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Effects of UV radiation on the photosynthesis of conchocelis of *Porphyra haitanensis* (Bangiales, Rhodophyta)

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Previous studies showed that photosynthesis and morphogenesis of *Porphyra* plants could be affected by solar UV radiation (UVR: 280–400 nm). However, little is known about the sensitivity of their conchocelis stage to UVR. We investigated the photosynthetic performance of *P. haitanensis* conchocelis under natural and simulated solar radiation with or without UVR and compared its responses among different developmental stages (vegetative and sporangial phases). High solar PAR accounted for most of the reduction of the effective quantum yield of PS II. Presence of UVR further reduced the yield by 53–55% in contrast to PAR alone treatment under solar radiation (UV-A of 33.2 W m^{-2} and UV-B of 0.85 W m^{-2}) or a xenon lamp (UV-A of 25.5 W m^{-2} and UV-B of 1.15 W m^{-2}). CO_2 fixation was more reduced by UVR in the free-living vegetative (38%) than in the sporangial conchocelis (14%). Photosynthetic tolerance of UVR increased from vegetative to sporangial phase, then to thallus stage, correlating with the increased contents of UV-absorbing compounds and/or differentiated structure.

KEY WORDS: CO_2 fixation, Conchocelis, Effective quantum yield, *Porphyra haitanensis*, UV-absorbing compounds, UVR

INTRODUCTION

Solar ultraviolet-B radiation (UV-B; 280–315 nm) reaching the Earth's surface has been increasing because of the depletion of the stratospheric ozone layer (Lubin & Jensen 1995; den Outer *et al.* 2005), which may affect many photosynthetic organisms because of its damage to the photosynthetic apparatus (Franklin & Forster 1997). Photosynthetic sensitivity to ultraviolet radiation (UVR: 280–400 nm) has been found to vary among life cycle stages of macroalgae. Early developmental stages are more sensitive to UVR than adult ones (Roleda *et al.* 2004; Bischof *et al.* 2006; Roleda *et al.* 2007) partially because of their simpler structure that allows easier penetration of UVR. Higher tolerance to UVR has also been found to be related to higher levels of UV-absorbing compounds, such as phlorotannins in *Fucus gardneri* (Henry & Van Alstyne 2004) and mycosporine-like amino acids (MAAs) in *Porphyra* (Misonou *et al.* 2003) and other algae (Oren & Gunde-Cimerman 2007).

Since *Conchocelis rosea* Batters was discovered as a phase in the life history of *Porphyra* spp. instead of an autonomous species (Drew 1949), the conchocelis stage (sporophyte) has been shown to form and release conchospores to initiate the thallus stage (gametophyte) (Tseng & Chang 1954), exhibiting a typical heteromorphic life history. Although the conchocelis lives beneath the inner layer of shells, it can be grown in a free-living state after liberated from the shells (Hollenberg 1958). Such a free-living conchocelis has been utilized for research as well as for seedling in *Porphyra* farming (Chen 1980; Sun & Tseng 1996; Tang & Fei 1998).

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Different life stages of *Porphyra* plants have been found to exhibit different photosynthetic characteristics. Light utilization efficiency in the thallus stage was much higher than that in conchocelis stage of *Porphyra yezoensis* (Zhang *et al.* 1997), and maximal net photosynthetic rate of the conchocelis was lower than that of the thalli (Tanaka 1985; Gao & Aruga 1987). Electron transfer inhibitor DCMU blocked the energy transfer from PS II to PS I in the thalli but not in the conchocelis of *P. yezoensis* (Pan *et al.* 2001). UVR was found to degrade photosynthetic pigments in both *Porphyra leucosticta* (Figueroa *et al.* 1997) and *Porphyra umbilicalis* (Aguilera *et al.* 1999) and to reduce the effective quantum yield of *P. leucosticta* (Figueroa *et al.* 1997), but it resulted in insignificant photoinhibition in *P. umbilicalis* (Gröniger *et al.* 1999). These studies have focused on the thallus stage of *Porphyra* spp. However, variation in UVR sensitivity among the different stages of *Porphyra* spp. has never been investigated. In nature, *Porphyra*-conchocelis lives in shells (Jao 1936) that are often found in shallow coastal waters and must be exposed to certain extent of UVR, but nothing is known about its photosynthetic responses to UVR. The aim of this study was to investigate the UVR impacts on the conchocelis stage of *Porphyra haitanensis* and compare the sensitivities among its different life cycle stages.

