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Full Length Article

Chlorophyll Fluorescence Characteristics Responses of Two Strains of *Porphyra haitanensis* to Emersion and Submersion

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Abstract

The chlorophyll fluorescence characteristics of two *Porphyry haitanensis* strains were examined under different lengths of emersion and submersion. A 6 h emersion treatment had no significant effect on the photosystem II relative electron transport rate (*r*ETR(II)) of the two strains. The *r*ETR(II) values reached their maxima under an activation light intensity of 209 μmol·m^{-2}·s^{-1} at 0 h and 6 h after emersion. The trends in the semi-saturation light intensity (I_k) values of the two strains resembled that of the maximum relative electron transfer rate (rETR$_{max}$), which was highest at 0 h and gradually decreased with emersion time. There were no significant differences in rETR$_{max}$ and I_k between the two strains, indicating that the tolerance of the two strains to water stress was equivalent. In the short submersion times of 0 h and 16 h, *r*ETR(II) reached its maximum value when the activation light intensity was 209 μmol·m^{-2}·s^{-1}. There was no significant decrease in *r*ETR(II) after 0 h and 16 h of submersion of the Dongtou local strain, but in the Eastern Zhejiang No. 1 strain, this value was significantly (P<0.05) reduced. This indicated that the Dongtou local strain was physiologically more active in the early period of submergence. As submersion time increased, the *r*ETR(II) values of both strains gradually decreased. The highest I_k value of the two strains of *P. haitanensis* was observed after 16 h of submersion, at which point the initial slope value was also at its minimum. The change in the fast light curve fluorescence of the two strains was basically consistent across the submersion times. Selecting strains that are tolerant to submerged conditions and creating appropriate short-term emersed environments are important for optimal growth and high yields in *P. haitanensis*.

Keywords: *Porphyra haitanensis*; Chlorophyll fluorescence; Rapid light curve; Emersion; Submersion

Introduction

Porphyra haitanensis, also called laver or nori, is an economically important red algae species, which is naturally distributed and cultivated in southern China (Wang *et al*., 2011). In the wild, *P. haitanensis* grows in intertidal zones, experiments were repeated in both emersed and submerged conditions with the changing tides. Thus, regular dehydration and re-hydration are the most significant events in their life cycles. The special hydrological conditions of the intertidal zone allowed *P. haitanensis* seedlings to avoid problems such as rot that was caused by long-term submersion. Typhoons often occur in their main habitats of southeastern coastal China, which causes long-term submersion and thus affects growth and yield. *P. haitanensis* faced strong light, ultraviolet radiation (UVR), osmotic pressure, and other stresses when it dried out (Jiang and Gao, 2009). The success of *P. haitanensis* cultivation is partially owing to its high stress tolerance.

One of the most important factors that restrict the development of photosynthetic organisms is water deficiency (Bukhov *et al*., 2004; Lin *et al*., 2009; Ma *et al.,* 2016). When exposed to high light and temperature stress, many species of *Porphyra* lose 85–95% of their cellular water during daytime low tides (Blouin *et al*., 2011). Laver has a strong resistance to drying out; it can endure 8–10 h of 90% desiccation (Liu and Gao, 1987). When laver dried out moderately, the loss of water on the surface of the thalli reduced the diffusion barrier of CO_2 in the aqueous phase, thereby increased photosynthetic activity, but further loss of water reduced its photosynthetic rate and photosynthetic efficiency (Gao and Aruga, 1987; Zou and Gao, 2002). Different *Porphyra* species have different reactions under the same water-deficient conditions, with some species being extremely tolerant to dehydration, while others were not (Smith *et al*., 1986). During the emersion process, *P. haitanensis* could continue photosynthesis and respond to CO_2 concentration changes in the air (Zou and Gao, 2002).

