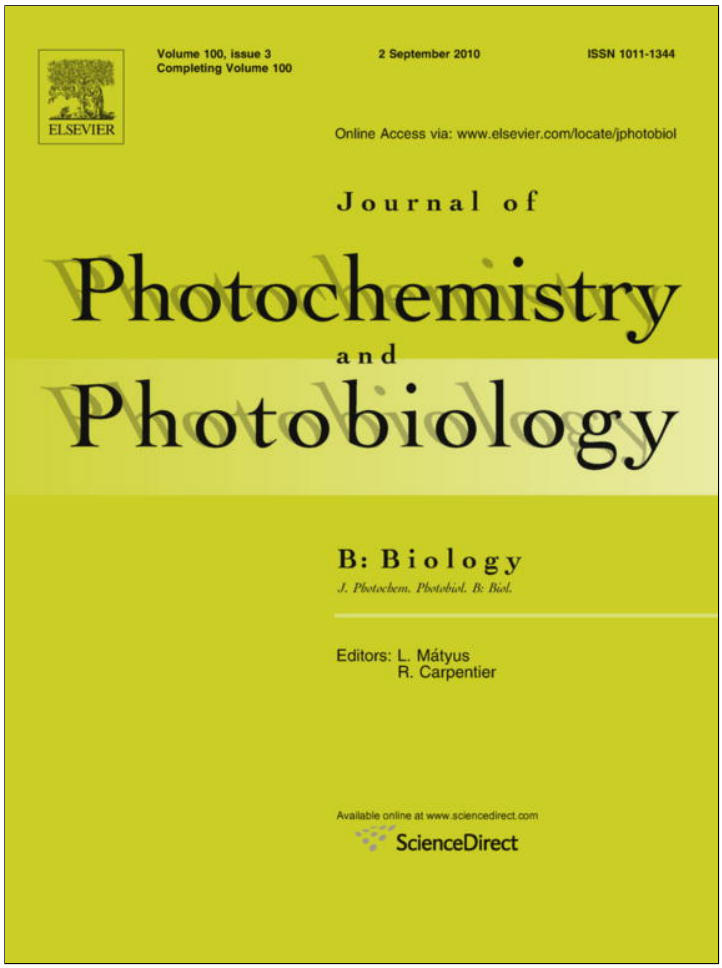

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UV-A enhanced growth and UV-B induced positive effects in the recovery of photochemical yield in *Gracilaria lemaneiformis* (Rhodophyta)

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ABSTRACT

The effects of solar UV radiation (280–400 nm) on growth, quantum yield and pigmentation in *Gracilaria lemaneiformis* were investigated when the thalli were cultured under solar radiation with or without UV for a period of 15 days. Presence of UV-A (315–400 nm) enhanced the relative growth rate, while UV-B (218–315 nm) inhibited it. The positive effect of UV-A and negative effect of UV-B counteracted to result in an insignificant impact of UVR on growth. During the noon period, both UV-A and UV-B resulted in the decrease of maximum quantum yield (Fv/Fm), but UV-B aided in the recovery of the yield in the late afternoon, reflecting that UV-B might be used as a signal in photorepair processes. UV induced the accumulation of UV-absorbing compounds (UVAC) to defend against the harmful UVR. However, the accumulation of UVAC took a much longer time compared to that previously reported, which was probably due to the lower levels of solar radiation and water temperature in the early spring period. Unknown UV-absorbing compounds (UVAC), which peaked at 265 nm, probably the precursor of MAAs ($UVAC_{325}$), accumulated under moderate levels of solar radiation and were transformed to MAAs under higher solar radiation.

1. Introduction

Marine photosynthetic organisms contribute to about half of global primary production. Macroalgae, mainly distributed in the coastal area, occupy less than 1% of the ocean area, but contribute to about 2% of the marine primary production [1]. Photosynthesis and growth of macroalgae can be influenced by global environmental changes, such as increase in atmospheric CO_2 concentration, SST and solar UV-B irradiance (280–315 nm) as well as sea level rise. Increased CO_2 concentrations to 1000 ppmv are shown to enhance the growth of some red algae [2,3] and photosynthesis of some intertidal red and brown species during emersion at low tides [4]. Increasing UV-B irradiance (280–315 nm) due to the thinning ozone layer in the stratosphere increases UV-related stresses on algae (see review by Häder et al. [5] and literatures therein).

