Short-term photoacclimation and photoregulation strategies of *Sargassum horneri* in response to temperature and light


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Abstract

*Sargassum horneri* (Turner) C. Agardh is a genus of brown algae and plays an important role in marine ecosystem. However, the inhabiting area of *S. horneri* has been decreasing sharply in China. To understand the photoacclimation and photoregulation strategies of *S. horneri* in responses to temperature and light, *S. horneri* was cultured under different temperatures [18℃ (LT) and 26℃ (HT)] and light intensities [60 μmol(photon) m−2 s−1 (LL) and 120 μmol(photon) m−2 s−1 (HL)] for 7 d, and then the chlorophyll a fluorescence parameters were measured. The results showed that the maximum electron transfer rate occurred at low temperature and high light (LT–HL) condition. The high temperature was the predominant factor for causing inhibition of PSII, lowering the effective quantum yield of PSII, and reducing the nonphotochemical quenching (NPQ). However, high light could improve the photoprotective ability via enhancing the NPQ. On the other hand, a strong linear relationship was observed between NPQ and the electron transport efficiency (α); the increase of NPQ could reduce the α value and avoid damage from high light stress to PSII. Therefore, *S. horneri* was found to be well adapted to grow under LT–HL conditions.

Keywords: photoacclimation; photoprotective ability; rapid light-response curves; *Sargassum horneri*; steady-state light-response curve.

Highlights

- High temperature damages PSII of *Sargassum horneri*
- High light improves the photoprotective ability in *S. horneri*
- *S. horneri* is adapted to grow under low temperature and high light conditions

Introduction

*Sargassum horneri* (Turner) C. Agardh is a genus of brown algae (Fucales, Phaeophyta) inhabiting rocky coasts along the northwest coast of the Pacific (Komatsu et al. 1982) in subtidal zone (3–4 m below the low tidal line) (Sun et al. 2010). Under normal conditions, it can form a flourishing forest in spring and provide a habitat for spawning, nursing, and feeding for marine organisms (Miki et al. 2016). On the other hand, *Sargassum* forest is an effective biofilter to purify effluent waters, playing an important role in marine ecosystems (Pang et al. 2009). Besides, *S. horneri* is often consumed in Asian countries as a bio-functional material source of fucoxanthin and other...
bioactive compounds (Murakami et al. 2011, Sanjeeewa et al. 2017). However, the natural Sargassum forest has been degenerating in recent years due to the following reasons: (1) land reclamation (Terawaki et al. 2003); (2) the grazing damage from herbivores, such as sea urchins, abalone, and holothurians (Zhang et al. 2008); and (3) the deterioration of marine environment, elevated temperature (Komatsu et al. 2014), limited transparency (Sun et al. 2010), misbalanced nutrition (Zhang et al. 2008), and increased pollution (Yu et al. 2019).

In China, Sargassum spp. were the dominant species in intertidal and subtidal zones in Gouqi Island, Zhejiang, China, where over 90% of the total biomass was *S. horneri* (Zhang et al. 2008). From 1960 to 1965, distribution of *S. horneri* was widespread although its abundance was lower than local dominant species (Sun et al. 2010). In the recent decade, the area of *S. horneri* beds has been shrinking quickly in China (Yu et al. 2019), especially, in Nanji Islands, Zhejiang, China from 1980 to 1985. Although the distribution of *S. horneri* was wide, its abundance was very low. From 2000 to 2007, *S. horneri* almost disappeared (Sun et al. 2010). The causes were most probably the elevated temperature (Zhang et al. 2008) and the limited light (Sun et al. 2010, Bi et al. 2014).

