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Decomposition of cyanobacteria and submerged macrophytes: impacts on carbon emissions and nutrient cycling in lake ecosystems

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Abstract

Aquatic primary producers, including submerged macrophytes and cyanobacteria, play essential roles in lake ecosystems by maintaining water quality and driving carbon cycling. However, the impact of their decomposition on greenhouse gas (GHG) emissions and nutrient dynamics remains poorly understood. This study examines how the decomposition of cyanobacteria and three submerged macrophyte species (*Ceratophyllum demersum*, *Vallisneria natans*, and *Potamogeton wrightii*) influences GHG emissions and nutrient cycling in lake systems. Over a 117-day period, microcosms were used to monitor decomposition and measure the release of methane (CH₄), carbon dioxide (CO₂), nitrogen, and phosphorus. Emission trends and water quality changes were modeled using the Generalized Additive Model, and the relationships between GHG emissions and nutrient release were analyzed. Our results indicate that cyanobacterial decomposition significantly increased GHG emissions and nutrient release. By day 25, the CH₄ emissions in the cyanobacteria treatment were 1.37 to 1.89 times higher than in the submerged macrophyte treatments, while final concentrations of nitrogen-related nutrients in the water column were 5.90 to 7.67 times greater. Among the submerged macrophytes, slight differences were observed in GHG emissions and nutrient release: *Vallisneria natans* exhibited a lower CO₂ release rate, while *Ceratophyllum demersum* showed reduced phosphorus release. These findings suggest that certain submerged macrophytes, particularly *Vallisneria natans* and *Ceratophyllum demersum*, can mitigate GHG emissions and regulate nutrient cycling. Promoting their growth may therefore serve as an effective strategy for lake restoration and eutrophication management. However, field validation and long-term monitoring are needed to assess their practical effectiveness and ecological stability under natural conditions.

Highlights

- One hundred seventeen-day lab incubation reveals GHG and nutrient impacts of plant decomposition.
- Cyanobacteria drive higher CH₄ and CO₂ emissions compared to submerged macrophytes.
- Cyanobacterial decomposition releases more nitrogen and phosphorus.

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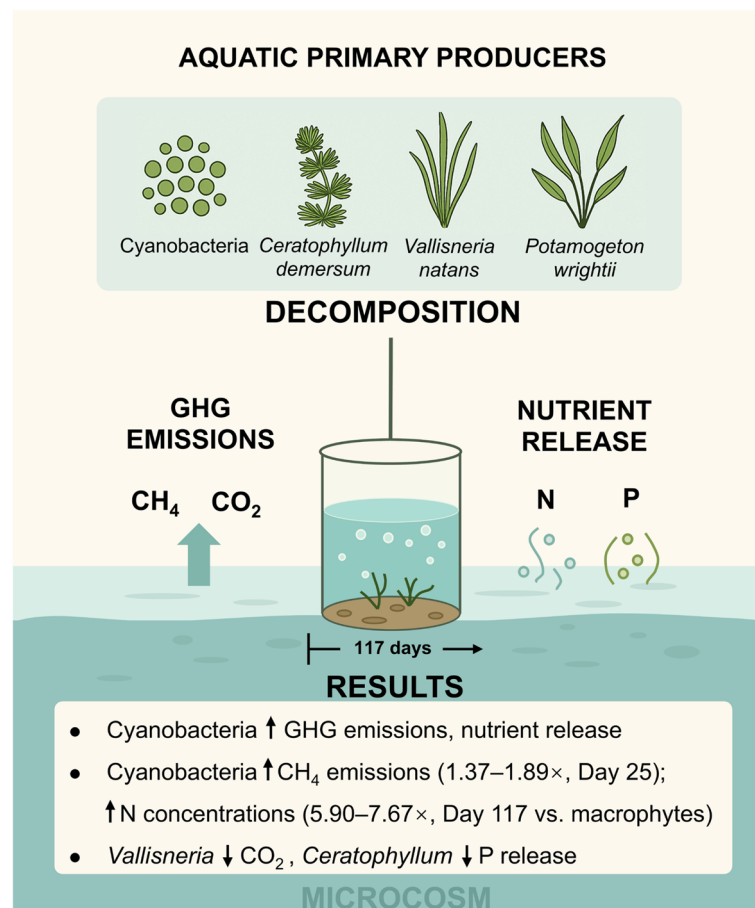
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- *Vallisneria natans* and *Ceratophyllum demersum* mitigate GHG emissions and nutrients.

Keywords Cyanobacteria, Submerged macrophytes, Greenhouse gases, Water quality, Lake restoration

Graphical Abstract



1 Introduction

Lakes play a pivotal role in global biogeochemical cycles by regulating carbon emissions and nutrient transformations. Despite covering only ~2% of Earth's surface, they exhibit high carbon burial rates, making them highly efficient carbon sinks compared to the vastly larger marine environment (Dean and Gorham 1998; Tranvik et al. 2009). This significant storage capacity also makes lakes major natural sources of greenhouse gases (GHGs), particularly methane (CH_4) and carbon dioxide (CO_2) (Kosten et al. 2010; Rosentreter et al. 2021). Lake GHG emissions are estimated to contribute roughly 20% of the annual CO_2 emissions from fossil fuel use (DeSontro et al. 2018). These emissions arise from complex biogeochemical processes, where sedimentary organic carbon

is metabolized by microorganisms, releasing CH_4 and CO_2 into the atmosphere (Tranvik et al. 2009; Sun et al. 2022; Zhou et al. 2024). These processes closely connect lake ecosystems to the global carbon cycle. As a result, even minor disturbances can trigger significant changes in GHG fluxes from lakes, leading to cascading effects on atmospheric GHG concentrations and the global carbon budget (Beaulieu et al. 2019).

