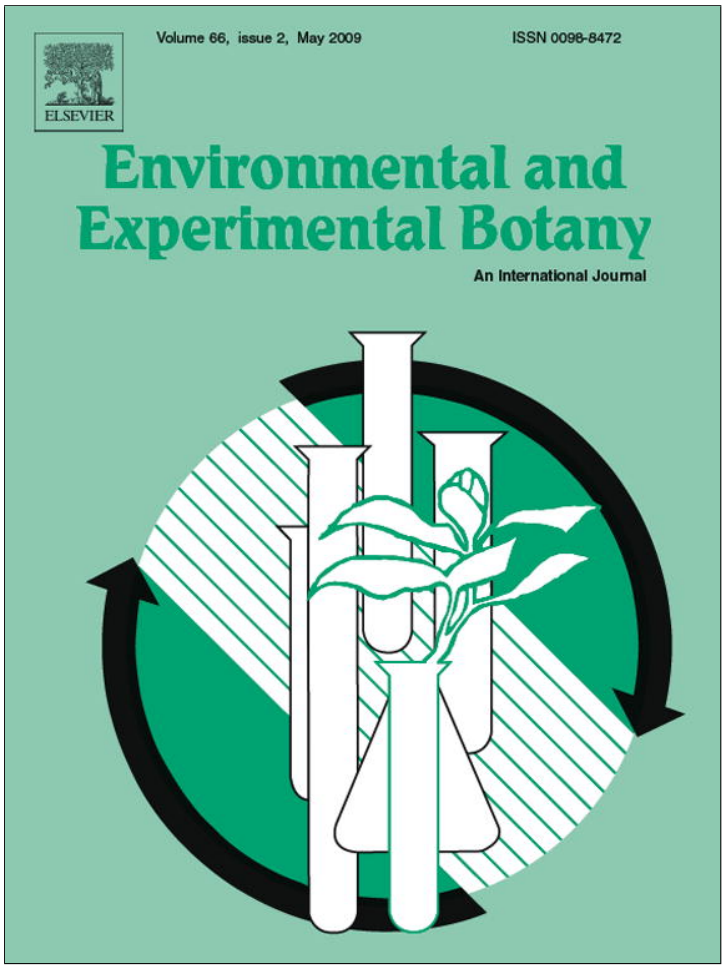

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Photosynthetically active and UV radiation act in an antagonistic way in regulating buoyancy of *Arthrospira* (*Spirulina*) *platensis* (cyanobacterium)

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ABSTRACT

Buoyancy provided by gas vesicles has been suggested to play an important role in regulating vertical distribution and nutrient acquisition in cyanobacteria. However, little is known about how changes in UV radiation (UVR, 280–400 nm) would affect the buoyancy. We have shown here that the floatation activity of the economically important cyanobacterium *Arthrospira platensis* (D-0083) decreased with increased photosynthetic rates associated with increased photosynthetically active radiation (PAR), but it decreased less in the presence of UVR, which resulted in inhibitory effects. When the cells were grown under isoenergetic levels of solar PAR or UVR alone, they migrated downward under PAR but maintained buoyant under UVR. The buoyancy regulation of *A. platensis* depended on the exposed levels of PAR as well as UVR, which affected photosynthesis and growth in an antagonistic way. The buoyancy of *A. platensis* in water columns is likely to be dependant on diurnal photosynthetic performance regulated by solar radiation, and can hardly be considered as an active strategy to gain more energy during sunrise/sunset or to escape from harmful irradiation during the noon period.

1. Introduction

Buoyancy in cyanobacteria is known to be provided by gas vesicles (Walsby, 1972, 1998). These cylindrical gas vesicles (hollow and gas-filled structure size from 340 to 750 nm in length and 60 to 110 nm in width) (Walsby, 1994), play an important role in regulating the buoyancy of cyanobacteria in various aquatic environments (Reynolds et al., 1987; Wallace and Hamilton, 1999; White et al., 2006), allowing the cells to receive sufficient light for photosynthesis, especially under light-limiting conditions, and to gain nutrients in ecosystems where a vertical separation between nutrients and light occurs (Walsby, 1994; Villareal and Carpenter, 2003). Vertical movement of cyanobacteria due to changes in buoyancy is accompanied with changes in solar visible (PAR, 400–700 nm) and UV radiation (UVR, 280–400 nm), the intensity of which becomes lower when the cells move downward since light is attenuated by water and the particles present in it at increasing depth (Häder et al., 2007).

