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Photosynthetic responses of a golden tide alga (*Sargassum horneri*) to ultraviolet radiation

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In recent years, massive *Sargassum* drifting on the sea surface, known as "golden tides," negatively impacted on the local marine ecology. However, the physiological mechanisms of its formation remain unclear. To investigate the photosynthetic responses of golden tide algae to UVR, one key factor for drifting *Sargassum* population, we cultivated thalli of *S. horneri*, a golden tide alga, under three light treatments: P (photosynthetically active radiation, PAR), PA (PAR+UVA) and PAB (PAR+UVA+UVB) for 120 mins, followed by low light recovery for 240 mins. The photosynthetic characteristics of alga were determined. The results showed that UVR exposure decreased photosynthetic activity, reflected by depressed maximum photochemical quantum yield (F_v/F_m) and contents of Chla and Chlc in the PA and PAB treatments. Higher content of malondialdehyde (MDA) was found in thalli exposed to UVR, which verified the damage of UVR. Electron transfer rate (ETR) was slowed down by UVR, accompanied by the increments of net closing rate of the reaction center and the energy absorbed and dissipated by unit reaction center in PSII. In these effects on photosynthesis of UVR, the PAB treatment expressed more significant inhibition, indicating a remarkable role of UVB. However, based on our results, *S. horneri* also took some strategies to protect itself from photodamage of UVR. UVR exposure enhanced the contents of UV-absorbing compounds (UVACs) and carotenoid, and simultaneously expedited heat consumption of excess light energy, indicated by the increased non-photochemical quenching coefficient (NPQ) in the PA and PAB treatments. Increased activities of superoxide dismutase (SOD) and peroxidase (POD), and higher content of PsbA (D1) protein were found in the treatments with UVR, which suggested that antioxidant system and the turnover of D1 protein played important roles in protection from UV-induced damages. Due to the above protection pathways, F_v/F_m and ETR gradually recovered when thalli were transferred to low light recovery. Therefore, we suggest that various protection and restoration pathways in *S. horneri* work together to effectively protect against UVR damage, which may be the reason why drifting populations can adapt to UVR on the seawater surface and form golden tide in case of suitable temperature and nutrients.

KEYWORDS

Sargassum horneri, UVR, photosynthesis, photodamage, photoprotection

Introduction

The golden tide is formed by the rapid growth of certain species of *Sargassum* drifting on the sea surface, which are naturally born in the subtidal zone (Smetacek and Zingone, 2013). In recent years, *Sargassum* golden tides broke out in many places in the world, for example, *S. fluitans* and *S. natans* golden tides broke out continuously in the Caribbean, West Africa, and the Gulf of Mexico from 2011 to 2016 (Schell et al., 2015; Wang et al., 2019; Qi et al., 2020), and *S. horneri* golden tides broke out in the East China Sea and the Yellow Sea from 2015 to 2017 (Xing et al., 2017; Qi et al., 2017; Liu et al., 2018). When the golden tide blooms as an invasive genus, mats of drifting *Sargassum* can change the ecosystem structure of the original sea area (van Tussenbroek et al., 2017; Caselle et al., 2018), negatively impact offshore tourism and maritime transport (Williams and Feagin, 2010; Milledge and Harvey, 2016), and lead to the deterioration of seawater quality after it sinks and decays (Cruz-Rivera et al., 2015). If an episode were to occur in aquaculture areas, golden tides could cause enormous losses to the local mariculture industry (Xing et al., 2017). When the golden tide breaks out, the ultraviolet radiation (UVR) received by *Sargassum* from the stationary water to the drifting state will be significantly enhanced due to the lack of the subtracting effect of the seawater layer (Tedetti et al., 2010). Excessive UVR often causes the decrease of photosynthetic capacity of algae, resulting in photoinhibition (Gao ang Xu, 2010). The main manifestations are the decrease of antenna pigment content (Xu and Gao, 2012), the degradation of D1 protein in the reaction center (Wu et al., 2011), the decrease of effective photochemical efficiency and electron transfer rate (Yakovleva and Titlyanov, 2001; Erin Cox and Smith, 2015), and the imbalance of reactive oxygen species, ROS) metabolism (Lesser, 1996), which ultimately affects the survival and growth of algae. However, how *Sargassum* spp. responds to such UV stress to maintain its rapid growth remains still unclear.

Sargassum horneri belongs to Phaeophyta, Fucales, Sargassaceae and *Sargassum*. It is an important part of coastal algal field. Because of its rapid growth, it can create a huge algal field to provide habitat, enemy avoidance and breeding place for many organisms (Terawaki et al., 2003). Additionally, the algae can absorb a lot of N, P and other nutrients from the surrounding seawater while growing rapidly, which has a good effect on the purification of water quality (Davis et al., 2000). On the other hand, because of the high adaptability and rapid growth of *S. horneri*, it often becomes an invasive species (Sfriso and Facca, 2013), which affects the local marine ecosystem (van Tussenbroek et al., 2017; Byeon et al., 2019). Especially in recent years, the *S. horneri* golden tide which appeared in drifting population has been outbreak in the North Pacific Ocean many times, which has attracted more and more attention from all walks of life in the world (Ma et al., 2020).

Considering that *S. horneri* drifting on the sea surface received more light (including UVR) during the golden tide, we speculate that it may have an efficient or special photosynthetic mechanism to adapt to UVR. Therefore, in this study, we focused on UVR, the key environmental factor for drifting population and investigated the photosynthetic responses, to reveal the mechanisms of photodamage and photoprotection in this alga exposed to UVR. Our results may provide data reference for the future study in the physiological and ecological mechanism of the formation of *Sargassum* golden tide.