MATERIAL AND METHODS

Plant materials and maintenance

Free-living vegetative conchocelis of *P. haitanensis* T.J. Chang & B.F. Zheng was obtained from Laboratory of

Marine Genetics and Breeding, Ocean University of China and cultured in 500-ml flasks with filtered (Whatman GF/F) and sterilized seawater enriched with F medium (Guillard & Ryther 1962) at 20°C and 40 μmol m^{-2} s^{-1} of PAR (Tang & Fei 1997) (12 L : 12 D) in an incubator (GXZ-300D, Jiangnan Instruments Ltd, Ningbo, China). Half of the enriched seawater in each flask was renewed every week. Sporangial conchocelis was obtained by culturing the vegetative conchocelis at 25°C for 2 months.

Thalli of *P. haitanensis* were collected from farmed areas around Nan'ao Island (23°24′N, 117°07′E) during January 2005 and were transported to the laboratory within 4 h. Pieces of vegetative tissue (3 × 2 cm) were cut from the middle part of the thalli with a scalpel and maintained in filtered, aerated (0.4–0.5 litres min^{-1}) seawater at room temperature (15–20°C) and ≤ 50 μmol m^{-2} s^{-1} of PAR before being used for the experiments the next day.

Experimental design

In order to avoid the self-shielding in the colonies of conchocelis, samples of both vegetative and sporangial phases were cut to fragments of 0.5 to 1 mm length with a sterilized household mixer and were then suspended and cultured for 3 days for recovery from the mechanical injury, which immediately resulted in 60% reduction of PS II photochemical efficiency measured directly after cutting. Concentration of chlorophyll *a* (chl *a*) was within a range of 150–200 μg l^{-1} in measurements of effective quantum yield and diluted to 13–16 μg l^{-1} in the determination of photosynthetic carbon fixation. During the experimental period, the temperature was controlled at 25–28°C under the solar simulator by air conditioning or at 22–26°C for outdoor incubations in a flow-through water bath.

PHOTOCHEMICAL PERFORMANCE OF THE CONCHOCELIS: Time courses of inhibition and recovery of effective quantum yield in the free-living vegetative conchocelis and sporangial conchocelis were investigated during and after 1 h exposure to different radiation treatments with or without UVR. The recovery was carried out under dim white light (5–10 μmol m^{-2} s^{-1}). All samples were placed in 250-ml quartz tubes (inner diameter, 5.4 cm) containing the enriched seawater, which was aerated (0.3–0.4 litres min^{-1}).

P-E CURVES IN THE CONCHOCELIS: Photosynthetic carbon fixation vs irradiance curves were determined under PAR alone or PAR + UVR in the free-living vegetative and sporangial phases of the conchocelis. Maximum irradiances were 69 W m^{-2} (317 μmol m^{-2} s^{-1}) for PAR, 15.2 W m^{-2} UV-A, and 0.73 W m^{-2} UV-B. DNA-weighted UV-B irradiance was 0.07 W m^{-2} (normalized to 1.0 at 300 nm, according to Setlow 1974). Neutral density nets were used to obtain a series of irradiances, and triplicate samples were set for each light level. The parameters of the *P* vs *E* curves were obtained according to Eilers & Peeters (1988).

COMPARISON OF PHOTOCHEMICAL PERFORMANCE BETWEEN THE CONCHOCELIS AND THE THALLI: Diurnal changes in photochemical efficiency were compared between the free-living sporangial conchocelis and the thalli. The conchocelis was exposed to 50% of incident solar radiation by covering one layer of neutral density net, and the effective quantum yield was monitored every 1.5 h on 4 April 2006. As for the thalli, the experiment was conducted on 11 January 2005, and 5–6 thallus discs (3 × 2 cm) were put in each quartz tube (inner diameter, 5.4 cm) with 600 ml enriched aerated seawater. Every two tubes received the same radiation treatment, and six measurements were made for each determination.

Radiation measurements and treatments

Outdoor and simulated solar radiations were measured with a broad-band filter radiometer (ELDONET, Real Time Computers, Erlangen, Germany). This instrument measures every second irradiance with wavelength bands of 400–700 nm (PAR), 315–400 nm (UV-A) and 280–315 nm (UV-B) and records the data (means over 60 s) at 1-min intervals with a PC (Häder *et al.* 1999; Korbee Peinado *et al.* 2004). It has been certified as having a correspondence error less than 0.5% in comparison with the most accurate instrument (certificate no. 2006/BB14/1) and has been calibrated regularly with assistance from the maker. A solar simulator (SOL 1200 W, Dr. Hönle AG, Munich, Germany) was used to provide simulated solar irradiance for indoor experiments.

Radiation treatments with or without UVR were implemented under natural or simulated solar radiation by using UV-cutting off foils: (1) samples exposed to PAR alone (P), covered with an Ultraphan 395 foil (UV Opak, Digefra, Munich, Germany), receiving light above 395 nm; (2) samples exposed to PAR + UV-A (PA), covered with a Folex 320 foil (Folex, Dreieich, Germany), receiving irradiances above 320 nm; and (3) samples exposed to PAR + UV-A + UV-B (PAB), covered with an Ultraphan 295 foil (Digefra, Munich, Germany), receiving wavebands above 295 nm. The transmission spectra of these foils were published elsewhere (Korbee Peinado *et al.* 2004).

