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Effects of solar UV radiation and temperature on morphology and photosynthetic performance of *Chaetoceros curvisetus*

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Abstract

This study investigated the effect of solar ultraviolet radiation (UVR) and temperature on a chain length and photosynthetic performance of diatom *Chaetorceros curvisetus*. The cells were cultured in large quartz tubes and exposed to PAR, PAR + UV-A (PA), or PAR + UV-A + UV-B (PAB) radiation at 20°C and 28°C for six days, respectively. After recovery for 1 h, the cells were exposed again to three different radiations for 1 h. Then, a change in the photochemical efficiency (Φ_{PSII}) was examined and UVR-induced photoinhibition was calculated. The percentage of long chains (more than five single cells per chain) in *C. curvisetus* significantly increased from 8.2% (PAR) to 38.9% (PAB) at 20°C; while it was not notably affected at 28°C. Mycosporine-like amino acids (MAAs) concentration obviously increased by irradiance increment from PAR to PAB at 20°C. Chlorophyll (Chl) *a* concentration significantly declined with increasing irradiance at 20°C. Both MAAs and Chl *a* concentrations were not obviously changed by irradiance at 28°C. Before and after reexposure, Φ_{PSII} was significantly reduced both at 20°C and 28°C. UVR-induced photoinhibition at 20°C (39%) was higher than that at 28°C (30.9%). Solar UV radiation, especially UV-B, could significantly influence the percentage of long chains of *C. curvisetus*, especially at low temperature. UVR-induced photoinhibition can be alleviated by higher temperatures.

Additional key words: photochemical efficiency; phytoplankton; solar ultraviolet radiation.

Introduction

Ultraviolet (UV) light refers to light with wavelength range of 100−400 nm, generally subdivided into three types, *i.e*., UV-A (315−400 nm), UV-B (280−315 nm), and UV-C (100−280 nm). Solar ultraviolet radiation (UVR) is a natural stress factor for phytoplankton (Beardall and Raven 2004, Häder *et al*. 2007), and UV-B radiation, in particular, can alter cyanobacterial morphology (Wu *et al*. 2005), and increase cell volume/size (Guan and Gao 2010a,b), thus may have certain influence on their suspension properties in water. UV-B radiation can also change the ultrastructure of chloroplasts (Buma *et al*. 1996) and affect Chl concentration (Gehrke 1999). Short exposures (≤ 30 min) to UVR can induce rapid decrease in PSII efficiency, but recovery of photosynthesis is possible if there is sufficient time for repair of UV damage (Marwood *et al*. 2000). Furthermore, long-term experiments (11 d) have discovered that phytoplankton may acclimate to UV radiation by synthesizing UV-absorbing compounds (Guan *et al*. 2011), such as mycosporine-like amino acids (MAAs) containing a central cyclohexenone or cyclohexenimine ring, which absorbs UV light and stabilizes free radicals, or produces quenching agents, *e.g*., carotenoids (Wu *et al*. 2009).

Meanwhile, temperature is another major ecological factor for growth of plants, including phytoplankton. Different diatom species exhibit varying optimum

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Abbreviations: Chl − chlorophyll; MAAs − mycosporine-like amino acids; PA − photosynthetically active radiation plus UV-A radiation; PAB − photosynthetically active radiation plus UV-A and UV-B radiation; PUFA − polyunsaturated fatty acids; UVR − ultraviolet radiation; Φ_{PSII} − photochemical efficiency of PSII.
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temperature ranges for their growth (Patrick 1971). Temperature also affects algal morphology (Mühling *et al*. 2003, Takabayashi *et al*. 2006) and Chl contents (Verity 1981). High temperatures have been reported to alleviate the UVR-caused photoinhibition (Vonshak 1997, Gao *et al*. 2008). *Chaetoceros* is probably the largest genus of marine planktonic diatoms, which spreads widely along the near shore in China. *Chaetoceros curvisetus* is a common diatom species growing in the East China Sea; it is a major marine diatom causing the red tide in recent years. Meanwhile, it is also a main larval diet in aquaculture, thus being an important primary producer in the marine ecosystem (Karthikeyan *et al*. 2013). Due to the depletion of stratospheric ozone layer, more and more UV light, especially UV-B, is reaching the Earth's surface. It has attracted increasing concern from humans as it has a significant impact on marine primary producers. In the meantime, global climate warming is an inexorable trend. Therefore, it is important to elucidate the effects of solar UVR and temperature on *Chaetoceros* species. In this study, *C. curvisetus* cells were exposed to three different irradiances [PAR; PAR + UV-A; and PAR + UV-A + UV-B] at 20 or 28°C, respectively. We anticipate that the results of this study could provide more information about the effects of solar UVR and temperature on the chain length and photosynthetic performance of *C. curvisetus*.

