Microb Ecol (2016) 71:802–813
DOI 10.1007/s00248-015-0719-z

MICROBIOLOGY OF AQUATIC SYSTEMS

Assessment of the Effects of Light Availability on Growth and Competition Between Strains of *Planktothrix agardhii* and *Microcystis aeruginosa*

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Received: 16 February 2015 / Accepted: 13 December 2015 / Published online: 21 December 2015

Abstract In this study, we tested the hypothesis that *Planktothrix agardhii* strains isolated from a tropical water body were better competitors for light than *Microcystis aeruginosa* strains. These cyanobacteria are common in eutrophic systems, where light is one of the main drivers of phytoplankton, and *Planktothrix* is considered more shade-adapted and *Microcystis* more high-light tolerant. First, the effect of light intensities on growth was studied in batch cultures. Next, the minimum requirement of light (I^*) and the effect of light limitation on the outcome of competition was investigated in chemostats. All strains showed similar growth at 10 μmol photons m^{-2} s^{-1}, demonstrating the ability of the two species to grow in low light. The optimum light intensity was lower for *P. agardhii*, but at the highest light intensity, *Microcystis* strains reached higher biovolume, confirming that *P. agardhii* has higher sensitivity to high light. Nonetheless, *P. agardhii* grew in light intensities considered high (500 μmol photons m^{-2} s^{-1}) for this species. *M. aeruginosa* showed a higher carrying capacity in light-limited condition, but I^* was similar between all the strains. Under light competition, *Microcystis* strains displaced *P. agardhii* and dominated. In two cases, there was competitive exclusion and in the other two *P. agardhii* managed to remain in the system with a low biovolume (≈15 %). Our findings not only show that strains of *P. agardhii* can grow under higher light intensities than generally assumed but also that strains of *M. aeruginosa* are better competitors for light than supposed. These results help to understand the co-occurrence of these species in tropical environments and the dominance of *M. aeruginosa* even in low-light conditions.

Keywords Cyanobacteria · Light limitation · Interspecific variability · Intraspecific variability · Continuous culture · Chemostats

Introduction

Cyanobacteria blooms are reported more frequently and with higher intensity in freshwater and coastal ecosystems [1, 2]. Cyanobacteria blooms can be highly variable in species compositions depending on a wide variety of environmental conditions [3]. The high flexibility of some cyanobacteria species to adapt to different environmental conditions (e.g., low nutrients, elevated temperature) may have provided them with an extra advantage to increase perennial blooms, especially in tropical regions [4].

Microcystis aeruginosa and *Planktothrix agardhii* are two of the most frequent bloom-forming cyanobacteria in tropical eutrophic aquatic ecosystems [5–8]. Both species are widely studied because they are potentially strong producers of microcystins, toxins that may have a significant negative impact on the aquatic ecosystem and present a hazard to human and animal health [9].

In general, *P. agardhii* is considered able to dominate the phytoplankton community under conditions of low light

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availability, and it is sensitive to high light intensity [5, 10, 11]. Therefore, *P. agardhii* is considered more shade-adapted. The dominance of *M. aeruginosa* is usually related to high nutrient concentrations, low turbulence, and high temperatures [9, 12]. But studies conducted in a hypereutrophic lake showed that the amount of light supplied to the water column may be the most important factor controlling the growth of *M. aeruginosa* [13]. *M. aeruginosa* is a species that may tolerate high light conditions [14–16]. Hence, *M. aeruginosa* is considered more high-light tolerant. This finds further support in a conceptual model, developed for shallow eutrophic lakes, that considered the underwater light availability as the major controlling variable to explain conditions under which the cyanobacterial assemblage is alternatively dominated by low light-adapted (*Oscillatoria* and *Lyngbya*) or high light-adapted (*Microcystis* and *Anabaena*) organisms [17].

It should be noted, however, that most of these considerations are based on works with temperate and subtropical systems. A recent study reported that *P. agardhii* occurred only in temperate and subtropical water bodies, but not in tropical waters [5]. However, *P. agardhii* has been found in the tropics [e.g., 7, 18], where it, for example, replaced *C. raciborskii* in a eutrophic reservoir when turbidity was less and water transparency greater [18]. In contrast, *M. aeruginosa* has been found blooming in turbid water [6]. Hence, the well-documented differences to light seem less clear for tropical *P. agardhii* and *M. aeruginosa*. To get more insight in the reaction to different light intensities we isolated two *P. agardhii* strains and two *M. aeruginosa* strains from a tropical water body and tested the hypothesis that also tropical *P. agardhii* is a better competitor for light than *M. aeruginosa*.

Methods

Organisms

The experiments were performed with two *P. agardhii* (Gomont) Anagnostidis & Komárek 1988 strains—Plank-03 and Plank-09—and two *M. aeruginosa* (Kützing) Kützing 1846 strains—MIC-03 and MIC-08. The cyanobacterium strains were isolated from Jacarepaguá Lagoon (22° 55′ S and 43° 17′ W, Brazil) between 2009 and 2011 and were maintained in culture collection of the Laboratory of Ecology and Physiology of Phytoplankton, University of Rio de Janeiro State (UERJ, Brazil). Three of the four studied strains are confirmed as producer of microcystins varieties (Table 1, determined by LC-MS/MS as described in [19]). *M. aeruginosa* strains were grown as single cells, not in colonies, except in some mixed culture. Cultures were not grown axenically, but regular microscopic inspection revealed that biomass of heterotrophic bacteria remained well under 1 % of total biovolume.

Table 1 Characteristics of the four strains used in this study

Species	Strain	Toxins
Microcystis aeruginosa	MIC-03	dmMC-LR, MC-LR
	MIC-08	MC-LR
Planktothrix agardhii	Plank-09	dmMC-RR, MC-RR, MC-YR
	Plank-03	Not determined

MC microcystin

Growth, Biovolume, Chlorophyll-a, Efficiency of Photosystem II (ϕ_{PSII}), and pH

Growth was monitored by cell counts using a hemocytometer (Neubauer chamber). At least 400 individuals were counted (error <10 %, $p < 0.05$ [20]). When colonies formation was observed, mucilage was dissolved using 0.03 M KOH warmed (≈50 °C) solution. The biovolume ($\mu m^3\ mL^{-1}$) of each strain was estimated from the product of the density population and mean cell volume of each strain. Cell volumes were estimated considering the average size of 100 individuals of each strain acclimated to the studied light intensities. Growth rates (μ, day^{-1}) of batch cultures were estimated using linear regression over natural log-transformed biovolume against time. Chlorophyll-*a* (Chl-a) concentration ($\mu g\ L^{-1}$) and efficiency of photosystem II (ϕ_{PSII}) were measured with the PHYTO-PAM phytoplankton analyzer (Heinz Walz GmbH, Effeltrich, Germany). Chlorophyll calibration was undertaken using the studied strains extracted in 90 % acetone according to [21]. The calibrations used cultures grown at 24 °C under five light intensities (10, 40, 60, 100, and 500 μmol photons $m^{-2}\ s^{-1}$). pH was monitored on alternate days using a pH electrode refillable Ag/AgCl (Sensoglass SC-09) calibrated in the range 4.0 to 7.0, with model PH-221 Lutron pH meter.

