

Photosynthetic Performance of the Red Alga *Pyropia haitanensis* During Emersion, With Special Reference to Effects of Solar UV Radiation, Dehydration and Elevated CO₂ Concentration

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ABSTRACT

Macroalgae distributed in intertidal zones experience a series of environmental changes, such as periodical desiccation associated with tidal cycles, increasing CO₂ concentration and solar UVB (280–315 nm) irradiance in the context of climate change. We investigated how the economic red macroalga, *Pyropia haitanensis*, perform its photosynthesis under elevated atmospheric CO₂ concentration and in the presence of solar UV radiation (280–400 nm) during emersion. Our results showed that the elevated CO₂ (800 ppmv) significantly increased the photosynthetic carbon fixation rate of *P. haitanensis* by about 100% when the alga was dehydrated. Solar UV radiation had insignificant effects on the net photosynthesis without desiccation stress and under low levels of sunlight, but significantly inhibited it with increased levels of desiccation and sunlight intensity, to the highest extent at the highest levels of water loss and solar radiation. Presence of UV radiation and the elevated CO₂ acted synergistically to cause higher inhibition of the photosynthetic carbon fixation, which exacerbated at higher levels of desiccation and sunlight. While *P. haitanensis* can benefit from increasing atmospheric CO₂ concentration during emersion under low and moderate levels of solar radiation, combined effects of elevated CO₂ and UV radiation acted synergistically to reduce its photosynthesis under high solar radiation levels during noon periods.

INTRODUCTION

Due to tidally driven immersion and emersion cycles, intertidal macroalgae are exposed periodically to air and experience variety of stresses, such as dehydration due to desiccation, increased exposures to irradiance levels, high or low salinity due to water loss or rainfall and dramatic temperature changes (1). Desiccation is one of the most important environmental stresses to many intertidal macroalgae. A decrease in thallus water content is known to affect their photosynthesis during the emersion and the extent of recovery upon re-immersion (2–5). Following severe desiccation, the photosynthetic machinery becomes more stressed and is eventually damaged, and the rate of photosynthesis sharply declines and the electron transport between photosystem II

(PSII) and photosystem I (PSI) is interrupted (6,7). Respiration of intertidal macroalgae was also affected by dehydration, which declined with increased water loss, then attributed to the decrease in net photosynthetic rate (2,8).

High light is another environmental stress to the intertidal macroalgae. Prolonged exposure of seaweeds to high light intensities can damage photosynthetic machinery and decrease both quantum efficiency and photosynthetic rates. In natural environments, solar UV radiation (280–400 nm) can negatively affect the growth (9,10), photosynthesis (9,11), contents of pigments (12) and key enzymes and DNA (13,14). UVA and/or UVB are found to alter the morphological structure or affect the morphological development (15,16) of macroalgae. These damages are further escalated when coupled with desiccation and/or temperature stress (1).

When macroalgae are exposed to air during emersion at low tide, CO₂ becomes the only exogenous carbon source because the large pool of HCO₃⁻ in seawater is no longer available. Considering almost 10 000 times higher diffusion rate of CO₂ in air than in water, the acquisition of CO₂ should be less constrained in air than in seawater (17). Once the surface water film has evaporated, CO₂ from the air can readily penetrate the cells to enhance photosynthesis (4,8), so that some intertidal macroalgae exhibit an increase in net photosynthetic rates following moderate desiccation compared to the fully hydrated state (2,18,19). Rising atmospheric CO₂ has been reported to enhance net photosynthetic rates of green, brown and red macroalgae during emersion regardless of the dehydration levels (4). However, such an influence of increasing CO₂ concentration in air has not been examined under multiple stressors, such as UV radiation and warming, which can interact with rising CO₂ to affect primary producers (20). When intertidal macroalgae are exposed to air during low tides, intensity of solar radiation exposed to them becomes much higher due to absence of seawater attenuation effect, which can lead to further physiological stresses in view of dehydration, increased temperature and UV exposures (20).