Materials and methods

Materials

Samples of *Sargassum horneri* were collected from a drifting population in Lidao Bay, Rongcheng City, Shandong Province, China (37°15′ N, 122°35′ E) on May 30, 2021. The collected samples were brought to the laboratory in an insulated cooler of 4°C in 2 hours. Healthy and unified individuals were selected and cleaned with autoclaved natural seawater (salinity, 30 PSU; NO_3^-, 25.0 mM; NH_4^+, 0.8 mM and DIP, 1.6 mM), and temporarily cultured for 24 hours. The temperature was set at 18°C, and the light level was 100 μmol m^{-2} s^{-1} with light and dark periods of 12 h: 12 h. The media were continuously aerated.

UVR treatments and low light recovery

The thallus branches of *S. horneri* with a total fresh weight (FW) of 1.0 g were cultured in a quartz tube (which can pass through UVR) filled with 500 mL of natural seawater. The quartz tube was placed in a water bath, and temperature was controlled at 18°C by a low-temperature thermostatic bath (YRDC-0506, China). Cultivation light radiations were provided by a solar simulator (Sol 1200, Hönle GmbH, Germany) and the PAR (photosynthetically active radiation, 400~700 nm), UVA (320~400 nm) and UVB (280~320 nm) irradiance were set at 1000 μmol m^{-2} s^{-1}, 47.1 W m^{-2} and 1.5 W m^{-2}, respectively, referring to the irradiance level on the sea surface when the golden tide of *S.horneri* broke out. The irradiance level was measured by a radiometer (Solar Light, PMA2100, USA). Quartz tubes were covered by different types of optical filters (Nantong Yinxing Optical Co., Ltd., China) to obtain different radiation treatments.

P treatment: The quartz tube was covered with ZJB-400 filter, which can only transmit light with wavelength above 400 nm, so that the algae in the quartz tube can only receive PAR (400~700 nm).

PA treatment: The quartz tube was covered with ZJB-320 filter. The ZJB-320 filter can only transmit light with wavelength

above 320 nm, and the algae can receive PAR+UVA radiation (320~700 nm).

PAB treatment: The quartz tube was covered with ZJB-280 filter, and the algae received the light radiation of PAR+UVA +UVB (280~700 nm).

According to the duration of high light at noon and low light in afternoon during the golden tide outbreak season under natural conditions, samples with three repetitions were cultured under different radiation treatments for 120 mins, and then allowed to recovery with lower visible light of 10 μmol m^{-2} s^{-1} for 240 mins in a light incubator (GXZ-380D, Ningbo Jiangnan Instrument, China), the temperature was set at 18°C.

Fluorescence measurement and parameterization

Chlorophyll fluorescence was measured using a dual-modulation kinetic fluorometer (FL6000, Photon Systems Instruments, Czech Republic). A multiple turnover saturating flash was applied to measure the maximum quantum yield of photochemistry of photosystem II (F_v/F_m) according to (F_m–F_0)/F_m. Where the difference between the maximum (F_m) and minimal fluorescence (F_0) is used to calculate the variable fluorescence (F_v) (van Kooten and Snel, 1990). The non-photochemical quenching coefficient (NPQ) was calculated as (F_m–F_m')/F_m', where F_m' is the maximum fluorescence measured in the presence of actinic light.

Polyphasic rise of Chl a fluorescence transients and JIP-test

Subsamples were dark adapted for 5 min, and the polyphasic rise of chlorophyll a fluorescence transients was measured by using a dual-modulation kinetic fluorometer (FL6000, Photon Systems Instruments, Czech Republic). The fluorescence signals were recorded within a time scale of 10 μs to 2 s. The JIP test was developed to characterize the fluorescence rise kinetics based on the theory of energy fluxes in the membrane in the photosynthetic apparatus (Strasser et al., 2000). According to this theory, the light system captures and absorbs light energy (ABS) through the light-trapping complex on the thylakoid membrane, a small part of which is used for heat dissipation (D) and fluorescence dissipation (F), and the rest is used for photochemical reaction (P). Most of the light energy (TR) captured by the reaction center (RCs) is used to reduce Q_A. After that, Q_A^- transfers electrons to Q_B for re-oxidation. In this process, the energy (ET) generated by electron transfer is used for subsequent reactions such as Calvin cycle. According to Strasser et al. (2000), the energy fluxes for absorption per reaction center (ABS/RC), the energy fluxes for dissipation per reaction center (DI_0/RC), the energy fluxes for trapping per reaction center (TR_0/RC), the energy flux for electron transfer from Q_A to Q_A^- per reaction center (ET_0/RC), the relatively variable fluorescence at J point (V_J), the net closing rate of PSII reaction center (M_0), and the probability of electron transport beyond Q_A (Ψ_0) were calculated by the following equations:

$$V_J = (F_J - F_0) / (F_m - F_0)$$

$$M_0 = 4 \times (F_{300\mu s} - F_0) / (F_m - F_0)$$

$$\psi_0 = 1 - V_J$$

$$ABS/RC = M_0 \times (1/V_J) \times (1/\varphi P_0)$$

$$TR_0/RC = M_0 \times (1/V_J)$$

$$ET_0/RC = M_0 \times (1/V_J) \times \psi_0$$

$$DI_0/RC = ABS/RC - TR_0/RC$$

Measurement of rapid light response curve

At room temperature, the rapid light response curves (LC) were obtained by using a palm top chlorophyll fluorescence instrument (AquaPen-C 100, Photon Systems Instruments, Czech Republic). Seven light intensity gradients (10, 20, 50, 100, 300, 500, 1000 μmol m^{-2} s^{-1}) were set, and the interval light adaptation time was 10 s. The algae samples were put into AquaPen-C100 for measurement after dark adaptation for 5 min. The PSII relative electron transfer rate (rETR) was calculated from the measured φPSII, and the formula was as follows (Jassby and Platt, 1976):

$$rETR = PFD \times \varphi PSII \times 0.5$$

In the formula, rETR is the relative electron transfer rate, PFD is the actinic light intensity, φPSII is the actual light quantum yield of PSII, and the coefficient of 0.5 indicates that about 50% of all absorbed light quantum is allocated to PSII.

