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Responses of two typical harmful cyanobacteria to extracts of *Phalaris arundinacea*, a dominant hygrophyte in Lake Poyang, China

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Abstract – The frequent occurrence of cyanobacterial blooms poses severe threats to the global environment and to local human health. Therefore, it is vital to develop effective methods to control blooms. *Phalaris arundinacea*, a dominant hygrophyte in the Lake Poyang wetland, decomposes when submerged during high-water-level periods. Through indoor cultivation experiments, we examined the effects of crude aqueous, ethyl acetate, dichloromethane and petroleum ether extracts of *P. arundinacea* on the growth of typical harmful bloom-forming cyanobacteria (*Microcystis aeruginosa* and *Dolichospermum flos-aquae*). The results revealed that the crude aqueous extract of *P. arundinacea* significantly inhibited the growth of *M. aeruginosa* and *D. flos-aquae*, with average inhibition rates of 86.77 per cent and 80.08 per cent, respectively. The inhibitory effect generally increased with time and dose, with maximum inhibition rates of 99.15 per cent for *M. aeruginosa* and 97.27 per cent for *D. flos-aquae*. *P. arundinacea* crude extracts obtained with ethyl acetate, dichloromethane and petroleum ether reduced the cell density and *chlorophyll a* concentration of *M. aeruginosa*. Among the extracts, the petroleum ether extract had the strongest inhibitory effect. Generally, the inhibition rates of these three crude organic solvent extracts peaked on Day 8 or Day 12 of the experiment. The results confirmed that *P. arundinacea*, a dominant hygrophyte in Lake Poyang, has significant potential for controlling harmful cyanobacterial blooms through the release of allelochemicals and likely plays an important role in this process in summer. Therefore, this study offers novel insights and materials for the prevention and management of cyanobacterial blooms in the future.

Keywords: *Phalaris arundinacea* / Harmful bloom-forming cyanobacteria / Extract / Inhibitory effects / Lake Poyang

1 Introduction

Owing to eutrophication and climate warming, freshwater ecosystems have experienced frequent cyanobacterial blooms, especially since the 2010s (Paerl and Barnard, 2020; Pal *et al.*, 2020; Wu *et al.*, 2021; Hou *et al.*, 2022). Cyanobacterial blooms lead to decreased dissolved oxygen content and poor water quality, reducing aquatic biodiversity and threatening animal and human health (Huisman *et al.*, 2018; Wu *et al.*, 2021). Consequently, mitigating cyanobacterial blooms has become a critical priority for safeguarding aquatic ecosystems and maintaining their functionality (Harris *et al.*, 2024).

Organisms compete through two strategies. The first involves resource competition, which occurs when specific resources are limited (Gao *et al.*, 2022; Mei *et al.*, 2022). In the second strategy (competition by interference), one organism

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directly or indirectly inhibits the growth of others through the secretion of chemicals, cell – cell interactions, or other behaviours (San Emeterio *et al.*, 2007; Zhang *et al.*, 2015; Pando *et al.*, 2022). Allelopathy, a specific form of interference-based competition, involves plants releasing specific chemicals into the environment to influence the growth and development of surrounding plants and microorganisms. Allelochemicals are environmentally friendly, and naturally derived, have short half-lives and good biodegradability and exhibit high application potential for ecological management (Zhu *et al.*, 2021; An *et al.*, 2022; Kostina-Bednarz *et al.*, 2023). Therefore, identifying effective and environmentally friendly natural allelochemicals as algaecides is important for environmental management.

Allelopathy (Molisch, 1938), refers to the beneficial or harmful effects of chemicals secreted by a plant or microorganisms on the growth of another plant (Rice, 1984). Secondary metabolites that exhibit allelopathic properties were termed allelochemicals by Whittaker and Feeny (1971). Allelochemicals secreted by plants inhibit the growth of phytoplankton (Kurashov *et al.*, 2021; Li *et al.*, 2021; Zhu *et al.*, 2021). For example, Xiao et al. (2010) reported that barley straw effectively inhibits the growth of cyanobacteria. Similarly, the by-products of terrestrial plants, including rice and wheat, effectively inhibit the growth of algae (Park *et al.*, 2006; Effiong *et al.*, 2020). Low-cost plant-derived allelochemicals demonstrate potential as eco-friendly tools for controlling cyanobacterial blooms in eutrophic freshwater bodies. To date, studies on the inhibitory effects of plants on phytoplankton have focused on aquatic macrophytes, as well as straws derived from rice, barley and other plants (Xiao *et al.*, 2010; Park *et al.*, 2006). However, hygrophytes, which are distributed across aquatic ecosystems, have not been extensively studied in terms of their allelopathic effects on phytoplankton.

Lake Poyang is the largest freshwater lake in China and is connected to the Changjiang River. The phytoplankton community in Lake Poyang is dominated by cyanobacteria and diatoms, and their growth is influenced mainly by underwater light conditions, temperature, nutrients, water exchange time, and water level (Wu *et al.*, 2013; Wu *et al.*, 2014a; Wu *et al.*, 2014b; Zhang *et al.*, 2018; Wu *et al.*, 2019; Xiong *et al.*, 2019). Notably, a significant increase in cyanobacteria has been detected in Lake Poyang during summer compared with other seasons, with the dominant genera including *Dolichospermum*, *Microcystis*, and *Planktothrix*, and cyanobacterial blooms have been frequently observed in some areas (Qian *et al.*, 2016). Therefore, more attention should be given to recent cyanobacterial development in Lake Poyang, as well as to site-specific cyanobacterial control methods.

Owing to its connection to a river, Lake Poyang undergoes periodic water level changes, leading to the transformation of lake areas to wetland areas and vice versa (Wang *et al.*, 2023). When the water level rises, many hygrophytes —moisture-loving plants that thrive in damp terrestrial habitats — decompose, affecting nutrient cycling and energy flow in the aquatic ecosystem. Hygrophytes are widely distributed in the wetlands around Lake Poyang, with an area reaching 3157.13 km^2 in the dry season, i.e., the period with a relatively low water level (Ji *et al.*, 2017). *Phalaris arundinacea* is a dominant hygrophyte in Lake Poyang, and its mean aboveground biomass in spring (relatively low water level period) was estimated to be 2262 $g\,m^{-2}$ (Wang *et al.*, 2016a). Our previous research revealed that the decomposition of *P. arundinacea* alters the aquatic environment and phytoplankton community structure (Ma *et al.*, 2021; Wu *et al.*, 2023). However, it remains unclear whether *P. arundinacea* affect phytoplankton, especially harmful bloom-forming cyanobacteria, through the release of allelochemicals. Considering the abundant distribution of *P. arundinacea* and the fact that it decomposes during inundation periods in Lake Poyang, studies on algal inhibition by this hygrophyte are needed to identify environmentally friendly and effective natural algaecides.

