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Different Photosynthetic Responses of *Pyropia yezoensis* to Ultraviolet Radiation Under Changing Temperature and Photosynthetic Active Radiation Regimes

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ABSTRACT

Macroalgae play a crucial role in coastal marine ecosystems, but they are also subject to multiple challenges due to tidal and seasonal alterations. In this work, we investigated the photosynthetic response of *Pyropia yezoensis* to ultraviolet radiation (PAR: 400–700 nm; PAB: 280–700 nm) under changing temperatures (5, 10 and 15°C) and light intensities (200, 500 and 800 µmol photons m^{-2} s^{-1}). Under low light intensity (200 µmol photons m^{-2} s^{-1}), *P. yezoensis* showed the lowest sensitivity to ultraviolet radiation, regardless of temperature. However, higher temperatures inhibited the repair rates (*r*) and damage rates (*k*) of photosystem II (PSII) in *P. yezoensis*. However, under higher light intensities (500 and 800 µmol photons m^{-2} s^{-1}), *P. yezoensis* showed higher sensitivity to UV radiation. Both r and the ratio of repair rate to damage rate (*r*:*k*) were significantly inhibited in *P. yezoensis* by PAB, regardless of temperature. In addition, higher temperatures significantly decreased the relative UV-inhibition rates, while an increased carbon fixation rate was found. Our study suggested that higher light intensities enhanced the sensitivity to UV radiation, while higher temperatures could relieve the stress caused by high light intensity and UV radiation.

INTRODUCTION

Macroalgae play critical roles in marine ecosystems in the intertidal zones of coastal areas (1). *Pyropia yezoensis*, previously known as *Porphyra yezoensis* (2), is an important economic red seaweed that serves as a raw material for food (3,4) and has been widely cultivated in shallow areas of north of China, Korea and Japan due to its high economic value (5,6) and increasing global demand (7,8). It is commonly cultivated using aquaculture rafts in the sea and is often subject to seasonal and tidal changes in light intensity, temperature and UV radiation (UVR) (5,9,10). Studies have shown that *P. yezoensis* adapts well to such changing environments (10,11). Recently, much more attention has been given to its growth and photosynthesis because of their close relationship with yield (12,13). However, the response of *P. yezoensis* to these conditions is not well understood.

It is well known that temperature and light intensity are key factors that affect algal assemblages (14). Previous studies have demonstrated that higher temperatures promote growth and increased metabolic rates in macroalgae (15,16) and increase photoprotection and photosynthesis for macroalgae in intertidal zones (17). Natural light intensity has been shown to affect photosynthesis in many macroalgae, especially when those thalli are transferred from deeper seawater to near the surface due to tides (18,19). High light intensity inhibits the growth of *P. yezoensis* due to changes in photosynthetic pigments (12,20). The optimal temperature and light intensity for the growth of *P. yezoensis* have also been studied (12). However, there are relatively few studies investigating the combined effects of these conditions on the photosynthesis of *P. yezoensis*.

For those algae that live in the intertidal zone, UVR has been recognized as an environmental stressor for marine macroalgae (10,21). UVR has been shown to cause serious damage to growth, photosynthesis, DNA synthesis, key enzymatic activities and spore germination of macroalgae (10,22), and UV-B can induce DNA damage and is involved in the recovery process of photoinhibition (23). Thus, macroalgae possess various mechanisms to protect themselves from the UVR-induced damage (24).

Red macroalgae contain various photosynthetic pigments, including chlorophyll, phycoerythrin (PE) and phycocyanin (PC). Light energy is absorbed by the light-harvesting complex and then transferred to the reaction centers via photosynthetic pigments (20). Higher intensity PAR and PAB are known to damage proteins and inhibit photosynthesis (10). However, high levels of UVR can also induce efficient defense and repair mechanisms (25–27). The two processes are completely different, and damage is attributed to higher light intensities (25) and higher temperatures (17), while the repair process is associated with the activity of enzymes in response to environmental changes (28).