Lakes can shift between two alternative stable states: clear-water systems dominated by submerged macrophytes and turbid systems dominated by cyanobacterial blooms. These shifts are primarily driven by nutrient enrichment associated with eutrophication (Janse 1997; Jackson 2003; Janssen et al. 2021; Zhou et al. 2022). In the submerged plant-dominated state, lakes tend to exhibit

clearer water, higher biodiversity, and more stable ecological processes because submerged macrophytes regulate nutrient cycling, reduce algal growth, and stabilize sediments (Kong et al. 2017; Fujibayashi et al. 2020; van Wijk et al. 2023; Mu et al. 2024). In contrast, systems dominated by cyanobacteria often lead to reduced water quality, increased nutrient loading, and elevated GHG emissions, particularly CH₄ and CO₂ (Bižić et al. 2020). Given these contrasting dynamics, restoring submerged macrophytes to re-establish clearer, more stable lake states is widely considered a key strategy for combating eutrophication and improving water quality (Grace et al. 2019). However, once submerged macrophytes decompose after senescence, they can release substantial amounts of GHGs, potentially offsetting some of the benefits they provide during growth, such as nutrient uptake, water clarity maintenance, and habitat provision (Han et al. 2019; Zhao et al. 2021; Grasset et al. 2019). Consequently, understanding the biogeochemical processes associated with the decomposition of both submerged macrophytes and cyanobacteria is crucial for fully assessing their ecological impacts, particularly in terms of nutrient cycling and GHG emissions.

The growth and decay of algae and submerged plants play a crucial role in regulating water quality and carbon cycling in lake ecosystems. Among these, decay processes are particularly important because they directly affect nutrient turnover and greenhouse gas emissions, primarily through interactions with microbial communities, nutrient availability, and environmental conditions (Grasset et al. 2016; Li et al. 2021; Liu et al. 2022; Wang et al. 2024). While the basic mechanisms of decomposition in cyanobacteria and submerged macrophytes are broadly similar, the rates and impacts of decay and the resulting GHG fluxes can vary considerably depending on the type of organic matter and the surrounding environmental factors. In phytoplankton-dominated systems, particularly those experiencing recurrent cyanobacterial blooms, rapid algal decay leads to oxygen depletion and the formation of anoxic zones, which in turn promote methanogenesis, a major pathway for CH₄ production (Bartosiewicz et al. 2021; Sun et al. 2021; Ji et al. 2024). Cyanobacterial decomposition also releases large quantities of nutrients and carbon substrates, intensifying internal nutrient cycling and creating a feedback loop that sustains prolonged CH₄ emissions (Nazari-Sharabian et al. 2018; Amorim and do Nascimento Moura 2021). In contrast, although submerged macrophytes follow similar decomposition pathways, the specific contributions of different species to GHG emissions can vary widely. The amount and density of plant material, as well as its organic matter content, are critical factors

that influence the magnitude of GHG emissions (Huang et al. 1997; Grasset et al. 2019; Theus et al. 2023). These species-specific traits influence sediment microbial activity and biogeochemical processes, ultimately influencing nutrient cycling and GHG fluxes (Li et al. 2010; Ma et al. 2020). Previous studies have substantially advanced our understanding of the decomposition dynamics of either cyanobacteria or submerged macrophytes. However, most investigations have examined these plant types in isolation or under varying environmental conditions, making it difficult to directly compare their biogeochemical impacts. Long-term, comparative studies involving multiple species under consistent experimental conditions are essential for clarifying their respective roles in greenhouse gas emissions and nutrient transformations in eutrophic lake systems.

In this study, we selected Taihu Lake as a representative site to investigate decomposition dynamics of dominant algae and submerged macrophytes. Taihu Lake is a large, shallow, and eutrophic lake located in eastern China. It has experienced persistent eutrophication and frequent cyanobacterial blooms over the past decades, making it a well-documented system for studying biogeochemical processes and GHG emissions (Qin et al. 2019; Song et al. 2024). A 117-day laboratory experiment was conducted to assess CH₄ and CO₂ emissions during decomposition, alongside measurements of key water quality parameters. The 117-day incubation period enabled us to capture both rapid, early-stage decomposition and slower, long-term biogeochemical changes, offering new insights into the roles of different plant types in shaping GHG fluxes and internal nutrient cycling. We hypothesize that: (1) due to their lower structural complexity and higher carbon lability, cyanobacterial decomposition would result in higher and more sustained CH₄ and CO₂ emissions compared to submerged macrophytes. Moreover, decomposition rates and associated GHG emissions are expected to vary among submerged plant species, depending on differences in tissue composition and nutrient stoichiometry (Grasset et al. 2019; Xu et al. 2024). (2) The decomposition of cyanobacterial biomass, due to its high nitrogen and phosphorus content, will result in faster and greater nutrient release. In contrast, submerged macrophytes will release nutrients more slowly, owing to their lower nutrient concentrations and more structurally complex, less degradable tissues (Elser et al. 2000; Grasset et al. 2019). By systematically comparing the decomposition of cyanobacteria and macrophytes, this study provides insights into their respective contributions to carbon cycling and water quality deterioration, offering practical strategies for lake management.

2 Materials and methods

2.1 Study area

The study area is located in Taihu Lake, a significant subtropical shallow lake and the third largest freshwater lake in China. Covering an area of approximately 2,338 km² with an average depth of 1.9 m, Taihu Lake presents a diverse range of ecosystems and environmental gradients (Qin et al. 2007; Luo et al. 2016). The dynamics of macrophytes and phytoplankton in the lake exhibit pronounced spatial heterogeneity. The northern region, particularly Zhushan Bay, experiences frequent cyanobacterial blooms due to high levels of eutrophication (Feng et al. 2018), in contrast to Xukou Bay in the lake's eastern region, where the growth of submerged macrophytes is more prominent (Luo et al. 2014). These two subregions have been well-documented in prior studies as representative of Taihu's contrasting ecological states, making them ideal sources of organic material for investigating the decomposition dynamics of cyanobacteria- and macrophyte-dominated systems (Deng et al. 2023; Shi et al. 2015).

