Influence of light availability on the specific density, size and sinking loss of *Anabaena flos-aquae* and *Scenedesmus obliquus**

HUANG Yingying (黄莹莹)[1], ZHANG Haichun (张海春)[2], GAO Rufeng (高如峰)[3], HUANG Xiaochen (黄晓琛)[4], YU Xiaojuan (于晓娟)[5], CHEN Xuechu (陈雪初)[1, 5, **]

[1] *Shanghai Key Lab for Urban Ecological Processes and Eco-Restoration, School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China*

[2] *Shanghai Environmental Monitoring Center, Shanghai 200235, China*

[3] *Shanghai Administration Center for Ocean Affairs, Shanghai 200050, China*

[4] *East Sea Information Center of State Oceanic Administration People's Republic of China, Shanghai 200137, China*

[5] *School of Environmental Science and Engineering, Shanghai Jiao Tong University, Shanghai 200240, China*

Abstract   Harmful algal blooms in eutrophic waters pose a serious threat to freshwater ecosystems and human health. In-situ light availability control is one of the most commonly used technologies to suppress algae in lakes and reservoirs. To develop a better understanding of the effects of light on algal growth, specific density, colony size and sinking loss, *Anabaena flos-aquae* (cyanobacteria) and *Scenedesmus obliquus* (green algae) were evaluated in varying light scenarios. The results showed that the specific density and colony size of these two species varied during growth, and there were obvious differences among the light scenarios. At the end of exponential phase, *S. obliquus* incubated under light-limited condition maintained a higher specific density and formed larger aggregates, whereas *A. flos-aquae* formed a longer filament length. Both species exhibited higher sinking loss rates with lower light availability. These results implied that the sinking loss rate was not always constant but should be considered as a variable response to the change of light availability, and in-situ light availability control might result in a significant increase of the sinking loss of algae due to the change of size and specific density, thereby further affecting the algal biomass in the water column.

Keyword: specific density; size; light availability control; sinking loss

1 INTRODUCTION

Eutrophic lakes are often dominated by cyanobacteria, including several potentially toxic species, such as *Anabaena*, *Microcystis* and *Aphanizomenon*. These cyanobacteria produce gas vesicles, which leads to lower specific density than water. When the water column is stable, the buoyant cyanobacteria float upwards forming dense surface blooms (O'Neil et al., 2012). These cyanobacteria cause considerable degradation of water quality due to the formation of blooms and the possible production of toxins and off-flavors.

Various technologies have been developed to restore eutrophic waters with cyanobacterial blooms (Ahn et al., 2003; Dockko et al., 2015). Among them, in-situ light availability control is one of the most commonly used technologies to suppress cyanobacteria in lakes and reservoirs (Jungo et al., 2001; Maestre-Valero et al., 2013). There are two common types of in-situ light availability control, "artificial mixing" and "surface light-shading". Artificial mixing entrains surface cyanobacteria into the aphotic layer with prolonged darkness. Due to the

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** Corresponding author: xcchen@des.ecnu.edu.cn

limited availability of light, the growth of cyanobacteria is inhibited (Jungo et al., 2001; Hudnell et al., 2010). Surface light-shading forces high-algal water to stay in a dark area for a certain period, leading to an efficient reduction of the cyanobacterial biomass (Chen et al., 2009a, 2009b). Previous researches suggested that light availability control would lead to a significant decrease of phytoplankton biomass and shift the dominant species from cyanobacteria to green algae and diatoms in the water column (Visser et al., 1996; Jungo et al., 2001; Burford and O'Donohue, 2006). Existing studies showed that this phenomenon could be produced by a light-competition model, developed by Huisman and co-workers from 1990s (Huisman and Weissing, 1994, 1995; Huisman, 1999; Huisman et al., 1999, 2004). This model suggests that cyanobacteria, due to its high "critical light intensity", would be competitively excluded by other species that can thrive under low light conditions, such as green algae and diatoms.

