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Short communication

Volatiles from submerged macrophytes in a large meso-oligotrophic lake

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ABSTRACT

The release of volatile organic compounds (VOCs) from freshwater macrophytes has received limited attention. Here, we used an exploratory approach to quantify net VOC release rates and their chemical diversity in submerged macrophyte species collected from an alpine lake (Lake Geneva, France). Holobionts of *Myriophyllum spicatum*, *Potamogeton perfoliatus*, and *Potamogeton lucens* were co-incubated and VOCs were analysed using a purpose-built purge-and-trap system followed by gas chromatography-mass spectrometry. In addition, *Lagarosiphon major* was individually incubated. The mean total net VOC release rates ranged from 397 to 1142 pmol g⁻¹ DW h⁻¹. Hydrocarbons and monoterpenoids accounted for 60–70% of the total net VOC release. Release of ketones and aldehydes as well as monoterpenoids and sesquiterpenoids varied between the co-incubated species. The macrophyte volatilomes consisted of both common and unique VOCs. This interspecific variability suggests that biodiversity but also temporal and spatial dynamics and environmental controls may affect the release of VOCs from macrophytes and their contributions to VOC fluxes in freshwater ecosystems.

1. Introduction

Volatile organic compounds (VOCs) are reactive compounds that are released by vegetation and serve diverse physiological, ecological and biogeochemical functions including defense and communication, carbon cycling, atmospheric chemistry, and climate (Laothawornkitkul et al., 2009). Terrestrial plants emit thousands of different VOCs amounting to approximately 1000 Tg of VOCs annually (Guenther et al., 2012). Aquatic plants (macrophytes) have critical functions in freshwater ecosystems, influencing both ecosystem structure and biogeochemical cycling. However, the diversity of VOCs (volatilomes) released by macrophytes and their epibionts, as well as their release rates, remain poorly quantified and are largely absent from Earth-system models estimating global VOC fluxes.

VOCs are emitted from lakes. For example, *in-situ* lake measurements of specific VOCs show isoprene concentrations of 0.18–0.72 nM in Lake Constance, Germany (Steinke et al., 2018), β -ionone concentrations ranging from 0.16 to 26.8 nM in Lake Taihu, China (Liu et al., 2017), and dimethyl disulfide concentrations between 0.02 and 6.3 nM in Canadian lakes (Richards et al., 1991). However, as comprehensive knowledge

about the sources of these VOCs is lacking, the extent to which aquatic macrophytes contribute remains unresolved.

A recent study examined VOCs released from whole plants, intact blades or apices of 34 common macrophytes from Liangzi Lake in China, revealing that macrophyte life form and phylogeny influenced VOC compositions (Peng et al., 2024). Studies on hydrodistilled macrophyte essential oils indicate that alcohols and hydrocarbons dominate the macrophyte volatilomes and that eutrophication of the aquatic ecosystem impacts volatilome diversity (Kurashov et al., 2016; Krylova et al., 2024). To our knowledge, macrophyte VOC release rates and volatilomes of entire vascular macrophyte holobionts (including stem, leaves, roots and potential epibionts) have not been investigated previously. Notably, this holobiont approach does not identify the specific sources of VOCs (e.g., macrophytes or their epibionts), nor the potential re-release of deposited VOCs on the plant leaves such as in terrestrial environments (e.g., Himanen et al., 2010). It additionally overlooks the biological and chemical production and consumption processes determining the ultimate yield of VOCs. Nevertheless, it provides a comprehensive description of macrophyte VOCs and the potential role of lakes as sources of VOCs to the atmosphere.

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Our aim was thus to use exploratory short-term incubations to characterize the diversity and net release rates of VOCs from the holobionts of four common species of submerged rhizophytic macrophytes in the meso-oligotrophic alpine lake, Lake Geneva (France).

2. Materials and methods

2.1. Macrophyte collection and experimental setup

Macrophytes (perennial phanerogams) and water for incubations were collected from Lake Geneva in Thonon-les-Bains at Plage de Saint-Disdille (46.401258°N, 6.502837°E). *Myriophyllum spicatum* L. (Haloragaceae), *Potamogeton lucens* L. (Potamogetonaceae) and *Potamogeton perfoliatus* L. (Potamogetonaceae) were collected at 3–5 m depth, 15 m from shore on 29 May 2024 (Fig. S1). *Lagarosiphon major* (Ridley) Moss (Hydrocharitaceae) was retrieved from shore at < 1 m depth on 9 June 2024, at INRAE CARRTEL research center, 5 km southwest of Saint-Disdille. Specimens were transported to the laboratory, and sediment and visible macro-epibionts (e.g., gastropods) were removed. Three morphologically similar replicates per species were selected. Macrophytes were stored in trays with lake water overnight.