Measurements of quantum yield and photosynthetic carbon fixation

For chlorophyll fluorescence measurements, a portable pulse amplitude modulated fluorometer (Water-PAM, Walz, Effeltrich, Germany) was used to obtain the effective quantum yield of PSII ($\Delta F/F_m'$; Genty *et al.* 1989). For measurements in the free-living conchocelis, the Water-ED Emitter-Detector Unit was connected to the PAM-Control Unit. As for the thalli, the Water-EDF Fiberoptics-Emitter-Detector Unit was applied, and the optic fiber probe was directly pointed at the surface of the thalli at 5 mm distance. $\Delta F/F_m' = (F_m' - F_t)/F_m'$, where F_t is the current steady-state fluorescence that was measured with an actinic red light of 300 μmol m^{-2} s^{-1} under a modulated red light of 0.3 μmol m^{-2} s^{-1} and F_m' is the maximal fluorescence yield of light adapted samples measured by a 0.8 s saturating pulse (white light, approx. 5600 μmol m^{-2} s^{-1}).

For determination of photosynthetic carbon fixation, 8–9 ml of suspended conchocelis fragments (13–16 μg chl *a* l^{-1}) were put in a 10-ml quartz tube and inoculated with

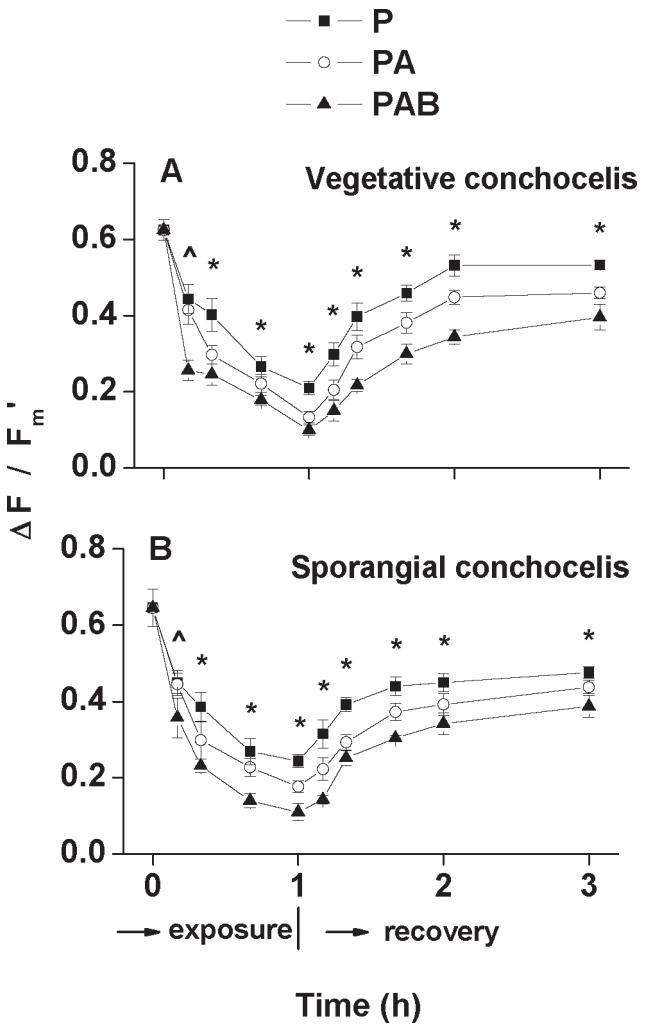

Fig. 1. Effective quantum yield of the free-living conchocelis of *Porphyra haitanensis* in its vegetative (A) and sporangial (B) stages when exposed to simulated solar irradiances (118 W m^{-2} PAR, 25.5 W m^{-2} UV-A and 1.15 W m^{-2} UV-B) under PAR, PAR + UV-A, and PAR + UV-A + UV-B for 1 h and then transferred to dim white light (5–10 μmol m^{-2} s^{-1}) for recovery. Data are the means ± *s* (*n* = 6). The symbol "*" indicates the differences among all treatments; "∧" indicates the differences between P and PAB treatments and between PA and PAB treatments.