UV radiation (UVR, 280–400 nm) are usually considered as a stressor to macroalage, damaging DNA molecules [6], reducing photosynthesis [7] and affecting enzymatic activities [8]. On the other hand, UV also shows undetected or even positive effects on algae. UVR is less damaging to photosynthesis than high PAR in several subtidal red algae [9]. No difference is found in the growth of *Ulva rigida* [10] and *Fucus serratus* [11] when the thalli are exposed to solar radiation with or without UV-B, in a long-term exposure. UV-A (315–400 nm) enhances DNA repair [12,13] and growth [14] in macroalgae, and is capable of driving the photosynthesis of phytoplankton and macroalgae in the absence of PAR [15–17].

Macroalgae protect themselves from UV by avoidance, repair and screening mechanisms [18–20]. They often exhibit high levels of UV-screening compounds, such as mycosporine-like amino acids (MAAs) [21,22], phlorotannins [23,24] and some unknown UV-B absorbing substance [25]. These compounds augment cellular content with increased UV exposure [23,25]. UV stimulates the accumulation of MAAs in *Gracilaria lemaneiformis* [26,27], *Chondrus crispus* [28] and *Porphyra columbina* [29]. The accumulation of MAAs depends on both dose and wavelength of solar radiation, higher accumulation being associated with higher doses and shorter wavelength [28,30].

In the previous studies, we found that the red alga *G. lemaneiformis* increased its cellular contents of MAAs in response to increased UV-exposures and nitrate concentrations [26], which alleviate the UV-induced inhibition of photosynthesis and growth; UV-A brought about enhancement of net photosynthesis [27], and increased availability of phosphate reverse the effects of UVA from the negative to the positive ones [31]. However, it remains unknown to what extent UVR would affect the photochemical machinery. The enhancement of photosynthesis as well as growth

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in *G. lemaneiformis* under moderate levels of UV-A could be attributed to either stimulated light or dark reactions of photosynthesis. In addition to the energy of UV-A that helps fuel PAR-limited photosynthesis [16], UV-A or/and UV-B might play positive roles in regulating the photochemical energy transfer. In this study, we evaluated the impacts of UV-A and UV-B on the photochemical efficiency and its recovery after UV-exposures, together with the impacts on growth rate, the balanced effects of UV-A and UV-B were discussed.

2. Materials and methods

2.1. Plant materials

G. lemaneiformis Bory was collected from areas where it is farmed at Nanao Island (116.6°E, 23.3°N), Shantou, China, in February, 2004. The collected thalli were transported to the laboratory within 3 h and maintained in a glass aquarium containing filtered natural seawater (salinity 32‰, enriched with 60 μM $NaNO_3$ and 6.0 μM NaH_2PO4) under 80 μmol photons m^{-2} s^{-1} at 20 °C (photoperiod: 12:12 h). The indoor maintenance under such a low level of PAR ensured that the thalli to be exposed to solar radiation were in similar photochemical status, showing a stable photochemical yield and Chl *a* content. Aeration was continuously provided and the seawater was renewed every other day before the thalli were used within a week for experiments under solar radiation.

2.2. Radiation treatments

Three different radiation treatments were implemented as follows: thalli receiving full solar radiation (PAB treatment) in uncovered quartz tubes; thalli receiving the irradiance above 320 nm (PA treatment) in quartz tubes covered with Folex 320 (Montagefolie, Nr. 10155099, Folex, Dreieich, Germany); and thalli receiving the irradiance above 395 nm (P treatment) in quartz tubes covered with Ultraphan film 395 (UV Opak, Digefra, Munich, Germany). The temperature was controlled at 18–20 °C, close to the SST in the coastal water of Shantou. Incident solar irradiance was continuously monitored using a broad band filter radiometer (Eldonet, Real Time Computer, Möhrendorf, Germany), which has three channels for photosynthetically active radiation (PAR, 400–700 nm), ultraviolet-A radiation (UV-A, 315–400 nm) and ultraviolet-B radiation (UV-B, 280–315 nm), respectively [32]. It measured the solar irradiance every second and recorded the means over each minute, and was calibrated with the support from the maker against a double monochromator spectroradiometer and a certified calibration lamp. The transmission spectra of the filters are shown elsewhere [26] and there is no significant difference (⩽4% transmission) in the PAR levels between the covered and uncovered tubes [15]. There was a 5 nm difference between the measured and exposed UV-A irradiance, which gives about a 2% higher percentage of UV-A than that the cells were actually exposed to.