Before the start of the incubation, macrophytes were placed in bottles with collected lake water. The bottles were secured to a floating frame in random order at approximately 20 cm depth at the INRAE port, ensuring uniform light exposure for the 4-hour incubation. Triplicate bottles without macrophytes served as controls to quantify background net release. Light and temperature were recorded. On 30 May 2024 (09:45–13:45; co-incubation of *M. spicatum*, *P. lucens* and *P. perfoliatus*), light intensity was 33766 Lux ($\sim 675 \mu\text{mol m}^{-2} \text{s}^{-1}$), and water temperature was 19.0 °C. On 10 June 2024 (12:00–16:00; individual incubation of *L. major*), light intensity and water temperature was higher, 63257 Lux ($\sim 1265 \mu\text{mol m}^{-2} \text{s}^{-1}$) and 21.8 °C. After incubation and VOC collection, the dry mass of each sample was determined following oven drying at 35 °C to constant weight.

2.2. VOC collection

After the incubation, VOCs were collected from water in each bottle using a purge-and-trap technique (Fig. S2). The sequence of water analyses alternated between macrophyte samples and lake water controls. Water samples were purged with air that was purified from particles, VOCs and ozone. Air flow was set to 200 mL min⁻¹ for 20 min directing purged VOCs through a stainless-steel adsorbent cartridge (150 mg Tenax TA and 200 mg Carboxograph 1TD; Markes International Limited). Independent checks using gas-chromatography with flame-ionization detection suggested that this procedure removed > 99% of isoprene from the water (data not shown). The adsorbent cartridges were refrigerated until analysis.

2.3. VOC analysis

The analysis of samples and 40 standard compounds (Table S1) was performed by gas chromatography-mass spectrometry (GC-MS) as described by Qin et al. (2025).

Chromatograms were analysed with PARADISE v6.1.5 software (Kromath). VOCs were identified using pure standards or matches from the NIST 23 Mass Spectral Library, the latter flagged as tentatively identified. See Supplementary material for details (Methods S1).

2.4. Data processing

Average VOC concentrations (ng L⁻¹; n = 3) in incubated lake water (controls) were subtracted from those in macrophyte samples to correct for plankton-mediated production or consumption. To facilitate comparisons between compounds of different molar masses, the corrected concentrations (ng L⁻¹) were normalized to macrophyte dry mass and

converted to molar units (pmol L⁻¹) based on the first hit in the NIST database. Compounds detected in only one of three replicates were removed from the dataset.

2.5. Hill Diversity analysis

Hill diversity was calculated using the R package *hillR* (Li, 2018) and used to assess the diversity of VOCs. The diversity order parameter *q*, determining the weighting of rare versus abundant compounds, was set to 0 (VOC species richness) and 1 (Hill-Shannon diversity). At *q* = 1, species richness and evenness of relative VOC abundances are considered, giving greater weight to more common compounds.

2.6. Statistical analyses

Due to small sample sizes, PERMANOVA with a dispersion test, 9999 permutations and Euclidean distances, was chosen for the investigation of between-species differences in net release for the co-incubation (R package *Vegan*, Table S2). Principal component analysis (PCA) was performed using SIMCA Version 17.0.2.34594 (Sartorius Stedim Data Analytics AB) to assess similarities in volatilome composition among macrophyte species. Net release rates from each VOC were unit variance-scaled and log-transformed. Compounds present in only a few samples were removed (19 compounds) with 72 compounds remaining for the PCA (Table S3). Data analysis was conducted using the R package *tidyverse* and Venny (Oliveros, 2015).

3. Results

3.1. Net release rates

Mean total net VOC release rate, summed across all compounds, ranged between 1142 pmol g⁻¹ DW h⁻¹ (*P. perfoliatus*) and 397 pmol g⁻¹ DW h⁻¹ (*M. spicatum*, Fig. 1a). Net VOC release rates for *L. major* and *P. lucens* fell between these (690 and 878 pmol g⁻¹ DW h⁻¹, respectively). Net release rate and multivariate dispersion did not differ significantly (PERMANOVA, pseudo-F = 4.23, R² = 0.59, *p* = 0.0824 and PERMDISP, *p* = 0.818).