Sinking loss is an important factor that may limit phytoplankton biomass in water column (Diehl et al., 2002; Padisák et al., 2003), and our previous study showed that sinking loss was the main mechanism for the cyanobacterial biomass reduction under light-shading (Huang et al., 2016). In the light competition model mentioned above, the specific sinking loss rate of phytoplankton have been considered as a constant that would not be influenced by light availability. Previous studies of light availability control rarely directly measured the sinking loss of phytoplankton, considering it as merely a small constant that would not significantly influence the biomass in the column. However, this presumption is questionable because the specific sinking loss rate of a given taxon may vary due to the change in cell (or colony) shape and size, as well as the specific density, and it may further influence the loss process (Jezberová and Komárková, 2007; Stoyneva et al., 2007; Chen et al., 2011). In particular, phytoplankton cell (or colony) size varied with the light gradient (Jezberová and Komárková, 2007; Kaiblinger et al., 2007). The findings of Naselli-Flores and Barone (2007) supported this statement that there were significant relationships between the daily availability of underwater light and the dominant morphology in the assemblage of a hypertrophic Mediterranean reservoir.

The objectives of this study were to investigate the variation trend of the specific density and the cell (or colony) size of two typical species, *Anabaena flos-aquae* and *Scenedesmus obliquus*, under different light incubation conditions and to discuss the constant of sinking loss rate in the light competition model. To simulate the sedimentation process, a mixing-static water column experimental apparatus was designed for this study. The sinking performance of two species was compared at the end of the experiment to investigate whether variations in the cell (or colony) size and specific density would further influence the sinking loss.

2 MATERIAL AND METHOD

2.1 Experimental design

Anabaena flos-aquae (FACHB 245) and *S. obliquus* (FACHB 416) were provided by the Freshwater Algae Culture Collection of the Institute of Hydrobiology, the Chinese Academy of Sciences (Wuhan, China). *Scenedesmus obliquus* normally forms four-celled colonies, known as coenobia, and *A. flos-aquae* forms filaments of 8–50 cells. The cells were maintained in a liquid axenic culture using BG11 medium. Illumination was provided using cool-white fluorescent light at a continuous intensity of 50 μmol photons/(m²·s) at the water surface. Then, the phytoplankton was cultured in 500 mL flasks containing 300 mL BG11 medium, with a 14 h:10 h light/dark cycle, at 25±1°C. The initial concentration was $(5×10^4)$–$(1×10^5)$ cells/mL. Adjustments of shade cloth were used to obtain different light incubation conditions, including 20, 60, 100, 200 and 300 μmol photons/(m²·s) for *S. obliquus* and 2, 10, 20, 60 and 100 μmol photons/(m²·s) for *A. flos-aquae*. Each treatment had three replicates. Samples of approximately 8 mL were taken every 4 d for measurements of Chlorophyll *a* (Chl *a*). The specific densities and colony sizes of the two species were measured during the experiment. The experiment lasted 22 d for *S. obliquus* and 35 d for *A. flos-aquae*, respectively, but the average specific growth rate (*μ*) was calculated according to the shortest exponential phase under different light intensity, as 10 d for *S. obliquus* and 31 d for *A. flos-aquae*, respectively. The average specific growth rate (*μ*) was calculated as:

$$\mu(/d) = \ln(N/N_0)/t, \qquad (1)$$

where N is the final concentration of Chl *a* (μg/L) at the end of the exponential phase, N_0 is the initial concentration of Chl *a* (μg/L), and t (d) is the experiment period.

According to the average specific growth rate, the light incubation conditions were divided into light-

limited condition, light-sufficient condition and light-inhibited condition.

At the end of the experiment, the sedimentation characteristics of suspended phytoplankton cultures were studied. A mixing-static water column experimental apparatus was designed for the simulation of sedimentation processes. The apparatus was a vertical glass cylinder (diameter, 5 cm; height, 50 cm) consisting of two chambers: (1) an upper mixing chamber (30 cm high), and (2) a lower settling chamber (15 cm high), which contained a honeycomb (Fig.1).