In order to better understand the relationship between temperature, light intensity and UV-radiation on *P. yezoensis*, we tested the hypothesis that higher temperatures can protect the thallus from the damage caused by UV-radiation and higher light intensities by measuring the changes of quantum yield, repair rate, damage rate and carbon fixation rate under various conditions.

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MATERIALS AND METHODS

Collection of plant materials. The thalli of *Pyropia yezoensis* (4–5 cm in length) were collected from cultivation rafts in the coastal area of Gaogong island (34°54′31″N; 119°31′57″E), Lianyungang, China. The collected algae were transported to the laboratory in a cooling box within 2 h. Thalli were cleaned with sterile seawater to remove any sediment and healthy samples were selected. The thalli of *P. yezoensis* were maintained in 1L balloon flasks containing sand-filtered natural seawater with Provasoli's enriched Seawater Medium (PSE) (29) (pH_{NBS}, 8.18), which were continuously aerated. Growth medium was changed every day before carrying out any experiments. The temperature was set at 10°C, the light intensity was supplied by cool fluorescent tubes at 80 μmol photons m^{-2} s^{-1}, with a light period of 10 L:14 D.

Experimental design. Experiments were performed under a solar simulator with a 1000 W xenon arc lamp as the light source. The difference in solar irradiation between PAB (PAR + UV-A + UV-B; 280–700 nm) and PAR (400–700 nm) was obtained using a cutoff-filter (ZJB 280, ZJB 400) that blocks radiation below 280 and 400 nm, respectively. Three levels of light intensity (200 μmol photons m^{-2} s^{-1}, LL; 500 μmol photons m^{-2} s^{-1}, ML; 800 μmol photons m^{-2} s^{-1}, HL) were controlled by the height of arc lamp and measured by Ultraviolet radiation photometer (QSL2100, US), and temperature (5, 10 and 15°C) were controlled with a cooling system (CTP 3000, Eyela).

Healthy samples of 0.03 g (fresh weight, FW) were weighed and transferred into 35 mL quartz tubes containing filtered natural seawater enriched with PSE medium, then three tubes were placed into water bath at 30 s intervals. The temperature was controlled by a thermostatic water bath (CTP3000, Eyela, Japan).

Chlorophyll fluorescence measurements. The initial effective quantum yield was recorded after 15 min dark-adapted with an AquaPen fluorometer (AP-C 100, PSI, China) before being placed in tubes, then these were measured after every 10 min of light exposure and placed back in the water bath immediately. After a total of 30 min exposure, samples were transferred to the water bath for recovery at the same temperature under dim light conditions (30 μmol photons m^{-2} s^{-1}). The effective quantum yield was determined at different time points (10, 30, 60, 120 and 240 min under dim light conditions).

Carbon fixation rate. Seawater pH was recorded with a pH meter probe (pH700, Eutech Instruments, Singapore) after 30 min of light exposure. Total inorganic carbon content was calculated using CO_2SYS (30) according to pH and total alkalinity (TA, fixed value: 2300) in seawater. The carbon fixation rate of *P. yezoensis* was calculated using the following formula (31):

$$\text{Carbon fixation rate} = \Delta C \times V/(W \times h).$$

where ΔC is the difference in total carbonate content between algae seawater and blank seawater; V is the volume of seawater; W is the fresh weight of algae, and h is the light exposure time.

Data analysis. After 30 min of light exposure, the relative UV inhibition on effective quantum yield was calculated as follows (32):

$$\text{Relative UV inhibition } (\%) = (P_{\text{PAR}} - P_{\text{PAB}})/P_{\text{PAR}} \times 100.$$

where P_{PAR} is the effective quantum yield under PAR treatment and P_{PAB} is the effective quantum yield under PAB treatment.

The rate of UV-induced damage to PSII (k, min^{-1}) and the repair rate (r, min^{-1}) under light exposure were calculated using the following Non-line fitting formula (25,33):

$$\frac{P_t}{P_0} = \frac{r}{k+r} + \frac{k}{k+r} e^{-(k+r)t},$$

where P_0 is the initial effective quantum yield, and P_t is the effective quantum yield after t minutes.