Hydrocarbons dominated the VOC profile of *P. lucens* (43% of the total) and *L. major* (39%), while *M. spicatum* exhibited a high proportion of isoprene (47%). *P. perfoliatus* had a notable dominance of monoterpenoids (27%) (Fig. 1b). These groups collectively accounted for ~60–70% of total net VOC release rates for each species. Sesquiterpenoids contributed 7% to the volatilome for *P. perfoliatus* but constituted less than 2% for the other co-incubated species. Sulfur-containing compounds made up 4% of the total VOCs for *M. spicatum* and 2% for *P. perfoliatus*. However, the analytical method was not optimized for sulfur compounds, which may interact with stainless-steel surfaces in thermal desorption tubes, leading to conservative concentration estimates.

Mean net isoprene release rates were 227 pmol g⁻¹ DW h⁻¹ for *P. lucens*, 188 pmol g⁻¹ DW h⁻¹ for *M. spicatum*, 158 pmol g⁻¹ DW h⁻¹ for *P. perfoliatus*, and 112 pmol g⁻¹ DW h⁻¹ for *L. major* (Fig. 1c). Release of monoterpenoids and sesquiterpenoids differed significantly among the co-incubated species (PERMANOVA, pseudo-F = 7.56, R² = 0.72, *p* = 0.02674 and pseudo-F = 35.2, R² = 0.92, *p* = 0.0083, respectively). Multivariate dispersion did not differ significantly (PERMDISP, *p* = 0.5398 and *p* = 0.3041, respectively). *P. perfoliatus* released at least ~14-fold more monoterpenoids than the other macrophytes. The highest release of sesquiterpenoids was also observed in *P. perfoliatus*, with 3–19 times higher rates than in *P. lucens* and *M. spicatum*. All co-incubated species released sulfur-containing compounds, while no release was detected for *L. major*. See Supplementary material for release rates of additional VOC groups (Fig. S3).

Most abundant individual VOCs released by *P. perfoliatus* were the monoterpene α -pinene (258 pmol g⁻¹ DW h⁻¹), isoprene, and