Growth-Irradiance Curves

Growth rates estimated for batch cultures were plotted against light intensities (Fig. 2). Maximum growth rate, μmax, the initial slope of the light-limited portion μ versus I curve, α, a parameter describing photoinhibition, β, and the irradiance at the onset of light saturation, I_k ($I_k = \mu max/\alpha$), were derived from a fitted model for which we replaced photosynthesis rates by growth rates [22].

Light Penetration (I_{out})

Light intensities (PAR from 400 to 700 nm) penetrating through cultures (I_{out}) were measured on alternate days with a quantum sensor LI-190SA attached to a light meter LI-250 (LICOR, Lincoln, Nebraska, USA) in 4 points vertically distributed on kitasato flask at the opposite side incident light. I_{out}

was measured as an estimate of species competitive abilities [23, 24]. This measure, although proposed by Huisman and Weissing (1994) for unidirectional light field, appears to be robust even when the assumption of unidirectionality is relaxed [24].

Evaluation of the Effect of Light Intensity on Growth and Morphology

The effect of light intensity on the growth of *P. agardhii* and *M. aeruginosa* strains were studied in batch cultures. The selected light intensities were based on field data obtained at the sub-surface (0.1 m) of Jacarepaguá Lagoon between 2007 and 2008 when the strains were isolated (M. Marinho, unpubl. data). The light intensities measured varied between 33 and 1498 μmol photons m^{-2} s^{-1}, with an average of 515 μmol photons m^{-2} s^{-1}. MIC-03, MIC-08, Plank-03, and Planck-09 strains, previously acclimated to a given experimental irradiance, were set up as batch monocultures in Erlenmeyer flasks containing 150 mL of slightly modified WC medium [25], under five light intensities (10, 40, 60, 100, and 500 μmol photons m^{-2} s^{-1}) at 24 ± 2 °C. Treatments were run in triplicate. Culture flasks were shaken several times a day. Initial biomass was low (2×10^6 μm^3 mL^{-1}) to minimize cell interactions due to competition for nutrients and light. Irradiance was provided continuously, from overhead cool white fluorescent lamps and measured with a quantum sensor LI-190SA attached to a light meter LI-250 (LICOR, Lincoln, Nebraska, USA). Growth was monitored for 10 days and samples were taken on alternate days. Changes in morphology were evaluated by the volume of the cells (all strains) and filament length of *P. agardhii* strains.

Evaluation of Light Competition Between Strains of *P. agardhii* and *M. aeruginosa*

Light competition between strains of *P. agardhii* and *M. aeruginosa* was studied in continuous cultures, performed in Kitasato flasks of 500 mL with a dilution rate of 0.3 day^{-1}. Chemostats were illuminated from one side to obtain a unidirectional light gradient. Incident light intensity (I_{in}) was set at 40 μmol photons m^{-2} s^{-1} of constant irradiance. To avoid nutrient limitation, concentration of phosphorus (K_2HPO_4) and nitrogen ($NaNO_3$) was seven times higher than that of the original WC medium [26]. Imposed limitations were confirmed by pilot experiments, and steady-state population biovolume increased only in response to an increase in the light supply. Bubbling with sterilized (0.2-μm membrane filters) air ensured both CO_2 supply and intense mixing throughout the total volume of the cultures.

First, monocultures of all strains were grown in light-limited chemostats for estimates of the biovolume, I_{out}, chlorophyll-*a*, and pH in steady-state conditions. Growth rates (r, day^{-1}) of chemostat monocultures were estimated using a solution for the classic logistic growth model through non-linear regression over biovolume against time.

$$N_t = \frac{N_0\, K}{N_0 + (K - N_0)e^{-rt}}$$

where N_t = biovolume, N_0 = initial biovolume, t = time, r = intrinsic rate of population increase, and K = carrying capacity.

Monocultures were maintained at steady state for 2 months. Steady-state traits were estimated based on the average of five measurements per monoculture, spaced at least 3 days apart. Then, strains of *P. agardhii* and *M. aeruginosa* were cultivated for 30 days in mixed culture for the competition experiment with the following pairs of strains: Plank-03/MIC-03, Plank-09/MIC-03; Plank-03/MIC-08, Plank-09/MIC-08. Each strain was inoculated with equal biovolume of 1.5×10^8 μm^3 mL^{-1} yielding initial total biovolume of the competition cultures 3.0×10^8 μm^3 mL^{-1}. Every 3 days, we measured the I_{out} and samples were withdrawn from culture flasks for cell counts and pH measurement.

Statistical Analysis

Growth rates were tested for differences between culture conditions and strains using two-way ANOVA. Pairwise multiple comparison procedures (Holm–Sidak method) were applied to distinguish means that were significantly different ($p < 0.05$). Cell volume and filament length were tested for differences using non-parametric Kruskall–Wallis one-way ANOVA with light intensity as the fixed factor, since variances were not equal. We tested pairwise differences with a Tukey post hoc test ($p < 0.05$). All the statistics were performed in the tool pack SigmaPlot version 12.5 (Systat Software, Inc).

Results

Growth of *M. aeruginosa* and *P. agardhii* at Different Light Intensities

The strains of *M. aeruginosa* (MIC-03 and MIC-08) showed similar growth curves, with a higher final biomass in intensities >60 μmol photons m^{-2} s^{-1} (Fig. 1a, b). The two strains showed lower growth in 10 μmol photons m^{-2} s^{-1} (Fig. 1a, b). Strains of *P. agardhii* (Plank-03 and Plank-09) showed variability in growth curves (Fig. 1c, d). Plank-03 grew better and had a higher final biomass in the intensity of 60 μmol photons m^{-2} s^{-1} and showed lower growth in 500 μmol photons m^{-2} s^{-1} (Fig. 1c). Plank-09 showed lower growth in 10 μmol photons m^{-2} s^{-1} and obtained the highest final biomass at 40 μmol photons m^{-2} s^{-1} (Fig. 1d).