2.2 Sample collection

In July 2019, cyanobacteria samples were collected from Zhushan Bay in Taihu Lake using a plankton net with a mesh size of 64 µm. Immediately after collection, the samples were washed with deionized water to remove any contaminants and stored in the dark at 4 °C to preserve their integrity. In contrast, three submerged macrophyte species—*Ceratophyllum demersum* (*C. demersum*), *Vallisneria natans* (*V. natans*), and *Potamogeton wrightii* (*P. wrightii*)—were harvested from Xukou Bay using a sickle. These species are common submerged macrophytes found in lakes. To standardize organic content and minimize microbial activity prior to incubation, the plant specimens were rinsed with deionized water, air-dried to remove excess moisture, and then oven-dried at 60 °C for 24 h. Following drying, the plants were cut into approximately 1 cm² pieces and thoroughly mixed.

Sediment samples were collected from both study areas using a gravity sediment sampler to a depth of approximately 10 cm, representing the active biogeochemical layer. After collection, the sediment was directly passed through a 0.15 mm mesh to remove larger particles such as stones, shells, and plant residues. The resulting fine-grained sediment was manually homogenized to ensure uniformity and stored at 4 °C for subsequent experiments. Additionally, water was collected from Caiyue Lake at the Xianlin Campus of Nanjing Normal University and pre-filtered through a 0.15 mm sieve to remove coarse debris and suspended solids before it was used as the culture medium in the microcosms.

2.3 Incubation experiments

Five different treatments were prepared in 500 mL head-space bottles to investigate the anaerobic decomposition of various plant materials: (a) water and sediment without organic matter addition (control); (b) water and sediment with cyanobacteria; (c) water and sediment with *C. demersum*; (d) water and sediment with *V. natans*; (e) water and sediment with *P. wrightii*. Each treatment was performed in triplicate (Fig. 1). For all treatments, 300 mL of water and 80 g of sediment were added. In treatments (b–e), plant materials were added to reach a target total organic carbon (TOC) level of approximately 350 mg: 1 g of cyanobacteria, 1.5 g of *C. demersum*, 1.5 g of *V. natans*, and 2 g of *P. wrightii*. The measured TOC values are provided in Appendix 1. The incubation was conducted in the dark at a constant temperature of 25 °C to simulate anaerobic freshwater decomposition (Zhang et al. 2009; Xu et al. 2024). To establish anaerobic conditions, the bottles were initially flushed with high-purity nitrogen gas for 15 min and sealed with butyl rubber stoppers (Nanchaiaiah and Venugopalan 2011; Li et al. 2025). A second nitrogen flush was performed 24 h later to ensure complete removal of oxygen. Anaerobic conditions were used to replicate the oxygen-depleted environments, commonly developed during the decomposition

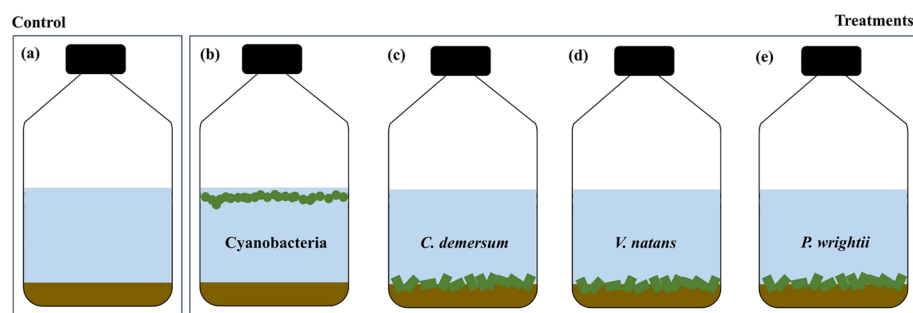


Fig. 1 Experimental grouping: (a) Control group without cyanobacteria or submerged macrophytes; (b) Experimental group with cyanobacteria; (c–e) Experimental groups with different submerged macrophyte species

of organic matter in lakes. Under such conditions, CH₄ is produced primarily by methanogenic microorganisms, while CO₂ is also generated through parallel anaerobic pathways such as fermentation. These processes together reflect the typical gas production dynamics during anaerobic degradation in aquatic systems (Gruca-Rokosz and Tomaszek 2015; Herndon et al. 2015). Gas and water samples were collected on days 1, 3, 5, 7, 11, 15, 19, 25, 31, 37, 43, 49, 61, and 117. A controlled, destructive sampling method was employed to minimize disturbance to the experiment. All collected samples were stored at −40 °C for subsequent analysis.

2.4 Analyses of GHGs and water

Gas samples (2 mL) were collected from the headspace of each treatment bottle using a 10 mL syringe and transferred to a 100 mL aluminum foil gas sampling bag with a double-valve system. Gas concentrations were determined using an Agilent 7890B gas chromatograph equipped with both a flame ionization detector (FID) and an electron capture detector (ECD). The FID was maintained at 200 °C, with high-purity nitrogen serving as the carrier gas at a flow rate of 30 mL/min. High-purity hydrogen and air were used as fuel gases at flow rates of 40 mL/min and 400 mL/min, respectively.

Water samples from each treatment were digested using K₂S₂O₈ and NaOH, and concentrations of total nitrogen (TN) and total phosphorus (TP) were measured using a UV–visible spectrophotometer (UV6100, Meipuda, China), based on the methods described by Raveh and Avnimelech (1979) and Ebina et al. (1983). Ammonia nitrogen (NH₄⁺) and nitrate nitrogen (NO₃[−]) concentrations were quantified with a water quality flow analyzer (AA3c, Bran Luebbe, Germany). TOC, total carbon (TC), and inorganic carbon (IC) concentrations were analyzed using a carbon/nitrogen analyzer (Multi N/C 3100, Jena, Germany). Prior to analysis, all water samples were filtered through a 0.45 µm glass fiber membrane.

2.5 Data analysis

The concentrations of CH₄ and CO₂ emissions from different treatments were calculated by measuring the gas concentrations in the headspace of the bottles, using the following formula:

$$m = 12CV/M$$

where m represents the cumulative release of CH₄ or CO₂ (mg); 12 is the molar mass of carbon; C is the concentration of CH₄ or CO₂ in the headspace (mmol·L^{−1}); V is the volume of the headspace in the bottle, which was 0.325 L for this study; M is the molar mass of CH₄ or CO₂.

