

Competition between toxic *Microcystis aeruginosa* and nontoxic *Microcystis wesenbergii* with *Anabaena* PCC7120

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Abstract To elucidate the changes in the proportions of microcystin (MC)-producing *Microcystis*, non-MC-producing *Microcystis* and *Anabaena* strains during cyanobacteria blooms, we compared their fitness under different initial biomass ratios. Culture experiments were carried out with three cyanobacterial strains: single-celled toxic *Microcystis aeruginosa* PCC7806 (*Ma7806*), single-celled nontoxic *Microcystis wesenbergii* FACHB-929 (*Mw929*) and filamentous *Anabaena* PCC7120 (*An7120*). Growth curves expressed as biovolume, *Ma7806* microcystin-LR (MC-LR) content (detected with HPLC and ELISA), and the culture medium dissolved total nitrogen and dissolved total phosphorous (DTP) were measured to monitor nutrient uptake. Results suggest that the dominant strain in competition experiments between *Ma7806* and *An7120* was mainly controlled by the initial biomass ratio of the two strains, but there was also evidence for allelopathic interactions, where MC-LR produced by *Ma7806* played an important role in the competition process. However, *Mw929* was always less competitive when co-cultured with *An7120* regardless of initial biomass ratio. Culture medium DTP showed significant differences between competition experiments

in all sets, suggesting that *Mw929* could be more suited to low phosphorus environments than *Ma7806* and *An7120*. Overall, the competitive ability of *Ma7806* was stronger than *Mw929* when co-cultured with *An7120* in the case of excess nutrients and the results could well unravel the seasonal succession process of cyanobacteria blooms.

Keywords Allelopathic effect · *Anabaena* · Competition · Cyanobacteria · Microcystin-LR · *Microcystis*

Introduction

The increasing input of nutrients, mainly nitrogen (N) and phosphorus (P), to water is leading to increased eutrophication in many regions across the globe (Cloern 2001). The most obvious effect of eutrophication is its alteration of the food web, resulting in high levels of phytoplankton biomass that can lead to algal blooms (Anderson et al. 2002; Smayda 2004). Occurrences of cyanobacteria blooms around the world have increased in recent decades, and under favorable conditions *Microcystis* is the most important cyanobacterial genus responsible for water blooms (Hudnell and Dortch 2008; Azevedo et al. 2002). Most known species of *Microcystis*, such as *Microcystis flos-aquae*, *M. aeruginosa*, *M. ichthyoblabe*, and *M. viridis*, have been reported to produce a family of nearly 80 hepatotoxic peptides called microcystins (MCs) (Briand et al. 2009). MCs are responsible for liver failure in wild animals, livestock and aquatic life, and are a health hazard for humans through the use of water for drinking and

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recreation (Hoeger et al. 2007). The release of chemicals and toxins by plants, that affect their potential competitors for resources, is known as allelopathy (Lampert and Sommer 2007). Previous studies have found that allelopathic compounds produced by phytoplankton are active in succession events (Jüttner and Wu 2000; Vardi et al. 2002). Also, allelopathic compounds produced by submerged macrophytes might affect the succession of phytoplankton (Gross et al. 2003, 2007). Tillmann (2003) and Granéli and Hansen (2006) have pointed out that allelopathy and toxin production are enhanced by stress factors, such as unbalanced N and P ratios at limiting concentrations. To understand toxin variations and allelopathy in natural blooms, most early investigations were focused on toxic cyanobacterial species in the laboratory. However, other nontoxic species of *Microcystis*, for example *M. wesenbergii* (Xu et al. 2008), which also plays an important role in cyanobacterial blooms succession, has received less attention despite being distributed widely around the world including Asia (Son et al. 2005), Europe (Jasprica et al. 2005), America (Oberholster et al. 2006), and Oceania (Wood et al. 2005).

Filamentous cyanobacterial blooms (i.e., *Anabaena* blooms) have been observed to occur simultaneously with, or alternatively to, *Microcystis* blooms (Aktan et al. 2009; Solis et al. 2009; Vesna et al. 2010). Furthermore, in hypertrophic lakes or reservoirs, water temperature and other abiotic factors interact to allow high phytoplankton production (Robarts and Zohary 1992). Therefore, we conducted competition experiments between two *Microcystis* strains and *Anabaena* PCC7120 (*An7120*) in order to unravel the seasonal succession process indirectly during cyanobacteria blooms. These results will be beneficial not only for water agencies but also for future prediction of algal blooms.

Materials and methods

Cyanobacterial strains *Microcystis aeruginosa* PCC 7806 (*Ma7806*) and *Anabaena* PCC 7120 (*An7120*) were originally obtained from the Pasteur Culture Collection

of Cyanobacteria, France, and were kindly provided by the Freshwater Algae Culture Collection of the Chinese Academy of Sciences (FACHB-Collection). The nontoxic strain *Microcystis wesenbergii* FACHB-929 (*Mw929*) was isolated from Lake Dianchi in China and was also obtained from the FACHB-Collection. Mean cell dimensions of the three strains were measured using an ocular micrometer at $\times 400$ magnification (Hill and Knight 1987). Cell densities of cultures were converted to biovolume ($\mu\text{m}^3 \text{L}^{-1}$) for each strain using the formula for the geometric shape roughly appropriate for the taxon (Hillebrand et al. 1999). In laboratory cultures, *Ma7806* and *Mw929* are single-celled and *An7120* is filamentous (Table 1).