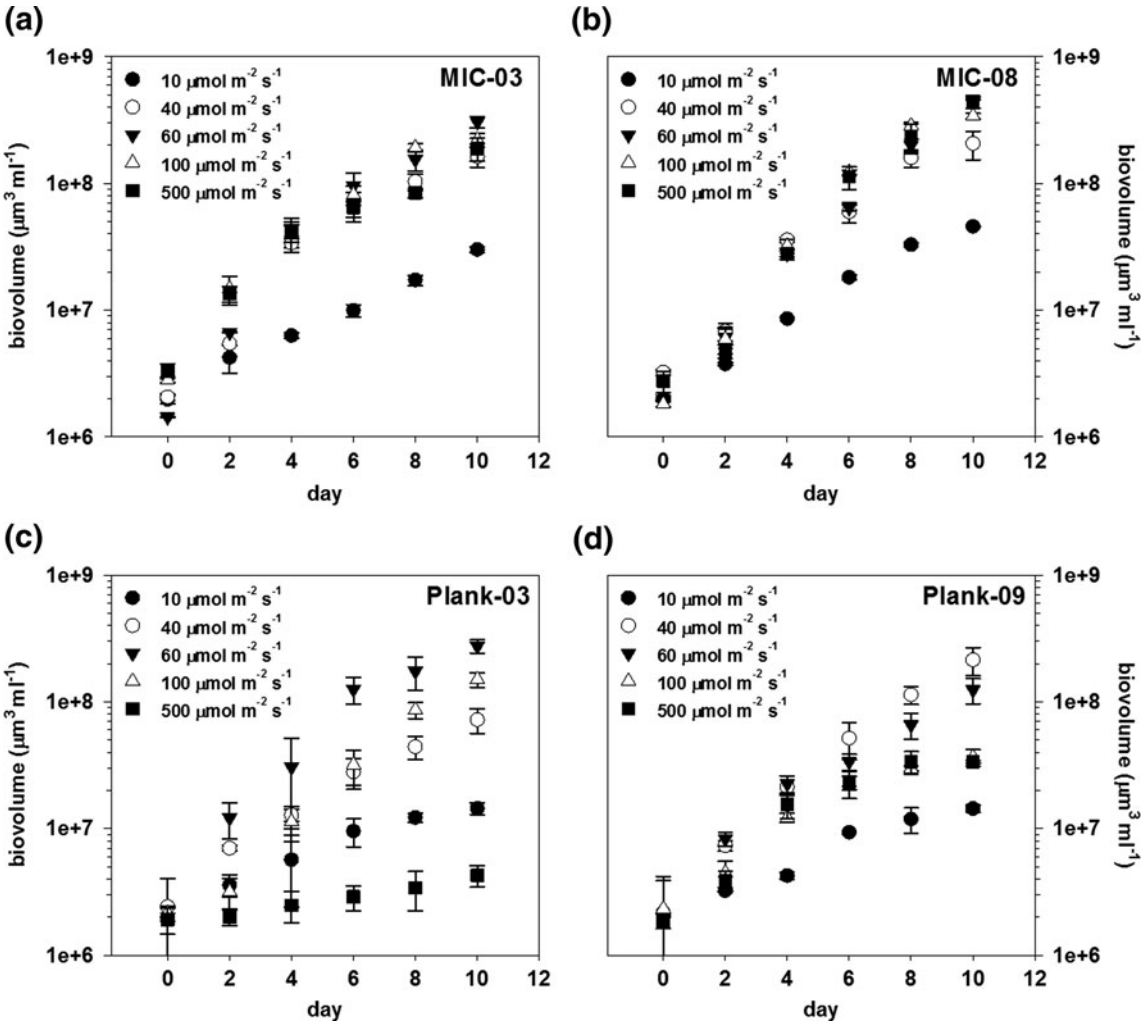

Fig. 1 Growth of *M. aeruginosa* and *P. agardhii* strains in different light intensities. **a** MIC-03. **b** MIC-08. **c** Plank-03. **d** Plank-09.

The strains of *M. aeruginosa* did not differ in growth rate at intensities ≤60 µmol photons m^{-2} s^{-1} (Fig. 2; Table 2). Both strains reached highest values at 60 µmol photons m^{-2} s^{-1}. However, the results obtained for 100 and 500 µmol photons m^{-2} s^{-1} showed significant differences (Table 2). MIC-03 growth rate reduced at intensities >60 µmol photons m^{-2} s^{-1}, while MIC-08 remained constant (Fig. 2). Growth rate of Plank-03 and Plank-09 differed at all light intensities tested but not at 10 µmol photons m^{-2} s^{-1} (Fig. 2; Table 2). Plank-03 presented the highest growth rate at 60 µmol photons m^{-2} s^{-1} and Plank-09 reached the highest growth rate at 40 µmol photons m^{-2} s^{-1} (Fig. 2). Plank-03 had a significant reduction in the growth rate at 100 to 500 µmol photons m^{-2} s^{-1} ($p < 0.05$), while Plank-09 maintained the growth rate similar to that found in the other intensities, with shorter exponential phase (Figs. 1d and 2). Thus, Plank-03 produced biovolume slowly but in a constant manner and Plank-09 grew rapidly until the sixth day, when entered the stationary phase (Fig. 1d).

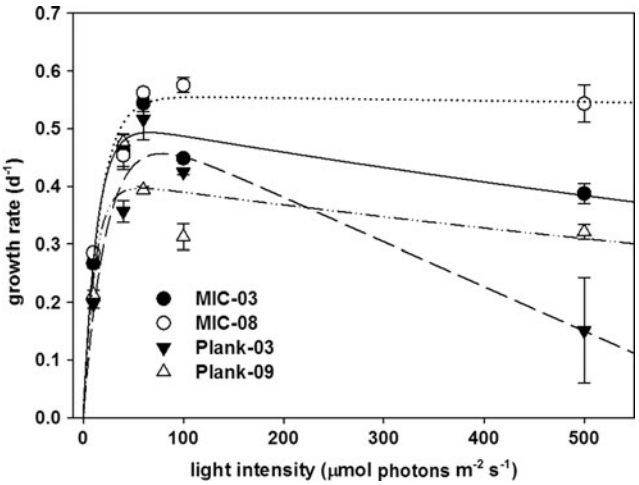

Fig. 2 Growth rate versus irradiance curves obtained for MIC-03, MIC 08, Plank-03, and Plank-09 strains. *Points* represent overall experimental growth rates obtained for batch monocultures, whereas *lines* represent modeled values adjusted to all points shown

Table 2 Two-way ANOVA table for effects of strains and light intensity on the growth rates of *M. aeruginosa* (MIC-03 and MIC-08) and *P. agardhii* (Plank-03 and Plank-09)