Gas concentrations were used to calculate cumulative CH₄ and CO₂ emissions over the incubation period for

each treatment. This cumulative approach provides a comprehensive measure of total gas production potential, which is particularly relevant for evaluating long-term effects of organic matter decomposition. It also facilitates comparison among treatments based on their total contribution to greenhouse gas release. To evaluate the significant differences in cumulative CH₄ and CO₂ emissions and water quality changes among treatment groups, we used a generalized additive model (GAM). This method is advantageous because it flexibly captures non-linear relationships without requiring a predefined parametric form. In this model, time was modeled as a smooth term, allowing the relationship between time and emissions to vary non-linearly for each treatment. The analysis was performed using the "mgcv" package (Wood 2004), and post hoc pairwise comparisons were conducted with the "emmeans" package (Lenth 2024) to identify significant differences between treatment groups. Additionally, Pearson correlation analysis with 999 permutations was used to explore relationships between cumulative emissions and environmental factors. Statistical significance was set at $p < 0.05$ for all tests. All analyses were carried out using R (version 4.4.0; R Core Team 2024).

3 Results

3.1 Cumulative CH₄ and CO₂ production in diverse treatments

During the 117-day incubation period, cumulative CH₄ and CO₂ emissions in all treatment groups increased rapidly at first, and then gradually stabilized (Fig. 2). The cyanobacteria-only treatment produced significantly higher cumulative CH₄ and CO₂ emissions (154.79 ± 16.16 mg-C and 69.49 ± 7.40 mg-C, respectively) compared to the submerged macrophyte treatments. In contrast, cumulative CH₄ emissions in the macrophyte treatments ranged from 109.22 to 115.35 mg-C for CH₄ and 57.68 to 59.19 mg-C for CO₂. Statistical analysis revealed significant differences in the CH₄ emission trend between the cyanobacteria treatment and the three submerged macrophyte treatments ($p < 0.05$), with no significant differences observed among the submerged macrophyte treatments themselves. Notably, by day 25, cumulative CH₄ emission in the cyanobacteria treatment was approximately 1.37 to 1.89 times higher than in the submerged macrophytes, reflecting its faster breakdown and greater availability of methanogenic substrates during early decomposition.

For CO₂ emissions, the cyanobacteria treatment showed significant differences only from the *P. wrightii* treatment. Specifically, CO₂ emissions from the cyanobacteria treatment were initially lower than those from *P. wrightii*, but later exceeded them. Additionally, CO₂ emissions from *P. wrightii* were significantly higher than

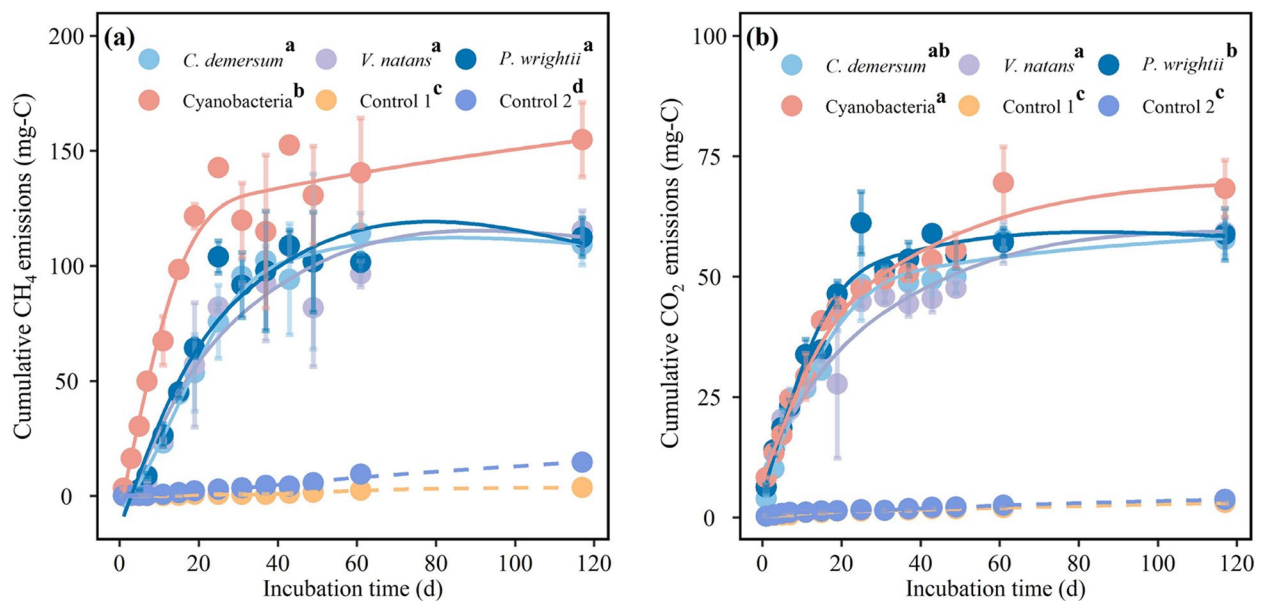


Fig. 2 Cumulative greenhouse gas (GHG) emissions under different treatment groups over the 117-day incubation period. The cumulative emission trends for each treatment were modeled using a generalized additive model (GAM), with data shown as means and error bars representing standard deviations (SD, $n = 3$). Different lowercase letters above each treatment group denote statistically significant differences at the $p < 0.05$ level. The solid line denotes the experimental group, while the dashed line represents the control group. **a** Cumulative CH₄ emissions over the 117-day cultivation period. **b** Cumulative CO₂ emissions over the 117-day cultivation period

those from *V. natans*, which may reflect differences in decomposition rates or microbial activity associated with these plant types.