The whole cylinder was filled with the phytoplankton culture to a height of 45 cm. The upper 30 cm of the water column, which was located in the mixing chamber, was continuously aerated with an airline at a flow rate of 0.5 L/min. The portion of the water column in the settling chamber remained undisturbed, preventing re-suspension of any material that had settled out of the mixing chamber. Eight milliliter of water samples were taken from the mixing chamber before and at the end of the 2-h experimental period, for Chl a measurements. Accordingly, the sinking loss rate over a 2-h period was calculated as:

$$\eta(\%)=(1-N_{2h}/N_0)\times100\%, \tag{2}$$

where N_{2h} is the final concentration of Chl a (μg/L) and N_0 is the initial concentration of Chl a (μg/L).

2.2 Analyses

The phytoplankton biomass, expressed as the concentration of Chl a, was determined using pulse-amplitude modulated fluorometry (PHYTO-PAM, WALZ, Germany, Phytowin v1.32).

The specific density of phytoplankton was measured using the Percoll density gradient centrifugation method (Pertoft, 2000). The Percoll solution was made by mixing 2.7 parts of Percoll with one part of the growth media (BG11 medium). Samples of approximately 2 mL were added to the mixture. The mixture was centrifuged at 14 000 r/min for 30 min. Next, a stable density gradient was formed, with the cells or colonies banded at their buoyant density during the centrifugation (Wolff, 1975). The specific density of each visible phytoplankton band was measured with a kerosene-CCl₄ column of a known density gradient (Condie and Bormans, 1997).

The colony sizes of A. flos-aqua and S. obliquus were expressed as the filament length and the aggregation size (cell number within aggregation),
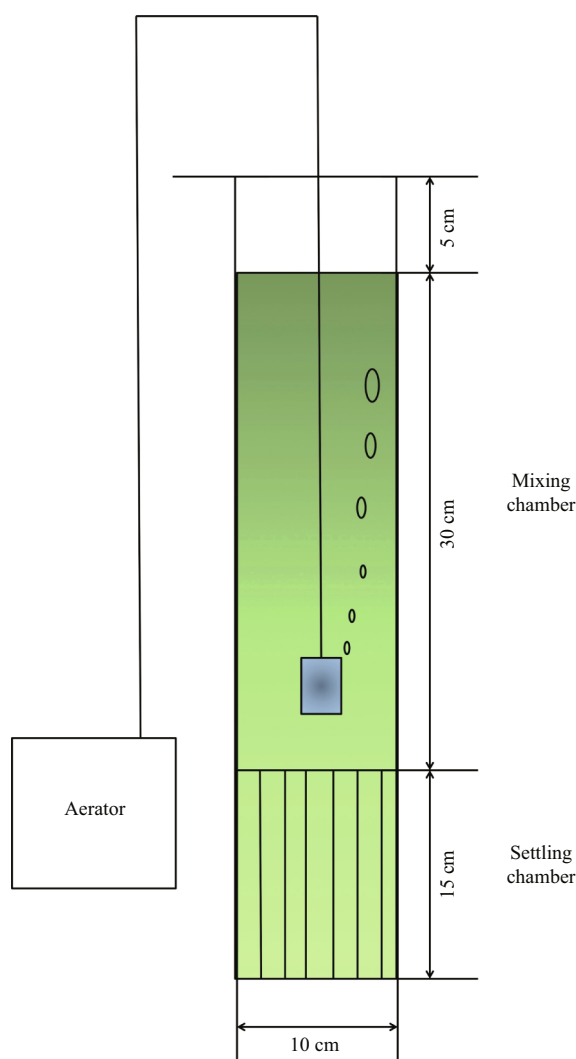

Fig.1 The mixing-static water column experimental system for simulation of sedimentation process

respectively. The colony sizes were observed and recorded with a fluorescence microscope (Eclipse E400 DS-Fi; Nikon, Melville, NY, USA). More than 50 photographs were taken for each sample to generate sufficient data for statistical analysis. The filament length of A. flos-aquae and the aggregation size of S. obliquus cells could be extracted from the photographs using the NIS elements microscopic photograph software.