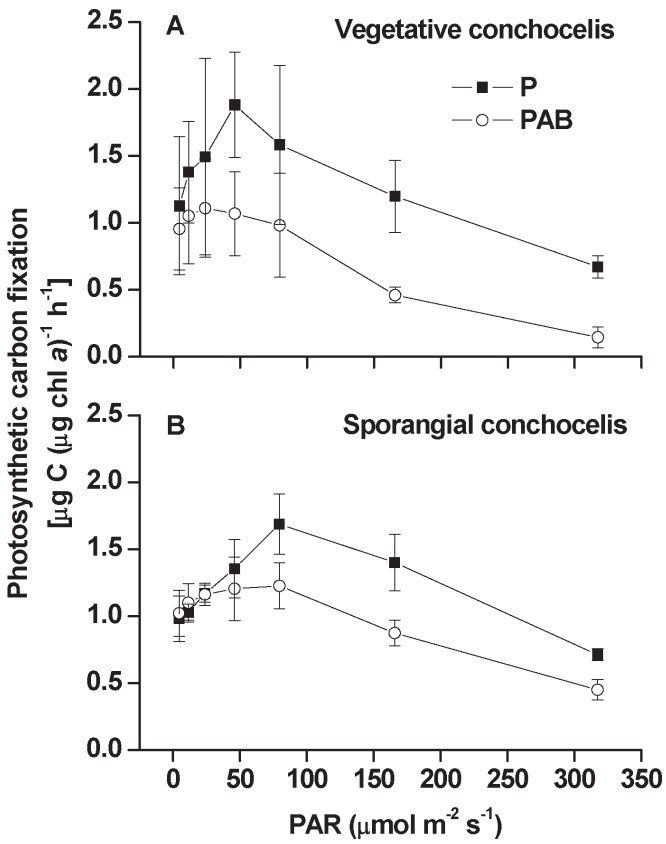

Fig. 2. Photosynthetic rates of the conchocelis of *Porphyra haitanensis* in its vegetative (A) and sporangial phases (B) when measured under PAR and PAR + UV-A + UV-B. Data are means ± *s* (*n* = 3). The ratios of PAR : UV-A : UV-B were 100 : 22.0 : 1.06.

0.1 ml-5 μCi (0.185 MBq) of labeled ($NaH^{14}CO_3$) sodium bicarbonate. After 2 h incubation, the samples were filtered onto Whatman GF/F glass fiber filters (25 mm), exposed to HCl fumes in darkness overnight to expel inorganic carbon as CO_2, and dried and dissolved in scintillation cocktail (PerkinElmer, Shelton, CT, USA) before the incorporated radioactivity counted with a liquid scintillation counter (LS 6500 Multi-Purpose Scintillation Counter (Beckman Coulter, Fullerton, CA, USA) (Holm-Hansen & Helbling 1995).

The relative photosynthetic inhibition (%) due to UVR, UV-A, or UV-B was calculated as

$$\mathrm{Inh_{UVR}}(\%) = (P_P - P_{PAB})/(P_P) \times 100,$$

$$\mathrm{Inh_{UV-A}}(\%) = (P_P - P_{PA})/(P_P) \times 100,$$

$$\mathrm{Inh_{UV-B}}(\%) = \mathrm{Inh_{UVR}}(\%) - \mathrm{Inh_{UV-A}}(\%),$$

where P_P, P_{PA}, and P_{PAB} represent the values after the exposure to PAR, PAR + UV-A, and PAR + UV-A + UV-B, respectively.

Determination of chl *a*, UV-absorbing compounds, and carotenoids

Chl *a*, UV-absorbing compounds (UVACs) and carotenoids were extracted in absolute methanol at 4°C for 24 h in darkness. After centrifugation at 5000 × *g* for 15 min, the supernatant was scanned with a spectrophotometer (Shimadzu UV-2501 PC, Shimadzu Corporation, Kyoto, Japan) to obtain the spectral absorption (250–750 nm). Triplicate samples of 100 ml free-living conchocelis were extracted, and another triplicate sample was dried (85°C, overnight) to obtain the dry mass. Vegetative tissues from the middle part of the thalli (about 0.1 g FW) were extracted, and the dry mass was measured separately as described previously. Chl *a* content was calculated according to Porra (2002), and the carotenoids concentration was estimated using the equations of Wellburn (1994). The concentration of UVACs was estimated on the basis of the absorption peak at 339 nm for the conchocelis or at 336 nm for the thalli by using the ratio of UVACs to chl *a* reported by Dunlap *et al.* (1995) and the chl *a* content. Concentrations of carotenoids and UVACs are normalized not only

Table 1. Photosynthetic parameters of free-living *Porphyra haitanensis* vegetative conchocelis and sporangial conchocelis under simulated solar PAR and PAR + UV-A + UV-B. P_{max}, the maximum photosynthetic rate (μg C [μg chl *a*]$^{-1}$ h^{-1}); E_k, the light saturation index (μmol m^{-2} s^{-1}); α, apparent photosynthetic efficiency (μg C [μg chl *a*]$^{-1}$ h^{-1}/μmol m^{-2} s^{-1}). Within each column of the data, values with different superscripts are significantly different at $P < 0.05$. Data were the means ± *s* ($n = 3$).

