Interspecific Competition between *Microcystis aeruginosa* and *Anabaena flos-aquae* from Taihu Lake, China

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Microcystis and *Anabaena* are the main cyanobacteria that cause cyanobacterial blooms in Taihu Lake, China. The mechanism of population competition between *M. aeruginosa* and *A. flos-aquae* was studied by co-cultivation in the laboratory. The growth of *M. aeruginosa* was inhibited, while the growth of *A. flos-aquae* was promoted. The degree of inhibition or promotion was related to the ratio of the initial cell densities. Both cell-free filtrates of *A. flos-aquae* and co-culture inhibited *M. aeruginosa* growth, while both cell-free filtrates of *M. aeruginosa* and co-culture promoted *A. flos-aquae* growth. Analysis of the cell-free filtrate by gas chromatography-mass spectrometry indicated that *M. aeruginosa* and *A. flos-aquae* may secrete some extracellular allelochemicals that inhibit (promote) the growth of *M. aeruginosa* (*A. flos-aquae*) in co-culture. These compounds included sulfur compounds, naphthalene derivatives, cedrene derivatives, quinones, phenol derivatives, diphenyl derivatives, anthracene derivatives, and phthalate esters. This study can help to understand the characteristics of *M. aeruginosa* and *A. flos-aquae* and to provide new concepts for the control of cyanobacterial blooms in Taihu Lake.

Key words: Cyanobacterial Blooms, *Microcystis aeruginosa*, Allelochemicals

Introduction

Taihu Lake, one of the five largest freshwater lakes in China, was seriously polluted because of rapid economic growth and urbanization, resulting in many environmental problems, such as eutrophication and cyanobacterial blooms. Cyanobacteria are well known and often dominant in the phytoplankton communities in eutrophic lakes and ponds (Yamamoto and Nakahara, 2009). Algal blooms usually occur with a few species but large quantities of algae (Wang and Lu, 2004). The cyanobacterial blooms are caused mainly by *Microcystis*, *Anabaena*, *Lyngbya*, *Aphanizomenon*, and *Oscillatoria* (Gao and Meng, 2009). Chen *et al.* (1999) studied the competition relationship of *M. aeruginosa* and the green alga *Scenedesmus quadricauda*, and first disclosed the reason why cyanobacteria became the dominant species under different kinds of algal competition conditions. Laboratory experiments demonstrated that competition between *Microcystis aeruginosa* PCC7806 and filamentous *Anabaena* PCC7120 in co-culture mainly depends on the initial biomass ratio between the two strains (Li and Li, 2012). A co-culture experiment between the hornwort *Ceratophyllum demersum* and *M. aeruginosa* showed that the growth of *M. aeruginosa* was significantly inhibited (Li *et al.*, 2008).

Allelopathy refers to the chemically mediated interaction between plants or microorganisms (Rice, 1984). These interactions are characterized by the release of allelopathic compounds (allelochemicals) into the surrounding medium, eliciting either a positive or deleterious response in a target organism (Rice, 1984). The allelopathic potential of cyanobacteria was recognized from observations in the field in the 1970s (Keating, 1978, 2007). Many dominant species, such as *Lyngbya majuscula*, produce a vast array of bioactive compounds. Cyanobacteria are a prolific source

of nearly 800 diverse bioactive secondary metabolites, which are mainly the products of nonribosomal peptide synthases or mixed polyketide synthase-nonribosomal peptide synthases (Welker and von Döhren, 2006; Tan, 2007). Several genera of cyanobacteria have been implicated in allelopathic phenomena, with targets ranging from other cyanobacteria to higher plants (Leão *et al.*, 2009). *Nodularia harveyana* was found to exhibit strong allelopathic activity against other axenic cyanobacteria (Gross, 2003). A certain concentration range of pyrogallol, caffeic acid, hydroquinone, and gallic acid can inhibit the growth of *M. aeruginosa* to different degrees (Ding and Zhang, 2007; Hua *et al.*, 2008). Certain concentrations of salicylic acid and cinnamic acid can inhibit the growth of *A. flos-aquae* (Wu *et al.*, 2008; He *et al.*, 2008).

