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The short- and long-term response of *Scrippsiella trochoidea* (Pyrrophyta) to solar ultraviolet radiation

W.C. GUAN[*,**] and S.H. LU[*+]

College of Life Science South China Normal University, Guangzhou, Guangdong, 510631, China[*]
School of Life Sciences, Wenzhou Medical College, Wenzhou, Zhejiang, 325035, China[**]

Abstract

To assess the short- and long-term impacts of UV radiation (UVR, 280–400 nm) on the microalga *Scrippsiella trochoidea*, we exposed cells to three different radiation treatments (PAB: 280–700 nm, PA: 320–700 nm, and P: 400–700 nm). A significant decrease in the photochemical efficiency (Φ_{PSII}) at high irradiance (100% of incident solar radiation, 216.0 W m^{-2}) was observed. Photoinhibition was reduced from 62.7 to 10.9% when the cells were placed in 12% solar radiation (26.1 W m^{-2}). In long-term experiments (11 days) using batch cultures, cell densities during the first 5 days were decreased under treaments P, PA, and PAB, reflecting a change in the irradiance experienced in the laboratory to that of incident solar irradiance. Thereafter, specific growth rates increased and UV-induced photoinhibition decreased, indicating acclimation to solar UV. Cells were found to exhibit both higher ratios of repair to UV-related damage, shorter period for recovery and increased concentrations of UV-absorbing compounds (UV_{abc}), whose maximum absorption was found to be at 336 nm. Our data indicate that *S. trochoidea* is sensitive to ultraviolet radiation, but was able to acclimate relatively rapidly (*ca.* 6 days) by synthesizing UV_{abc} and by increasing the rates of repair processes of D1 protein in PSII.

Additional key words: growth; photochemical efficiency; *Scrippsiella trochoidea*; UVR; Φ_{PSII}.

Introduction

Solar ultraviolet radiation (UV-B; 280–315 nm) is known to be a natural stress factor for phytoplankton (Beardall *et al.* 2004, Häder *et al.* 2007). Depletion of ozone caused by industrial activities has caused increased UV-B irradiance reaching the earth surface (Beardall *et al.* 2004, Häder *et al.* 2007). Although the rate of stratospheric chloride increase has slowed since the adoption of the Montreal Protocol, the recovery of the ozone layer is delayed due to global tropospheric warming that leads to cooling in the stratosphere (Weatherhead and Andersen 2006). UV-B is known to damage DNA and proteins of phytoplankton (Boelen *et al.* 2000, Xiong 2001), alter cyanobacterial morphology (Wu *et al.* 2005), and reduce photosynthetic activity (Guan and Gao 2008) and nutrient uptake (Behrenfeld *et al.* 1995). However, the light history of cells also affects the biological response to solar UVR (Guan and Gao 2008). Alternatively, positive effects of UVR have also been shown, such as UV-A-aided repair of damaged DNA (Karentz *et al.* 1991), UV-driven photosynthetic carbon fixation in the absence of PAR (Gao *et al.* 2007), and UV-A-enhanced photosynthesis in the presence of PAR (Neori *et al.* 1988, Barbieri *et al.* 2002, Helbling *et al.* 2003, Mengelt and Prézelin 2005).

Short-term (<day) experiments have demonstrated photoinhibition and irreversible photodamage of photosystem II (PSII) in some phytoplankton (Guan and Gao 2008, 2010a,b). This is related to the damage and disruption of the D1 protein in PSII, causing a decrease in the rates of electron transport (Renger *et al.* 1989,