The three strains were axenic and inoculated in BG₁₁ liquid medium, under a 12L/12D cycle with a light intensity of $30 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ provided by cool white fluorescent tubes at $25 \pm 1^\circ\text{C}$. Experiments were carried out in 500-mL conical flasks containing 300 mL BG₁₁ liquid medium. All samples were run in triplicate and all flat-bottomed bottles were shaken by hand three times per day during the maintenance and experimental stages. Subsamples were taken at predetermined intervals from day 1 during the incubation period to determine cell numbers, examine dissolved total phosphorous (DTP) and dissolved total nitrogen (DTN) and extract MCs.

The initial biomass of each culture was determined from the concentration of chlorophyll *a*, then the cell number was counted and converted to biovolume. Two co-cultures were prepared: *Ma7806* and *An7120*; *Mw929* and *An7120* (Table 2). Each sample was run in triplicate and was divided into subsamples for cell counting, for determination of MC content and for determination of extracellular DTN and DTP contents in the medium.

Measurement of cell number and biovolume

After staining with 1% acidified Lugol's iodine solution, the cyanobacterial cells were counted under a microscope using a haemocytometer. The cells of *An7120* and *Mw929* were separated by sonication before counting. Cell counts

Table 1 Characteristics of the three strains used in this study

Characteristics	Morphology	Toxins	N-fixation ability	Cell diameter (μm)	Origin
<i>Microcystis aeruginosa</i> PCC7806	Single-celled	MC-LR	–	3.0	PCC
<i>Microcystis wesenbergii</i> FACHB-929	Single-celled	None	–	6.2	Lake Dianchi, China
<i>Anabaena</i> PCC7120	Filamentous	None	+	3.2	PCC

PCC Pasteur Culture Collection of Cyanobacteria

Table 2 The initial biomass of the strains studied in competition experiments

Initial biomass ratios	Ma7806/An7120			Mw929/An7120		
	Set a ^a	Set b ^a	Set c ^a	Set a ^a	Set b ^a	Set c ^a
Chla/chla	1/9	1/1	9/1	1/9	1/1	9/1
Cell N/Cell N ^b ($\times 10^7$ cells L ⁻¹)	5.1 \pm 0.4/35 \pm 1.1 ^c	25 \pm 0.1/20 \pm 0.2	45 \pm 0.1/4 \pm 0.02	0.79 \pm 0.04/34.9 \pm 0.8	3.6 \pm 0.1/20 \pm 0.5	6 \pm 0.2/4 \pm 0.01
BioV/BioV ^d ($\times 10^7$ μm^3 L ⁻¹)	73 \pm 5.9/609 \pm 20	353 \pm 1.4/346 \pm 5.0	636 \pm 1.5/69 \pm 0.45	89 \pm 0.4/432 \pm 21	399 \pm 6.5/215 \pm 6.2	671 \pm 26/69 \pm 0.3

^a The initial chlorophyll *a* ratio of *M. aeruginosa* PCC7806 to *Anabaena* PCC7120 and *M. wesenbergii* to *Anabaena* PCC7120 was 1:9, 1:1 and 9:1, respectively

^b Cell number

^c Each value in the table represents the mean of three measurements \pm SD except for that in the Chla/chla row

^d Biovolume

were ultimately converted to biovolume by multiplying cell count by the estimated volume per cell.

Examination of DTN and DTP

Subsamples (10 mL) from the cultures were taken at predetermined intervals. The samples were firstly placed in Ultrasonic cleaning device (KQ 5200E) for 5 min, which promoted cells sinking to the bottom of the tube, as both *Microcystis* and *Anabaena* are known for the gas vesicles to assist buoyancy. Then they were centrifuged at 10,000 rpm for 12 min, and the supernatant was used to determine DTP and DTN after persulfate oxidation to nitrate (D'Elia et al. 1977) and orthophosphate, respectively. The nitrate was determined with a Szechrome NB reagent (Wynne and Rhee 1986), and the orthophosphate was determined by the phosphomolybdate method.

Microcystin extraction and analysis

Extraction of intracellular microcystin-LR (MC-LR) followed the method developed by Harada et al. (1988). Lyophilized cells were firstly sonicated and extracted three times with 5% (v/v) acetic acid. The extract was centrifuged at 8,000 rpm for 10 min and the supernatant was then transferred to a C18 cartridge (Sep-Pak; Waters Association). The C18 cartridge was activated with 10 mL methanol and 20 mL Millipore water and then impurities were eluted with 20% and 30% methanol separately prior to eluting MC-LR with 75% methanol. Finally, the eluted solutions were evaporated to dryness in a rotary vacuum evaporator, and then re-dissolved with 1 mL 50% methanol and stored at -20°C for high-performance liquid chromatography (HPLC) analysis.

