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Motility and photosynthetic responses of the green microalga *Tetraselmis subcordiformis* to visible and UV light levels

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Abstract To test the effects of photosynthetic active radiation (PAR, 400–700 nm) and ultraviolet radiation (UVR, 280–400 nm) on phototaxis and photosynthesis of free swimming microalgae, experiments were performed with *Tetraselmis subcordiformis* (Wille) Butcher under a solar simulator. In particular, we evaluated the effects of different PAR levels and radiation regimes (i.e., PAR only and PAR+UVR) on those two processes. We found that the cells preferred to move to a particular area (e.g., receiving 100 W m^{-2} PAR) with little photochemical suppression or inhibition of carbon fixation. Adding UV-A to high PAR decreased its swimming capacity and photosynthetic capability, and further adding UV-B led to more inhibition. The suppression of the moving capability of *T. subcordiformis* was reversible but the cells exposed to PAR combined with UVR needed longer time intervals to recover their motility as compared with those irradiated only with PAR. Based on the above results, we postulate that in nature, the motile capability and photosynthesis of free swimming the green microalga might be impaired by enhanced solar UVR. On the other hand, the cells can reduce the damage caused by high irradiances (and even get the optimum light level for photosynthesis) by a behavioral swimming response.

Keywords Effective photochemical quantum yield · Migration · PAR · *Tetraselmis subcordiformis* · Photosynthesis · Phototaxis · UVR

Introduction

Phototactic flagellate algae orient their movement axis with respect to the direction of environmental light stimulus (Häder and Häder 1989; Tirlapur et al. 1993). In general, cells show positive phototaxis (i.e., swimming toward the light source) at moderate intensities, but at high ones they present a negative phototaxis (i.e., swimming away from the light source; Takahashi et al. 1992; Sgarbossa et al. 2002). These responses are important to keep cells under optimal conditions for both growth and survival. Special attention has been put on questions such as how these small organisms are capable of precisely detecting the direction of the light (Takahashi et al. 1992). In this sense, the phototaxis of *Chlamydomonas* sp., used as model organism, has been widely studied (Ebrey 2002; Sineshchekov et al. 2002; Berthold et al. 2008; Jékely 2009). The light signal, sensed by the photoreceptor rhodopsin (Kröger and Hegemann 1994; Berthold et al. 2008) elicits a sensory transduction chain, which eventually causes a flagellar reorientation, resulting in a controlled vectorial movement with respect to the light direction: towards or away from the light source

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and in some cases at a certain angle, diaphototaxis (Wemmer and Marshall 2004; Jékely 2009).

Solar radiation drives photosynthesis, but also harms the photosynthetic machinery (Aro et al. 1993). In particular, solar ultraviolet radiation (UVR, 280–400 nm) has negative effects on aquatic primary producers (Beardall and Stojkovic 2006; Häder et al. 2007). UVR inhibits growth and photosynthesis (Heraud and Beardall 2000; Gao et al. 2007), damages proteins and the DNA molecule (Karentz et al. 1991; Bouchard et al. 2005; Gao et al. 2008), harms cell membrane and other pigments complexes by inducing reactive oxygen species (Kramer et al. 1991; Ma and Gao 2010), and even suppresses nutrient uptakes by inhibiting the protein channels (Murphy 1983; Behrenfeld et al. 1995; Sobrino et al. 2004). Also, the motility and orientation of some organisms with respect to different stimuli, such as light and gravity, may be impaired by exposure to UVR (Richter et al. 2007). This is ecologically important, as organisms may become incapable of migration in the water column to find the best conditions for growth and survival (Häder and Worrest 1991). These kinds of damage have been studied in several microorganisms, and the results stressed the variable sensitivity to UVR and the molecular mechanisms involved in this process (Häder and Brodhun 1991; Ekelund 1994).

