent in *T. latifolia*. This herbivorous moth larva feeds endophytically on *Typha* stems from spring until July/August, when it pupates and flies out (Teder & Tammaru 2002).

Experiment 1: CH₄ emissions from three paludicrops

To assess how CH₄ emissions are affected by the three paludicrops, CH₄ emissions (diffusion and ebullition) and pore water concentrations were measured in B2 (average water table in 2020: +17.5 cm, see Figure A1 in the Appendix; for water chemistry, see Table 1) during 14 sampling campaigns (ten with manual and four with automated chambers) throughout 2020. To enable GHG emission measurements in *Typha* without soil disturbance, three wooden frames were installed below the water table in each *Typha* compartment (total n = 6 frames; Figure A2). Manual chamber measurements were carried out on 10 March, 23 April, 14 May, 04 June, 18 July, 04 August, 08 September, 20 October, 09 November and 08 December. For both *Typha* species we used transparent Perspex chambers (diameter 50 cm) that could be stacked to match the height of the plants. Each chamber element was equipped with a fan powered by a power bank. The top part additionally contained a temperature logger and a PAR logger (both HOBO onset, Onset Computer Corporation, Bourne, MA, USA). For *Azolla* we used a floating transparent Perspex chamber (diameter 29 cm, height 26 cm) equipped with a HOBO temperature logger, and PAR was measured with a handheld device (PAR Quantum sensor SKP 215, Skye Instruments, Llandrindod, Wales, UK). Chambers were connected in a closed loop with gastight tubing to either a LI-COR 7810 portable GHG analyser (LI-COR Inc.,

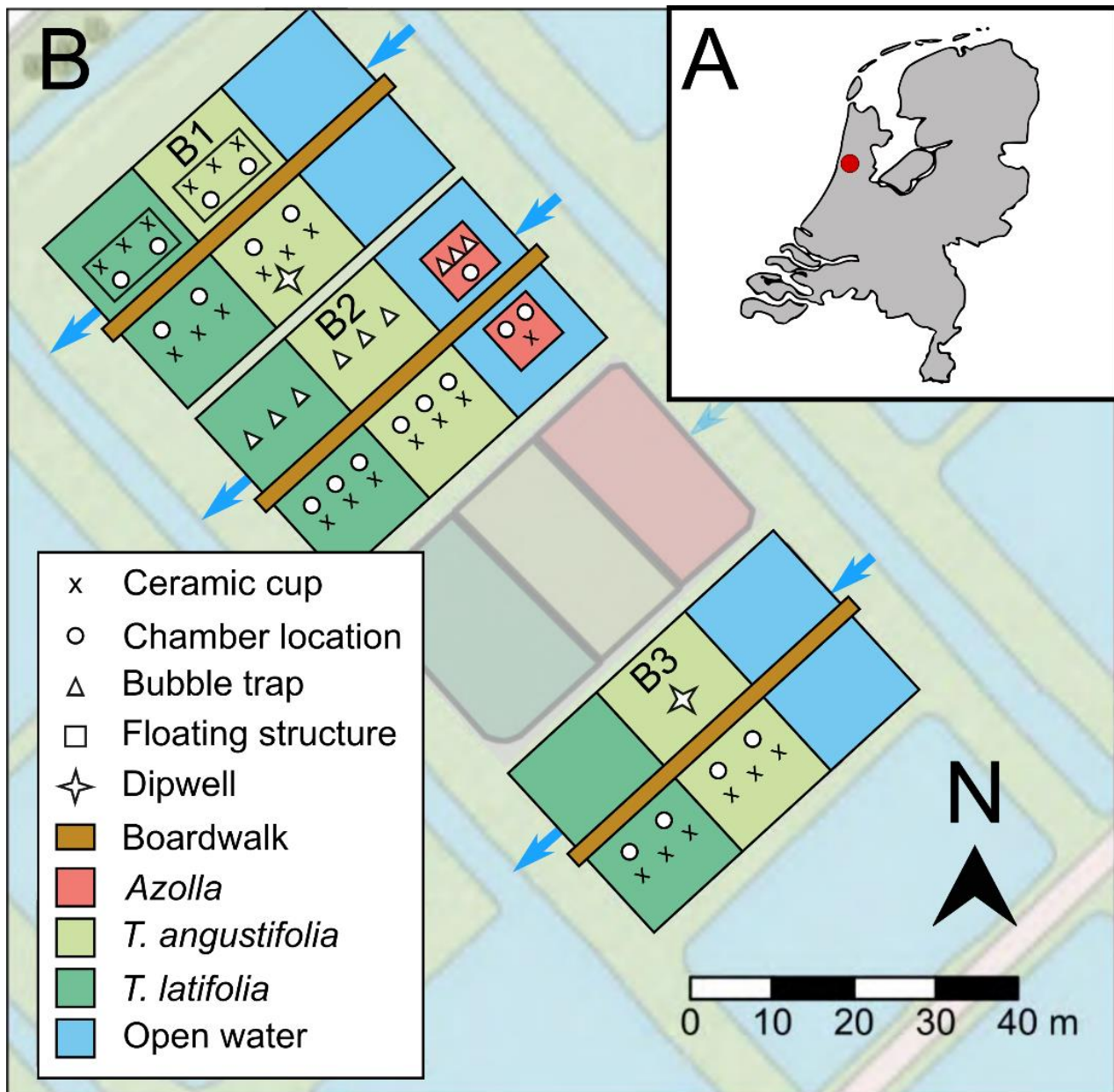


Figure 1. A: Location of the field site in The Netherlands; and B: overview of the experimental paludiculture basins. Measurements were conducted in B1 (Experiment 2), B2 (Experiments 1 and 2), and B3 (Experiment 2). Blue arrows indicate the direction of irrigation water flow. The water table was kept at around the peat surface in B1 and around +20 cm in B2 and B3 throughout the study period. Note that icons are used to indicate the setup per compartment, and are neither to scale nor fully accurate spatially.

Lincoln, NE, USA) or a Los Gatos Ultra-Portable GHG analyser (ABB - Los Gatos Research, San Jose, CA, USA) that measured CH₄ concentrations every second. Measurements were carried out during daytime and lasted three minutes each. At every flux measurement point (n=3 for *Azolla*, *T. latifolia*, *T. angustifolia* and open water (unvegetated control, measured in the *Azolla* basins next to the floating structures containing *Azolla*); total n=12), three transparent measurements and three opaque chamber

measurements were carried out during each campaign. To estimate the biomass of *Typha* spp. in the measurement plots, ten living shoots of each species were harvested outside of the measurement plots in September 2020 (n = 1 per basin and species). These shoots were dried at 70 °C for 72 hours, and dry weight per cm shoot length was calculated. This was then multiplied by the number of living shoots and the average shoot height at each measurement time and in each measurement plot.

Table 1. Porewater and surface water characteristics of basin B2, measured monthly in 2020. Values are given as average (min, max). Letters indicate significant differences ($p < 0.05$) between vegetation types. DOC = dissolved organic carbon, NO_3^- = nitrate, NH_4^+ = ammonium, PO_4^{3-} = phosphate, P = phosphorous, Cl = chloride, and H_2S = hydrogen sulphide. For methodological details, see van den Berg *et al.* (2024).

Water type	Variable	Unit	Inflow ditch	<i>Azolla</i>	<i>T. angustifolia</i>	<i>T. latifolia</i>
Surface water	pH	-	7.65 (7.34, 8.35)	7.41 (6.98, 8.36)	7.39 (6.99, 7.72)	7.77 (7.14, 8.6)
	DOC	mmol L ⁻¹	3.37 (2.68, 4.85)	3.59 (2.65, 4.83)	3.67 (2.51, 4.95)	4.29 (2.21, 6.35)
	NO_3^-	$\mu\text{mol L}^{-1}$	8.89 (0.65, 57.62)	4.1 (0.55, 16.72)	4.08 (0.5, 19.58)	2.6 (0.3, 12.93)
	NH_4^+	$\mu\text{mol L}^{-1}$	43.51 (3.07, 110.49)	28.18 (1.67, 81.63)	10.92 (1.88, 20.25)	10.96 (1.88, 14.55)
	PO_4^{3-}	$\mu\text{mol L}^{-1}$	5 (0.97, 9.22)	3.34 (0.7, 5.19) ^a	0.97 (0.17, 2.05) ^b	1.41 (0.16, 2.4) ^{ab}
	Cl	mmol L ⁻¹	39.66 (5.68, 59.05)	38.35 (5.76, 49.69)	37.08 (5.73, 47.67)	35.79 (5.69, 44.53)
Pore water	pH	-		6.38 (6.2, 6.66) ^a	4.83 (4.72, 5) ^b	6.42 (6.19, 6.65) ^a
	DOC	mmol L ⁻¹		24.14 (7.16, 58.64)	9.88 (6.3, 18.32)	5.38 (4.99, 5.79)
	NH_4^+	$\mu\text{mol L}^{-1}$		339.07 (128.99, 648.67) ^a	11.89 (0.91, 28.35) ^b	6.97 (2.94, 13.51) ^b
	P	$\mu\text{mol L}^{-1}$		31.27 (9.29, 55.8) ^a	3.17 (1.14, 6.6) ^b	1.79 (1.07, 2.9) ^b
	Cl	mmol L ⁻¹		32.81 (5.69, 52.8)	43.58 (5.8, 75.62)	41.25 (5.7, 55.96)
	H_2S	$\mu\text{mol L}^{-1}$		0.02 (0, 0.07)	0.05 (0.01, 0.13)	0.02 (0.01, 0.05)

In addition to manual measurements, we carried out automatic chamber measurements at the beginning of March, end of May, end of June and beginning of November 2020. For this, four Perspex chambers (diameter 35 cm) were placed in one vegetation type at a time. The chambers consisted of 0.5 m segments that could be stacked to match vegetation height. Rubber liners and tightening screws prevented leakage between the segments, and guy wires were used to secure the chambers at their maximum height. These chambers were equipped with fans and temperature loggers. They also had hinged lids controlled by a connected Raspberry Pi computer (Raspberry Pi Foundation, Cambridge, UK) and were connected with gastight tubing in four closed loops to a Los Gatos Microportable Greenhouse Gas Analyser. The four chambers were measured in succession, by closing the lid of the requisite chamber for 3 minutes of which the first 30 seconds were excluded from analysis due to flushing time of the tubing. After each measurement the chambers were flushed with atmospheric air for one minute, and then the lid of the next chamber was closed. During the closing time of one chamber, the other chambers remained open. This sequence was continued for three to five days in each vegetation type, providing high resolution data including diel variation in emissions.