PAR drives photosynthesis, but also results in photoinhibition at high levels. UVR has been known to inhibit photosynthesis (Sinha et al., 2001a; Gao and Ma, 2008), damage DNA (Sinha et al., 2001b) and proteins (Sass et al., 1997) and alter morphology (Wu et al., 2005; Li and Gao, 2008) of cyanobacteria. However, reduced levels of UVR might act as cues controlling vertical migration of cyanobacteria in microbial mats (Bebout and Garcia-Pichel, 1995; Kruschel and Castenholz, 1998) and enhance photosynthetic carbon fixation by phytoplankton (Gao et al., 2007). It is likely that changing levels of PAR as well as UVR affect the buoyancy of cyanobacteria in different ways, since they often act antagonistically on photosynthesis. However, this aspect remains unknown.

Arthrospira platensis, an important cyanobacterium, has been commercially produced for decades. Buoyancy is essential for *Arthrospira* spp. to position themselves in the water column and plays an important role in production harvest (Kim et al., 2005). We have previously shown that presence of solar UVR resulted in broken and/or compressed spirals and damaged DNA in *A. platensis*, and such impacts depended on temperature (Wu et al., 2005; Gao et al., 2008). Here, we have shown that changing levels of PAR and UVR affected the buoyancy of *A. platensis* in an antagonistic way.

2. Materials and methods

2.1. Organism

A. platensis (D-0083) was obtained from Hainan DIC Microalgae Co. Ltd., Hainan, China. A single healthy spiral was selected

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and all the trichomes were propagated from it. The cells were cultured in Zarrouk's medium (Zarrouk, 1966) at 30 °C, irradiated with 40 μmol m^{-2} s^{-1} of cool-white fluorescent light (12 h:12 h light:dark cycle) and aerated with ambient air (360 ppmv CO_2). Samples in the exponential growth phase were used in the following experiments.

2.2. Radiation treatments

Buoyant filaments (those which floated to the medium surface in 1 h when maintained still in a 10 cm depth of culture) were collected and transferred to fresh Zarrouk's medium in quartz tubes (Ø4 cm, 16 cm long) at a biomass density of 330 mg dry weight L^{-1} (optical density of 0.3 at 560 nm). The tubes (placed in a water bath for temperature control at 30 °C) were illuminated under a solar simulator (Sol 1200W, Dr. Hönle, Martinsried, Germany), and were exposed to three different radiation treatments: (1) PAB (PAR + UV-A + UV-B), tubes covered with Ultraphan 295 foil (Ultraphan, Digefra, Munich, Germany), transmitting UVR (295–400 nm) and PAR; (2) PA, tubes covered with Folex 320 filter (Montagefolie, no. 10155099, Folex, Dreieich, Germany) to allow the cells to receive UV-A (320–400 nm) and PAR; (3) P, tubes covered with Ultraphan 395 film (UV Opak, Digefra, Munich, Germany), transmitting PAR alone. UV-B (280–315 nm), UV-A (315–400 nm) and PAR (400–700 nm) irradiances were measured with a broadband filter radiometer (ELDONET, Real Time Computer Inc., Germany). The incident radiations of PAR, UV-A and UV-B were 173.9 (800 μmol m^{-2} s^{-1}), 40.5 and 1.3 W m^{-2}, respectively. Since there was a 5 nm difference between the measured and exposed irradiance for UV-A, the cells received about 2% less than the measured amount of UV-A. Transmission of the cut-off foils has been published elsewhere (Korbee-peinado et al., 2004) and these foils reflected 4% of PAR under water. Considering the reflection and transmission of the cut-off foils, cells in the quartz tubes received 150.2 (700 μmol m^{-2} s^{-1}) for PAR, 36.5 for UV-A and 1.2 W m^{-2} for UV-B, respectively. The biologically weighted UV-B irradiance was 0.12 W m^{-2} (normalized at 300 nm) (Setlow, 1974). Triplicate samples were taken from each light treatment.