Specific growth rate and specific density of the two species under different light incubation conditions were compared using an ANOVA, followed by an S-N-K (s) test. Correlations among specific density, filament length or aggregation size, incubation light, and sinking loss at the end of experiment were analyzed by Pearson correlation. P-values less than 0.05 and 0.01 were considered as significant and extremely significantly, respectively.
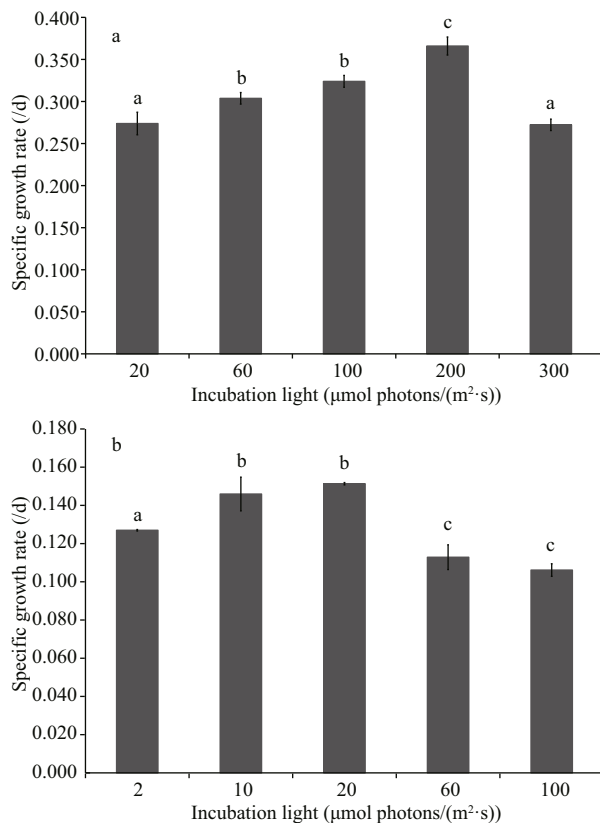
Fig.2 The specific growth rate of *Scenedesmus obliquus* (a) and *Anabaena flos-aquae* (b) under different light incubation conditions

Different letters indicate significant differences.

3 RESULT

3.1 Growth of two species under different light incubation conditions

For *S. obliquus* (Fig.2a), the specific growth rate increased from 20 µmol photons/(m²·s) to 200 µmol photons/(m²·s). When the incubation light was as high as 300 µmol photons/(m²·s), the rate decreased obviously ($P<0.05$), suggesting the growth of *S. obliquus* was inhibited due to excessive light. Accordingly, it could be inferred that *S. obliquus* experienced light-limited and light-inhibited conditions under 20 µmol photons/(m²·s) and 300 µmol photons/(m²·s), respectively, whereas incubation light of 200 µmol photons/(m²·s) supplied sufficient light for the growth of *S. obliquus*. Similarly, for *A. flos-aquae* (Fig.2b), with increasing amounts of light, the specific growth rate first increased gradually and then decreased sharply after peaking; however, there were no significant differences between the specific growth rates under 10 µmol photons/(m²·s) and 20 µmol photons/(m²·s) ($P>0.05$), and between

the specific growth rates under 60 µmol photons/(m²·s) and 100 µmol photons/(m²·s) ($P>0.05$). The light-limited, light-sufficient and light-inhibited conditions were approximately 2 µmol photons/(m²·s), 20 µmol photons/(m²·s) and 100 µmol photons/(m²·s), respectively.

3.2 Variation of specific density under different light incubation conditions

For *S. obliquus* (Fig.3a), the specific density was influenced by both incubation time and light availability. Under light-limited condition (20 µmol photons/(m²·s)), the specific density gradually increased for approximately 14 d, until it achieved the maximal value of 1.070. Under light-sufficient condition (200 µmol photons/(m²·s)), a similar variation trend of the specific density with incubation time was observed. However, the specific density increased more rapidly during the first 3 d but achieved a lower maximal value of 1.045 after 8 d of incubation. Under the light-inhibited condition (300 µmol photons/(m²·s)), the specific density continually increased during the experiment, and the final specific density value was approximately 1.039. The maximal values of the specific density under three light incubation conditions were significantly different ($P<0.05$). At the end of the experiment, the specific density under the light-limited condition was obviously higher than that under the light-sufficient condition and the light-inhibited condition ($P<0.05$), but there was no difference between the specific densities under the latter two conditions ($P>0.05$).