2.3. Measurement of growth

Relative growth rate (RGR) was estimated as follows: $RGR = 100 * (lnN_t - lnN_0)/t$, where N_0 is the initial fresh weight and N_t that after t days. About 1.3 g (fresh weight) thalli were placed in a quartz tube (6.9 cm in inner diameter and 40 cm long, about 1.5 L) with the seawater. Fresh weight of the thalli was measured every 2 days after the seawater (enriched with 60 μM $NaNO_3$ and 6.0 μM NaH_2PO_4) was renewed. Aeration was provided continuously at 0.6 L min^{-1}.

2.4. Chlorophyll fluorescence measurements

Photochemical efficiency was determined as the maximal quantum yield (Fv:Fm) using a Plant Efficiency Analyser (Hansatech Instruments, England). Maximum excitation irradiance of 3200 μmol photons m^{-2} s^{-1} (peak wavelength 650 nm) was applied to gain the maximal fluorescence (Fm) and F_0 was attained by extrapolation of the initial few microseconds of the rise of the Kautsky curve back to t_0. Fv:Fm was used as an indicator of the maximal quantum yield of photosystem II [33], where Fv indicates

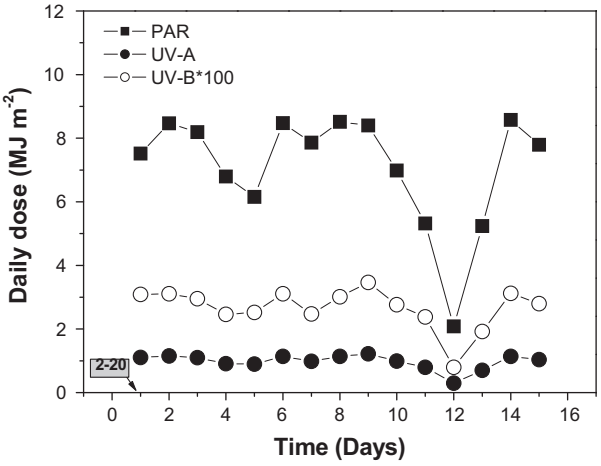

Fig. 1. Change in daily doses of solar PAR, UV-A and UV-B irradiance during the growth of *G. lemaneiformis* from February 19 to March 5, 2004.

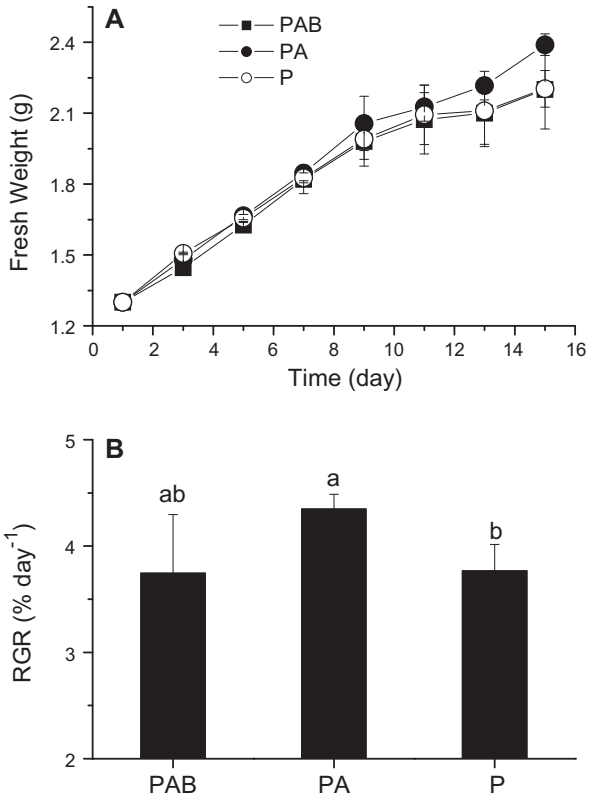

Fig. 2. Change in fresh weight (A) and RGR (B) of *Gracilaria lemaneiformis* thalli under different solar radiation treatments (PAB, PAR + UV-A + B; PA, PAR + UV-A; P, PAR) with time from February 20 to March 5. The RGR of *Gracilaria lemaneiformis* was attained by comparing the values before and after 15 days. Different letters show significant ($P < 0.05$) differences among the treatments.

the variable fluorescence (Fv = Fm − F_0). Fv:Fm of thalli treated under different radiation (P, PA and PAB treatments) was measured at 8:00, 12:30 and 17:30 at days 1, 5, 9 and 14 during the period February 19 to March 5, 2004. All the thalli were dark-adapted for 10 min before photochemical efficiency measurement.