Conchocelis stages	Treatment	P_{max}	E_k	α
Vegetative	P	1.91 ± 0.07^{a}	35.05 ± 3.08^{a}	0.37 ± 0.14^{ab}
	PAB	1.19 ± 0.18^{bc}	17.26 ± 5.25^{b}	0.47 ± 0.19^{ab}
Sporangial	P	1.44 ± 0.10^{b}	47.03 ± 1.50^{c}	0.30 ± 0.06^{a}
	PAB	1.24 ± 0.05^{c}	22.43 ± 2.95^{b}	0.67 ± 0.14^{b}

to dry mass but also to chl *a*, for photosynthetic rates were normalized to chl *a*.

Statistics

All data were expressed as mean ± standard deviation ($n =$ 3–6). Statistical significance among different treatments was tested with *t* test or analysis of variance at a level of $P <$ 0.05.

RESULTS

When the free-living conchocelis was exposed to PAR (118 W m^{-2}, 543 μmol m^{-2} s^{-1}), PAR + UV-A (25.5 W m^{-2}) or PAR + UV-A + UV-B (1.15 W m^{-2}) for 1 h, its effective quantum yield was quickly reduced during the first 10-min exposure in both the vegetative and the sporangial phases (Fig. 1). Presence of UV-A or UV-B resulted in further reduction of the yield. UVR-induced inhibition was much higher in the vegetative conchocelis (42%) (Fig. 1A) than the sporangial phase (21%) (Fig. 1B) after 10 min of exposure. The yield decreased by 66% (P), 79% (PA) and 84% (PAB) in the vegetative conchocelis (Fig. 1A) and by 62% (P), 73% (PA) and 83% (PAB) in the sporangial phase (Fig. 1B) at the end of 1-h exposure. In both phases, UV-B–induced inhibition appeared earlier in 10 min than that caused by UV-A ($P < 0.05$); however, UV-A caused 11–21% higher inhibition than UV-B at the end of the exposures. After being transferred to dim light for recovery for 20 min, the effective quantum yield recovered to 64% (P), 51% (PA) and 35% (PAB) of the initial value (before the exposures) in the vegetative conchocelis and to 61% (P), 45% (PA) and 39% (PAB) in the sporangial phase (Fig. 1). The recovery showed biphasic kinetics with a steep increase during the first hour followed by a slower rise during the next hour. At the end of the 2-h recovery period, the yield in the conchocelis previously exposed to P, PA and PAB treatments reached 74–85%, 62–70% and 60–63% of the initial value prior to the exposures, respectively. No significant differences were found in the recovered photochemical efficiency between the vegetative and sporangial phases of the conchocelis.

The relationship of photosynthetic carbon fixation rate vs irradiance with or without UVR was established for the free-living vegetative and sporangial conchocelis (Fig. 2). The maximum photosynthetic rate (P_{max}) was 33% higher in the vegetative conchocelis than in the sporangial conchocelis under P treatment (Table 1). UVR reduced the P_{max} by 38% in the vegetative and by 14% in the sporangial conchocelis. The light-saturating point (E_k) was significantly lower in the vegetative than in the sporangial conchocelis under P treatment. Presence of UVR lowered the E_k values in both conchocelis stages. The apparent photosynthetic efficiency (α) was significantly ($P < 0.05$) higher in the sporangial with UVR than without it (Table 1). However, α was not different between the radiation treatments with or without UVR in the vegetative stage.

The photochemical efficiencies of the conchocelis (sporangial) and the thalli were compared under the natural solar radiation (Figs 3, 4). On 4 April 2006, the conchocelis received 50% of the incident solar radiation, with the maximal PAR of 184 W m^{-2} (846 μmol m^{-2} s^{-1}), UV-A of 33.2 W m^{-2} and UV-B of 0.85 W m^{-2}, respectively (Fig. 3A). In contrast, on 11 January 2005, the thalli were exposed to the full incident solar radiation, with the maximal PAR of 327 W m^{-2} (1504 μmol m^{-2} s^{-1}), UV-A of 48 W m^{-2} and UV-B of 1.3 W m^{-2}, respectively (Fig. 4A). The effective quantum yield decreased with increasing irradiance until noontime under all radiation treatments and then increased with decreasing irradiance in the late afternoon in both the conchocelis and the thalli (Figs 3B, 4B). In the conchocelis, the yield decreased to 17% (P), 10% (PA) and 4% (PAB) at noontime and recovered in the late afternoon to 33% (P), 28% (PA) and 21% (PAB) of the initial value, respectively (Fig. 3B). While in the thalli, no significant difference in the yield was found between P and PA treatment throughout the day (Fig. 4B), reflecting no additional harm caused by UV-A. The yield decreased to 30% (P), 32% (PA) and 22% (PAB) at noontime and recovered in the late afternoon to 53% (P), 68% (PA) and 57% (PAB) of the initial value, respectively (Fig. 4B). In contrast to the initial value in the morning, the effective quantum yield was reduced under all radiation treatments, and high levels of PAR accounted for most of the reduction of the yield. When compared with the value in samples exposed to PAR alone, UV-A or UV-B related inhibition was 31 or 22% in the conchocelis and 0 or 34% in the thalli in terms of the means for the daytime period. In both the conchocelis and the thalli, UV-B-induced inhibition was the highest at noontime compared to those in the early morning and late afternoon. Absorption characteristics (OD/dry weight) showed obvious difference in wavelength bands shorter than 360 nm, standing for (UVACs, between the conchocelis (Fig. 3C) and the thalli (Fig. 4C). The ratios of peak at 336–339 nm to 665 nm or 480 nm were higher in the thalli than the conchocelis.