Microcystis aeruginosa and *Anabaena flos-aquae* are the cyanobacteria that are the main cause of blooms in Taihu Lake. The goal of the present study was to evaluate the competition between *M. aeruginosa* and *A. flos-aquae* in laboratory experiments, and to disclose a possible allelopathy between the two cyanobacterial species through analysis of secondary metabolites in the culture medium using gas chromatography-mass spectrometry (GC-MS). Our experiments make a contribution to uncovering the mechanism of cyanobacterial blooms in a freshwater lake and provide information on the control of cyanobacterial blooms in Taihu Lake.

Materials and Methods

Culture conditions

The experiments were carried out with two species of cyanobacteria: *Microcystis aeruginosa* FACHB-905 and *Anabaena flos-aquae* FACHB-245. These two strains had been isolated from Taihu Lake and were provided by the Freshwater Algae Culture Collection of the Chinese Academy of Sciences (Wuhan, China). Medium preparation and cultivation procedures strictly followed the instructions provided by the suppliers. The strains were cultured axenically in the laboratory in autoclaved BG11 medium, which is suitable for both *M. aeruginosa* and *A. flos-aquae* (Stanier *et al.*, 1971). The only organic constituents of BG11 medium are EDTA (ethylenediaminetetraacetic acid) and citric acid. Stock cultures of both species were first inoculated into growth medium and incubated in axenic condition until the cell density indicated optimal growth for further sub-culturing. Sub-cultured samples were run in triplicate and all 1-L conical glass flasks were shaken by hand three times per day during the maintenance and experimental stages. Cultures were kept under a 12-h light/12-h dark cycle with a light intensity of 2,500 – 3,000 lux provided by cool white fluorescent tubes at $(25 \pm 1)\,^{\circ}$C. Sufficient sterile aeration was supplied. Cells sticking together were separated from each other by sonication before counting their number under a microscope with a haemocytometer. Optical density was also measured to support the results of cell counting. All measurements were taken at least three times.

Co-cultivation at different initial cell ratios

This experiment was carried out in 3,000-mL Erlenmeyer flasks containing 1,500 mL BG11 liquid medium, with aeration. *M. aeruginosa* and *A. flos-aquae* were co-cultured at different ratios of initial cell densities. Sub-samples were taken every second day for determination of cell numbers. Two single cultures and three co-cultures were prepared. Cells of the two species were easy to distinguish, as *M. aeruginosa* grows as single cells under the experimental conditions, while *A. flos-aquae* grows in filaments.

Effect of cell-free filtrates

In order to study the factor(s) having an influence on the growth and competition between *M. aeruginosa* and *A. flos-aquae*, apart from the nutrients, we used cell-free filtrates of the culture media. Sub-samples (200 mL) from each culture (*M. aeruginosa* single culture, *A. flos-aquae* single culture, and co-culture with an initial cell ratio of 1:1) were taken during the entire growth phase (5, 10, 15, and 20 d). After centrifugation at approximately $2{,}680 \times g$ for 12 min and carbon dioxide decompression filtration through 0.2-μm membrane filters under sterile conditions, cell-free filtrates were obtained and preserved at $-20\,^{\circ}$C.

Before the experiments, concentrations of nitrogen and phosphorus in the cell-free filtrates were measured. $NaNO_3$ and K_2HPO_4 were added to adjust the levels of nitrogen and phosphorus to that in fresh BG11 medium. Thus three types of new culture media were obtained. The experiment was carried out in 50-mL Erlenmeyer flasks containing 30 mL of the respective culture medium. *M. aeruginosa* was grown in the cell-free filtrate of *A. flos-aquae* and the co-culture filtrate, while *A. flos-aquae* was grown in the cell-free filtrate of *M. aeruginosa* and the co-culture filtrate. The initial cell density of each culture was $5 \cdot 10^4$ cells/mL.