Microcystis aeruginosa and *Dolichospermum flos-aquae* are typical harmful bloom-forming cyanobacteria in freshwater lakes. Owing to their short growth cycles, sensitivity to pollutants, and wide distribution, they are often used as model organisms in aquatic experiments. To address the above issues, we used *M. aeruginosa* and *D. flos-aquae* as experimental algae in this study. These species were co-cultured with crude aqueous, ethyl acetate, dichloromethane and petroleum ether extracts of *P. arundinacea*, and their growth characteristics were recorded. These three organic solvents, which have been commonly used in similar studies, were selected based on polarity to extract different components of *P. arundinacea* (Li *et al.*, 2022; Xu *et al.*, 2019), and their performance in inhibiting cyanobacteria growth was tested. The main objectives of this research were to 1) determine whether *P. arundinacea* can limit the growth of typical bloom-forming cyanobacteria and 2) identify the influence of exposure time and dose on the effects of *P. arundinacea* crude extracts. The findings of this study provide new insights and guidance for the control of cyanobacterial blooms.

2 Materials and methods

2.1 Culture of *M. aeruginosa* and *D. flos-aquae*

M. aeruginosa (FACHB 905) and *D. flos-aquae* (FACHB 1255) strains were obtained from the Institute of Hydrobiology, Chinese Academy of Sciences. They were cultured in an illuminated incubator with BG-11 medium under a light intensity of 2000 lux, with a light:dark ratio of 12 h:12 h, and the temperature was approximately 25 °C (Hao *et al.*, 2025). The culture medium and containers were sterilised, and all operations throughout the experiment were performed on an ultraclean workbench. The algal cultures were shaken three times per day.

2.2 Preparation of crude aqueous and organic solvent extracts of *P. arundinacea*

Fresh *P. arundinacea* were collected from the Lake Poyang Wetland Observation and Research Station of the Chinese Academy of Sciences. First, the roots were removed, and the stems and leaves were manually cleaned, dried, and cut into 2 cm pieces. A total of 100 g of cut *P. arundinacea* was placed in a 5 L conical flask and soaked in distilled water for five days. After soaking, the residue was removed, and the

solution was filtered through a 0.2 μm membrane to obtain 100.0 g/L aqueous extract, which was stored at 4°C.

The plants were also extracted with three organic solvents. First, the plants were pulverised into a powder and sieved through a 50-μm mesh. A total of 50 g of plant powder was added to a 500 mL conical flask, and the powder was extracted three times, with 80 mL of petroleum ether, ethyl acetate, or dichloromethane. The supernatant was filtered through a 0.45 μm organic filter membrane twice (to eliminate interference from particles). The organic phase was mixed and dried via rotary evaporation (100 r/min) at 40°C for petroleum ether and dichloromethane and 60°C for ethyl acetate. The extract was weighed and dissolved in dimethyl sulfoxide (DMSO) (<1.0 per cent, v/v) to obtain a final organic solvent extract concentration of 4.8 g/L. The solution was filtered through a 0.22 μm organic filter membrane under aseptic conditions to eliminate microbial contamination, and the filtrate was stored at 4°C in the dark.

2.3 Experimental design

2.3.1 Crude aqueous extract

For each species of algae, there were 6 treatments, including 1 control group (medium only) and 5 groups with different concentrations of extract (5.0, 10.0, 20.0, 40.0, and 80.0 g/L), with 4 replicates per group. To obtain the target concentrations, 50.0, 100.0, 200.0, 400.0, and 800.0 mL of the aqueous extract (100 g/L) were added and diluted to 1 L with distilled water in conical flasks.

Batch cultures were performed in 250 mL conical flasks. Because the aqueous extract of *P. arundinacea* releases relatively high nutrient concentrations (Ma *et al.*, 2021) and has a rapid inhibitory effect, provisional algal assay procedure (PAAP) medium, which has relatively low nutrients contents (4.200 mg/L N and 0.186 mg/L P), was used for the aqueous extract addition experiments (Miller *et al.*, 1978). Two milliliters of cultured algae at a concentration of 1×10^8 cells/mL and 16 mL of the designed concentration of aqueous extract were added and diluted to 200 mL with PAAP medium. Therefore, the initial algal concentration was 1×10^6 cells/mL. Throughout the study, all culture experiments were performed under controlled laboratory conditions (25 ± 1°C, 2000 lux light intensity, 12 h:12 h light/dark cycle). We collected phytoplankton samples from each flask every 3 days, which were fixed with Lugol's iodine solution (1 per cent v/v) in situ and counted using a microscope (Leica DM2500, Germany).

2.3.2 Crude ethyl acetate, dichloromethane and petroleum extracts

Crude organic extracts addition experiment was conducted in 100 mL conical flasks and consisted of 16 treatments, i.e., a control (medium only, without ethyl acetate, dichloromethane or petroleum) and ethyl acetate, dichloromethane and petroleum ether treatments with concentrations of 0.01, 0.02, 0.04, 0.08, and 0.16 g/L; each treatment had 4 replicates. Precultured *M. aeruginosa* in the logarithmic growth phase was added to the flasks, and the initial concentration was 1.0×10^6 cells/mL. Sterile medium was added to achieve a final volume of 60 mL. The culture conditions were the same as those in the crude aqueous extract experiment. Phytoplankton samples were collected from each flask every 4 days. At the end of the experiment, i.e., Day 16, we determined the *chlorophyll a (*chla) content via the acetone method. Briefly, a 1 mL sample was collected, 9 mL of 90 per cent acetone was added, and the mixture and kept in the dark for 24 h at 4 °C before centrifugation. The absorbance was analysed at 665 and 750 nm with an ultraviolet spectrophotometer (TU-1810, Beijing, PR China). The components of the crude extracts were determined via liquid chromatography–mass spectrometry (LC–MS). More detailed information is available in Dodder et al. (2007).