To calculate fluxes from both manual (daytime fluxes) and automatic chambers, a plot of CH₄ concentration against time was made for a visual check on linearity. Measurements with significant departures from linearity (due to ebullition or other causes) were rejected. Fluxes were then calculated by linear regression of the gas concentration in the chamber, according to Almeida *et al.* (2016).

To assess CH₄ ebullition from the three paludicrops, we installed three bubble traps in each vegetation type (total $n=9$). Each trap consisted of a glass tube connected to a funnel (diameter 20 cm) which was kept floating by a small foam raft (Figure A2). Toothpicks were inserted into the foam rafts to prevent ducks from sitting on them and flipping over the traps. A butyl stopper was fitted at the top of each glass tube to enable gas extraction. Gas volume was determined every 1.5–3 weeks by removing the accumulated gas with a syringe. To determine CH₄ concentrations, gas was sampled once a month (April, May, November, December) or twice a month (June–October): 1 mL of gas was transferred to a 118 mL bottle closed with a butyl stopper. Subsequently, 1 mL of diluted gas was injected into a Los Gatos Ultraportable GHG analyser using an open loop of gastight tubing. The CH₄ concentration was then determined by calculating the area under the

curve. As the CH₄ concentrations in the sampled gas were very high (>3%), atmospheric CH₄ concentrations (~0.0002%) in the bottles and the greenhouse gas analyser inflow were negligible. Next, ebullitive CH₄ fluxes were calculated by multiplying the gas volume by the CH₄ content and dividing by bubble trap deployment time and area of the funnel.

To assess porewater CH₄ concentrations, ceramic cups were installed in the top 10 cm of soil in each compartment ($n=1$ per plant species). Pore water samples were collected in gastight evacuated 12 mL glass exetainers (Labco, Lampeter, UK) containing 1 mL of 0.5 M hydrochloric acid (HCl) for sample preservation. Samples were taken after manual chamber measurements were completed, on 11 March, 24 April, 14 May, 05 June, 23 July, 05 August, 09 September, 21 October, 10 November and 09 December 2020. Pore water CH₄ was measured in the headspace of the exetainers using 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). The original concentrations in the pore water were calculated using Henry's law (Sander 2015).

Experiment 2: Effect of water table and nutrient loading on *Typha* CH₄ emissions

To assess the effect of water table and nutrient loading on CH₄ emissions from both *Typha* species, sampling campaigns were carried out in B1 (average water table -4.5 cm in 2021), B2 and B3 (average water table for both was +19.5 cm in 2021 (Figure 1, Figure A1)). To measure emissions, wooden structures similar to those in B2 were installed in B3 (see Experiment 1, $n=3$ per species); whereas in B1, two PVC rings (40 cm height, 50 cm diameter) per treatment and species were inserted ± 20 cm into the soil ($n=8$ rings in total). In basins B1 and B3, a nutrient treatment was applied using the artificial fertilisers urea (CO(NH₂)₂) and triple superphosphate (45% P). In 2020, a total of 210 kg ha⁻¹ yr⁻¹ of N and 48 kg ha yr⁻¹ of P was applied, in three applications during the period May–July. In 2021, a total of 140 kg ha⁻¹ yr⁻¹ of N and 32 kg ha yr⁻¹ of P was applied, divided over four occasions in the months April–July. Fertiliser was added directly to the surface water in B3, whereas in B1 the fertiliser was applied in one of the 2 × 4 m enclosures made of wooden boards per species.

Diffusive CH₄ fluxes were measured eight times using manual chambers in 2021 (07 and 28 April, 18 May, 09 June, 07 and 21 July, 04 and 25 August), according to the above-mentioned methods. We used opaque chambers, since we did not see differences

between transparent and opaque chamber measurements in the previous experiment. Diffusive CH₄ flux (including plant transport) was measured at two sampling points per treatment combination and *Typha* species (n = 16 sampling points in total), and two replicate measurements were taken per sampling point during each sampling campaign.

To compare porewater CH₄ concentrations between treatments, ceramic cups were placed in triplicate in the vicinity of the CH₄ flux measurement points in each treatment combination (total n = 24 cups). Porewater was sampled on 07 and 28 April, 18 May, 09 June, 07 and 21 July, and 04 and 25 August 2021, according to the above-mentioned methods.

In August 2021, biomass was harvested from 1 × 1 m plots of to determine biomass production. For each treatment, two plots were chosen that were not in the proximity of any GHG measurement setup. In the fertilised 0 cm water table treatment, only one plot per species was harvested due to the small treatment plot size. *Typha* shoots were cut down to ~5 cm above the water table or ~10 cm above the soil surface (to realistically represent harvesting), weighed, and dried at 70 °C for 72 hours to determine dry weight (mass).

Statistical analyses

All statistical analyses and visualisations were done in RStudio v 4.0.3 using packages ggplot2 (Wickham 2016), nlme (Pinheiro *et al.* 2018) and emmeans (Lenth 2022). Differences between treatments in manually measured diffusive CH₄ fluxes, ebullitive CH₄ fluxes and porewater CH₄ concentrations were assessed using general linear (mixed) models followed by Analysis of Variance (ANOVA). Several models were created for each comparison, including the relevant main effects (vegetation type, date, water table, nutrient addition) and their two-way interactions with, in addition, (i) measurement plot as a random intercept, (ii) a temporal autocorrelation structure, (iii) both (i) and (ii), or (iv) neither. Then, models were compared using ANOVA, and the model with the lowest Aikake Information Criterion (AIC) was chosen. If AICs did not differ significantly based on an ANOVA test, the model with the simplest structure was selected. Residual plots were created for visual assessment of variance normality and homogeneity. To obtain variance normality, CH₄ diffusion and ebullition were log-transformed. Differences between individual treatments were assessed using Tukey post-hoc tests. A significance threshold of p < 0.05 was used. Values are reported in the text as means ± standard error.

RESULTS

Experiment 1: CH₄ emissions from three paludicrop stands

As CH₄ fluxes in manual transparent and opaque chamber measurements did not differ significantly (p = 0.30), diffusive CH₄ flux values were averaged over all six measurements per measurement point (n = 3 points per species) and date. A strong seasonal trend in CH₄ emissions was observed in all treatments, with low emissions during winter months (December, March) and peak emissions during summer months (July–September) (Figure 2A). Overall, diffusive CH₄ emissions differed significantly between plant species (p < 0.001). Specifically, emissions were lowest in the *Azolla* stand (9.8 ± 1.6 mg m⁻² d⁻¹), followed by open water (36.4 ± 6.0 mg m⁻² d⁻¹) and *T. angustifolia* (64.5 ± 8.4 mg m⁻² d⁻¹). Emissions were substantially higher in *T. latifolia* (187.0 ± 29.4 mg m⁻² d⁻¹). There was no difference in estimated biomass production between *T. angustifolia* and *T. latifolia* (p = 0.97).

CH₄ diffusion measured by automated chambers showed distinct diel fluctuations during some months, depending on the species (Figure 3). In March, before the growing season, no patterns could be distinguished. In May, however, CH₄ diffusion in *Azolla* was higher during the night. In June/July, *T. latifolia* had higher emissions during the day, whereas *T. angustifolia* had the highest emissions during the night. In September/October, both *Typha* species again had higher emissions during the day, although the fluctuations were less pronounced. No diel patterns were distinguished in *Azolla* in June/July and September/October. The presence of these diel patterns could lead to a mismatch of daytime (manual) measurements with actual emissions (over 24 h). For instance, measuring *Azolla* at noon in May (6 mg m⁻² d⁻¹) would under-estimate average emissions over 24 hours (35 mg m⁻² d⁻¹) by more than fivefold. A similar underestimation, albeit less extreme, would occur for *T. angustifolia* in June/July (300 vs. 325 mg m⁻² d⁻¹ at noon and over 24 hours, respectively), while fluxes from *T. latifolia* would be over-estimated (472 vs. 379 mg m⁻² d⁻¹ at noon and over 24 hours, respectively, in June/July).

CH₄ ebullition was highly variable, with peak emissions in June and August (Figure 2B). Average ebullitive CH₄ emissions were significantly lower in *T. angustifolia* (16.7 ± 5.40 mg m⁻² d⁻¹) than in *Azolla* (91.5 ± 22.2 mg m⁻² d⁻¹; p < 0.001) and in *T. latifolia* (46.6 ± 12.2 mg m⁻² d⁻¹; p = 0.042), with no significant difference between the latter two (p = 0.245). The average contribution of ebullition to total CH₄ fluxes was highest in *Azolla* (69 %), and substantially lower