The maximum relative electron transfer rate ($rETR_{max}$) and the initial slope (α) of the rapid light response curve were obtained by fitting formula, and the light saturation point E_k was calculated by $rETR_{max}$ and α, and the formula were as follows:

$$rETR = rETR_{max} \times \tanh(\alpha \times PAR/rETR_{max})$$

$$E_k = rETR_{max}/\alpha$$

Analysis of oxidative stress response

At the end of 120 mins UVR exposure and 240 mins low light recovery, approximately 0.2 g FW samples were collected and frozen in liquid nitrogen (-80°C) for subsequent analysis of oxidative stress response. Before determination, 1.8 mL volume of homogenate medium (physiological saline) were added. The mixture was ground into 10% tissue homogenate in ice-water bath (0°C). After the homogenizedextract was centrifuged at 3500 rpm (4°C) for 10 mins, MDA contents, SOD and POD activities were tested through assay kits (Nanjing Jiancheng Biological Engineering Company, China), respectively. The content of MDA was measured by condensation of MDA in lipid peroxide degradation products with thiobarbituric acid (TBA) to form a red product with the maximum absorption peak at 532 nm. One unit of SOD activity was defined as the amount of enzyme which resulted in a 50% inhibition of the rate of nitro-blue tetrazolium reduction at 560 nm. Based on the principle of catalysing hydrogen peroxide reaction by peroxidase, the POD activity was obtained by measuring the change of absorbance at 420 nm.

Determination of photosynthetic pigment

Approximately 0.1 g FW of thalli were ground with 90% acetone, and then adjusted constant volume to 8 mL. After the dark extraction for12 hours at 4°C, extracting solution was centrifuged for 15 mins at 4000 rpm at 4°C, and the absorbance of supernatant was determined with ultraviolet spectrophotometer (UV-2600, Shimadzu, Japan). The contents (mg g^{-1} FW) of chlorophyll (Chla, Chlc) and carotenoids (Car) were calculated as described by Jeffrey and Humphrey (1975) and Parsons et al. (1984), respectively.

$$Chla(mg/g) = (11.47 \times A_{664} - 0.40 \times A_{630}) \times V/M$$

$$Chlc(mg/g) = (24.36 \times A_{630} - 3.73 \times A_{664}) \times V/M$$

$$Car(mg/g) = [7.6 \times (A_{480} - 1.49 \times A_{510})] \times V/M$$

Where A_{664}, A_{630}, A_{480}, A_{510} indicated the absorption values at wavelengths of 664, 630, 480 and 510 nm, respectively. V represented the volume of 90% acetone, and M represented FW of algae.

Determination of UV-absorbing compounds content

Approximately 0.1 g FW of algae were ground and then extracted in 10 mL methanol for 24 hours at 4°C, and the solution was centrifuged for 15 mins at 4000 rpm. The absorbance of supernatant was scanned from 250 nm to 750 nm with ultraviolet spectrophotometer (UV-2600, Shimadzu, Japan). The ratio of peak height at 335 nm to FW of algae was used to express the relative content of UV-absorbing compounds (UVACs).

Relative quantitation of D1 proteins by immunoblotting

Algal thylakoid membrane proteins were extracted in cool extracting medium (50 mM Tris–HCl, pH 7.6, 5.0 mM $MgCl_2$, 10 mM NaCl, 0.4 M sucrose, and 0.1% BSA) according to Ma et al. (2016). Protein concentration determined by the Bradford method. And 10 μg of extracted proteins were used for 12% separating gel (pH 8.9) in Tris-glycine buffer (pH 8.3). For immunoblotting, the SDS-PAGE gel was transferred to a PVDF membrane with a DYY-6C Transblot semi-dry transfer apparatus, according to the manufacturer's instructions. Membranes were blocked for 60 min with 5% skimmed milk in TBS (20 mM Tris, 150 mM NaCl, pH 7.4) at 37°C. Rabbit anti-the C-terminal part of PsbA (AgriSera; 1:50000) and goat anti-rabbit IgG-HRP (1:1000) antibodies used as primary and second antibodies, respectively. All incubations were performed at room temperature. The membranes were developed with 3′3-diminobenzidine (DAB) substrate. After scanning the membranes, scan strips are analyzed by Image J image processing software, and the average optical density value of each strip was used as the relative amount of D1 protein.

Data analysis

Results were expressed as mean ± standard deviation (n = 3). SPSS 17.0 was used for statistical analysis. One-way ANOVA (Duncan) was used for difference analysis, and the difference significance level was set as $P<0.05$.

Results

Maximum photochemical quantum yield (F_v/F_m)

The maximum photochemical quantum yields (F_v/F_m) of *S. horneri* during UVR exposure and low light recovery were shown in Figure 1. F_v/F_m with the initial value of 0.750 ± 0.007 at time 0 decreased sharply by 49.47%, 57.07% and 72.40% after exposed to P, PA and PAB treatments for 120 mins, respectively. There were significant differences among the three treatments ($P<0.001$). In the following process of low light recovery, F_v/F_m rose to 84.93%, 78.80% and 72.00% for P, PA and PAB treatments respectively as compared with the initial value after 240 mins, there were significant difference between these treatments ($P<0.001$).

Electron transfer and energy flow distribution

In order to study the effect of UV radiation on PSII electron transfer reaction, we determined the fast chlorophyll fluorescence induction of *S. horneri* during the P, PA and PAB exposure and the subsequent low light recovery. The results of ABS/RC, DI_0/RC, TR_0/RC and ET_0/RC were shown in Figure 2. ABS/RC, DI_0/RC and TR_0/RC values gradually increased during high light exposure, PAB treatment led to the highest value of 4.74 for ABS/RC, 6.00 for DI_0/RC and 1.65 for TR_0/RC after 120 mins exposure, which is 2.96 times, 15.11 times and 1.54 times of P treatment, respectively. When shifted to low light, ABS/RC, DI_0/RC and TR_0/RC decreased, but still higher than the initial value measured before the high light treatment, the highest value was still kept under PAB treatment. However, ET_0/RC declined gradually 37.99%, 43.99% and 51.46% under P, PA and PAB treatments respectively as compared with the original value, and recovered to 93.67%, 88.96% and 85.23% after 240 min recovery. In contrast to the increase of ABS/RC, DI_0/RC and TR_0/RC by PAB treatment, ET_0/RC showed the opposite changes.