Source of variation	Growth rate
Strain	$F_{3,52} = 75.70$
	$p < 0.001$
Light intensity	$F_{4,52} = 86.14$
	$p < 0.001$
Strain × light intensity	$F_{12,52} = 27.38$
	$p < 0.001$

Multiple comparison (Holm–Sidak method) results

Comparisons for growth rate: strains × light intensity

	10	40	60	100	500
MIC-03	A1	B1	B1	AB1	A1
MIC-08	A1	B1	B1	C2	B2
Plank-03	A2	B2	C1	D3	E3
Plank-09	A2	B1	C2	C4	C1

The letters indicate homogeneous groups of each strain at different light intensities, and the numbers indicate homogeneous groups of the different strains for each light intensity according with the post hoc Holm–Sidak test ($p < 0.05$)

M. aeruginosa and *P. agardhii* species showed distinct growth responses depending on the tested light intensity. At 10 μmol photons m^{-2} s^{-1} *P. agardhii* showed lower growth rate than *M. aeruginosa* (Fig. 2; Table 2). Growth curves evidenced light limitation at this intensity for both species, as all strains grew better at 40 than 10 μmol photons m^{-2} s^{-1} (Fig. 1). An increased growth rate with similar growth curves was observed for *M. aeruginosa* (MIC-03, MIC-08) and Plank-03 at 60 μmol photons m^{-2} s^{-1} (Figs. 1 and 2). But *P. agardhii* Plank-09 showed inhibition and the lowest growth rate among the strains in this condition (Table 2; Fig. 2). At 100 μmol photons m^{-2} s^{-1}, MIC-08 showed the highest growth rate, Plank-09 the lowest growth reaching the stationary phase on the sixth day of the experiment and MIC-03 and Plank-3 presented similar growth rates (Table 2; Figs. 1 and 2). Although with significant decreased growth rates (except MIC-08), all the strains were able to grow at 500 μmol photons m^{-2} s^{-1} (Table 2). MIC-08 presented the highest growth rate and Plank-03 the lowest (Fig. 2). Growth rates of *M. aeruginosa* strains were higher than those of *P. agardhii* (Fig. 2). The growth curves showed that strains of *M. aeruginosa* can achieve greater biovolume than *P. agardhii* in this condition (Fig. 1). The model fitted to the growth-irradiance curves indicated strong similarities for *Microcystis* strains. However *Planktothrix* strains showed differences under light-limited and high light conditions (indicated by α, I_k, and β). Plank-09 had the lowest maximum growth rate and Plank-03 was the only strain with a $\beta < 0$ (Table 3).

Table 3 Growth parameters under different light intensities (maximum growth rate: μmax, day^{-1}; initial slope of the light-limited portion of the curve: α, day^{-1} μmol photons m^{-2} s^{-1}; photoinhibition parameter: β, day^{-1} μmol photons m^{-2} s^{-1}; and the irradiance at the onset of light saturation: I_k, μmol photons m^{-2} s^{-1})

Strains	μmax	α	β	I_k
MIC-03	0.51	0.04	0.000	13
MIC-08	0.56	0.03	0.000	16
Plank-03	0.54	0.02	−0.001	23
Plank-09	0.41	0.04	0.000	11

Cell Volume and Size of Filaments

Changes in cell volume and filaments length were observed during the experiments. Cells of *M. aeruginosa* increased in volume from 10 to 60 μmol photons m^{-2} s^{-1} (MIC-03) or 100 μmol photons m^{-2} s^{-1} (MIC-08) (Table 4). At light intensities >100 μmol photons m^{-2} s^{-1} no changes were observed for both strains. In general, MIC-03 showed higher cell volume than MIC-08, evidencing the difference between the strains of *M. aeruginosa* (Table 4).

The cell volume in Plank-09 filaments remained similar at the different light intensities tested, but cell volume in Plank-03 decreased gradually with increasing light intensities from 10 to 500 μmol photons m^{-2} s^{-1} (Table 4). In general, Plank-03 showed higher cell volume than Plank-09 (Table 3). The average filaments length also showed variations depending on light intensity. Plank-03 showed higher variability for filaments length than Plank-09. The smallest filaments were obtained when cultivated at lower intensity (10 μmol photons m^{-2} s^{-1}) and mainly at the highest intensity (Table 4).

Growth of *M. aeruginosa* and *P. agardhii* in Chemostats—Monocultures

The growth of the strains in monoculture promoted the reduction of the passage of light through cultivation (I_{out}) until the carrying capacity and the steady state of each system was achieved. Monocultures reached stability around the tenth day of culture (Fig. 3). MIC-08 and Plank-03 showed some incidental events with tubing and supply of the culture medium, with consequent reduction of biovolume on days 25–30 and 11–20, respectively. After exchanged capillaries, the strains returned to steady-state reached previously (Fig. 3).

Both strains of *M. aeruginosa* achieved higher biovolume at steady state than the strains of *P. agardhii*, but the biovolume was similar among strains of the same species (Table 5). MIC-03, MIC-08, and Plank-09 had similar I_{out} values and Plank-03 showed the lowest I_{out} among the strains tested. The I_{out} of MIC-03 was higher than Plank-03 (Table 5). The strain with higher minimum requirement of light was

Table 4 Average cell volume ($\mu m^3 \pm 1$ standard deviation), filament length ($\mu m \pm 1$ standard deviation), and surface/volume ratio (S/V—μm^{-1}) of *M. aeruginosa* (MIC03, MIC-08) and *P. agardhii* (Plank-03, Plank-09) strains, measured at five different light intensities (μmol photons m^{-2} s^{-1}) including χ^2 and p values of non-parametric Kruskall–Wallis one-way ANOVAs

