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Research Note

Photosynthetic contribution of UV-A to carbon fixation by macroalgae

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Abstract: Previous studies showed that energy of ultraviolet light A (UV-A) (315–400 nm) could be used for photosynthesis by some macroalgae; however, little has been documented on the extent of such photosynthetic contribution among different macroalgal taxa. We selected 11 macroalgal species, representing red, brown and green phyla, and investigated their ability to utilize UV-A for photosynthesis. Our results showed that, in the absence of photosynthetically active radiation (PAR), UV-A alone triggered photosynthetic carbon fixation rates in all the selected species. The gross photosynthetic rates of the tested macroalgae when exposed to UV-A ranged from 6.5 ± 0.3 to 52.3 ± 1.8 μmol C g (fresh weight)$^{-1}$ h^{-1}, with the highest rate found in the green alga *Ulva lactuca* Linnaeus. The ratio of gross photosynthesis driven by UV-A alone to that by saturating PAR varied from 14% to 22%. The present work demonstrated that macroalgae are capable of utilizing UV-A irradiance to drive photosynthetic carbon fixation, and this was consistent for all the species tested across green, red and brown algae.

Key Words: Macroalgae, Photosynthesis, Photosynthetic pigments, UV-A

INTRODUCTION

In aquatic ecosystems, photosynthetic production by algae and cyanobacteria contributes to nearly 50% of the global primary production (Behrenfeld *et al*. 2006), and most of it is due to phytoplankton. However, macroalgae in coastal waters also play an important role in the carbon cycle. Since most macroalgae are distributed in shallow waters, they are usually exposed to high solar visible (400–700 nm) and ultraviolet (UVR, 280–400 nm) radiation. Therefore, it is of general concern to see how solar UV irradiance influences primary production of macroalgae (Groniger & Häder 2001). Previous studies have documented the impacts of UVR on photosynthetic production of macroalgae (Hanelt *et al*. 1997; Flores-Moya *et al*. 1999; Wiencke *et al*. 2000; Dring *et al*. 2001; Garbary *et al*. 2004; Gao & Xu 2010).

Solar UV-B radiation is known to inhibit the growth rate (Altamirano *et al*. 2000; Han & Han 2005; Davison *et al*. 2007), reduce photosynthetic performance (Häder *et al*. 2001; Gao & Zheng 2010; Xu & Gao 2012), damage photosynthetic pigments (Aguilera *et al*. 1999; Vass 1997), key enzymes (Bischof *et al*. 2002) and even DNA molecules (Buma *et al*. 2003) and affect community structure (Bischof *et al*. 2006). It can also affect the early development (Huovinen *et al*. 2000, Henry & Van Alstyne 2004) and spore germination (Wiencke *et al*. 2000; Han *et al*. 2004; Jiang *et al*. 2007) of macroalgae. On the other hand, UV-A (315–400 nm) can stimulate photosynthesis and growth in some macroalgae (Henry & Van Alstyne 2004; Gao & Xu 2008; Xu & Gao 2010). Although high levels of UV-A inhibit growth and photosynthesis of macroalgae (Xu & Gao 2010), moderate levels of UV-A radiation can enhance the growth of embryos of the brown alga *Fucus gardneri* Silva (Henry & Van Alstyne 2004) and stimulate morphogenesis of *Porphyra haitanensis* Chang & Zheng (Jiang *et al*. 2007). UV-A was also found to enhance the photorepair of UV-B-induced DNA damage (Buma *et al*. 2003). Halldal (1964) detected photosynthetic O_2 evolution when a green alga *Ulva lactuca* Linnaeus and a red alga *Trailliella intricat*e Batters were exposed to UV-A. However, little has been documented on the contribution of solar UV-A to photosynthetic production of macroalgae, and there has been no comparison of this among different phyla.

To understand to what extent solar UV-A radiation contributes to photosynthetic production in different phyla of macroalgae, we investigated photosynthetic carbon fixation and O_2 evolution under UV-A alone or under photosynthetically active radiation (PAR) alone in 11 macroalgal species and estimated their UV-A-utilizing ability relative to PAR utilization.