The red macroalga *Pyropia haitanensis*, an economically important marine crop in the southern China, distributed at upper part of intertidal zone, is exposed daily to air following tidal cycles. *P. haitanensis* is known to be able to endure long periods of desiccation. While in its sea-farming areas, it is also periodically exposed to air to stamp out fouling algae (such as *Ulva* and benthic diatom species). Periodical desiccation decreases photosynthetic carbon fixation of *P. haitanensis* (8), but it also

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plays a key role in maintaining high concentration of mycosporine-like amino acids that absorbs UV irradiances (21). Since photosynthesis of *P. haitanensis* cannot be saturated by the ambient CO₂ concentration during emersion under light-saturating conditions, increasing atmospheric CO₂ level has been suggested to enhance it (8). On the other hand, since incident UV-B (218–315 nm) irradiance is increasing with depletion of ozone and climate changes (22), and atmospheric CO₂ level is predicted to rise to up to 800–1000 ppmv by the end of this century on the basis of a fossil-fuel intensive emission scenario (A1F1) (23), therefore, intertidal seaweeds are influenced simultaneously by UV and elevated CO₂ concentrations. Obviously, *P. haitanensis* is to be exposed to multiple climate change factors during low tides. Since little is known about the combined effects of the multiple stressors, this study aimed to investigate the co-effects of desiccation, CO₂ and solar UV radiation on the photosynthetic performance of *P. haitanensis* and to evaluate its responses to future environmental changes. We found here that solar UV significantly decreased the enhancing effects of elevated CO₂ levels on the net photosynthetic performance of *P. haitanensis*, especially when highly dehydrated.

MATERIALS AND METHODS

Plant materials. The thalli of *Pyropia haitanensis* were collected every morning from its farmed rafts in Shen'ao bay, Nanao island (116.6 °E, 23.3 °N), Shantou, China in December, 2006. The samples were immediately transported to Nan'ao Marine Biological Station of Shantou University, where the experiments were carried out. We selected young and intact plants, and maintained them in sand-filtrated running-through seawater (Salinity, 31, pH_{obs}, 8.18) before carrying out the experiment during the noon period.

Experimental design. All the experiments were carried out during noontime on the sunny days (December, 2006), to obtain comparable data under relatively stable levels of solar radiation. The first experiment was designed to examine net photosynthetic carbon fixation, while the alga was suffering from continuous dehydration in air under different levels of CO₂ and different solar radiation treatments (see below). Water loss of the thalli was determined by pretests to establish the relation of water loss levels with time spans during the emersion (Fig. 1). The second experiment was set to check how different solar light levels affect the interactions of water loss, CO₂ and solar UV. Three solar light levels and three water loss levels were used in this experiment, respectively. Solar PAR light levels were set as low, 40 (LL), intermediate, 120 (ML) and high, 230 (HL) W m⁻² (about 196, 588 and 1127 μmol photons m⁻² s⁻¹, respectively), and water loss levels were 10% (A), 30% (B) and 55% (C), respectively. Different levels of solar radiation were achieved by covering neutral density screens on the chamber. In all the experiments, we used different thalli for different CO₂ or UV treatments.

Solar radiation measurements and treatments. Incident solar irradiance was continuously monitored using an ELDONET broad band radiometer (Real Time Computer, Möhrendorf, Germany), which has three channels, respectively, for photosynthetically active radiation (PAR, 400–700 nm), UV-A (UV-A, 315–400 nm) and UV-B radiation (UV-B, 280–315 nm). The device was installed on the roof of the Nan'ao Marine Biological Station of Shantou University. Three different radiation treatments were implemented as follows: thalli receiving full solar radiation (PAB treatment) in uncovered quartz tubes; thalli receiving UV-A and PAR (PA treatment) in quartz tubes covered with Folex 320 (Montagefolie, Nr. 10155099, Folex, Dreieich, Germany), transmitting irradiances above 320 nm; and thalli receiving only PAR (P treatment) in quartz tubes covered with Ultraphan film 395 (UV Opak, Digepra, Munich, Germany), transmitting the irradiances above 395 nm.