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[+]Corresponding author; fax: +86-020-85217621; e-mail: lusonghui1963@163.com
Abbreviations: Chl *a* – chlorophyll *a* ; F_m' – the instantaneous maximum fluorescence; F_t – the steady-state fluorescence of light-adapted cells; *k* – damage rate; P – photosynthetically active radiation; PA – photosynthetically active radiation + ultraviolet A; PAB – photosynthetically active radiation + ultraviolet A+B; PSII – photosystem II; *r* – repair rate; UVA – ultraviolet A; UVB – ultraviolet B; UV_{abc} – the UV-absorbing compounds; UVR – ultraviolet radiation; Y_{PAR} – the Φ_{PSII} after 1 hour exposure to solar PAR; Y_X – the Φ_{PSII} after 1 hour exposure to PA or PAB; Φ_{PSII} – photochemical efficiency of PSII.
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Demmig-Adams *et al.* 1992). However, a rapid synthesis of the D1 protein enabled the effects of the photodamage to be counteracted, and thus populations of *Synchocystis* sp. (PCC6803) were not inhibited (Barber 1995). In addition, UV-induced inhibition of photochemical efficiency could be remediated within several minutes or hours for different species after the stress of high irradiance was eliminated (Gao *et al.* 2007, Guan and Gao 2008).

Over relatively long-time scales (several days or weeks), phytoplankton might acclimate and protect themselves by the synthesis UV-absorbing compounds (UV_{abc}), such as mycosporine-like amino acids (MAAs) (Gao *et al.* 2007, Guan and Gao 2010b), or by the production of quenching agents (*e.g.* carotenoids) (Wu *et al.* 2009). UV_{abc} absorb UVR at wavelengths between 310 and 360 nm, and can be synthesized by a variety of phytoplankton (Gao *et al.* 2007, Wu *et al.* 2009, Guan and Gao 2010b). The protective role of MAAs have been demonstrated in previous studies (Garcia-Pichel 1994, Sommaruga and Garcia-Pichel 1999).

Scrippsiella trochoidea is a red tide alga, which forms intense spring or summer blooms in East China Sea, such as in Changjiang estuary. Blooms have been reported at 2004 and 2006 (Wang and Wu 2009). However, very little information is available on the potential effect of UV on this species. The data presented here focus on the short- and long-term effects of ultraviolet radiation (UVR) on photochemical efficiency and growth of *S. trochoidea*, as well as the mechanism by which this species copes with solar UVR.

Materials and methods

Species and culture conditions: *S. trochoidea* was isolated at Changjiang estuary, East China Sea at 2007, maintained in f/2 medium (Guillard and Ryther 1962), and grown under cool-white fluorescent lights at ~50 μmol(photon) m^{-2} s^{-1} (12L:12D) and 20°C in a growth chamber (*XT5401-CC275TLH*, *Huayan*, Shanghai China). 1 W m^{-2} ≈ 4.6 μmol(photon) m^{-2} s^{-1}. Experiments to evaluate the effects of solar UVR on *S. trochoidea* were conducted at the Marine Biology Institute, Shantou University (23°26'N, 116°42'E) during June, 2009. The cells were cultured for 12 days (batch culture) under 400 μmol(photon) m^{-2} s^{-1} before the cells were used for short- or long-term experiments. The PAR in the growth chamber was measured by an *Illuminometer* (*ST-80C, Photoelectric Instrument Factory*, Beijing Normal University, China). Cells in the exponential phase (4.0×10^4 cells ml^{-1}) were diluted to 2.9×10^4 cells ml^{-1} with fresh medium before the experiments began. Experiments were conducted in small (2 cm in diameter, 7 cm long) or large (5.9 cm in diameter, 35 cm long) quartz tubes maintained in a water bath (20 ± 0.5°C; *CAP-3000*, *Rikakikai*, Tokyo, Japan).

Experimentation: Short-term exposures were completed to investigate the photochemical efficiency (Φ_{PSII}) responses to UVR, and long-term exposures were designed to assess how the cells acclimate to solar radiation and the extent of the influence of solar UVR on growth. To analyze the acclimation mechanisms of *S. trochoidea*, the UV-absorbing compounds (UV_{abc}) were analyzed and quantified, and the ratios of repair to damage rates of D1 protein were calculated before and after acclimation.