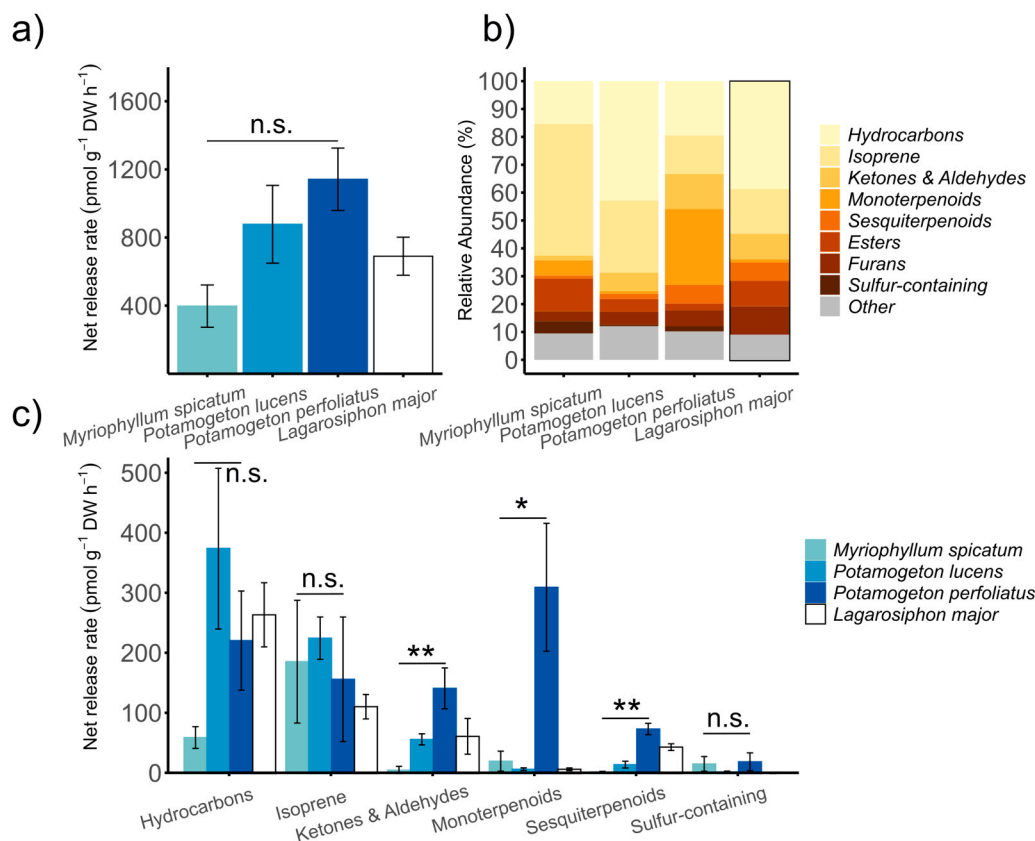


Fig. 1. Net VOC release rates for the submerged macrophytes *Myriophyllum spicatum*, *Potamogeton lucens*, *Potamogeton perfoliatus* and *Lagarosiphon major*. *L. major* was individually incubated (black outline). (a) Total hourly VOC release rates (pmol g⁻¹ DW h⁻¹, mean ± SE, n = 3), (b) Relative abundances of different VOC groups (%), (c) Net release rates of selected VOC groups (pmol g⁻¹ DW h⁻¹, mean ± SE, n = 3). The co-incubated species (*M. spicatum*, *P. lucens* and *P. perfoliatus*) were tested for differences using PERMANOVA (* $p \leq 0.05$; ** $p \leq 0.01$; n.s., not significant).

tentatively identified sesquiterpenoid trans- β -ionone (75 pmol g⁻¹ DW h⁻¹) (Fig. 1c and Table S4). *P. lucens* released high levels of isoprene along with the tentatively identified ketone 3-pentanone (51 pmol g⁻¹ DW h⁻¹) and the tentatively identified alkane cyclohexane (51 pmol g⁻¹ DW h⁻¹). In *M. spicatum*, dominant VOCs were isoprene, a tentatively identified ester (27 pmol g⁻¹ DW h⁻¹), and an unknown compound (18 pmol g⁻¹ DW h⁻¹). Dominant VOCs released by *L. major* were the tentatively identified alkene ectocarpene (158 pmol g⁻¹ DW h⁻¹),

isoprene, and the furan 2-methylfuran (70 pmol g⁻¹ DW h⁻¹).

3.2. Volatilomes

Principal component analysis (PCA) based on full volatilomes from the co-incubation demonstrated a clear separation between species, indicating differences in the relative compound compositions (Fig. 2a). For *P. perfoliatus*, monoterpenoids, hydrocarbons and sulfur-containing

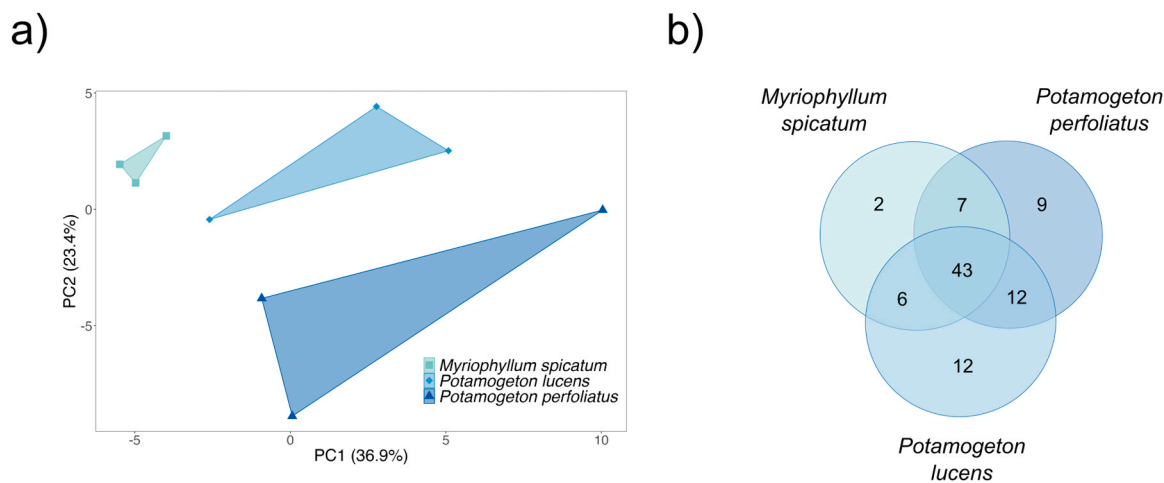


Fig. 2. Volatilomic differences between the co-incubated submerged macrophytes *Myriophyllum spicatum*, *Potamogeton lucens* and *Potamogeton perfoliatus*. (a) Principal component analysis score plot showing the triplicates for each species. Variance explained by each principal component is shown in parentheses. (b) Venn diagram illustrating common and unique compounds among the three co-incubated macrophytes based on the presence/absence of the 91 detected VOCs.