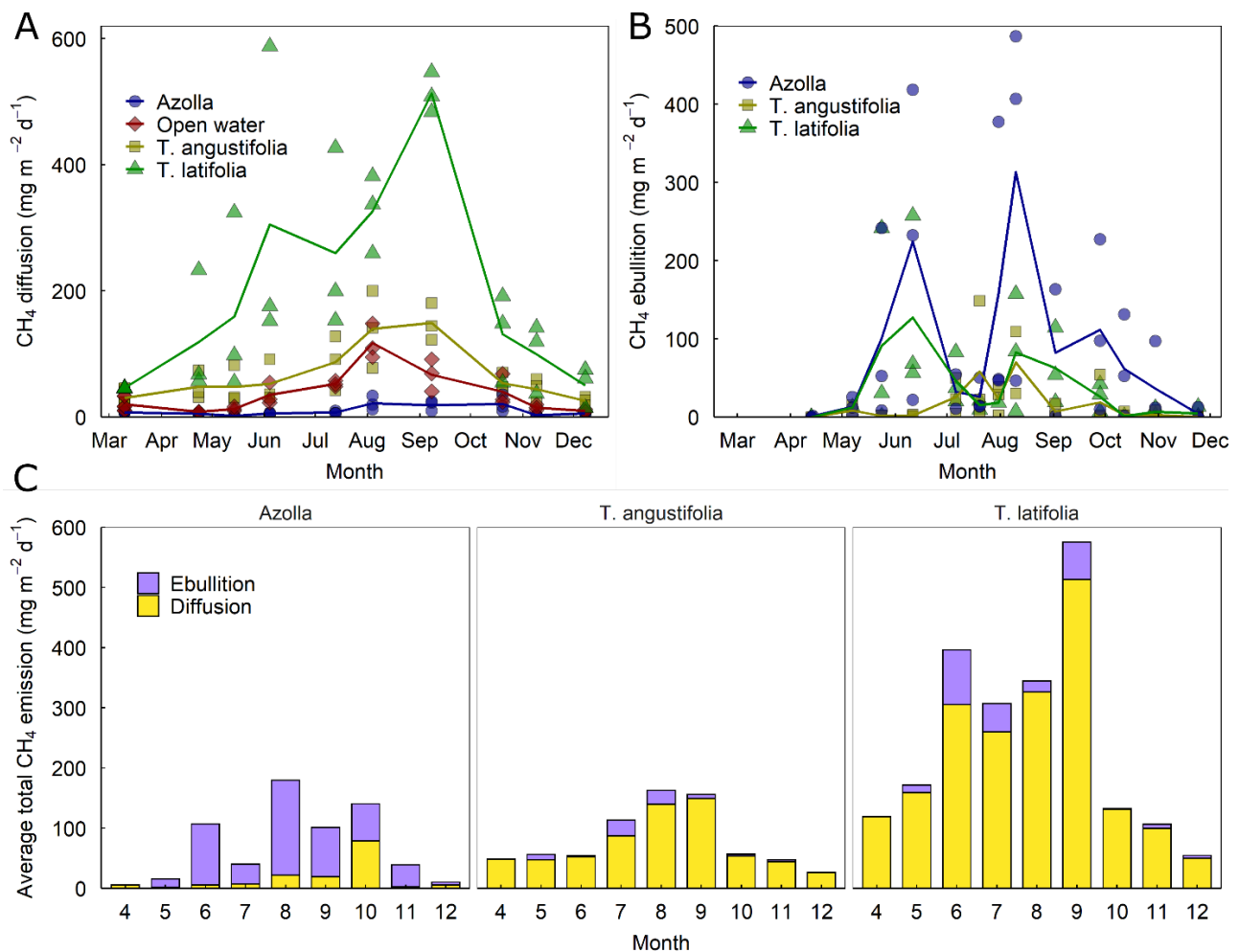


Figure 2. A: Diffusive CH_4 fluxes (includes water–atmosphere fluxes and plant-mediated transport) for the three vegetation types and open water; B: Ebullitive CH_4 fluxes (not measured in open water); and C: Total CH_4 fluxes (diffusion + ebullition) for each vegetation type. Bars show averages for the three subplots. Symbols indicate individual measurements at subplots (for diffusion, averaged over $n = 6$ repeat measurements over time). Lines indicate average emissions per vegetation type.

in both *Typha* species (9 % in *T. latifolia*, 8 % in *T. angustifolia*) (Figure 2C). Average annual total CH_4 fluxes were highest in *T. latifolia* ($245.4 \pm 57.1 \text{ mg m}^{-2} \text{ d}^{-1}$), followed by *T. angustifolia* ($80.2 \pm 16.9 \text{ mg m}^{-2} \text{ d}^{-1}$, $p = 0.020$) and *Azolla* ($71.1 \pm 21.0 \text{ mg m}^{-2} \text{ d}^{-1}$, $p = 0.012$), with no significant differences between the latter two ($p = 0.938$).

Porewater CH_4 concentrations (top 10 cm of sediment) remained rather stable ($\sim 80 \mu\text{mol L}^{-1}$) over time in both *Typha* species whereas a clear accumulation was observed in *Azolla*, rising from $47 \mu\text{mol L}^{-1}$ in March to $1305 \mu\text{mol L}^{-1}$ in November (Figure 4). Overall, mean porewater CH_4 concentrations were significantly higher in *Azolla* ($481 \pm 129 \mu\text{mol L}^{-1}$) than in *T. angustifolia* ($50 \pm 13 \mu\text{mol L}^{-1}$; $p < 0.001$) and *T. latifolia* ($111 \pm 31 \mu\text{mol L}^{-1}$, $p < 0.001$), and did not differ between *T. latifolia* and *T. angustifolia* ($p = 0.056$).

Experiment 2: Effect of water table and nutrient loading on *Typha* CH_4 emissions

Biomass yield for both *Typha* species was higher in the +20 cm WT conditions, with the more marked increase in *T. latifolia* (Figure 5A). Similarly, nutrient addition increased the biomass yield of both species, but more prominently of *T. latifolia*. *T. latifolia* dry biomass was 0.41 (0 cm WT) and 1.96 (+20 cm WT) kg m^{-2} in the unfertilised treatment and 0.53 (0 cm WT) and 3.81 (+20 cm WT) kg m^{-2} in the fertilised treatment. *T. angustifolia* dry biomass was 0.87 (0 cm WT) and 1.35 (+20 cm WT) kg m^{-2} in the unfertilised treatment and 0.62 (0 cm WT) and 2.23 (+20 cm WT) kg m^{-2} in the fertilised treatment.

As in Experiment 1, diffusive CH_4 emissions were substantially lower (65 % on average) in *T. angustifolia* than in *T. latifolia* at the high WT

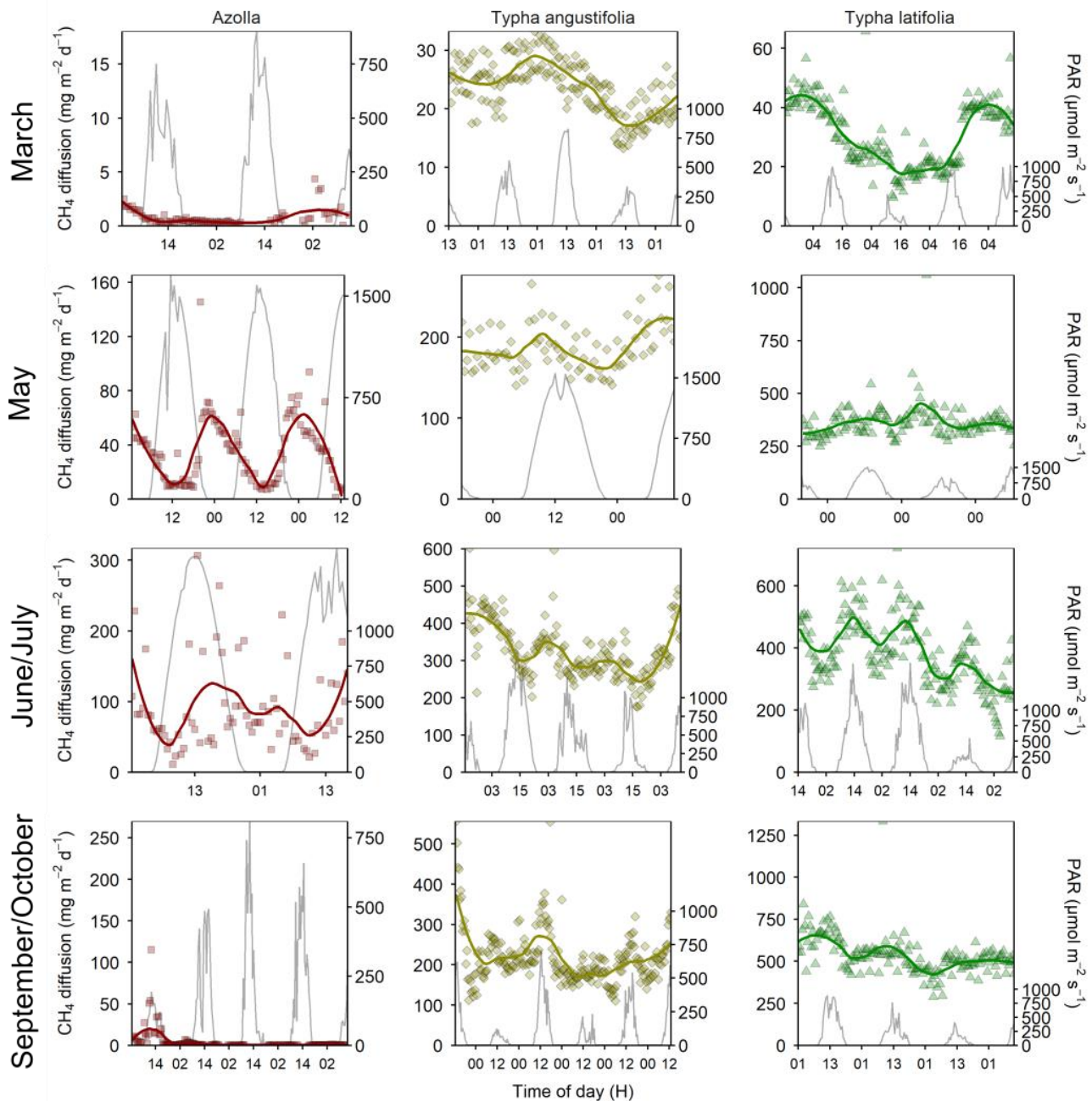


Figure 3. Diel patterns of CH₄ fluxes in the three vegetation types measured using automated chambers. Locally estimated scatterplot smoothing (loess) models are shown by the coloured lines. Grey lines represent PAR values at the times of measurements. NB: y-axis scales vary. *Azolla* was not yet present in March.

($p < 0.001$) (Figure 5B). At the low WT, however, emissions did not differ significantly between the two species ($p = 1.000$). Overall, emissions were substantially lower at the low WT ($p < 0.001$). This difference was more prominent in *T. latifolia* (87 % lower, 466.7 ± 57.5 and 53.0 ± 10.6 mg m⁻² d⁻¹ at the high and low WT, respectively), but also substantial in *T. angustifolia* (71 % lower, 123.8 ± 11.9 and 35.4 ± 2.2 mg m⁻² d⁻¹ at the high and low WT,

respectively). Despite its effect on biomass production, nutrient addition had no effect on CH₄ emissions ($p = 0.342$).

Porewater CH₄ concentrations were more than ten times higher at the +20 cm WT than at the 0 cm WT (283 ± 30 μmol L⁻¹ and 23 ± 5 μmol L⁻¹, respectively, $p < 0.001$) (Figure 5C). Porewater CH₄ concentrations did not differ between plant species ($p = 0.086$) or fertilisation treatments ($p = 0.606$).