Figure 3 exhibited the changes in the relative variable fluorescence (V_J), variation of net closure rate (M_0) and the probability of electron transport beyond Q_A (Ψ_0) during UVR exposure and the subsequent low light recovery. The value of V_J increased by 53.59%, 61.75% and 69.12% under exposure to P, PA and PAB for 120 mins respectively, and then exhibit a trend of decrease during the recovery period. (Figure 3A). Through JIP-test, we also found Ψ_0 was gradually reduced with the prolonged UVR exposure and showed recovery when *S. horneri* was shifted to low light, which further indicated high light exposure, particularly for UV radiation, could inhibit electron transfer from Q_A^- to Q_B. M_0 expressed the net closing rate of reaction centers during the high light exposure, it increased as the exposure prolonged, but decreased when *S. horneri* was transferred to low light. The presence of UVR resulted in much higher M_0 value than P treatment (P<0.001).

Rapid light response curve

Figure 4 showed initial slope (α), maximum relative electron transfer rate ($rETR_{max}$) and light saturation point (E_k) obtained from rapid light response curve (LC) of alga. High light exposure remarkably decreased α and $rETR_{max}$ (P<0.001). Compared with PAR, the presence of UVA led to a further decrease of 55.04% and 63.11% for α and $rETR_{max}$ respectively, while the presence of UVB 61.75% and 74.80%. During the following low light recovery, both α and $rETR_{max}$ gradually increased, and at the end of 240 min recovery, α recovered to 82.84%, 75.75% and 65.86%, while $rETR_{max}$ to 90.92%, 82.88% and 77.71% of the initial value under P, PA and PAB treatments, respectively. In contrast, the light saturation point (E_k) expressed unobvious changes with insignificant difference between three radiation treatments.

Non-photochemical quenching (NPQ)

NPQ of thalli gradually increased during high light exposure (Figure 5). After 120 min exposure in P, PA and PAB treatments, NPQ increased 2.91, 3.32 and 3.62 times over that of the initial value. And then after 240 mins of low light recovery, NPQ of alga exposed to these radiation treatments relaxed.

Oxidative stress response

Figure 6 showed the content of MDA and the activities of SOD and POD during UVR exposure and following low light

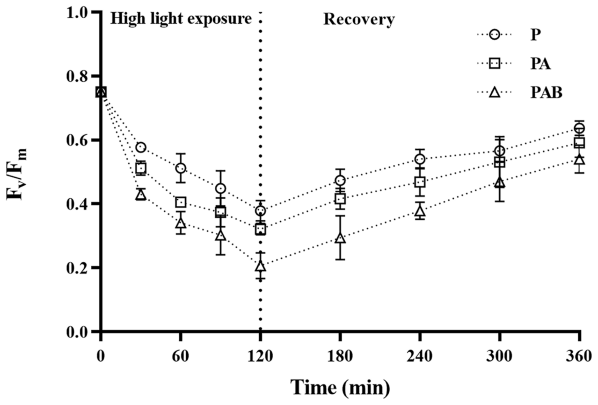

FIGURE 1
Changes of the maximum photochemical quantum yield (F_v/F_m) in *Sargassum horneri* during P, PA and PAB exposure and low light recovery. Data are means ± SD (n = 3).

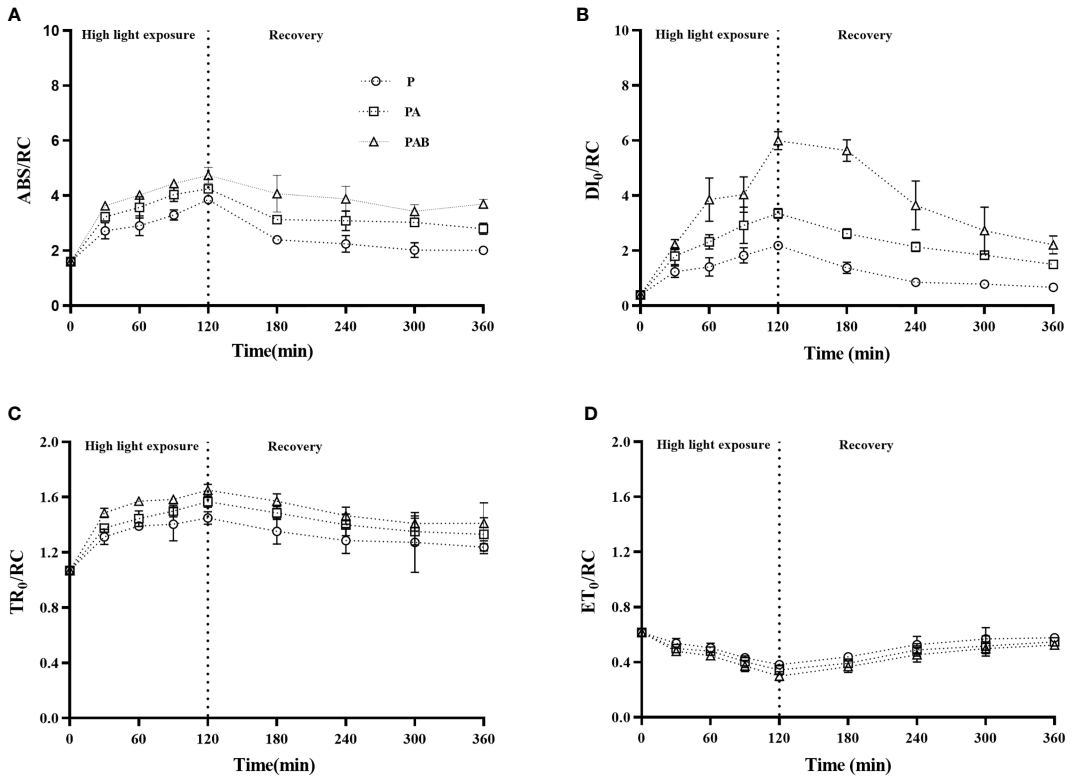

FIGURE 2
The energy fluxes for absorption per reaction center, ABS/RC **(A)**, the energy fluxes for dissipation per reaction center, DI_0/RC **(B)**, the energy fluxes for trapping per reaction center, TR_0/RC **(C)**, and the energy fluxes for electron transfer from Q_A to Q_A- per reaction center, ET_0/RC **(D)** versus time in *S. horneri* during P, PA and PAB exposure and low light recovery. Data are means ± SD (n = 3).