3.2 Changes in water quality in different treatment methods

During the 117-day incubation period, the decomposition of cyanobacteria and submerged macrophytes exhibited distinct carbon dynamics. In the cyanobacteria treatment, TC concentration declined sharply

from $709.52 \pm 53.50 \text{ mg L}^{-1}$ to $289.77 \pm 13.66 \text{ mg L}^{-1}$ within the first 19 days. This was followed by a gradual increase in TC, reaching a peak of $940 \pm 9.26 \text{ mg L}^{-1}$ by day 117. In contrast, TC concentration in the submerged macrophyte treatments initially rose during the first 7 days, then decreased back to baseline levels, followed by a slower secondary increase (Fig. 3a). A similar trend was observed for TOC concentrations (Fig. 3b). IC concentrations increased rapidly in the first 31 days, declined modestly over the next 18 days,

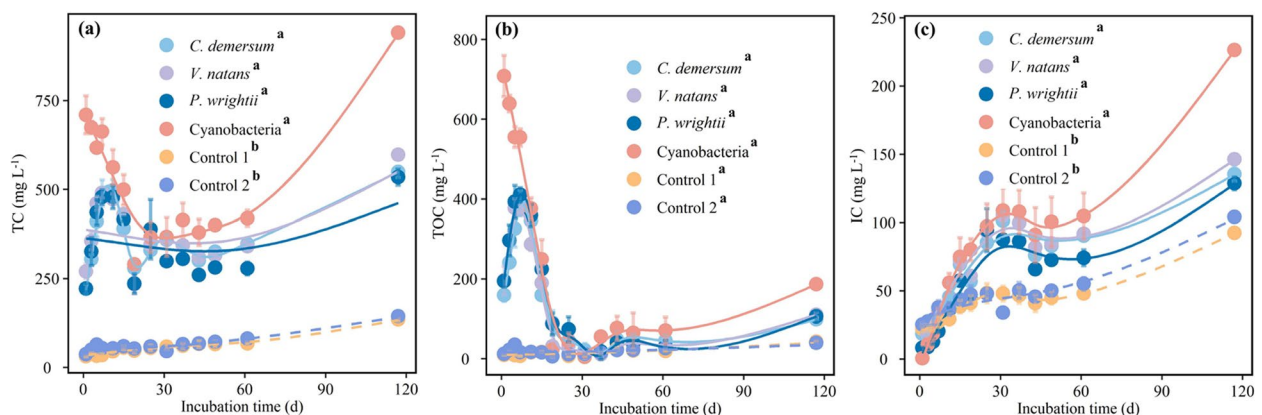


Fig. 3 Cumulative trends of carbon under different treatment groups over the 117-day incubation period. **a** Total Carbon (TC); **b** Total Organic Carbon (TOC); **c** Inorganic Carbon (IC). Different lowercase letters above each treatment group denote statistically significant differences at the $p < 0.05$ level

and then increased again through day 117. The cyanobacteria treatment consistently exhibited the highest IC levels, peaking at $226.29 \pm 1.34 \text{ mg L}^{-1}$ on day 117 (Fig. 3c). Although distinct trends were observed, statistical analysis indicated no significant differences among treatments ($p > 0.05$), suggesting that while the temporal patterns of carbon transformation differed, the overall carbon release during decomposition was comparable across treatments.

The decomposition of cyanobacteria and submerged macrophytes significantly affected the physical and chemical properties of the overlying water. During the 117-day incubation period, the concentrations of TN and NH_4^+ continued to increase in both the cyanobacteria and submerged macrophyte treatments, while NO_3^- concentrations gradually decreased. The cyanobacteria treatment exhibited significantly higher TN and NH_4^+ concentrations, reaching peaks of $276.42 \pm 7.68 \text{ mg L}^{-1}$ and $276.33 \pm 7.67 \text{ mg L}^{-1}$, respectively, by the end of the experiment. In contrast, TN and NH_4^+ concentrations in all three submerged macrophyte treatments remained below 50 mg L^{-1} throughout the study, indicating much lower nitrogen released from their decomposition. Statistical analysis revealed significant differences in the cumulative trends of TN and NH_4^+ concentrations between the cyanobacteria and submerged macrophyte treatments ($p < 0.05$), with no significant differences observed among the three submerged macrophyte treatments ($p > 0.05$). These results suggest that cyanobacteria release nitrogen more rapidly and in greater amounts compared to submerged macrophytes. Conversely, NO_3^- concentrations did not differ significantly between the cyanobacteria, macrophyte treatments, and control ($p > 0.05$), implying that neither decomposition type strongly influenced NO_3^- levels in the overlying water.

For TP, the cyanobacteria treatment had the highest initial concentration at $17.27 \pm 1.37 \text{ mg L}^{-1}$, which gradually decreased throughout the experiment. The TP concentrations in the three submerged macrophyte treatments also showed a decreasing trend, but the initial concentrations differed. At the start of the experiment, *P. wrightii* had the highest TP concentration, followed by *V. natans* and *C. demersum*. Throughout the study, TP in *C. demersum* remained consistently low, below 5 mg L^{-1} . Statistical analysis indicated that the TP trend in *C. demersum* differed significantly from the other treatments ($p < 0.05$), while no significant differences were observed between the other two submerged macrophyte treatments ($p > 0.05$). These results suggest that *C. demersum* released phosphorus more slowly, likely due to its lower tissue nutrient content or reduced microbial degradability (Fig. 4).

3.3 Correlation analysis between cumulative CH_4 and CO_2 production as well as environmental parameters

The cumulative emissions of CH_4 and CO_2 from cyanobacteria and three submerged macrophyte treatments showed similar correlations with water physicochemical factors, suggesting that their decomposition kinetics may follow comparable patterns. Both GHG emissions were significantly positively correlated with IC, and significantly negatively correlated with TOC, but showed no significant relationship with TC (Fig. 5). Additionally, cumulative CH_4 and CO_2 emissions were significantly positively correlated with TN and NH_4^+ , and significantly negatively correlated with TP and NO_3^- .