Measurements of photosynthetic carbon fixation. Photosynthetic rate of *Pyropia haitanensis* while exposed to air was determined as CO₂ uptake by infrared gas analysis using an infrared gas analyzer (CGT-700; Shimadzu, Japan), with a quartz leaf chamber (4 cm inner diameter, 15 cm long). This method can detect changes in CO₂ concentration between inlet and outlet, and has been applied to measure photosynthesis

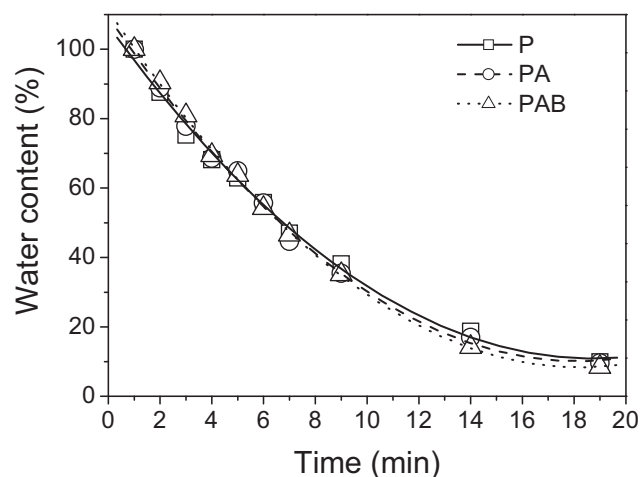


Figure 1. The changes in water content of *Pyropia haitanensis* thalli as a function of time when the thalli was exposed to high solar PAR (P), PAR+UV-A (PA) and PAR+UVR (PAB) at noon time on sunny days. The data shown in the figure are the mean values of three measurements with variations less than 8%. The data were fitted with quadratic equation ($R^2 > 0.99$). There were no significant difference among the light treatments P, PA and PAB.

during emersion of macroalgae or terrestrial cyanobacteria from 1980s (2,4,8,24,25). A single layer of thalli (0.4–0.7 g fresh weight) was placed on a stainless steel net (4 cm width * 14 cm long). Temperature was controlled at $19 \pm 1^\circ\text{C}$ by maintaining the leaf chamber in a temperature-controlled shallow tank with running fresh seawater. Two levels of CO₂ concentrations in air (ambient and 800 ppmv) were set to determine the net photosynthetic rates under different radiation treatments with or without UV. The concentration of 800 ppmv CO₂ was obtained by injecting pure CO₂ into an air bag (1 m³) and mixed with ambient air. Gas flow rate was set as 0.2 L min⁻¹. The percentages of water loss (WL, %) was estimated as follows: $WL = (W_0 - W_t) / (W_0 - W_d) * 100$, where W_0 is the initial wet weight, measured after removing surface water drops by lightly blotting with tissue paper, W_t is the desiccated weight after a known time interval and W_d is the dry weight (80°C, 24 h).

Net photosynthetic rate (P_n) (μmol CO₂ g (DW)⁻¹ h⁻¹) was calculated as follows: $P_n = C \times F \times 60 \times 273 / [(273 + T) \times 22.4 \times DW]$, where C is the difference in CO₂ concentration (mL m⁻³) between the inlet and outlet air, F is the gas flow rate (L min⁻¹), T is temperature (°C) and DW is the dry weight of the thalli used (g). The inhibition of photosynthetic rates caused by UV (I_{UVA} , I_{UVB} and I_{UVR}) was attained as follows:

$$I_{UVA} = \frac{P_{PAR} - P_{PA}}{P_{PAR}} \times 100\%$$

$$I_{UVR} = \frac{P_{PAR} - P_{PAB}}{P_{PAR}} \times 100\%$$

$$I_{UVB} = I_{UVR} - I_{UVA}$$

where P_{PAR} , P_{PA} and P_{PAB} represent net photosynthetic carbon fixation rates under P, PA and PAB treatments, respectively.