recovery. Significant accumulation of MDA was induced after 120-min exposure for all three radiation treatments when compared with the initial level at time 0, and further accumulation occurred during the subsequent recovery. Obviously, the presence of UVR provoked significant cumulative ROS toxicity.

The activity of SOD increased 2.47, 2.52 and 2.66 times over that of the initial value at time 0 by P, PA and PAB treatments respectively, with significant difference between P and PAB treatments (P<0.001), and showed stabilization during the 240-min recovery. The activity of POD showed a similar trend of increase during the P, PA and PAB exposure, but decreased when shifted to low light.

Pigments and UV-absorbing compounds (UVACs)

Contents of photosynthetic pigments and UVACs in thalli were exhibited in Figure 7. Compared with the initial value, both contents of Chla and Chlc reduced during UVR exposure and following low light recovery, with no significant difference between P and PA treatments. However, contents of these two pigments expressed lower value in PAB treatment than in P and PA treatments, whether after UVR exposure or low light recovery (Figures 7A, B). Additionally, after 240 min low light recovery, Chla content of alga cultured in P, PA and PAB treatments returned to 90.91%, 87.25% and 72.86% of the initial value, respectively (P=0.002).

Contrarily, content of Car dramatically increased after P, PA and PAB exposure (P<0.05). Furthermore, PA and PAB treatments respectively enhanced it by 14.60% and 36.50%, compared with the P treatment. After 240 min low light recovery, the content of Car decreased to the initial value level in P and PA treatments (P=0.139), while still maintained a relatively high value in PAB treatment.

UVACs was not induced by P treatment. However, PA and PAB treatments enhanced it by 1.71 and 2.89 times after UVR exposure, respectively, indicating that both UVA and UVB promoted the synthesis of UVACs in alga. After 240 min low light recovery, UVACs content in PAB treatment still remained higher than the other radiation treatments.

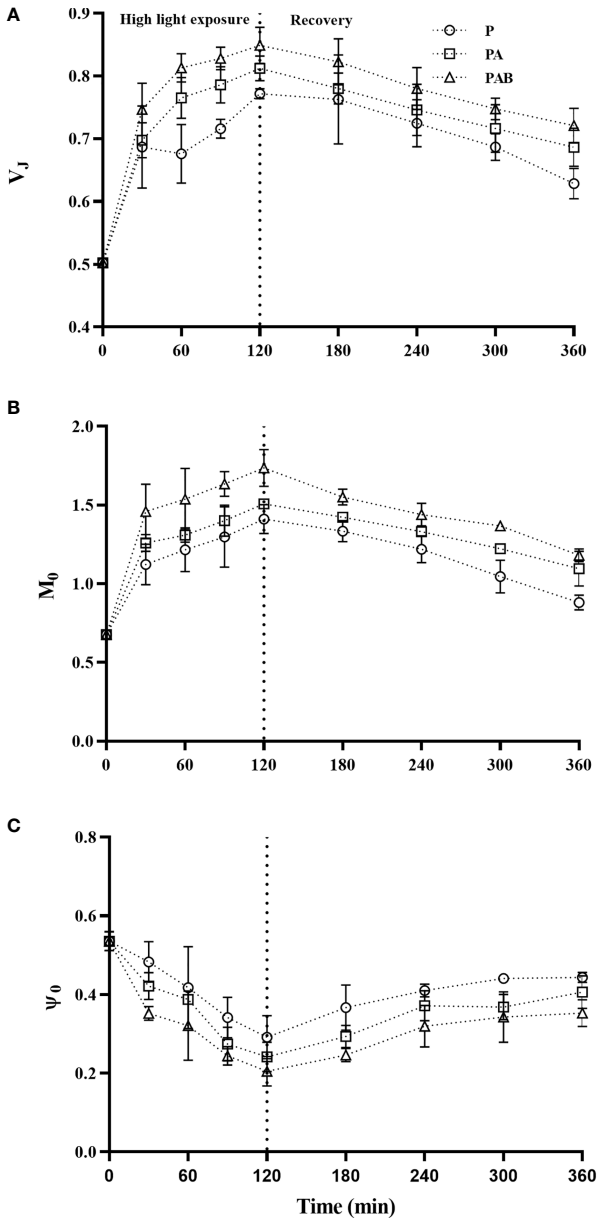

FIGURE 3
The relative variable fluorescence (V_J, **A**), approximated initial slope of the fluorescence transients (M_0, **B**) and the probability of electron transport beyond Q_A (Ψ_0, **C**) in *S. horneri* during P, PA and PAB exposure and low light recovery. Data are means ± SD (n = 3).

Relative quantitation of D1 proteins

Figure 8 showed the relative D1 protein content in alga during UVR exposure and low light recovery. The D1 protein content was enhanced by UVR exposure, especially UVB. After low light recovery for 240 mins, D1 protein content increased in P and PA treatment, but decreased in PAB treatment, compared with that under high-light exposure.