For *A. flos-aquae* (Fig.3b), the variation trend of specific density was more complex. Under light-limited condition (2 µmol photons/(m²·s)), the specific density decreased obviously during the first two d ($P<0.05$) and then fluctuated from 1.091 to 1.097. At the end of the experiment, it achieved the maximal value of 1.116. Under light-sufficient condition (20 µmol photons/(m²·s)), the specific density also decreased obviously during the first two d ($P<0.05$) and then increased until it achieved the maximal value of 1.116. After that, the variation of specific density was not obvious ($P>0.05$). Under light-inhibited condition (100 µmol photons/(m²·s)), the specific density increased rapidly to the maximal value of 1.171 during the first 10 d, which was significantly higher than the maximal values under light-limited condition and light-sufficient condition ($P<0.05$), and then it decreased sharply. Unlike *S. obliquus*, the specific density of *A. flos-aquae* showed no significant
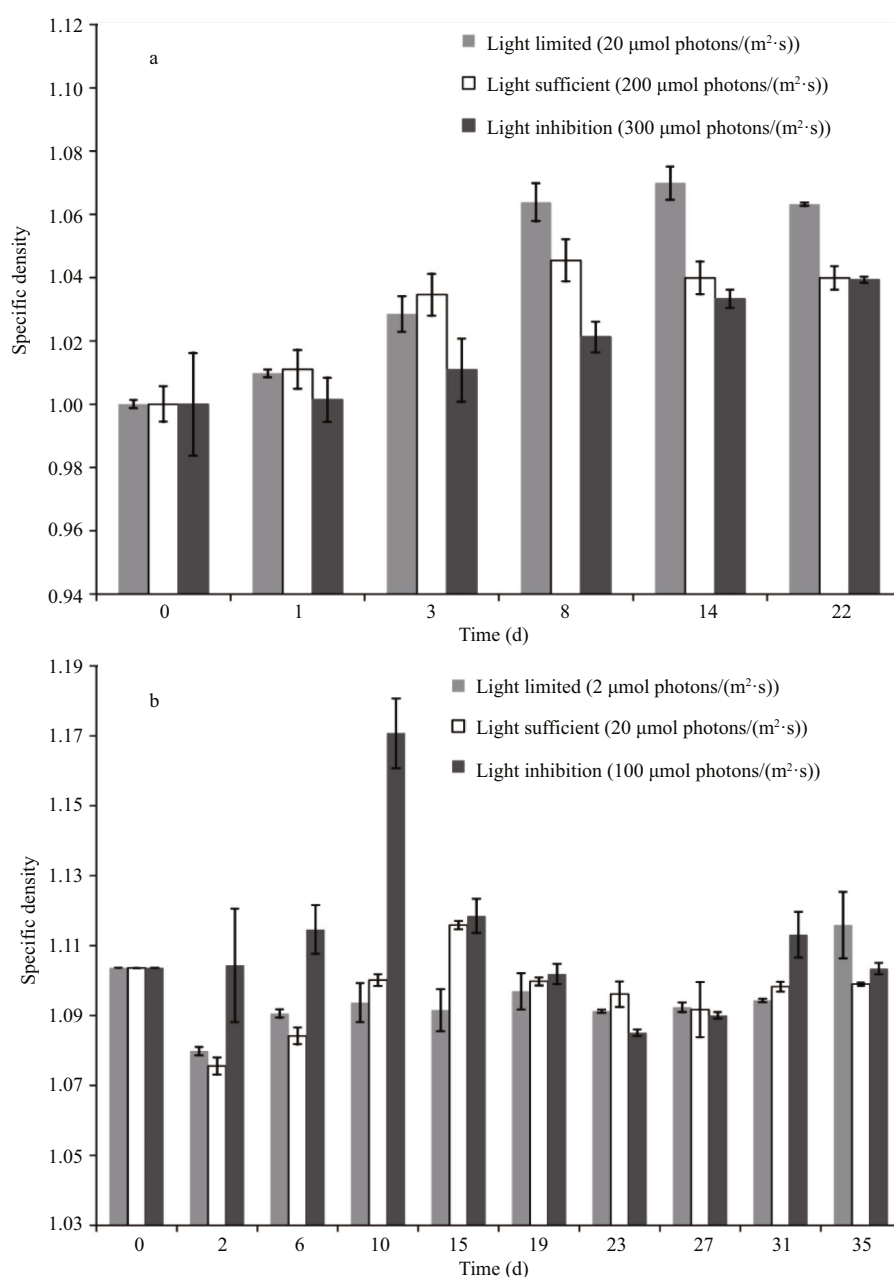
Fig.3 Variation of specific density of *Scenedesmus obliquus* (a) *and Anabaena flos-aqua* (b) under different light incubation conditions