Statistical analysis. Differences among the treatments were tested using one-way or multiple-way analysis of variance (Tukey) with SPSS (version 19.0). A confidence level of 95% was used in all analyses.

RESULTS

The water contents of *P. haitanensis* thalli correlated well with the time intervals of desiccation ($R^2 > 0.99$, quadratic equation), with the water loss reaching 50% in about 6 min and over 90% in 19 min after emersion under sunlight (Fig. 1). Under the

high light level, net photosynthetic rate of the thalli measured in ambient CO_2 or high CO_2 level showed similar relationship with water loss, that shows a slight increase under low water loss and subsequent quick decline when the water loss further increased (Figs. 2 and 3A). Compared with the initial net photosynthetic rates, no significant differences were found during the beginning of water loss among all the radiation treatments ($P > 0.05$), however, with increased dehydration, presence of UVB inhibited it (Fig. 3). The inhibition observed caused by UVB was higher under HC than LC at higher levels of water loss ($P < 0.05$) (Fig. 3A). Under the ambient CO_2 condition, UVA showed no significant effect on the net photosynthetic rate of *P. haitanensis* under lower water loss ($P > 0.05$), and it started to inhibit it with increased water loss ($P < 0.05$) (Fig. 3B). UVB also had no significant effect when the water loss of the thalli was low, but it significantly ($P < 0.05$) decreased the net photosynthetic carbon rate when the water loss exceeded 30% (Fig. 2A). Under the high CO_2 condition, the net photosynthetic carbon rate of *P. haitanensis* exposed to PA treatment was higher than that to PAR alone, though the difference was not significant between them ($P > 0.05$). UVB-induced inhibition was not found below 30% water loss, but it increased with further dehydration ($P < 0.05$) (Figs. 2B and 3B). In general, when the thalli were exposed to high light and dehydration levels, the elevated CO_2 acted synergistically with UVB to increase the photosynthetic inhibition ($P < 0.05$) (Fig. 3B).

The ratio of the net photosynthetic carbon rates under HC to that under LC in *P. haitanensis* increased in the presence of UVA and reached the highest value at about 45% water loss, then decreased with further water loss (Fig. 4). In the presence

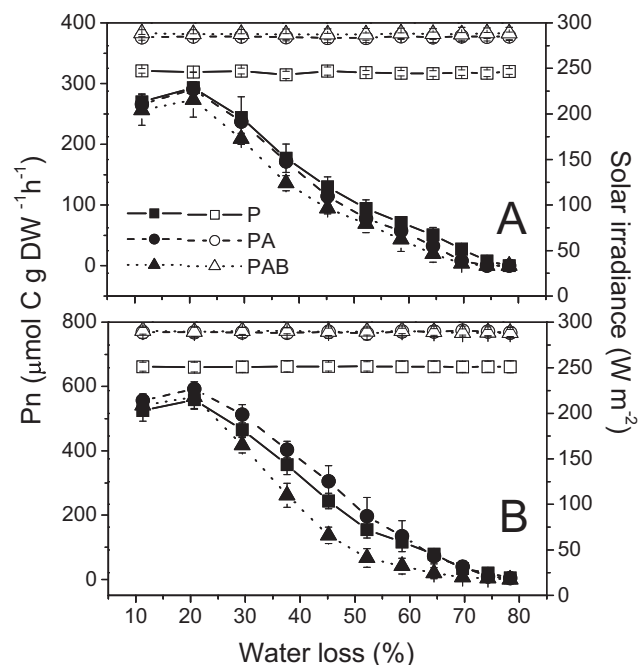


Figure 2. The change in net photosynthetic carbon fixation rate (closed symbols) of *Pyropia haitanensis* under different solar radiation treatments (PAB, PA and P, open symbols) with water loss at ambient CO_2 (A, 380 ppmv) and high CO_2 condition (B, 800 ppmv). The experiments were carried out during noon period on sunny days under relatively constant levels of solar radiation (open symbols). The data are the means of three measurements.