Discussion

Photosynthesis is the most basic and important physiological activity of algae, which can quickly respond to UV radiation. Generally, UV radiation directly acts on photosynthetic organs, and PSII is the most sensitive to UV radiation, especially UV-B, and suffers the most serious light suppression (Spetea et al., 1996; Vass et al., 2002). The maximum

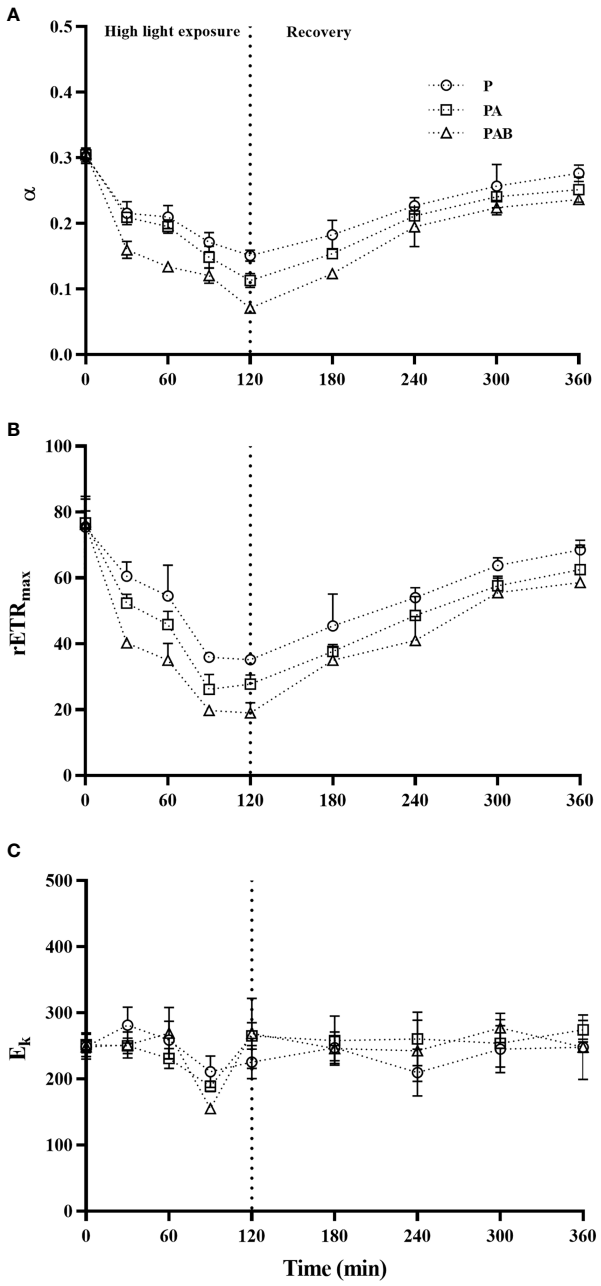

FIGURE 4
The photosynthetic efficiency parameter (α, **A**), maximum relative electron transfer rate ($rETR_{max}$, **B**) and light saturation point (E_k, **C**) versus time in *S. horneri* during P, PA and PAB exposure and low light recovery. Data are means ± SD (n = 3).

photochemical quantum yield of PSII (F_v/F_m) reflects the quantum yield when all PSII reaction centers are open, and it will decrease significantly when algae are under environmental stress. Therefore, F_v/F_m is an important index to study the effects of photoinhibition or various environmental stresses on photosynthesis (Kolber and Falkowski, 1988). In this study, F_v/F_m of *S. horneri* decreased under strong light treatment, and this stress was aggravated by UVA and UVB. Meanwhile, the stress degree of algae was related to the duration UVR exposure, and the longer the time, the higher the stress degree. This might be due to damaged reaction center pigments and reduced electron transfer rate by UVR. In fact, it was found in the present study that UVR exposure decreased the contents of Chla and Chlc, and inhibited the electron transfer from to Q_B in *S. horneri*, reflecting

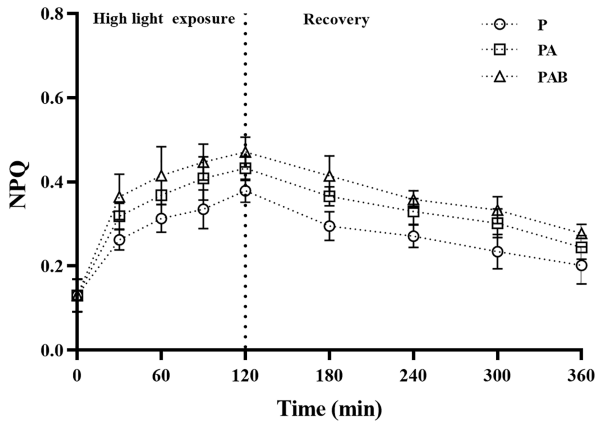

FIGURE 5
The non-photochemical quenching (NPQ) versus time in *S. horneri* during P, PA and PAB exposure and low light recovery. Data are means ± SD (n = 3).

by increased V_J and decreased Ψ_0 (Strasser et al., 2000). Therefore, α and $rETR_{max}$ also decreased with UVR exposure, indicating that the number of active PSII reaction centers of *S. horneri* decreased by UVR, which was consistent with the results in *Porphyra leucosticte*, *P. umbilicalis* and *Grateloupia lanceola* (Korbee et al., 2005; Huovinen et al., 2006).

Furthermore, under UVR stress, electrons are hard to transfer from Pheo on the receptor side to Q_A on the secondary electron acceptor in time, resulting in increased Q_A and $P680^+$. Eventually, PSII will be damaged by $^1O_2$ and $P680^+$, which have strong oxidizability (reviewed by Nishiyama and Murata, 2014). In this study, the MDA contents of *S. horneri* cultured in PA and PAB treatments were significantly higher than that in the P treatment, reflecting the increased productions of reactive oxygen species (ROS) during UVR exposure, which led to membrane lipid peroxidation (Saber et al., 2020). Similar result was found in *Chlorococcum* sp. (Abo-Shady et al., 2008).