Tetraselmis subcordiformis, a unicellular free swimming oceanic green microalga, belonging to the family Chlamydomonadaceae (Chlorophyta), is an important food complement for zooplankton, fish, shrimp, and shellfish (Xie et al. 2001; Li et al. 2008). It has been found that its growth rate, chlorophyll *a* and carotenoid contents decreased but the superoxide anion radicals and malodiadehyde (MDA) contents increased when exposed to UV-B radiation (280–315 nm; Yu et al. 2004; Zhang et al. 2005). In spite of the ecological and economic importance of this microalga, photosynthesis and phototaxis under different radiation regimes had received little attention (Halldal 1961; Yu et al. 2004). As it was previously reported that the buoyancy regulation of a non-motile cyanobacterium under solar radiation was tightly linked to photosynthesis (Ma and Gao 2009), we hypothesized that behavioral swimming responses of *T. subcordiformis* help the cells to reduce UVR-induced damages and to avoid photoinhibition under high levels of PAR and UVR.

Materials and methods

Tetraselmis subcordiformis (Wille) Butcher was obtained from the State Key Laboratory of Marine Environmental Science (Xiamen University). Organisms were grown in f/2 medium (Guillard and Ryther 1962) at 20 °C and illuminated with cool-white fluorescent light at a PAR irradiance of 60 μmol photons m^{-2} s^{-1} (12L:12D). The cultures were routinely shaken (two to three times per day) and cells were harvested for experimentation (see below) at the end of the dark period and during the exponential growth phase.

Light sources and illumination measurements

All the experiments were conducted in the laboratory using an artificial radiation source provided by a solar simulator (Sol 1200 W, Dr. Hönle, Martinsried, Germany) under irradiances of 250.2, 55.3 and 2.4 W m^{-2} for PAR, UV-A and UV-B, respectively, so that the ratio PAR/UV-A/UV-B was 104/23/1. It should be noted though that the solar simulator spectrum output had slightly higher intensities for UV-A and UV-B as compared to that of solar radiation in tropical China during mid spring (Villafañe et al. 2007). The irradiances were measured using a broadband ELDONET filter radiometer (Real Time Computer, Germany) that has three channels for PAR (400–700 nm), UV-A (315–400 nm) and UV-B (280–315 nm), respectively. This instrument is routinely calibrated yearly using sun calibration factors.

Evaluation of movement and cell concentration measurements

The motility responses of *T. subcordiformis* were estimated by means of the cell concentration changes caused when cells were exposed to the different radiation treatments: The decrease in cells concentration under a particular light treatment was an indication that the organism swam away (i.e., avoidance strategy) whereas the increase indicated aggregation under the irradiance/treatment imposed to the cells (i.e., accumulation of cells).

To calculate cell concentrations, an aliquot of 2 mL were fixed with buffered formalin (0.4 % final concentration of formaldehyde) and counted using a Beckman Coulter Z2™ Counter (Beckman Coulter, UK).

Measurement of chlorophyll fluorescence

The effective photochemical quantum yield (F_v'/F_m') of cells was measured at the beginning and at the end of each incubation period; the optimal quantum yield (F_v/F_m) was determined when the cells were kept in darkness for 15 min (Wei and Berry 1987; Genty et al. 1989). Fluorescence measurements were performed with a xenon-pulse amplitude modulated fluorometer (XE-PAM; Walz, Germany), with the actinic light set to 100 μmol photons m^{-2} $s^{-1}$and the saturating pulse of ~5,000 μmol photons m^{-2} s^{-1} lasting for 0.8 s.

Experiments to test behavior response and photosynthesis under increasing PAR levels