It was reported that the global sea surface temperature has been considerably increasing at a rate of ~ 0.12°C per decade in recent 30 years (IPCC 2013). The predicted ocean warming posed a threat to the survival of *S. horneri*; the southern limit of *S. horneri* distribution would move northward and may disappear in 2100 (Komatsu et al. 2014). The elevated ocean temperature was known to affect the primary productivity by directly or indirectly altering algal physiological performance (Gao et al. 2017). Photosynthesis is highly sensitive to high temperature and often inhibited before other cellular functions are impaired. Photosystem II (PSII) and ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) are the major attacked targets; high temperature can damage PSII and reduce the Rubisco activity by inactivating the Rubisco activase (Koch et al. 2013). Additionally, sensitivity of other main cellular components is directly subject to high temperature (Harley et al. 2012). The membrane properties and intracellular milieu could be changed by high temperature and thus cell functions are impaired. An increase in fluidity of thylakoid membranes caused by high temperature could dislodge PSII light harvesting (Mathur et al. 2014).

In addition, subtidal macroalgae are sensitive to the excess and fluctuating light (Li et al. 2014). In a shallow coastal zone, light could fluctuate on different time scales (from seconds to days) in predictable (day length, tidal period, and solar angle) or unpredictable (sunshine, cloud, turbidity, and rain) manner (Williamson et al. 2018). Excess or fluctuating light may result in photoinhibition and the accumulation of reactive oxygen species (ROS) in photosynthetic apparatus, especially the PSII. Protein D1 is one of sensitive targets to photodamage. When protein D1 is damaged, it will be removed and replaced by *de novo* synthesized proteins during the D1 repairing cycle. When the rate of photodamage exceeds the D1 repair capacity, photoinhibition will take place. The imbalance between energy absorption and consumption can lead to production of ROS and damage the membrane fluidity of the thylakoid membranes, while D1 repairing cycle is tightly dependent on the membrane fluidity of the thylakoid membranes (Yamamoto 2016).

Being exposed to the changing environmental stress, macroalgae must optimize their photosynthetic performance through photoacclimation. Otherwise, the photodamage to the photosynthetic system would occur, resulting in the markedly inhibition of photosynthesis (Müller et al. 2001). Photoacclimation (hours to days) is a phenotypic acclimation in response to environmental conditions through changing the size or number of photosynthetic units (Williamson et al. 2018). While under a sudden environmental stress, photoregulation (seconds to minutes) is needed to guarantee the safe dissipation of surplus absorbed energy as heat to prevent photodamage to the photosynthetic system (Lavaud and Lepetit 2013). In addition, nonphotochemical quenching (NPQ) is one of the most important photoprotective mechanisms for phototropic organisms (Ocampo-Alvarez et al. 2013). By the help of the xanthophyll cycle (XC) during NPQ, excess absorbed energy is dissipated as heat (Esteban et al. 2009, Garcia-Mendoza et al. 2011, Ocampo-Alvarez et al. 2013). Thus, for macroalgae, photoacclimation and photoregulation are high-efficiency strategies to adjust photosynthetic performances to multiple environmental stresses.

The pulse amplitude modulated (PAM) fluorometry is an efficient technology to measure chlorophyll (Chl) a fluorescence, which includes rich information about photosynthetic apparatus (Sterbet and Govindjee 2011). The evident advantage of PAM is instantaneous and nondestructive measurement of real-time activity of photosynthesis (White and Critchley 1999). One technique of PAM is using the rapid light-responses curves (RLC), allowing to rapidly (<2 min) detect the adjustments in photosynthetic performance (short-term photoacclimation), related mainly to the carbon metabolism, photoprotective mechanism, and photoinhibition (Ralph and Gademann 2005). In opposition to RLC, the steady-state light-response curves (LC) characterize the long-term photoacclimation status. LC represents the potential response to long-term light exposure conditions, while the RLC aims at the acclimation status to recent light history (Serôdio et al. 2006). Discrepancy between RLC and LC was shown in the nonphotochemical quenching (NPQ) processes, during which extra absorbed light energy could be dissipated. RLC and LC have been successfully applied to study the photosynthetic performance of benthic diatom and provide an effective way to detect the photoacclimation of other algae. At present, however, details of the inter-action between seawater temperature and light on the photosynthetic performance of *S. horneri* remain poorly understood.