2.4 Data analysis

The phytoplankton inhibition rate was calculated using the following formula:

$$IR = \left(1 - \frac{N}{N_0}\right) \times 100\%\text{percent} \quad (1)$$

where N is the cell density of phytoplankton in the treatment group and N_0 is the cell density of phytoplankton in the control.

When the data passed the normality and homogeneity of variance tests, one-way analysis of variance (ANOVA) was used for significant difference analysis; otherwise, the Kruskal–Wallis test was used. The normality test, the homogeneity of variance test, one-way ANOVA, and the Kruskal–Wallis tests were performed using SPSS version 24. The effects of time, dose, and their interaction on cell density were analysed via a generalised linear model, with time, dose, and their interaction as fixed effects and the culture flask ID as a random effect. The generalised linear model was calculated in R version 4.3.4.

3 Results

3.1 Effects of *P. arundinacea* crude aqueous extract on the growth of *M. aeruginosa* and *D. flos-aquae*

3.1.1 Cell density

The cell densities of *M. aeruginosa* in all the aqueous extract groups were lower than those in the control group at the same sampling time (Fig. 1A). The results of the Kruskal–Wallis test revealed significant differences between the control group and each extract group (all $P < 0.05$), indicating that the *P. arundinacea* crude aqueous extracts significantly reduced the cell density of *M. aeruginosa* regardless of concentration. Over time, the cell density in the control group gradually increased, whereas in the aqueous extract treatment groups, the cell density initially decreased but then fluctuated. On Day 15, the average cell densities in the treatments were 0.59×10^6 cells/mL (5.0 mg/L), 0.34×10^6 cells/mL (10.0 mg/L), 0.24×10^6 cells/mL (20.0 mg/L), 0.18×10^6 cells/mL (40.0 mg/L), and 0.02×10^6 cells/mL (80.0 mg/L), all of which were lower than the corresponding values in the control group (2.84×10^6 cells/mL) and the initial cell density (1.00×10^6 cells/mL). Additionally, the mean cell density decreased with increasing concentrations of crude aqueous extract, except in the 10.0 mg/L group on Day 9, in which the cell density was slightly greater than that in the 5.0 mg/L group (Fig. 1).

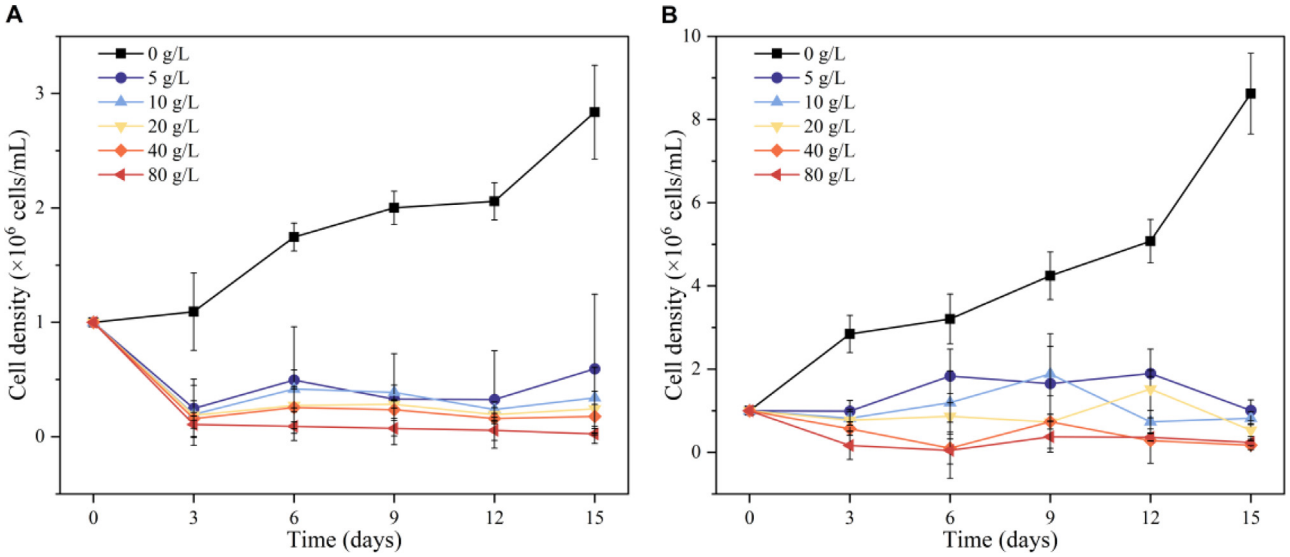

Fig. 1. Effects of the *P. arundinacea* crude aqueous extract on the cell densities of *M. aeruginosa* (A) and *D. flos-aquae* (B). The data points represent the mean values (n = 4), and the error bars indicate the standard deviation (SD).

Similar to the trends for *M. aeruginosa*, *D. flos-aquae* growth was significantly inhibited by the crude *P. arundinacea* aqueous extract, with lower cell densities in the crude aqueous extract treatments from Day 3 to Day 15 (Fig. 1B). For example, on Day 15, the cell densities were 1.01×10^6 cells/mL (5.0 mg/L), 0.82×10^6 cells/mL (10.0 mg/L), 0.53×10^6 cells/mL (20.0 mg/L), 0.17×10^6 cells/mL (40.0 mg/L), and 0.24×10^6 cells/mL (80.0 mg/L), all of which were lower than the corresponding cell density in the control group (2.84×10^6 cells/mL). Overall, the mean *D. flos-aquae* cell density decreased with increasing concentrations of the crude aqueous extract, especially on Days 3 and 6. The results of the Kruskal–Wallis test revealed significant differences between the control and crude aqueous extract treatments (all $P < 0.05$), regardless of time.

3.1.2 Inhibition rate

The *P. arundinacea* crude aqueous extract strongly inhibited the two typical bloom-forming cyanobacteria, with average inhibition rates of 86.77 per cent (*M. aeruginosa*) and 80.08 per cent (*D. flos-aquae*). In the later stages of the experiment (Days 12 and 15), the rate of *M. aeruginosa* growth inhibition by *P. arundinacea* crude aqueous extract at concentrations of 20 g/L and above exceeded 90 per cent (Fig. 2A). In the treatments with *P. arundinacea* extract at concentrations of 40 g/L or greater, the inhibition of *D. flos-aquae* growth exceeded 90 per cent (Fig. 2B). Notably, the inhibition rate of 80 g/L *P. arundinacea* crude aqueous extract was greater than 90 per cent for both species of bloom-forming cyanobacteria throughout the experiment.