MATERIAL AND METHODS

Eleven macroalgal species were used in the experiment, five red macroalgae, *Porphyra haitanensis* Chang & Zheng, *Gymnogongrus flabelliformis* Harvey, *Gracilaria lemaneiformis* (Bory) Weber-van Bosse, *Pterocladia tenuis* Okamura and *Laurencia okamurai* Yamada; four brown macroalgae, *Dictyota dichotoma* (Hudson) Lamouroux, *Sargassum hemiphyllum* (Turner) C.Agardh, *Sargassum fusiforme* (Harvey) Setchell and *Colpomenia sinuosa* (Mertens *ex* Roth) Derbès & Solier; and two green macroalgae, *Ulva lactuca* Linnaeus and *Codium fragile* (Suringar) Hariot. All macroalgal species

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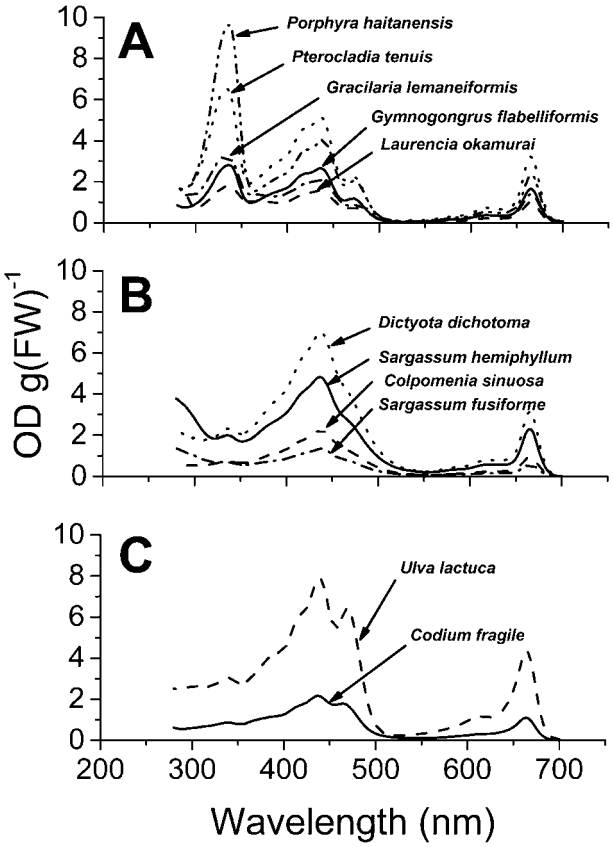

Fig. 1. Absorption spectra of red (A), brown (B) and green (C) macroalgae. The thalli were extracted in 10 ml of absolute methanol for 24 h at 4°C in darkness.

were collected from the coastal water of Nanao Island, Shantou (116.6°E, 23.3°N), China. The collected plants were cleaned of epiphytes and maintained in the laboratory for 24 h in filtered natural seawater (30‰ salinity) at 20°C, and 100 μmol photons m^{-2} s^{-1} of PAR (12:12 light:dark) before conducting the experiments.

Photosynthetic carbon-fixation rates were determined on the inorganic carbon removal from the seawater during incubations (Gao *et al.* 1993). The measurement was carried out on clear sunny days at midday (11:30 AM to 12:30 PM). Solar irradiance levels during the incubation periods were about 461.4 W m^{-2} for PAR (about 2290 μmol photons m^{-2} s^{-1}), 83.6 W m^{-2} for UV-A and 2.6 W m^{-2} for UV-B, respectively. About 0.1 g of thalli was placed into each quartz tube containing 15 ml of filtered seawater. The quartz tubes were maintained in an opaque plastic box, in the top of which a PAR cutoff filter, UG11 (Schott, Mainz, Germany), and a Folex 320 cutoff foil (Montagefolie, Nr. 10155099, Folex, Dreieich, Germany), were sealed to screen PAR and UV-B irradiance. The UG11 filter cuts off 100% of PAR and transmits 53.7% of UV-A and 63.8% of UV-B. The Folex 320 cutoff foil blocks 100% of UV-B and allows 70.5% of UV-A to go through. The intensity of UV-A that the thalli actually received was about 31.6 W m^{-2}. The box was maintained in a water bath in which water temperature was controlled at 20°C ± 1°C using a cooling unit (CAP-3000, Rikakikai, Tokyo, Japan). Dissolved inorganic carbon concentration ([DIC]) of seawater was measured by a total organic carbon (TOC) meter (TOC-5000, Shimadzu Corp., Kyoto, Japan) that automatically measures DIC as well as total carbon in a liquid. The photosynthetic carbon-fixation rates were estimated from the following equation:

