

LETTER

Rooted macrophytes reduce sediment CH₄ storage and net production: An experimental approach using a novel scanning method

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Scientific Significance Statement

Methane (CH₄) is a potent GHG, and freshwater ecosystems are among the largest natural sources. However, our capacity to estimate these emissions remains limited, especially in vegetated zones where plants influence CH₄ fluxes. This study shows how various types of aquatic plants, influence CH₄ storage in sediments and its emissions to the atmosphere. By combining a novel scanning method with emission measurements in a controlled experiment, we show that plant characteristics, particularly root biomass and growth form, strongly influence CH₄ production, storage, and emission pathways. Importantly, we demonstrate that changes in sediment gas storage is a major but often overlooked component of freshwater CH₄ budgets. Our scanning method is an effective new approach to quantify CH₄ storage in aquatic ecosystems and can help unravel plant-specific characteristics affecting CH₄ production and emissions.

Abstract

Methane (CH₄) emissions from freshwater ecosystems are significant but rarely quantified in vegetated zones. We assessed the influence of five macrophyte species that root in the sediment differing in growth form and root biomass on CH₄ emissions and sediment gas storage. Using a novel scanning method, we visualized sediment bubbles and root structures over time. Macrophyte growth form influenced diffusive as well as ebullitive emissions. Bubbles occupied a smaller volume in vegetated sediments (~19%) than in control treatments (~53%). Extensive root systems were associated with reduced sediment CH₄ accumulation, likely due to enhanced CH₄ oxidation and/or transport. Total CH₄ production was lower in vegetated (~54 mg CH₄ m⁻² d⁻¹) than in control treatments (103 mg CH₄ m⁻² d⁻¹), of which a substantial part was stored in sediment bubbles. Our findings highlight the importance of including changes in sediment CH₄ storage in CH₄ budgets and demonstrate how macrophyte characteristics shape CH₄ dynamics.

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Methane (CH₄) is a potent greenhouse gas (GHG), with a global warming potential 27 times greater than carbon dioxide (CO₂) over a 100-yr timeframe (Forster et al. 2021). Freshwaters account for nearly half of the global CH₄ emissions (Rosentreter et al. 2021). However, estimates remain highly uncertain, largely due to limited data on ebullition (bubble-mediated emissions) and emissions from vegetated zones (Bodmer et al. 2024; Rosentreter et al. 2021). Most research on aquatic CH₄ emissions has focused on open water zones, often overlooking vegetated areas despite their potentially significant role in governing CH₄ emissions (Bodmer et al. 2024). Reducing these uncertainties is crucial for improving global GHG budgets and advancing our understanding of CH₄ dynamics in freshwater systems.

Recognizing the role of vegetated areas is essential, as macrophytes regulate CH₄ production, oxidation, and transport. Studies comparing vegetated and non-vegetated areas show that macrophytes can reduce CH₄ emissions, although the extent varies depending on species-specific characteristics, gas exchange mechanisms, and environmental factors (Bastviken et al. 2023; Bodmer et al. 2024; Struik et al. 2022). Through aerenchyma, macrophytes transport oxygen to their roots, releasing it into sediments, a process known as radial oxygen loss (ROL). Radial oxygen loss creates oxic zones around the roots that promote CH₄ oxidation (Lemoine et al. 2012; Mueller and Megonigal 2024). Simultaneously, some species transport CH₄ from sediments to the atmosphere through their aerenchyma, bypassing oxidation in the upper sediment layer and water column (Villa et al. 2020). Little is known about the relative importance of these two contrasting macrophyte effects on CH₄ emissions and how they relate to macrophyte characteristics, such as growth form and root biomass.

While various methods exist to quantify CH₄ emissions from vegetated areas (see Bodmer et al. 2024), approaches to measure CH₄ storage within sediments are less established. This is an important limitation because understanding bubble characteristics and dynamics is crucial for predicting ebullition and developing process-based CH₄ models (Katsman et al. 2024; Marcon et al. 2022; Peltola et al. 2018). CH₄ is stored in sediments either dissolved in porewater or as free gas (bubbles), which form when solubility limits are exceeded. Dissolved CH₄ storage can be estimated by multiplying porewater CH₄ concentrations by porewater volume (Hilgert et al. 2015). However, the amount of CH₄ stored in bubbles is rarely quantified. This is noteworthy since up to ~18% of sediment volume may consist of bubbles (Liu et al. 2016), and they are often largely composed of CH₄ (Langenegger et al. 2019).

Current methods for estimating bubbles in sediments include ground-penetrating radar, a non-invasive technology for use in laboratory and field settings. However, it is limited to shallow systems and provides only partial environmental information (Knight 2001; Mustasaar and Comas 2017). Another method, x-ray computed tomography, requires freezing the sediment, introducing uncertainties by disturbing

sediment structure and compromising repeated measurements (Dück et al. 2019; Liu et al. 2018). Emerging techniques such as inverse geoacoustic methods and echo sounding demonstrate strong potential for estimating sediment gas content in reservoirs and lakes, but lack vertical spatial resolution (Katsnelson et al. 2017; Marcon et al. 2022; Uzhansky et al. 2020). Hence, despite advances, direct in situ measurements of bubbles in sediment remain limited.