Materials and methods

Diatom species: *Chaetoceros curvisetus* (strain Y1), collected from Tolo Harbour, Hong Kong, China (22°30'N, 114°20'E) on 28 February 2009, was cultured in F/2 medium after isolation (Guillard *et al*. 1962) under cool-white fluorescent irradiation [~50 μmol(photon) m^{-2} s^{-1}, 12/12 h of light/dark cycle], at 20°C in a growth chamber (*XT5401-CC275TLH*, *Huayan*, Shanghai, China). Experiments for evaluating the effects of solar UVR and temperature on *C. curvisetus* were carried out at the Marine Biology Institute, Shantou University (23°26'N, 116°42'E) in June, 2009.

Solar radiation treatments and culture conditions: *C. curvisetus* cells in the exponential phase with cell density of 1.2×10^6 cells ml^{-1} were first diluted to 1.3×10^4 cells ml^{-1} with a fresh medium and then cultured in large quartz tubes (5.9 cm in diameter, 35 cm long) for 6 d at 20°C and at 28°C water bath (± 0.5°C, *CAP-3000*, *Rikakikai,* Tokyo, Japan) using running water to control temperature outdoors, respectively. *C. curvisetus* cells at the same initial density cultured under cool-white fluorescent tube providing 50 μmol(photon) m^{-2} s^{-1} indoors (20°C) were used as the control.

Incident solar radiation was monitored continuously using a broadband *ELDONET* filter radiometer (*Real Time Computer*, Möhrendorf, Germany) with three channels for PAR (400−700 nm), UV-A (315−400 nm) radiation, and the UV-B (280−315 nm) radiation, respectively (Häder *et al*. 1999), of which the cut-off filters can reduce 4% PAR in water due to reflection (Gao *et al*. 2007). This device has been universally recognized (certificate No. 2006/BB14/1) and was calibrated regularly in the laboratory. *C. curvisetus* cells, cultured at each temperature, were exposed to the following three treatments: (*1*) PAB (PAR + UV-A + UV-B), tubes were covered with a 295 nm cut-off filter (*Ultraphan*, *Digefra*, Munich, Germany), with transmission irradiance of above 295 nm; (*2*) PA (PAR + UV-A), tubes were covered with a 320 nm cut-off filter (*Montagefolie*, *Folex*, Dreieich, Germany), with transmission irradiance of above 320 nm; and (*3*) PAR, tubes were covered with a 395 nm cut-off filter (*Ultraphan UV Opak*, *Digefra*, Munich, Germany) (Zheng and Gao 2009). The solar irradiance doses for the 6-d treatment were set as dynamics according to the natural solar irradiance outdoor. The highest and lowest solar doses were 7.27 and 2.76 MJ m^{-2} (PAR), 1.17 and 0.59 MJ m^{-2} (UV-A), and 0.033 and 0.015 MJ m^{-2} (UV-B), respectively (Fig. 1). Three replications were used for each radiation treatment, as well as for the control.