Solar radiation monitoring and radiation treatments: Incident solar radiation was continuously monitored using a broadband *ELDONET* filter radiometer (*Real Time Computer*, Möhrendorf, Germany) which has 3 channels for photosynthetically active radiation (PAR, 400–700 nm), ultraviolet-A (UV-A, 315–400 nm) and ultraviolet-B radiation (UV-B, 280–315 nm), respectively (Häder *et al*. 1999). This device has been universally recognized (certificate No. 2006/BB14/1) and was calibrated regularly. The cut-off filters reduce 4% of PAR in water due to reflection (Gao *et al*. 2007). There was about 5 nm difference between the measured and exposed UV-A wave lengths. Therefore, the cells received about 2% less UV-A and about 4% less PAR than suggested by the measured irradiances.

The cells were exposed to the following treatments: (*1*) PAB (PAR+UV-A+UV-B), tubes covered with a 295 nm cut-off filters (*Ultraphan, Digefra*, Munich, Germany), transmitting irradiances above 295 nm; (*2*) PA (PAR+UV-A), tubes covered with 320 nm cut-off filters (*Montagefolie, Folex*, Dreieich, Germany), transmitting irradiances above 320 nm; and (*3*) P (PAR), tubes covered with a 395 nm cut-off filters (*Ultraphan UV Opak, Digefra*, Munich, Germany). The transmission spectra of these filters have been previously reported (Zheng and Gao 2009). For the cells to acclimate to the incident solar radiation, a long-term exposure was run during June 3–13, 2009. Solar radiation levels were adjusted using layers of neutral density screen as needed, so that the cells received 50 and 100% of incident solar radiation in the first (day 1–4) and second (day 5–11) phase, respectively. The cell density was set at 2.9×10^4 cells ml^{-1}, and the Chl *a* concentration was 0.14 μg(Chl *a*) ml^{-1}. The quartz tubes were covered by 1 layer of neutral density screen to reduce the incident solar radiaton by 50%. During the long-term experiments, the cultures received 100% solar radiation. To avoid sedimentation of cells, the tubes were gently shaken two times each day at approximately 12-h intervals. Cells were counted under light microscopy (*BX50F4, Olympus optical Co. Ltd*., Japan) using a haemacytometer, and growth rates calculated from an exponential equation using the cell abundance data.

Φ_{PSII} versus irradiance curves with or without UVR were determined under three quality radiation treatments (P, PA, and PAB) and under six levels of solar radiation (to simulate the irradiance at different depths in the water column) by covering the tubes with a variable number of neutral density screens. The irradiance thus varied from 100 to 3%. Incubations lasted 1 h.

Determination of Φ_{PSII}: Φ_{PSII} was measured with a pulse-amplitude-modulated fluorometer (*PAM - WATER-ED*, Walz, Germany) according to Genty *et al.* (1989) and was quantified as follows:

$$\Phi_{PSII} = \Delta F/F_m' = (F_m' - F_t)/F_m', \quad (1)$$

where F_m' represents the instantaneous maximum fluorescence and F_t the steady-state fluorescence of light-adapted cells. The saturating light pulse was 5,300 μmol(photon) m^{-2} s^{-1} with 0.8-s duration. Light at measurement is about 0.3 μmol(photon) m^{-2} s^{-1}, and the actinic irradiance is 10 μmol(photon) m^{-2} s^{-1}.

The rates of UVR-induced damage to the photosynthetic apparatus (k, min^{-1}) and corresponding repair rate (r, min^{-1}) were estimated according to the previous studies (Lesser *et al.* 1994, Heraud and Beardall 2000), and the details shown in Guan and Gao (2008). UVR-induced inhibition of Φ_{PSII} was calculated as (the synergic effects for UV-A and UV-B were neglected):

$$\text{Inh}\ (\%) = (Y_{PAR} - Y_X) \times Y_{PAR}^{-1} \times 100, \quad (2)$$

where Y_{PAR} is the Φ_{PSII} after 1-h exposure to solar PAR, and Y_X is the Φ_{PSII} after 1-h exposure to PA or PAB.