At all time points, the rates of *M. aeruginosa* and *D. flos-aquae* growth inhibition by *P. arundinacea* crude aqueous extract generally increased with increasing extract concentration; this trend was particularly apparent for *M. aeruginosa* (Fig. 2). On Day 15, the average inhibition rates of *M. aeruginosa* in the treatments were 79.06 per cent (5.0 mg/L), 88.00 per cent (10.0 mg/L), 91.39 per cent (20.0 mg/L), 93.77 per cent (40.0 mg/L), and 99.15 per cent (80.0 mg/L) (Fig. 2A); the corresponding average inhibition rates for *D. flos-aquae* were 88.31 per cent, 90.51 per cent, 93.85 per cent, 98.03 per cent, and 97.27 per cent, respectively (Fig. 2B). In terms of the mean inhibition rate, the treatments with lower crude aqueous extract concentrations (5, 10, and 20 g/L) had greater inhibitory effects on *M. aeruginosa* than on *D. flos-aquae* throughout the experiment except on Day 15, particularly on Day 3, when the difference was significant ($P < 0.05$).

3.2 Effects of *P. arundinacea* crude organic solvent extracts on *M. aeruginosa*

3.2.1 Cell density

Fig. 3 shows the effects of the three crude organic solvent extracts of *P. arundinacea* on the cell density of *M. aeruginosa*. Compared with that of the control group, the cell density was lower in all three crude extract treatments, regardless of concentration. The results of the Kruskal–Wallis test revealed significant differences (all $P < 0.05$) between the control group and the petroleum ether extract groups at all concentrations except 0.01 g/L. Significant differences were also observed between the control and the dichloromethane extract treatments at 0.04 and 0.16 g/L (all $P < 0.05$). However, there were no significant differences between the control group and any of the ethyl acetate extract treatment groups. On Day 16, the cell density generally decreased with increasing crude extract concentration, particularly in the ethyl acetate extract treatments (Fig. 3B).

Regardless of concentration, the average cell density at each time point was similar for the ethyl acetate and dichloromethane crude extract treatments, and the cell densities for both extracts were greater than those for the petroleum ether crude extract. For example, on Day 16, the

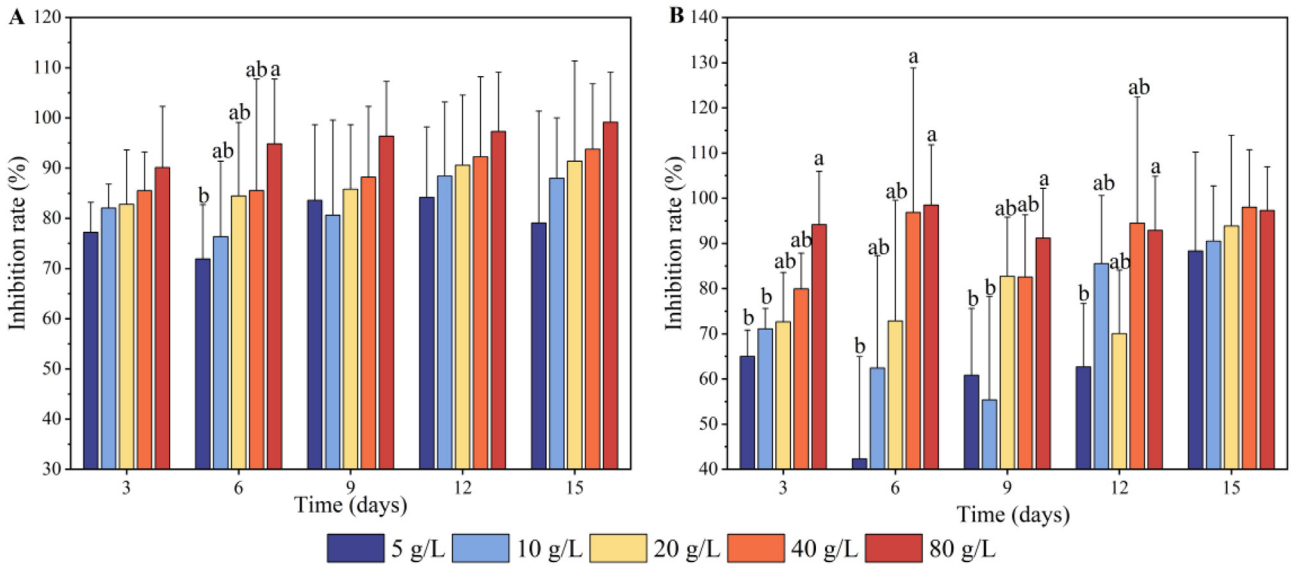

Fig. 2. Effects of *P. arundinacea* crude aqueous extract on the inhibition of *M. aeruginosa* (A) and *D. flos-aquae* (B). The data points represent the mean values (n = 4), and the error bars indicate the standard deviation (SD). Significant differences ($P < 0.05$) among different concentrations at the same sampling time are indicated by different letters (a and b).

average cell densities in the ethyl acetate and dichloromethane extract treatments were 25.29×10^6 cells/mL and 25.18×10^6 cells/mL, respectively, whereas the corresponding value was 22.01×10^6 cells/mL in the petroleum ether treatment.

Table 1 shows a significant effect of time on the cell density of *M. aeruginosa* in all three crude organic solvent extract treatments. Additionally, in the dichloromethane extract treatment, dose had a significant effect on the cell density of *M. aeruginosa*. Among the three crude extract treatments, the interaction between time and dose had no significant effect on cell density.

Additionally, we analysed the chemical composition of the crude organic solvent extracts (Table S1) via LC–MS. All three crude organic solvent extracts contained alkaline nitrogenous organic matter.