This study shows how macrophyte species that root in the sediment, with different growth forms (submerged vs. floating-leaved) and root biomass, influence CH₄ storage and emissions. We compare vegetated and unvegetated systems. Our hypotheses are: H1: Macrophytes reduce total net CH₄ production compared to non-vegetated systems. H2: Macrophytes with floating leaves emit more CH₄ than submerged macrophytes by providing a pathway for gas exchange between sediments and the atmosphere. H3: Root biomass is negatively correlated with sediment bubble CH₄ stock, as root systems facilitate gas transport and enhance oxygenation at the sediment–root interface. To test these hypotheses, we conducted a controlled microcosm experiment with five macrophyte species and a non-vegetated control, using a novel technique to measure CH₄ storage in sediments.

Materials and methods

Experimental design

The experiment lasted 7 weeks (April to June 2023) and was conducted in a greenhouse at Radboud University, the Netherlands (51°49'21"N, 5°52'26"E). Thirty microcosms (50 × 34 × 18 cm) were filled with sediment (~20 cm depth) collected from a ditch in a peat meadow (Zegveld, the Netherlands; 52°8'25"N, 4°50'18"E) and rainwater (~20 cm depth). The sediment, containing 15% organic matter, was sieved (mesh size 0.5 cm) to remove invertebrates and macrophyte propagules. Water levels were maintained by adding rainwater to offset evaporation. The greenhouse had natural light (~16 h 32 min light/7 h 28 min dark) at ~24°C.

Each microcosm was equipped with a water circulation pump (200 L h⁻¹) and a transparent acrylic tube positioned diagonally at a 61° angle, allowing for the insertion of a scanner ("Scanning method for gas bubbles and roots" section).

The experiment included six treatments: five macrophyte species that root in the sediment (*Callitriche palustris*, *Potamogeton natans*, *Potamogeton crispus*, *Elodea nuttallii*, and *Myriophyllum spicatum*) and a non-vegetated control, each with four replicates. The selected species represent different growth forms common in European temperate freshwater ecosystems: *C. palustris* and *P. natans* have floating leaves, while *P. crispus*, *E. nuttallii*, and *M. spicatum* are fully submerged. Macrophytes were acclimated in the greenhouse for 1 month, during which no noticeable differences in growth were observed. Following planting in the microcosms, an establishment period of 2 weeks was provided to reduce potential

disturbance effects. All microcosms started with ~ 120 g fresh weight of macrophyte biomass.

Water-atmosphere diffusion of CH₄

Water-atmosphere CH₄ emissions, including diffusive and plant-mediated emissions, were measured weekly during the day and night using a chamber connected to a GHG analyzer (Picarro-G2508). Diel emission intensities were calculated based on the weighted average according to the hours of daylight. For details, see Supporting Information Methods section (M1).

CH₄ ebullition

Ebullition was quantified weekly using two permanently installed bubble traps (Ø 0.08 m) per microcosm. Gas samples were analyzed for CH₄ concentration by gas chromatography. Weekly ebullitive emissions were calculated from gas volume, CH₄ concentration, funnel area, and deployment time. The average ebullition intensity was used to calculate the total emission during the experiment. For details, see Supporting Information Methods section (M2).

Scanning method for gas bubbles and roots

We developed a novel scanning method (hereafter “scanner”) to assess bubble and root areas using a CI-600 CanoScan imager (CID Bio-Science), a portable cylindrical device (105 cm long) with a 360° rotating head capturing high-resolution images (~ 23.6 px mm⁻¹). Water-sealed acrylic tubes (Ø 70 mm) were permanently installed diagonally in each aquarium to enable scanning (Supporting Information Fig. S1). Scans were taken once per week in all the microcosms throughout the experiment. Images were analyzed using FIJI/ImageJ software for semi-automatic annotation of bubbles and roots, quantifying their area, distribution (in *X* and *Y*-axes), and shape (bubbles with roundness > 0.4 were considered circular, and those with roundness ≤ 0.4 were considered elongated).

Bubbles were distributed along the entire perimeter of the acrylic tube, with no visible accumulation on its surface (Supporting Information Fig. S1). The sum of individual bubble areas per image, expressed as a percentage of the total image area, was used as a proxy for the proportion of sediment volume composed of bubbles. The same approach was applied to the root area. Assuming that the scans represent random cross-sections of bubbles, we translated the area to volume, using the total sediment volume. Detailed methods for assessing gas content in sediment and water column (free gas and dissolved gas) are described in the Supporting Information Methods section (M3 and M4).

Data analysis

The contribution of diffusion to total CH₄ emissions was calculated for each microcosm as the diffusive emission divided by the sum of diffusive and ebullitive emissions, multiplied by 100. The few (minor) negative diffusive emissions (i.e., uptake) were excluded to focus on emissions only.

Total net CH₄ production during the experiment was estimated by summing emission and accumulation components,

expressed in mg CH₄ m⁻². Emissions included total water-atmosphere CH₄ fluxes (diffusive and ebullitive), integrated over the experimental period. Net CH₄ accumulation was calculated as the net increase (final minus initial) in three compartments: (1) CH₄ stored in sediment gas bubbles (estimated from the change in bubble volume between the start and end of the experiment—calculated from images—multiplied by the final CH₄ concentration in the sediment bubbles [assuming CH₄ bubble concentration stayed constant]); (2) dissolved CH₄ in porewater (using initial and final porewater CH₄ concentration, and porewater volume); and (3) dissolved CH₄ in surface water (using initial and final surface water CH₄ concentration and surface water volume). All components were summed to estimate total net CH₄ production per microcosm (Supporting Information Methods section, M5).

To further assess macrophyte impact on water-atmosphere gas exchange, we calculated the gas transfer velocity (*k*; Supporting Information Methods section, M6). For treatments with macrophytes, *k* represents an apparent exchange velocity, plant-mediated transport may also play a role.