Analysis of organic compounds in cell-free filtrates

Extracellular organic compounds were extracted from the cell-free filtrates into dichloromethane, and the extract concentrated to approximately 2 mL by rotary evaporation under vacuum and further concentrated to 1 mL under a gentle stream of nitrogen. The samples were then analysed by GC-MS in an HP6890-HP5975 apparatus (Agilent Technologies Inc., Santa Clara, CA, USA). A HP-5 fused silica capillary column (30 m × 0.25 mm, 0.25 μm i.d.) was used for separation with helium as the carrier gas at a constant flow rate of 0.8 mL/min. Oven temperature was programmed as follows: hold at 60 °C for 0.5 min, raised at 10.0 °C/min to 300 °C, held for 30 min. The injection was set on splitless mode at 280 °C. An 1.0-μL sample was injected with a 2.0-min solvent delay. Detection was conducted by a mass selective detector (MSD) with electron impact ionization (EI). The mass scanning ranged from m/z 20 to 650. Mass spectra were compared to those of reference compounds in the National Institute of Standards and Technology (NIST) library and compounds identified by comparison or by co-injection with standards whenever possible. The relative concentration of each compound was quantified based on the peak area integrated by the analysis program.

Data processing and statistical analysis

To study the inhibitory (or promoting) effect of the treatment on cyanobacterial growth, relative degrees of inhibition (or promotion) were calculated as follows:

$$\text{relative degree of inhibition (or promotion)} = \frac{|(\text{cell density})_{\text{treatment}} - (\text{cell density})_{\text{control}}|}{(\text{cell density})_{\text{control}}} \cdot 100\,\%.$$

Data were expressed as means ± S.D. and displayed a normal distribution by parametric test. Statistical evaluation by Student's t-test was performed when only two value sets were compared using Microsoft Office Excel 2003 (Microsoft Corporation, Redmond, WA, USA), and one-way analysis of variance (ANOVA) followed by Dunnett's test when the data involved three or more groups using SPSS 13.0 for windows (IBM Corporation, Armonk, NY, USA). A difference of $P < 0.05$ was considered to be significant.

Table I. Initial cell densities of *Microcystis aeruginosa* and *Anabaena flos-aquae* in the competition experiments.

Culture	*M. aeruginosa* [cells/mL]	*A. flos-aquae* [cells/mL]
Single culture 1	$5 \cdot 10^4$	–
Single culture 2	–	$5 \cdot 10^4$
Co-culture 1	$5 \cdot 10^4$	$2.5 \cdot 10^4$
Co-culture 2	$5 \cdot 10^4$	$5 \cdot 10^4$
Co-culture 3	$5 \cdot 10^4$	$1 \cdot 10^5$
Co-culture 4	$1 \cdot 10^5$	$5 \cdot 10^4$
Co-culture 5	$5 \cdot 10^4$	$5 \cdot 10^4$
Co-culture 6	$2.5 \cdot 10^4$	$5 \cdot 10^4$

Results

Interaction between the two cyanobacterial species in co-culture

The initial cell density of each culture is shown in Table I. The growth curves of *M. aeruginosa* and *A. flos-aquae* in single culture and co-culture showed that *M. aeruginosa* was inhibited while *A. flos-aquae* was promoted (Fig. 1). The degree of inhibition or promotion was related to the ratio of the initial cell densities of the two species. Compared to the control, the maximum biomass of *M. aeruginosa* was strongly reduced while the maximum biomass of *A. flos-aquae* changed only little. Statistical evaluation of the data revealed that the relative degree of inhibition of *M. aeruginosa* appeared significantly different ($P < 0.05$), while the relative degree of promotion of *A. flos-aquae* was not significantly different ($P > 0.05$). Figure 2 shows the relative degree of inhibition of *M. aeruginosa* on day 16 (logarithmic phase) and the relative degree of promotion of *A. flos-aquae* on day 12 (also in the logarithmic phase). When the initial ratio of the cell density between *M. aeruginosa* and *A. flos-aquae* was varied (M:A = 1:2, 1:1, or 2:1), the degrees of inhibition of *M. aeruginosa* were significantly different from each other ($P < 0.05$), and the degrees of promotion of *A. flos-aquae* were also significantly different from each other ($P < 0.05$). However, when the initial cell inoculation ratio between *M. aeruginosa* and *A. flos-aquae* was M:A = 2:1, *A. flos-aquae* was not promoted any more.