To compare the filaments' buoyancy at isoenergetic levels of PAR and UVR, the cells were grown at 0.94 MJ m^{-2} of solar PAR or UVR from 8:00 to 16:00 (16 September 2006). UVR alone was obtained under the UG11 filter (which cut-off 100% PAR and transmitted 53.7% of UV-A and 63.8% of UV-B under the solar radiation) sealed in a lightproof cassette (18 cm × 10 cm × 5 cm); PAR was maintained to the same energy level as UVR using neutral filters and Ultraphan film 395 (UV Opak, Digefra, Munich, Germany). The intensities of UVR and PAR were estimated according to the measured solar radiation and the transmission of UG11 filter as follows: $UVR_{rec} = UVA \times 53.7\% + UVB \times 63.8\%$ and $PAR_{rec} = PAR \times T_1 \times T_2$, where UVR_{rec} and PAR_{rec} represented the irradiances which the cells actually received; T_1 and T_2, the transmissions of Ultraphan film 395 and neutral filters, respectively. The culture tubes were placed within the cassettes, which were placed in a water bath for temperature control at 30 ± 1 °C. Floatation activity was measured at the end of incubation. At least triplicate samples were measured for each treatment.

2.3. Measurement of photosynthesis

The filaments in their exponential phase, precultured under indoor conditions, were used to measure the photosynthetic rate. Photosynthetic evolution of O_2 was monitored with a Clark-type oxygen electrode (YSI Model 5300, Ohio, USA). Various levels of PAR were obtained by adjusting the distance between a halogen lamp and the reaction chamber. The maximal net photosynthetic rates obtained under halogen or Xenon lamps were identical under PAR. Triplicate samples were measured for photosynthesis and the time interval for each measurement was about 5 min.

2.4. Evaluation of floatation activity

To assess buoyancy, 6 mL of each of the cultures under different radiation treatments were sampled at the end of incubation and vigorously mixed to obtain homogenous distribution of the spirals in a transparent tube of 8 cm high (Ø1.3 cm), which was thereafter left under indoor conditions (30 °C, 10 μmol m^{-2} s^{-1}) for 1 h. The cell densities (OD_{560nm}) in the upper (D_U) and lower parts (D_L) of the water column (divided at the middle) were determined and the floatation activity (FA) was estimated as follows: $FA = 100\% \times D_U/(D_U + D_L)$. The filaments that floated to the surface or sank to the bottom were respectively defined as positively or negatively buoyant trichomes. Although such a partition was arbitrary since the floating or sinking velocity of different individual filaments can be time-dependent, a period of 1 h after mixing proved to be long enough to reflect the changes in buoyancy.

2.5. Temperature control

During culture, the tubes were placed in a water bath, the temperature of which was controlled with a circulating refrigerator (Eyela, CAP-3000, Tokyorikakikai Co. Ltd., Tokyo, Japan). To further confirm the effect of photosynthesis on the buoyancy of the filaments, the light-saturated photosynthesis and the floatation activity were measured at 15, 20, 25 and 30 °C.

2.6. Statistical analysis

Data were analyzed using one-way ANOVA followed by a multiple comparison using the Tukey test. A confidence level of 95% was used in all analyses.

3. Results

3.1. Relationship of floatation activity with photosynthesis

The floatation activity decreased while net photosynthesis (Pn) increased with increasing intensities of PAR during the incubation periods for either 1 or 10 h (Fig. 1A and B), but the floatation activity decreased more ($p < 0.01$) in 10 h with increasing levels of PAR than in the 1 h incubation. It declined to a minimum when the Pn increased to a maximum at PAR higher than 600 μmol m^{-2} s^{-1}. The initial slope as a function of light, for Pn, was about 1.1, while for the floatation activity, it was about −0.9 for 10 h incubation. At the highest PAR level of about 800 μmol m^{-2} s^{-1}, 10 h period of incubation reduced the floatation activity by 86%, while 1 h incubation by about 50%. The required levels of PAR for the floatation activity to decrease by 50% were 450 and 170 μmol m^{-2} s^{-1} for 1 and 10 h incubations, respectively.