4 Discussion

Cyanobacteria and submerged macrophytes are key primary producers in freshwater ecosystems and play a critical role in GHG emissions from lakes and wetlands. Our study revealed that the decomposition of cyanobacteria led to higher CH_4 and CO_2 emissions compared to the three submerged macrophytes, with cyanobacteria showing a notably faster CH_4 release in the early stages of decomposition. These findings align with our first hypothesis. The rate of decomposition of plant materials under anaerobic conditions is generally negatively correlated with the carbon-to-nitrogen (C/N) ratio (Grasset et al. 2019). Both CH_4 and CO_2 are by-products of organic matter mineralization, and the composition of the organic matter, along with its decomposition rate, plays a critical role in determining GHG emissions (Duc et al. 2010; Xu et al. 2020). Cyanobacteria typically have lower C/N ratios and contain fewer complex structural compounds (such as lignin and cellulose), making them more readily decomposed by microorganisms (Lamb et al. 2006; Mao et al. 2024; Xu et al. 2024). This enhanced early-stage anaerobic decomposition releases substrates that are efficiently utilized by methanogens, thereby leading to higher CH_4 production (West et al. 2012; Casas et al. 2013). In contrast, submerged macrophytes have higher C/N ratios and more complex organic compounds that decompose more slowly, resulting in a more gradual release of substrates and a delayed increase in GHG emissions (C/N ratios for all plant materials are provided in Appendix 2). This slower decomposition process limits the availability of methanogenic substrates, leading to lower CH_4 emissions in the short term (Duarte 1992; Lamb et al. 2006; Assunção et al. 2017).

Among the submerged macrophytes studied, *P. wrightii* exhibited significantly higher initial decomposition rates, particularly for CO_2 emissions, than *V. natans* and *C. demersum*. However, this trend was not clearly associated with its C/N ratio, which was comparable to the other two species (Appendix 2). This suggests that

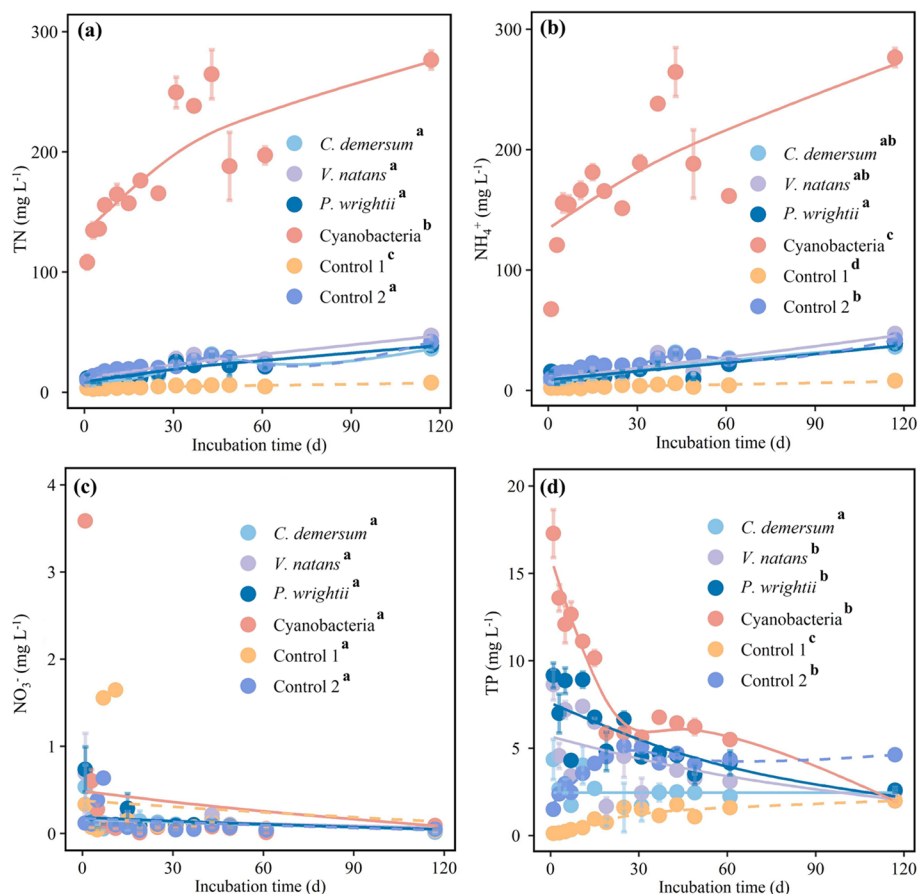


Fig. 4 Cumulative water quality trends under different treatment groups during the 117-day incubation period. **a** Total nitrogen (TN); **(b)** Ammonium nitrogen (NH₄⁺); **(c)** Nitrate nitrogen (NO₃⁻); **(d)** Total phosphorus (TP). Different lowercase letters above each treatment group denote statistically significant differences at the $p < 0.05$ level

factors beyond the bulk C/N ratio, such as differences in tissue structure, the proportion of labile organic compounds, or species-specific microbial interactions may play a more dominant role in driving early-stage carbon mineralization. Further studies focusing on detailed biochemical composition (e.g., soluble sugars, structural carbohydrates, and lignin content) are needed to clarify the mechanisms underlying interspecific variation in decomposition dynamics and GHG emissions.

The decomposition of both cyanobacteria and submerged macrophytes plays a significant role in carbon dynamics within freshwater ecosystems (Wu et al. 2017; Reitsema et al. 2018; Liu et al. 2019). In our study, the decomposition of submerged macrophytes led to a marked increase in TOC concentrations during the first 7 days, followed by a sharp decline by day 31. This pattern suggests that submerged macrophytes release labile organic carbon early in the decomposition process, stimulating microbial activity and subsequent GHG production. The initial increase in TOC likely reflects

the leaching of soluble, easily degradable organic compounds (e.g., monosaccharides and amino acids), which microorganisms rapidly consume (Bottino et al. 2016). As microbial activity progresses, these labile carbon sources are depleted, leading to the observed decline in TOC. The negative correlations between CH₄ and CO₂ fluxes and TOC concentrations (Fig. 5) further support this hypothesis, aligning with previous research (Reitsema et al. 2018; Zhang et al. 2022). In contrast, TOC concentrations in the cyanobacteria treatment decreased rapidly, with a reduction of 95.03% to 98.85% within the first 19 days. This decline reflects the high proportion of labile carbon in cyanobacterial biomass, which is immediately released and rapidly consumed by microorganisms (Yan et al. 2017; Xue et al. 2024). Thus, the rapid decrease in TOC is attributable to the rapid release and consumption of labile carbon by microorganisms.