		Light intensity					χ^2	p
		10	40	60	100	500		
Cell volume	MIC-03	43.0 (±0.0)^{A}	55.9 (±0.0)^{AB}	65.4 (±0.0)^{B}	65.4 (±15.4)^{B}	65.4 (±15.4)^{B}	23.3	<0.001
	MIC-08	25.8 (±10.0)^{A}	33.5 (±0.0)^{AB}	39.9 (±13.1)^{AB}	46.3 (±16.5)^{B}	43.1 (±15.4)^{B}	15.1	<0.05
	Plank-03	56.8 (±6.7)^{A}	49.2 (±17.0)^{AB}	47.1 (±10.1)^{A}	46.4 (±13.6)^{AB}	34.8 (±6.2)^{B}	21.3	<0.001
	Plank-09	36.6 (±4.1)	38.9 (±4.0)	39.4 (±14.9)	42.3 (±7.8)	39.0 (±7.1)	4.1	>0.05
Filament length	Plank-03	385.3 (±122.9)^{A}	737.9 (±247.8)^{B}	594.0 (±129.2)^{BC}	540.1 (±127.8)^{C}	77.0 (±41.9)^{D}	310.6	<0.001
	Plank-09	418.3 (±100.5)^{A}	532.1 (±144.2)^{B}	469.7 (±93.2)^{AB}	512.8 (±174.3)^{B}	188.8 (±83.1)^{C}	226.9	<0.001
S/V	MIC-03	1.4 (±0.14)^{A}	1.3 (±0.14)^{A}	1.2 (±0.001)^{B}	1.2 (±0.001)^{B}	1.2 (±0.001)^{B}	23.3	<0.001
	MIC-08	1.7 (±0.26)^{A}	1.5 (±0.001)^{A}	1.4 (±0.12)^{B}	1.4 (±0.15)^{B}	1.4 (±0.14)^{B}	15.1	<0.001
	Plank-03	0.8 (±0.06)^{A}	0.9 (±0.10)^{A}	0.8 (±0.001)^{A}	1.0 (±0.08)^{A}	1.1 (±0.11)^{B}	34.3	<0.001
	Plank-09	1.0 (±0.06)	1.0 (±0.001)	0.9 (±0.10)	1.0 (±0.06)	1.0 (±0.003)	30.2	>0.05

Superscript letters indicate homogeneous groups according to the Tukey test

Plank-09 (1.01 μmol photons m^{-2} s^{-1}), as opposed to another strain of *P. agardhii* Plank-03 (0.62 μmol photons m^{-2} s^{-1}). The growth rates estimated through the fits of logistic equation (r) was similar for MIC-03, MIC-08, and Plank-09, but Plank-03 showed the lowest growth rate among the strains tested (Table 5). The chlorophyll contents were different, except for MIC-03 and Plank-09 that produced similar amounts of chlorophyll per cell (Table 3). MIC-08 produced the lowest amount (0.37 pg $cell^{-1}$) and Plank-03 produced the highest amount of chlorophyll (0.89 pg $cell^{-1}$). The pH of the cultures showed values below 9.0 for most of the time (Table 5).

Competition for Light

The results of the competition experiment under light limitation showed that *M. aeruginosa* always dominate or displaced *P. agardhii* regardless the pair of competing strains (Fig. 4). In the experiment with the pair *M. aeruginosa* MIC-03 × *P. agardhii* Plank-03, the total biovolume reached steady state after 15 days (on average 7.8×10^8 μm^3 mL^{-1}). The I_{out} dropped to an average value of 0.82 ± 0.12 μmol photons m^{-2} s^{-1}. *M. aeruginosa* MIC-03 displaced *P. agardhii* Plank-03 and became the dominant species, but *P. agardhii* Plank-03 remained in the chemostat with a contribution around 15 % (Fig. 4a). *M. aeruginosa* MIC-03 also dominated and virtually excluded *P. agardhii* Plank-09 (contribution <2 % at the end of experiment) (Fig. 4b). Total biovolume reached the steady state around the 20th day (on average 9.5×10^8 μm^3 mL^{-1}) and average I_{out} was 0.76 ± 0.20 μmol photons m^{-2} s^{-1}. The contribution of *M. aeruginosa* MIC-03 was >98 % by the end of the experiment (Fig. 4b).

In the experiment with the pair *M. aeruginosa* MIC-08 × *P. agardhii* Plank-03 (Fig. 4c), the total biovolume reached the steady state after 20 days (on average 7.9×10^8 μm^3 mL^{-1}). The I_{out} decreased more slowly than in the previously described pairs and the average value at steady state was lower (0.61 ± 0.09 μmol photons m^{-2} s^{-1}). Although the competitive exclusion was not observed in the time span of the experiment, *M. aeruginosa* MIC-08 contributed with more than 97 % of the total biovolume by the end of the experiment (Fig. 4c). In the light competition experiment, *M. aeruginosa* MIC-08 displaced *P. agardhii* Plank-09 and became the dominant species, but complete exclusion could not be observed in the time span of the experiment, where *P. agardhii* Plank-09 showed a contribution around 15 % by the 30th day (Fig. 4d). Steady state was reached after 15 days with an average total biovolume of 9.4×10^8 μm^3 mL^{-1} and low I_{out} values (average 0.61 ± 0.10 μmol photons m^{-2} s^{-1}). The final biovolume of *M. aeruginosa* strains in mixed cultures was similar to the average biovolume found during the steady state under monoculture. However, the final biovolume of *P. agardhii* strains in competition was lower than that observed for monoculture.

Discussion

In this study we tested the hypothesis that two *P. agardhii* strains isolated from a tropical water body were better competitors for light than two *M. aeruginosa* strains. Both species were able to grow in the different light intensities provided. All the strains showed similar growth at intensity of 10 μmol photons m^{-2} s^{-1}, demonstrating the ability of the two species to grow in low light. But at the highest light intensity (500 μmol photons m^{-2} s^{-1}), both *M. aeruginosa* strains had higher biovolume than *P. agardhii*, confirming that *P. agardhii* has higher sensitivity to high light. Under light competition,