To assess the potential photomovement of *T. subcordiformis* under different PAR levels, rectangular aquaria (50×6× 10 cm, length × wide × depth) made of black plastic were used. Each aquarium was equally divided into six chambers by symmetrical grooves on the sides and bottom, into which plastic plates could be slid in perpendicularly to isolate each chamber from each other at any time. The length of each chamber was ~8 cm and the depth of water column in each one was ~8 cm. Each aquarium lay horizontally, so that the maximum possible depth was 10 cm; the aquarium was placed at a distance of 80 cm from the solar simulator. Cultures of *T. subcordiformis* with a concentration of ~10^5 cells mL^{-1} were transferred to the aquarium (without the sliding plates) and gently shaken to allow the individuals to be homogeneously distributed before exposure. Five different treatments (i.e., different PAR levels) were used in this experiment: 50, 100, 150, 200, and 250 W m^{-2} (1,150 μmol photons m^{-2} s^{-1}) which were obtained by putting layers of wire net filters (which reduce intensity of all wavelengths proportionally) on top of each chamber a dark treatment (chamber covered with an opaque plastic) was also done. During the exposure, the cells were allowed to move freely around the irradiated areas. The aquaria were maintained in a big water tank and the temperature was kept at 20 °C with a circulating cooler. Each exposure lasted 30 min and, after that period, the plates were perpendicularly inserted to isolate the chambers receiving the different PAR levels. The water was gently mixed to homogenize the cells in each particular chamber, and the effective photochemical quantum yield was measured (as above). A sub-sample of each radiation treatment was obtained from each chamber and cells counted as described before. Three experiments with three replicates each were done, and the data are reported as means and standard deviation for each irradiance level.

Experiments to test behavior response and photosynthetic activity under different radiation treatments

To investigate whether *T. subcordiformis* could avoid UVR-induced stress by means of a behavioral response, cells (concentration of ~10^5 cells mL^{-1}) were placed into the aquaria (only four adjacent chambers were used in this experiment, the other two chambers were separated with the plates). The treatments were obtained by putting different materials/cut-off filters on the top of the chambers as follows: (1) Darkness, control, covered with a black plastic; (2) PAR, (P) treatment, chamber covered with a GG395 Schott filter (Mainz, Germany), cells receiving irradiances > 395 nm; (3) PAR+UV-A, (PA) treatment, chamber covered with a WG320 Schott filter, cells receiving irradiances > 320 nm; (4) PAR+UV-A+UV-B (PAB) treatment, chamber covered with a WG280 Schott filter, cells receiving irradiances > 280 nm. The aquarium was maintained in a water bath for temperature control at 20 °C and the cells of *T. subcordiformis* were allowed to freely swim to their preferred irradiated areas under irradiances of PAR, UV-A and UV-B of 250.2 (1,150 μmol photons m^{-2} s^{-1}), 55.3 and 2.4 W m^{-2}, respectively. After exposures of 10, 20 and 30 min the plates were perpendicularly inserted to separate each chamber under the different radiation treatments. The cell concentration in each compartment was calculated at the above mentioned intervals and the effective photochemical quantum yield of the cells after 30 min exposure was measured (as described above). Three experiments with three replicates each were done, so the data are reported as means and standard deviation for each combination of time interval/radiation treatment.

Experiments to test the effects of different radiation treatments on swimming capability

To test the effects of different radiation wavebands on the behavior responses of *T. subcordiformis*, the cells were put in aquaria (25×6×10 cm, length × wide × depth, separated in three chambers as above) and exposed to three radiation treatments: P, PA, and PAB (as above). Cells were exposed for 30 min to irradiances of PAR, UV-A and UV-B of 250.2 (1,150 μmol photons m^{-2} s^{-1}), 55.3 and 2.4 W m^{-2}, respectively. A dark treatment was used as control. After exposure, the solar simulator was turned off, the filters in each aquarium were removed and cells were gently mixed. Then, immediately, 80 % (20 cm in length) of each aquarium was covered with a light-proof dark plastic while the open end (5 cm) was illuminated with PAR of 100 μmol photons m^{-2} s^{-1}. The cell concentrations at the "illuminated end" and on the opposite side—"dark end" were determined every 20 min (for a total time of 120 min) by withdrawing 2 mL of sample, fixed and counted as above. The changes in cell concentration of those pre-cultured in darkness for 30 minutes were used as control. In addition, sub samples (2 mL) were taken to measure the effective photochemical quantum yield every 20 min.