differences among the three different light incubation conditions at the end of the experiment (P>0.05).

3.3 Variation of colony size under different light incubation conditions

For *S. obliquus*, there was no observed change in shape during the exponential phase of growth under different light incubation conditions. However, a phenomenon of cell aggregation was observed at the end of the exponential phase. As shown in Fig.4, the size of the aggregation decreased with the increase of

light availability. Furthermore, the cell numbers were counted within observed aggregations under different light incubation conditions. It appeared that *S. obliquus* formed smaller aggregations under higher light availability conditions.

For *A. flos-aquae*, a notable morphological characteristic is filament length. Figure 5 shows the variation in filament length (n≥50) under the three light conditions. Under light-limited condition, the median filament length showed an increasing trend during the experiment, from an initial value of 118 μm
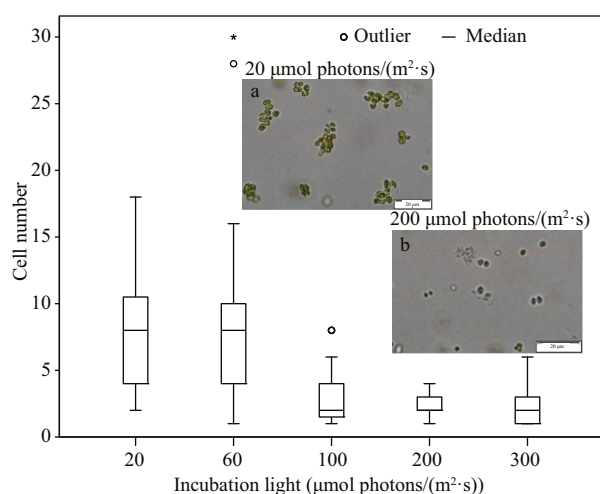
Fig.4 Frequency distribution of cell number within aggregate and microscopic photos of *Scenedesmus obliquus* under different light incubation conditions

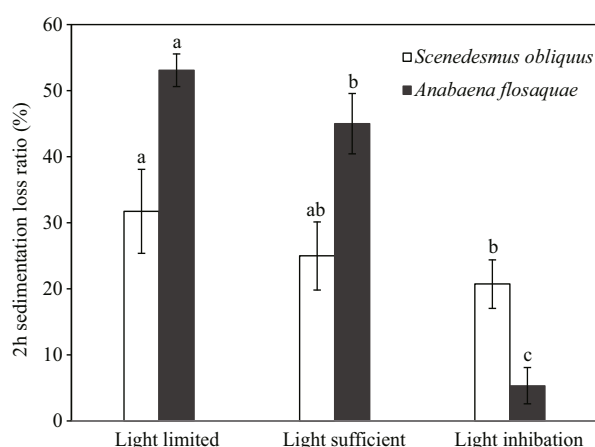a. 20 μmol photons/(m²·s); b. 200 μmol photons/(m²·s).

Fig.6 Two-hour sinking loss rate of *Scenedesmus obliquus* and *Anabaena flos-aqua* under different light incubation conditions

Different letters indicate significant differences.

to a final value of 490 μm, indicating that the filament length increased with incubation time when the light was limited. Under light-sufficient and light-inhibited conditions, the variation trend of filament length was similar. Both filament lengths increased from the beginning of experiment until they achieved maximal values of 495 μm and 284 μm, respectively, and thereafter decreased to 59 μm and 47 μm, respectively. In addition, it seemed that higher light availability could induce *A. flos-aquae* to achieve its maximal filament length more quickly.