Effect of cell-free culture filtrates on the cyanobacterial growth

To test the hypothesis that inhibition and promotion, respectively, of the cyanobacterial growth was re-

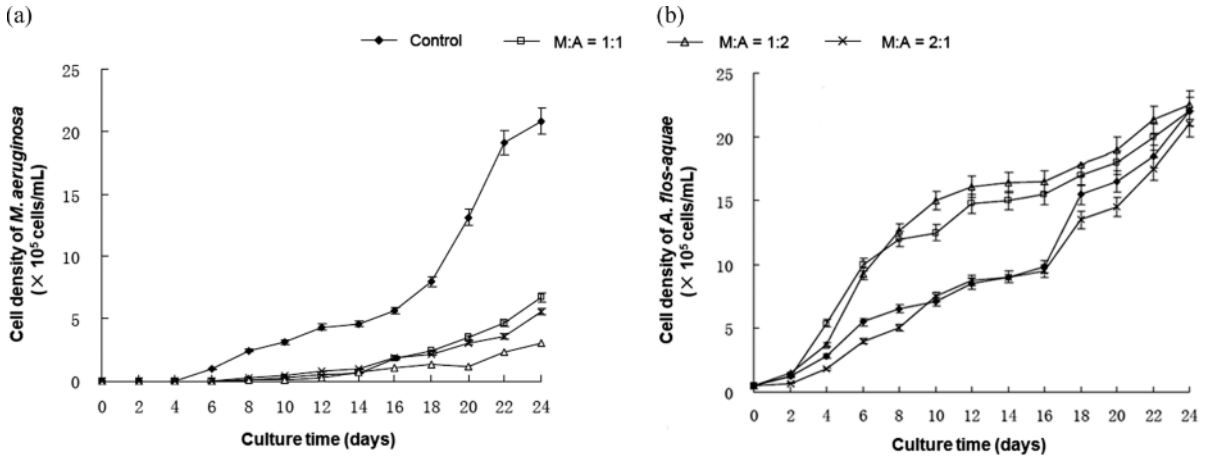


Fig. 1. Growth curves of (a) *M. aeruginosa* and (b) *A. flos-aquae*, alone or co-cultured with (a) *A. flos-aquae* or (b) *M. aeruginosa*, with different initial ratios of cell densities as indicated. The initial cell densities of the two species were $5 \cdot 10^4$ cells/mL.

lated to chemicals released into the medium, we let the cyanobacteria grow in cell-free filtrates of the cultures studied above. Figure 3 shows the relative degree of inhibition of *M. aeruginosa* on day 16 and the respective promotion of *A. flos-aquae* by different cell-free filtrates. When *M. aeruginosa* (or *A. flos-aquae*) was grown in the cell-free filtrates of *A. flos-aquae* (or *M. aeruginosa*) or co-culture, the growth of *M. aeruginosa* (or *A. flos-aquae*) was inhibited (or promoted) markedly by both types of filtrates. The relative degrees of inhibition (or promotion) caused by the two kinds of filtrates were significantly different ($P < 0.05$). The relative degrees of inhibition of *M. aeruginosa* by cell-free filtrates taken at different times during *A. flos-aquae* culture or co-culture (except for 20 d *A. flos-aquae*) were also significantly different from each other ($P < 0.05$). The relative degrees of

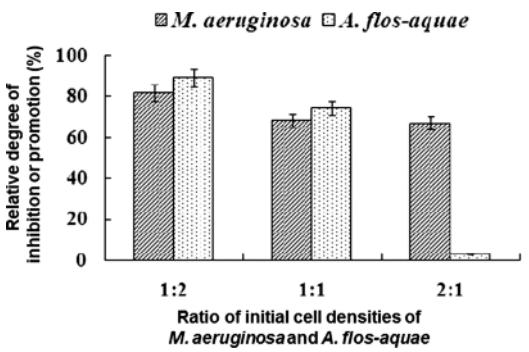


Fig. 2. Relative degree of inhibition or promotion of the cyanobacterial growth in co-cultivation with different ratios of initial cell densities. The inhibition of *M. aeruginosa* was calculated from the cell density on day 16, while promotion of *A. flos-aquae* was calculated from the cell density on day 12, when the cyanobacteria were in the logarithmic phase of growth.