$$\mathrm{Pn} = V \times (\mathrm{C1} - \mathrm{C2}) \times T^{-1} \times \mathrm{FW}^{-1}$$

where V is the volume of seawater in the tube, C1 and C2 are DIC concentrations of seawater before and after the incubation over a period of T (min), respectively, and FW is the fresh weight of the thalli.

During the measurements, the pH of the seawater medium under the PAR treatment changed rapidly when similar amounts of the algal thalli were used as under UV-A with the carbon removal method. As a consequence, we used the oxygen evolution method, which allowed for changes in O_2 concentration over a short time (less than 10 min) with negligible change of pH. Accordingly, photosynthetic O_2 evolution of the macroalgae under PAR alone were measured with a Clark-type oxygen electrode (YSI model 5300, Yellow Springs, Ohio USA), and the thalli were cut into fragments and kept in seawater for about 2 h to minimize the damage from cutting. About 0.03–0.2-g samples were transferred to the cuvette containing 8 ml of filtered fresh seawater, and the temperature was controlled at 20°C using a cooling unit. The light for photosynthetic O_2 evolution and dark respiration rate measurements were set as 850 μmol photons m^{-2} s^{-1} (saturation light) and zero (aluminum foil covered), respectively.

The samples for pigment analyses were stored at –20°C after the determination of their FW. About 200 mg (FW) of thalli were extracted in 10 ml of absolute methanol for 24 h at 4°C in darkness. After centrifugation at 5000 × *g* for 10 min, the extract was used to obtain absorption spectra with a scanning spectrophotometer (UV 530, Beckman Coulter, Fullerton, California, USA) (for red macroalgae, phycobiliproteins were not extracted with this solvent because they are water soluble). Chlorophyll *a* (Chl *a*) concentration was estimated according to Wellburn (1994).

Incident solar irradiance was monitored using an ELDONET radiometer (Real Time Computer, Möhrendorf, Germany) with three channels, respectively, for PAR (400–700 nm), UV-A (315–400 nm) and UV-B radiation (280–315 nm). The device was installed on the roof of the Nan'ao Marine Biological Station of Shantou University, where the experiments were carried out.

Gross photosynthetic rate of the macroalgae was attained by adding the dark respiration rate to net photosynthetic rate (assuming the ratio of photosynthetic O_2 evolution to net carbon fixation rate as 1). The data were expressed as means ± standard deviation (SD). Statistical significance of the data was tested with a one-way analysis of variance, and subsequently with Tukey's post hoc test. A confidence level of 95% was used in all analyses.

RESULTS

In terms of the absorption spectra of the thalli (Fig. 1), the red algae showed an absorption peak in the UV band (300–

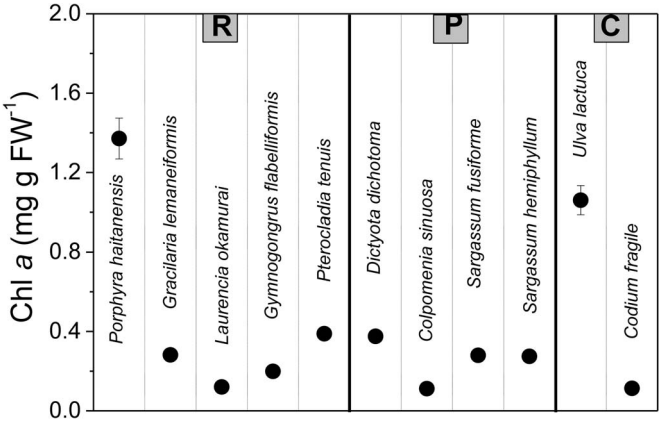

Fig. 2. Chl *a* contents of 11 macroalgae. Vertical bars represent ± SD of the means ($n = 5$). R, P and C represent Rhodophyta, Phaeophyta and Chlorophyta, respectively.