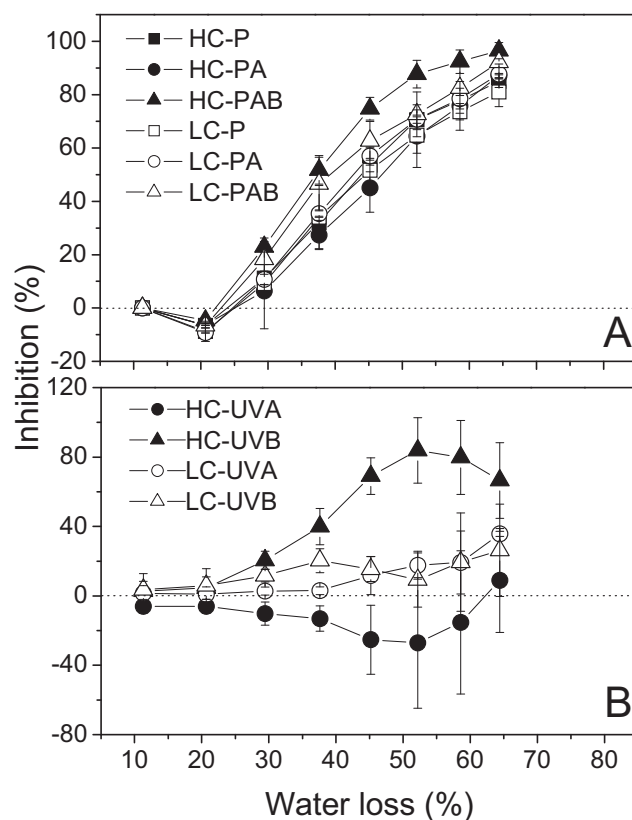


Figure 3. The changes of inhibition of net photosynthetic carbon fixation rate of *Pyropia haitanensis* induced by water loss (A) and by UV-A/UV-B (B) with the water loss at ambient CO_2 (LC, 380 ppmv) and high CO_2 condition (HC, 800 ppmv). All the data derived from Fig. 2.

of UVB, the ratios slightly decreased with water loss, and then sharply decreased with the water loss over 38%, being < 1 at higher levels of water loss (Fig. 4). The ratio under PAR alone changed relatively less with increased dehydration compared to those in the presence of UV irradiances.

In the ambient CO_2 condition, when the water loss of the thalli was low (10%), no significant difference in the net photosynthetic carbon rates was found among the UV treatments regardless of light intensities (Fig. 5A). When the water loss reached 30%, no significant difference in the net photosynthetic carbon rates was also found among the UV treatments when the thalli were exposed to low light intensity, but both UVA or UVR reduced the net photosynthetic carbon rates of the thalli exposed to middle light intensity ($P < 0.05$), and UVB or UVR showed the same result when the thalli were exposed to high light (Fig. 5B). When the water loss of the thalli was high (55%), no significant difference ($P > 0.05$) of the net photosynthetic carbon rates was found among the UV treatments at low light level, while under middle or high light treatments, it showed the significant decrease in the net photosynthetic carbon rates when the thalli measured under PAB treatment compared with P or PA treatments ($P < 0.05$) (Fig. 5C).