UV_{abc} and pigments: The absorption by pigments was determined by filtering 15–25 ml of the culture (the volume varied as a function of the different cell concentrations) on a *Whatman GF/F* filter, extracting in absolute methanol (5 ml) overnight at 4°C, and centrifuging (10 min at 1,500 × *g*) before measuring with a scanning spectrophotometer (*DU530 DNA/Protein Analyzer, Beckman*, Coulter, USA). The concentration of UV-absorbing compounds was expressed by the peak height (310–360 nm) of optical density (OD). In addition, the concentration of Chl *a* was calculated from the equation of Porra (2002).

Data analysis: A one-way analysis of variance (*ANOVA*) (*Tukey* test) was used to determine significant difference among the radiation treatments. A confidence level was set a priori at p=0.05. The number of replicates is 8, it means that 4 samples were measured from each of 2 cultures.

Results

For the cells cultured with different levels of solar radiation, there was an overall decrease in Φ_{PSII} with increasing irradiance (Fig. 1). The data were fit using a second-order exponential decay function ($y = A_1\exp(-x/t_1) + A_2\exp(-x/t_2) + y_0$, $R \geq 0.95$). At 100% of incident solar radiation (261.64 W m^{-2}), the highest inhibition was 62.7%. The inhibition of UV-A and UV-B was 48.3 and 14.7%, respectively. However, the UVR-induced inhibition of Φ_{PSII} for the cells exposed to 12% solar irradiance (26.1 W m^{-2}) was 5 times less than that of cells at 100% E_0 (that is, the irradiance at the water surface). For the cell at 3% of incident solar radiation (3.34 W m^{-2}), the deleterious effect of UVR almost could not have been tested.

There were two phases reflected in growth rates during the long-term acclimation period. In the first, cell density of *S. trochoidea* decreased slightly during the first five days (Fig. 2*A*) for three treatments (P, PA and PAB) while 50% incident solar radiation was provided. Although there was no increase in cell density during the first phase, this probably reflected the effects of the irradiance change when the cultures were moved from the lab (low irradiance and without UVR) to outside. During the second phase (from 6 to 11 days) cell density increased among all three treatments (P, PA, and PAB). The specific growth rates (μ) during the second phase were 0.18, 0.17, and 0.12 d^{-1} for the P, PA, and PAB treatments, respectively. The specific growth rate was significantly lower for PAB than that of both P and PA (p<0.05). For Φ_{PSII}, the variety has two phases and is similar with that of growth (Fig. 2*B*). The daily doses received by cells during the long-term experiment are shown in Fig. 2*C*.

When the cells of *S. trochoidea* were moved outdoors and exposed to solar radiation treatments without UVR

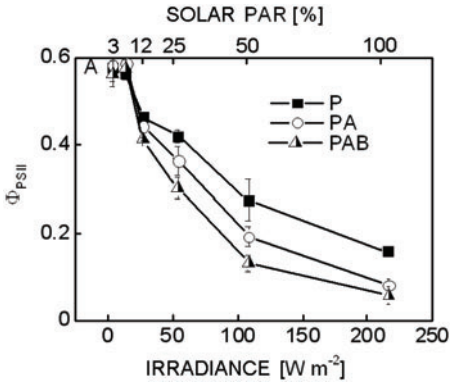

Fig. 1. Mean photochemical efficiency (Φ_{PSII}) as a function of solar PAR (W m^{-2}) in a second-order exponential decay function $y = A_1\exp(-x/t_1) + A_2\exp(-x/t_2) + y_0$, ($R \geq 0.96$) when *S. trochoidea* cells exposed to P, PA, and PAB treatments. The vertical lines indicate SD (n = 8), representing 4 samples from each of 2 cultures. The mean solar irradiances during 60-min exposure for PAR, UV-A, and UV-B were 261.6, 42.1, and 1.4 W m^{-2}, respectively.