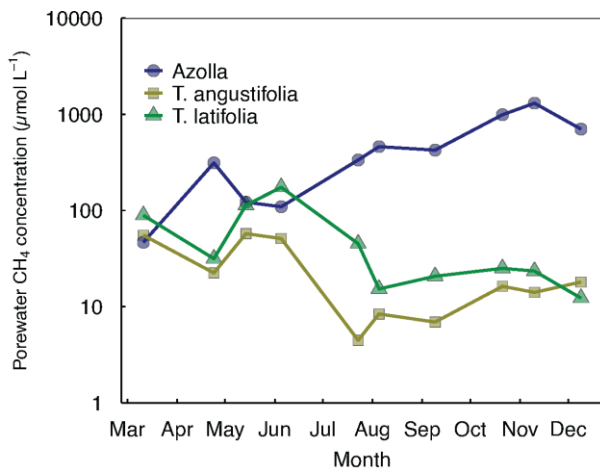


Figure 4. Porewater CH₄ concentrations (note the logarithmic y-axis scale) for the three vegetation types through time.

DISCUSSION

Paludiculture can halt intense CO₂ emissions from formerly drained peatlands and substantially decrease negative climate effects compared to drainage, despite coinciding increases in CH₄ emissions (Günther *et al.* 2020). Moreover, CH₄ emissions, particularly occurring in flooded conditions with high carbon and nutrient concentrations, could be minimised by informed management choices, including the choice of paludicrop species (Antonijević *et al.* 2023, van den Berg *et al.* 2024). In our field study conducted in the third and fourth year after rewetting, we found that the magnitude and pathways of CH₄ emissions were paludicrop-dependent in stands that had not yet been harvested. CH₄ emissions were diffusion-dominated in the emergent *Typha* spp., but ebullition-dominated in the free-floating *Azolla*. *T. latifolia* stands had substantially higher total emissions than stands of its congener *T. angustifolia* or of *Azolla*. CH₄ emissions in *Typha* were substantially lower at a water table of 0 cm than of +20 cm. N and P addition led to higher biomass production in *Typha* at both water tables, but did not affect CH₄ emissions.

CH₄ emissions in free-floating *Azolla* were ebullition-dominated

This experiment was the first to quantify in-situ CH₄ emissions from *Azolla* outside of rice paddy systems, and the first to quantify CH₄ ebullition in an outdoor water body covered by *Azolla*. Previous studies in rice paddies showed that *Azolla* dual cropping generally led to lower diffusive CH₄ emissions than growing rice alone, potentially as a result of higher

dissolved O₂ concentrations in surface water and, thus, a higher sediment redox potential (Xu *et al.* 2017, Bharati *et al.* 2000). In our study *Azolla* appeared to be a good candidate paludicrop in terms of CH₄ emissions, with lower diffusive emissions than the open water control (although open water ebullitive emissions were not quantified here). Lower diffusive emissions may be explained by reduced CH₄ diffusion through the floating *Azolla* mat, ROL from *Azolla* roots to the surface water and/or presence of methanogens on *Azolla* roots, leading to enhanced CH₄ oxidation (Kosten *et al.* 2016). ROL may also explain the diel CH₄ patterns in May, with lower fluxes during the day (O₂ production and release through photosynthesis) than the night. Alternatively, higher night-time CH₄ fluxes may be explained by heat loss from the warmer water to the air, resulting in convective mixing and increased CH₄ diffusion (Anthony & Macintyre 2016). In June/July, automated chamber measurements took place in a part of the *Azolla* stand that was particularly affected by *S. rufinusus*, explaining the absence of this pattern and the discrepancy between automated and manual measurements (undertaken in a healthy part of the stand). Additionally, shading by the *Azolla* mat may have led to lower sediment temperatures and, therefore, lower rates of methanogenesis (Segers 1998). However, porewater CH₄ concentrations in *Azolla* stands did show a steady increase during our experiment. When *Azolla* is not rooted in the sediment, the lack of a plant-transport pathway can result in sediment CH₄ accumulation and bubble formation (Van Der Nat & Middelburg 1998, van den Berg *et al.* 2020). The observation that ebullitive CH₄ emissions exceeded diffusive CH₄ emissions highlights the importance of quantifying this pathway in systems with *Azolla* or other floating plants. In the longer term, release of organic material from the *Azolla* mat may lead to enhanced CH₄ production and ebullition, as was observed in a two-year mesocosm experiment (Vroom *et al.* unpublished results). However, our bubble trap funnels were positioned below the floating vegetation which is likely to lead to over-estimation of the ebullitive flux that reaches the atmosphere. Bubbles rising up from the sediment may be retained naturally by the floating plants and, from there, part of the trapped CH₄ may diffuse into the water or be oxidised in the rhizosphere. Bubble retention has been found to be around 10 % at an *Azolla* cover of 100 % (Kosten *et al.* 2016). Additionally, ebullitive fluxes are likely to be underestimated for all species, since ‘trapped’ bubbles may be oxidised or dissolve in between bubble trap sampling times.

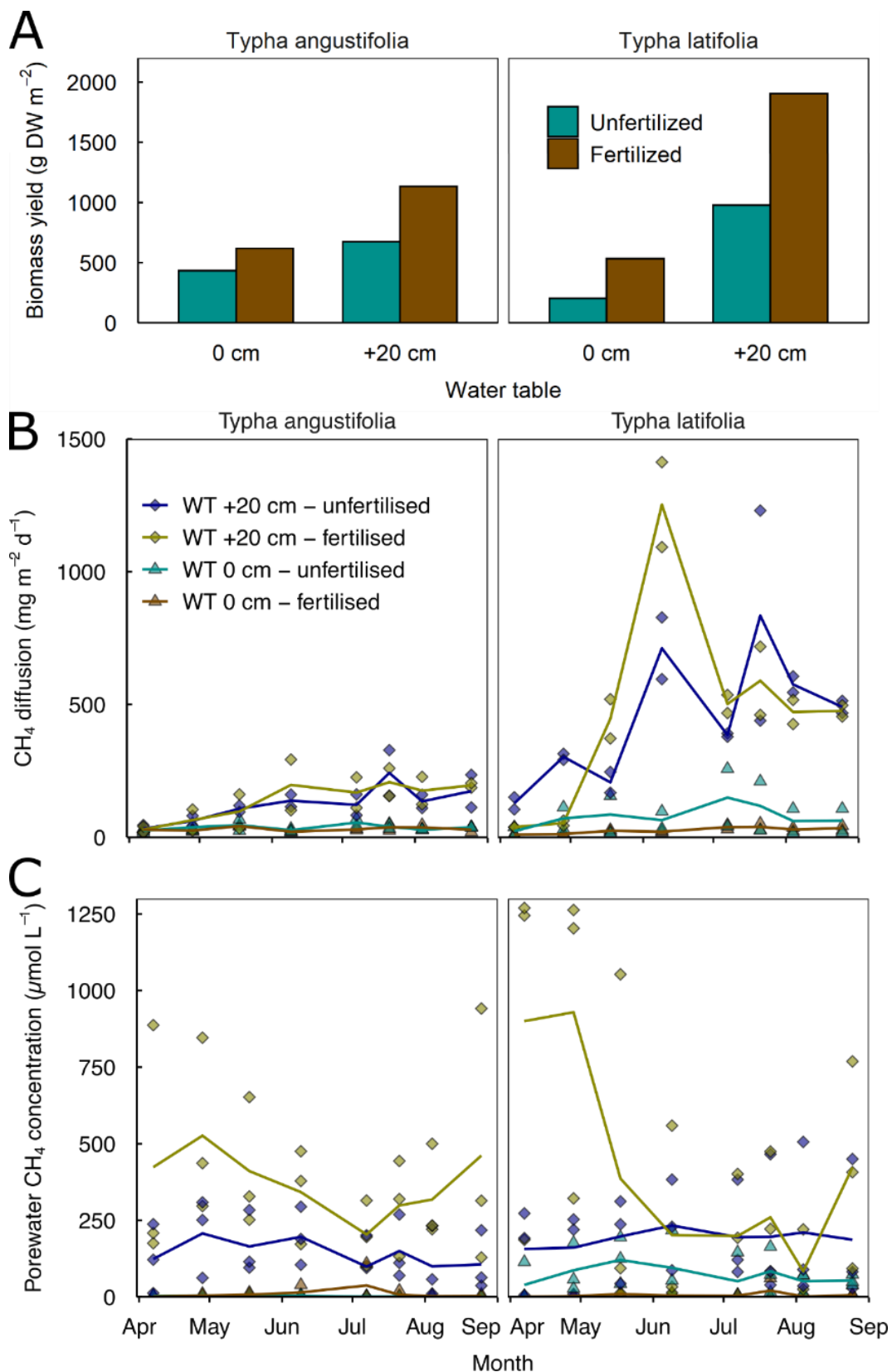


Figure 5. A: Average biomass yield measured at the end of August 2021 ($n=2$ per treatment, $n=1$ for the 0 cm WT, fertilised treatment). B: diffusive CH₄ fluxes measured in 2021 at 0 cm and +20 cm WT, with and without fertiliser application, for both *Typha* species. Symbols indicate the average of three measurements per plot ($n=2$ plots per treatment for CH₄ diffusive flux, $n=3$ samples per treatment for CH₄ concentration). Lines indicate average emissions per WT and fertilisation treatment.

CH₄ emissions from *Typha* stands were species-dependent

Typha productivity in our field site was relatively low (< 1.5 kg m⁻² dry mass), which can be explained by high Cl concentrations, low nutrient availability and *N. typhae* invasion. Still, CH₄ fluxes from *Typha* were generally high (> 100 mg m⁻² d⁻¹), especially during the summer months. This magnitude is in line with previous field studies of *T. latifolia* stands in a boreal lake (Desrosiers *et al.* 2022), a subtropical swamp (Whiting & Chanton 1996) and a temperate wetland (Yavitt 1997), but higher than *T. latifolia* in a temperate rewetted fen (Günther *et al.* 2014) and higher than expected after the substantial topsoil removal that took place (Quadra *et al.* 2023). Fewer studies exist on *T. angustifolia*: much higher CH₄ emissions (> 1000 mg m⁻² d⁻¹ during the warm season) were found in a temperate marsh (Strachan *et al.* 2015), while slightly lower emissions were found in one EC study in a temperate *T. angustifolia* stand (annual average 73 mg m⁻² d⁻¹) (Fritz & van Giersbergen 2023) and two mesocosm studies (~80 mg m⁻² d⁻¹) (Kao-Kniffin *et al.* 2010, 2011).