The floatation activity also decreased with increasing net photosynthesis when water temperature was raised from 15 to 30 °C (Fig. 2A and B). However, such a reduction was much ($p < 0.01$) less compared with that as a function of light. The rate of Pn increased about twice, while the floatation activity decreased by 56% in 1 h and by 86% in 10 h. Compared with that in 1 h incubation, floatation activity was much lower in 10 h incubation. The ratio of floatation activity of 1–10 h incubation was 1.9 at 15 °C and 4.2 at 30 °C, respectively. The temperature quotient of floatation activity (decreased floatation activity by 10 °C increase in

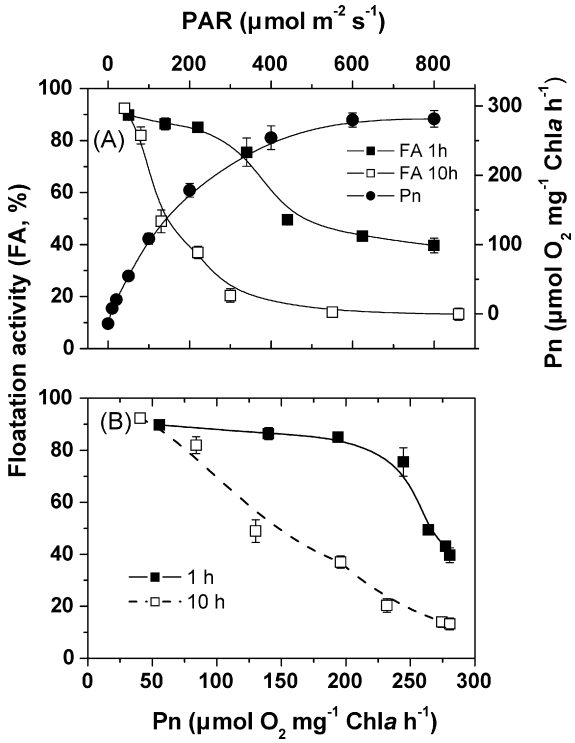

Fig. 1. Floatation activity (FA) and photosynthetic O_2 evolution rate as a function of PAR (A) and the change of FA with increased photosynthesis in *A. platensis* (D-0083) at 30 °C (B). The FA was determined after incubation at each PAR level for 1 or 10 h, respectively. Mean ± S.D. (n = 3).