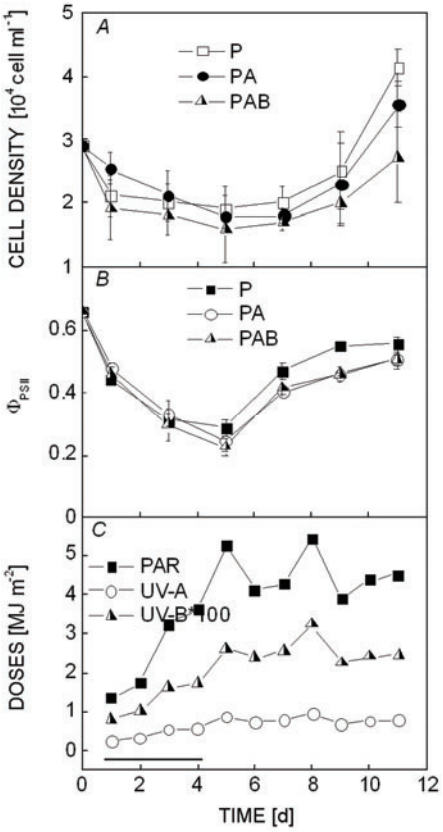

Fig. 2. Acclimation of *S. trochoidea* cells to solar radiation with UV-A (PA) and UVR (PAB) or without UVR (P) during the period of June 3–13, 2009. *A*: cell density; *B*: photochemical efficiency (Φ_{PSII}); *C*: daily doses of solar PAR, UV-A, and UV-B received by cells. 50% of the solar radiation was adjusted using 1 layer neutral density screen at the first four days. The vertical lines indicate SD (n = 8), representing 4 samples from each of 2 cultures. The Φ_{PSII} was measured at 17:00 h (local time) during the experiment.

(PAR only), Φ_{PSII} decreased from 0.51 to 0.11 (P), and thereafter remained constant. When UV-A or UVR were added, they induced more damage in PSII, and the Φ_{PSII} decreased to 0.04 (PA) and 0.03 (PAB), respectively (Fig. 3*A*). After 11 days, the pattern for Φ_{PSII} was the same as that on the first day (Fig. 3*B*). However, as indicated by the Φ_{PSII} ratio from day 1 to 11 (Fig. 3*C*), the decreased Φ_{PSII} was small when compared with that at day 1 (t_0). The UVR-induced inhibition was significantly decreased after 11 days under solar radiation (p<0.05). Compared with day 1, the inhibition decreased from 77.5 to 29.3% in the UVR. On the first day the photochemical efficiency became constant after 15-min exposure to solar radiation (Fig. 3*A*). However, Φ_{PSII} reached steady-state in 5 min for three radiation treatments after 11 days (Fig. 3*B*). Furthermore, the repair rate under PAR alone was 0.070 min^{-1}at t_0 and 0.253 at t_{11}, respectively. In the presence of UV-A, however, the repair rate was 0.216 min^{-1}at t_{11}, or about 5 times faster than that on t_0 (0.036 min^{-1}), while with UVR it was 0.188 min^{-1}at t_{11}, 4.3 times faster than that in t_0 (0.035 min^{-1}). The ratios of r and k, estimated from the constant levels of Φ_{PSII} under P, PA, and PAB radiation treatments, were much faster at t_{11} than at t_0 (Fig. 4). In contrast to the first day (t_0), the ratio of r to k at t_{11} was 1.4, 5.0, and 5.2 times greater under P, PA, and PAB treatments, respectively (Fig. 4).