In the present study, the short-term photoacclimation and photoregulation strategies of *S. horneri* in responses to temperature and light were investigated. We hope that the results may provide an insight to photosynthetic characteristics of *S. horneri* and a support to the protection of Sargassum forest.
Materials and methods

Materials: *S. horneri* were sampled in a subtidal Sargassum forest in Changdao Island (38°21′22.48′′N, 120°54′30.78′′E), Shandong Province, China, in September 2019. The thalli were washed and delivered to laboratory in cooler box in 48 h. After arriving to laboratory, algae were further cleaned with sterile seawater gently to remove debris and epiphytes and cultured in water tank in 200 L of sterile natural seawater enriched with 100 μM NaN3 and 10 μM KH2PO4. The culture medium was bubbled with ambient air and refreshed daily; light intensity was set as 120 μmol(phonon) m−2 s−1 in photoperiod of 12 h (L):12 h (D).

Experimental design: To investigate the effects of temperature and light on *S. horneri* growth, approximately 0.1 g of thalli fresh mass (FM) were incubated in 500-mL flasks, then grown at two temperatures (18 and 26℃) and two light intensities [60 and 120 μmol(photon) m−2 s−1] in photoperiod of 12 h (L):12 h (D) (triplicate for each treatment). The medium was sterile natural seawater enriched with f/2, gently bubbled with ambient air, and renewed daily. The chosen temperature of 18℃ was the optimal growth temperature of *S. horneri* (Sun et al., 2008), while that of 26℃ was the upper threshold of *S. horneri* survival (Yu et al., 2019). The chosen light intensities were low but higher than the light-compensation point to provide high light intensity range above the saturating irradiance [100 μmol(phonon) m−2 s−1], which was close to the maximum midday light intensity at the sample collection site. Chl a fluorescence parameters were measured after being cultured for 7 d.

Chl a fluorescence parameters: The fluorescence parameters were measured with a pulse amplitude modulated fluorometer (DIVING-PAM, Walz, Effeltrich, Germany). All measurements were made with dark leaf clip (DIVING-LC) plus adapter positioning fiber optics tips perpendicularly above the algae at a constant distance of 3 mm. Samples were placed in natural seawater at a culture temperature controlled by air conditioner. After 30-min dark adaption under the same conditions as the culture environment (except for light), the rapid light curves (RLC) and steady-state light curves (LC) were measured according to the protocol of Serôdio et al. (2006). After dark adaptation, F0 and Fm were measured using the saturating pulses [3,577 μmol(phonon) m−2 s−1 for 800 ms]. RLC was created by exposing samples to eight increasing levels of light intensity [38, 104, 186, 322, 463, 621, 893; and 1,189 μmol(phonon) m−2 s−1] for 10 s. At each actinic light, F and Fm were determined every 90 s until the steady state was achieved (about 4.5–15 min). An RLC was constructed immediately after each light level of the LC and was termed the steady-state rapid light curves (SRLC). After the completion of the SRLC, the sample was subjected to the next LC light level and allowed to reach a new steady state.

The following parameters were calculated based on the studies of Bilger and Björkman (1990), Hendrickson et al. (2004), and Belshe et al. (2007):

1. Maximum PSII quantum yield:
   \[ F_v/F_m = (F_m - F_0)/F_m \]  

2. Effective quantum yield of PSII:
   \[ Y_{(m)} = F_v/F_m' = (F_m' - F_v)/F_m' \]  

3. Nonphotochemical quenching:
   \[ NPQ = (F_m - F_m')/F_m' \]  

4. Quantum yield of regulated energy dissipation:
   \[ Y_{(NPQ)} = (F_v/F_m') - (F_v/F_m) \]  

5. Quantum yield of nonregulated energy dissipation:
   \[ Y_{(NO)} = F_v/F_m' \]

6. The relative electron transfer rate:
   \[ rETR = \frac{rETR_{max} \times \tanh \left( \frac{x \times I}{rETR_{max}} \right)}{I} \]

7. Where AF is the light absorption capacity that used the most common value 0.84; PAR is the actinic photosynthetically active radiation; and 0.5 is the relative distribution of absorbed energy to PSII. The parameters of the RLC and LC were calculated from the rETR curves following the models (Jassby and Platt, 1976):