To test the effect of macrophyte species on diffusive and ebullitive CH₄ emissions over time, we used linear mixed-effects models. CH₄ diffusion was log-transformed (log[*x* + 1]) to ensure all values were positive and included in the analysis, and ebullitive emissions were square root-transformed to improve normality of residuals. To test the effect of treatments on the percentage of sediment occupied by roots and gas bubbles, we used generalized linear mixed models (GLMMs), specifying a Gamma distribution with a log-link function to account for non-normality of residuals. To assess the relationship between root and bubble volume, we applied a non-parametric Spearman rank correlation, as the data did not meet normality assumptions.

All mixed models included treatment as a fixed effect, with microcosm ID and time as random effects. Additional GLMMs were used to explore relationships between bubble and root volume and ebullition.

Differences in total CH₄ emissions over the experiment and net CH₄ production were analyzed using linear models (LMs). Log-transformed total emissions were compared across macrophyte species and growth forms (floating vs. submerged) using standard LMs. Residuals, Shapiro–Wilk, and correlations confirmed model assumptions. Data are available at DANS repository (Cabrera-Lamanna et al. 2025).

Results

Root and shoot biomass

The macrophytes developed differently during the experiment. *Potamogeton natans*, *E. nuttallii*, and *M. spicatum* reached the highest above-sediment biomass by the end of the experiment, while *P. natans*, *P. crispus*, and *M. spicatum* reached the highest root biomass (Supporting Information Table S1). The significantly higher root biomass in these three

treatments was also evident from the scanner images (“Scanner-derived bubble and root characteristics” section).

CH₄ emission

Ebullitive emissions varied widely among replicates in the control and submerged macrophyte treatments (Fig. 1A) but remained consistently low in treatments with floating-leaved macrophytes. The ebullition rate showed no clear pattern throughout of the experiment (Supporting Information Fig. S2). Although mean ebullition did not differ significantly between treatments, analysis by growth form showed that ebullitive emissions were significantly higher in submerged than floating-leaved macrophyte treatments (LM, $p = 0.01$). Root volume was not significantly related to ebullition (GLMM, $p = 0.33$).

Diel diffusive fluxes ranged from -0.99 to 3.49 mg CH₄ m⁻² d⁻¹, with *P. natans* showing significantly higher mean emissions than all other treatments (Fig. 1B, LM, $p = 0.006$). Diel diffusive emissions showed no clear pattern throughout the experiment (Supporting Information Fig. S2). Emissions during day and night did not differ significantly (Supporting Information Fig. S3). Diel diffusive CH₄ emissions, including plant-mediated transport, represented only a small fraction of the total CH₄ emissions. Contribution

ranged from $0.3\% \pm 0.25\%$ (mean $\pm$ SD) in *M. spicatum*, to $7.38\% \pm 0.03\%$ in *P. natans*, with intermediate values in *E. nuttallii* ($0.47\% \pm 0.37\%$), *P. crispus* ($1.52\% \pm 1.89\%$), and the control ($0.67\% \pm 1.03\%$).

Scanner-derived bubble and root characteristics

Root volume in the sediment differed significantly among treatments (GLMM, $p < 0.001$; Fig. 2A), with *P. natans* and *P. crispus* showing the highest percentage of sediment occupied by roots. The scans also revealed species-specific differences in root depth distribution. For instance, *P. natans* had peak root volume near the sediment surface, while *P. crispus* peaked at a depth of 9–12 cm (Supporting Information Fig. S4D).

The cross-sectional area of individual bubbles ranged from 5.0×10^{-4} to 1.9975 cm², with a median of 2.34×10^{-2} cm² (see Supporting Information Results section, R1). Bubbles made up 0.16% to 3.06% of the sediment volume. Bubble volume was positively correlated with ebullition rates (GLMM, $p = 0.0007$) and differed among treatments (GLMM, $p < 0.001$), with the highest values in control and lowest in species with extensive root systems (*P. natans*, *P. crispus*, and *M. spicatum*; Fig. 2B). When grouping all species, root volume was significantly negatively correlated with bubble volume