Determination of photosynthesis at six wavebands

To determine photosynthesis at different wavebands, six different quality radiation treatments were done by using Schott filters that cut-off radiation at 280, 295, 305, 320, 350 and 395 nm. The transmission spectra of these filters have been published elsewhere (Villafañe et al. 2003). The irradiances of PAR, UV-A and UV-B were 200 (920 μmol photons m^{-2} s^{-1}), 44.2 and 1.92 Wm^{-2}, respectively. The

cells were dispensed into 30 mL quartz tubes and inoculated with 10 μCi (0.37 MBq) $NaH^{14}CO_3$ (ICN Radiochemicals, USA) and incubated for 2 h beneath the surface (2 cm) in a water bath with circulating water for temperature control at 20 °C. After the incubations, cells were filtered onto a Whatman GF/F filter (25 mm), which were then placed in 20 mL scintillation vials, exposed to HCl fumes overnight and dried in oven at 45 °C. The activity of the fixed radiocarbon was determined with a scintillation counter (LS 6500 Multi-Purpose Scintillation Counter, Beckman Coulter, USA) after filters were digested in the cocktail (Wallac Optiphase HiSafe 3, Perkin Elmer Life and Analytical Sciences, USA). The photosynthetic carbon fixation was estimated from the CPM counts (Holm-Hansen and Helbling 1995).

The effectiveness a quantum to decrease photosynthesis in the six waveband intervals were obtained by using the biological weighting function model (Neale and Kieber 2000). The mean energy between each filter interval was calculated according to the transmission of the Schott filters and the spectrum of the solar simulator. An exponential decay function was used to fit the data in each experiment, and the exponent of the function was expressed as a third-degree polynomial function ($Y=aX^3+bX^2+cX+d$; a, b, c, and d are the adjust parameters), the best fit was obtained by iteration.

Statistical analysis

One-way ANOVA, non-parametric analysis (Kruskal–Wallis analysis) and Kendall tests were used to establish differences among treatments, with a significant level set at 5 % ($p=0.05$). An ANCOVA multiple regression analysis was used to determine the main factors controlling the photosynthesis inhibition and behavior responses.

Results

Effects of increasing radiation levels on behavior response and photosynthesis

Results from the experiment devoted to determine behavior response and photosynthesis under increasing levels of PAR (Fig. 1) indicated that the preferred area i.e., that of higher concentration of cells was the one that received 100 W m^{-2} (Fig. 1a). Comparing the cell concentrations with that at the beginning of the experiment, it was seen that it decreased 10.5 % in the area under 50 W m^{-2} but increased 15.8 % and 2.3 % in areas receiving 100 and 150 W m^{-2}, respectively. The concentration of cells in areas under high irradiances (i.e., 200 and 250 W m^{-2}), as well as in the dark treatment, were similar to that at the beginning of the experiment. In

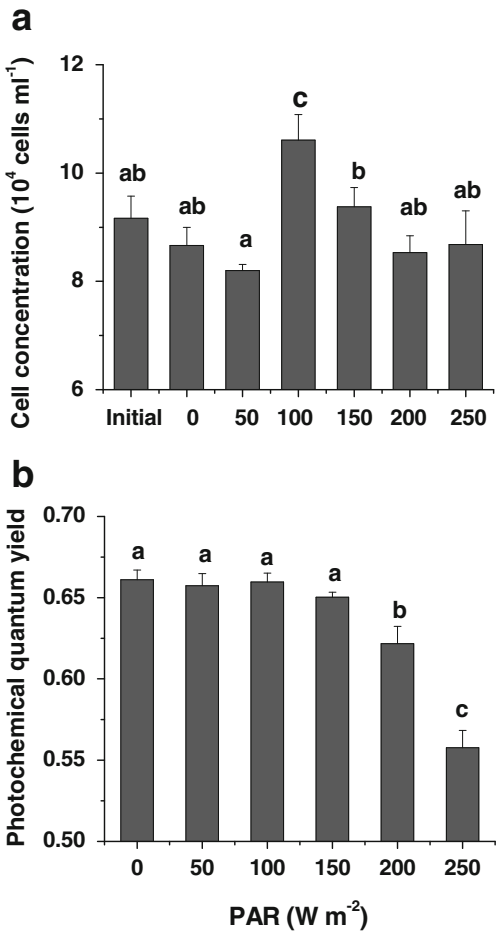

Fig. 1 Effects of increasing PAR levels on *Tetraselmis subcordiformis* after 30 min of exposure at 20 °C. **a** Mean cell concentration (in 10^4 cells mL^{-1}) and, **b** photochemical effective quantum yield (F_v'/F_m'). Each sample (triplicates) was measured two times and the mean and standard deviation were calculated ($n=6$). The different *letters* indicate significant differences between treatments at $p<0.05$ level