3.4 Sedimentation performance of two species

At the end of the experiment, the sinking loss of *S. obliquus* and *A. flos-aquae* was studied through a

Fig.5 Frequency distribution of chain length of *Anabaena flos-aquae* under different light incubation conditions

a. light-limited condition (2 μmol photons/(m²·s)); b. light-sufficient condition (20 μmol photons/(m²·s)); c. light-inhibition condition (100 μmol photons/(m²·s)).

mixing-static column experiment. This experiment indicated that the sinking loss rates of both species tended to decrease with higher light availability. As shown in Fig.6, the maximal 2-h sinking loss rates of both taxa were observed under the light-limited

Table 1 Correlations among specific density, filament length or aggregation size, incubation light, and sinking loss according to values observed at the end of experiment

	Incubation light	2-h sinking loss rate
Anabaena flos-aquae		
Specific density	-0.418 ($P<0.01$)	0.473 ($P<0.01$)
Filament length	-0.626 ($P<0.01$)	0.688 ($P<0.01$)
2-h sinking loss rate	-0.777 ($P<0.01$)	/
Scenedesmus obliquus		
Specific density	-0.955 ($P<0.01$)	0.460 ($P<0.01$)
Cell number within aggregation	-0.764 ($P<0.05$)	0.830 ($P<0.05$)
2-h sinking loss rate	-0.409 0 ($P<0.01$)	/

condition, having values as high as 31.75% and 53.09%, respectively. Under the light-sufficient condition, the 2-h sinking loss rates of the two taxa decreased to 25.00% and 45.04%, respectively. Under the light-inhibited condition, the 2-h sinking loss rate was the lowest, showing the values of 20.73% and 5.36%, respectively. Interestingly, *A. flos-aquae* showed a better sinking performance than *S. obliquus* under light-limited and light-sufficient conditions, whereas *S. obliquus* showed a better sedimentation performance under the light-inhibited condition.

4 DISCUSSION

4.1 Specific density, colony size and sinking loss in response to light availability

Sinking loss of phytoplankton is an important factor that limits the phytoplankton biomass in a water column. To obtain enough light for survival, phytoplankton populations dwell in the well-illuminated upper regions of the water column. However, most phytoplankton species have specific densities somewhat higher than the surrounding medium and, consequently, move downwards on average even in turbulent waters (Bright and Walsby, 1999; Ptacnik et al., 2003). The specific sinking loss of a given taxon depends strongly on its sinking velocity. The sinking velocity (w_s) of a small phytoplankton that satisfies the condition of laminar flow, without frictional drag ($Re<0.1$), can be predicted by the modified Stokes equation (Reynolds, 2006). According to this equation, sinking velocities vary among different species, depending mainly on cell (or colony) size, cell shape and specific density (Padisák et al., 2003; Naselli-Flores et al., 2007; Kruk et al., 2011). Nevertheless, most models describing

the dynamics of phytoplankton populations in water columns implicitly assume that the changes in these three parameters are very slight and would not influence the sinking velocity and specific sinking loss of particular species.

Actually, a few of studies have shown changes in cell (or colony) size, cell shape and specific density in response to the environment (Naselli-Flores and Barone, 2007; Yamamoto and Nakahara, 2009), and cell (or colony) size would affect specific density and further influent their sinking performance (Li et al., 2016). Similarly, the result of our experiment indicated that colony size and specific density might vary significantly during the exponential growth phase. This experiment also suggested that light availability could affect the colony size and specific density. The variation trend of these parameters showed significant differences under the different light incubation conditions (Figs.4, 5). In particular, when the growth of phytoplankton was ceased at the end of the experiments, *S. obliquus* maintained a higher specific density and formed larger aggregates under the light-limited condition, whereas *A. flos-aquae* showed a longer filament length. Similarly, Li et al. (2015) also found that unicellular forms of *S. obliquus* increased when light availability increased up to 40 μmol photons/(m²·s). To further evaluate the influence of light availability, the correlations among specific density, filament length or aggregation size, incubation light, and sinking loss were calculated based on the values observed at the end of the experiment. As shown in Table 1, for both species, incubation light showed a negative correlation with all the other parameters, and there were significant positive correlations between the sinking loss rate and the specific density and between the sinking loss rate and either filament length or aggregate size. These results indicated that the changes in specific density and size responses to light availability could further affect the sinking loss of a certain species.