In the high CO_2 condition, when the water loss of the thalli was low (10%), no significant difference of the net photosynthetic carbon rates was found among the UV treatments regardless of light intensities (Fig. 5D). When the water loss reached 30%, no significant difference of the net photosynthetic carbon rates was also found among the UV treatments when the thalli

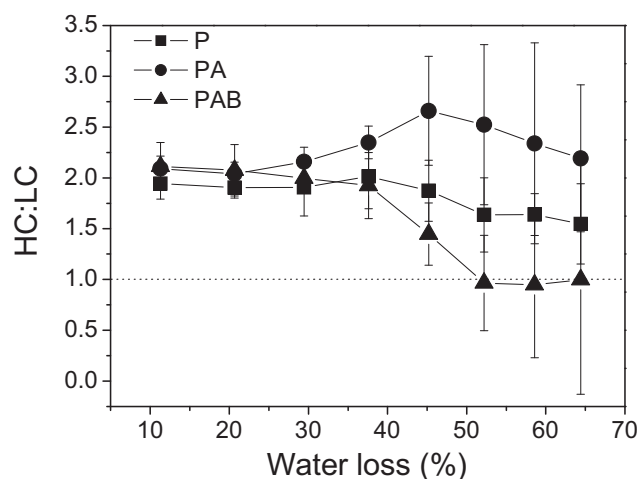


Figure 4. The ratios of HC:LC of net photosynthetic carbon fixation rate of *Pyropia haitanensis* under different solar radiation treatments (P, PA and PAB) derived from Fig. 2 as function of water loss.

exposed to low light intensity, but UVB and UVR reduced the net photosynthetic carbon rates of the thalli exposed to middle and high light intensities ($P < 0.05$) (Fig. 5E); the same trends was also found in the thalli which water loss reached 55% (Fig. 5F).

In different CO_2 levels, UV had no significant effects on the net photosynthetic carbon rates in the thalli measured under low light or low water loss (Fig. 5). When both the light and water loss increased, UVA/UVB or UVR, all showed significant inhibition effects. The rates of inhibition increased from 15% to 31% for UVA/UVB and 19% to 40% for UVR in the LC treatments, and they increased from 20% to 59% for UVB and 19% to 59% for UVR in the HC treatments. Compared with LC treatment, the rates of inhibition of UV in HC treatment were higher especially under the condition of high light and high water loss.

According to the results of multiple-way ANOVA analysis (Table 1), any of the four forcing factors played a significant role to affect the net photosynthetic carbon rates in *P. haitanensis* during emersion ($P < 0.001$). There are significant interactions between the two ($P < 0.05$), but no significant differences among the three factors ($P > 0.05$), except for that among the water loss, CO_2 and light intensity ($P < 0.05$). The effects of a combination of water loss, CO_2 , solar UV radiation and light intensity were statistically significant ($P < 0.05$).

DISCUSSION

There are different patterns in photosynthesis behavior between emersion and submersion. The photosynthesis of macroalgae usually saturated at the actual dissolved inorganic carbon concentration in the seawater since they can use bicarbonate, but when the thalli was exposed to air, HCO_3^- is no longer present and atmospheric CO_2 is the only exogenous carbon source, then the enhanced CO_2 levels has been reported to enhance photosynthesis of many macroalgae during emersion (4). With the increase in atmospheric CO_2 , more carbon resource is supplied to the red macroalga *Pyropia haitanensis* when it is exposed to air at low tide, and then the net photosynthetic carbon rates were enhanced (Fig. 2). Slight water loss can increase the emerged photosynthesis