relation to the photosynthetic responses, it was seen that the effective photochemical quantum yield (Fig. 1b) was not suppressed by PAR levels <150 W m^{-2} but it was significantly inhibited i.e., by 6 and 15.6 %, respectively, when cells were exposed for 30 min to PAR levels of 200 and 250 W m^{-2}.

Effects of different radiation treatments on behavior response and photosynthesis

After exposure to different radiation treatments for 10 min, there were no significant ($p>0.05$) differences in cell concentrations under darkness and under the P but they were significantly lower ($p<0.05$) than under the PA treatment; samples under the PAB had an intermediate cell concentration as those under the P, darkness and PA treatments (Fig. 2a). When the exposure lasted 20 min, the cell densities under the P, PA, and PAB treatments were similar

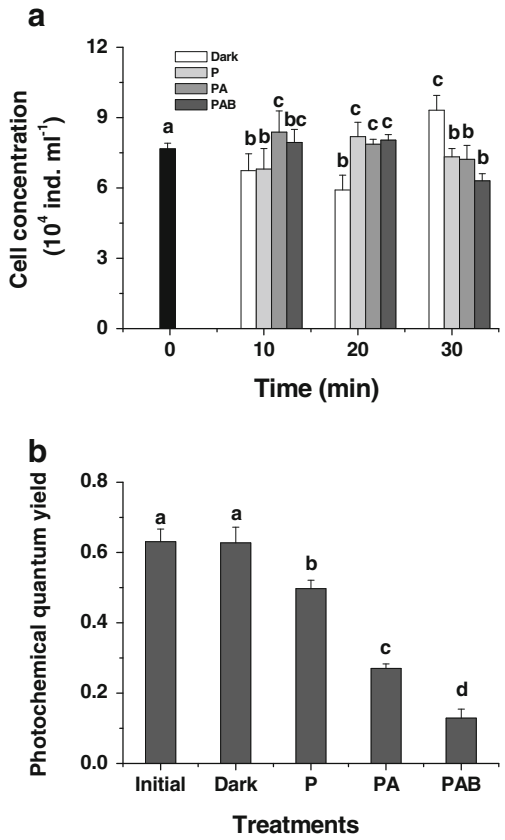

Fig. 2 Effects of different radiation regimes on *Tetraselmis subcordiformis*: **a** Mean cell concentration (in 10^4 cells mL^{-1}) after 10, 20 and 30 min of exposure at 20 °C and, **b** photochemical effective quantum yield (F_v'/F_m') after 30 min of exposure at 20 °C. The irradiance levels were 250.2, 55.3, and 2.4 W m^{-2} for PAR, UV-A, and UV-B, respectively. Each sample (triplicates) was measured two times and thus the mean and standard deviation were calculated (n=6). The different *letters* indicate significant differences between treatments at p<0.05 level

among them but significantly higher (p<0.05) than that in darkness. However, when the exposure time lasted 30 min, the cell concentration in darkness was significantly higher (p<0.05) than those under the other three treatments. It should be noted that the cell concentrations in darkness after 10- and 20-min exposures were significantly lower (p<0.05) than that at time zero, however, it was much higher (p<0.01) when the incubations lasted 30 min (Fig. 2a).

The photosynthetic responses of *T. subcordiformis* during these experiments are shown in Fig. 2b. The effective photochemical quantum yield after 30 min of exposure was significantly inhibited by PAR, and adding UV-A and UV-B to PAR led to further inhibition (Fig. 2b). As compared with the cells kept in darkness, the effective photochemical quantum yield of *T. subcordiformis* cells under the P, PA, and PAB treatments decreased about 21, 57, and 80 %, respectively.