The recovery rate (R, min^{-1}) of *P. yezoensis* under dim light conditions was calculated by a fitting equation (25,33):

$$y = y_0 + c(1 - e^{-\alpha t}).$$

where y represents the effective quantum yield after t minutes during the dim light recovery period, α represents the recovery rate and y_0 and c are constant values.

The results were expressed as means of replicates ± standard deviation. Data were processed by SPSS 18.0 software. Three-way ANOVA was used to analyze the statistics of the effects of light intensity, temperature and ultraviolet radiation on repair rate, damage rate, *r:k*, rate constant of recovery, relative UV inhibition and carbon fixation rate. One-way analysis of variance (ANOVA, origin 7.0) was used to compare the repair rate, damage rate, *r:k*, rate constant of recovery, relative UV inhibition and carbon fixation rate at different light intensities and temperatures. Tukey's honest significant difference (Tukey HSD) was used for ANOVA. A confidence level of 95% was set for all analyses.

RESULTS

The initial effective quantum yield of *P. yezoensis* was approximately 0.60 for all treatments; however, a significant decrease was observed at the end of the 30-min irradiation exposure period. Meanwhile, compared to PAR treatment, the quantum yield was lower under PAB irradiation ($P < 0.05$, Fig. 1). During the dim light recovery period, light intensity had a significant influence on the quantum yield of *P. yezoensis*, while there was no significant difference in yield between PAR and PAB treatments under LL conditions. However, under HL conditions, PAB-treated samples only recovered to ~60% of the initial values, while the quantum yield recovered to ~95% after the same treatment time (60 min) under PAR at 5°C (Fig. 1a). At 10 and 15°C, the general patterns were similar to those treated at 5°C for 60 min

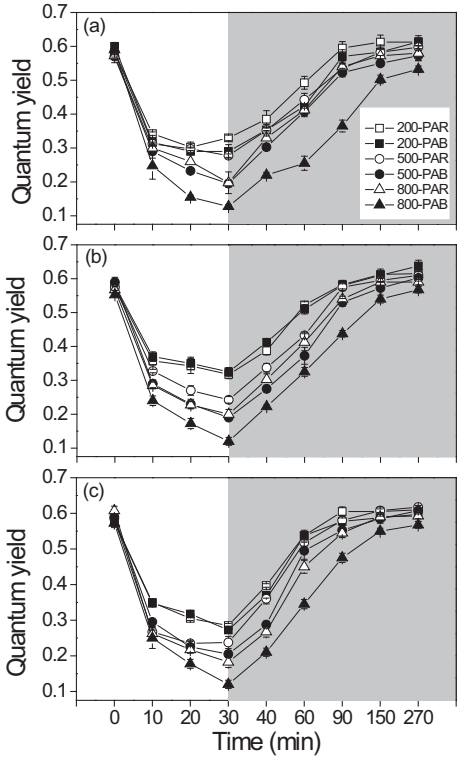

Figure 1. Quantum yields of *Porphyra yezoensis* under LL; ML and HL treated by PAR (400–700 nm) or PAB (280–700 nm) for 30 min and subsequent recovery under dim light (gray area) for 4 h at 5°C (a), 10°C (b) or 15°C (c). Results are expressed as means of replicates ± standard deviation. $n = 3$.