4.2 Implication for in-situ light availability control

It has been observed that in-situ light availability control would lead to a decrease of cyanobacterial biomass, shifting the dominant species from buoyant cyanobacteria to green algae and diatoms in water column (Visser et al., 1996; Jungo et al., 2001; Burford and O'Donohue, 2006). The existing theory shows the phenomenon is attributed to the occurrence of light-limited condition, and the growth process of certain algae will be inhibited due to the lack of

available light (Diehl et al., 2002; Huisman et al., 2004). The light competition model suggests that the population dynamics in well-mixed waters depends on the "critical light intensities" of the species. Under light-limited condition, the species with lowest critical light intensity should competitively exclude all other species (Diehl et al., 2002; Huisman et al., 2004). However, the results of our experiments indicated another possible mechanism that might regulate the community structure. For instance, *A. flos-aquae* showed a better sinking performance than *S. obliquus* under the same light incubation condition of 20 µmol photons/(m²·s). Moreover, there was a significant positive correlation between the sinking loss rate and specific density, as well as filament length or aggregation size. Artificial aeration in reservoirs or deep lakes and light-shading at more than 30% of the water surface can create light-limited conditions for algae (Kojima, 2000; Kim et al., 2007). Our results indicated that in-situ light availability control might result in an increase of sinking loss of cyanobacteria due to the change of size and specific density, which would further promote the decrease in cyanobacterial biomass in the column. However, further studies should be conducted to confirm this hypothesis.

On the other side, the well-known light competition model predicts that the increase of phytoplankton population in column will absorb more light and thus make the overall light condition become less sufficient for growth, and negatively affects the specific growth rate (Huisman and Weissing, 1994, 1995; Huisman, 1999). Accordingly, during the period of light-limited growth, the phytoplankton experience variable but prolonged light-limited condition. Our experiments suggested that under prolonged light-limited condition, the size and specific density of *S. obliquus* and *A. flos-aquae* would vary gradually, and leaded to a significant increase of sinking loss compare to the ones grew under light-sufficient condition. As shown in Table 1, specific density of both species was negatively related to light availability ($P<0.01$). For *S. obliquus*, lower specific density under higher light availability might be related to smaller size of cell and cell number within aggregation under higher light availability conditions (Fig.4). For *Anabaena flos-aqua*, the mechanism for lower specific density under higher light availability might involve increased cell turgor pressures at higher light intensities which resulted in collapse of gas vacuoles (Spencer and King, 1989). These results implied that the sinking loss rate was not always stable as expected, but should be consider as a variable response to the change of light availability. Therefore, to a certain extent, the light competition model should be revised considering the influence of light availability on the morphology and specific density of certain phytoplankton. However, further studies should be conducted to confirm this hypothesis.

5 CONCLUSION

1) With increasing amounts of light, the specific growth rates of these two species first increased gradually and then decreased sharply after peaking. The specific density was influenced by incubation time and light availability. However, the specific density of *A. flos-aquae* showed no significant differences among the three light incubation conditions at the end of the experiment.

2) Under light-limited condition, the median filament length of *A. flos-aquae* showed an increasing trend during the experiment. Under light-sufficient and light-inhibited conditions, the median filament length increased, and thereafter decreased to very short lengths. For *S. obliquus*, a phenomenon of aggregation was observed at the end of the exponential phase. The size of the aggregation decreased with the increase of light availability.

3) The sinking losses of *S. obliquus* and *A. flos-aquae* were not always stable but tended to decrease with higher light availability. Their sinking loss should be considered as a variable response to the change of light availability.

6 DATA AVAILABILITY STATEMENT

The authors declare that all data supporting the findings of this study are available within the article.

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