8. **Results**

   Fv/Fm ratio variation with temperature and light: The Fv/Fm ratio decreased with the increase of temperature and light (Fig. 1). The maximum Fv/Fm value of 0.7288 occurred at low temperature and low light (LT–LL), while the Fv/Fm dropped to 0.7053 under high temperature and high light (HT–HL), the difference between them was significant. Two-way ANOVA showed that temperature and light were the main factors causing the decrease of Fv/Fm. However, temperature and light had no significant interactive effect on Fv/Fm (Table 1).
PHOTOACCLIMATION OF SARGASSUM HORNERI

rETR and NPQ vs. PAR curves: After growth under different temperature and light conditions for 7 d, the relationship of rapid light curves (RLC) and steady-state light curves (LC) to temperature and light was significantly different (Fig. 2). The photoacclimation status could be inferred from the photosynthetic parameters (Table 2). In the RLC, the high light decreased the electron transport efficiency (α), and the differences were not significant compared to that of the low light, whilst under the high light, the α in the LC showed no change. Besides, the differences between all α values estimated from RLC and LC were not significant. Comparison in rETR$_{\text{max}}$ of the S. horneri samples revealed that rETR$_{\text{max}}$ in LC was higher than that in RLC under the same treatment conditions. On the other hand, the rETR$_{\text{max}}$ estimated from RLC was not obviously different between those of the LT–LL, LT–HL, and HT–LL, but all of them were significantly higher than that of HT–HL in a range from 26 to 40%. Two-way ANOVA showed that temperature and light had an interactive effect and both temperature and light exerted a main effect on the rETR$_{\text{max}}$. As shown in Table 2, the high light boosted the inhibition to the rETR$_{\text{max}}$ by the high temperature. Conversely, the increase of light did not significantly alter the rETR$_{\text{max}}$ in LC under the high temperature, whilst high light obviously increased the rETR$_{\text{max}}$ under the low temperature. Regarding $I_k$, the patterns of responses to temperature and light in RLC and LC were generally the same as the rETR$_{\text{max}}$. In RLC, the maximum and minimum $I_k$ was observed at LT–HL and HL respectively.

Table 1. Two-way analysis of variance in the effects of temperature and light on maximum PSII quantum yield ($F_v/F_m$), maximum electron transport rate of a rapid light curve (ETR$_{\text{max(RLC)}}$), electron transport efficiency of the initial slope of a rapid light curve ($\alpha_{RLC}$), saturated irradiance of a rapid light curve ($I_{k(RLC)}$), nonphotochemical quenching of a rapid light curve (NPQ$_{RLC}$), maximum electron transport rate of a steady-state light curve (ETR$_{\text{max(LC)}}$), electron transport efficiency of the initial slope of a steady-state light curve ($\alpha_{LC}$), saturated irradiance of a steady-state light curve ($I_{k(LC)}$), and nonphotochemical quenching of a steady-state light curve (NPQ$_{LC}$) of Sargassum horneri. Temperature × light represents the interactive effect between these two factors; df represents degrees of freedom; and $F$ represents the value of the $F$ statistic.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>$F$</th>
<th>$P$ value</th>
<th>Source</th>
<th>df</th>
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</tr>
</thead>
<tbody>
<tr>
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<td>Temperature</td>
<td>1</td>
<td>11.43</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Light</td>
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<td>19.651</td>
<td>&lt;0.05</td>
<td>Light</td>
<td>1</td>
<td>8.97</td>
<td>&lt;0.05</td>
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<td>Temperature × light</td>
<td>1</td>
<td>0.228</td>
<td>&gt;0.05</td>
<td>Temperature × light</td>
<td>1</td>
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<tr>
<td>$\alpha_{RLC}$</td>
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<td>&gt;0.05</td>
<td>Temperature</td>
<td>1</td>
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<td>&gt;0.05</td>
</tr>
<tr>
<td>Light</td>
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<td>6.93</td>
<td>&lt;0.05</td>
<td>Light</td>
<td>1</td>
<td>0.10</td>
<td>&gt;0.05</td>
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<tr>
<td>Temperature × light</td>
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<td>Temperature × light</td>
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<td>11.09</td>
<td>&lt;0.05</td>
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<tr>
<td>NPQ$_{RLC}$</td>
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<td>&lt;0.01</td>
<td>Temperature</td>
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<td>94.32</td>
<td>&lt;0.001</td>
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<tr>
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<td>113.20</td>
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<td>Light</td>
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<td>25.08</td>
<td>&lt;0.01</td>
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<td>Temperature × light</td>
<td>1</td>
<td>14.60</td>
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</tr>
<tr>
<td>$\alpha_{LC}$</td>
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<td>Temperature</td>
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<td>68.38</td>
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<tr>
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<td>0.00</td>
<td>&gt;0.05</td>
<td>Light</td>
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<td>14.62</td>
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<td>NPQ$_{LC}$</td>
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<td>&lt;0.05</td>
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HT–HL, respectively. However, differences between all the treatments were not significant (Table 2). Compared to RLC, the \( I_k \) levels estimated from LC were relatively higher under the same treatment conditions. Additionally, the high temperature induced lower \( I_k \) regardless of light intensity as shown in the LC.