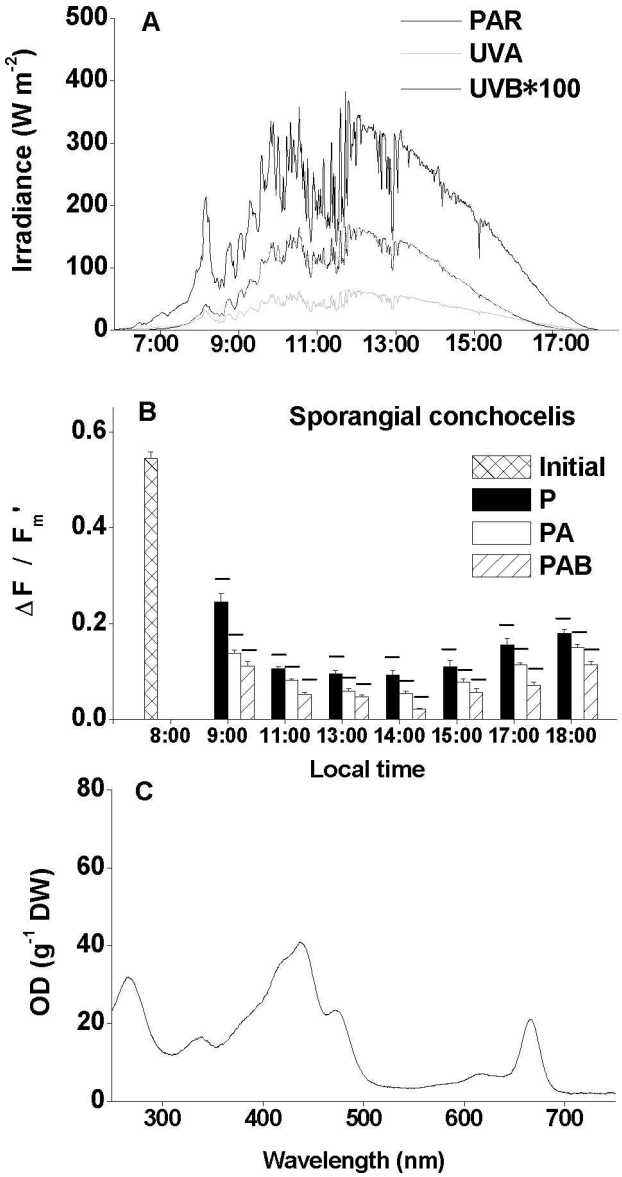

Fig. 3. (A) Irradiances of solar PAR, UV-A and UV-B*100 (W m^{-2}) at 50% of their natural levels on 4 April 2006 to which the conchocelis was exposed with the maximal PAR of 184 W m^{-2} (846 μmol m^{-2} s^{-1}), UV-A of 33.2 W m^{-2} and UV-B of 0.85 W m^{-2}, respectively. (B) Effective quantum yield of the sporangial conchocelis under the solar radiation treatments with or without UVR. (C) Absorption characteristics (OD/dry weight) of the sporangial conchocelis. Data are means ± *s* (n = 6). Horizontal lines over the histograms indicate the differences among treatments.