Effects of different radiation treatments on swimming capability and photosynthesis

Pre-exposure to diverse treatments i.e., P, PA, PAB, and dark, clearly demonstrated the alteration of the motile capability of *T. subcordiformis*, as seen through the evaluation of cell concentration changes in the "light end" (Fig. 3a) and "dark end" (Fig. 3b) of the containers. The cell concentration of *T. subcordiformis* pre-cultured in darkness and then stimulated with 100 μmol photons m^{-2} s^{-1} PAR quickly increased at the "light end". However, those pre-cultured under the P, PA, and PAB treatments showed a delayed increase in cell concentrations (Fig. 3a) but then increased

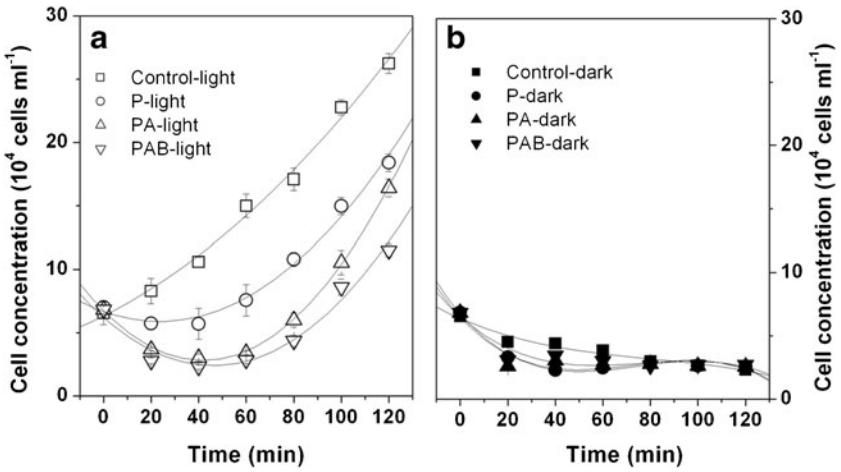

Fig. 3 Changes in cell concentration of *Tetraselmis subcordiformis* at the "light end" (**a**) and at the "dark end" (**b**) when using 100 μmol photons m^{-2} s^{-1} PAR as a stimulus to swim to the "dark end" or to the "light end" in cells pre-exposed to PAR (P), PAR+UV-A (PA) and PAR+UV-A+B (PAB) or kept in darkness (Control) for 30 min at 20 °C (full explanation in the text). The irradiance levels for PAR, UV-A and UV-B during the pre-exposure were 250.2, 55.3, and 2.4 W m^{-2}, respectively. Each sample (triplicates) was measured two times and thus the mean and standard deviation were calculated (n=6). Mean±standard deviation (n=3). The different *letters* indicate significant differences between treatments at p<0.05 level

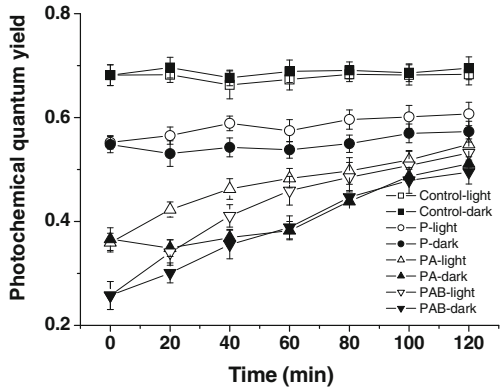

Fig. 4 Changes in the photochemical effective quantum yield (F_v'/F_m') of *Tetraselmis subcordiformis* at the "light end" (clear symbols) and at the "dark end" (*dark symbols*) after the cells had been pre-exposed to PAR (P), PAR+UV-A (PA) and PAR+UV-A+B (PAB) or kept in darkness (control) for 30 min at 20 °C. The irradiance levels for PAR, UV-A and UV-B during the pre-exposure were 250.2, 55.3, and 2.4 W m^{-2}, respectively. Each sample (triplicates) was measured two times and the mean and standard deviation were calculated (n=6)

after 60–80 min of PAR exposure. At the "dark end" (Fig. 3b), the cell concentrations decreased with time under all treatments and no significant (p>0.05) differences could be found among them.