The Φ_{PSII} recovered as a first order exponential function of time (R≥0.95) when shifted to a low PAR of 10 μmol m^{-2} s^{-1} (Fig. 3*D*,*E*). As indicated by the photochemical efficiency (Φ_{PSII}) ratio from day 1 to 11 (Fig. 3*F*), the increased Φ_{PSII} was higher when compared with that at day 1 (t_0). The initial slope (α) of the fitted curves was used as an estimated of the recovery rate of Φ_{PSII}, so a higher α indicates a faster recovery. The initial slope (α) is 0.013, 0.013, and 0.012 min^{-1} for P, PA, and PAB at the end of experiment, and faster than that at the beginning (P: 0.012, PA: 0.009, PAB: 0.009 min^{-1}). The Φ_{PSII} increased much faster at t_{11} than that at t_0; in 70 min, the yield reached 0.51 at t_{11}, while that at t_0 recovered to 0.39 for P and 0.32 for PA and PAB (Fig. 3*D*,*E*). The recovery of Φ_{PSII} at t_0 has significant difference for the cells exposed to P, while compared with PA and PAB, respectively. However, there is no significant difference for PA and PAB (Fig. 3*D*).The absorption characteristics of *S. trochoidea* (Fig. 5*A*) suggested the presence of UV-absorbing compounds with a maximum absorption at 336 nm. The peak height of optical density (OD_{Peak}) increased from 0.189 to 0.389, 0.346, and 0.184 after 11 days of PAR+UVR (PAB), PAR+UV-A (PA), and PAR treatment, respectively (Fig. 5*B*). There was no significant difference between t_0 and t_{11} for PAR alone (Fig. 5*B*).

Discussion

Photosynthesis of microalgae can be significantly inhibited by solar ultraviolet radiation over short time scales (Helbling *et al.* 2003, Guan and Gao 2010a,b). However, cells have different mechanisms to cope with excessive solar energy over short time periods (Franklin and Forster 1997). One example of photoprotection, based on the xanthophyll cycle, occurs in many algae (Wu *et al.* 2009) and higher plants (Demmig-Adams *et al.* 1992, Franklin and Forster 1997), and refers to dissipation of excitation energy in the antennae pigments (Franklin and Forster 1997). However, photoinactivation, due to damage to the D1 protein of PSII, is an effective protection mechanism by causing a decrease in the electron transport rate (Renger *et al.* 1989, Demmig-Adams *et al.* 1992). Over longer time periods (several days or weeks), however, cells can show different degrees of acclimation through the synthesis of UV-absorbing compounds (Gao *et al.* 2007, Wu *et al.* 2009) or a rapid synthesis of D1 protein