Observation of *C. curvisetus* colonies: After 6-d exposure, the number of *C. curvisetus* cells per chain was counted with a compound microscope (*Zeiss Axioplan 2*, *Carl Zeiss*, Germany). A colony consisting of 2−4 cells per chain was considered as a short chain, and that consisting of 5 cells or more per chain was considered as the long chain. For each treatment, a total of 400 colonies of different sizes (the single cell, short chain, and long chain) in 20 fields were examined, and the percentage of each colony type was calculated. Digital images were recorded with a *Zeiss Axicam* camera and analyzed with a *Vision Analysis System* (*AxioVision 3.0*).

MAAs and Chl *a* content: After 6-d exposure, 25−40 ml of *C. curvisetus* cell culture was collected, followed by

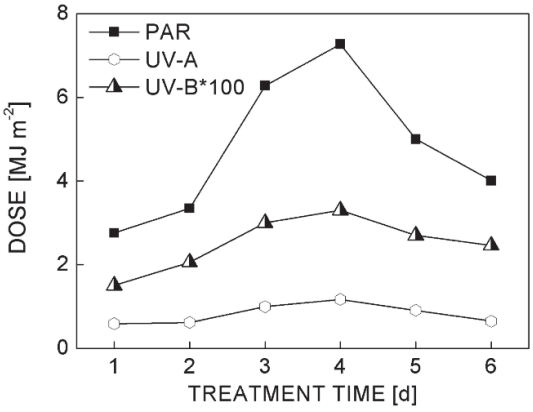

Fig.1. Daily doses of solar photosynthetically active radiation (PAR), ultraviolet-A (UV-A), and ultraviolet-B (UV-B) during the experiment.

filtering with a *Whatman GF/F* filter paper. Subsequently, the precipitate was extracted by 5 ml of absolute methanol overnight at 4°C, followed by centrifugation at 1,500 rpm for 10 min. Afterwards, the absorption of the supernatant was measured (250−750 nm) using a scanning spectrophotometer (*DU530 DNA/ Protein Analyzer*, *Beckman Coulter*, USA). The MAAs concentration was determined from the peak height (310−360 nm) according to Helbling *et al*. (1996). Meanwhile, Chl *a* concentration was calculated using a more reliable post-Arnon equation presented by Porra *et al.* (1989).

Photochemical efficiency (Φ_{PSII}): After being exposed to solar radiation for 6 d, *C. curvisetus* cultures were taken indoors and recovered for 1 h under cool-white fluorescent irradiation of 50 μmol(photon) m^{-2} s^{-1} at 20°C and 28°C correspondingly, in order to recover PSII. Afterwards, samples were diluted to 1.3×10^4 cells ml^{-1} by a fresh medium and re-exposed to solar PAR, PA, and PAB treatments for another 1 h from 10:30 to 11:30 h on 13 June, 2009, respectively. The treatments were followed by a determination of Φ_{PSII}, during which the mean solar irradiance was 233.23 W m^{-2} (PAR), 39.70 W m^{-2} (UV-A), and 1.22 W m^{-2} (UV-B), respectively. Meanwhile, the control cultures, which were incubated indoors under 50 μmol(photon) m^{-2} s^{-1}, were also taken outdoors and exposed to solar PAR, PA, and PAB treatments for 1 h, respectively.

Φ_{PSII} was measured with a pulse amplitude modulated fluorometer (*PAM-Water-ED*, *Walz*, Germany) according to the study of Genty *et al*. (1990) as follows:

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

where F_m' represents the instantaneous maximum fluorescence, F_t the steady-state fluorescence of light-adapted cells, and ΔF is the difference of F_m' minus F_t. The saturating light pulse was 5,300 μmol(photon) m^{-2} s^{-1} with a 0.8-s duration. Measuring light was about 0.3 μmol(photon) m^{-2} s^{-1}, and the actinic irradiance was 10 μmol(photon) m^{-2} s^{-1}. UVR-induced inhibition of Φ_{PSII} was calculated as:

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

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

UVR-induced inhibition was calculated as the difference of Φ_{PSII} after re-exposed to solar UVR between PAR and PAB treatments; UV-A-induced photoinhibition was not calculated.