Fig. 2C,D illustrates typical responses of nonphotochemical quenching (NPQ) in RLC and LC to the temperature and light. Higher NPQs were found in LC, and the differences between RLC and LC were significant. The maximum NPQ in RLC was observed under LT–HL (Table 2), which was higher than those of other treatments (LT–LL, 34.1% of LT–HL; HT–LL, 48.8% of LT–HL; and HT–HL, 41.5% of LT–HL). In LC, LT–HL induced the highest NPQ, while differences between other treatments were not significant.

Steady-state rapid light curve: The short-term photoacclimation and photoregulation were reflected by the responses of steady-state rapid light curve (SRLC) to ambient light (Fig. 3). The light responses of \( \text{rETR}_{\text{max}, \text{SRLC}} \) in acclimated cultures under different temperature and light conditions were significantly different. In low temperature (LT–LL and LT–HL) treatments, \( \text{rETR}_{\text{max}, \text{SRLC}} \) increased with the increasing ambient light under \( \text{PAR} < 463 \mu\text{mol(photons)} \text{m}^{-2} \text{s}^{-1} \) to a maximum value, and then decreased under the light above the PAR value. In addition, the high light induced greater \( \text{rETR}_{\text{max}, \text{SRLC}} \) than that at the low light acclimation (Fig. 3A). Besides, in the high-temperature samples (HT–LL and HT–HL), maximum \( \text{rETR}_{\text{max}, \text{SRLC}} \) were found at 322 \mu\text{mol(photons)} \text{m}^{-2} \text{s}^{-1} and slightly decreased with the increasing light. However, the difference of \( \text{rETR}_{\text{max}, \text{SRLC}} \) between high and low light was not significant, which is inconsistent to the responses of \( \text{rETR}_{\text{max}, \text{SRLC}} \) to ambient light in low temperature acclimated cultures. The light responses of light-saturation (\( I_k, \text{SRLC} \)) showed that it increased almost linearly with the increasing PAR. In addition, LT–HL samples presented...
Phytoplankton, S. horneri  – maximum electron transport rate; 
Compared to RLC, relatively lower Y(NO) is seen in LC. As the increase in temperature and light intensity (C, D).

38 μmol(photon) m⁻² under low light, until reaching the maximum value under and low light; HT–HL – high temperature and high light. Values with the increasing PAR, and the differences between all treatments were minor.

**Δα vs. NPQ:** A linear relationship was observed between NPQ and the high light-induced decrease of Δα under low light for each light group (Fig. 5; Serôdio et al. 2006). NPQ was the NPQ measured under the steady state for S. horneri. Δα = αm − αa, where αm is the maximum value of αa vs. PAR. Correlations between Δα and NPQ were highly significant in all cases. The difference of slopes of the regressions of Δα on NPQ calculated from the different cultivations were significant (F₃,₈ = 140.935, P<0.001; ANOVA test for homogeneity of slopes).