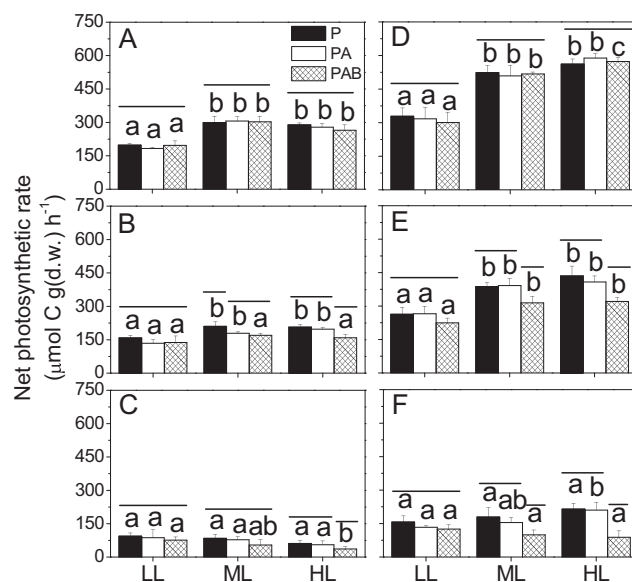


Figure 5. The changes in net photosynthetic carbon fixation rate of *Pyropia haitanensis* measured at ambient CO_2 (380 ppmv) under different solar radiation treatments (P, PA and PAB) at PAR levels of 40 (LL), 120 (ML) and 230 (HL) W m^{-2} (about 196, 588 and 1127 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, respectively) at 10% (A), 30% (B) and 55% (C) levels of water loss. D, E and F are the change in net photosynthetic carbon fixation rate measured at high CO_2 condition (800 ppmv) at 10%, 30% and 55% levels of water loss, respectively. The data are the means of three measurements. Different letters and horizontal lines represent significant differences among the light intensities (LL, ML and HL) and light treatments (P, PA and PAB), respectively.

Table 1. Multiple-way ANOVA analysis of individual and interactive effects among Water loss (WL), CO_2 concentration (CO_2), Light intensity (LI) and Solar UV radiation (UV) at $P < 0.05$ level.

Treatments	<i>P</i>	df	<i>F</i>	Significant
WL	<0.001	2	1475.679	Yes
CO_2	<0.001	1	1607.437	Yes
LI	<0.001	2	208.746	Yes
UV	<0.001	2	34.443	Yes
LI \times CO_2	<0.001	2	70.735	Yes
LI \times WL	<0.001	4	65.883	Yes
LI \times UV	0.030	4	2.768	Yes
$\text{CO}_2 \times$ WL	<0.001	2	103.430	Yes
$\text{CO}_2 \times$ UV	<0.001	2	9.694	Yes
WL \times UV	<0.001	4	5.732	Yes
LI \times $\text{CO}_2 \times$ WL	<0.001	4	7.259	Yes
LI \times $\text{CO}_2 \times$ UV	0.518	4	0.814	No
LI \times WL \times UV	0.615	8	0.787	No
$\text{CO}_2 \times$ WL \times UV	0.057	4	2.358	No
LI \times $\text{CO}_2 \times$ WL \times UV	0.040	8	2.093	Yes

of *P. haitanensis*, but the net photosynthetic carbon rate significantly decreased with further water loss (Figs. 2 and 3). The positive effect of CO_2 was not affected by water loss except that in the presence of UVB which significantly decrease it. That is, the inhibition effect of UVB was enlarged in the future ocean, especially during low-tide condition. Because atmospheric CO_2 is the only carbon source of intertidal macroalgae at low tides, *P. haitanensis* must be sensitive to the rising of ambient CO_2 levels. Although some macroalgae showed the saturated emersed

photosynthesis at the ambient CO₂ levels (26,27), the photosynthesis of more intertidal macroalgae were enhanced by rising CO₂ concentration (4,28–31). In natural condition, about one time enhancement of net photosynthetic carbon rate was found in *P. haitanensis* measured under double ambient CO₂ concentration, which was in accord with the results attained in lab experiment with constant PAR light (8). Solar UV radiation is a permanently existing environmental factor that macroalgae are usually exposed to, one of the flaws in lab studies is that the photosynthetic performance has been mainly investigated without considering the effects of UVR. Our study showed that UV had no significant effects on the net photosynthetic carbon rate when the water loss was low even in high light at noon time. This can be attributed to the high levels of mycosporine-like amino acids (MAAs) in *P. haitanensis* (21), which can reduce UV-related damage and play a protective role in resisting solar UVR (32).