Statistical analysis: The two-way analysis of variance (*ANOVA*) and *Tukey*'s test were used to determine the significant difference among different radiation and temperature treatments at the P=0.05 level.

Results

Effect of UVR and temperature on chain length of *C. curvisetus*: After being treated at 20°C for 6 d, the percentage of *C. curvisetus* single cells decreased significantly from 49.4% (PAR) to 25.3% (PA), and 21.1% (PAB). The percentage of the long chains (≥ 5 cells per chain) at 20°C increased significantly from 8.2% (PAR) to 14.3% (PA) and 38.9% (PAB). At 28°C, the percentage of the single cells (34.5%) was lower than that at 20°C in the PAR treatment, but the percentages of the long chains (24.1%) was significantly higher than that at 20°C in the PAR treatment. Furthermore, the percentage of the long chains did not increase significantly at 28°C in either PA or PAB compared with that of the PAR treatment (Table 1). The combination of the temperature increment from 20°C to 28°C and both UV-B and UV-A increased the percentage of *C. curvisetus* of both long (from 8.2% to 24.4%) and short chains (from 42.4% to 52.6%), whereas it decreased the percentage of the single cells of *C. curvisetus* (from 49.4% to 23.1%).

Table 1. Percentage of *Chaetoceros curvisetus* colonies of different sizes (single cell, short chain, and long chain) after 6-day exposure to PAR), PA (PAR + UV-A), and PAB (PAR + UV-A + UV-B) treatment at 20°C or 28°C, respectively. For each treatment, a total of 400 colonies were observed. *– significant difference between different treatments at the same temperature, P<0.05; # – significant difference between 28°C and 20°C, P<0.05.

Treatment	Percentage [%]					
	Single cell		2−4 cells per chain		≥ 5 cells per chain	
	20°C	28°C	20°C	28°C	20°C	28°C
PAR	49.4	34.5#	42.4	41.4	8.2	24.1#
PA	25.3*	19.8*	60.4*	58.1*	14.3*	22.1
PAB	21.1*	23.1*	40.0	52.6*	38.9*	24.4

Effect of UVR and temperature on MAAs concentration: After the treatment for 6 d, MAAs concentration was detected in all cultures exposed to different radiation treatments at either 20°C or 28°C. At 20°C, there was an obvious rising trend in MAAs concentration as irradiance increased through UV-A to UV-B radiation; the MAAs concentrations in the PA and PAB treatments were significantly higher than that of the control cultures (Fig. 2). However, the upward trend in MAAs concentration was not apparent as irradiance increased through UV-A to UV-B radiation at 28°C, although in each treatment it was significantly higher than that of the control cultures. There was significant difference in the MAAs concentration under PAR treatment between two different temperature conditions.

Effect of UVR and temperature on Chl *a* concentration: There was a notable declining trend in Chl *a* concentration at 20°C as the radiation treatment increased from PAR to PAB treatment (Fig. 3). The Chl concentrations in the PAR (0.043 μg ml^{-1}) and PA (0.039 μg ml^{-1}) treatments were higher than that of the control cultures (0.030 μg ml^{-1}), while the Chl concentration in the PAB treatment (0.024 μg ml^{-1}) was lower than that of the control cultures. However, there was no obvious declining trend in Chl concentration at 28°C. The Chl concentration at 28°C was significantly lower than that at 20°C in the PA and PAR treatment.

Effect of UVR and temperature on Φ_{PSII} and photoinhibition: For *C. curvisetus* cultures, which were exposed to the radiation treatments before the recovery, the Φ_{PSII} was around 0.5 in each of the three treatments after recovery for 1 h indoors. After the cultures being re-exposed to PAR radiation, PA radiation, and PAB radiation for 1 h, Φ_{PSII} in each treatment decreased markedly at 20°C compared to the value before exposure