Generally, high CH₄ emissions in our site (despite top soil removal) may be explained by high dissolved organic carbon (DOC) concentrations (> 2.7 mmol L⁻¹) in the incoming surface water, supplying a carbon source for methanogenesis (Chanton *et al.* 1995, Liu *et al.* 2012). Especially in summer months, when evapotranspiration rates and water demand were high, DOC inflow may have been substantial. On the other hand, DOC concentrations in surface water and pore water were equally high in all vegetation types, ruling out the explanation that differences between vegetation types were caused by spatial differences in DOC concentrations. Our outcomes warrant further research into the effect of DOC loading and composition, and rewetting methods (e.g. flooding or ditch irrigation), on paludiculture CH₄ emissions.

Diffusion (including plant mediated transport) was the dominant CH₄ emission pathway in both *Typha* species. Porewater CH₄ concentrations became very low during the growing season, and ebullitive CH₄ emissions were low in both *Typha* species compared to *Azolla*. This indicates that plant transport substantially reduced the sediment dissolved CH₄ pool (Chanton 2005, Green & Baird 2012). CH₄ emissions were substantially higher in *T. latifolia* than in *T. angustifolia*, even though both species transport CH₄ through pressurised gas flow (Tornbjerg *et al.* 1994). However, *T. angustifolia* generally grows in deeper water and has higher pressurised flow rates and ROL rates than *T. latifolia* (Bendix *et al.* 1994, Inoue & Tsuchiya 2008). This

could result in higher root zone CH₄ oxidation rates in *T. angustifolia* and subsequently lower CH₄ emissions, which is supported by the observed lower sediment pH in *T. angustifolia* (on average 7.39 compared to 7.77 in *T. latifolia*). A low pH could also directly affect CH₄ dynamics, e.g. by reducing methanogenesis (Segers 1998). Additionally, although aboveground biomass did not differ, the *T. angustifolia* stand may have been healthier compared to *T. latifolia*, as it was less affected by *N. typhae* and *T. angustifolia* has a higher salt tolerance (McMillan 1959). This may have concurred with a higher root density and, therefore, increased ROL.

Observed dips in *T. angustifolia* CH₄ emissions during daytime in June could be explained by decreased pressurisation and gas flow rates under illumination in this species (Bendix *et al.* 1994). The opening of stomata at sunrise increases the effective pore size above the optimum diameter (~ 0.2 µm) and could thereby reduce pressurisation efficiency (Inoue & Tsuchiya 2008, Vroom *et al.* 2022b) and CH₄ transport. However, ROL is not affected by illumination in this species, because the lower pressurised flow is compensated by higher photosynthetic rates and, thus, O₂ concentrations (Inoue & Tsuchiya 2008). Higher emissions during daytime than during night-time in *T. latifolia*, on the other hand, correspond with earlier findings of increased pressurised flow rates during daytime in this species (Chanton *et al.* 1993). It is likely that *T. latifolia* has longer and/or more tortuous sub-stomatal air pathways, increasing resistance to mass flow and explaining why illumination does not decrease pressurisation in this species (Sorrell & Brix 2003, Inoue & Tsuchiya 2008). However, increased temperatures during the day do increase internal pressurisation, and, therefore, gas flow rates (Vroom *et al.* 2022b). The presence of these diel dynamics in paludicrops emphasises the importance of capturing both day and night emissions, especially during the summer months, when creating carbon balances in paludiculture. In our case, daytime measurements may have led to an emission over-estimation for both *Typha* species during summer months, with the exception of *T. angustifolia* in June/July which had potential emission under-estimation.

Our biogeochemical data show no substantial differences between compartments, and we found no structural differences in CH₄ emissions between measurement spots within compartments. However, due to the experimental design, we cannot fully exclude potential spatial effects on CH₄ emissions (e.g. effects of the basin margins). We therefore recommend future studies to further unravel

differences between both *Typha* species in different environmental conditions (e.g. healthier stands, different water tables). Additionally, the effect of a closed chamber on gas flow through *Typha* plants (by altering e.g. temperature and humidity) warrants future investigation.

***Typha* CH₄ emissions were driven by water table, but not by nutrient addition**

As expected, a water table just below the soil surface led to decreased CH₄ emissions, but also to lower *Typha* biomass production compared to a flooded (WT +20 cm) situation. As the water table increases from (far) below the surface to above the surface (flooded), microbial breakdown shifts from respiration and CH₄ oxidation (CO₂-dominated fluxes) to methanogenesis (CH₄-dominated fluxes), due to a decrease in O₂ availability (Blain *et al.* 2014, Minke *et al.* 2016). Assessing the balance by quantifying CO₂ emissions, plant carbon storage, site hydrology and economic value of the produced biomass are necessary when choosing an optimal water table. Water tables close to the surface may be more realistic for paludiculture in temperate climates, given a water surplus of 200–300 mm during winter and spring that is consumed by evapotranspiration in May through July. Water tables below the surface from June onwards would, therefore, be more common when *Typha* stands approach peak biomass (Günther *et al.* 2014).

Although nutrient addition led to a biomass increase in both *Typha* species, it did not affect CH₄ diffusion. This corroborates previous findings from mesocosm experiments (e.g. Bhullar *et al.* 2013, Boonman *et al.* 2023) and suggests that increasing biomass leads not only to an increase in plant-mediated CH₄ transport and labile carbon release, but also to an increase in ROL and subsequent CH₄ oxidation. Additionally, added nutrients could have affected methanogenesis (Bodelier *et al.* 2000, Veraart *et al.* 2015). Our findings imply that the admission of surface water that is rich in nutrients, particularly NH₄⁺ and PO₄³⁻ at moderate concentrations, can boost biomass production without exacerbating CH₄ emissions in the establishment phase of *Typha* paludiculture.

Recommendations and implications for paludiculture

Limiting CH₄ emissions in paludiculture could accelerate carbon sink restoration and increase stakeholder support for implementation. Examples of CH₄ emission drivers that can be actively managed include water table, nutrient input and paludicrop choice (Karki *et al.* 2014, Günther *et al.* 2015, Vroom

et al. 2018). We found similar CH₄ emissions in *Azolla* and *T. angustifolia* stands during the first period after rewetting, whereas emissions from *T. latifolia* were substantially higher. Although these results arise from only one paludiculture site with high water table and limited biomass production, and only in the third and fourth year after rewetting, this implies that even congeners with very similar morphology may have drastically different effects on carbon cycling in paludiculture. In our study, growth of *Azolla* and *Typha* was hampered by low nutrient availability as a result of substantial topsoil removal. Despite initial concerns expressed by scientific advisors, this occurred during site construction for various (practical and bureaucratic) reasons. If high biomass production is desired, we would recommend a lower amount (~10 cm) of topsoil removal, to still limit CH₄ emissions and nutrient mobilisation while allowing substantial biomass production (Quadra *et al.* 2023). Growth of our paludicrops was further limited by *S. rufinasus* and *N. typhae*. Further research on insect herbivory in paludiculture and possible ways to prevent infestation is recommended before scaling up to larger paludicrop ‘monocultures’ when high biomass production is an (economic) incentive. Meanwhile, the tradeoff between lower CH₄ emissions and lower biomass production at a (summer) water table around the peat surface needs to be addressed, for instance using life cycle analysis. Future research could add insights by focusing on CH₄ production at different soil depths and relating this to plant rooting depths at different WTs. If CH₄ is produced in deeper layers, emissions may be substantial even at WTs below the peat surface. Bubble release may be impacted, in turn, by plant roots. Assessing carbon dynamics in simple pilot field trials may aid in paludicrop species choice prior to scaling up; however, the effect of the incoming water (e.g. carbon input) needs critical evaluation. Lastly, to fully assess carbon dynamics in paludiculture, the effect of harvesting (including the use of machinery) on CH₄ emissions should be assessed, for instance by the use of eddy covariance towers during a harvest.

ACKNOWLEDGEMENTS

We thank all the volunteers who made the field campaigns possible during the pandemic. We thank Eva Kuipers for help with fieldwork and Sebastian Krosse for laboratory analyses. The measurements on the paludiculture site were part of the Peat Innovation Program initiated by the Association for Agricultural Nature and Landscape Management; Water, Land &

Dijken (WLD) and the landscape conservation organisation Landschap Noord-Holland (LNH). RV and BvdR were supported by the NWO-TTW-project AZOPRO (Project no. 16294).

AUTHOR CONTRIBUTIONS

RV planned and carried out fieldwork, analysed data, and is the lead author. TG planned and carried out fieldwork, analysed data. JvH and CvH carried out automated chamber measurements and analysed data. AS, SK and BvdR conceptualised and supervised the study and acquired funding. MvdB conceptualised and supervised the study and the manuscript, analysed data, and validated outcomes. All versions of the manuscript were written by RV and revised by TG, JvH, CvH, AS, SK, CF and MvdB. All authors approved the final manuscript.