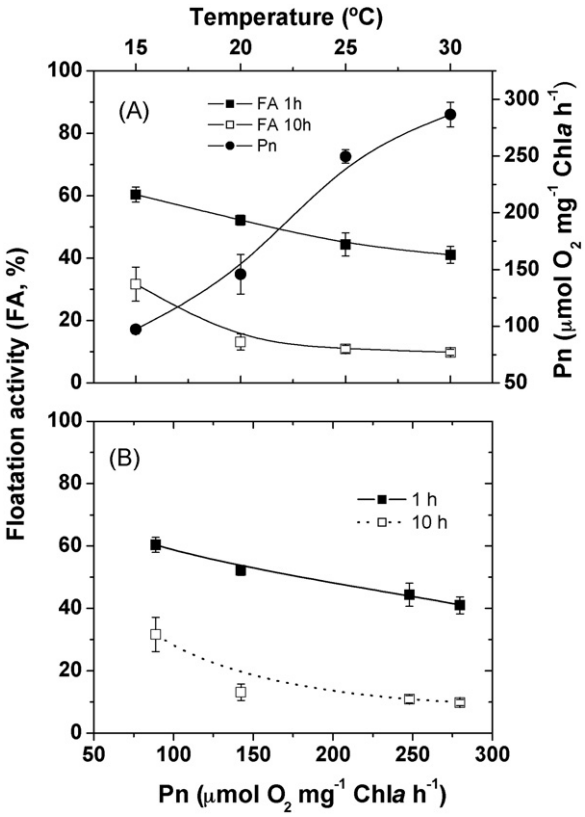

Fig. 2. Floatation activity and photosynthetic O_2 evolution rate as a function of temperature (A) and the change of FA with increased photosynthesis in *A. platensis* (D-0083) under high PAR (800 μmol m^{-2} s^{-1}) (B). The floatation activity at each level of temperature was determined after incubation for 1 and 10 h at a PAR level of 800 μmol m^{-2} s^{-1}. Mean ± S.D. (n = 3).

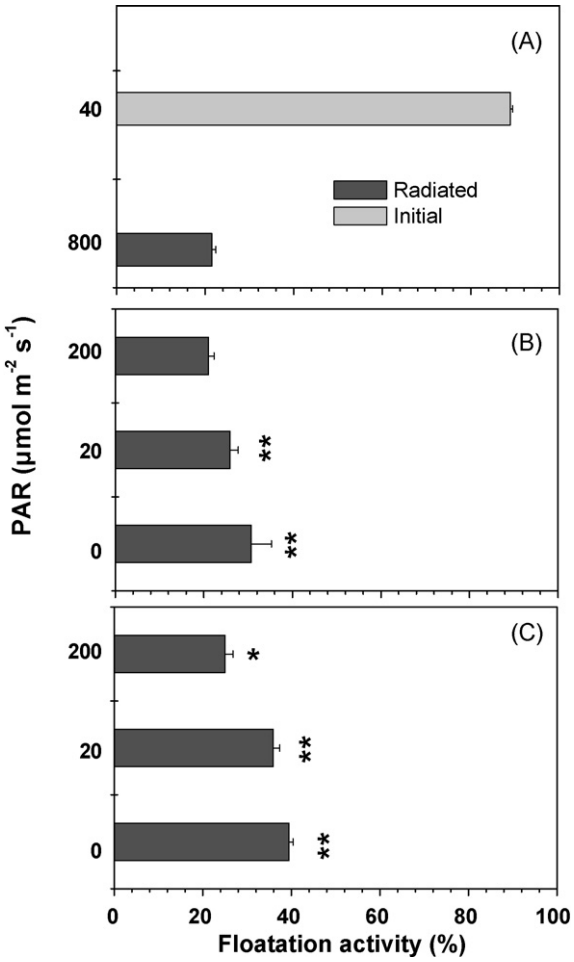

Fig. 3. Changes in floatation activity of *A. platensis* (D-0083) exposed to high PAR (800 μmol m^{-2} s^{-1}) for 10 h (A), and then shifted to reduced PAR levels (i.e. 0, 20 and 200 μmol m^{-2} s^{-1}) for 12 h (B) or 24 h (C). Mean ± S.D. (n = 3). The symbols "*" and "**" indicate significant differences at $p < 0.05$ and $p < 0.01$.

temperature, Q10) was 0.32 and 0.69 for 1 and 10 h incubations, respectively.

3.2. Restoration of the floatation activity

The floatation activity increased after the cells (exposed to 800 μmol m^{-2} s^{-1} for 10 h) were transferred to the lower light levels or darkness (Fig. 3B and C). It increased by 5.5 and 10.8% respectively when transferred to 20 μmol m^{-2} s^{-1} PAR or darkness for 12 h (Fig. 3B), but no ($p > 0.05$) increase was observed at 200 μmol m^{-2} s^{-1}. However, 24 h later (Fig. 3C), the cells' floatation activity increased by 4.4, 16.7 and 20.6% at 200, 20 and 0 μmol m^{-2} s^{-1} PAR, respectively.