**Discussion**

Under various environmental factors, short-term photosynthetic acclimation to ambient light and temperature is an important photoprotective way by which the light energy capture and metabolic energy consumption were balanced via effective energy distribution (Davison and Pearson 1996, Ensminger et al. 2005). Photoacclimation could be realized by changing the size or the number of photosynthetic units (Williamson et al. 2018). Under a suitable growth temperature, low light (LL) acclimation of S. horneri could increase the number of photosynthetic units to enhance the light-utilization efficiency (α) but had low rETRmax as illustrated in the rapid light curve (RLC), which is similar to the results of Beer et al. (2014). Conversely, in the steady-state light curve (LC), the α values between LL and HL showed no difference, implying that the size of photosynthetic units was changed by HL. The significantly higher rETRmax indicated that photoacclimation could be achieved mainly by changing the size of photosynthetic units and enhancing the light energy utilization to prevent the photodamage to PSII under HL conditions (Williamson et al. 2018).

PSII is known as one of the most thermosensitive components of photosynthetic apparatus (Havaux 1996). Under a high temperature stress, the fluidity of thylakoid membranes could be increased, causing the light-harvesting complexes of PSII dislocate from thylakoid membrane (Mathur et al. 2014). It was reported that the reasons for inhibition of PSII caused by high temperature
stress is mainly the dissociation of Ca\(^{2+}\), Mn\(^{2+}\), Cl\(^{-}\), and the release of extrinsic 18, 24, and 33-kDa polypeptides from oxygen-evolving complex (OEC) (Yang et al. 2018). The PSII inhibition caused by high temperature stress was also affected by light (Yan et al. 2013). In the present study, high light intensity promoted the inhibition of rETR\(_{\text{max}}\) in S. horneri at high temperature. As shown in the RLC, the rETR\(_{\text{max}}\) of high temperature and high light acclimated treatments was significantly smaller than those of other treatments, suggesting that the electron transport at the PSII acceptor side was inhibited (Yang et al. 2018). In addition, as shown in the LC, high light treatment produced the highest rETR\(_{\text{max}}\) under low temperature, reflecting the actual photosynthetic performance of S. horneri. Therefore, it is likely that the high temperature stress was the predominant factor for the inhibition of PSII.