REFERENCES

- Abel, S., Kallweit, T. (2022) *Potential Paludiculture Plants of the Holarctic*. Proceedings of the Greifswald Mire Centre 04/2022, Greifswald, 440 pp. (self-published, ISSN 2627-910X)
- Aben, R.C.H., Oliveira Junior, E.S., Carlos, A.R., van Bergen, T.J.H.M., Lamers, L.P.M., Kosten, S. (2022) Impact of plant species and intense nutrient loading on CH₄ and N₂O fluxes from small inland waters: An experimental approach. *Aquatic Botany*, 180, 103527, 10 pp. <https://doi.org/10.1016/J.AQUABOT.2022.103527>
- Almeida, R.M., Nóbrega, G.N., Junger, P.C., Figueiredo, A.V. and 26 others (2016) High primary production contrasts with intense carbon emission in a eutrophic tropical reservoir. *Frontiers in Microbiology*, 7, 717, 13 pp. <https://doi.org/10.3389/fmicb.2016.00717>
- Anthony, K.W., Macintyre, S. (2016) Nocturnal escape route for marsh gas. *Nature*, 535, 363–365.
- Antonijević, D., Hoffmann, M., Prochnow, A., Krabbe, K., Weituschat, M., Couwenberg, J., Sigrid, E., Zak, D., Augustin, J. (2023) The unexpected long period of elevated CH₄ emissions from an inundated fen meadow ended only with the occurrence of cattail (*Typha latifolia*). *Global Change Biology*, 29, 3678–3691. <https://doi.org/10.1111/gcb.16713>
- Bastviken, D., Treat, C.C., Pangala, S.R., Gauci, V., Enrich-Prast, A., Karlson, M., Gålfalk, M., Romano, M.B., Sawakuchi, H.O. (2023) The importance of plants for methane emission at the ecosystem scale. *Aquatic Botany*, 184, 103596, 14 pp. <https://doi.org/10.1016/j.aquabot.2022.103596>
- Bendix, M., Tornbjerg, T., Brix, H. (1994) Internal gas transport in *Typha latifolia* L. and *Typha angustifolia* L. 1. Humidity-induced pressurization and convective throughflow. *Aquatic Botany*, 49(2–3), 75–89. [https://doi.org/10.1016/0304-3770\(94\)90030-2](https://doi.org/10.1016/0304-3770(94)90030-2)
- Bharati, K., Mohanty, S.R., Singh, D.P., Rao, V.R., Adhya, T.K. (2000) Influence of incorporation or dual cropping of *Azolla* on methane emission from a flooded alluvial soil planted to rice in eastern India. *Agriculture, Ecosystems Environment*, 79(1), 73–83. [https://doi.org/10.1016/S0167-8809\(99\)00148-6](https://doi.org/10.1016/S0167-8809(99)00148-6)
- Bhullar, G.S., Iravani, M., Edwards, P.J., Olde Venterink, H. (2013) Methane transport and emissions from soil as affected by water table and vascular plants. *BMC Ecology*, 13, 32, 9 pp. <https://doi.org/10.1186/1472-6785-13-32>
- Blain, D., Murdiyarso, D., Couwenberg, J., Nagata, O., Renou-Wilson, F., Sirin, A., Strack, M., Tuittila, E-S., Wilson, D. (2014) Rewetted organic soils. In: *2013 Supplement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories: Wetlands*, Hiraiishi, T., Krug, T., Tanabe, K., Srivastava, N., Baasansuren, J., Fukuda, M., Troxler, T.G. (eds.), IPCC, Geneva, Switzerland, 3.1–3.42.
- Bodelier, P., Hahn, A., Arth, I., Frenzel, P. (2000) Effects of ammonium-based fertilisation on microbial processes involved in methane emission from soils planted with rice. *Biogeochemistry*, 51, 225–257. <https://doi.org/10.1023/A:1006438802362>
- Bodmer, P., Vroom, R., Stepina, T., Del Giorgio, P., Kosten, S. (2021) Methane fluxes of vegetated areas in natural freshwater ecosystems: Assessments and global significance. Preprint, *EarthArXiv*, 35 pp. <https://doi.org/10.31223/X5ND0F>
- Boonman, C.C.F., Heuts, T.S., Vroom, R.J.E., Geurts, J.J.M., Fritz, C. (2023) Wetland plant development overrides nitrogen effects on initial methane emissions after peat rewetting. *Aquatic Botany*, 184, 103598, 8 pp. <https://doi.org/10.1016/j.aquabot.2022.103598>
- Brouwer, P., Bräutigam, A., Külahoglu, C., Tazelaar, A.O.E., Kurz, S., Nierop, K.G.J., van der Werf, A., Weber, A.P.M., Schlupepman, H. (2014) *Azolla* domestication towards a biobased economy? *New Phytologist*, 202(3), 1069–1082.
- Canadell, J.G., Monteiro, P.M.S., Costa, M.H., da Cunha, L.C. and 13 others (2021) Global carbon and other biogeochemical cycles and feedbacks. In: Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L. and 15 others (eds.) *Climate Change 2021: The Physical Science Basis*.



- Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, Cambridge, UK, 673–816.
- Chanton, J.P. (2005) The effect of gas transport on the isotope signature of methane in wetlands. *Organic Geochemistry*, 36(5), 753–768. <https://doi.org/10.1016/J.ORGEOCHEM.2004.10.007>
- Chanton, J.P., Whiting, G.J., Happell, J.D., Gerard, G. (1993) Contrasting rates and diurnal patterns of methane emission from emergent aquatic macrophytes. *Aquatic Botany*, 46(2), 111–128. [https://doi.org/10.1016/0304-3770\(93\)90040-4](https://doi.org/10.1016/0304-3770(93)90040-4)
- Chanton, J.P., Bauer, J.E., Glaser, P.A., Siegel, D.I., Kelley, C.A., Tyler, S.C., Romanowicz, E.H., Lazrus, A. (1995) Radiocarbon evidence for the substrates supporting methane formation within northern Minnesota peatlands. *Geochimica et Cosmochimica Acta*, 59(17), 3663–3668. [https://doi.org/10.1016/0016-7037\(95\)00240-Z](https://doi.org/10.1016/0016-7037(95)00240-Z)
- Desrosiers, K., DelSontro, T., del Giorgio, P.A. (2022) Disproportionate contribution of vegetated habitats to the CH₄ and CO₂ budgets of a boreal lake. *Ecosystems*, 25(7), 1522–1541. <https://doi.org/10.1007/s10021-021-00730-9>
- Dinsmore, K.J., Skiba, U.M., Billett, M.F., Rees, R.M. (2009) Effect of water table on greenhouse gas emissions from peatland mesocosms. *Plant and Soil*, 318, 229–242. <https://doi.org/10.1007/s11104-008-9832-9>
- Fritz C., van Giersbergen, Q. (2023) *Monitoring Mechanistic Processes Affecting the GHG Balance in Paludicultures Compared to Irrigate-Drained Grasslands on Peat in 2021–2022*. Report, National GHG Monitoring on Organic Soils, Nijmegen, The Netherlands, 48 pp.
- Frolking, S., Roulet, N.T., Moore, T.R., Richard, P.J.H., Lavoie, M., Muller, S.D. (2001) Modeling northern peatland decomposition and peat accumulation. *Ecosystems*, 4, 479–498. <https://doi.org/10.1007/s10021-001-0105-1>
- Frolking, S., Talbot, J., Jones, M.C., Treat, C.C., Kauffman, J.B., Tuitilla, E.S., Roulet, N. (2011) Peatlands in the Earth's 21st century climate system. *Environmental Reviews*, 19, 371–396. <https://doi.org/10.1139/a11-014>
- Gaudig, G., Krebs, M., Prager, A., Wichmann, S. and 30 others (2018) Sphagnum farming from species selection to the production of growing media: a review. *Mires and Peat*, 20, 13, 30 pp.
- Georgiev, G., Theuerkorn, W., Krus, M., Kilian, R., Grosskinsky, T. (2014) The potential role of cattail-reinforced clay plaster in sustainable building. *Mires and Peat*, 13, 09, 13 pp.
- Green, S.M., Baird, A.J. (2012) A mesocosm study of the role of the sedge *Eriophorum angustifolium* in the efflux of methane - including that due to episodic ebullition - from peatlands. *Plant and Soil*, 351(1–2), 207–218. <https://doi.org/10.1007/s11104-011-0945-1>
- Günther, A.B., Huth, V., Jurasinski, G., Glatzel, S. (2014) Scale-dependent temporal variation in determining the methane balance of a temperate fen. *Greenhouse Gas Measurement and Management*, 4(1), 41–48.
- Günther, A.B., Huth, V., Jurasinski, G., Glatzel, S. (2015) The effect of biomass harvesting on greenhouse gas emissions from a rewetted temperate fen. *GCB Bioenergy*, 7, 1092–1106. <https://doi.org/10.1111/gcbb.12214>
- Günther, A.B., Barthelmes, A., Huth, V., Joosten, H., Jurasinski, G., Koebsch, F., Couwenberg, J. (2020) Prompt rewetting of drained peatlands reduces climate warming despite methane emissions. *Nature Communications*, 11, 1644, 5 pp. <https://doi.org/10.1038/s41467-020-15499-z>
- Haldan, K., Köhn, N., Hornig, A., Wichmann, S., Kreyling, J. (2022) *Typha* for paludiculture—Suitable water table and nutrient conditions for potential biomass utilization explored in mesocosm gradient experiments. *Ecology and Evolution*, 12(8), e9191, 21 pp. <https://doi.org/10.1002/ECE3.9191>
- Hemes, K.S., Chamberlain, S.D., Eichelmann, E., Knox, S.H., Baldocchi, D.D. (2018) A biogeochemical compromise: The high methane cost of sequestering carbon in restored wetlands. *Geophysical Research Letters*, 45(12), 6081–6091. <https://doi.org/10.1029/2018GL077747>
- Inoue, T.M., Tsuchiya, T. (2008) Interspecific differences in radial oxygen loss from the roots of three *Typha* species. *Limnology*, 9(3), 207–211. <https://doi.org/10.1007/s10201-008-0253-5>
- Jespersen, D.N., Sorrell, B.K., Brix, H. (1998) Growth and root oxygen release by *Typha latifolia* and its effects on sediment methanogenesis. *Aquatic Botany*, 61(3), 165–180. [https://doi.org/10.1016/S0304-3770\(98\)00071-0](https://doi.org/10.1016/S0304-3770(98)00071-0)
- Joosten, H. (2009) *The Global Peatland CO₂ Picture: Peatland Status and Drainage Related Emissions in all Countries of the World*. Wetlands International, Ede, 36 pp. Online at: <https://www.wetlands.org/publication/the-global-peatland-co2-picture/>, accessed 11 Sep 2023.
- Joosten, H., Sirin, A., Couwenberg, J., Laine, J., Smith, P. (2016) The role of peatlands in climate regulation. In: *Peatland Restoration and Ecosystem Services: Science, Policy and Practice*, Cambridge University Press, Cambridge, United Kingdom, 63–76. <https://doi.org/10.1017/CBO>