Chlorophyll fluorescence has recently been used as an independent method for assessing algal physiology in aquatic environments (Lin *et al*., 2009; Prasil *et al*., 2008). Compared with the apparent gas exchange index, pulse amplitude modulated (PAM) fluorescence instruments can be used to study chlorophyll fluorescence parameters that reflect their intrinsic physiological characteristics. The chlorophyll fluorescence kinetics technique is a fast, noninvasive assay for measuring leaf photosynthetic function, especially in photosystem II (PS(II)) functional studies (Schreiber *et al*., 1994; Zhao *et al*., 2010). In particular, PAM fluorometry has been widely used in investigating photosynthetic properties of algae (Lin *et al*., 2009; Li *et al*., 2013; Liu *et al*., 2017; Wang *et al*., 2016), making it possible to study the chlorophyll fluorescence characteristics of *P. haitanensis* in both emersed and submersed conditions.

The regularly changing tides of the intertidal zone periodically dry and dehydrate *P. haitanensis*, which have tremendous impact on its natural growth and cultivation. This aspect need to be theoretically and empirically researched. In this study, two strains of *P. haitanensis* were cultured in Dongtou in Wenzhou, China. The responses of chlorophyll fluorescence parameters to emersion and submersion were studied, in order to explore the tolerance of *P. haitanensis* to dehydration and submergence.

Materials and Methods

Sample Collection

Two strains of *P. haitanensis* were collected on the shore of Wenzhou (27°51′–27°52′N, 121°4′–121°5′E), China. Their thalli were collected on November 15, 2014 as part of a second harvest of laver. One of the strains of *P. haitanensis* was the Dongtou local strain, which is the local traditional strain cultivated in Dongtou. The other strain of *P. haitanensis* was Eastern Zhejiang No. 1, which is a newly introduced strain. Within 2 h, *P. haitanensis* samples were transported back to the laboratory immersed in their original sea water, where the experiments were immediately conducted. The basic physical and chemical parameters of seawater were determined by using an Ap2000 AQUAread water quality analyzer (AQUAread, Kent, UK), which were: temperature, 20.48°C; pH 7.95; EC 51.89 dS/m; DO 8.03 mg/L; salinity 34.12‰ and seawater specific gravity 24.73 σt.

Experimental Treatments

In the emersion treatment, *P. haitanensis* were suspended in the laboratory to allow them to naturally dehydrate. After air drying for 6 h, 50 h and 120 h, the samples were measured immediately after the thalli were slightly soaked in their original seawater. In the submersion experiments, *P. haitanensis* were immersed in their original sea water. The samples were selected after being submersed for 16 h, 48 h, and 68 h, and the samples were tested immediately after they were emersed.

Water Content Determination

The absolute water content (AWC) of the thalli was defined using the formula (Lin *et al*., 2009):

$$AWC = (W_t - W_d) \times 100 / (W_0 - W_d)$$

W_0 is the weight of the fresh thalli immediately after the gentle removal of surface water (wet weight), W_d is the weight of the thalli after 24 h at 60°C in a dry box (dry weight), W_t is the weight of thalli after a set time (6 h, 50 h, and 120 h) of dehydration. Water absorbent paper was used to remove water from the surfaces of thalli in order to avoid the formation of salt crystals (Gao *et al*., 2016).

Photosynthetic Measurements

Four to six complete *P. haitanensis* thalli were selected from each strain (Dongtou local strain and Eastern Zhejiang No.1 strain). The surface water of thalli was removed by water absorbent paper before measurement. The rapid light curve was measured at various times during emersion and submersion using a DUAL-PAM-100 fluorescence spectrometer (Heinz Walz GmbH, Germany). In order to prevent rapid water loss in the determination process, *P. haitanensis* were wrapped in a plastic film. Measurements were taken at the thalli base using an activated light source with red and blue light; a gradient of eight activated light intensities were selected ranging from 0 to 341 μmol/m^2/s. The measurements conducted immediately after the thalli were taken out their water, directly after being transported to the laboratory, were recorded as the 0 h submersion measurements. After 16 h submersions, *P. haitanensis* thalli were air dried, after which, the 0 h emersion measurement was recorded. The used samples were discarded and not re-used for subsequent measurements. This avoided the problem of repeatedly submerged or dried samples having been effected by the continuous stress of recurrent emersions and submersions.