Macroalgae have evolved in a series of protective mechanisms under UVR stress (Gao and Xu, 2020). Photosynthetic pigments, located on the surface of thylakoid membrane, firstly capture excess energy under UVR (Conde et al., 2004), leading to its structural disintegration, but also protecting the reaction center of PSII (Franklin et al., 2003). Therefore, in this study, the decrease of Chla and Chlc in *S. horneri* might play an important role in UVR protection of photoreaction centers. Significantly, the content of carotenoids in *S. horneri* increased with UVR exposure in this study. Carotenoids are important antenna pigments, which can not only capture light energy, but also protect cells from damage through antioxidation (Conde et al., 2004). UVR can induce cells to produce ROS, which will cause structural and compositional damage to photosynthetic organs, for example, resulting in elevated MDA as shown in this study. Carotenoids have antioxidant effects in two ways. One is to quench the excited chlorophyll by self-epoxidation, so as to prevent the production of active oxygen; the other is to directly quench active oxygen. Therefore, the increase of carotenoid content is a protection strategy for algae (Lvarez-Gómez et al., 2019). Additionally, the content of UVACs in *S. horneri* also increased in PA and PAB treatments, with an absorption peak in UV band, which could shield UVR and protect important intracellular organelles from UV stress (Peinado et al., 2010; Lvarez-Gómez et al., 2019; Gao and Xu, 2020). Actually, it has been reported in many species of alga, including micro- and macroalgae, that UVA and/or UVB can induce the synthesis of UVACs (Yakovleva and Titlyanov, 2001; Han and Han, 2005; Xu and Gao, 2012; Lvarez-Gómez et al., 2019; Gao and Xu, 2020).

In the present study, UVR forced algae to improve the efficiency of the remaining active reaction center, that was, under UV stress, the energy absorbed (ABS/RC) and dissipated (DIo/RC) by the unit active reaction center of *S. horneri* increased, thus dissipating the excess energy in the electron transfer chain (Gert et al., 2010). Additionally, UVR, especially UVB, increased the NPQ of *S. horneri* in this study. Xanthophyll cycle can partially resist or accelerate the recovery of algae damaged by UVR through dissipating energy (Zudaire and Roy, 2001). The higher NPQ is related to the accumulation of zeaxanthin in algae (Garcia-Mendoza et al., 2011). Therefore, *S. horneri* might improve the photo-protective ability to UVR through NPQ related to xanthophyll cycle.

Antioxidant system is another effective way for algae to protect themselves from UVR damage (Foyer et al., 1994), for example, superoxide dismutase (SOD) can catalyze the decomposition of superoxide anion radical (O_2^-) in algae into hydrogen peroxide and molecular oxygen (Grene et al., 2002); and peroxidase (POD) can remove hydrogen peroxide and

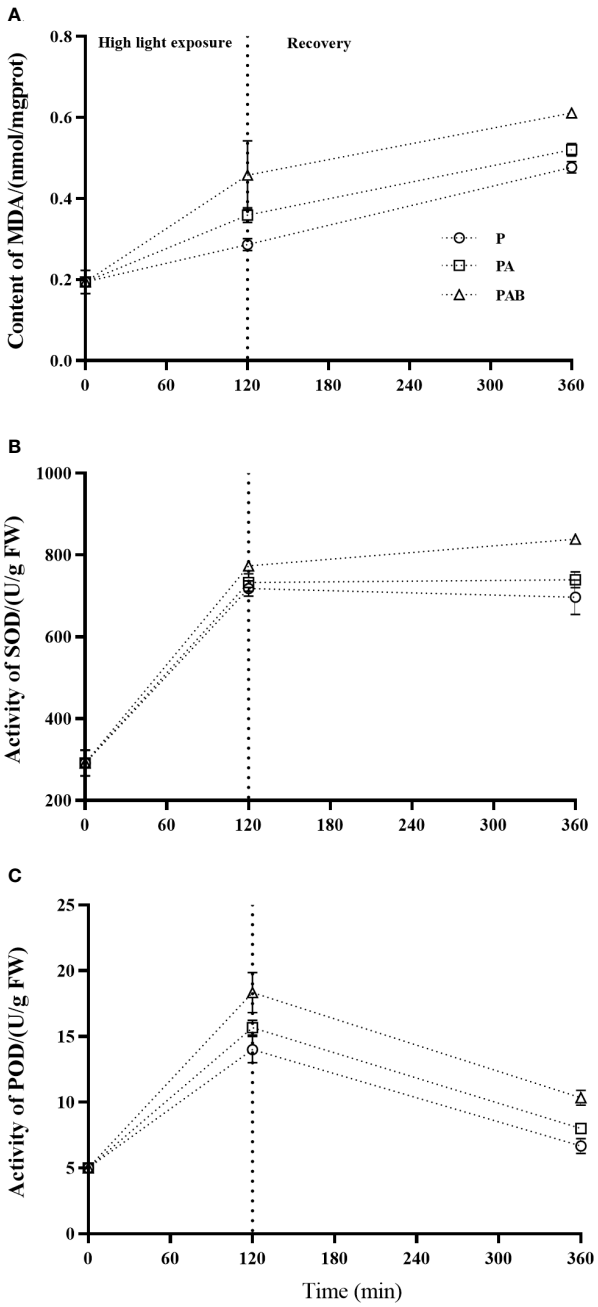

FIGURE 6
The MDA content **(A)**, SOD **(B)** and POD **(C)** activities versus time in S. horneri during P, PA and PAB exposure and low light recovery. Data are means ± SD (n = 3).

effectively avoid the accumulation of hydrogen peroxide and organic peroxide in algae (Zhang and Kirkham, 1993). The enzyme activities of SOD and POD in brown algae are generally at a lower level, compared with those in green and red algae. However, Aguilera et al. (2002) found that the activities of these two enzymes in *Monostroma affarcticum* significantly increased after UVR exposure when the ice broke. Similarly, *S. horneri* exposed to UVR had higher activities of SOD and POD in this study, which may play an important role in damage repair for drifting thalli to adapt to UVR stress on the sea surface.