- 9781139177788.005
- Kao-Kniffin, J., Freyre, D.S., Balsler, T.C. (2010) Methane dynamics across wetland plant species. *Aquatic Botany*, 93(2), 107–113. <https://doi.org/10.1016/j.aquabot.2010.03.009>
- Kao-Kniffin, J., Freyre, D.S., Balsler, T.C. (2011) Increased methane emissions from an invasive wetland plant under elevated carbon dioxide levels. *Applied Soil Ecology*, 48(3), 309–312. <https://doi.org/10.1016/j.apsoil.2011.04.008>
- Karki, S., Elsgaard, L., Audet, J., Lærke, P.E. (2014) Mitigation of greenhouse gas emissions from reed canary grass in paludiculture: effect of groundwater level. *Plant and Soil*, 383, 217–230. <https://doi.org/10.1007/s11104-014-2164-z>
- Kollah, B., Patra, A.K., Mohanty, S.R. (2016) Aquatic microphylla *Azolla*: a perspective paradigm for sustainable agriculture, environment and global climate change. *Environmental Science and Pollution Research*, 23, 4358–4369. <https://doi.org/10.1007/s11356-015-5857-9>
- Kosten, S., Piñeiro, M., de Goede, E., de Klein, J., Lamers, L.P.M., Ettwig, K. (2016) Fate of methane in aquatic systems dominated by free-floating plants. *Water Research*, 104, 200–207. <https://doi.org/10.1016/j.watres.2016.07.054>
- Lenth, R.V. (2022) *emmeans: Estimated Marginal Means, aka Least-Squares Means*. R package version 1.7.4-1. Online at: <https://CRAN.R-project.org/package=emmeans>
- Liu, D., Ding, W., Jia, Z., Cai, Z. (2012) The impact of dissolved organic carbon on the spatial variability of methanogenic archaea communities in natural wetland ecosystems across China. *Applied Microbiology and Biotechnology*, 96(1), 253–263. <https://doi.org/10.1007/s00253-011-3842-x>
- Mandal, B., Vlek, P.L.G., Mandal, L.N. (1999) Beneficial effects of blue-green algae and *Azolla*, excluding supplying nitrogen, on wetland rice fields: A review. *Biology and Fertility of Soils*, 28, 329–342. <https://doi.org/10.1007/s003740050501>
- Martens, M., Karlsson, N.P.E., Ehde, P.M., Mattsson, M., Weisner, S.E.B. (2021) The greenhouse gas emission effects of rewetting drained peatlands and growing wetland plants for biogas fuel production. *Journal of Environmental Management*, 277, 111391, 9 pp. <https://doi.org/10.1016/J.JENVMAN.2020.111391>
- McInerney, E., Helton, A.M. (2016) The effects of soil moisture and emergent herbaceous vegetation on carbon emissions from constructed wetlands. *Wetlands*, 36(2), 275–284. <https://doi.org/10.1007/s13157-016-0736-9>
- McMillan, C. (1959) Salt tolerance within a typha population. *American Journal of Botany*, 46(7), 521–526. <https://doi.org/10.1002/j.1537-2197.1959.tb07044.x>
- Minke, M., Augustin, J., Burlo, A., Yarmashuk, T., Chuvashova, H., Thiele, A., Freibauer, A., Tikhonov, V., Hoffmann, M. (2016) Water level, vegetation composition, and plant productivity explain greenhouse gas fluxes in temperate cutover fens after inundation. *Biogeosciences*, 13(13), 3945–3970. <https://doi.org/10.5194/bg-13-3945-2016>
- Muster, C., Gaudig, G., Krebs, M., Joosten, H. (2015) Sphagnum farming: the promised land for peat bog species? *Biodiversity and Conservation*, 24(8), 1989–2009. <https://doi.org/10.1007/s10531-015-0922-8>
- Pazourek, J. (1977) The volumes of anatomical components in leaves of *Typha angustifolia* L. and *Typha latifolia* L. *Biologia Plantarum*, 19(2), 129–135.
- Peters, G., Meeks, J. (1989) The *Azolla-Anabaena* symbiosis: basic biology. *Annual Review of Plant Physiology and Plant Molecular Biology*, 40, 193–210.
- Pieterse, A.H., De Lange, L., Van Vliet, J. (1977) A comparative study of *Azolla* in the Netherlands. *Acta Botanica Neerlandica*, 26(6), 433–449.
- Pijlman, J., Geurts, J., Vroom, R., Bestman, M., Fritz, C., van Eekeren, N. (2019) The effects of harvest date and frequency on the yield, nutritional value and mineral content of the paludiculture crop cattail (*Typha latifolia* L.) in the first year after planting. *Mires and Peat*, 25, 04, 19 pp. <https://doi.org/10.19189/MaP.2017.OMB.325>
- Pinero-Rodríguez, M.J., Fernández-Zamudio, R., Arribas, R., Gomez-Mestre, I., Díaz-Paniagua, C. (2021) The invasive aquatic fern *Azolla filiculoides* negatively impacts water quality, aquatic vegetation and amphibian larvae in Mediterranean environments. *Biological Invasions*, 23(3), 755–769. <https://doi.org/10.1007/s10530-020-02402-6>
- Pineiro, J., Bates, D., DebRoy, S., Sankar, D., R Core Team (2020) *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-149. Online at: <https://CRAN.R-project.org/package=nlme>
- Quadra, G.R., Boonman, C.C.F., Vroom, R.J.E., Temmink, R.J.M., Smolders, A.J.P., Geurts, J.J.M., Aben, R.C.H., Weideveld, S.T.J., Fritz, C. (2023) Removing 10 cm of degraded peat mitigates unwanted effects of peatland rewetting: a mesocosm study. *Biogeochemistry*, 163, 65–84. <https://doi.org/10.1007/s10533-022-01007-6>
- Sander, R. (2015) Compilation of Henry's law constants (version 4.0) for water as solvent. *Atmospheric Chemistry and Physics*, 15(8), 4399–



4981. <https://doi.org/10.5194/acp-15-4399-2015>
- Sebacher, D.I., Harriss, R.C., Bartlett, K.B. (1985) Methane emissions to the atmosphere through aquatic plants. *Journal of Environmental Quality*, 14(1), 40–46. <https://doi.org/10.2134/jeq1985.00472425001400010008x>
- Segers, R. (1998) Methane production and methane consumption: a review of processes underlying wetland methane fluxes. *Biogeochemistry*, 41, 23–51.
- Sheppard, A.W., Shaw, R.H., Sforza, R. (2006) Top 20 environmental weeds for classical biological control in Europe: A review of opportunities, regulations and other barriers to adoption. *Weed Research*, 46(2), 93–117. <https://doi.org/10.1111/j.1365-3180.2006.00497.x>
- Sorrell, B.K., Brix, H. (2003) Effects of water vapour pressure deficit and stomatal conductance on photosynthesis, internal pressurization and convective flow in three emergent wetland plants. *Plant and Soil*, 253(1), 71–79. <https://doi.org/10.1023/A:1024517510541>
- Strachan, I.B., Nugent, K.A., Crombie, S., Bonneville, M.C. (2015) Carbon dioxide and methane exchange at a cool-temperate freshwater marsh. *Environmental Research Letters*, 10(6), 065006, 10 pp. <https://doi.org/10.1088/1748-9326/10/6/065006>
- Tanneberger, F., Tegetmeyer, C., Busse, S., Barthelmes, A. and 55 others (2017) The peatland map of Europe. *Mires and Peat*, 19, 22, 17 pp. <https://doi.org/10.19189/MaP.2016.OMB.264>
- Tanneberger, F., Appulo, L., Ewert, S., Lakner, S., Ó Brolcháin, N., Peters, J., Wichtmann, W. (2021) The power of nature-based solutions: How peatlands can help us to achieve key EU sustainability objectives. *Advanced Sustainable Systems*, 5(1), 2000146, 10 pp. <https://doi.org/10.1002/adsu.202000146>
- Tanneberger, F., Birr, F., Couwenberg, J., Kaiser, M., Luthardt, V., Nerger, M., Pfister, S., Oppermann, R., Zeitz, J., Beyer, C., van der Linden, S., Wichtmann, W., Närmann, F. (2022) Saving soil carbon, greenhouse gas emissions, biodiversity and the economy: paludiculture as sustainable land use option in German fen peatlands. *Regional Environmental Change*, 22(2), 69, 15 pp. <https://doi.org/10.1007/s10113-022-01900-8>
- Teder, T., Tammaru, T. (2002) Cascading effects of variation in plant vigour on the relative performance of insect herbivores and their parasitoids. *Ecological Entomology*, 27(1), 94–104. <https://doi.org/10.1046/J.0307-6946.2001.00381.X>
- Temmink, R.J.M., Fritz, C., van Dijk, G., Hensgens, G., Lamers, L.P.M., Krebs, M., Gaudig, G., Joosten, H. (2017) Sphagnum farming in a eutrophic world: The importance of optimal nutrient stoichiometry. *Ecological Engineering*, 98, 196–205. <https://doi.org/10.1016/j.ecoleng.2016.10.069>
- Tiemeyer, B., Albiac Borraz, E., Augustin, J., Bechtold, M. and 19 others (2016) High emissions of greenhouse gases from grasslands on peat and other organic soils. *Global Change Biology*, 22(12), 4134–4149. <https://doi.org/10.1111/gcb.13303>
- Tornbjerg, T., Bendix, M., Brix, H. (1994) Internal gas transport in *Typha latifolia* L. and *Typha angustifolia* L. 2. Convective throughflow pathways and ecological significance. *Aquatic Botany*, 49(2–3), 91–105. [https://doi.org/10.1016/0304-3770\(94\)90031-0](https://doi.org/10.1016/0304-3770(94)90031-0)
- van den Berg, M., van den Elzen, E., Ingwersen, J., Kosten, S., Lamers, L.P.M., Streck, T. (2020) Contribution of plant-induced pressurized flow to CH₄ emission from a *Phragmites* fen. *Scientific Reports*, 10(1), 12304, 9 pp. <https://doi.org/10.1038/s41598-020-69034-7>
- van den Berg, M., Gremmen, T.M., Vroom, R.J.E., Van Huissteden, J., Boonman, J., Van Huissteden, C.J.A., Van Der Velde, Y., Smolders, A.J.P., Van De Riet, B.P. (2024) A case study on topsoil removal and rewetting for paludiculture: effect on biogeochemistry and greenhouse gas emissions from *Typha latifolia*, *Typha angustifolia*, and *Azolla filiculoides*. *Biogeosciences*, 21, 2669–2690. <https://doi.org/10.5194/bg-21-2669-2024>
- Van Der Nat, F.J.W.A., Middelburg, J.J. (1998) Seasonal variation in methane oxidation by the rhizosphere of *Phragmites australis* and *Scirpus lacustris*. *Aquatic Botany*, 61(2), 95–110. [https://doi.org/10.1016/S0304-3770\(98\)00072-2](https://doi.org/10.1016/S0304-3770(98)00072-2)
- Van Der Nat, F.-J.W.A., Middelburg, J.J., Van Meteren, D., Wielemakers, A. (1998) Diel methane emission patterns from *Scirpus lacustris* and *Phragmites australis*. *Biogeochemistry*, 41(1), 1–22. <https://doi.org/10.1023/A:1005933100905>
- Veraart, A.J., Steenbergh, A.K., Ho, A., Kim, S.Y., Bodelier, P.L.E. (2015) Beyond nitrogen: The importance of phosphorus for CH₄ oxidation in soils and sediments. *Geoderma*, 259–260, 337–346. <https://doi.org/10.1016/j.geoderma.2015.03.025>
- Vroom, R.J.E., Xie, F., Geurts, J.J.M., Chojnowska, A., Smolders, A.J.P., Lamers, L.P.M., Fritz, C. (2018) *Typha latifolia* paludiculture effectively improves water quality and reduces greenhouse gas emissions in rewetted peatlands. *Ecological Engineering*, 124, 88–98. <https://doi.org/10.1016/j.ecoleng.2018.09.008>
- Vroom, R.J.E., Geurts, J.J.M., Nouta, R., Borst, A.C.W., Lamers, L.P.M., Fritz, C. (2022a) Paludiculture crops and nitrogen kick-start ecosystem service provisioning in rewetted peat