The photosynthetic responses of cells pre-cultured under the different radiation treatments are shown in Fig. 4. The effective photochemical quantum yield of *T. subcordiformis* pre-cultured under darkness did not change either at "the light end" or at the "dark end" and presented the highest values i.e., ~0.7. However, in the cells pre-cultured under the P, PA, and PAB treatments, the effective photochemical quantum yield was significantly reduced at the beginning of measurements, with the decrease being most evident under PAB, but it recovered with time at both ends. Within a particular treatment, the effective photochemical quantum yield was significantly higher (p<0.05) in the "light" than in the "dark end" (Fig. 4).

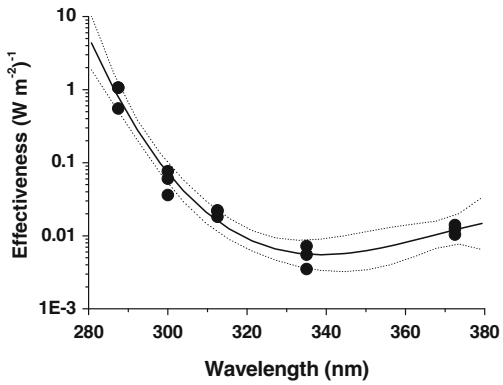

Fig. 5 Quantum effectiveness to inhibit carbon fixation of *Tetraselmis subcordiformis* incubated at 20 °C as a function of wavebands (W m^{-2})$^{-1}$. Mean±standard deviation (n>3)

Determination of photosynthesis at six wavebands

The average quantum effectiveness to decrease photosynthesis of *T. subcordiformis* as a function of wavelength is shown in Fig. 5. It is clear that different UVR wavebands had differential impacts on the carbon fixation, with higher sensitivity of the cells at shorter wavelengths of UV-B, but lower ones in the UV-A range. In fact, the effectiveness in the range 340–380 nm were ~0.01 (W m^{-2})$^{-1}$ whereas at 300 nm it was about 100 times higher.

Discussion

In this study, we demonstrated that behavioral response and photosynthesis of *T. subcordiformis* are clearly conditioned by the quality and quantity of radiation imposed during the experiments. We further determined that these two processes are tightly coupled so that this organism had to balance the benefits of moving towards a light level, which do not significantly affect photosynthesis or growth. It is known that phototactic flagellate algae orient their movement axis with respect to the direction of the environmental light stimulus (Takahashi et al. 1992). Cells of *T. subcordiformis* swam to the area with moderate radiation levels (Fig. 1a) that did not induce significant photoinhibition, such as 100 and 150 Wm^{-2} PAR (Fig. 1b); lower radiation levels such as 50 Wm^{-2} PAR, instead, while not affecting photosynthesis, seemed to be unsuitable for this algae. Indeed, light seems to be the dominant factor influencing the spatial and temporal distribution, migration, depth regulation and succession of phytoplankton flagellates in freshwater ecosystems (Clegg et al. 2004). Nevertheless, the actual preferred levels show an important component of species-specificity, as seen in studies devoted to evaluate vertical migration within the water column (Richter et al. 2007). In our study, however, the motile capability of this organism may be weakened or even completely suppressed by the sudden environmental stimulus before they could move to a "safe" place. In fact, we showed that phototaxis of *T. subcordiformis* to light stimulus was very sensitive as changes in cell density could be detected even within 20 min and at a distance of 8 cm (Fig. 2a).

Phototactic responses are found in five out of the six major eukaryotic groups; both single-celled and multicellular eukaryotic phototactic organisms are polarized, swim in a spiral and use cilia for swimming and phototactic steering (Jékely 2009). Signaling can happen via direct light-triggered ion currents, adenylyl cyclases or trimeric G-proteins (Häder and Jori 2001), and signaling in all cases eventually modifies the beating activity of cilia/flagella. In the best studied green alga, *Chlamydomonas reinhardtii*, phototaxis is mediated by rhodopsin pigments (Foster et

al. 1984; Nagel et al. 2002, 2003) which act as light-gated cation channels and trigger depolarizing photocurrents (Sineshchekov et al. 2002; Berthold et al. 2008). In our study, when the cells were observed under the microscope after being exposed to PAR, UV-A, and UV-B levels of 250.2, 55.3, and 2.4 W m^{-2} for 30 min, the spiral swimming of *T. subcordiformis* completely disappeared and some of the cells sank to the bottom of the vessel (data not shown). As previously mentioned, *T. subcordiformis* preferred to aggregate under a moderate PAR level (Fig. 1) and this may be an integration of negative and positive phototaxis. The switch from positive to negative phototaxis beyond an intensity threshold can be the result of evolving to minimize photodamage.