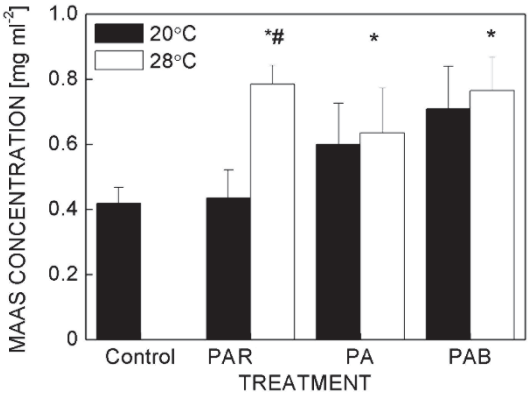

Fig. 2. Mycosporine-like amino acids (MAAs) concentration after 6-day exposure to different radiation treatments. * – significant difference between the experimental group and the control, # – significant difference in the same treatment between 20°C and 28°C, P<0.05. PAR − photosynthetically active radiation; PA − photosynthetically active radiation plus UV-A radiation; PAB − photosynthetically active radiation plus UV-A and UV-B radiation.

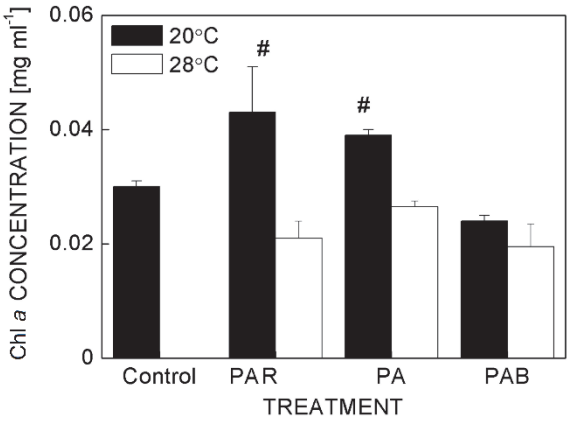

Fig. 3. Chlorophyll (Chl) *a* concentration after six days of exposure to different radiation treatments. # – significant difference between 28°C and 20°C in the same treatment, P<0.05. PAR − photosynthetically active radiation; PA − photosynthetically active radiation plus UV-A radiation; PAB − photosynthetically active radiation plus UV-A and UV-B radiation.

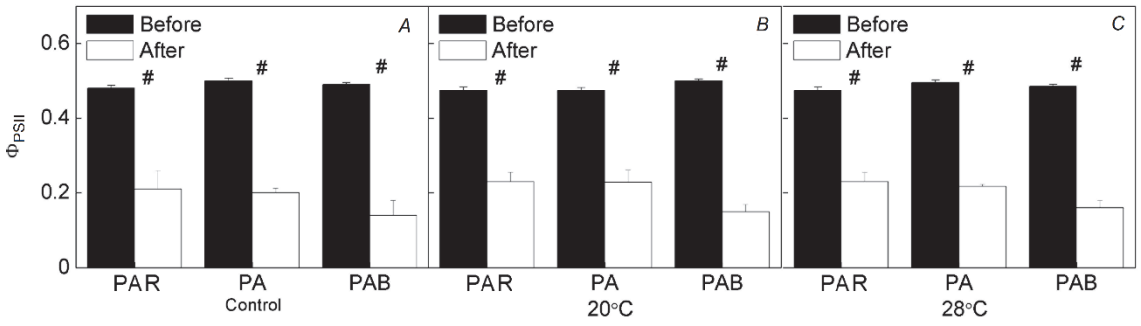

Fig. 4. The photochemical efficiency (Φ_{PSII}) of cultures before and after reexposure to solar radiation at 20°C and 28°C. # – significant differences before and after reexposure. PAR − photosynthetically active radiation; PA − photosynthetically active radiation plus UV-A radiation; PAB − photosynthetically active radiation plus UV-A and UV-B radiation.