compounds were predominant, while hydrocarbons, sulfur-containing compounds and 'other' VOCs, were the most influential groups for *M. spicatum*.

Of the 126 VOCs from all four macrophytes, 18 (14.3%) were identified with standards (Table S4, highlighted in bold). The "common" volatilome for the co-incubation consisted of 43 VOCs (47.3%) out of the 91 different VOCs detected (Fig. 2b). The common volatilome across all four species consisted of 25 VOCs including isoprene, seven hydrocarbons, one furan, two esters, eight 'other' VOCs, two ketones and aldehydes, one monoterpenoid, and two sesquiterpenoids (Table S4). The unique volatilome for each macrophyte in the co-incubation ranged from two unique compounds in *M. spicatum* to 12 compounds in *P. lucens*.

The VOC species richness (Hill diversity) and the Hill-Shannon diversity, which account for both VOC richness and evenness, did not differ significantly among macrophyte species (PERMANOVA, pseudo-F = 0.8741, $R^2 = 0.72$, $p = 0.45664$ and pseudo-F = 35.2, $R^2 = 0.92$, $p = 0.0083$, respectively). Neither did the multivariate dispersion (PERMDISP, $p = 0.5398$ and $p = 0.3041$, respectively). *P. perfoliatus* and *P. lucens* had the highest mean VOC species richness among co-incubated species, reaching 60, while *M. spicatum* VOC richness was 51 (Fig. S4).

4. Discussion

This is the first study to estimate net release rates of VOCs from entire freshwater vascular macrophytes including their epibionts. We found that the studied macrophyte species differed in their VOC release rates and that their volatilomes comprised both common and unique VOCs, many of which are also found in terrestrial plants.

The macrophyte volatilomes were dominated by isoprene and other hydrocarbons, which accounted for 33–69% of the total net VOC release. Isoprene plays a well-documented role in enhancing plant tolerance to mild stress (Sharkey and Monson, 2017) and is the most abundantly emitted VOC from terrestrial vegetation, contributing ~50% of global biogenic VOC emissions (Guenther et al., 2012). Isoprene release has been detected in microalgae cultured from lake surface water (Yu et al., 2019) and in macrophytes such as *Potamogeton malaianus* Miquel (Potamogetonaceae) (Peng et al., 2024). Isoprene fluxes from lakes ranging 0.004–1 nmol m⁻² s⁻¹ have been documented (Steinke et al., 2018; Seco et al., 2020). Hydrocarbon abundance in our study was similar to that of the essential oil of the floating aquatic macrophyte *Spirodela polyrrhiza* (L.) Scheiden (Araceae) (36%, Kurashov et al., 2016) and aligned with previous findings indicating that hydrocarbons are among the most abundant VOCs in freshwater environments (Qin et al., 2025). Our findings highlight the potential role of macrophytes in contributing to isoprene and hydrocarbon fluxes in lake ecosystems.

The most-abundant sulfur-containing compound was tentatively identified carbon disulfide, which has been previously detected in freshwater ecosystems (Fritz and Bachofen, 2000). This was followed by tentatively identified dimethyl disulfide (DMS), also reported in freshwater environments (Richards et al., 1991). Carbon disulfide is emitted by terrestrial plants and phytoplankton and is formed photochemically from organic sulfur precursors in natural waters (Piluk et al., 2001; Modiri Ghahrevaran and Shah, 2018), while DMS can be produced by freshwater algae (Caron and Kramer, 1994). Our measurements likely underestimate sulfur-containing compounds as our analytical conditions were optimized for broad detection of VOCs, not for sulfur compounds. Notably, highly reactive sulfur-containing compounds, such as dimethyl sulfide (DMS) (Steinke et al., 2018) and methanethiol (Caron and Kramer, 1994), were not detected in our study. DMS plays an important role in marine environments, where it is primarily produced by phytoplankton (Hopkins et al., 2023), but it has also been observed in terrestrial plant VOC emissions (Rinnan et al., 2014) and lake water (Steinke et al., 2018). Methanethiol has been detected in freshwater algae cultures (Caron and Kramer, 1994). Despite the

limitations of our analysis, our results suggest that macrophytes may represent a source of carbon disulfide in lake ecosystems.