The increased and decreased cell concentrations at the "light end" and "dark end" both proved its photomovement (Fig. 3a, b), and the higher increase rate in the "light end" and lower decrease rate in the "dark end" indicated the higher motile capability of the cells. After pre-cultured in the P, PA, and PAB treatments for 30 min, the concentration of cells in the "light end" decreased firstly and then increased (Fig. 3a). This was due to the sinking of cells that lost their swimming capability during the pre-exposures—some cells sank out to the bottom of the aquarium and could not be sampled. The higher decrease rate of pre-cultured cells under the different treatments in the "dark end" was caused by the same reason (Fig. 3b). The delayed time for the increase in cell concentration at the "light end" indicated a longer interval needed for recovering capability of movement and the prolonged delay time meant further damage on the flagellar swing, i.e., adding UV-A or UV-A+UV-B to PAR led to further suppression. Moreover, shorter wavelengths (i.e., higher energy) produced higher damage to the swimming capability and photosynthesis of *T. subcordiformis*.

Under light, the D1 protein undergoes a permanent turnover cycle of synthesis, degradation, and replacement in the thylakoid membrane. As soon as the rate of damage exceeds the rate of repair, the function of the reaction center is impaired and the photosynthetic apparatus is destructed (Aro et al. 1993) in a process called photoinactivation (Franklin et al. 2003). The absorption of the highly energetic UVR by sensitive target molecules within the photosynthetic apparatus (e.g., the reaction center or Rubisco) causes further photoinactivation, as seen in our study (Figs. 2b and 4). Photorepair by the enzyme photolyase, using UV-A/blue light as energy source (Menck 2002), is a major mechanism to reduce UVR-induced DNA damage (Sinha and Häder 2002). Indeed, this may be responsible for the faster effective photochemical quantum yield recovery of *T. subcordiformis* in the "light end" as compared with those in "light end".

Migration (Bebout and Garcia-Pichel 1995; Sinha et al. 2001) and accumulation of photo-protective pigments (Dillon et al. 2002; Liu et al. 2004) are effective strategies to avoid harmful radiation in phytoplankton. However, the photosynthetic components and the flagella swing of *T. subcordiformis* were still damaged by high PAR, especially in the presence of UV-A and UV-B.

In view of the high quantum effectiveness at shorter wavebands on photosynthetic carbon fixation and the decreased motility associated with photosynthetic inhibition, motile algal cells may migrate vertically to deeper depths or stop active movement so they sediment in water column to avoid the shorter UVR wavelengths or higher surface UVR irradiances. Such a behavior may, in turn, increase the food supply to the zooplankton they also migrate vertically to avoid UVR (Rhode et al. 2001; Williamson et al. 2001; Alonso et al. 2004).

The results of our study highlight important ecological implications. As an important food source in nature, *T. subcordiformis* often faces regular changes in solar radiation conditions; therefore, the migratory response of the cells could alleviate the damage caused by high light stimulus and even get optimum light levels for growth and survival. On the other hand, the avoidance and accumulation of *T. subcordiformis* cells to light levels is consistent with the migration of herbivorous zooplankton (Ma et al. 2010): they migrate vertically or horizontally to illuminated but less than photo-damaged area. The coupled responses of *T. subcordiformis* and zooplankton to illumination might be favorable for cell photosynthesis and zooplankton grazing. However, the suppression of photosynthesis and motile activity of *T. subcordiformis* caused by high PAR and UVR before they could migrate to suitable position may decrease the food supply to herbivorous zooplankton.

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