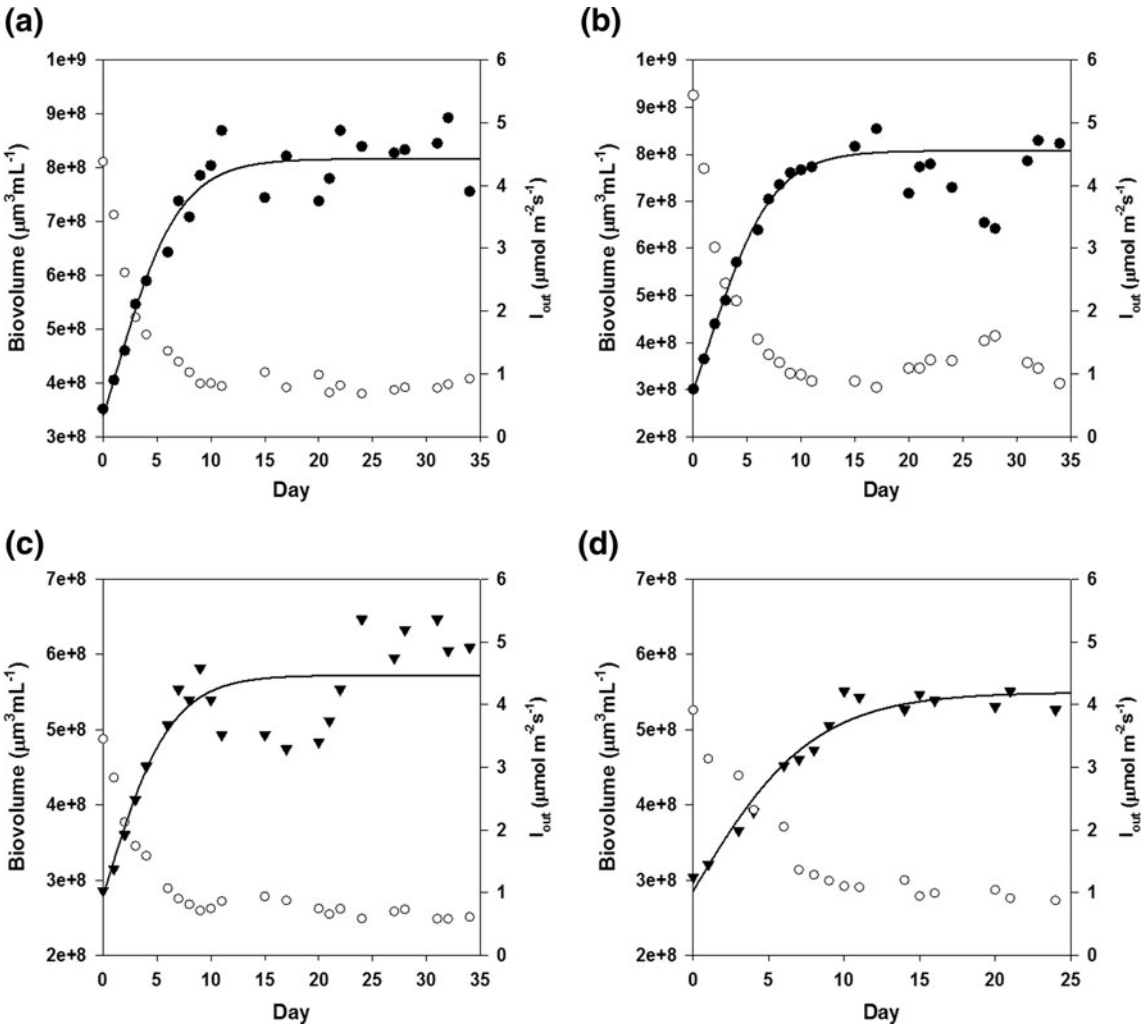

Fig. 3 Biovolume of *M. aeruginosa* (*closed circle*) and *P. agardhii* (*closed inverted triangle*) strains in chemostat monocultures. **a** MIC-03. **b** MIC-08. **c** Plank-03. **d** Plank-09. *Open circles*—light penetration through cultures (I_{out}). The *solid line* represents the fitted growth by regression according to the logistic equation

M. aeruginosa exceeded *P. agardhii* immediately after the start of the experiment. This rapid growth resulted in the dominance of *M. aeruginosa* for all four pairs of strains tested. Our findings not only show that *P. agardhii* can grow under higher light intensities than generally assumed but also that *M. aeruginosa* is a better competitor for light than supposed.

Evaluation of the Effect of Light Intensity on Growth and Morphology

The theory of competition for light predicts that species with lower minimum light requirements will be the strongest competitors [27]. When the phytoplankton biomass is sufficiently

Table 5 Steady-state data of each strain grown in monoculture under light limitation

	Microcystis aeruginosa		*Planktothrix agardhii*	
	MIC-03	MIC-08	Plank-03	Plank-09
Biovolume (μm^3 mL^{-1})	8.2×10^8 ($\pm 5.9 \times 10^7$)	8.0×10^8 ($\pm 4.5 \times 10^7$)	6.2×10^8 ($\pm 2.1 \times 10^7$)	5.4×10^8 ($\pm 9.8 \times 10^6$)
I_{out} (µmol photons m^{-2} s^{-1})	0.83 (±0.13)	0.96 (±0.18)	0.62 (±0.07)	1.01 (±0.13)
Chl *a* content (pg $cell^{-1}$)	0.66 (±0.03)	0.37 (±0.03)	0.89 (±0.04)	0.70 (±0.04)
r (day^{-1})	0.33 (±0.04)	0.34 (±0.07)	0.33 (±0.09)	0.25 (±0.03)
pH	8.87 (±0.39)	8.72 (±0.43)	8.52 (±0.16)	8.37 (±0.33)