Statistical Analysis

The rapid light curve parameters were fit according to the method described by Platt *et al*. (1980), which determines the initial slope (α), the maximum relative electron transfer rate (*r*ETRmax), and the semi-saturation light intensity (I_k) using the following formula:

$$P = Pm(1 - e^{-\alpha PAR/Pm}) \cdot e^{-\beta PAR/Pm}$$

Where P is the PS(II) relative electron transport rate (*r*ETR) under certain light intensities (Li *et al*., 2015); α is the rapid light curve of the initial slope; *P*m is the (*r*ETRmax); and the semi-saturated light intensity (I_k) is the ratio of *P*m to α.

Excel 2003 was used for data processing, drawing graphs, and calculating regression coefficients. Rapid light curve fitting and other all statistical analyses were conducted with SPSS 17.0 statistical software; comparisons between the two strains were analyzed via a one-way analysis of variance.

Results

Chlorophyll Fluorescence Characteristics Responses to Different Emersion Lengths

Table 1 shows absolute water contents of the two strains, which decreased with the emersion time, but the absolute water content after a 120 h emersion was higher than that after a 50 h emersion; this may be caused by an increase in the absolute water content caused by thalli becoming waterlogged. After 6 h, the absolute water content of both strains was still above 17%, but the water loss exceeded 96% after 50 h. The absolute water content of Eastern Zhejiang No. 1 strain thalli was higher than that of the Dongtou local strain at any given emersion time, but there were no significant differences between the two strains.

Under the same activation light intensity, the *r*ETR(II) values of the two strains did not exhibit significant differences between 0 h and 6 h emersion treatments (P>0.05), though it was higher than that of 120 h emersion treatments and lowest for 50 h treatments (Fig. 1). The *r*ETR(II) value reached its maximum at 50 h of emersion under the lower activation light intensity of 61 $\mu mol \cdot m^{-2} \cdot s^{-1}$, and *r*ETR(II) decreased as activation light intensity increased. The *r*ETR(II) of the Dongtou local strain was highest under an activation light intensity of 209 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at 0 h, 6 h, and 120 h of emersion. When the *r*ETR(II) of Eastern Zhejiang No. 1 strain reached its maximum at 0 h and 6 h of emersion, the activation light intensity was also 209 $\mu mol \cdot m^{-2} \cdot s^{-1}$. However, when *r*ETR(II) reached its maximum at 120 h of emersion, the activation light intensity was 61 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The rapid light curve of the two strains consistently took similar values under the same emersion times.

Table 2 shows the α values of the two strains of *P. haitanensis*, where the 50 h emersion exhibited the maximum value, indicating a high utilization efficiency of light activation. The two *P. haitanensis* strains showed the lowest α value after 120 h of emersion, which indicated the low initial utilization efficiency of activated light. The I_k trends in the two strains were similar to those of *r*ETRmax, which was the highest at 0 h and gradually decreased with emersion time, ultimately reaching its lowest point at 120 h. The difference in α between the two strains was significant (P < 0.05), but there were no significant (P>0.05) differences in I_k and *r*ETR$_{max}$.

The correlations among *r*ETRmax, I_k, and absolute water content were strong, with all determination coefficients (R^2) exceeding 0.93. There were no significant correlations among *r*ETRmax, I_k, and absolute water content in the Dongtou local strain. However, there were significant correlations between *r*ETR$_{max}$ and absolute water content (P < 0.05), and I_k was highly significantly correlated with water content (P < 0.01) in the Eastern Zhejiang No.1 strain.