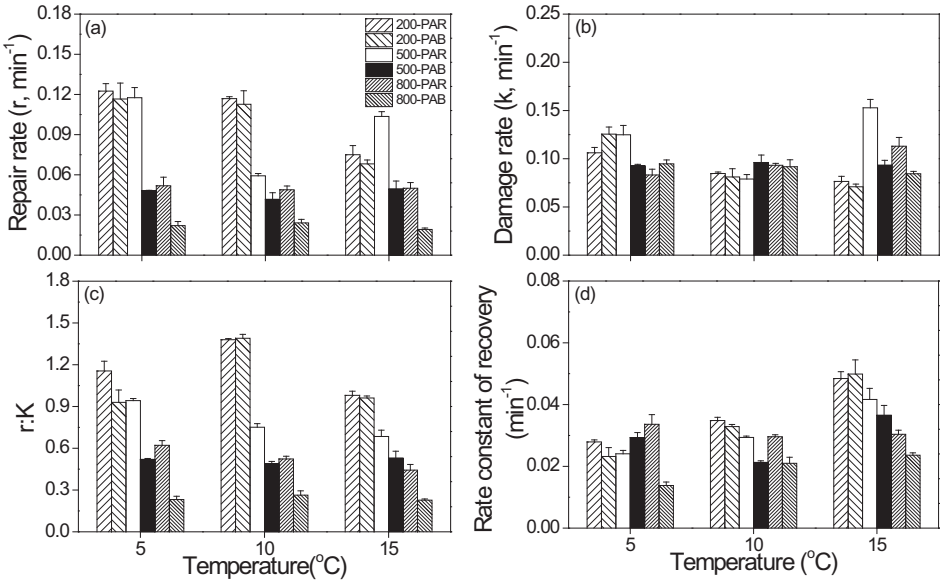

Figure 2. The repair rate (a) and damage rate (b) of PSII in *Porphyra yezoensis* at LL; ML and HL treated by PAR (400–700 nm) or PAB (280–700 nm) exposure at different temperatures. The ratio of repair to damage rate (c), and the rate constants of recovery (d) for *P. yezoensis* under dim light. Results are expressed as means of replicates ± standard deviation. $n = 3$.

(Fig. 1b,c); however, the difference in quantum yield between the PAR and PAB irradiated algae was small but still significant ($P < 0.001$, Fig. 1b; $P < 0.05$, Fig. 1c).

During high radiation exposure, under LL condition, the repair rates (r) and damage rates (k) of PSII for *P. yezoensis* showed decreasing patterns with increasing temperature, with the highest values at 5°C (Tables S1 and S2; Fig. 2a, 2b). However, the ratio of repair rate to damage rate (r:k) was different, with a peak value at 10°C and the lowest value at 15°C for PAR treatment under LL condition, and there was no significant difference between PAB treatment at 5 and 15°C (Table S3; Fig. 3c). Meanwhile, the r:k results showed a decreasing pattern with increasing light intensity, regardless of temperature and UVR. Temperature had no significant effect on repair rates or damage rates in *P. yezoensis* treated by PAB under higher light conditions (500 and 800 μmol photons m^{-2} s^{-1}) (Fig. 2a,b). The r:k ratio had a similar pattern (Fig. 2c).

During the dim light recovery phase, the recovery rate constants for *P. yezoensis* increased with increasing temperature both for PAR and PAB treatments, regardless of light intensity (Table S4; Fig. 2d). Under the highest light intensity, the rate constants of recovery for *P. yezoensis* were lower when treated with PAB compared to PAR, and the lowest values were observed at 5°C (Fig. 2d), suggesting that recovery was better under warmer conditions.

Temperature and light intensity had an interactive influence on relative UV inhibition in *P. yezoensis* (Table S5). Comparing the values of UV inhibition at 5°C, there was a decrease in relative UV inhibition of 39% at LL, 52% at ML and 9.7% at HL at 15°C (Fig. 3), which indicated that temperature had a positive effect on UV inhibition under different light conditions (Fig. 3). The minimum values for UV inhibition occurred at 10°C under low light intensity condition, indicating an optimal condition for photosynthesis of *P. yezoensis*.