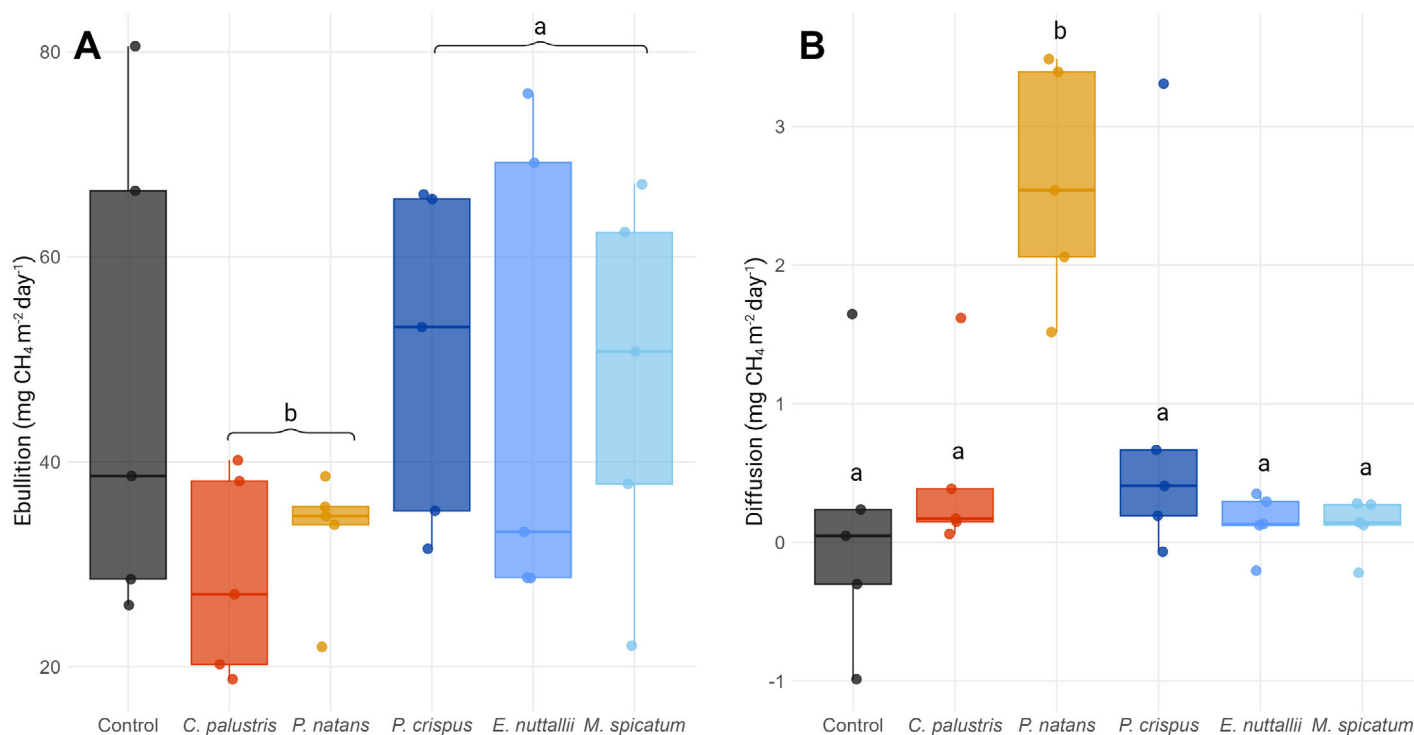


Fig. 1. Average methane fluxes via (A) ebullition, and (B) diel diffusion including plant-mediated transport. Boxplots display the median (horizontal line), interquartile range (box), and whiskers extending to 1.5 times the interquartile range. Statistical differences between treatments were determined using simple linear models followed by Tukey's post hoc test and are indicated by different letters (based on post hoc pairwise comparisons, $p < 0.05$). In (A) brackets group macrophyte growth-forms, with floating leaved species (*Callitriche palustris*, *Potamogeton natans*) significantly differing from submerged species (*Potamogeton crispus*, *Elodea nuttallii*, *Myriophyllum spicatum*).