2.5. Determination of UV-absorbing compounds and photosynthetic pigments

UV-absorbing compounds (UVACs) and photosynthetic pigments were determined at the end of the experiment. About 100 mg (FW) thalli was extracted in 10 mL absolute methanol for 24 h at 4 °C in darkness, which resulted in complete extraction [27]. The extract was centrifuged at 5000*g* for 10 min and absorbance of the supernatant was scanned from 250 nm to 750 nm using a spectrophotometer (UV 530, Beckman Coulter, Fullerton, CA, USA). UVACs and Chl *a* contents were obtained according to [34,35], respectively. Phycocyanin and phycoerythrin concentration was determined after extraction in 0.1 M phosphate buffer (pH 6.8) [36].

2.6. Statistical analysis

Differences among the treatments were tested using one-way analysis of variance (Turkey test) or T-test with SPSS (version 11.5). A confidence level of 95% was used in all analyses.

3. Results

From February 20 to March 5, 2004, the daily doses of solar PAR ranged from 2.08 to 8.57 MJ m^{-2}, with a daily average of 7.13 MJ m^{-2}; while that of UV-A ranged from 0.30 to 1.14 MJ m^{-2}, with a daily average of 0.98 MJ m^{-2}, and UV-B from 0.008 to 0.03 4 MJ m^{-2}, with the daily average of 0.027 MJ m^{-2} (Fig. 1). The noontime irradiances were 303 for PAR, 42 for UV-A and 1.4 W m^{-2} s^{-1} for UV-B. The ratio of UV-B to PAR ranged from 0.4 to 0.5%; whereas that of UV-A to PAR from 13% to 17%. During this period, the fresh weight of the thalli under different solar radiation treatments increased with time by about 69.2% (PAB), 83.8% (PA) and 69.4% (P) (Fig. 2A). RGR derived from the end changes in fresh biomass was higher in the thalli under PA than those under P or PAB treatments. UV-A enhanced the RGR by 15%, whilst UV-B inhibited it by about 16% (Fig. 2B).

The maximum quantum yield (Fv/Fm) of *G. lemaneiformis* thalli showed different extents of inhibition induced by UV during the morning (8:00), noon (12:30) and afternoon (5:30) (Fig. 3). UV-A resulted in significant decrease in the yield at days 9 and 14 during the noon period due to high daily doses (Fig. 3B and b). In the afternoon, the recovery of Fv/Fm was found in all treatments, and the Fv/Fm of the thalli receiving PAB treatments was significantly higher than those under PA treatments at days 5 and 9 (Fig. 3C). UV-B-induced inhibitions in the late afternoon were all negative, reflecting its positive role in photochemical recovery (Fig. 3c).

UVACs in the *G. lemaneiformis* thalli were detected at 265 and 325 nm (Fig. 4). The content of $UVAC_{325}$ increased significantly in the presence of UV-A or UV-A + B in contrast to the radiation treatment without UV (Fig. 5A). At day 15, the contents of $UVAC_{325}$ in the thalli were higher than those at day 12 when solar radiation was low, but the difference was only found in the thalli grown under the full spectrum of solar irradiance. The content of $UVAC_{265}$ showed the opposite pattern to that of $UVAC_{325}$ (Fig. 5A), showing their highest values at day 12 (rainy day), and then decreasing at day 15 (Figs. 4 and 5B).

No significant ($P > 0.1$) difference was found in Chl *a* content among the different solar radiation treatments (Fig. 6A), whilst PE and PC contents significantly ($P < 0.01$) decreased in the thalli in the presence of UV-A or UV-A + B, and there was no significant difference between PA and PAB treatments (Fig. 6B and C).