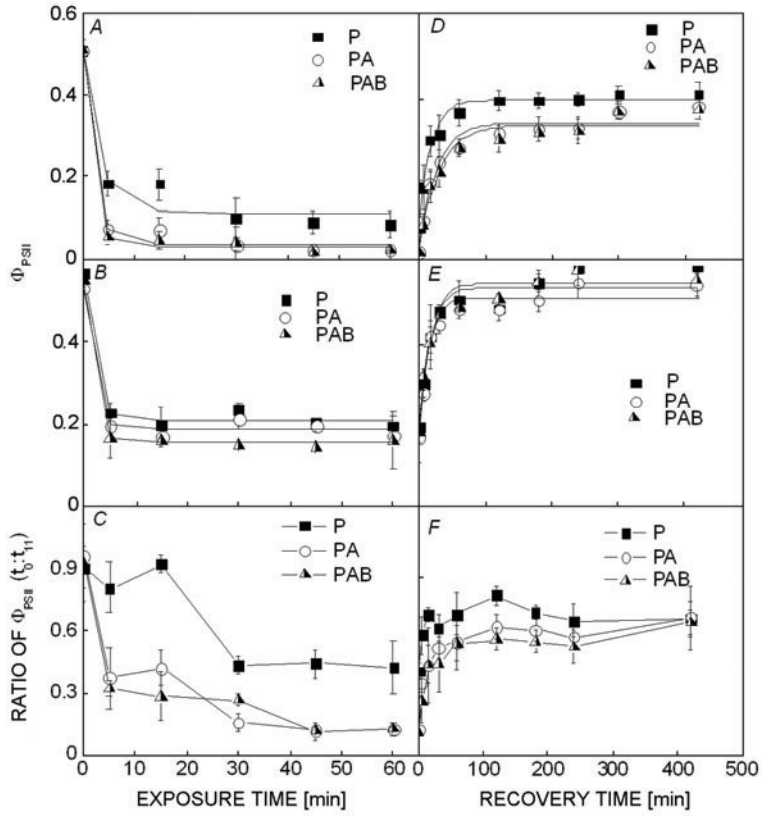

Fig. 3. Changes in the photochemical efficiency (Φ_{PSII}) in *S. trochoidea* during 60-min exposures to P, PA, or PAB before (*A*) or after 11-day (*B*) acclimation to solar radiation. *C*: Φ_{PSII} ratio of t_0 to t_{11} during the exposure periods. Recovery of Φ_{PSII} of *S. trochoidea* under 10 μmol(photon) m^{-2} s^{-1} after 60-min exposures to P, PA, or PAB before (*D*) or after 11-day (*E*) acclimation to solar radiation. *F*: Φ_{PSII} ratio of t_0 to t_{11} during the recovery periods. The vertical lines indicate SD (n = 8, 2 cultures, 4 samples from each culture). The mean irradiance during the 60-min exposure (from 12:00 to 13:00) were 285.1 (PAR), 44.5 (UV-A), and 1.5 W m^{-2} (UV-B). Differences in PAR between the two days was less than 0.15%.

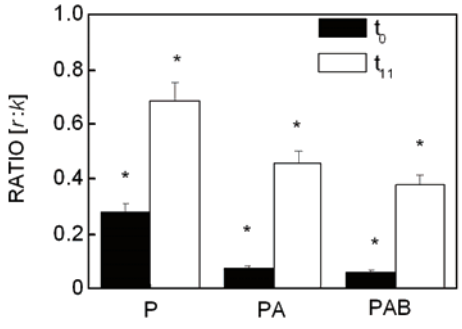

Fig. 4. The ratios of repair (r) to damage (k) rates of PSII under P, PA, or PAB (Fig. 3*A*,*B*). The vertical bars indicate SD (n = 8, 2 cultures, 4 samples from each culture). The asterisks mean the significant difference (p<0.05).

(Guan and Gao 2010b). Simultaneously, non-photochemical quenching must be another important mechanism for cell acclimation.

UVR resulted in the significant photoinhibition (Fig. 1, Fig. 3*A*) and decreased cell growth (Fig. 2*A*) when cells were exposed to incident solar radiation. *S. trochoidea* cells incurred the most serious damage by UVR at the higher solar energies, similar to when the water column becomes stratified and blooms form. However, vertical movement within the water column can relieve the deleterious effect of solar UVR (Fig. 1) (Guan and Gao 2008). Usually, if the bloom of *S. trochoidea* lasted several days, it would be negatively affected by solar UVR before cells could acclimate to the higher UVR at the surface. Our data showed that *S. trochoidea* cells need *ca*. 7 days at a new irradiance for acclimation (Fig. 2*A*), but the time scale also was dependent on the light history of the cultures (Guan and Gao 2008) and environmental conditions, such as absolute incident irradiance and temperature, nutrient availability, and the effect of self-shading which was an important factor to modulate the recovery after UVR-induced damage (Gao *et al.* 2007). The protection mechanisms were observed after 7-day acclimation, when cell density began to increase (Fig. 2*A*) along with the faster repair rate of D1 protein (Figs. 3, 4) and the higher content of UV_{abc} (Fig. 5). Similar results have been found showing an increasing protection of the cell against the deleterious effects of UVR as the UV_{abc} content increased (Gao *et al.* 2007, Wu *et al.* 2009, Guan and Gao 2010b) and the faster repair rate for D1 protein in PSII (Guan and Gao 2010b). The protective role of MAAs has been shown in previous studies (Garcia-Pichel 1994, Helbling *et al.* 1996, Sommaruga and Garcia-Pichel 1999), but this function depended on the cell diameter. Specifically, the MAAs can be effectively used as a photoprotective mechanism for microplankton (cell radii, 10~100 μm), but not for picoplankton (cell radii, <1 μm). Among nanoplankton (cell radii, 1~10 μm), sunscreens can afford considerable benefits, but only at the expense of relatively heavy investments of energy and with restricted efficiencies (Garcia-Pichel 1994). Although *S. trochoidea*,

