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Highly efficient photoprotective responses to high light stress in *Sargassum thunbergii* germlings, a representative brown macroalga of intertidal zone

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ABSTRACT

Photosynthetic responses to sudden exposure to high light stress (600 μmol photons m^{-2} s^{-1}) and the potential for subsequent recovery were assessed in *Sargassum thunbergii* germlings grown under three different light intensities of 10 μmol photons m^{-2} s^{-1} (low light, LL), 60 μmol photons m^{-2} s^{-1} (moderate light, ML) and 300 μmol photons m^{-2} s^{-1} (high light, HL). The photosynthetic activity (maximum photochemical efficiency, F_v/F_m; rapid light curves, RLCs; non-photochemical quenching, NPQ) was estimated by chlorophyll fluorescence using a pulse amplitude modulated fluorometer. All treatments exhibited high capacity for dynamic photoinhibition, with the fast reaction kinetics of F_v/F_m during both inhibition and recovery period, and with the rapid induction of maximum NPQ (within minutes). HL-germlings characteristically demonstrated a high NPQ value of approx. 5.5, allowing a flexible and reversible response to stress. Besides the significant contribution of NPQ to photoprotection, photosynthetic capacity (ETR_{max}) in LL-germlings was as great as that in HL-germlings, suggesting that energy dissipation through photochemical electron transport system could also reduce probability of photodamage. NPQ in *S. thunbergii* germlings appeared to be not directly controlled by a transthylakoid proton gradient (ΔpH) due to the lack of "light activated state". Furthermore, inhibition of xanthophyll cycle with DTT considerably blocked NPQ_{pre} induction of preillumated germlings, and a slow NPQ relaxation occurred upon disruption of ΔpH by NH_4Cl, collectively indicating the importance of xanthophyll cycle to NPQ. These results suggested that *S. thunbergii* germlings could tolerate sudden high light by down-regulation of photosynthetic capacity, based on highly efficient photoprotective responses, including energy dissipation through xanthophyll cycle and photosynthetic electron transport. The photoprotection was efficiently independent on the light history of germlings. The high photosynthetic plasticity with immediate response to rapidly changing light may be a central feature explaining the survival of germlings in highly variable light environments of intertidal habitat.

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1. Introduction

When light energy input exceeds the capacity for energy utilization, an active regulatory process by a decrease of photosynthetic efficiency occurs, which is described as photoinhibition (Osmond, 1994). According to Osmond (1994), dynamic photoinhibition, as a photoprotective mechanism, is related with the dissipation of excessive absorbed photons harmlessly as heat. By contrast, chronic photoinhibition is followed by a nonreversible damage of the photosynthetic apparatus with corresponding degradation of the D_1 protein. Different mechanisms can contribute to the energy dissipation (NPQ) in higher plants and green macroalgae, including, e.g., state transitions, xanthophyll cycle, photosystem II (PSII) reaction center quenching and inactivation of PSII (Goss and Jakob, 2010). However, based on evolutionary divergence, brown macroalgae demonstrate unique light harvesting pigments and protein compositions (Goss and Jakob, 2010).Enhanced heat dissipation by xanthophyll cycle represents the major photoprotective mechanism in brown macroalgae (Fernández-Marín et al., 2011; García-Mendoza and Colombo-Pallotta, 2007).

Photosynthetic responses of brown macroalgae to high light stress have been studied mainly in the subtidal species such as *Laminaria* (Rodrigues et al., 2002), and *Macrocystis* (García-Mendoza and Colombo-Pallotta, 2007), which are exposed to relatively slow changes in the incident light intensity. By contrast, the situation may become further complicated by the fact that irradiance pattern encountered by intertidal macroalgae are controlled by the daily cycle, tidal rhythm and changing cloud cover (Schagerl and Möstl, 2011). Consequently, intertidal macroalgae must have evolved anatomical and physiological mechanisms to cope with such irradiance fluctuations and maintain an optimal photosynthetic rate (Davison and Pearson, 1996). Compared with species that inhabit deeper waters, intertidal species are less susceptible to photoinhibition and have greater recovery capacity after a photoinhibitory treatment (Pearson et al., 2000; Rodrigues et al., 2002; Yu et al., 2013). This capacity has been attributed to their efficient

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photoprotective mechanisms (Harker et al., 1999), which enable the maintenance of the crucial balance between energy absorption and photosynthetic light utilization through carbon fixation, thereby preventing photo-oxidative damages in PSII (Perkins et al., 2006). To our knowledge, few studies have been done to investigate the photosynthetic responses of intertidal brown macroalgae to dramatic changes of light regime.