To avoid the photodamage to PSII, plants have evolved a series of tolerance mechanisms to adapt stresses, including ion transporters, induction of antioxidant defense, and accumulation of osmoprotectants (Mathur et al. 2014). In case of a sudden stress, nonphotochemical quenching (NPQ) is a fast and flexible photoprotective mechanism to avoid the damage to the photosynthetic apparatus by dissipating excess absorbed light energy (Müller et al. 2001). Higher capacity of NPQ means generally a better adaptation to high light (Pniewski et al. 2017). As shown in Fig. 2C and Table 2, the LT–HL acclimation resulted in the highest NPQ value in all cases, suggesting that the greater size of XC pigments pool (ΣXC) was accumulated in LT–HL after 30-min dark treatments, where ΣXC is the sum of violaxanthin (VX) plus antheraxanthin and zeaxanthin (ZX). Because NPQ depends on the size and de-epoxidation state of ΣXC, a greater ΣXC would result in a faster NPQ induction (Ocampo-Alvarez et al. 2013). Additionally, in the LC, high light condition induced greater NPQ, especially under low temperature, while high temperature or low light caused lower NPQ, and the difference between them was not significant, implying that high temperature reduced the size of ΣXC but induced a faster VX to ZX conversion. If excess energy exceeds the photochemical and nonphotochemical capacities, the reactive oxygen species (ROS) could be produced, which would damage the PSII reaction centers (Wilson et al. 2006). A high quantum yield of nonregulated energy dissipation [Y\(_{\text{NO}}\)] is often used to indicate that both photochemical and nonphotochemical capacity are...
inefficient (Hendrickson et al. 2004, Wang et al. 2009). In both RLC and LC (Fig. 4), a lower $Y_{(NO)}$ was found at LT–HL, implying that high light enhanced the photochemical and nonphotochemical capacity. The $Y_{(NO)}$ values in all the treatments showed a marked increase in RLC, while relatively stable $Y_{(NO)}$ occurred in LC, suggesting that the rapid strong light induced more ROS production and lowered the photochemical and nonphotochemical capacity. A high $Y_{(NPQ)}$ means that the light intensity is excessive, but the plant has the capacity to protect itself (Wang et al. 2009). In the RLC, we found that high temperature could destroy the capacity of protection, and no difference was observed between low and high light treatments, while high light showed a better regulation than the low light did under low temperature conditions. Therefore, high temperature was the main factor of destructing the capacity of regulation, and the low light was harmful, too. On the other hand, in the LC, it is easily to find that the $Y_{(NPQ)}$ showed the same pattern to that in the RLC, while $Y_{(NPQ)}$ in the LC was higher than that in the RLC. All these clearly indicate that the PSII reaction centers (RCIIs) stay completely open and the photosynthetic yield is determined largely by the changes in NPQ in LC (Kramer et al. 2004). Conversely, the rapid strong light could cause the closure of RCIIs during RLC. The reasons for differences between LC and RLC may be that there is no fast phase of NPQ ($\Delta$PH-dependent quenching) in brown algae, resulting in slow NPQ induction (García-Mendoza and Colombo-Pallotta 2007, García-Mendoza et al. 2011). The lasting time in RLC is relatively short compared to that in LC, it may not be enough to induce the NPQ generation completely ($NPQ_{RLC} < NPQ_{LC}$). Therefore, excess absorbed light energy could lead to the overproduction of Q$_A$ as well as closure of the RCIIs and the quenching of reaction center due to nonradiative charge recombination between Q$_A$ and the primary donor of PSII (Ivanov et al. 2008). With the illumination time lasting, high light increased the electron turnover through the PSII and activated the Calvin-Benson cycle enzyme (Pniewski et al. 2018), so that the reaction center could gradually be opened again. Meanwhile, NPQ gradually appeared during light, so $Y_{(NPQ)}$ Fise, while $Y_{(NO)}$ remains stable. This suggests that $S. horneri$ relies more on ‘nonregulated’ $Y_{(NO)}$ than on ‘regulated’ $Y_{(NPQ)}$ energy dissipation for photoprotection [$Y_{(NO)} > Y_{(NPQ)}$] in RLC during exposing to short periods of high light; while during a long duration of high light, NPQ is main mechanism to deal with the excess absorbed light energy.

It is reported that the inhibition of $\alpha_{RLC}$ under high light stress is most likely caused by the operation of reversible photoprotective NPQ processes (Serôdio et al. 2006). The conversion of VX to ZX takes place under high light and the back conversion takes place in darkness or under low light intensity (Ocampo-Alvarez et al. 2013). The accumulation of ZX decreases the transfer efficiency of absorbed energy to RCIIs (Serôdio et al. 2006), which is supported by the fact that the tight correlations between $\Delta$SA and NPQ were found in all cases. As shown in Fig. 5, the $\Delta$SA of low light acclimation was more sensitive to NPQ than that of high light acclimation, indicating that the transfer efficiency of absorbed energy to the RCIIs under low light acclimation treatments was more likely affected by high light stress, and high light acclimation had a better photoprotective mechanism (larger $\Sigma XC$) to avoid photodamage under a high light stress. Additionally, as shown in Fig. 5, high temperature enhanced the sensitivity of $\Delta$SA to NPQ under high light acclimation treatments, which is in coincidence with the fact that high temperature reduced the size of $\Sigma XC$.

In conclusion, we illustrated the short-term photo-acclimation and photoregulation strategies of $S. horneri$ in responses to temperature and light changes. $S. horneri$ was adapted to grow under low temperature and high light conditions. High temperature was the predominant factor for causing the inhibition of PSII, while high light could improve the photoprotective ability. Under the global warming scheme, improving the water quality in coastal areas is an effective measure to protect $Sargassum$ beds.

References

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