3.2.2 Inhibition rate

All three crude organic solvent extracts inhibited *M. aeruginosa* growth (Fig. 4). For example, on Day 16, the average inhibition rates across the concentration gradient ranged from 24.37 per cent to 38.65 per cent for petroleum ether treatments, 9.34 per cent to 33.65 per cent for the ethyl acetate extract treatments and 18.14 per cent to 29.50 per cent for the dichloromethane extract treatments. In terms of cell density, the crude petroleum ether extract had relatively high inhibition rates against *M. aeruginosa* growth. Across all the concentrations, the average inhibition rates of the petroleum ether extract were 34.72 per cent (Day 4), 49.80 per cent (Day 8), 47.78 per cent (Day 12), and 34.19 per cent (Day 16), all of which were higher than those of the other two extracts. At the same concentration, the highest inhibition rates were observed in the crude petroleum ether extract treatment throughout the experiment (except at 0.16 g/L, which inhibition was slightly higher that in the crude dichloromethane extract treatment). For example, at 0.08 g/L, the maximum inhibition rate for the petroleum ether extract treatments was 53.47 per cent, and the corresponding values were 38.89 per cent and 35.83 per cent for the crude dichloromethane and ethyl acetate extract treatments, respectively.

In general, the inhibition rate tended to first increase but then decrease over time in all the treatments, particularly in the treatments with the petroleum ether and dichloromethane extracts (Fig. 4). Except for ethyl acetate treatments with relatively low concentrations (0.01 and 0.02 g/L), the maximum inhibition rates in the three crude organic solvent extract treatments were observed on either Day 8 or Day 12. For example, at low concentrations (0.01–0.04 g/L), the maximum inhibition rates of the crude dichloromethane extract treatments were observed on Day 8, i.e., 27.26 per cent (0.01 g/L), 36.40 per cent (0.02 g/L), and 44.02 per cent (0.04 g/L); for the higher concentration treatments, the maximum inhibition rates were observed on Day 12, with values of 38.88 per cent (0.08 g/L) and 57.21 per cent (0.16 g/L).

The inhibition rate generally increased with increasing crude extract concentration. For example, the inhibition rates in the dichloromethane extract treatments were 22.52 per cent (0.01 g/L), 23.96 per cent (0.02 g/L), 24.79 per cent (0.04 g/L), 33.17 per cent (0.08 g/L), and 35.44 per cent (0.16 g/L). The inhibitory effect of the petroleum ether extract slightly decreased in the 0.08 and 0.16 g/L treatments, with inhibition rates of 36.43 per cent (0.01 g/L), 39.63 per cent (0.02 g/L), 44.83 per cent (0.04 g/L), 44.37 per cent (0.08 g/L), and 42.85 per cent (0.16 g/L).

3.2.3 Final chla concentration

Compared with that of the control group, the chla content strongly decreased in the crude organic solvent extract treatments, especially for the petroleum ether extract (with an average reduction of 56.64 per cent), followed by the ethyl acetate extract (36.05 per cent) and dichloromethane extract (35.91 per cent) (Fig. 5). Additionally, the chla content was the

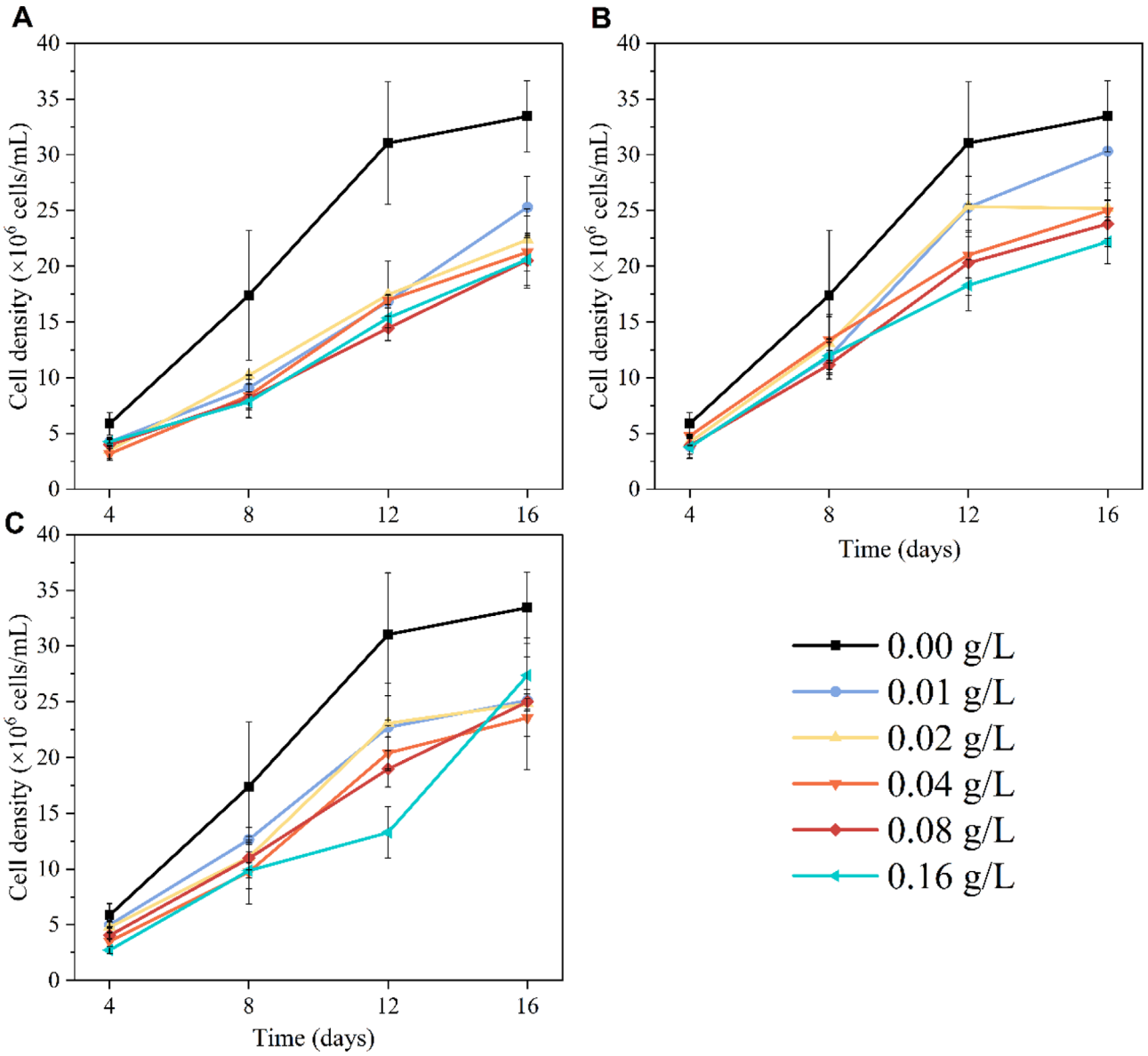

Fig. 3. Effects of three *P. arundinacea* crude extracts (petroleum ether (A), ethyl acetate (B), and dichloromethane (C)) on the cell density of *M. aeruginosa*. Data points represent mean values ($n = 4$), and the error bars represent the SDs.

lowest in the petroleum ether extract treatment, regardless of concentration, with values that were at least 62.34 per cent and 27.88 per cent lower than those in the ethyl acetate and dichloromethane extract treatments, respectively. The chla content was the highest in the crude dichloromethane extract treatment, except at 0.01 mg/L.