Several studies did direct comparison in the susceptibility of early versus adult life stages of macroalgae to ultraviolet radiation stress, such as red macroalgae *Mastocarpus*, *Chondrus* and *Gracilaria*, and green macroalgae *Urospora* (Roleda et al., 2004, 2009, 2012). As for the photoprotective responses to photosynthetically active radiation stress especially in brown macroalgae, most studies have only focused on the adult thalli, with little examination of early life stages (e.g. germlings). In natural habitats, early stages generally operate as shade adapted organisms, since they live sheltered under adult canopies or in pores of the substrata (Coelho et al., 2000); however, they are also inevitably exposed to high solar radiation within the euphotic layer. Survival of early stages is critical for the successful recruitment of populations due to their vulnerability to radiation stress (Roleda et al., 2007), and thereby physiological studies on the early life stages of brown macroalgae in response to light stress remain as an important matter to be investigated.

Sargassum thunbergii (Sargassaceae, Phaeophyta), a common dioecious macroalga distributed widely in the intertidal zone of northwestern Pacific coast (Liu et al., 2012; Zhang et al., 2009), is now used as a candidate for the restoration of intertidal seaweed beds due to its high economic and ecological value (Chu et al., 2012a,b; Yu et al., 2012a,b). To increase the understanding of ecological adaptation of this species, the photosynthetic characteristics of *S. thunbergii* germlings following sudden exposure to high light stress were investigated in the present study. Our objective was to examine (1) photoinhbition of photosynthesis; (2) NPQ development; and (3) the effect of inhibitors on NPQ.

2. Materials and methods

2.1. Collection and culture of germlings

Fertile thalli of *S. thunbergii* were collected from the rocky intertidal zone of Zhanqiao (37°31′44″N, 121°26′4″E), Yantai, Shandong Province, China, on June 23, 2012. Selected thalli were healthy and yellowish-brown in appearance with intact and inflated receptacles which had no obvious shedding. Following removing surface epiphytes, 2 kg thalli were stored in a plastic foam box full of crushed ice and transported to the laboratory where they were placed on aerated 75 L plastic tanks filled with filtered seawater. The tank were kept at 22 °C, 10 μmol photons m^{-2} s^{-1} and a 10 L: 14 D (light: dark cycle) photoperiod. At 24 h post-fertilization, a total of 3.0×10^5 released germlings were obtained followed the method by Chu et al. (2012a,b). Subsequently, they were transferred to a 3 L glass tank filled with sterile filtered seawater and stirred even to produce a homogeneous suspension, and then immediately poured into each Petri dish (60 mm × 15 mm). Germlings attached to the Petri dishes were cultured under three light intensities: 10, 60, and 300 μmol photons m^{-2} s^{-1} in three incubators, which were referred as low light germlings (LL-germlings), moderate light germlings (ML-germlings), and high light germlings (HL-germlings) respectively. All treatments were kept for 12 days with a photoperiod of 10 L: 14 D at 25 °C. During light time, the illumination was provided by a LED lamp (LI-6400-04; Li-Cor, Lincoln, NE, USA), with a color temperature ranging from 5000 K to 6000 K which is comparable to sunlight. Sterile filtered seawater was used as the culture medium and changed once a day to avoid contamination and nutrition deficiency problems. Irradiance within the wavelength range 400–700 nm was measured using a Li-Cor LI-250 light meter equipped with a LI-190SA quantum sensor. Moderate and low light intensities chosen were according to Zhao et al. (2009). Since light treatment at the minimum saturating irradiance (E_k) would cause the least photoinhibitory stress (Kirst and Wiencke, 1995), in order to estimate the photoacclimation capacity of germlings, high light intensity was about twice as much as E_k (approx. 130 μmol photons m^{-2} s^{-1}) in germlings about 24 h after fertilization.