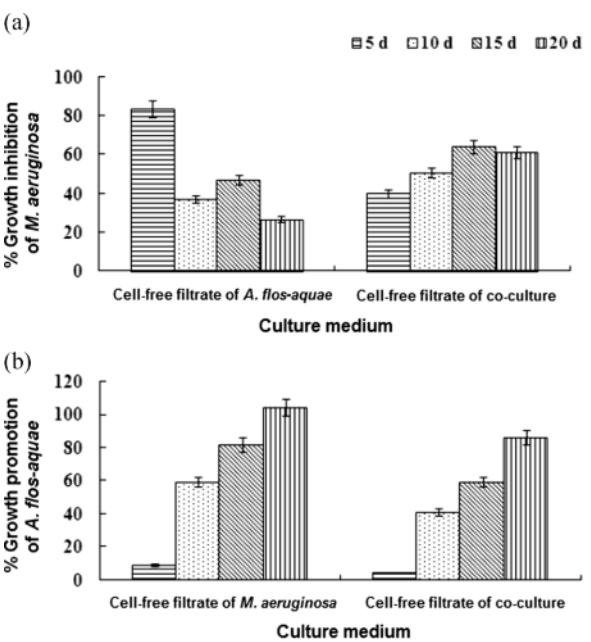


Fig. 3. Relative degree of (a) inhibition and (b) promotion of cyanobacterial growth in the presence of different nutrient supplemented cell-free filtrates. Cell-free filtrates were prepared from the respective single cultures, and the growth of the two species with an initial 1:1 ratio of cell densities was followed for 20 days. Inhibition and promotion were calculated as in Fig. 2.

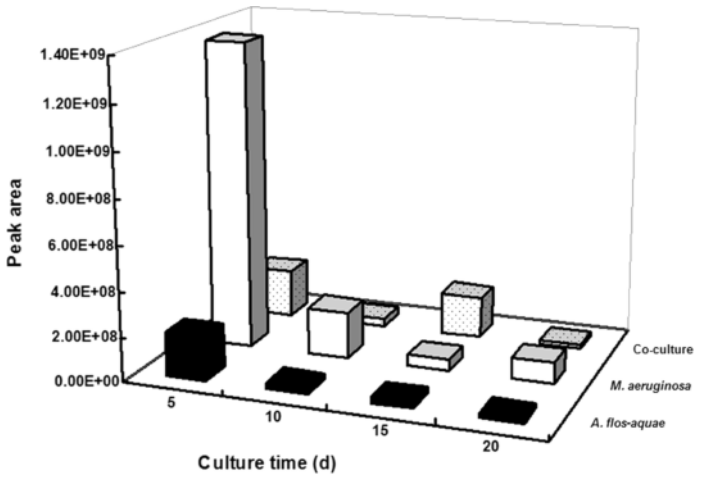


Fig. 4. Relative amounts of total compounds in cell-free filtrates. Cell-free filtrates were prepared from single cultures of the two cyanobacterial species and from a co-culture with an 1:1 ratio of initial cell density. Filtrates were extracted with dichloromethane and analysed by GC-MS. The relative concentrations of total compounds were quantified based on the peak areas integrated by the analysis program.

promotion of *A. flos-aquae* by cell-free filtrates taken at different times during *M. aeruginosa* culture or co-culture (except for 5 d *M. aeruginosa* and 5 and 10 d of co-culture) also appeared significantly different from each other ($P < 0.05$). These results suggest that, indeed, some interacting substance might be released by one or the other (or both) species.

GC-MS analysis of organic compounds released into the culture medium and identification of their structure

Extracts were analysed by means of GC-MS, and the structures of organic compounds were identified. Figure 4 shows that the total amounts of compounds in the extracts differed over time. In the single culture of both *M. aeruginosa* and *A. flos-aquae*, their content was highest on the 5th day (end of the lag phase) and thereafter decreased, but the amounts were much higher in the case of *M. aeruginosa*. In the co-culture, as compared to the single cultures, *A. flos-aquae* effectively inhibited the massive release of compounds from *M. aeruginosa* in the lag phase.