4 Discussion

4.1 Inhibitory effects of *P. arundinacea* on typical harmful bloom-forming cyanobacteria

This study revealed that *P. arundinacea*, a dominant hygrophyte in Lake Poyang, can effectively inhibit the growth of two typical harmful bloom-forming cyanobacteria, namely, *M. aeruginosa* and *D. flos-aquae*. On Day 15, 20 g/L *P. arundinacea* aqueous extract resulted in more than 90 per cent inhibition of *M. aeruginosa* growth, and the inhibition rate exceeded 97 per cent for both *M. aeruginosa* and *D. flos-aquae* when the concentration was 80 g/L. The three organic solvent extracts of *P. arundinacea* also had significant inhibitory effects on *M. aeruginosa* growth, with maximum inhibition rates of 54.96 per cent (petroleum ether), 41.12 per cent (ethyl acetate), and 57.21 per cent (dichloromethane). Researchers have conducted numerous studies on the allelopathic effects of plants on algae. Typical terrestrial plant products with algicidal properties include rice straw, barley straw, and *Spartina alterniflora*. Yuan et al. (2020) demonstrated that the inhibitory effect of *S. alterniflora* aqueous extract on *M. aeruginosa* growth increased with increasing concentration, with maximum

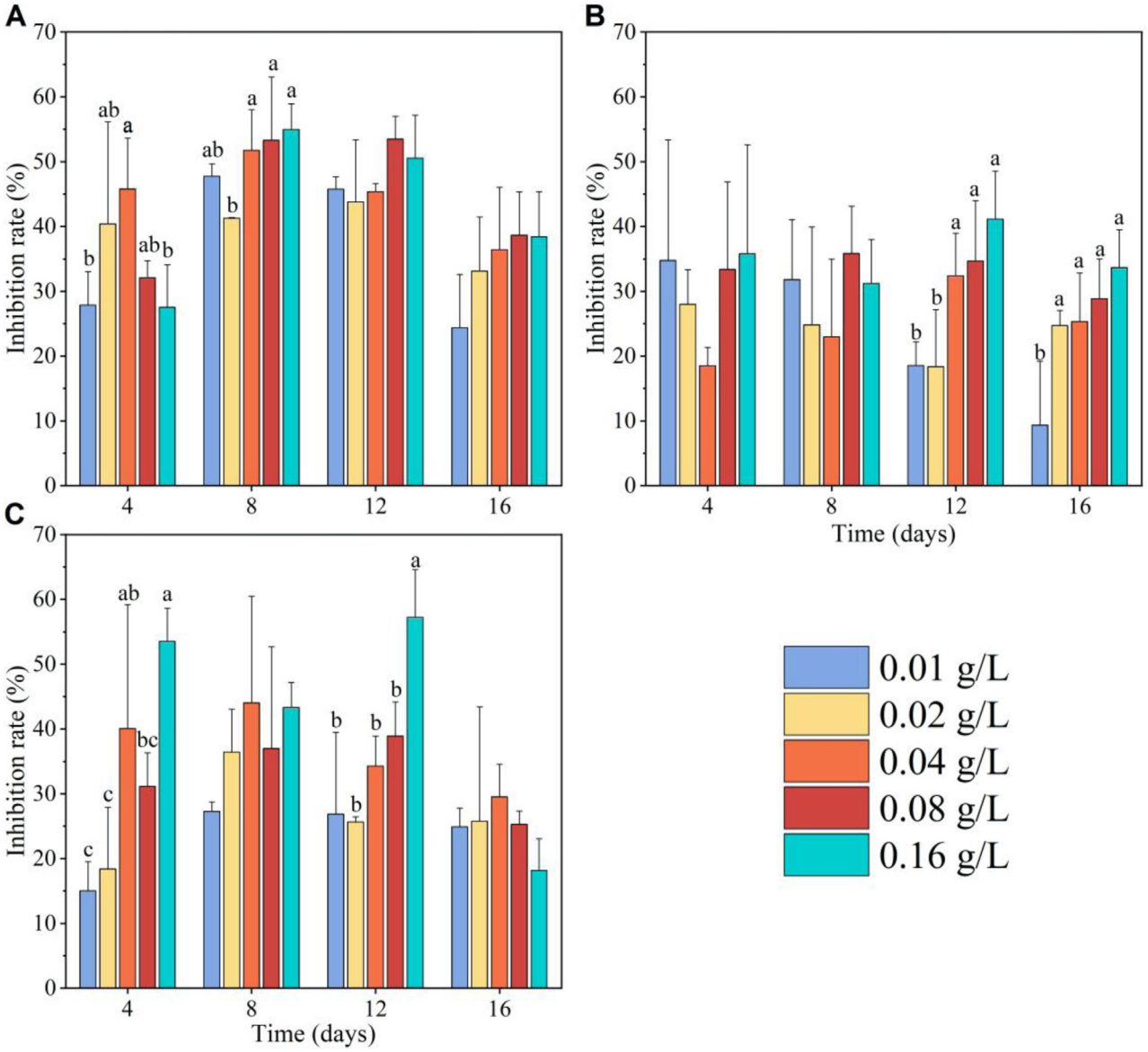

Fig. 4. Effects of three crude organic solvent extracts of *P. arundinacea* (petroleum ether (A), ethyl acetate (B), and dichloromethane (C)) on the rate of *M. aeruginosa* growth inhibition. The data points represent the mean values (n = 4), and the error bars represent the SDs. Significant differences ($P < 0.05$) among different concentrations at the same sampling time are indicated by different letters (a, b, and c).