In regard to the carbon fixation rate for *P. yezoensis*, an increasing tendency was observed under LL and ML conditions

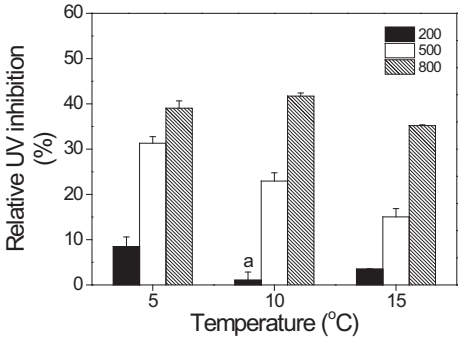

Figure 3. The relative UV inhibition on PSII for *Porphyra yezoensis* induced by PAB on the PSII after 30 min exposure at LL, ML and HL at different temperatures (5, 10 and 15°C). Results are expressed as means of replicates ± standard deviation. $n = 3$.

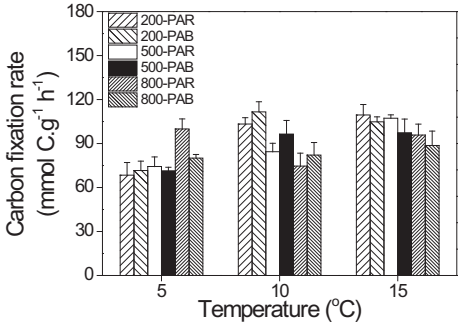

Figure 4. The carbon fixation rate of *Porphyra yezoensis* after 30 min exposure at different temperatures (5, 10, and 15°C) at LL, ML and HL treatment with PAR (400–700 nm) and PAB (280–700 nm). Results are expressed as means of replicates ± standard deviation. $n = 3$.

with increasing temperature (Table S6; Fig. 4), but there was no significant difference. Higher light intensities enhanced carbon fixation at 5°C, while the trend was the opposite at higher

temperatures. Meanwhile, no significant difference in carbon fixation rates can be found at 15°C.

DISCUSSION

In the present study, we found that *P. yezoensis* showed higher sensitivity to UVR with increasing light intensity. Meanwhile, relative UV inhibition significantly increased with increasing light intensity and higher temperatures relieved the negative effects of UV inhibition in *P. yezoensis*. These results suggested that the tolerance to environmental stresses is related to the environment in which *P. yezoensis* is living. Furthermore, these results also demonstrated that both light intensity and temperature are the most important factors that can alter the response of *P. yezoensis* to UVR. Meanwhile, different species have different mechanisms to respond to environmental change (34).

Macroalgae cultured in the natural environment are often affected by multiple stressors concomitantly (35). An increase in light intensity is often accompanied by rising temperature and UV radiation due to seasonal changes, which is critical for the operation of PSII in photosynthesis, and PSII is sensitive to high light exposure (13). In our study, under low light conditions, *P. yezoensis* showed the lowest sensitivity to UVR, while higher sensitivity to UVR was found with increasing light intensity. High light levels have negative effects on photon absorption by light-harvesting complexes (36,37). In our study, the *r*:*k* ratio of *P. yezoensis* showed a decreasing pattern with increasing light intensity, regardless of temperature and UVR (Fig. 1c), which was caused by a decrease in repair rates and stable damage rates in coastal algae under higher light intensities at all temperatures. Excess absorption of light energy also can induce protective mechanisms (38,39) and these may contribute to the stability of the damage rate at higher light intensities. In the present study, compared to PAR, the damage rate of *P. yezoensis* was not significantly different between higher light intensity conditions (500 and 800 μmol photons m^{-2} s^{-1}) treated by PAB, regardless of temperature.

As a critical environmental factor, temperature affects all metabolic pathways (40), while, algae also have alternate mechanisms to respond to temperature (41). A previous study demonstrated that macroalgae are able to optimize their growth and photosynthesis over a wide range of temperatures (42,43). In our study, the results showed that increasing temperature significantly decreased the repair rates (*r*), damage rates (*k*) of PSII and relative UV inhibition in *P. yezoensis* under low -light intensity (200 μmol photons m^{-2} s^{-1}), However, the ratio of repair rate to damage rate (*r*:*k*) showed a different tendency, with the highest *r*:*k* found at 10°C, which may be caused by a higher repair rate and lower damage rate (Fig. 1b). Meanwhile, in the temperature range used in the present study, the relative UV inhibition was lowest at 10°C under low light intensity, and those results support the notion that 10°C is the optimal growth temperature under low light conditions. In addition, during the dim light recovery phase, the effective quantum yield of *P. yezoensis* rapidly regained the highest value, and the rate constants for recovery in *P. yezoensis* increased with increasing temperature. Meanwhile, the increased of carbon fixation rate may be caused by increased photosynthetic, suggesting that macroalgae may have broader adaptability to cope with highly varying temperatures in the natural environment (16,42,43), which may be caused. Higher temperatures can accelerate the metabolic activities of algae, which may allow them to better repair induced damage (24,44).