Standard MC-LR was received as a gift from Dr. Wei Chen, IHB, CAS (>95% purity) (Chen et al. 2009) and MC-LR samples were analyzed by a Shimadzu CLASS-LC10 HPLC with a reverse C18 column (4.6 and 250 mm) in a run with 60% solution A (100% methanol) and 40% solution B (0.05% aqueous trifluoroacetic acid) over 20 min and diode array detector at 238 nm. The results showed that retention time of the MC-LR was 13.5 min.

Extracellular microcystin concentrations would be possibly below the detection limit of the high-performance liquid chromatograph (2 ng L^{-1}). Therefore, they were determined using an enzyme-linked immunosorbent assay, which was performed according to the protocol of the microcystin plate kit (EnviroLogix, Inc.; Catalog no. EP022). This method is sensitive for low levels of microcystin (Pyo et al. 2005; Carmichael and An 1999). The assays were run in 96-well plates containing 0.1 mU enzyme (recombinant protein phosphatase 1A, catalytic subunit, Roche Applied Science), 1.05 mg para-nitrophenyl phosphate (Sigma) and 10 μL of sample or microcystin-LR (Sigma Biochemical). Water samples (5 mL per sample) were taken and stored at -20°C . In order to avoid false-negative or false-positive effects, we firstly transferred the supernatant to a C18 cartridge (Sep-Pak; Waters), eluting impurities. And then the diluted MC-LR extracted from water samples of 100 μL were added to test tubes pre-coated with polyclonal antibodies followed by addition of an enzyme-linked substrate. The antibodies were specific to MC-LR at low concentrations. Activity of the bound peroxidase was assayed as rate of hydrolysis of TMB (3,3',5,5'-tetramethylbenzidine), stopped with 1N HCl, and measured spectrophotometrically at 450 nm (absor-

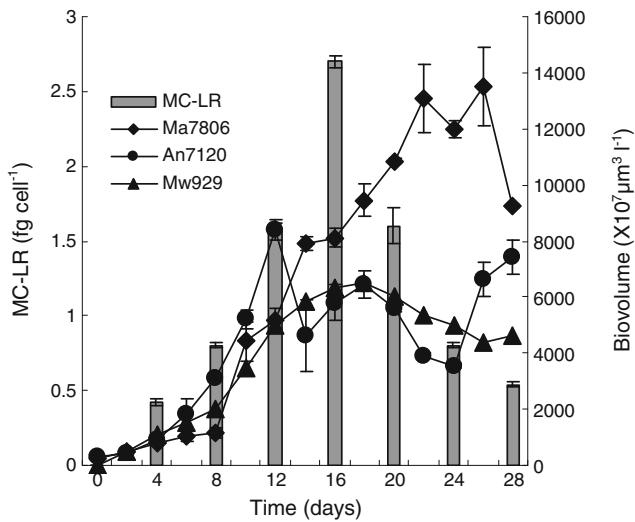


Fig. 1 Growth curves of *Ma7806*, *Mw929*, and *An7120* (symbols + lines) and changes of the microcystin-LR content (column) of *Ma7806* in the monoculture experiments

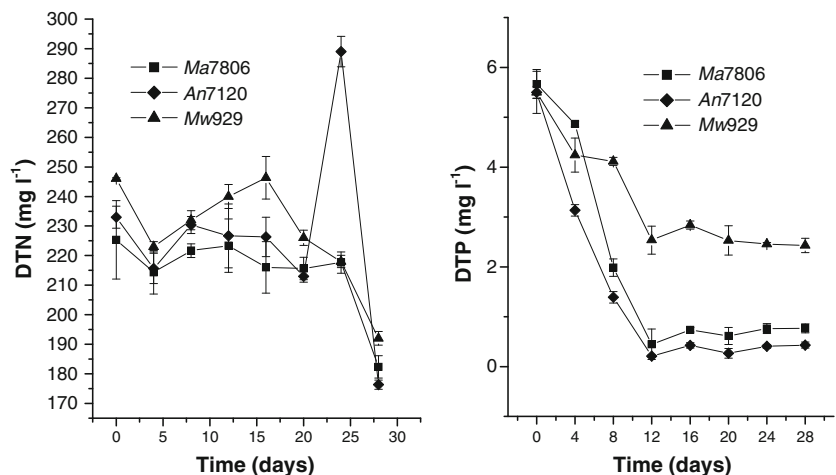
bance peak) and 650 nm (turbidity blank) over 1 h. In the results, all reported toxin concentrations are microcystin-LR equivalents. And the detection limit was between 0.1 and 5 $\mu\text{g L}^{-1}$.

In the results, all reported toxin concentrations are microcystin-LR equivalents. Unknowns, standards, and controls were all run in duplicate.