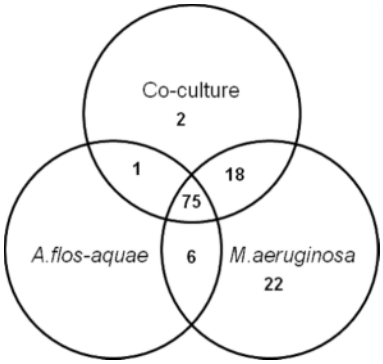


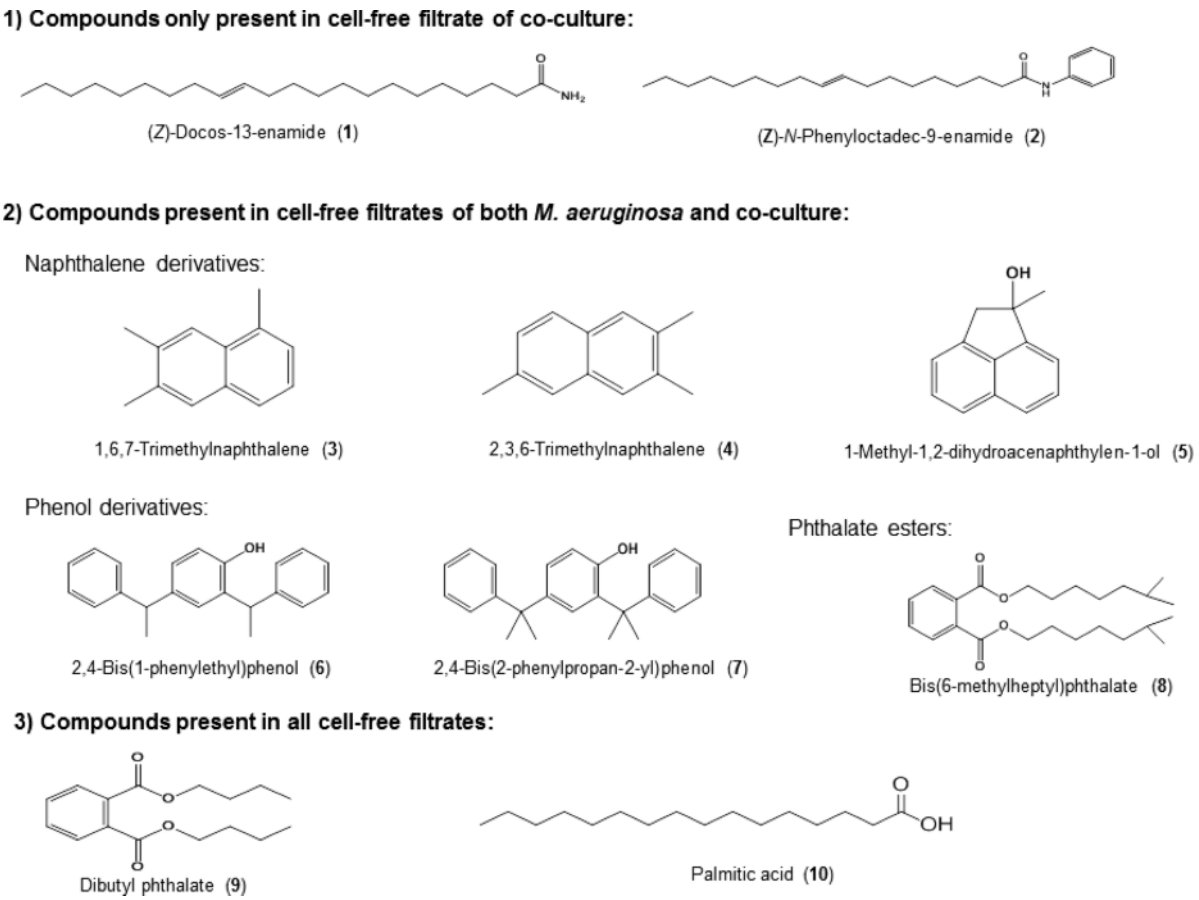
Fig. 5. Number of compounds present in cell-free filtrates at various times of (co-)culture. Conditions were as in Fig. 4.