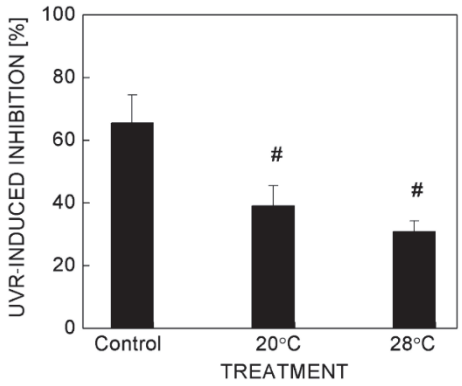

Fig. 5. UVR-induced inhibition based on photochemical efficiency. # – significant difference between 28°C and 20°C, $P<0.05$.

(Fig. 4), especially in the PAB treatment, with a value of 0.14, lower than that in either PAR or PA treatment. For the control cultures after 1-h radiation, the Φ_{PSII} in the PAB treatment was also the lowest, lower than that in either PAR treatment or PA treatment. There was no significant difference in Φ_{PSII} between the PAR and PA treatment. For the cells cultured at 28°C, there was a similar trend in Φ_{PSII} change as at 20°C (Fig. 4*B,C*). UVR-induced photoinhibition was 39% and 30.9% in the cells cultured at 20°C and 28°C, respectively, and each was significantly lower than that of the control cultures (65.5%, Fig. 5).

Discussion

The results of this study showed that both solar UVR and ambient temperature affected the morphology of *C. curvisetus*. Our results demonstrated that the combination of higher temperature and UV treatment reduced the number of the single cells in *C. curvisetus*. However, the percentage of both short and long chain *C. curvisetus* increased with temperature increment and UV treatment. Thus, we may anticipate that more and more *C. curvisetus* cells are going to appear in chains instead of single cells as more solar UV-B is arriving to the Earth and temperature is increasing in the future.

As previously reported, temperature strongly affected the growth rates of PAR-limited diatom species *via* affecting the composition of PUFA accounting for a high percentage in thylakoid membranes and chloroplast envelopes (Cohen *et al*. 1988, Reiter *et al*. 2014, Shatwell *et al*. 2014). The increment of temperature could decrease the percentage PUFA in membranes of diatoms and thus reduce the fluidity to acclimate to the increasing temperatures (An *et al*. 2013, Dodson *et al*. 2014). Moreover, Takabayashi *et al*. (2006) showed the chain length of PAR-limited diatom species *Skeletonema costatum* (*S. costatum*) strain showed dominance by longer chains under higher temperatures. This was inconsistent with our results, *i.e*., the higher temperature facilitated the dominance of the longer-chain *C. curvisetus*, indicating that the percentage of PUFA in the thylakoid membranes of *C. curvisetus* might decrease by increasing temperature.

However, the fact that the high PUFA content protects thylakoid membranes from oxidation (Kneeland *et al*. 2013) confirmed a vital role of PUFA in maintaining the integrity of thylakoid membranes, which contain PSII, and protecting membranes from being damaged by UV radiation (Ogata *et al*. 2013). Diatoms are excellent sources of long chain PUFAs, and UV radiation have been demonstrated to elevate the amount of PUFAs (Leu *et al*. 2006 a), or at least not to reduce the amount of PUFAs (Leu *et al*. 2006 b) These results showed that temperature and UV radiation might have complementary effects on PUFAs. In this study, we indicated that both the exposure to UV and the increment of temperature could increase the chain length of *C. curvisetus*.

Moreover, Smayda and Boleyn (1966) discovered that the sinking rate of a chain-shaped diatom *S. costatum* was inversely related to colony length, thus long chains were more resistant to sinking due to their increased surface area to volume ratio, accordingly facilitating their suspension in the upper part of water column, where light and nutrient conditions are more favorable for their growth. At 28°C under the PAR treatment, the percentage of the long chains was higher than that at 20°C. However, the percentage did not increase significantly when the solar irradiance was not enhanced, suggesting that temperature may also affect the effect of UVR on the chain length, which is consistent with the conclusion that morphological changes in *A. platensis* are temperature-dependent (Vonshak 1997, Gao and Li 2008).