Statistics

Data are presented as mean \pm SD (standard deviation). All statistical analyses were computed with one-way analysis of variance (ANOVA) statistics using SPSS (Version 16.0), except for DTP in medium, which was analyzed with the *t* test for *Mw929* co-culturing with *An7120*.

Fig. 2 Changes of DTN and DTP concentration in medium of the three strains in monocultures



Results

Monocultures

All three strains flourished throughout the monoculture experiments, although their specific growth rates changed with time (Fig. 1). The growth rates of *Ma7806*, *An7120*, and *Mw929* were 0.184, 0.285, and 0.117 day^{-1} , respectively, in the exponential phase. Changes in MC-LR content showed a similar tendency to those of *Ma7806* growth and reached a maximum in the mid exponential growth phase, but decreased in the late exponential growth phase (Fig. 1).

Changes in culture medium DTN and DTP were also estimated (Fig. 2). No significant differences in DTN concentrations were observed among the three strains (ANOVA, $p>0.05$). However, a significant difference in DTP between *Mw929* and *An7120* was observed (ANOVA, $p=0.046<0.05$).

Co-cultures of *Ma7806* and *An7120*

The dominant strain under competition mainly depends on the initial inoculation biomass, that is, when *Ma7806* dominated at the beginning, it continued to dominate until the end (Fig. 3a) and similarly with *An7120* (Fig. 3c). However, when the initial inoculation amount of *Ma7806* and *An7120* was almost equal, both strains achieved similar growth rates (0.107 and 0.113 day^{-1}) for the first 15 days, at which point *An7120* started to grow faster than *Ma7806* (Fig. 3b). However, both strains converged to similar biovolume densities by the end of the experiment (28 days). The maximum biovolume of *An7120* in set (a) was much larger than that during the monoculture experiments while the growth of *An7120* was seriously suppressed in set (c).

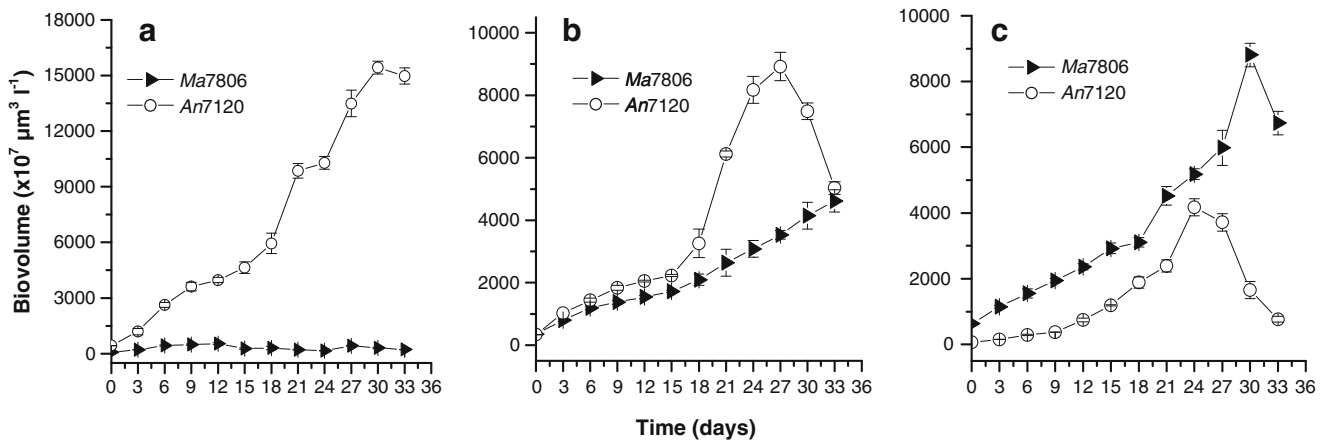


Fig. 3 Time course of biovolumes in competition experiments between *Ma7806* and *An7120*. **a–c** The initial chlorophyll *a* ratios of *Ma7806* to *An7120* were 1:9, 1:1, and 9:1, respectively