As shown in Fig. 5, a total of 124 compounds were identified in all extracts taken together. Of these, two compounds were found exclusively in the cell-free filtrate of the co-culture, 18 in the filtrates of both *M. aeruginosa* and the co-culture, six in those of both *M. aeruginosa* and *A. flos-aquae*, 22 only in the filtrate of *M. aeruginosa*, and 75 were commonly found in all three types of cell-free filtrates.

We assume that some of these compounds might be allelochemicals, including sulfur compounds, derivatives of naphthalene, cedrene, diphenyl, and anthracene, as well as phenols, quinones, and phthalate esters. The structures of some of these potential allelochemicals are shown in Scheme 1. Further screening of the allelopathic activities of these compounds is in progress and will be reported in subsequent publications.

Discussion

In aquatic ecosystems, allelopathy is being regarded an important process in the shaping of mi-



Scheme 1. Structures of some potential allelochemicals in the cell-free filtrates.

crobial communities (Gross, 2003; Strom, 2008; Hay, 2009). Different ecological roles have been attributed to the production of allelochemicals by cyanobacteria, including phytoplankton succession, bloom formation, resource and interference competition (Leflaive and Ten-Hage, 2007), and invasive fitness (Figueredo *et al.*, 2007). Compounds released by the freshwater cyanobacterium *Oscillatoria* sp. have been shown to inhibit the growth of the green microalga *Chlorella vulgaris* (Leão *et al.*, 2010). Many studies have shown that cyanobacteria are able to interfere with other organisms in their communities through the release of compounds into the surrounding medium (Leflaive and Ten-Hage, 2007).

We have shown here that in co-culture of the two cyanobacterial species, growth of *M. aeruginosa* was inhibited while that of *A. flos-aquae* was promoted. After eliminating nutrients as a possible cause, we hypothesized that allelochemicals released by the two species into the culture medium were responsible for this effect. Many phenolic acids, phthalate esters, and long-chain fatty acids have been identified as allelopathic compounds (Wendel and Jüttner, 1996; Jüttner, 2001; Leflaive and Ten-Hage, 2007). Among them, dibutyl phthalate (Scheme 1) had been proven to be an allelochemical (Wang *et al.*, 2008). At the same time, stronger allelopathic activity of phenolic acids had been proven (Nakai *et al.*, 1999, 2000). In our experiments, we found two compounds, (*Z*)-docos-13-enamide and (*Z*)-*N*-phenyloctadec-9-enamide, only existing in the cell-free filtrate of the co-culture (Scheme 1), that may be related to allelopathy. Both of the two compounds are long-chain fatty acid amides, and the former has surfactant activity. Thus, we speculate that the two compounds may affect membrane permeability (Smith and Doan, 1999).

There were larger amounts of various naphthalene derivatives in the cell-free filtrate of *M. aeruginosa* as compared to that of the co-culture. Thus, *A. flos-aquae* may inhibit the release of some naphthalene derivatives from *M. aeruginosa*, and these derivatives may promote the growth of *A. flos-aquae*.

Recent molecular biological studies have accelerated the elucidation of the biosynthesis of these secondary metabolites. These metabolites may be changed to useful compounds using information obtained from the molecular studies (Harada, 2004).

Conclusions

When co-cultured, the growth of *Microcystis aeruginosa* was inhibited and the growth of *Anabaena flos-aquae* was promoted. Through the study on the effect cell-free filtrates, it can be concluded that the extracellular compounds may play crucial roles in the interspecific competition between the two cyanobacteria. After chemical analysis, most of the organic compounds in the filtrates were identified, and some of them were the potential allelochemicals. Therefore, further investigation on the allelochemic activities of these compounds is needed to disclose the competition mechanism.

Acknowledgement

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