inhibition rates exceeding 99 per cent . Recent studies have also shown that watermelon rind aqueous extract inhibits the growth of *D. flos-aquae*, with the inhibition rate increasing with increasing extract concentration (Yan *et al.*, 2022). Aquatic plants release allelochemicals that diffuse through the water environment and act on phytoplankton, thereby inhibiting phytoplankton growth (Tang *et al.*, 2021). For example, Dong et al. (2018) reported that the effect of cattail leaf extract on *M. aeruginosa* was concentration dependent, with a maximum inhibition rate of 72.35 per cent . Li et al. (2023) reported that extracts of three submerged plant taxa (*Vallisneria*, *Myriophyllum spicatum*, and *Ceratophyllum*) affected the growth of *M. aeruginosa*, promoting growth at low concentrations (0.5 and 1.0 g/L) and inhibiting growth at high concentrations (5 and 10 g/L). *P. arundinacea* is dominant in Lake Poyang wetlands (Xu *et al.*, 2020). When the water level rises in Lake Poyang, hygrophytes are submerged; this condition persists from May to September. Given its high biomass, submerged *P. arundinacea* may release relatively high quantities of allelochemicals that inhibit the growth of harmful bloom-forming cyanobacteria.

Notably, the highest inhibition rates for the crude extracts of the three organic solvents occurred on Day 8 or Day 12. One possible reason for this finding is that after prolonged exposure to stress conditions, the algal cells adapt and self-regulate under stress (Zhu *et al.*, 2010). Su et al. (2014) reported that *M. aeruginosa* cells recovered to some extent after prolonged exposure to high concentrations of rice straw extract relative to their state at the beginning of the experiment. The experimental duration employed in this study may have also affected the results. Li et al. (2022) tested the inhibitory effects of crude extracts of *Landoltia punctata* on *M. aeruginosa* in a 10-day experiment. Tazart et al. (2021) explored the inhibitory

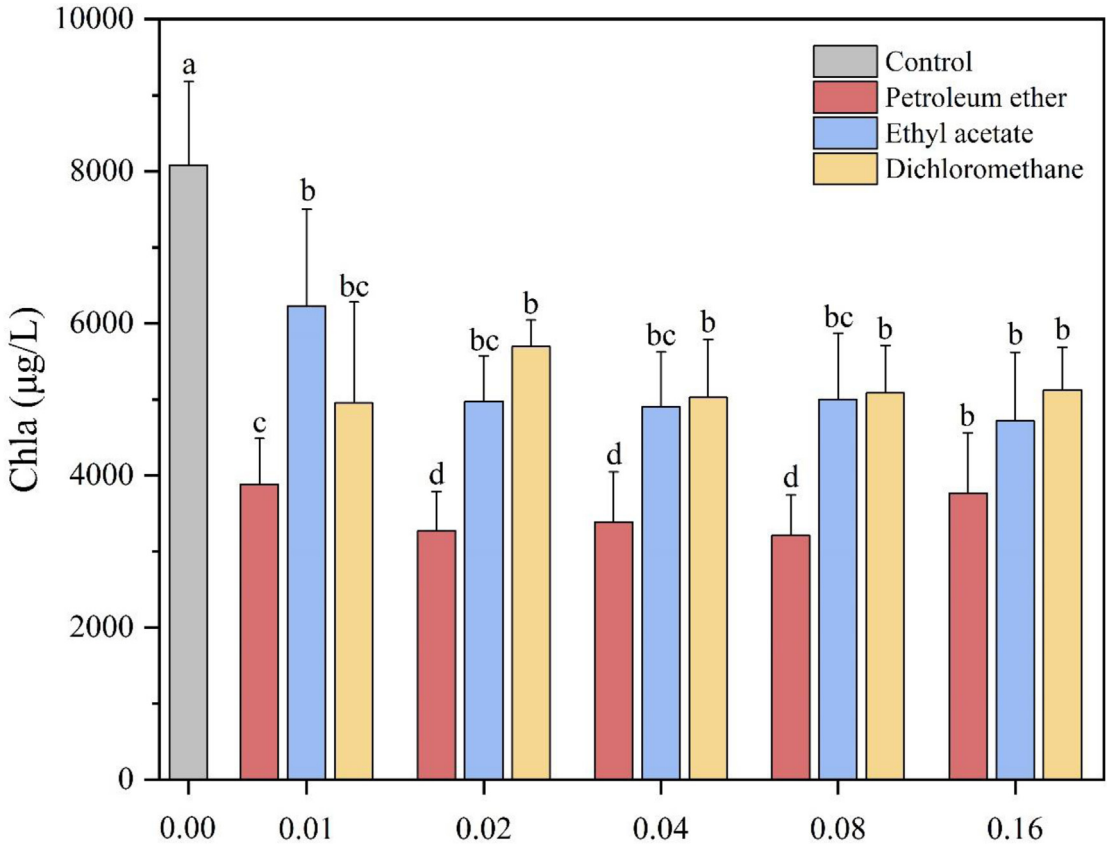

Fig. 5. Chla concentration of *P. arundinacea* in the control group and the three crude organic solvent extract groups. The data points represent the mean values (n = 4), and the error bars represent the SDs. Different letters (a, b, c) represent significant differences within the treatments.

effects of crude extracts from three macrophytes on *M. aeruginosa* in an experiment that lasted 8 days. Compared with previous studies, this study used a longer duration, potentially leading to changes in the internal conditions of the culture system, which may explain the decrease in the inhibition rate observed on Day 16. The degradation of allelochemicals, due to light and other factors may also account for the observed temporal variation in inhibition rates (Sanna *et al.*, 2004).

Nutrients are critical probably factors influencing phytoplankton growth and likely affect the inhibitory effects of *P. arundinacea* on typical harmful bloom-forming cyanobacteria. Due to the relatively high nutrient concentrations released by aqueous extracts of *P. arundinacea* (Ma *et al.*, 2021) and the observed rapid inhibition, we used provisional algal assay procedure (PAAP) medium, which has relatively low nutrient contents (4.200 mg/L N and 0.186 mg/L P), for the aqueous extract addition experiments (Miller *et al.*, 1978). Therefore, nutrients were not a limiting factor for algal growth in our study.