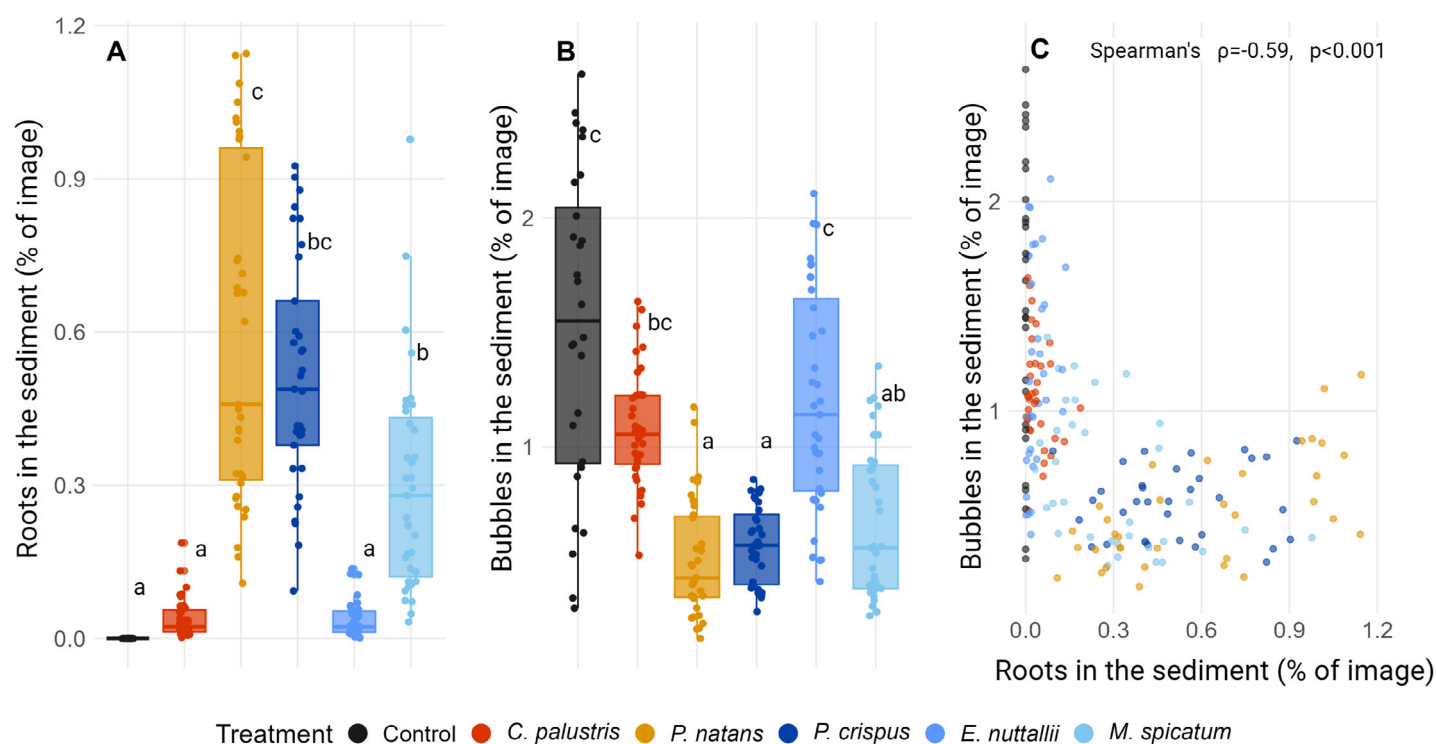


Fig. 2. Sediment root and gas bubble volume (weekly measurements over 7 weeks; $n = 5$ per treatment) and their relationship. **(A)** Sediment root area expressed as a percentage of the image area. **(B)** Sediment area occupied by gas bubbles, also expressed as a percentage of the image area. **(C)** Relationship between sediment root area and gas bubble area across all treatments. Boxplots are formatted as described in Fig. 1. Statistical differences among treatments in **(A, B)** were assessed using GLMMs with microcosm ID and time as random effects (Gaussian distribution). Treatments not sharing a letter differ significantly from each other (post-hoc pairwise comparisons, $p > 0.05$). In **(C)**, Spearman rank correlation indicated a significant negative relationship ($\rho = -0.59$, $p < 0.001$).

(Spearman's $\rho = -0.59$, $p < 0.001$; Fig. 2C). When testing each species separately, no clear trends emerged.

Sediment and water gas content and gas exchange velocity

Sediment bubbles consisted predominantly of CH₄ (~99%; Supporting Information Table S2). At the end of the experiment, porewater CH₄ ranged from 1.28 to 2.00 mg L⁻¹, with no significant treatment differences. Surface water CH₄ remained low (0.1 µg L⁻¹) across treatments. Porewater dissolved inorganic carbon (DIC) did not differ significantly, although *P. natans* tended to have slightly higher concentrations than the control (LM, $p = 0.08$; Supporting Information Table S3). Apparent gas exchange velocity (k) was highest in *P. natans* (0.789 ± 0.492 m d⁻¹) than in all other treatments (LM, $p < 0.001$; Supporting Information Table S3), and lowest in the control (0.004 ± 0.220 m d⁻¹).

Stocks and fluxes: Net CH₄ production

During the experiment, most of the net CH₄ produced was emitted to the atmosphere, while a smaller proportion remained in the system, primarily in sediment bubbles (Fig. 3). Net CH₄ production was highest in the control (LM, $p = 0.011$), with the produced CH₄ divided nearly evenly between emissions and retention bubbles. In macrophyte

treatments, ~19% of the net CH₄ production was retained in sediment bubbles. The highest accumulation was observed in *E. nuttallii* (31%), and the lowest in *C. palustris* (8%).

Discussion

Net CH₄ production, as reflected in the sum of total emissions and CH₄ accumulation in the sediment, was consistently and significantly lower in macrophyte treatments than in the unvegetated control, supporting hypothesis 1. This finding underscores the important role of rooted macrophytes in regulating CH₄ dynamics in freshwater sediments. By limiting net CH₄ production, either by increasing oxidation or by decreasing production, macrophytes help reduce CH₄ emissions, playing a key role in GHG mitigation.

To gain deeper insight into sediment CH₄ stored in bubbles and monitor spatial and temporal variations in bubbles across treatments, we used a novel scanner method. The images provided information on individual bubbles in sediment as well as on the distribution of roots. Bubble sizes (Ø) in our experiment (median: 1728 µm; maximum: ~15,950 µm) fall within the range reported by Liu et al. (2016), who used a digital photo camera to observe bubbles up to 18,200 µm in

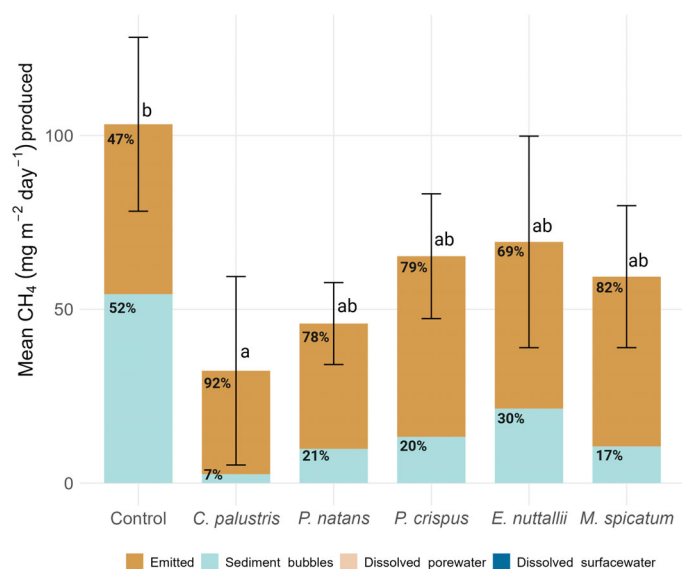


Fig. 3. Fate of net CH₄ production over a seven-week experiment across macrophyte treatments. Bars represent mean net CH₄ production (mg m⁻² d⁻¹) and its partitioning between two main compartments: CH₄ emitted to the atmosphere and CH₄ accumulated in sediment bubbles. Contributions from dissolved CH₄ in porewater and surface water (<0.1%) are not visible in the figure. Error bars represent the standard deviation of total net CH₄ production (i.e., the sum of all compartments). Different letters above bars indicate statistically significant differences among treatments based on a linear model followed by Tukey's post hoc test ($p < 0.05$). Most of the CH₄ was emitted, followed by accumulation in bubbles. Percentages within the bars indicate the relative contribution of each compartment.

clay- and silt-rich sediments. Our values also align with those reported by Liu et al. (2018), who, using x-ray microtomography, observed bubble diameters up to 6100 μ m in clay and 3500 μ m in sand. Differences in sizes may be influenced by imaging technique, resolution, and sediment properties, especially elasticity and fracture behavior, which are known to strongly influence bubble size (Katsman 2024).