In addition, IC concentrations increased steadily throughout the incubation period in both the cyanobacteria and submerged macrophyte treatments, showing

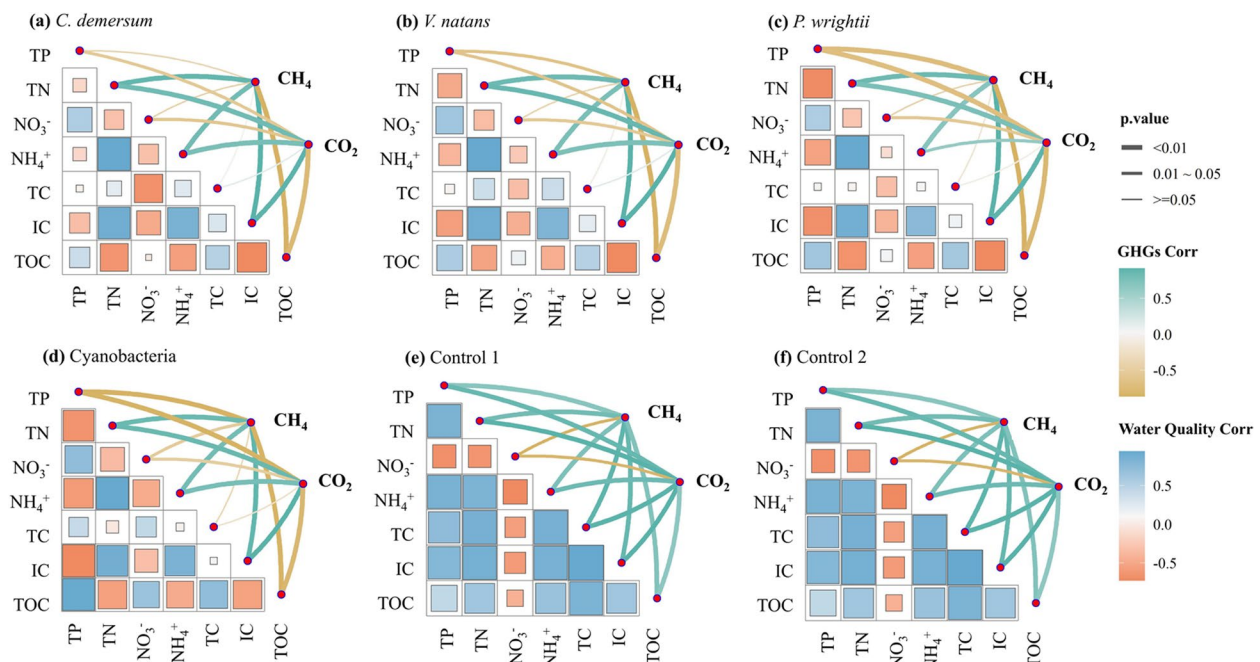


Fig. 5 Correlation between cumulative GHG emissions and water environmental factors across treatment groups in the water and sediment matrix. The line thickness represents the significance of the correlation, with thicker lines indicating stronger significance. **a** *C. demersum*; **b** *V. natans*; **c** *P. wrightii*; **d** Cyanobacteria; **e** Control 1; **f** Control 2

a significant positive correlation with CO_2 release. This trend likely reflects the accumulation of CO_2 produced during the decomposition of organic matter and its subsequent dissolution into the water column. In freshwater systems, dissolved CO_2 typically reacts with water to form carbonic acid (H_2CO_3), which then dissociates into bicarbonate (HCO_3^-) and hydrogen ions (H^+) (Ferdush and Paul 2021). The formation of HCO_3^- likely contributed to the observed rise in IC and represents a notable internal carbon sink (Titus and Pagano 2002). By temporarily retaining CO_2 in dissolved form, this process may partially mitigate atmospheric emissions and buffer greenhouse gas fluxes from aquatic ecosystems.

Our study revealed significant differences in nitrogen and phosphorus dynamics between cyanobacterial and submerged plant treatments. Cyanobacterial decomposition led to a marked increase in TN and NH_4^+ concentrations in the water column, suggesting that cyanobacteria release nitrogen more efficiently during decomposition, particularly in the form of ammonium. This finding supports our second hypothesis. Previous studies have shown that nitrogen can stimulate microbial enzyme activity, thereby accelerating decomposition rates (Chen et al. 2021b; Dong et al. 2022; Li et al. 2022). Consequently, the rapid nitrogen release from cyanobacterial decomposition may enhance microbial activity, further promoting the breakdown of organic matter and

the subsequent emission of GHGs. The significant positive correlations between CH_4 and CO_2 emissions and NH_4^+ and TN concentrations provide strong support for this hypothesis. However, it is important to note that the rapid and efficient nitrogen flux associated with cyanobacterial decomposition could have broader implications for eutrophication. Elevated nitrogen concentrations can disrupt nutrient balance in freshwater systems, leading to nutrient cycling feedback loops that exacerbate eutrophication (Bergström and Jansson 2006; Conley et al. 2009). Over time, the continuous release of nitrogen may fuel the growth of nitrogen-fixing microorganisms and further contribute to nutrient enrichment in the system, which may increase the overall nutrient load and support a cycle of prolonged eutrophic conditions. In contrast, nitrogen release from submerged macrophytes was more limited, with no significant differences observed between species. This suggests that submerged macrophytes contribute less to nitrogen mineralization during decomposition, likely due to their higher C/N ratios, which slow decomposition and reduce the availability of nitrogen to microbial communities (Fog 1988; Geurts et al. 2010; O'Brien et al. 2014). As a result, submerged macrophytes may contribute to a more stable nitrogen balance, potentially reducing the risk of further nutrient enrichment and mitigating the acceleration of eutrophication in freshwater ecosystems.