Monoterpenoids and sesquiterpenoids are well-known VOCs produced in high amounts by terrestrial plants (Laothawornkitkul et al., 2009). Our findings indicate that the macrophytes studied here released these compounds to varying degrees, although the low number of replicates limits the statistical power of these findings. *P. perfoliatus* exhibited particularly high release of monoterpenoids (α -pinene) and sesquiterpenoids (tentatively identified trans- β -ionone). Both compounds have been previously reported for macrophytes (Peng et al., 2024). In addition, *L. major* released oxygenated sesquiterpenes that were not detected in other species. Whether this was due to differences in environmental conditions between the incubations or species-specific differences, remains uncertain.

We found that the most abundantly released 'common' volatiles among the four macrophyte species were also among the highest for each individual species, suggesting their substantial contribution to macrophyte volatilomes. These five compounds (isoprene, tentatively identified 3-pentanone, 2-methylfuran, tentatively identified ectocarpene, and tentatively identified trans- β -ionone) have all been previously identified in terrestrial plants or associated with fruit volatiles. Some of these compounds, including β -ionone, 3-pentanone, and isoprene, have also been detected in macrophyte VOC emissions (Peng et al., 2024).

The lack of differences in the diversity of VOCs from the different macrophyte species aligns with previous findings that macrophytes with similar life form – in this case submerged species – have comparable relative VOC compositions (Peng et al., 2024). Furthermore, this agrees with a study of the volatilomes in four seagrass species that exhibited no differences in their VOC chemical richness and diversity (Coquin et al., 2024).

In our study, the macrophytes were incubated on two different days, resulting in higher temperature and light intensity during the incubation period for *L. major*. Light and temperature are well-known factors influencing VOC emissions in plants (Laothawornkitkul et al., 2009). While we cannot directly infer the effects of varying temperatures and light intensities from our data, it is possible that the higher light intensity during incubation enhanced VOC release from *L. major*, or contributed to stress-induced physiological acclimation, potentially increasing release rates and VOC diversity by bringing additional compounds above the detection limit. Notably, *L. major* exhibited 35 unique VOCs. This distinct volatilome could also stem from genetic differences between the species; *L. major* is an invasive species, and invasive plants are known to use secondary metabolites as allomones against native plant populations (Hierro and Callaway, 2003).

Our study shows that freshwater macrophytes release substantial amounts of VOCs and that volatilomes vary across species. These findings underscore the need for further investigations into the temporal and spatial dynamics of macrophyte VOC release to better assess their contribution to overall VOC release in freshwater ecosystems. Additionally, identifying the environmental factors that regulate climate-relevant VOC release is crucial, particularly as a changing climate could alter water temperature, light exposure, and other stressors. Given that macrophyte species composition is also expected to shift with changing climate conditions (Patrick et al., 2012), expanded mapping of macrophyte volatilomes will be essential for predicting future trends in lake VOC emissions.

CRediT authorship contribution statement

Lasse Riemann: Writing – review & editing, Supervision. **Riley Hughes:** Writing – review & editing, Investigation, Conceptualization. **Geneviève Chiapusio:** Writing – review & editing, Methodology, Conceptualization. **Riikka Rinnan:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition. **Michael Steinke:** Writing – review & editing, Resources, Methodology, Funding

acquisition, Conceptualization. **Ellen Salamon Slater:** Writing – original draft, Visualization, Investigation, Formal analysis. **Isabelle Laurion:** Writing – review & editing, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Viet Tran Khac:** Writing – review & editing, Investigation. **Stéphan Jacquet:** Writing – review & editing, Investigation.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.aquabot.2026.104039](https://doi.org/10.1016/j.aquabot.2026.104039).

Data availability

Data and metadata are available in the Environmental Research Data Archive (<https://www.erdarc.org/archives/731ccd9514403a29471c-caeed3c64eaa/published-archive.html>).

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