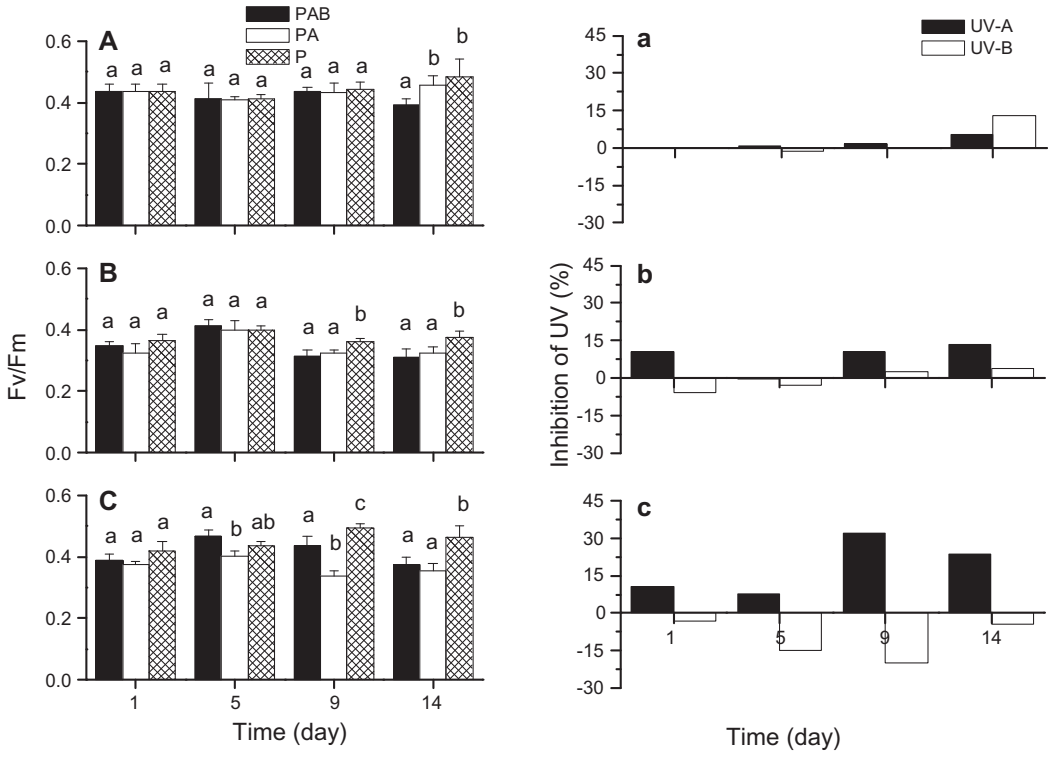

Fig. 3. Maximal quantum yield (Fv/Fm) of *Gracilaria lemaneiformis* thalli grown under different solar radiation treatments (PAB, PAR + UV-A + UV-B; PA, PAR + UV-A; P, PAR) measured during early morning (8:00, A), noon (12:30, B) and late afternoon (17:30, C). UV-A or UV-B induced inhibitions are correspondingly shown in parallel (a, morning; b, noon, c, afternoon). Different letters show significant ($P < 0.05$) differences among the treatments.