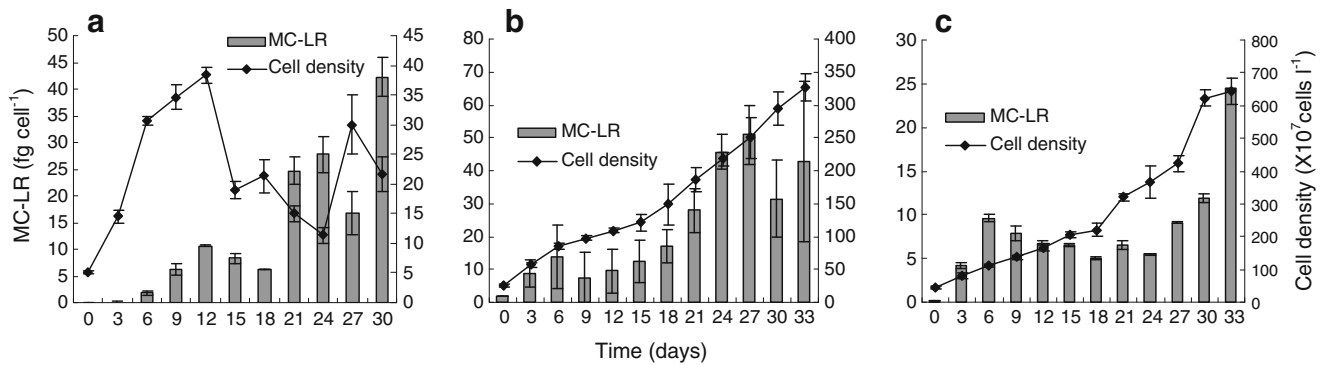


Fig. 4 Time course of cell density and MC-LR contents of *Ma7806* in competition experiments between *Ma7806* and *An7120* under different initial ratios of chlorophyll *a*. **a–c** The initial chlorophyll *a* ratios of *Ma7806* to *An7120* were 1:9, 1:1, and 9:1, respectively. *Line*, cell density; *column*., cellular MC-LR content

For MC-LR, the microcystin contents (fg cell^{-1}) in sets (a) and (b) were much higher than that in set (c) (Fig. 4). The microcystin contents showed significant differences between sets (a) and (c) (ANOVA, $p < 0.05$) and between sets (b) and (c) (ANOVA, $p < 0.01$). Additionally, in set (b), the microcystin contents were positively correlated with the *Ma7806* cell density, but were negatively correlated in set (c). Moreover, the extracellular fraction of MC-LR in the medium varied between different growth stages and growth conditions (Fig. 5).

No significant differences in culture medium DTN or DTP ($p > 0.05$; $F = 0.173$; $df_1 = 2$; and $df_2 = 33$) were found throughout the competition experiments between *Ma7806* and *An7120* in sets (a–c) (Fig. 6).

Co-cultures of *Mw929* and *An7120*

An7120 biovolume eventually exceeded *Mw929* biovolume for all three initial chlorophyll *a* ratios tested (Fig. 7). At

the same time, the DTN (ANOVA, $p > 0.05$) showed almost the same trends (Fig. 8) for all three sets, while DTP showed significant differences between the three sets (t test, $p < 0.05$).

Discussion

In order to elucidate the changes in the proportions of MC-producing *Microcystis*, non-MC-producing *Microcystis* and *Anabaena* strains during cyanobacteria blooms, we compared their fitness under different initial biomass ratios. When *Ma7806* and *An7120* were cultured together, the dominant strain was largely determined by the initial biomass ratio between them. This result could further be attributed to the difference in growth rates between the two strains in the monoculture experiments, where the strains had no competitors. Oberhaus et al. (2007) carried out monoculture and competition experiments to

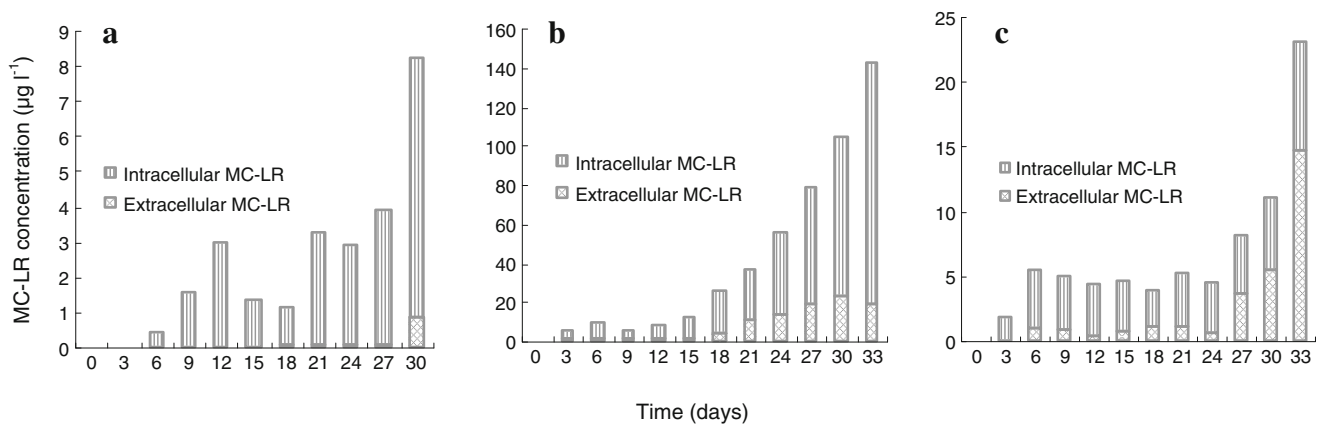


Fig. 5 Time course of intracellular and extracellular MC-LR in competition experiments between *Ma7806* and *An7120*. **a–c** The initial chlorophyll *a* ratios of *Ma7806* to *An7120* were 1:9, 1:1, and 9:1, respectively. *Line*, cell density; *column*, MC-LR content

compare the fitness of cyanobacterial strains *Planktothrix rubescens* and *P. agardhii*, cultured under various different conditions of temperature and light, and showed that there are significant differences in the growth rates of *P. rubescens* and *P. agardhii* in monoculture and competition experiments.