Temperature and light intensity have an interactive effect on some sensitive species, while increasing light intensity is often accompanied by rising temperature and UV radiation due to seasonal changes, and temperature could alleviate UV inhibition in marine phytoplankton (45). In our study, the relative UV inhibition on PSII activity for *P. yezoensis* increased with increasing light intensity and decreased with increased temperature (Fig. 4). Meanwhile, the highest UV-inhibition rate was found at 5°C, and UV tolerance for macroalgae was modulated by temperature, which may be due to its role in damage repair (24). This offers a better understanding of why those algae can live in their natural niche environments.

Intertidal algae are the least sensitive to PAB-radiation, which may be associated with adaptation to their environment (18,46); UV-B can induce PSII damage and is involved in the recovery process of photoinhibition (23,47). In our study, *P. yezoensis* had higher sensitivity to UV radiation and PAB significantly inhibited the repair rate of *P. yezoensis*, which has a greater impact on *r*:*k* under higher light intensity conditions. Upon exposure to high light intensity conditions, UV absorbing compounds (UVACs) can be synthesized to protect algal cells from UV damage (48). In the temperature range used in these experiments, PAB-radiation had no effect on *r*:*k* of *P. yezoensis* under higher light intensity conditions and increased temperature alleviated the negative effects of *r*:*k*. However, photosynthesis and variable fluorescence for algae were also inhibited by UV-irradiation, even under the present PAB-radiation conditions (18,46). A previous study demonstrated that the effect of solar UV on *Graciliaria lemaneiformis* depended on light intensity (49) as well as the synthesis of UV absorbing compounds (UVACs) (50).

The present study showed the differential responses of *P. yezoensis* to UVR under altered temperatures and light intensities. Based on these experiments, *P. yezoensis* living in coastal areas responds to UV radiation related to their environments. Higher light intensities enhanced the sensitivity of *P. yezoensis* to UV radiation, while higher temperatures can relieve the pressure caused by high light intensity and UV radiation.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article:

Table S1. Three-way analysis of variance for the effect of ultraviolet radiation, light intensity and temperature on the repair rate for *P. yezoensis*, df represents degree of freedom, *F* represents the value of *F* statistic and Sig. represents *P*-value.

Table S2. Three-way analysis of variance for the effect of ultraviolet radiation, light intensity and temperature on the damage

rate for *P. yezoensis*. df represents degree of freedom, F represents the value of *F* statistic and Sig. represents *P*-value.

Table S3. Three-way analysis of variance for the effect of ultraviolet radiation, light intensity and temperature on the ratio of repair to damage (*r*:*k*) for *P. yezoensis*. df represents degree of freedom, F represents the value of F statistic and Sig. represents *P*-value.

Table S4. Three-way analysis of variance for the effect of ultraviolet radiation, light intensity and temperature on the rate constant of recovery for *P. yezoensis*. df represents degree of freedom, *F* represents the value of *F* statistic and Sig. represents *P*-value.

Table S5. Three-way analysis of variance for the effect of light intensity and temperature on the UV inhibition for *P. yezoensis*. df represents degree of freedom, *F* represents the value of *F* statistic and Sig. represents *P*-value.

Table S6. Three-way analysis of variance for the effect of ultraviolet radiation, light intensity and temperature on the rate of carbon fixation rate for *P. yezoensis*. df represents degree of freedom, *F* represents the value of *F* statistic and Sig. represents *P*-value.

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