In this study, the concentration of Chl *a*, a major green pigment involved in oxygenic photosynthesis for diatom, was reduced with the increasing UV irradiance at 20°C. This result was inconsistent with that from Beardall *et al.* (1997?) who studied the impact of UV-B radiation on *Selenastrum capricornutum* and *Aphanizomenon flos-aquae.* However, UVR-induced reduction in the Chl *a* concentration is not consistent for different plant species, as some plants, which have adopted to UV-B radiation, are able to retain high Chl contents during the UV-B exposure, and thus are more UV-tolerant (Bornman and Vogelmann 1991, Greenberg *et al*. 1997). Meanwhile, temperature also affects the Chl content, as Chl synthesis is temperature-dependent (Barrett *et al*. 1964). In this study, the Chl *a* concentrations under different treatments at 28°C were found to be always lower than their counterparts at 20°C, indicating a negative influence of high temperature

on Chl *a* in *C. curvisetus*.

The Φ_{PSII} dropped notably after reexposure to PAR radiation to about 0.2 comparing with 0.5 prior the re-exposures. It indicated that the PAR treatment heavily reduced the Φ_{PSII}, especially, PAR plus UV-A and UV-B at either 20 or 28°C. These results implied that UV-B might negatively impact Φ_{PSII} and this might be attributed to UV-B-induced degradation of D1 protein in PSII (Friso *et al*. 1995, Jansen *et al*. 1998, Guan *et al.* 2011). However, the main influence might contribute to the PAR due to the low dose of actinic light [50 μmol(photon) m^{-2} s^{-1}] used in this study. This was inconsistent with the result of our previous study (Guan *et al.* 2011) that short time (1 h) exposure of *C. curvisetus* cells to solar UVR decreased Φ_{PSII}, which may be attributed to the acclimation of *C. curvisetus* cells to long-term exposure to solar UVR.

The UVR-induced photoinhibition at 28°C was significantly lower than that at 20°C, suggesting a beneficial role of higher temperature in reducing UVR-induced photoinhibition. It might be attributed to the fact that synthesis of D1 protein involved in the repair process is temperature-dependent and higher temperatures can reduce the detrimental consequences of UV radiation (Gong and Nilsen 1989, Roos and Vincent 1998). Furthermore, the UVR-induced photoinhibition at either 28°C or 20°C was lower than that of the control cultures, indicating that cultures exposed to the long-time (6 d) UV radiation have developed an acclimation mechanism to the radiation and can diminish the UVR-induced photoinhibition to some extent; it could be related to MAAs increment in the cultured cells.

Synthesizing MAAs has been extensively adopted by phytoplankton as a selfprotection and acclimation strategy in response to UV, especially UV-B stress (Sinha and Häder 2008). In our study, MAAs was also detected in the cultures after their exposure for 6 d to radiation treatments at either 20 or 28°C. It is consistent with most studies that reported the synthesis of this substance after long-term exposure to UVR (Zheng and Gao 2009, Guan *et al.* 2011). Moreover, the MAAs concentration revealed an upward trend with the increasing irradiance at 20°C, indicating a positive correlation between the MMAs concentration and irradiance under this temperature, as reported by Zheng and Gao (Zheng and Gao 2009). However, this positive correlation was not observed at 28°C. Nevertheless, the MAAs concentrations under all the three radiation treatments at 28°C were higher compared to their counterparts at 20°C, indicating that higher temperature may boost the generation of MMAs.

Therefore, we can conclude that enhanced solar UVR can alter *C. curvisetus* morphology by extending the chains; it can also decrease the Chl *a* concentration and photochemical efficiency and cause more significant photoinhibition of *C. curvisetus* cultures. Meanwhile, temperature was found to affect also the chain length of *C. curvisetus* and its Chl *a* concentration, but the higher temperature can alleviate UVR-induced photoinhibition. Additionally, *C. curvisetus* developed a selfprotection mechanism to reduce the UV-induced damage by synthesizing MAAs, a UV-absorbing compound, which is a kind of acclimation to the long-term UV radiation.

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