Moreover, the MC-LR concentration of *Ma7806* was much higher in competition experiments than that inoculated in monoculture experiments; in particular, the concentrations of MC-LR in sets (a) and (b) were much higher than that in set (c), implying that the greater the competitive pressure the higher the cellular MC-LR content in competition experiments. This phenomenon results from two factors. The first can be assessed in terms of the costs and benefits of producing MC. MC is biosynthesized via a multi-enzyme complex requiring a high energy input, implying a high cost for the cell. Briand et al. (2008) suggested that, under cell growth-limiting conditions, the benefits of producing MC would outweigh the costs. In the monoculture experiment, *Ma7806* had no competitor, so it did not invest resources in MC production. Meanwhile,

Ma7806 did produce large amounts of MCs in order to outweigh other strains in competition experiments. The second factor is the possible allelopathic effect of *Ma7806* on *An7120* (Pflugmacher 2002; Schagerl et al. 2002; Sedmak and Elerseck 2005), particularly when *Ma7806* and *An7120* were inoculated by similar amounts. In this case, their growth rates were initially similar (0.107 and 0.113 day⁻¹, respectively), before *An7120* became suddenly dominant from day 18 to day 27. Conversely, after day 27 the continually increasing MC-LR concentration suggests that the allelopathic effect was effective only if the intracellular content of MC-LR was sufficient to be released into the medium, when it would suppress the growth of *An7120* (Pflugmacher 2002; Schagerl et al. 2002; Sedmak and Elerseck 2005). In particular, MCs can function as inhibitors of photosynthetic activity (Hu et al. 2004; Sukenik et al. 2002). Therefore, to verify whether the allelopathic effect exists, the physiological experiments were analyzed (Fig. 9). The growth of *An7120* was promoted or restrained when the concentration of MC-LR was below 0.1 µg L⁻¹ or above 1 µg L⁻¹, respectively.

Fig. 6 Time course of DTN and DTP in competition experiments between *Ma7806* and *An7120*. **a–c** The initial chlorophyll *a* ratios of *Ma7806* and *An7120* were 1:9, 1:1, and 9:1, respectively

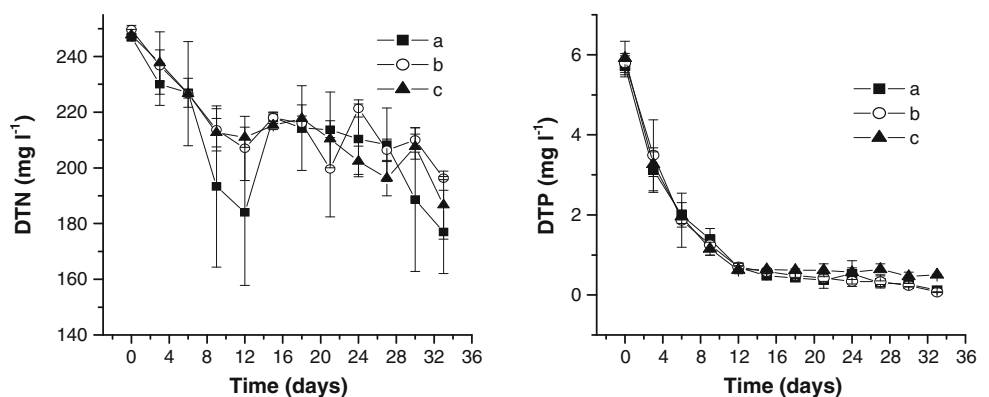
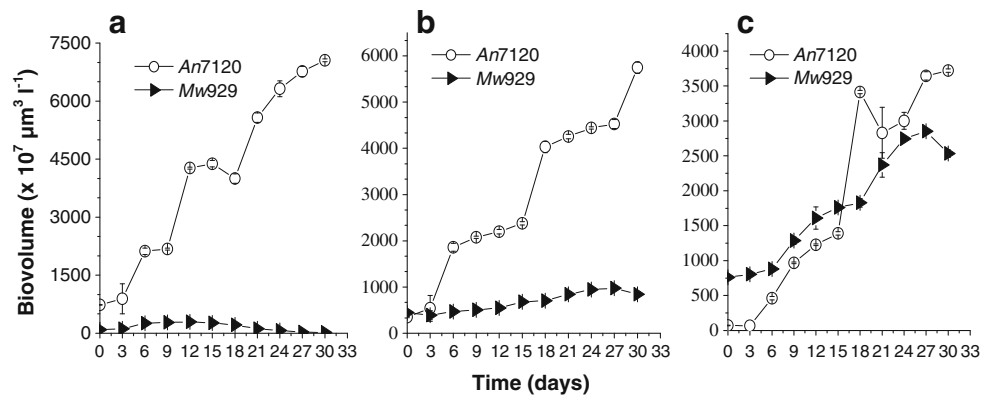