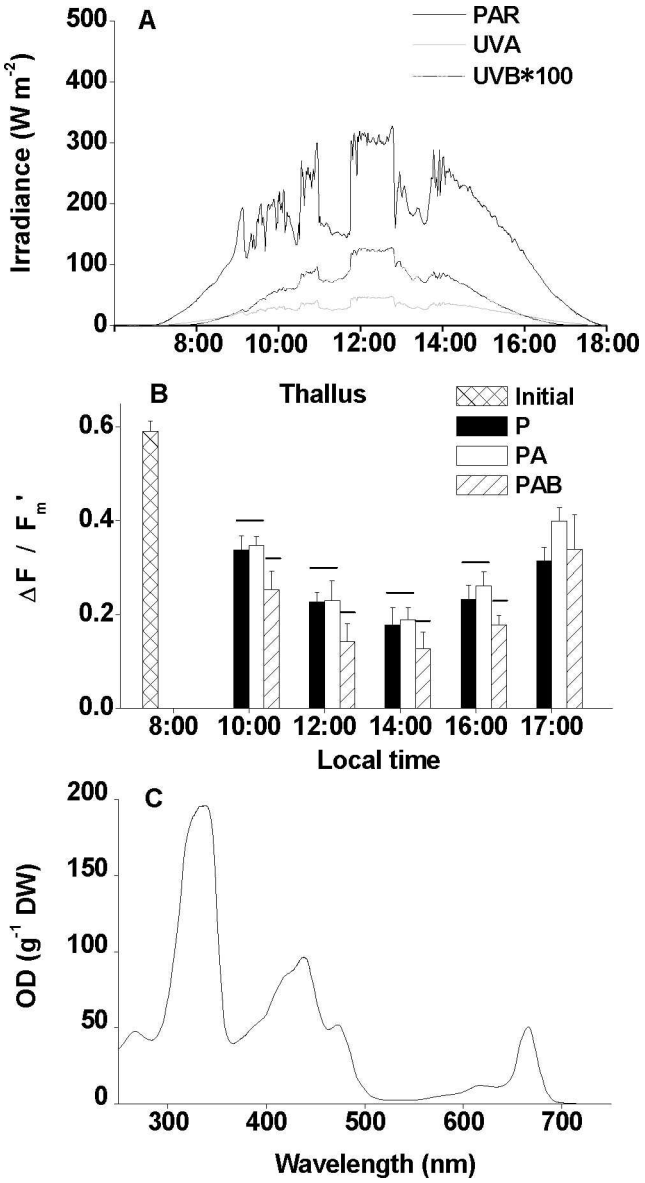

Fig. 4. (A) Irradiances of solar PAR, UV-A and UV-B*100 (W m^{-2}) on 11 January 2005 when *Porphyra haitanensis* thalli were exposed to. (B) Effective quantum yield of the thalli under PAR, PAR + UV-A or PAR + UV-A + UV-B. (C) Absorption characteristics (OD/dry weight) of the thalli. Data are the means ± *s* (n = 6). Horizontal lines over the histograms indicate the differences among treatments.

Contents of chl *a*, carotenoids and the absorptivity of UVACs were much higher in the thalli than those in the conchocelis and higher in the sporangial conchocelis than those in the vegetative stage (Fig. 5A). Both the ratios of carotenoids and UVACs to chl *a* for the thalli were much higher than those for the conchocelis, except for the ratio of carotenoids to chl *a* in the sporangial conchocelis (Fig. 5B). The ratios of carotenoids and UVACs to chl *a* were, respectively, 23 and 120% higher in the sporangial than those in the vegetative conchocelis.

DISCUSSION

The conchocelis stage of *P. haitanensis* showed higher sensitivity than the thallus to UVR as well as PAR of high levels. The conchocelis became more resistant to photodamage in terms of carbon fixation when it developed into the sporangial phase, although the PS II photochemical activity was identically affected by UVR. Photosynthetic carbon fixation could be more susceptible to UV-B damage than PS II electron transport (Franklin *et al.* 2003) since activity of carboxylation-related enzymes could be affected. Higher contents of carotenoids and higher absorptivity of UVACs were found in the sporangial conchocelis and the

thalli that showed less photoinhibition than the vegetative conchocelis. UVACs in *Porphyra* plants have been identified as mycosporine-like amino acids (MAAs) (Misonou *et al.* 2003; Helbling *et al.* 2004; Korbee Peinado *et al.* 2004) as well as in *Bangia* plants (Karsten & West 2000; Hoyer *et al.* 2001). MAAs absorb mainly in the UV-A waveband but are known to protect against both UV-A and UV-B as demonstrated in the red algae *Devaleraea ramentacea* (Karsten *et al.* 1999) and *Chondrus crispus* (Franklin *et al.* 1999). The absorptivity of UVACs in the thalli of *P. haitanensis* was about 40–100 times that of the conchocelis. Such a difference was also found between the sporophytic conchocelis and the gametophyte of *Bangia atropurpurea* and *B. fuscopurpurea* (Boedeker & Karsten 2005). On the other hand, acclimation to the indoor low PAR conditions of the conchocelis may also reflect high sensitivity to UVR in contrast to the thalli grown under natural solar radiation in the sea. Despite of the inhibitory effects of UVR, high levels of solar PAR were found to be responsible for most of the reduction of the photosynthetic yield in chonchocelis stage. *Porphyra* gametophytes that distributed at upper levels of intertidal zones were shown to be less photoinhibited since their acclimation to higher solar radiation (Herbert & Waaland 1988). Either for the natural shell-dwelling or indoor grown conchocelis, cells are acclimated to much lower levels of light compared with sea-farmed thalli.