After 12 days of culture, the size of germlings was measured in terms of surface area (μm^2) using a calibrated Olympus BX43 microscope (Olympus Optical Co., Ltd., Tokyo, Japan) at 4 × 10 magnification. Subsequently, a total of 45 Petri dishes with attached germlings equally in each (40 ± 5 germlings per square centimeter) were selected for the following experiments, including photoinhibition, NPQ development and inhibitor treatments. Three independent replicates were used for each experiment. Fluorescence characteristics of two areas from each dish were assessed using three replication dishes per treatment. During the experiments, germlings were maintained in a temperature-controlled incubator (25 °C) with an electric fan within the incubators that circulated air through the gap between Petri dish and lights.

2.2. Photoinhibition experiments

The photosynthetic activity was measured with a portable pulse amplitude modulated (PAM) fluorometer (Diving-PAM; Walz, Effeltrich, Germany). For the determination of the maximal photochemical efficiency of PSII (F_v/F_m) and the rapid light response curves (RLCs), germlings were dark-adapted for 10 min. The minimum fluorescence, F_o, was induced by low irradiation of the red measuring light (approx. 0.15 μmol photons m^{-2} s^{-1}), and maximum fluorescence F_m was obtained after application of a single saturating pulse of light (0.8 s duration, approx. 5000 μmol photons m^{-2} s^{-1}). Variable fluorescence, F_v, was calculated as the difference between F_o and F_m. Immediately following this, germlings were illuminated with actinic white light to detect RLCs, whose actinic illumination was incremented in eight steps for duration of 10 s. At each light intensity step, the effective quantum yield ($\Delta F / F_m'$) was determined whereby a saturation flash was applied. $\Delta F / F_m'$ was calculated as $(F_m' - F) / F_m'$ following Harker et al. (1999). Electron transport rate (ETR) was then calculated as $ETR = \Delta F / F_m' \times PAR \times 0.5 \times 0.84$, where PAR is the photosynthetically active radiation, 0.84 is the absorption factor of ETR, and this equation assumes that PSII absorbs half (0.5) the quanta of available light (Andreev et al., 2012). To obtain the photosynthetic parameters α (photosynthetic efficiency under non-saturating irradiances, as ETR/PAR) and ETR_{max} (maximum rate of electron transfer to PSII under saturation irradiances), RLCs were fitted to a double exponential decay curve as described by Ralph and Gademann (2005).

All the treatments were dark adapted for 3 h before photoinhibition experiment, and then immediately exposed to 600 μmol photons m^{-2} s^{-1} white light for 3 h. Following that, germlings were transferred to dim light (20–30 μmol photons m^{-2} s^{-1}) to allow photosynthesis to recover for 3 h. Since *S. thunbergii* germlings generally grow under the canopy of adult macroalgae where light is certain to be limited (Zhao et al., 2009), the irradiance 600 μmol photons m^{-2} s^{-1} was high enough to cause light stress of photosynthesis in germlings (Coelho et al., 2000). During the inhibition and recovery periods, the F_v/F_m and RLCs of each treatment was measured every 30 min by the fluorescence method described above. The $t_{1/2}$ of F_v/F_m changes, time necessary to reach half of the maximal response, was calculated by fitting the data to the kinetics model proposed by Hanelt (1998). The inhibition phase was described by: $Y_{inh} = P_{fast}\exp(-at) + P_{slow}\exp(-bt)$ and the recovery phase was described by: $Y_{rec} = F_v/F_m - (P_{fast}\exp(-at) + P_{slow}\exp(-bt))$. Y_{inh} and Y_{rec} represent the F_v/F_m at time (t) during the inhibition and recovery phase; P_{fast} and P_{slow} describe the amplitude of the fast and slow reaction phase, respectively; F_v/F_m in the recovery formula is the initial value before high light exposure.

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