Chlorophyll Fluorescence Responses to Different Submersion Times

Under the same activation light intensity, the *r*ETR(II) value of the Dongtou local strain was very low at 0 h and 16 h, while it was higher than that after a 48 h submersion and lowest after a 68 h submersion (Fig. 2). Under the same activation light intensity, the *r*ETR(II) of the Eastern Zhejiang No.1 strain at 0 h was significantly higher than that of other submersion times, while the lowest value was observed at 48 h. At the longest submersion time (68 h), the *r*ETR(II) of the Dongtou local strain reached the highest value at a low activation light intensity of 61 $\mu mol \cdot m^{-2} \cdot s^{-1}$, while the *r*ETR(II) of the Eastern Zhejiang No.1 strain reached a maximum at a low activation light intensity of 34 $\mu mol \cdot m^{-2} \cdot s^{-1}$ with *r*ETR(II) decreasing with activation light intensity afterward. In contrast, at short submersion times of 0 h and 16 h, *r*ETR(II) reached its maximum with an activation light intensity of 209 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

Table 3 shows the α and *r*ETR$_{max}$ values of the two strains of *P. haitanensis* were highest at a submersion time of 0 h, indicating the high utilization efficiency of light activation. Two *P. haitanensis* strains showed the lowest α values after 16 h of submersion, indicating the low initial utilization efficiency of activated light. The *r*ETR$_{max}$ of the Dongtou local strain decreased to a minimum when submerged for 68 h, while the Eastern Zhejiang No.1 strain exhibited the lowest value at 48 h. The highest I_k values of both strains were observed after 16 h of submersion, which was related to the lowest α value at this time. The trends in the fast light curve fluorescence of the two strains were basically consistent across the different submersion times.

Discussion

The *P. haitanensis* is a red algae inhabiting the mid-high tide zone, which is regularly exposed to air and submerged in seawater. Accordingly, the species is often exposed to water stress. Its monolayer cell membrane structure permits rapid water loss. *P. haitanensis* dries out twice daily (Li *et al*., 2011); in the spring, exposure and desiccation in the air for up to 4 h or more can cause water loss exceeding 90%, which forces thalli to fully utilize their strong tolerant to water loss and rehydration (Xie *et al*., 2014). In this study, 50 h emersions of the two strains of *P. haitanensis* resulted in water loss of 96% or more. This slow water loss may be related to the air temperature, humidity, and other factors. It has been reported that photosystem II activity is sensitive to drought stress (Gao *et al*., 2013). Laver dried for 2 h and then rehydrated for 3 h showed recoveries of photosynthetic rates up to 100%.

Table 1: The absolute water content of *P. haitanensis* after various emersion times

AWC %	0 h	6 h	50 h	120 h
Dongtou local strain	100 ± 0.00	17.66 ± 0.09	2.71 ± 0.00	4.23 ± 0.00
Eastern Zhejiang No.1 strain	100 ± 0.00	21.80 ± 0.09	3.19 ± 0.01	4.81 ± 0.01

Mean ± standard deviation

Table 2: Photosystem II rapid light curve parameters under different emersion times

Strain	Emersed time	α	$r\mathrm{ETR}_{max}$	I_k ($\mu mol \cdot m^{-2} \cdot s^{-1}$)
Dongtou local strain	0 h	0.074 ± 0.008	6.104 ± 0.80	82.604 ± 9.97
	6 h	0.069 ± 0.011	5.595 ± 1.02	81.055 ± 6.36
	50 h	0.077 ± 0.011	3.683 ± 0.07	47.831 ± 4.55
	120 h	0.065 ± 0.012	2.917 ± 0.46	44.886 ± 2.40
Eastern Zhejiang No.1 strain	0 h	0.060 ± 0.008	5.652 ± 0.18	93.505 ± 7.15
	6 h	0.065 ± 0.012	3.526 ± 0.46	54.118 ± 5.09
	50 h	0.067 ± 0.007	2.986 ± 0.26	44.567 ± 4.00
	120 h	0.052 ± 0.007	2.130 ± 0.33	41.130 ± 5.68

Mean ± standard deviation

Table 3: Photosystem II rapid light curve parameters under different submersed time

Strain	Emersion time	α	$r\mathrm{ETR}_{max}$	I_k ($\mu mol \cdot m^{-2} \cdot s^{-1}$)
Dongtou local strain	0 h	0.109 ± 0.014	7.735 ± 0.54	70.963 ± 8.66
	16 h	0.074 ± 0.008	6.104 ± 0.80	82.604 ± 9.97
	48 h	0.104 ± 0.016	3.570 ± 0.38	34.437 ± 4.59
	68 h	0.090 ± 0.012	2.977 ± 0.36	33.041 ± 4.26
Eastern Zhejiang No.1 strain	0 h	0.095 ± 0.009	7.568 ± 0.62	79.992 ± 9.92
	16 h	0.060 ± 0.008	5.652 ± 0.18	93.505 ± 7.15
	48 h	0.071 ± 0.008	2.095 ± 0.16	29.460 ± 3.15
	68 h	0.086 ± 0.017	2.349 ± 0.19	27.314 ± 2.47