Morphological differences among life stages can affect the energy transfer of UVR in the tissue, resulting in different responses to UVR in the red algae *Mastocarpus stellatus* and *C. crispus* (Roleda *et al.* 2004; Bischof *et al.* 2006). The thallus stage of *P. haitanensis* is foliose with the thickness of 60–110 μm, while the conchocelis stage is filamentous with the cell width of 2–4 μm in the vegetative and of 10–16 μm in the sporangial stages. Thus, longer path length for the absorbed UVR energy in sporangial and thallus cells might reduce its damaging effects, as UV-B-induced DNA damage was found to be lower in larger cells of diatoms (Karentz *et al.* 1991).

In the present studies, presence of UV-A resulted in either negative or insignificant effects on the photochemical efficiencies (Figs 3, 4) in the sporangial conchocelis or the thalli that contained higher levels of UVACs (Fig. 5). Such a phenomenon contrasts with the positive effects reported for UV-A on the photosynthetic carbon fixation of phytoplankton (Gao *et al.* 2007). The sporangial conchocelis exhibited much higher value of α under the treatment with UVR than without UVR (Table 1), suggesting possible utilization of UVR for the photosynthetic carbon fixation at low light levels.

In nature, the conchocelis stage of *Porphyra* spp. is found under the shading of the shell flake, receiving much reduced levels of solar PAR and UVR, while the thallus stage grows at upper parts of the intertidal zone, receiving higher levels of solar radiation. In addition, the vegetative conchocelis grows during late spring to develop to the sporangial stage during summer, when the solar radiation and temperature are increasing. Although the sporangial conchocelis and the thalli of *P. haitanensis* possess higher levels of UVACs and carotenoids (Fig. 5), which provide protection against UVR, and high levels of PAR, they still showed significant

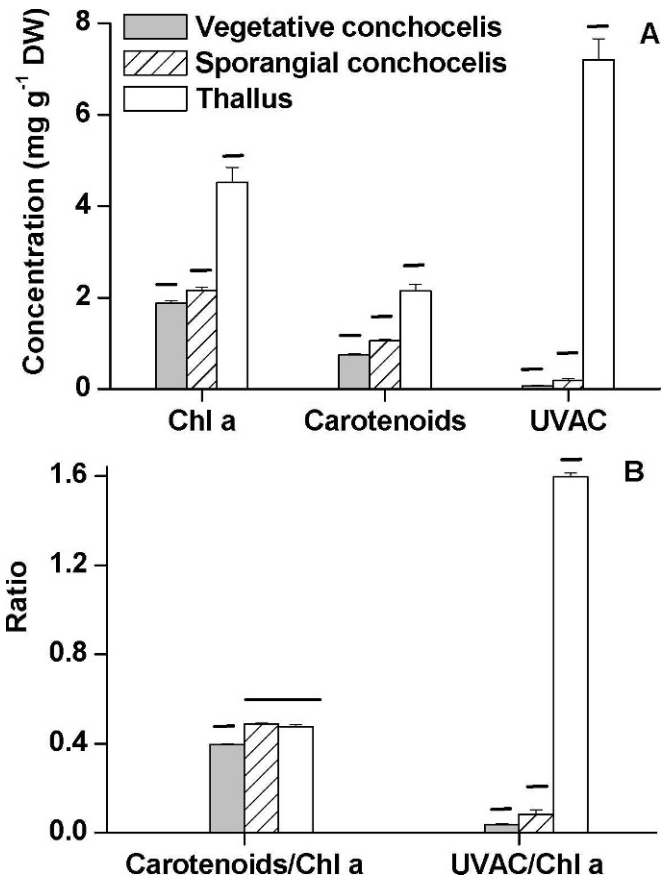

Fig. 5. Concentrations (mg g^{-1} dry weight) of chl *a*, carotenoids and UV-absorbing compounds (UVACs) (A), the ratios of carotenoids and UVACs to chl *a* (B) in the free-living vegetative conchocelis, sporangial conchocelis, and the thalli of *Porphyra haitanensis*. Data are means ± *s* (n = 3). Horizontal lines over the histograms indicate the differences among samples.

sensitivity to the incident levels of UV-B (Figs 3, 4). Increased solar UV-B irradiances at the Earth's surface have been reported in other latitudes besides the Antarctic areas (Bischof *et al.* 2006; McKenzie *et al.* 2007). Therefore, increased solar UV-B radiation may lead to more damage to both the conchocelis and the thallus stages of *Porphyra*. In the present study, the ratio of UV-B to PAR was 0.97–1.06% under the solar simulator and ranged 0.53–0.78% under sunlight. A higher proportion of UV-B during noontime or under the solar simulator did lead to higher or faster inhibition of photochemical efficiencies in the thalli as well as in the conchocelis.

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