The cyanobacterial treatment also revealed an increase in phosphorus concentration during the early stages of decomposition, followed by a rapid decline. This pattern likely reflects the release of soluble phosphorus from cyanobacterial biomass during initial decomposition (Gao et al. 2013; Zhang et al. 2018; Yan et al. 2024). Prior research suggests that phosphorus released from decomposing cyanobacteria is primarily in the form of labile peptides, while phosphorus released from submerged macrophytes tends to be more associated with aliphatic hydrocarbons and highly unsaturated, low-oxygen substances (He et al. 2016; Chen et al. 2021a, b). The observed differences in release patterns between treatments are consistent with these compositional contrasts. Given that phosphorus is a limiting nutrient in many freshwater systems, the initial release of labile phosphorus by cyanobacteria may serve as a critical nutrient source for microorganisms, promoting microbial activity and accelerating decomposition and GHG production (Rejmánková and Houdková, 2006; Mehnaz et al. 2019). However, this initial pulse of labile phosphorus may also exacerbate eutrophication by stimulating further algal growth and microbial respiration (Conley et al. 2009). As decomposition progresses and phosphorus is consumed, the release rate declines. Nevertheless, the residual phosphorus load may continue to support nutrient cycling, potentially extending the eutrophic state of the lake. In contrast, phosphorus released by submerged macrophytes typically exhibits low bioavailability, which may reduce the risk of sustained nutrient pulses and limit further nutrient enrichment, thereby contributing to more stable nutrient dynamics and potentially mitigating long-term eutrophication in freshwater ecosystems.

In addition, nitrogen and phosphorus dynamics exhibited contrasting trends, reflecting fundamental differences in their biogeochemical behavior. NH_4^+ tends to remain dissolved in the water column due to its high solubility (Neuhausen and Patrick, 2002; Thomas et al., 2002), whereas phosphorus is more readily removed from the water column through microbial uptake or adsorption onto sediment particles (Du et al., 2011; Huang et al., 2011). This decoupling led to a progressive increase in the nitrogen-to-phosphorus (N/P) ratio over time, particularly in the cyanobacterial treatment. An elevated N/P ratio can shift the microbial community toward phosphorus limitation, which may reduce microbial growth efficiency and alter enzyme allocation strategies (Güsewell and Gessner 2009). Under phosphorus-limited conditions, microbes may upregulate oxidative enzymes (e.g., phenol oxidase) to access organic phosphorus, thereby accelerating the degradation of organic matter (Chen et al. 2021b; Zhang et al. 2022). These shifts in microbial metabolism may enhance carbon mineralization and

influence greenhouse gas emissions. In contrast, the submerged plant treatment maintained a more stable N/P ratio, likely supporting more balanced microbial nutrient uptake, slower organic matter decomposition, and reduced GHG production.

Considering the differences between cyanobacteria and submerged macrophytes in terms of GHG emissions and nutrient dynamics, promoting the growth of submerged macrophytes with lower decomposition rates, higher carbon-to-nitrogen ratios, and reduced phosphorus release, such as *V. natans* and *C. demersum*, appears to be a promising strategy for restoring eutrophic lakes and mitigating GHG emissions in freshwater ecosystems. Their higher C/N ratios and slower release of labile organic matter suggest a greater potential for organic carbon retention in sediments, which could contribute to long-term carbon storage. However, widespread use of such macrophytes also requires caution. Excessive biomass accumulation can lead to nighttime oxygen depletion due to respiration, creating hypoxic conditions that threaten fish and other aerobic organisms (Miranda and Hodges 2000; Flint et al. 2012). In addition, if the introduced species is non-native or invasive, its rapid expansion may displace native aquatic plants and disrupt habitat structure and biodiversity (Kagami et al. 2019). Therefore, balancing the benefits of macrophyte restoration with the potential risks to ecosystem function is critical. Developing a comprehensive research agenda will help refine restoration strategies and provide a clearer pathway for sustainable management practices in eutrophic lakes and wetlands.

5 Conclusion

Our study highlights the complex relationship between the decomposition of cyanobacteria and three submerged macrophytes in lake ecosystems, with respect to GHG emissions and water quality dynamics. Our results demonstrate that cyanobacterial decomposition significantly increases the release of CH_4 and CO_2 , while also accelerating the release of essential nutrients such as nitrogen and phosphorus into the water. This process is likely to intensify the carbon cycling in the lake and exacerbate eutrophication, creating a positive feedback loop that contributes to global warming. In contrast, the decomposition of submerged macrophytes results in lower emissions of GHGs and nutrients, although slight differences were observed between species. For lake restoration and GHG mitigation, we recommend prioritizing submerged macrophyte species with lower GHG and nutrient release, such as *V. natans* and *C. demersum*, to help mitigate eutrophication and reduce the impact of GHG emissions in eutrophic lakes.

Abbreviations

<i>C. demersum</i>	<i>Ceratophyllum demersum</i>
CH ₄	Methane
GHG	Greenhouse gas
GHGs	Greenhouse gases
C/N	Carbon-to-nitrogen
CO ₂	Carbon dioxide
ECD	Electron capture detector
FID	Flame ionization detector
GAM	Generalized additive model
H ⁺	Hydrogen ions
HCO ₃ [−]	Bicarbonate
H ₂ CO ₃	Carbonic acid
IC	Inorganic carbon
N/P	Nitrogen-to-phosphorus
NH ₄ ⁺	Ammonia nitrogen
NO ₃ [−]	Nitrate nitrogen
<i>P. wrightii</i>	<i>Potamogeton wrightii</i>
SD	Standard deviations
TC	Total carbon
TN	Total nitrogen
TOC	Total organic carbon
TP	Total phosphorus
<i>V. natans</i>	<i>Vallisneria natans</i>

Supplementary Information

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Supplementary Material 1.

Authors' contributions

All authors contributed to the study conception and design. Hanrui Wang and Yanzhi Cui performed material preparation, data collection, analysis, and wrote the first draft of the manuscript. Ming Ji, Fei He, and Guodong Bian contributed to material preparation, data collection, and analysis. Jie Ma, Zhipeng Pei, and Xiaoguang Xu contributed to writing—review and editing. Jie Ma supervised the project and acquired funding. All authors commented on previous versions of the manuscript and read and approved the final manuscript.

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Data availability

Data will be made available on request.

Declarations

Competing interests

The authors declare that they have no competing interests.

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