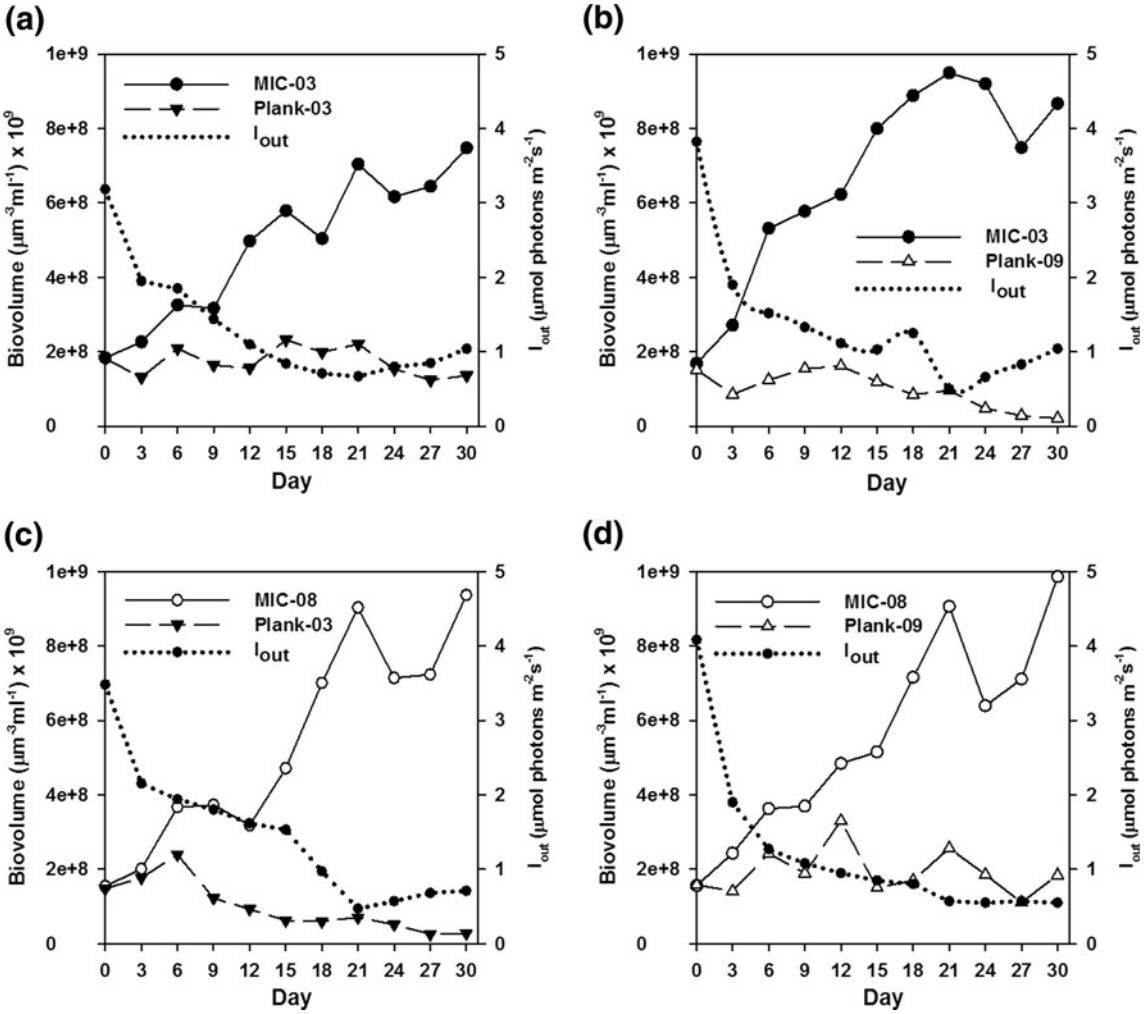

Fig. 4 Competition experiments under light-limited conditions. **a** MIC-03/Plank-03. **b** MIC-03/Plank-09. **c** MIC-08/Plank-03. **d** MIC-08/Plank-09. ddotted Dotted line—light penetration through cultures (I_{out})

concentrated, an ideal condition of self-shading is created in which *Planktothrix* becomes dominant, since it has a greater affinity for light than *Microcystis* [10]. In this case, *Microcystis* possibly will lose the competition. In contrast, at lower concentrations of biomass, the growth of *Planktothrix* is adversely affected due to photoinhibition, and under such conditions, *Microcystis* can win the competition [9]. However, such species level generalizations should be met critically as among strain variability might cause strong overlap with species belonging to the same, but also different genera [26].

The results of this study demonstrate that there is variability in the response of strains of the same species to the availability of light. This variability in responses can change the conception that *Planktothrix* will always win the competition at low light intensities and *Microcystis* at high intensities. *P. agardhii* suffered a strong inhibition of growth in higher light intensities used in the experiment, but in different ways depending on the strain. While *Planktothrix* Plank-09 reduced its growth at 60 µmol photons m^{-2} s^{-1}, possibly indicating photoinhibition, the other strain, *Planktothrix* Plank-03, at this same intensity, obtained its highest value of growth rate among the tested intensities, showing decrease of growth only at 100 µmol photons m^{-2} s^{-1} (Fig. 1). Tonk et al. [28] observed similar results for continuous cultures that demonstrated an increased growth rate of *P. agardhii* until 60 µmol photons m^{-2} s^{-1}, while above 100 µmol photons m^{-2} s^{-1}, the growth appears to be inhibited. Inhibition of growth of *P. agardhii* was also observed when exposed to light intensity above 180 µmol photons m^{-2} s^{-1} for extended periods [29]. It is noteworthy that both studied strains, especially *Planktothrix* Plank-09, could grow up to 500 µmol photons m^{-2} s^{-1}. This can be related with the environment from which the strains studied were isolated, where light intensity on the surface can reach 500–1500 µmol photons m^{-2} s^{-1} variation over a year (M. Marinho, unpubl. data).

M. aeruginosa is a species known for their high resistance to photoinhibition and high light availability [17, 30]. The growth rate of *M. aeruginosa* MIC-08 remained high at 100 and

500 μmol photons m^{-2} s^{-1}. These results were similar to those observed by [31], where the growth rate of *M. aeruginosa* PCC7806 increased to an intensity of 80 μmol photons m^{-2} s^{-1} and was constant between 80 and 403 μmol photons m^{-2} s^{-1}. Raps et al. [32] observed increased growth rate of *M. aeruginosa* with elevated levels of light intensity. According to their results, the light intensity capable of saturating growth appeared to exceed 565 μmol photons m^{-2} s^{-1}, values not investigated in our experiments. Reduction in growth rates were observed only at levels below 40 μmol photons m^{-2} s^{-1} [32], which is similar to our study. These studies and our results for MIC-08 seem to underpin the high incident light tolerance of *M. aeruginosa*. On the other hand, *M. aeruginosa* MIC-03 showed decreased growth rates at intensities >100 μmol m^{-2} s^{-1}, probably due to photoinhibition. *M. aeruginosa* MIC-03 reached their highest growth in 60 μmol m^{-2} s^{-1}, possibly indicating that this strain is adapted to conditions of lower light intensity than *M. aeruginosa* MIC-08.

The data of growth at 10 μmol photons m^{-2} s^{-1} demonstrated that strains of *M. aeruginosa* and *P. agardhii* grow similarly in low light (Fig. 2). Hence, the *M. aeruginosa* strains we have tested were at least as equally shade tolerant as the *P. agardhii* strains.

Light intensity also affected the morphology observed by the change in cell volume and size of the filaments. Shorter length of the filament in cyanobacteria may be associated with lower growth rates and physiological stress [23, 33]. Our data show a positive correlation between growth rate and length of filament ($r = 0.62$; <0,001; $n = 26$), also observed by Poulíčková et al. [34]. The lower growth rates obtained in the batch experiments of light were observed in the extreme intensities, 10 and 500 μmol photons m^{-2} s^{-1}, and were coincident with the filaments of shorter length (Fig. 2; Table 4). The shortest filaments were found at 500 μmol photons m^{-2} s^{-1}, possibly related to the stress of high light intensity. Filament size reduction can be regarded as a mechanism to reduce the cost of cellular maintenance under conditions of high temperature and irradiation [35], or to prevent the high radiation damage [34]. Energy use must be higher in order to avoid light stress (light dissipation mechanisms require energy such as synthesis of the D1 protein and the synthesis of protective carotenoids), and hence, their growth is affected [36]. The intraspecific variability of the average length of the filaments observed also appears to be associated with growth rates. In each light intensity, the strain that showed the higher growth rate also showed higher filament length.

Evaluation of Light Competition Between Strains of *P. agardhii* and *M. aeruginosa*

Chemostat monocultures revealed inter and intraspecific variability in relation to chlorophyll content, but the minimum requirement of light (I_{out}) was rather similar for each strain (Table 3). *P. agardhii* Plank-03 showed the lowest I_{out}, probably due to the greater amount of chlorophyll per cell of all the four strains tested, but Plank-03 did not win the competition for light (Fig. 4a, c). The I_k values estimated from the growth-light curves were in the range (7 to ~20 μmol photons m^{-2} s^{-1}) of species considered adapted to low-light conditions [5, 37]. These results indicate that all studied strains can be considered shade tolerant.