360 nm), with *Porphyra haitanensis* having the highest among all tested species. Such a UV absorption peak was not found in the green and brown macroalgae. The Chl *a* contents of all the species ranged from 1.37 ± 0.10 to 0.11 ± 0.01 mg g $(FW)^{-1}$. *Porphyra haitanensis* showed the highest concentration of Chl *a* among all the species ($P < 0.05$), and *Ulva lactuca* showed the second highest Chl *a* content (Fig. 2). The gross photosynthetic rates of the tested algae ranged from 6.5 ± 0.3 to 52.3 ± 1.8 μmol C g $(FW)^{-1}$ h^{-1} under the UV-A-alone radiation treatment. Different species showed differential capabilities to use UV-A irradiance (Fig. 3A). The green alga *U. lactuca* had the highest gross photosynthetic rate, and *P. haitanensis* also showed the relative higher value compared with other tested species ($P < 0.001$). The brown alga *Colpomenia sinuosa* had the lowest gross photosynthetic rate of all the tested species. Similar trends were found in the gross photosynthetic rate driven by PAR (Fig. 3B). The ratio of gross photosynthesis driven by UV-A alone to that by saturating PAR varied from 14% to 22% (Fig. 4).

DISCUSSION

Visible wavelengths (400–700 nm) have been considered as PAR for decades; however, there is some evidence that the energy for photosynthesis can be extended to the infrared region (Chen *et al*. 2010) or UV bands (McLeod & Kanwisher 1962; Halldal 1964; Gao *et al*. 2007; Xu & Gao 2010). UV-A (320–400 nm) was not included in the definition of PAR because of its limited potential as one of the energy sources in solar radiation (Amthor 2010). Another important aspect is that UV-A can inhibit electron transport of photosystem II 60-fold more effectively than PAR per unit quanta (Vass *et al*. 2002) by similar mechanisms of UV-B damage. However, our results showed that all species can utilize the energy of UV-A irradiance to drive macroalgal photosynthesis.

The species with higher content of Chl *a* showed higher UV-A-driven gross photosynthetic rates; therefore, it is most

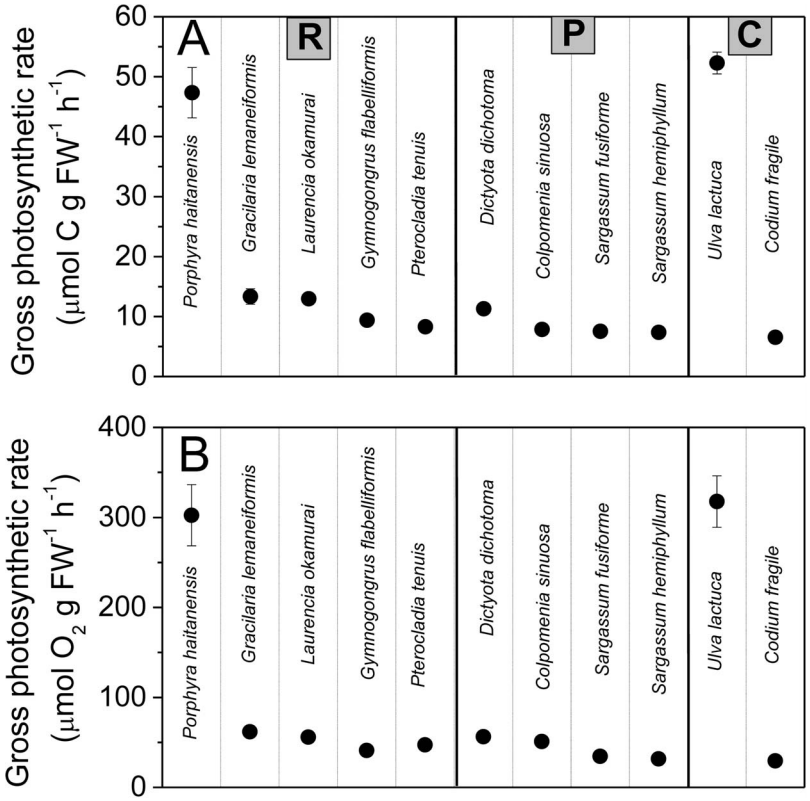

Fig. 3. Gross photosynthetic rates of the 11 macroalgae under UV-A alone (A) and PAR (B). Vertical bars show means ± SD, $n = 3$. R, P and C represent Rhodophyta, Phaeophyta and Chlorophyta, respectively.