Fig. 7 Time course of biovolumes in competition experiments between *Mw929* and *An7120*. **a–c** The initial chlorophyll *a* ratios of *Mw929* to *An7120* were 1:9, 1:1, and 9:1, respectively



Therefore, the allelopathic effect occurred throughout the competition experiments. The maximum extracellular concentration of MC-LR was $0.0875 \mu\text{g L}^{-1}$ in set (a), while the maximum biomass of *An7120* was much larger than that in the monoculture experiment. In set (c), the maximum extracellular concentration of MC-LR was $14.706 \mu\text{g L}^{-1}$ while the growth of *An7120* was greatly suppressed by MC-LR, consistent with the physiological experiments. In natural water, the concentration of MC-LR varies dynamically and plays an important role in diversified algae biovolume construction. Moreover, the percentage of extracellular MC-LR in the medium ranged from 0.3% to 10.55% in set (a), from 13% to 23.47% in set (b) and from 0.244% to 63.7% in set (c), although Sedmak and Elersek (2005) reported that the extracellular fraction of MC-LR in the medium only accounts for approximately 1% the intracellular fraction, which might result from the different culture conditions. Above all, the results indicated that the

more the biomass proportion of *M. aeruginosa*, the larger the concentration of MC-LR in medium. And hence, the quantity of MC-LR released into the natural waters varies during cyanobacteria blooms.

Additionally, neither DTN nor DTP showed significant differences in any experimental sets, which might result from the excess nutrients in the BG11 medium making competition between strains for nutrients unnecessary. Additionally, the initial total inoculated biomass was nearly identical in the competition experiments (Table 2), and total biovolume and cell size for each set were close so that the relative surface areas of the two strains were similar. This leads to similar rates of nutrient uptake, consistent with the monoculture experiments.

In the *Mw929* and *An7120* mixed culture experiments, *Mw929* were eventually competitively suppressed by *An7120* for all tested inoculation ratios. This result is mainly a function of two factors. The first is the subtle

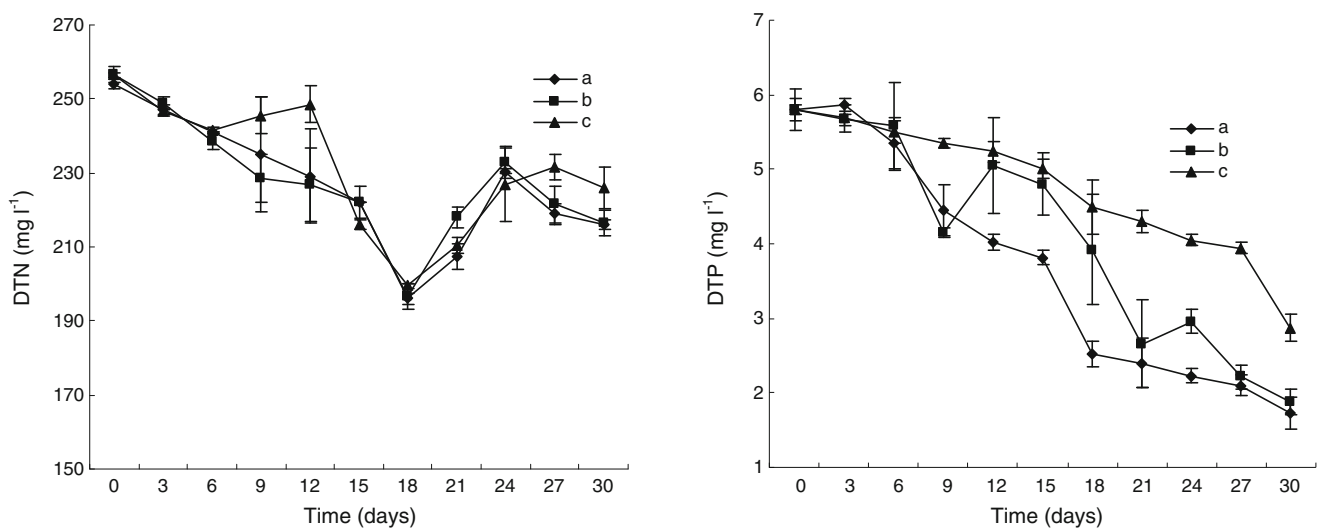


Fig. 8 Time course of DTN and DTP in competition experiments between *Mw* and *An7120*. **a–c** The initial chlorophyll *a* ratios of *Mw929* to *An7120* were 1:9, 1:1, and 9:1, respectively