3.3. Flotation activity and growth under P, PA and PAB treatments

In contrast to the floatation activity under a PAR level of 700 μmol m^{-2} s^{-1}, addition of UV-A (PA treatment) at 36.5 W m^{-2} slowed down the loss of buoyancy, and presence of both UV-A and UV-B (PAB treatment) further ($p < 0.01$) retarded it (Fig. 4A). While the PAR alone treatment (P) steadily decreased the floatation activity, presence of UV-A and UV-B prevented this decrease by 3.5 and 6.0% in 10 h, respectively. Presence of UV-A and UV-B together (PAB treatment) or UV-A alone (PA) reduced the cell concentration (OD_{560nm}) by 9.1 and 8.0% compared with PAR alone (P) after 10 h incubation (Fig. 4B).

3.4. Floatation activity under isoenergetic PAR and UVR

To further confirm the effect of UVR on the buoyancy of *A. platensis*, the filaments were exposed to an isoenergetic dose of UVR or PAR at 0.94 MJ m^{-2} on a sunny day (from 8:00 to 18:00, 16 September 2006). Most of the filaments, irradiated with PAR, lost buoyancy and sank to the tube bottom (Fig. 5A), while those exposed to UVR alone held their buoyancy and stayed at the surface (Fig. 5B).

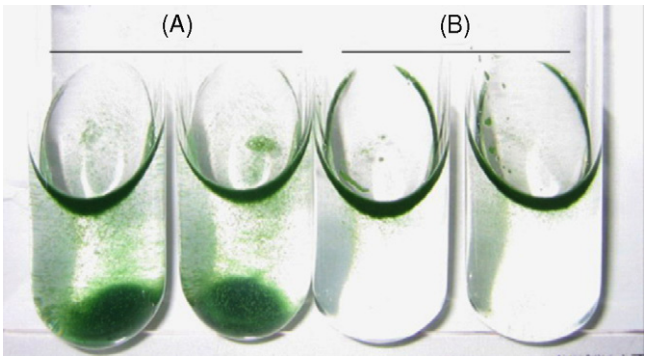

Fig. 5. Comparative floatation activity of *A. platensis* (D-0083) filaments when exposed to the isoenergetic level (0.94 MJ m^{-2}) of solar PAR (A) or UVR (B) from 8:00 to 18:00 on 16 September 2006.

4. Discussion

The floatation activity of *A. platensis* (D-0083) decreased with increasing photosynthetic rates associated with increasing PAR or temperature, but it decreased less in the presence of UVR, which resulted in inhibitory effects. Buoyancy regulation depended on the exposure levels of PAR as well as UVR, which affected photosynthesis and growth in an antagonistic way. Cyanobacteria can regulate buoyancy by collapse or formation of gas vesicles or changes in biochemical components (Oliver and Walsby, 1988). Lost buoyancy of *A. platensis* was restored when the cells were transferred to darkness or low light conditions (Fig. 3B and C). It appeared that respiration enhanced the buoyancy of *A. platensis*. Accumulation of carbohydrates by photosynthesis and consumption of them during respiration must have counteracted each other to regulate the buoyancy. Decreased floatation activity in some cyanobacterial species, such as *Trichodesmium* spp., is linked to accumulation of carbohydrates (Villareal and Carpenter, 2003; White et al., 2006). On the other hand, dilution of the vacuole due to cell division leads to loss of buoyancy (Walsby et al., 1983). In the present study, growth was higher under PAR and was inhibited by the presence of UVR, which can also result in the antagonistic effects of PAR and UVR on buoyancy. However, since the inhibitory effect on photosynthesis of UVR happened at a faster pace than growth, light-mediated carbohydrate loading probably played a larger role in regulation.