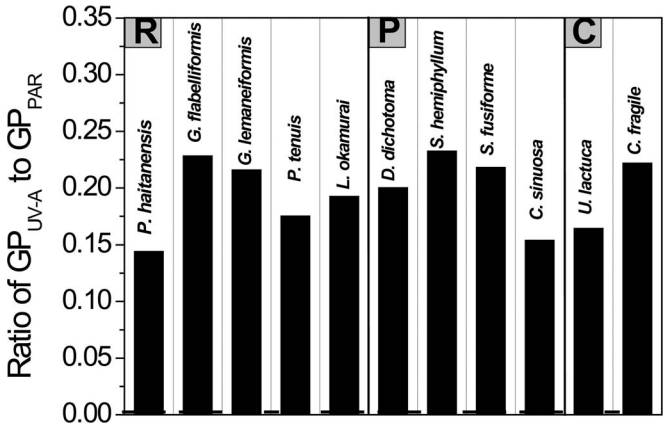

Fig. 4. The ratio of photosynthetic rates driven by UV-A (GP_{UV-A}) to that by PAR (GP_{PAR}). The levels of UV-A and PAR are 31.6 W m^{-2} and 850 μmol photons m^{-2} s^{-1}, respectively. R, P and C represent Rhodophyta, Phaeophyta and Chlorophyta, respectively.

likely that Chl *a* absorbs some extent of UV-A in view of its absorption tails into the UV band (Harris & Zscheile 1943). Alternatively, UV-A can be used indirectly via the carotenoid lutein (Turnbull *et al*. 2013). On the other hand, phycobiliproteins, the main antenna pigment in red macroalgae, have small absorption peaks within the UV band, which might contribute to UV-driven photosynthetic activities (Neori *et al*. 1986, 1988; Gao & Xu 2008). Another possibility is that macroalgae use UV-A irradiance for absorption by UV absorption compounds, such as mycosporine-like amino acids (MAAs), that absorb UV-A within the 310–360-nm waveband, to function as antenna pigments channeling the energy to the photosynthetic apparatus (Sivalingam *et al*. 1976, Gao *et al*. 2007). This is despite the fact that UV energy absorbed by MAAs is dissipated nonradioactively and considered hardly available for photosynthesis (Shick & Dunlap 2002).

The ratio of solar UV-A to PAR varies from 14% to 21% during different seasons in the study area (Wu *et al*. 2010). This ratio is coincidentally close to the photosynthetic contribution ratio of UV-A to PAR (Fig. 3). Although apparent photosynthetic efficiency for UV-A is significantly lower than that of PAR, the maximal rate of photosynthetic O_2 evolution driven by UV-A alone in *Gracilaria lemaneiformis* can amount to 18% of that by PAR. Coincidentally, such a photosynthetic contribution ratio is close to that of UV-A to PAR in natural solar radiation. The ratios can only reflect the potentialities of the macroalgae to the UV-A energy, since UV-A irradiance in natural solar radiation always acts together with visible light. However, when the sunlight is low, such as during twilight periods or under heavy cloud cover, UV-A was shown to stimulate photosynthesis in the red alga *G. lemaneiformis* (Gao & Xu 2008; Xu & Gao 2010). High levels of UV-A, like PAR, usually cause photoinhibition of the photosynthetic machinery (Gao & Xu 2010). Moderate or reduced levels of UV-A and longer wavelength of UV-B can contribute significantly to photosynthetic carbon fixation (Li & Gao 2013). The integrated effects of UV-A and UV-B during a day or over some time period determine its net influence on primary productivity of a macroalga or macroalgal community. Therefore, *in situ* measurements of photosynthetic rates over long terms will explore the contribution of UV-A to marine algal carbon fixation.

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