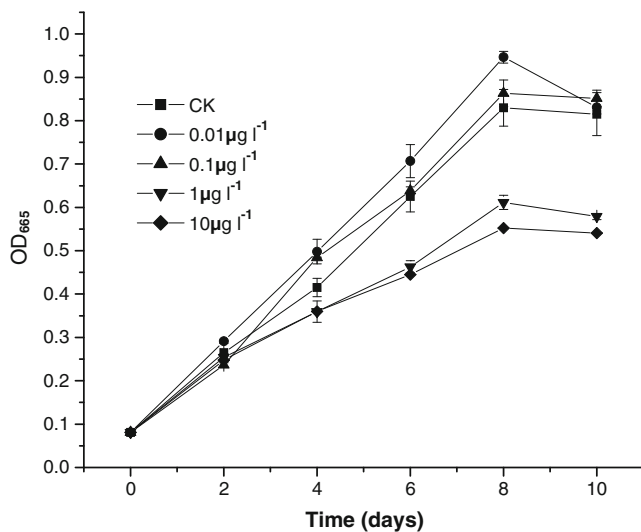


Fig. 9 Effects of different MC-LR concentrations on the growth of *An7120*

difference in growth rates between the two strains in the monoculture experiments, which inevitably affects their growth in the competition experiments. The second factor is cell size: *Mw929* cells are much larger than *An7120* cells. Mathematical theory predicts that the relative surface area of *Mw929* will be much smaller than that of *An7120*; hence the latter will absorb nutrients more efficiently than the former. Furthermore, the decreases of nitrogen resources during the experiment will result in growth limitation of the cells (Fig. 7). However, under conditions of nitrogen deficiency, the nitrogen-fixing heterocysts will differentiate from vegetative cells in *An7120* (Kaneko et al. 2001), and this characteristic will allow it to gain eventual dominance. Overall, *Mw929* appeared to be weaker during competition with co-cultured *An7120*.

On the other hand, in Fig. 7, we could infer that the larger the proportion of *Mw929* the greater the DTP in the medium when co-cultured with *An7120*, which indicates that *Mw929* should be well accustomed to phosphorous deficiency conditions. Hence, the concentration of phosphorous could serve as a forecast of *Mw929* blooms. Phosphorus often limits *Microcystis* growth in the natural aquatic environment. There are many reports of interactions between *Microcystis* and phosphorus. However, these reports focus mainly on the uptake of different forms of phosphorus by *Microcystis* (Yang et al. 2005) or its competitive utilization with other algae (Takeya et al. 2004) other than *M. wesenbergii*.

As we know, in most natural lakes in China, *Microcystis* blooms usually occur from early summer to late autumn. To a large extent, the phenomenon requires a suitable temperature. *Microcystis* have been found to have an optimal temperature for growth and photosynthesis at, or

above, 25°C (Takamura et al. 1985; Robarts and Zohary 1987; Reynolds 2006; Jöhnk et al. 2008; Paerl and Huisman 2008). In natural waters, the temperature would be below 25°C from spring to early summer and hence *Anabaena* blooms could occur under favorable conditions; when the temperature reaches above 25°C, *Microcystis* species (i.e., *M. aeruginosa* and *M. wesenbergii*) would begin to grow rapidly and then *Microcystis* blooms would occur until late autumn; in late autumn, *Anabaena* blooms would occur again due to low temperature. During *Microcystis* blooms, the three strains always co-exist but their biomass proportion varies considerably at different periods. The biomass of *M. aeruginosa* is much larger than *M. wesenbergii* in the early period of *Microcystis* blooms, which our experiment results suggest is due to *M. aeruginosa* having a stronger competitive ability than *M. wesenbergii* under favorable conditions. Conversely, in the late period of *Microcystis* blooms, when the concentration of phosphorous in natural waters decreased markedly, the process of *Microcystis* blooms as well as that our experiment showed that *M. wesenbergii* was more tolerant to low phosphorus than *M. aeruginosa*. At the same time, the biomass of *Anabaena* varies considerably as well. According to our results, allelopathic effects of MC-LR on *An7120* exist and the extracellular MC-LR concentration varies with different biomass proportion. When the temperature was below 25°C in spring, the biomass proportion of *M. aeruginosa* was usually smaller than *Anabaena* and the concentration of MC-LR released to natural waters would be much lower leading to promoting the growth of *Anabaena*. With increased temperature, the biomass proportion of *M. aeruginosa* would increase and the concentration of MC-LR in natural waters would also increase thus restraining the growth rate of *Anabaena* so that *M. aeruginosa* dominated for a long period. In the late period of *Microcystis* blooms, *M. wesenbergii* would dominate relatively for a short period until the temperature decreases to about 25°C and then *Anabaena* would dominate again. Overall, temperature, nutrients and microcystin jointly drive the succession of cyanobacteria blooms. Besides this, some other abiotic factors should be studied further.

In conclusion, our laboratory experiments demonstrate that the *M. aeruginosa* strain has a stronger competitive ability than *M. wesenbergii* under favorable conditions when co-cultured with *An7120*. The dominant strain in competition experiments between *Ma7806* and *An7120* mainly depends on the initial biomass ratio between the two strains. Differences in morphological forms and allelopathic effects of MC-LR produced by *M. aeruginosa* are considered to be the main factors controlling growth. Finally, we found that *M. wesenbergii* was tolerant to low phosphorus.

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