Mean ± standard deviation

The ability to maintain a basal photosynthetic rate during dry times is important for the total photosynthetic productivity of marine algae (Li *et al*., 2011).

As emersion times increased, the *r*ETR(II) values decreased to their lowest level after a 50 h emersion, but increased slightly at 120 h, perhaps as a result of the long-term desiccation activating a protective mechanism that increased *r*ETR(II). The initial utilization efficiency of *P. haitanensis* was higher at 50 h after emersion, but at 120 h after emersion, *P. haitanensis* exhibited a low initial utilization efficiency of activated light. This was likely caused by the emersion time being too long, thereby leading to a difficult recovery of photosynthetic capacity under low light intensity. The $r\mathrm{ETR}_{max}$ and I_k of the two strains reached its maximum at 0 h and gradually decreased with emersion time down to a minimum at 120 h. This showed that the emersion process restrained the electron transport rate and reduced the saturation light intensity, which could explain the decrease in the photosynthetic rate at long emersion times. There was no significant difference in $r\mathrm{ETR}_{max}$ and I_k between the two strains, indicating that the tolerance of the two strains to desiccation stress was roughly equivalent.

The transport of photosynthetic electron in algae is largely influenced by desiccation stress (Gao *et al*., 2013a, b; Gao and Wang, 2013). Water loss has a great impact on the photosynthetic capacity of algae in the intertidal zone (Lipkin *et al*., 1993). The net photosynthetic rate of *P. haitanensis* decreased with the prolongation of drying time. The steady decrease in photosystem II activity during dehydration decreased the rates of linear electron flow (Heber and Walker, 1992; Golding and Johnson, 2003). However, the photosynthetic rate of *P. haitanensis* was not negative within 12 h after drying (Liu and Gao, 1987; Zou and Gao, 2002). As the drying time increased, the time needed to fully recover photochemical efficiency increased (Jiang and Gao, 2009).

When the tide is high, the intertidal *P. haitanensis* thalli are submersed in seawater, then exposed to two potential sources of exogenous carbon [dissolved CO_2 and bicarbonate (HCO_3^-)] for photosynthesis. Chlorophyll a and phycobiliproteins are important photosynthetic pigments in laver. Phycobiliproteins containing phycoerythrin and phycocyanin are multi-subunit protein pigment complexes that are sensitive to light (Cai *et al*., 2014). In the cells of macroscopic red algae, light energy utilization activity of phycobiliproteins is higher than that of chlorophyll (Haxo and Blinks, 1950). In general, the higher the phycobiliproteins content, the stronger the photosynthetic capacity (Glazer, 1984). If *P. haitanensis* is submersed for a long time, bacterial growth is promoted along with other detrimental effects to healthy algal growth. Intertidal *P. haitanensis* thalli alternately spend part time exposed to the atmosphere and part time emersed in seawater throughout the day, fluctuating with the tidal level, which ensures its healthy growth.

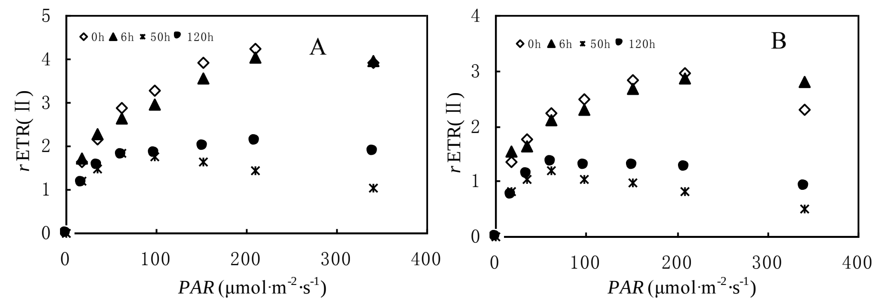

Fig. 1: The rapid light curve of *r*ETR(II) under different emersion times for (A) the Dongtou local strain and (B) Eastern Zhejiang No. 1 strain