Although the total volume of bubbles differed among treatments (Fig. 2B), we did not find indications for macrophytes impacting individual bubble size (Supporting Information Fig. S4). The spatial distribution of bubbles revealed clear depth patterns: larger, rounder bubbles were concentrated near the sediment surface, while smaller, more elongated bubbles appeared deeper, consistent with previous observations (Boudreau 2012; Liu et al. 2018) and likely reflecting vertical pressure gradients in the sediment.

Our results show that a considerable portion of the CH₄ produced in sediments can be stored in gas bubbles, and that the abundance of roots in sediment strongly affects this storage. Yet, current assessments of ecosystem CH₄ budgets, as well as the impact of vegetation on these budgets, focus mostly on water-atmosphere fluxes (Bodmer et al. 2024) and do not account for variations in the sediment CH₄ stock.

Although some models include sediment CH₄ stock to predict ebullition dynamics, they assume a constant bubble size and gas content (Peltola et al. 2018). Our analysis shows that sediment CH₄ stocks are dynamic. Between the start and end of the experiment, mean bubble volume increased by 29% in *C. palustris* treatment and by 261% in control treatment. Therefore, accounting for variation in sediment CH₄ storage linked to vegetation could improve estimates of spatial and temporal CH₄ dynamics (Katsman et al. 2024; Liu et al. 2016), thereby improving our understanding of emission drivers and enhancing CH₄ budget estimations.

Supporting hypothesis 3, we observed a significant negative relationship between roots and gas bubbles, suggesting that macrophytes with extensive root systems reduce sediment CH₄ stocks. This may either result from a decrease in net CH₄ production, for example, via ROL, enhancing CH₄ oxidation (Kosten et al. 2016; Lai et al. 2012) or an increase in plant-mediated CH₄ transport to the atmosphere (Bhullar et al. 2013; Oliveira Junior et al. 2018).

Although we did not directly measure oxidation, our results suggest that both plant-mediated transport and oxidation occurred. First, net CH₄ production was consistently lower in vegetated systems compared to the control (Fig. 3), likely in part due to ROL increasing CH₄ oxidation and/or inhibiting methanogenesis. In particular, the relatively high porewater dissolved inorganic carbon concentrations in the *P. natans* treatment (Supporting Information Table S3) may reflect CO₂ production from CH₄ oxidation (Lemoine et al. 2012). Moreover, *M. spicatum* and *P. crispus* have been found to exhibit considerable ROL (Laskov et al. 2006). Furthermore, most—if not all—aquatic plant leaves and stems can act as a niche for methanotrophs further enhancing CH₄ oxidation (e.g., Esposito et al. 2023; Yoshida et al. 2014). Second, supporting hypothesis 2, we found indications of plant-mediated transport. It was most evident in *P. natans* treatments, which showed the highest diffusive CH₄ emissions, particularly during the day (Supporting Information Fig. S3), and the highest apparent gas exchange coefficient (k -value; Supporting Information Table S3), suggesting active gas transport (Vroom et al. 2022). This finding aligns with indications of considerable CH₄ transport in other floating leaved macrophytes including *Nuphar lutea* (Ribaudo et al. 2012) and *Pontederia crassipes* (formerly *Eichhornia crassipes*) (Oliveira Junior et al. 2018, 2020).

Although *C. palustris* is also a floating-leaved macrophyte, it lacked indicators of plant-mediated transport, possibly, because it has smaller floating leaves than *P. natans* and many of its leaves are submerged. Nevertheless, ebullition in the systems with *C. palustris* was lower than in those with the submerged species (*M. spicatum*, *P. crispus*, *E. nuttallii*; Fig. 1A), despite its low root biomass (Fig. 2A). *Callitriche palustris* may facilitate CH₄ transport from the sediment to its submerged floating leaves and prolific water-column roots, promoting subsequent oxidation. Hence, while CH₄ transportation has

been found to scale with plant surface area and biomass within a single species (Struik et al. 2022), intra-specific differences (e.g., stomata regulation) may strongly impact plant-mediated CH₄ fluxes (see also Villa et al. 2020; Bodmer et al. 2024), making generalization difficult.

Overall, our findings reveal general patterns across species: all rooted macrophytes studied here decreased net CH₄ production, but the extent to which they affected net CH₄ production differed between species. Broad classifications such as submerged and floating-leaved may fall short in explaining the differences, as variation within each group was substantial. As in the floating-leaved macrophytes, similar variation occurred in sediment CH₄ storage within submerged macrophytes. For instance, *E. nuttallii*, having low root volume, had much less CH₄ stored in gas bubbles compared to large root macrophytes *P. crispus* and *M. spicatum* (Fig. 2A,B). Hence, although growth form and root biomass explain part of the variation in net CH₄ production and emission, species-specific characteristics (e.g., aerenchyma porosity, root morphology, ROL barriers) can also shape CH₄ dynamics (Vroom et al. 2022). The consistent difference in CH₄ dynamics between unvegetated and vegetated conditions, clearly indicates both should be considered when quantifying whole-system CH₄ emissions.