- soils. *Plant and Soil*, 474, 337–354. <https://doi.org/10.1007/s11104-022-05339-y>
- Vroom, R.J.E., van den Berg, M., Pangala, S., van der Scheer, O., Sorrell, B. (2022b) Physiological processes affecting methane transport by wetland vegetation - A review. *Aquatic Botany*, 182, 103547, 13 pp. <https://doi.org/10.1016/j.aquabot.2022.103547>
- Wagner, G.M. (1997) *Azolla*: A review of its biology and utilization. *The Botanical Review*, 63, 1–26. <https://doi.org/10.1007/BF02857915>
- Whiting, G.J., Chanton, J.P. (1996) Control of the diurnal pattern of methane emission from emergent aquatic macrophytes by gas transport mechanisms. *Aquatic Botany*, 54(2–3), 237–253. [https://doi.org/10.1016/0304-3770\(96\)01048-0](https://doi.org/10.1016/0304-3770(96)01048-0)
- Wichtmann, W., Schröder, C., Joosten, H. (eds.) (2016) *Paludiculture, Productive Use of Wet Peatlands: Climate Protection, Biodiversity, Regional Economic Benefits*. Schweizerbart Science Publishers, Stuttgart, 272 pp.
- Wickham, H. (2016) *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York. Online at: <https://ggplot2.tidyverse.org>
- Xu, H., Zhu, B., Liu, J., Li, D., Yang, Y., Zhang, K., Jiang, Y., Hu, Y., Zeng, Z. (2017) *Azolla* planting reduces methane emission and nitrogen fertilizer application in double rice cropping system in southern China. *Agronomy for Sustainable Development*, 37(4), 9 pp. <https://doi.org/10.1007/s13593-017-0440-z>
- Yavitt, J.B. (1997) Methane and carbon dioxide dynamics in *Typha latifolia* (L.) wetlands in central New York State. *Wetlands*, 17(3), 394–406. <https://doi.org/10.1007/BF03161429>
- Submitted 05 Dec 2023, revision 20 Aug 2024*
Editors: Gerald Jurasinski and Olivia Bragg

Author for correspondence: Renske Vroom, Peatland Studies and Palaeoecology, Institute of Botany and Landscape Ecology, Soldmannstraße 15, 17489 Greifswald, Germany.
Tel: +49 3834 420-4179; E-mail: renske.vroom@uni-greifswald.de

Appendix

Pictures of the *Typha* stands during the 2020 field season can be found at: <https://doi.org/10.5281/zenodo.13348040>

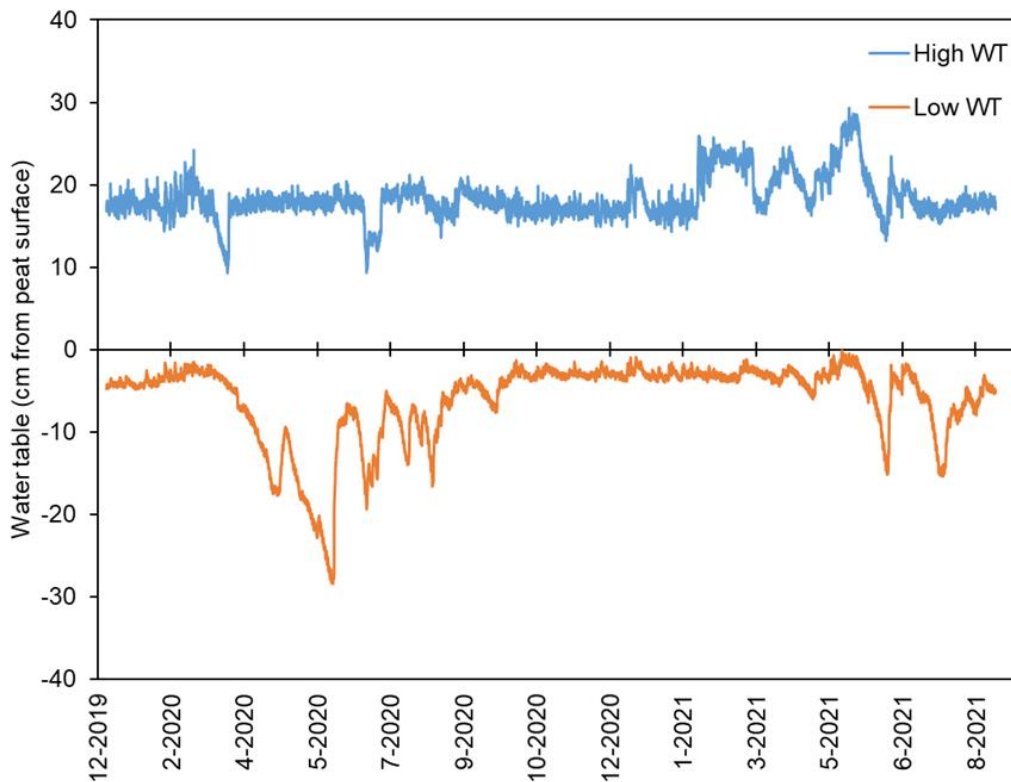


Figure A1. Water table height in the +20 cm WT (B2, B4) and 0 cm WT (B1) basins.

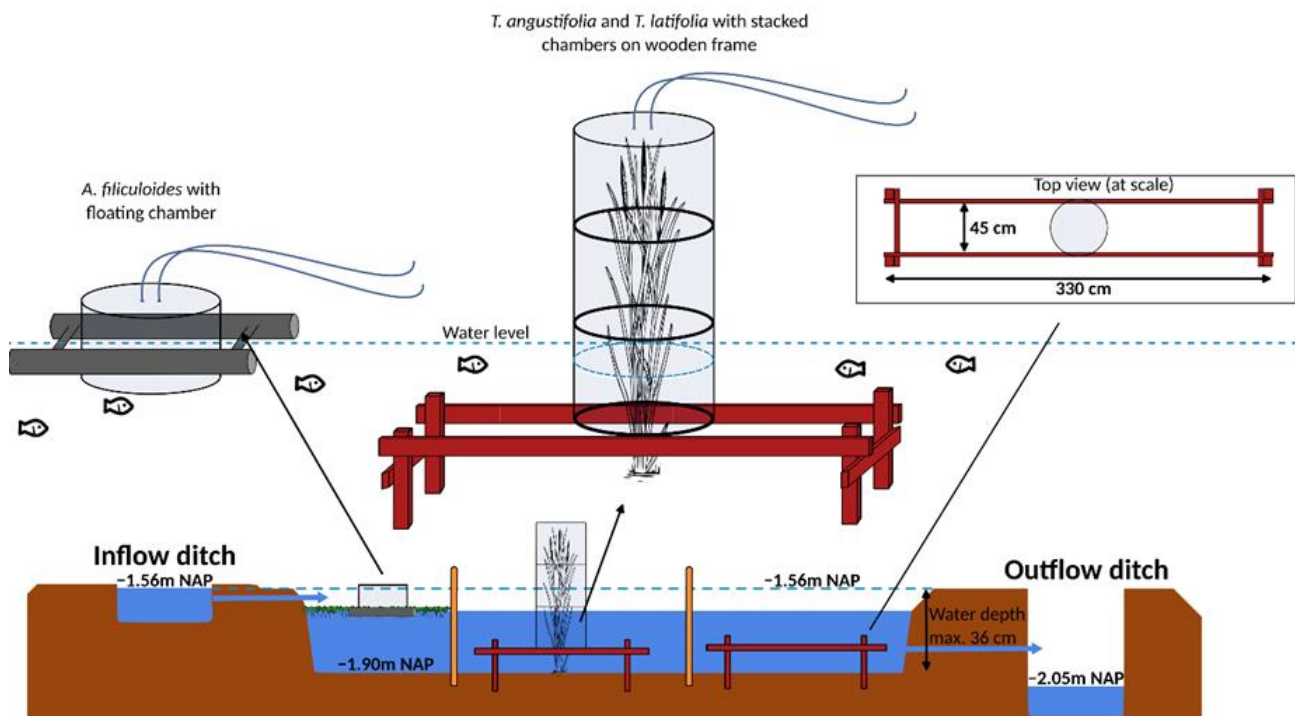


Figure A2. Visual representation of the diffusive flux measurement setup (see also van den Berg *et al.* 2024). Water tables are relative to Amsterdam Ordnance Datum (NAP).