The uncertainty in the algal inhibition effect may also be related to the sterile culture conditions and the scale of the microcosm experiments. Studies have shown that phytoplankton is closely associated with other microorganisms in the environment (Sun *et al.*, 2018; Tan *et al.*, 2022). Therefore, the absence of microorganisms (sterile conditions) may lead to deviations in algal growth compared with that under natural conditions. Additionally, the microcosms employed in this study were closed systems, and dynamic changes occurring in open water bodies, such as water flow and nutrient exchange, could not be simulated. This may have led to discrepancies between the experimental results and actual conditions.

4.2 Different crude organic solvent extracts exhibit varying degrees of algal inhibition

In this study, the three crude organic solvent extracts inhibited *M. aeruginosa* growth to various degrees, and overall, the crude petroleum ether extract had the greatest inhibitory effect. Li et al. (2022) investigated the effects of *L. punctata* extracts using petroleum ether, dichloromethane, and ethyl acetate as organic solvents on the growth of *M. aeruginosa* and reported that the ethyl acetate extract had the strongest inhibitory effect. Patil et al. (2024) reported that a crude methanol extract of *Pyropia haitanensis* had a more significant inhibitory effect on algae than did an acetone extract. Differences in the quantity and type of allelochemicals extracted by different solvents are key factors influencing the inhibitory effects of crude extracts (Wang and Liu, 2023). Yuan et al. (2020) reported that extracts of *S. alterniflora* enriched with petroleum ether yielded more organic components than those enriched with ethyl acetate, chloroform, or n-butanol, with the petroleum ether extract having the greatest inhibitory effect. The main categories of allelochemicals include polyphenolics, nitrogen-containing compounds, fatty acids

and esters, and terpenoids (Zhu *et al.*, 2021). Zhu et al. (2020) demonstrated that alkaline nitrogen-containing compounds inhibit the growth of *M. aeruginosa* 4–52 times more effectively than do phenolic acids, fatty acids and ester chemosensitizers.

Allelochemicals can disrupt the structure and function of the photosynthetic system of algae through various pathways, ultimately inhibiting algal growth (Zhu *et al.*, 2021). Chla is one of the primary components of algal pigments. When algal cells are exposed to allelochemicals, reactive oxygen species (ROS) levels increase, leading to the oxidative degradation of chla and a significant reduction in chla content (Wang *et al.*, 2016b; Ni *et al.*, 2018). Additionally, allelochemicals may interfere with photosystem II (PS II) in algae, reducing the efficiency of light energy capture and conversion by chla (Zhu *et al.*, 2010; Jiang *et al.*, 2014).

4.3 Insights for the management of Lake Poyang

Owing to the high water levels, the phytoplankton density in Lake Poyang is dominated by cyanobacteria and diatoms and exhibits an increasing trend at the interannual scale (Xiong *et al.*, 2019). Notably, Lake Poyang has recently been in a state of eutrophication, with moderate nutrient levels and water quality primarily classified as Class IV according to the "Environmental Quality Standard for Surface Water (GB3838-2002)" of PR China (Lou *et al.*, 2023). Additionally, the total nitrogen (TN) and total phosphorus (TP) concentrations have shown increasing trends in recent years (Li *et al.*, 2020). In particular, during the high water level period of 2021-2022, the average concentrations of total nitrogen (TN) and total phosphorus (TP) were 1.68 and 0.12 mg/L, respectively, both of which exceeded the Class IV standard limits specified in GB3838-2002 (Jiang *et al.*, 2023). Nutrients are among the key factors influencing phytoplankton community structure (Wu *et al.*, 2014b; Zebek and Szymanska, 2017). Notably, certain areas of the lake have already experienced cyanobacterial blooms (Liu *et al.*, 2020; Hu *et al.*, 2024).

This study demonstrated that allelochemicals released by *P. arundinacea* can limit the growth of typical bloom-forming cyanobacteria to a certain extent. The water level of Lake Poyang fluctuates by nearly 10 m annually, and the floodplain wetland vegetation is submerged during the high water level period. *P. arundinacea* is dominant in the wetland plant communities of Lake Poyang and has abundant aboveground biomass. For example, in Bang Lake, a sublake of Lake Poyang, the average aboveground biomass of *P. arundinacea* is 2262 g/m^2 (Wang *et al.*, 2016a). Ji (2017) reported that the biomass of *P. arundinacea* communities in Lake Poyang can exceed 6000 g/m^2. When the water level rises in Lake Poyang, large amounts of *P. arundinacea* become inundated and decompose, releasing allelochemicals that can alter the phytoplankton community structure, particularly by inhibiting the growth of harmful bloom-forming cyanobacteria. Therefore, this study may provide valuable insights and materials for the control of cyanobacterial blooms in Lake Poyang in the future. Additionally, the inhibitory effect of *P. arundinacea* is likely another important factor limiting phytoplankton growth under relatively high nutrient concentrations, as are low underwater light conditions, water flow.

It should be emphasized that the results of this study were based on indoor microcosm experiments and need to be further validated in the field. In particular, Lake Poyang can still freely exchange with the Yangtze River, which increases water flow and material exchange and increases the uncertainty of the algal inhibition effect. Additionally, microorganisms can influence the response of phytoplankton to *P. arundinacea* to some extent.

5 Conclusions

Our study demonstrated that both crude aqueous and organic solvent extracts of *P. arundinacea* significantly inhibited the growth of typical bloom-forming cyanobacteria. With increasing time and concentration, the inhibitory effect of *P. arundinacea* aqueous extract increased, peaking on Day 15 with maximum inhibition rates of 99.15 per cent (*M. aeruginosa*) and 97.27 per cent (*D. flos-aquae*). Among the three organic solvent extracts, the inhibition rates generally increased with increasing crude extract concentration, and the petroleum ether extract was the most effective at inhibiting *M. aeruginosa* growth. The strongest inhibitory effects were observed on Day 8 and Day 12 of the experiment.

P. arundinacea, a dominant hygrophyte in Lake Poyang, inhibits the growth of typical harmful bloom-forming cyanobacteria by releasing allelochemicals when it is submerged and decomposes during the summer high-water level period. These findings suggest that *P. arundinacea* has the potential to serve as an environmentally friendly material for managing cyanobacterial blooms.

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Supplementary material

Table S1. Chemical composition of the crude organic solvent extracts.

The Table S1 is available at https://doi.org/10.1051/kmae/2025003/olm.

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