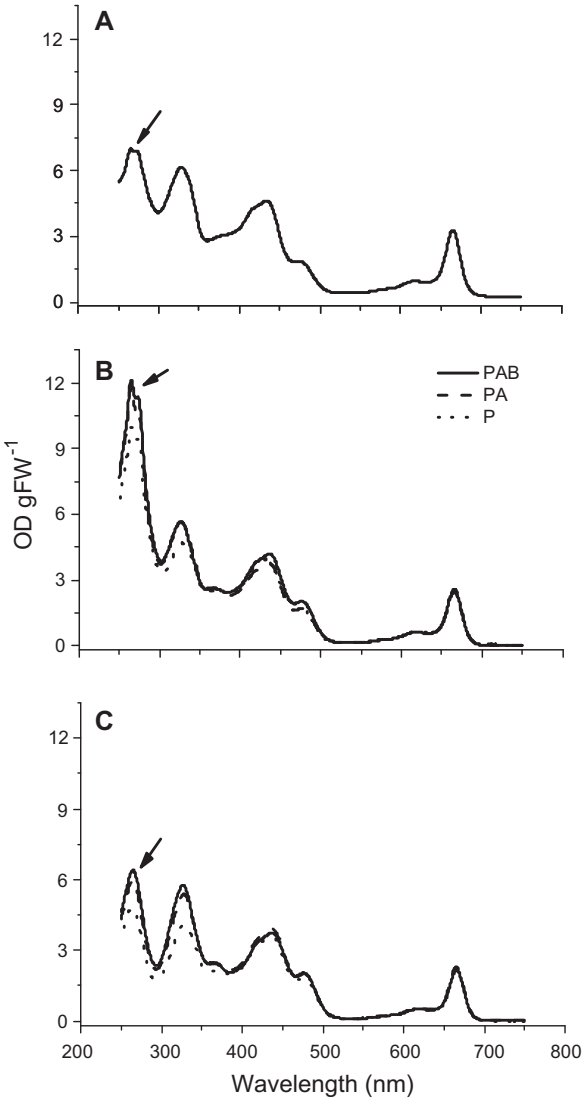

Fig. 4. Absorption spectra of the methanol-extracts from the *Gracilaria lemaneiformis* thalli grown under different radiation treatments (PAB, PAR + UV-A + UV-B; PA, PAR + UV-A; P, PAR). A, the initial levels at day 1; B, the values obtained at day 12; C, at day 15. Arrows indicate the absorption peak at 265 nm.

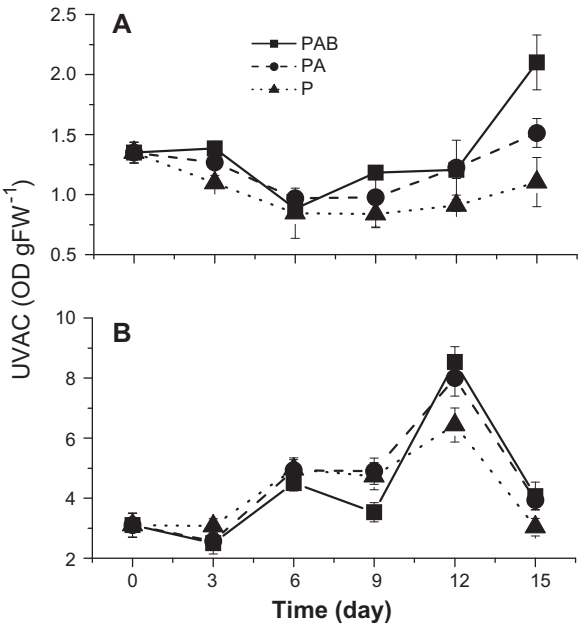

Fig. 5. The contents of $UVAC_{325}$ (A) and $UVAC_{265}$ (B) of *Gracilaria lemaneiformis* thalli grown under the radiation treatments PAB, PAR + UV-A + UV-B; PA, PAR + UV-A; and P, PAR during the period February 20–March 5, 2004.

4. Discussion

Solar UVR is usually regarded as a negative environmental factor. In this study, high levels of UV-A or UV-B decreased the photochemical efficiency of *G. lemaneiformis*. However, presence of UV-A significantly enhanced the growth rate at the end of the exposure that lasted for 15 days, and presence of UV-B appeared to play a positive role in recovery of the photochemical efficiency during late afternoon when solar radiation decreased. The contents of phycoerythrin and phycocyanin decreased, while that of UVACs increased in the presence of UV, reflecting UV-induced bleaching effects and a protective response. Excessive levels of PAR or high levels of UV-A or UV-B are known to cause damage to D1 protein in photosystem II [37], which leads to decreased photochemical efficiency. Nevertheless, solar UV-B irradiance could be involved in the recovery process of the photosynthetic machinery in *G. lemaneiformis*. Such beneficial effects of UV-B on the recovery of photoinhibition are reported in the brown alga *Dictyota dichotoma* [38]. UV-B irradiance might be used as a signal to induce photoprotective and/or photorepair processes. UV-B stimulates the turnover of the D1 protein in the higher plants *Spirodela oligorrhiza* [39] and *Brassica napus* [40]. Higher maximum quantum yields were reported in several subtidal red algae during recovery after exposure to solar UV-A or UV-A + UV-B as compared with exposure to PAR alone or PAR + UVR [11].

Change in growth rate reflects the total net balance among the effects of an environmental stress on the biochemical and physiological processes within the cell. Natural or enhanced levels of UVR are known to inhibit growth of macroalgae [10,25,41,42]. However, moderate levels of UV-A stimulate photosynthesis and growth in both micro and macroalgae [15,27]. In the present study, the presence of UV-A stimulated the growth rate by 15% in *G. lemaneiformis*. During the experimental period of late February to early March, solar radiation (daily dose) was lower by about 12% compared to the previous study period from April 9th to 17th [27]. The reduced level of UV-A must have ministered to the alga's photosynthesis and led to an enhanced growth rate (Fig. 2). In *U. rigida* [10] and *F. serratus* [11], no difference is found in growth between samples exposed to solar radiations with or without UV-B in long-term experiments. UV-A stimulates the growth rate in the brown alga *Fucus gardneri* embryos [14], aids in photorepairing UV-B-induced damage in *Rhodymenia pseudopalmata* [12] and enhances the carboxylation efficiency in *G. lemaneiformis* under phosphorus-replete conditions [31].