Author Contributions

Lucía Cabrera-Lamanna: conceptualization, writing – original draft, formal analysis, data curation, investigation, methodology, visualization, writing – review and editing. Ilenia Marquina-Luevano: conceptualization, investigation, methodology, writing – review and editing. Eric J. W. Visser: supervision, writing – review and editing. Dick van Oevelen: conceptualization, supervision, writing – review and editing. Andreas Lorke: conceptualization, writing – review and editing. Sarian Kosten: conceptualization, supervision, writing – review and editing.

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Data Availability Statement

All data supporting the findings of this study are available in the DANS life sciences repository URL: <https://doi.org/10.17026/LS/G7PTWH> (Cabrera-Lamanna et al. 2025).

References

- Bastviken, D., C. C. Treat, S. R. Pangala, et al. 2023. “The Importance of Plants for Methane Emission at the Ecosystem Scale.” *Aquatic Botany* 184: 103596. <https://doi.org/10.1016/j.aquabot.2022.103596>.
- Bhullar, G. S., M. Iravani, P. J. Edwards, and H. Olde Venterink. 2013. “Methane Transport and Emissions From Soil as Affected by Water Table and Vascular Plants.” *BMC Ecology* 13: 1–9. <https://doi.org/10.1186/1472-6785-13-32>.
- Bodmer, P., R. J. E. Vroom, T. Stepina, P. A. del Giorgio, and S. Kosten. 2024. “Methane Dynamics in Vegetated Habitats in Inland Waters: Quantification, Regulation, and Global Significance.” *Frontiers in Water* 5: 1332968. <https://doi.org/10.3389/frwa.2023.1332968>.
- Boudreau, B. P. 2012. “The Physics of Bubbles in Surficial, Soft, Cohesive Sediments.” *Marine and Petroleum Geology* 38, no. 1: 1–18. <https://doi.org/10.1016/j.marpetgeo.2012.07.002>.
- Cabrera-Lamanna, L., I. Marquina-Luevano, E. J. W. Visser, and S. Kosten. 2025. *Methane Emissions and Sediment Gas Storage in Freshwater Microcosms with Rooted Macrophytes*. DANS Data Station Life Sciences, V1. <https://doi.org/10.17026/LS/G7PTWH>.
- Dück, Y., L. Liu, A. Lorke, I. Ostrovsky, R. Katsman, and C. Jokiel. 2019. “A Novel Freeze Corer for Characterization of Methane Bubbles and Assessment of Coring Disturbances.” *Limnology and Oceanography: Methods* 17, no. 5: 305–319. <https://doi.org/10.1002/lom3.10315>.
- Espósito, C., T. P. A. Nijman, A. J. Veraart, et al. 2023. “Activity and Abundance of Methane-Oxidizing Bacteria on Plants in Experimental Lakes Subjected to Different Nutrient and Warming Treatments.” *Aquatic Botany* 185: 103610. <https://doi.org/10.1016/j.aquabot.2022.103610>.
- Forster, P., T. Storelvmo, K. Armour, et al. 2021. “The Earth’s Energy Budget, Climate Feedbacks, and Climate Sensitivity.” In *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, 1–204. Cambridge University Press.
- Hilgert, S., F. Gauger, S. Hölzlwimmerl, and S. Fuchs. 2015. “Development of a Flexible Dialysis Pore Water Sampler Placement System: Easy Handling and Related Error Sources.” *Journal of Limnology* 74, no. 2: 414–420. <https://doi.org/10.4081/jlimnol.2014.1054>.
- Katsman, R. 2024. “Mechanics of Methane Bubbles in Consolidated Aquatic Muds.” *Earth-Science Reviews* 257: 104908. <https://doi.org/10.1016/j.earscirev.2024.104908>.
- Katsman, R., E. Uzhansky, A. Lunkov, and B. Katsnelson. 2024. “Methane Gas Dynamics in Sediments of Lake Kinneret, Israel, and Their Controls: Insights From a Multi-annual Acoustic Investigation and Correlation Analysis.”