But, with the increase in water loss, the inhibition of UV gradually appeared and showed the highest values in high water loss and high light intensity. Desiccation is an important stress factor faced by intertidal macroalgae, mainly triggered by daily tide changes (33,34). It was demonstrated that desiccation in *Pyropia columbina* induced an overproduction of reactive oxygen species (ROS) (35), which can be extremely harmful at high concentration. Although some research showed that desiccation can play a positive role in the thermotolerance of intertidal macroalgae, the photosynthesis is severely decreased in high water loss, which affects reactions catalyzed by water-soluble enzymes and by enzymes at the membrane–water interface (36). While solar UV, especially UV-B is known to inhibit the growth, photosynthesis, pigments, key enzyme, D1 protein of photosystem II reaction center and even DNA of macroalgae (37). UV can also affect the cellular ultrastructure of macroalgae, resulting in the changes of mitochondria, damage of chloroplast and phycobilisomes in red macroalgae (11). When desiccation is coupled with UV radiation, the double stress makes the photosynthesis to decrease further. With the seasonal depletion of stratospheric ozone concentration, enhanced solar UV would show more stress on the thalli under high water loss.

The inhibition induced by UV was higher in the HC condition compared with LC treatment, especially under HL and high water loss condition. That is, the benefit of enriched CO₂ concentration was cut down by UV radiation. Because water loss and UV radiation could both damage photosystem reaction center, the photosynthetic performance was severely inhibited when the thalli were exposed to high UV and water loss condition together. At this time, the only exogenous carbon source, atmosphere CO₂, was not the limiting factor for the net photosynthetic carbon rate of *P. haitanensis*, moreover, the high water loss can further inhibit the absorption of CO₂ for the cells. So the enhancement of CO₂ in thalli was decreased with water loss, especially in the present of high solar UV radiation. The co-effect of UV and CO₂ on algae were also studied in some researches, UV and CO₂ together decreased the calcification in the coralline algae *Coralina sessilis* (38) and *C. officinalis* (39), changed the phytoplankton composition (40) and CO₂ can eliminate the deleterious influence of UVR on photosynthesis (41). Nevertheless, the roles of CO₂ in all of these researches were focused on not only the acquisition of carbon resource in the carbonate system, but also pH change in culture medium. At this point, the effect of CO₂ on the emersed thalli of *P. haitanensis* might be clearer to understand compared with submerged thalli.

As one of typical intertidal macroalgae, *P. haitanensis* always experiences periodic exposure with tidal cycle, and the thalli must be adjusted to dehydration due to desiccation, solar high UV radiation and other environmental stresses. Although short-term exposure can increase the ability for absorption of CO₂ in *P. haitanensis* and it will be benefited to elevated atmospheric CO₂ concentration with industrial processes, the benefit of CO₂ is relieved with the increase in water loss and/or in the presence of solar UV radiation when the thalli is exposed to air for long time (it usually occurs because this macroalga is distributed in the upper parts of intertidal zone). In conclusion, in natural condition, *P. haitanensis* will benefit from the CO₂ concentration increase in the future when the exposed time is low or in the very low light conditions such as early morning, late afternoon or very cloudy days. But, this benefit will be severely relieved with the exposed time increased under high light condition due to the synergistic effects of solar UV and desiccation.

While impacts of the environmental changes on photosynthesis at daily (or longer) time scale would be very limited since stimulation or inhibition of photosynthesis may be transitory for some intertidal macroalgae. However, for most *Pyropia* (*porphyra*) species, their thalli can be dehydrated over 90% (42), and *Pyropia haitanensis*, being distributed at the upper part of intertidal zone, is known to endure long period of desiccation. Slightly desiccated (at the disappearance of the water film) condition stimulated the emersed photosynthesis of intertidal species, which is transitory (4). CO₂, solar UV radiation, water loss and levels of solar PAR, each showed significant effect on the net photosynthetic rates of *P. haitanensis*, and significant interactions were found among the environmental factors. Nevertheless, antagonistic effects appeared to exist when three forcing factors were combined. Therefore, to predict the effects of the ongoing global changes on intertidal algae, interactions among multiple stressors should be explored.

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