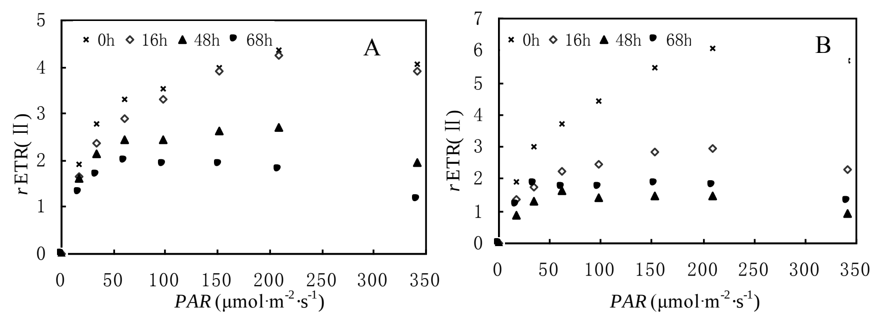

Fig. 2: The rapid light curve of *r*ETR(II) at various submersion times for (A) the Dongtou local strain and (B) Eastern Zhejiang No. 1 strain

The study showed that the *r*ETR(II) values of Dongtou local strain were very close between 0 h and 16 h under submersed conditions, but the *r*ETR(II) of the Eastern Zhejiang No. 1 strain at 16 h was significantly lower than that of 0 h, indicating that the Dongtou local strain was more tolerant to the stresses of submersion in the early period of submergence. As submersion time increased, the *r*ETR(II) of Dongtou local strain decreased gradually, but the Eastern Zhejiang No. 1 strain exhibited a recovery after 48 h. This indicates that the Eastern Zhejiang No. 1 strain may have a strong self-protection mechanism, which was consistent with its higher α value and initial utilization efficiency of activated light after a 68 h submersion. Under the different submergence times, the trends in the fast light curve parameters of the two strains differed. This may have been caused by the different adaptation mechanisms of the different strains of *P. haitanensis* to submersion.

The decreased photosynthetic electron transfer efficiency of *P. haitanensis* was consistent with the rate of the open PS(II) reaction center decreasing, indicating that the photosynthetic electron transport was blocked, and the light energy was absorbed by the PS(II) pigment used in the photochemical electron transfer. Light conversion efficiency and potential activity decreased, thereby reducing normal photosynthesis. Submersion may reduce respiration and promote accumulation of oxygen free radicals in cells, which damages the structure of chloroplast membranes and accelerates the decomposition of chlorophyll, leading to a decrease in the chlorophyll content of thalli. Because chlorophyll is the main chemical substance of photosynthesis, it absorbs and transmits light energy. However, it also plays a vital role in the process of electron transfer, a necessary component of photosynthesis. Total chlorophyll/carotenoids showed the strongest association with fluorescence parameters such as quantum efficiency and PS(II) yield (Singh *et al*., 2017). The decreased chlorophyll content in thalli may have decreased photosynthetic electron transport efficiency during submersion. It is also important to investigate the synergistic effects of environmental factors when determining the conditions for optimum photosynthetic efficiency of PS(II) in seaweeds (Green and Neefus, 2016).

Conclusion

The *r*ETR(II) of the two *P. haitanensis* strains reached their maxima under a low activated light intensity of 209 $\mu mol \cdot m^{-2} \cdot s^{-1}$ after short emersion times (0 h and 6 h) and submersion times (0 h and 16 h). The tolerance of the two strains to water stress was equivalent, but the Dongtou local strain was more tolerant to submersion in its early period. In order to achieve healthy growth and high yields in *P. haitanensis*, strains should be selected that are tolerant to submerged conditions and creating environments with short-term emersion.

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