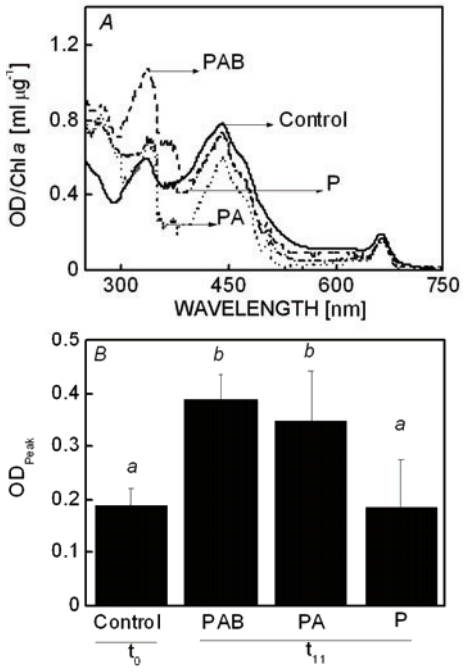

Fig. 5. *A*: Spectral absorption characteristics of *S. trochoidea* (methanol extraction) at the beginning (t_0) and the end (t_{11}) of the long-term experiment. *S. trochoidea* exposed to P, PA, and PAB treatments. *B*: Peak height (310–360 nm) of optical density (OD_{Peak}) before and after 11-day acclimation. The letters on top of bars indicate significant difference at p=0.05, so for the same letters, there is no significant difference among the data. "Control" was for the cells that had not been exposed to solar radiation (t_0).

with a mean cell diameter of 26 μm, seems to be marginally suited for an effective use of UV_{abc} (Garcia-Pichel 1994), our data suggest that these compounds had an influence in photoprotection of cells during the long-term experiments. Some other species, such as *Emilinia huxleyi* (Guan and Gao 2010b), *Heterosigma akashiwo* (Gao *et al.* 2007) and two centric diatom species (Helbling *et al*. 1996), also can synthesize UV_{abc} protection compounds, although the cell diameters were also only marginally suited for an effective use of UV_{abc} (Garcia-Pichel 1994). Our data also show that UV-A can induce the synthesis of UV_{abc} in *S. trochoidea* cells, but not PAR or UV-B, although it has been found that other species produce UV_{abc} upon stimulation by PAR or UV-B also (Gao *et al.* 2007). On the other hand, previous researches had shown that the cellular or plastidal changes of polyamines are the primary cellular mechanism for regulation of response of the algae or plants to enhance UVR (Sfichi *et al.* 2004, Lütz *et al.* 2005, Sfichi-Duke *et al.* 2008).

S. trochoidea cells grown under indoor conditions for 3 years, when re-exposed to solar UVR, were found to be sensitive to solar UVR radiation (Figs. 2*A*, 3*A*). This reflects the effects of light histories on cellular defensive strategies against solar UVR or strong PAR. The same phenomenon has been observed in many species, such as *S. costatum* (Guan and Gao 2008), *H. akashiwo* (Gao *et al.* 2007) and *E. huxleyi* (Guan and Gao 2010b). Cells which had been cultured in the laboratory for several years had not genetically adapted to the low PAR and UVR-free environment, since they retained the ability to respond to UVR during acclimation. Thus, this may be an important strategy for cells to acclimate to solar UVR *in situ*.

The data presented in this study indicate that although the red tide alga *S. trochoidea* was sensitive to solar ultraviolet radiation, cells had mechanisms to cope with increased energy flux, and that any future increase of UV-B may have little impact in this species over long time scales.

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