It has been reported in some micro- and macroalgae that UV-induced ROS damaged D1 protein in reaction center proteins of PSII, resulting in decreased content of it

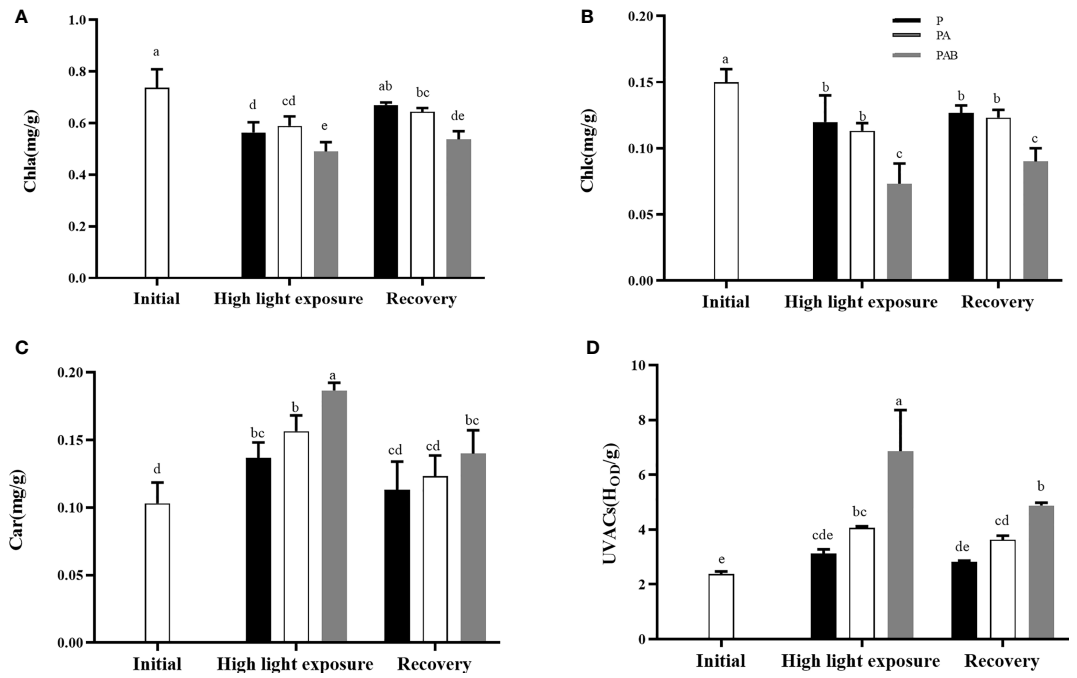

FIGURE 7
The contents of Chla **(A)**, Chlc **(B)**, Car **(C)** and UV-absorbing compounds (UVACs, **(D)** versus time in *S. horneri* during P, PA and PAB exposure and low light recovery. Data are means ± SD (n=3). Significant (P<0.05) differences among the treatments are indicated by different lowercase letters.

(Nishiyama and Murata, 2014). Correspondingly, algae under environmental stress could alleviate damage to the photosystem by accelerating the synthesis of D1 protein, whose starting time and speed varied with the species of algae, reflecting the role of D1 protein synthesis in repairing damage (Zhang and Aro, 2002; Wu et al., 2011; Ma et al., 2020). In the present study, the content of D1 protein in *S. horneri* increased significantly after 120min PAB exposure, with the increased SOD and POD activities, indicating that the accelerated synthesis of D1 protein had started rapidly due to the removal of ROS by SOD and POD. This might suggest that the rapid turnover of D1 protein play an important role in the repair of

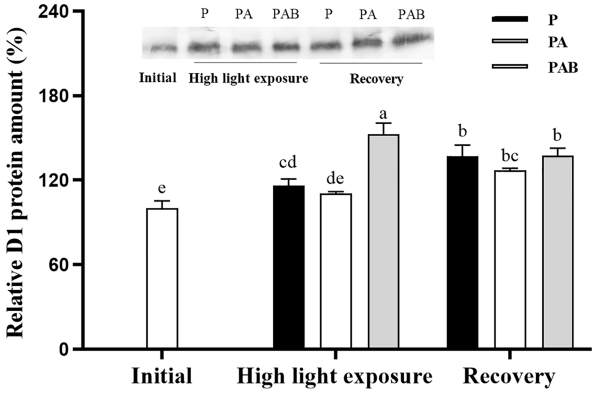

FIGURE 8
Changes of the relative D1 protein content in *S. horneri* after exposed to P, PA and PAB treatments and low light recovery. The data are shown after normalization to the value at the initial. Data are means ± SD (n = 3). Significant (P < 0.05) differences among the treatments are indicated by different lowercase letters.

photodamage of *S. horneri*. Actually, we have subsequently confirmed this conclusion by adding streptomycin to inhibit D1 protein synthesis, and found that the F_v/F_m of *S. horneri* exposed to UVR decreased sharply in a short time (Our unpublished data). Moreover, during the 240 min low light recovery period, D1 protein maintained high content in this study, accompanied by the recovery of F_v/F_m and electron transfer rate, which also verified the key role of D1 protein synthesis in UVR protection of *S. horneri*.

Conclusion

Drifting *S. horneri* is exposed to increased UVR, resulting that the membrane system is damaged, the maximum photochemical quantum yield decreases, electron transfer rate reduced, and the photosynthetic pigment content decreases. However, this alga can protect and repair its photosynthetic system through a series of efficient pathways, such as synthesizing UVACs, enhancing NPQ, improving SOD and POD activities, and accelerating D1 protein turnover. Various protection and restoration pathways in *S. horneri* work together to effectively protect against UVR damage, which enable the *S. horneri* to adapt to the UVR on the sea surface, and thus may form a golden tide when temperature and nutrition conditions are appropriate.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding authors.

Author contributions

ZX and LXL conceived of and designed the experiment with help from YM and HW. ZX and LXL carried out the experiment, with help from HJ and FY. The data analyses were performed by ZX and LXL, with help from HJ, FY, LJL, and SZ. ZX and LXL wrote the manuscript with contributions from HJ, FY, LJL, SZ, YM, and HW. All authors reviewed and gave their approval for the final manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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