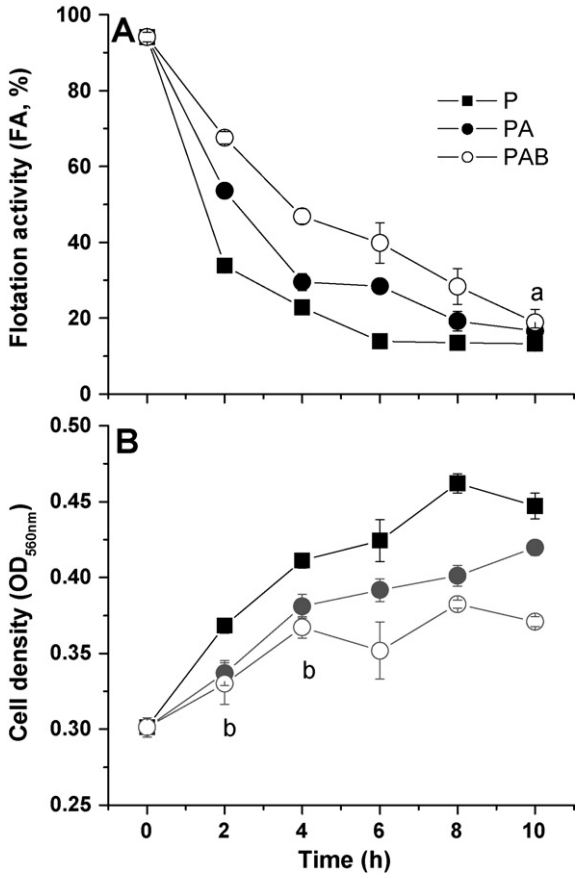

Fig. 4. Floatation activity (A) and biomass density (B) of *A. platensis* (D-0083) grown under P, PA and PAB at 30 °C. P, PA and PAB are the abbreviations for PAR, PAR + UV-A, and PAR + UV-A + UV-B. Mean ± S.D. ($n = 3$). The letters "a" or "b" denote insignificant difference between P and PA treatments or PA and PAB treatments at $p = 0.05$ level.

Less efficient photosynthesis under resource-limited or photoinhibited conditions can promote buoyancy due to the lower amounts of polysaccharides accumulated. On the other hand, the amount of gas vacuoles increases with increasing levels of PAR (Van Eykelenburg, 1979) or at low levels of PAR (50 μmol m^{-2} s^{-1}) in the presence of UV-B (Rajagopal et al., 2005). It appears that the accumulation of carbohydrate played a major role in regulating the buoyancy in *A. platensis*, since the carbohydrate contents increased significantly with increased photosynthetic rate under high levels of PAR (data unpublished).

Filamentous and unicellular cyanobacteria are shown to move downwards in response to high levels of PAR (Ramsing et al., 1997; Wallace and Hamilton, 1999; Wallace et al., 2000; Villareal and Carpenter, 2003) as well as UVR (Bebout and Garcia-Pichel, 1995; Kruschel and Castenholz, 1998), which has been thought to be effective strategy to avoid harmful radiation (Bebout and Garcia-Pichel, 1995; Sinha et al., 2001a). However, our results showed that the presence of UVR slowed down the loss of buoyancy of *A. platensis* observed in the cultures exposed to PAR. Since UVR and PAR acted in an antagonistic way in regulating the floatation activity, and lower levels of UVR might result in enhanced photosynthetic carbon fixation (Gao et al., 2007), there must be an irradiance and/or dose dependency of floatation activity on UVR. UVR levels equal to or higher than that in the present study can stimulate floatation by negatively affecting photosynthesis, while reduced levels of UVR may not affect the floatation when its damage to the photosynthetic apparatus is negligible.

Floatation activity of *A. platensis* (D-0083) decreased with increasing levels of PAR or temperature which stimulate photosynthesis. However, it was reduced to a much lower extent as a function of increasing temperature compared with that of raised PAR levels even within the same range of photosynthetic rates. Such a disproportional change appeared to be caused by differential accumulations of carbohydrate (data not shown). Transformation of carbohydrate to lighter molecules, such as proteins, might be performed at a faster rate at increasing temperature levels in contrast to the carboxylation rate (Visser et al., 1995).

Solar radiation can regulate the buoyancy and vertical migration of *A. platensis* in nature or commercial ponds according to its diurnal photosynthetic performance. The buoyancy of *A. platensis* peaked near sunrise, decreased with increasing solar radiation towards noon and increased with declining sunlight towards sunset. Such a migration pattern could enable the cells to receive more

light during twilight periods and to lessen photoinhibition during the noon period. However, this diurnal vertical movement in *A. platensis* may be passively driven by photosynthesis rather than by an active strategy to escape from harmful irradiations.

Acknowledgements

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