Photosynthetic antennae are highly sensitive targets of solar UV radiation. In the present study, UVR decreased the concentrations of phycoerythrin (PE) and phycocyanin (PC), but did not affect the content of Chl *a*. PE and PC are known to be more easily destroyed by UV [43,44]. To counteract the photodamage induced by UV, photosynthetic organisms have developed a number of photoprotective compounds, such as scytonemins in cyanobacteria, MAAs in cyanobacteria and algae and several other UV-absorbing substances of unknown chemical structure [45]. *G. lemaneiformis* regulates its content of MAAs quickly when it is transferred from indoor low light to outdoor high solar radiation, or vice versa [26]. In the present study, accumulation of MAAs took a much longer time to reach their maximum compared to the results of a previous study [26]. This was probably due to the lower

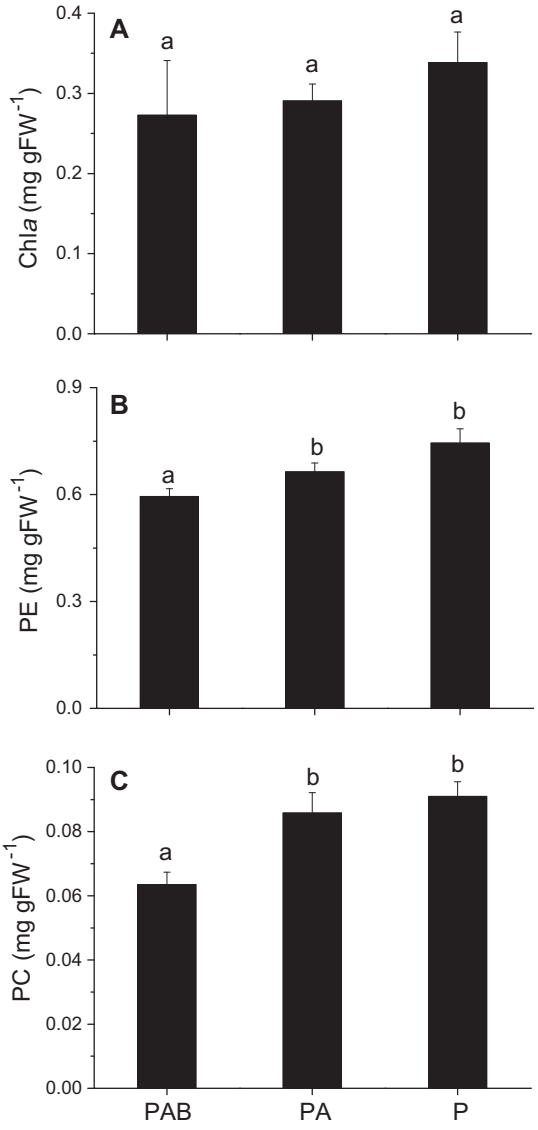

Fig. 6. The contents of phycoerythrin (PE, A), phycocyani (PC, B) and Chl *a* (C) of *Gracilaria lemaneiformis* thalli grown under different radiation treatments with or without UV (PAB, PAR + UV-A + UV-B; PA, PAR + UV-A; P, PAR) after 15 days culture. Different letters show significant ($P < 0.05$) differences among the treatments.

levels of solar radiation and temperature during the study period. The biosynthesis of MAAs is suggested to be associated with the shikimate pathway [46]. In this work, unknown UV-absorbing compounds peaked at 265 nm were found (Fig. 5B), which decreased rapidly with the increase of $UVAC_{325}$. These unknown UVACs were also detected previously [26]. It was possible that the unknown UVACs accumulated under moderate levels of solar radiation and transformed to MAAs upon exposure to higher solar radiation. The $UVAC_{265}$ could be the precursor of $UVAC_{325}$, the synthesis of which requires higher levels of solar radiation.

Acknowledgements

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