- Science of the Total Environment* 918: 170480. <https://doi.org/10.1016/j.scitotenv.2024.170480>.
- Katsnelson, B., R. Katsman, A. Lunkov, and I. Ostrovsky. 2017. "Acoustical Methodology for Determination of Gas Content in Aquatic Sediments, With Application to Lake Kinneret, Israel, as a Case Study." *Limnology and Oceanography: Methods* 15, no. 6: 531–541. <https://doi.org/10.1002/lom3.10178>.
- Knight, R. 2001. "Ground Penetrating Radar for Environmental Applications." *Annual Review of Earth and Planetary Sciences* 29, no. 1: 229–255. <https://doi.org/10.1146/annurev.earth.29.1.229>.
- Kosten, S., M. Pineiro, E. de Goede, J. de Klein, L. P. M. Lamers, and K. Ettwig. 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>.
- Lai, W.-L., Y. Zhang, and Z.-H. Chen. 2012. "Radial Oxygen Loss, Photosynthesis, and Nutrient Removal of 35 Wetland Plants." *Ecological Engineering* 39: 24–30. <https://doi.org/10.1016/j.ecoleng.2011.11.010>.
- Langenegger, T., D. Vachon, D. Donis, and D. F. McGinnis. 2019. "What the Bubble Knows: Lake Methane Dynamics Revealed by Sediment Gas Bubble Composition." *Limnology and Oceanography* 64, no. 4: 1526–1544. <https://doi.org/10.1002/lno.11133>.
- Laskov, C., O. Horn, and M. Hupfer. 2006. "Environmental Factors Regulating the Radial Oxygen Loss From Roots of *Myriophyllum spicatum* and *Potamogeton crispus*." *Aquatic Botany* 84, no. 4: 333–340. <https://doi.org/10.1016/j.aquabot.2005.12.005>.
- Lemoine, D. G., F. Mermillod-Blondin, M.-H. Barrat-Segretain, C. Massé, and E. Malet. 2012. "The Ability of Aquatic Macrophytes to Increase Root Porosity and Radial Oxygen Loss Determines their Resistance to Sediment Anoxia." *Aquatic Ecology* 46, no. 2: 191–200. <https://doi.org/10.1007/s10452-012-9391-2>.
- Liu, L., T. De Kock, J. Wilkinson, et al. 2018. "Methane Bubble Growth and Migration in Aquatic Sediments Observed by X-Ray μ CT." *Environmental Science & Technology* 52, no. 4: 2007–2015. <https://doi.org/10.1021/acs.est.7b06061>.
- Liu, L., J. Wilkinson, K. Koca, C. Buchmann, and A. Lorke. 2016. "The Role of Sediment Structure in Gas Bubble Storage and Release." *Journal of Geophysical Research: Biogeosciences* 121, no. 7: 1992–2005. <https://doi.org/10.1002/2016jg003456>.
- Marcon, L., K. Sotiri, T. Bleninger, A. Lorke, M. Männich, and S. Hilgert. 2022. "Acoustic Mapping of Gas Stored in Sediments of Shallow Aquatic Systems Linked to Methane Production and Ebullition Patterns." *Frontiers in Environmental Science* 10: 876540. <https://doi.org/10.3389/fenvs.2022.876540>.
- Mueller, P., and J. P. Megonigal. 2024. "Redox Control on Rhizosphere Priming in Wetlands." *Nature Geoscience* 17, no. 12: 1209–1217. <https://doi.org/10.1038/s41561-024-01584-1>.
- Mustasaar, M., and X. Comas. 2017. "Spatiotemporal Variability in Biogenic Gas Dynamics in a Subtropical Peat Soil at the Laboratory Scale Is Revealed Using High-Resolution Ground-Penetrating Radar." *Journal of Geophysical Research: Biogeosciences* 122, no. 9: 2219–2232. <https://doi.org/10.1002/2016jg003714>.
- Oliveira Junior, E. S., Y. Tang, S. J. P. van den Berg, S. J. Cardoso, L. P. M. Lamers, and S. Kosten. 2018. "The Impact of Water Hyacinth (*Eichhornia crassipes*) on Greenhouse Gas Emission and Nutrient Mobilization Depends on Rooting and Plant Coverage." *Aquatic Botany* 145: 1–9. <https://doi.org/10.1016/j.aquabot.2017.11.005>.
- Oliveira Junior, E. S., T. J. H. M. van Bergen, J. Nauta, et al. 2020. "Water Hyacinth's Effect on Greenhouse Gas Fluxes: A Field Study in a Wide Variety of Tropical Water Bodies." *Ecosystems* 24, no. 4: 988–1004. <https://doi.org/10.1007/s10021-020-00564-x>.
- Peltola, O., M. Raivonen, X. Li, and T. Vesala. 2018. "Technical Note: Comparison of Methane Ebullition Modelling Approaches Used in Terrestrial Wetland Models." *Biogeosciences* 15, no. 3: 937–951. <https://doi.org/10.5194/bg-15-937-2018>.
- Ribaudo, C., M. Bartoli, D. Longhi, S. Castaldi, S. C. Neubauer, and P. Viaroli. 2012. "CO₂ and CH₄ Fluxes across a *Nuphar lutea* (L.)." *Journal of Limnology* 71, no. 1: 200–210. <https://doi.org/10.4081/jlimnol.2012.e21>.
- Rosentreter, J. A., A. V. Borges, B. R. Deemer, et al. 2021. "Half of Global Methane Emissions Come From Highly Variable Aquatic Ecosystem Sources." *Nature Geoscience* 14, no. 4: 225–230. <https://doi.org/10.1038/s41561-021-00715-2>.
- Struik, Q., E. S. Oliveira Junior, A. J. Veraart, and S. Kosten. 2022. "Methane Emissions through Water Hyacinth Are Controlled by Plant Traits and Environmental Conditions." *Aquatic Botany* 183: 103574. <https://doi.org/10.1016/j.aquabot.2022.103574>.
- Uzhansky, E., B. Katsnelson, A. Lunkov, and I. Ostrovsky. 2020. "Spatial and Temporal Variability of Free Gas Content in Shallow Sediments: Lake Kinneret as a Case Study." *Geo-Marine Letters* 40, no. 4: 491–505. <https://doi.org/10.1007/s00367-019-00629-4>.
- Villa, J. A., Y. Ju, T. Stephen, C. Rey-Sanchez, K. C. Wrighton, and G. Bohrer. 2020. "Plant-Mediated Methane Transport in Emergent and Floating-Leaved Species of a Temperate Freshwater Mineral-Soil Wetland." *Limnology and Oceanography* 65, no. 7: 1635–1650. <https://doi.org/10.1002/lno.11467>.

- Vroom, R. J. E., M. van den Berg, S. R. Pangala, O. E. van der Scheer, and B. K. Sorrell. 2022. "Physiological Processes Affecting Methane Transport by Wetland Vegetation – A Review." *Aquatic Botany* 182: 103547. <https://doi.org/10.1016/j.aquabot.2022.103547>.
- Yoshida, N., H. Iguchi, H. Yurimoto, A. Murakami, and Y. Sakai. 2014. "Aquatic Plant Surface as a Niche for Methanotrophs." *Frontiers in Microbiology* 5: 30. <https://doi.org/10.3389/fmicb.2014.00030>.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

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