The concept of minimum light requirement is only able to predict the result of competition for light when the requirements of competing species are sufficiently different [38]. In the experiments of light competition conducted by Huisman et al. (1999), the data observed for minimum light requirement also did not correspond to the results of competition. *Aphanizomenon flos-aquae* showed lower I_{out} than *Microcystis* sp. but did not win the competition for light [38]. In this case, the I_{out} values obtained in the monoculture experiment were similar for both species, but values of minimum requirement of light obtained from modeling [27] were better able to explain the results of the competition. The differences between the values of minimum requirement of light observed in the experiment and fitted by the model were attributed to differences in light absorption spectrum of the species and the way how the data were calculated [38].

The studied strains of *M. aeruginosa* and *P. agardhii* showed differences in biovolume reached at the steady state in monoculture chemostat (Fig. 3; Table 5). Although the competing pairs MIC-03/Plank-03 and MIC-08/Plank-09 showed similar I_{out} values (Table 5), the higher biomass indicates that *M. aeruginosa* strains performed better under light-limited condition and can accumulate more biomass than *P. agardhii*. However, *P. agardhii* strains could maintain their biovolume close to the initial value of the inoculum over the 30 days of experiment (Fig. 4a, d). The theory predicts that competitive exclusion will be extremely slow since the competitors are sufficiently similar to coexist for prolonged periods of time [39].

Cyanobacteria can reach up to 90 % of the total phytoplankton biomass during some year seasons in Jacarepaguá lagoon, when *M. aeruginosa* is the dominant species [8]. But *M. aeruginosa* and *P. agardhii* have presented an alternate dominance in this phytoplankton community during high nutrient and elevated temperature periods [40]. Although our results cannot be directly transported to the nature, we can think about the mechanism involved in this shifts in dominance. If the environmental conditions that maintain the dominance of *M. aeruginosa* changes, then a coexistent inoculum of *P. agardhii* could grow and became dominant. Nevertheless, depending on the combination of the strains tested, *P. agardhii* was excluded in pairs MIC-03/Plank-09 and MIC-08/Plank-03 (Fig. 4b, c). These data demonstrate the importance of intraspecific diversity for the maintenance of the species in the environment.

M. aeruginosa exceeded the biovolume of *P. agardhii* immediately after the start of the competition experiment, resulting in their dominance before beginning competition for light (Fig. 4). The biovolume maintained during the steady-state monoculture showed that *M. aeruginosa* under the same conditions of growth of *P. agardhii* reached higher biovolume and, consequently, higher carrying capacity. The mechanism by which *Microcystis* strains displaced *Planktothrix* strains can be related to the growth strategy showed by the strains in terms of speed and capacity. Microcystis strains showed higher growth rates at low light (Fig. 1), and during the steady state (Fig. 3) *M. aeruginosa* reached higher biovolume than *P. agardhii* under the same conditions of growth and, consequently, higher carrying capacity. Other studies also found that differences in growth rates/capacities explained the results of light competition [41–43]. Considering the competing pairs where we observed exclusion (MIC-03/Plank-09 and MIC-08/Plank-03), *Microcystis* strains had higher growth rates and carrying capacities, and for MIC-08/Plank-03 also lower I_k value (Tables 3 and 5). This is a key factor, as a rapid growth capacity in one species subsequently impairs the growth of the less fit species [41]. *Microcystis* strains showed higher *S*/*V* ratios than *Planktothrix* at low-light conditions (Table 4), resulting in higher capacity of light acquisition and consequently growth rate.

Microcystis strains showed higher capacity to produce biomass than *Plankthotrix* under low-light conditions. This also can apply to the results regarding MIC-08/Plank-09. But, in this case, Plankthotrix Plank-09 was not excluded, probably due to its lower I_k. The lower I_k also can explain why MIC-03 outcompeted Plank-03, although the growth rates were similar.

The competition experiment demonstrated that *M. aeruginosa* growth in mixed culture was slower than monocultures. It took more time to reach the equilibrium and the minimum I_{out} (Figs. 3 and 4; Table 5), probably due to species interaction. Also, the growth of *P. agardhii* was reduced; in several cases, *P. agardhii* did either not change biomass (Fig. 4a, d) or even showed a decrease (Fig. 4b) from the start of the competition experiment, even though growth should still be possible when comparing the I_{out} values with those obtained in the monocultures. This suggests some inhibition of its growth from the start of the experiment. Since substances that exhibit activity against photosynthetic organisms were identified and isolated in strains of *Microcystis* [44, 45], the hypothesis of allelopathic interactions between species cannot be ruled out. The production of inhibitors of growth was also reported for *Planktothrix rubescens*, and this ability can vary between different strains of *Planktothrix* [46]. Based on this information, we can think of an alternative hypothesis that the dominance of *M. aeruginosa* during the competition may also be related to inhibition of growth of *P. agardhii* due to production and release of some allelopathic compounds by *M. aeruginosa*. In this study, we did not test neither allelopathic effects interactions nor our experimental design was adequate to infer this kind of interaction among the strains. Specific experiments will be required to evaluate the potential allelopathic interactions between the studied strains.

According to the conceptual model of Scheffer et al. [10], underwater light availability is the major controlling variable to explain conditions under which the cyanobacterial assemblage is dominated by low light-adapted species, because these shade-tolerant cyanobacteria are able to cause an increase in turbidity that favors their competitive advantage. So the ideal condition of self-shading is created in which *Planktothrix* becomes dominant, since it has a greater affinity for light than *Microcystis*. In this case, *Microcystis* possibly lose the competition. *P. agardhii* is usually considered a species with high tolerance to light limitation, and many studies use this feature to explain its dominance in turbid conditions [e.g., 5, 47]. But, our results strikingly contradict this conceptual model. The theory of competition for light predicts that species with lower minimum light requirements will be the strongest competitors [27]. Apart from our results, another two studies already showed that strains of *Microcystis* can present similar, or even lower critical light intensities than filamentous species of cyanobacteria [26, 38]. So *Microcystis* can be as a good light competitor as *Planktothrix*, and in some cases, probably the light is not the only factor that drives the dominance of filamentous cyanobacteria.

Acknowledgments Camila A. Torres' MSc scholarship was funded by FAPERJ (Fundação de Apoio a Pesquisa do Rio de Janeiro) and by CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior). This study was conducted under the flag of the CAPES (Brazil)/ Wageningen University (The Netherlands) CAPES-WUR project 004/ 2008.

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