

Effects of Temperature and Light on Growth Rate and Photosynthetic Characteristics of *Sargassum horneri*

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(Received February 25, 2020; revised October 27, 2020; accepted November 3, 2020)

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Abstract The changing environmental factors exerted great influences on coastal macroalgal communities. To study the responses of the brown seaweed *Sargassum horneri* to temperature and light, *S. horneri* was cultured under three temperatures (20, 25 and 30°C) and three light intensities (30, 60, and 120 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) for seven days. The growth rate, chlorophyll *a* (Chl *a*) and carotenoids (Car) contents, chlorophyll fluorescence, and photosynthetic oxygen evolution rate were measured. The results show that the highest relative growth rate (RGR), maximal electron transport rate ($r\text{ETR}_{\text{max}}$); the net photosynthetic rate (P_n) were observed at the lowest temperature (20°C) and highest light intensity (120 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$); and the RGR and P_n were significantly inhibited by the highest temperature (30°C), especially at the lowest light intensity (30 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) ($P < 0.05$). Additionally, the highest light intensity enhanced the non-photochemical quenching (NPQ) even under the highest temperature (30°C), indicating that the higher light intensity could induce photo-protection reaction of thalli. These results suggest that the higher temperature and lower light intensity exerted negative influences on *S. horneri*.

Key words chlorophyll fluorescence parameter; ocean warming; oxygen electrode; photosynthetic activity; *Sargassum horneri*; transparency

1 Introduction

Global climate change has caused ocean warming (Ji *et al.*, 2016), which exerts great influences on the marine ecosystem (Diaz-Pulido *et al.*, 2011; Wernberg *et al.*, 2016; Khan *et al.*, 2018). The elevated temperature has exerted a notable impact on the biochemical components of algae and physiological characteristics (Liu *et al.*, 2017). According to Gao *et al.* (2018a), the chemical composition of algae, such as amino acids, fatty acids and lipid, was increased with culture temperature within a certain range. It also has been proved that temperature determines the performance of seaweeds by influencing enzymatic activities as well as diffusional rate and membrane transport efficiencies (Hoegh and Bruno, 2010; Harley *et al.*, 2012). Moderate increment of temperature would increase light-harvesting pigments content, promote enzyme activity, and accelerate metabolic levels, which could enhance the photosynthesis and growth of algae, but the mortality risk would significantly increase also and local populations might decline or even extinct once the threshold was exceeded (Hoegh and Bruno, 2010; Wu *et al.*, 2019). Furthermore, the elevated temperature

has changed the biodiversity and species composition of coastal ecosystems (Olabarria *et al.*, 2013), reshaped the distribution of macroalgae (Müller *et al.*, 2009), and even caused the extinction of several hundred species (Wernberg *et al.*, 2011), which has been reported worldwide (Bartsch *et al.*, 2012). Under the ocean warming scheme, warm water species will intrude into formerly colder regions (Ji *et al.*, 2016), and this trend has been predicted by North-Atlantic rocky intertidal model (Jueterbock *et al.*, 2013). For instance, in the reef system in Australia, kelp forests have extensively shrunk, and temperate species have been replaced by subtropical and tropical ones (Wernberg *et al.*, 2016).

In addition, the eutrophication and the re-suspension of sediments in the coastal zone has reduced the seawater transparency, thus changed the light environment (Zhang *et al.*, 2013; Chen *et al.*, 2014; Rahman *et al.*, 2015). It is known that light is a vital environmental factor for the growth and development of plant, and affects the photosynthetic characteristics through a variety of processes (Su *et al.*, 2014). In general, macroalgae have their own optimal light intensity ranges for growth, sub- and supra-optimal conditions will negatively influence their physiological characteristics (Pan and Guo, 2016; Li *et al.*, 2017). Furthermore, as a signal molecule, light can activate the corresponding regulatory mechanism in the cell, exerting an impact on the growth and development of

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plants (Wang *et al.*, 2009; Gutu *et al.*, 2013). Additionally, light is a determinant for macroalgae depth distribution. A series of studies have reported that algae have their own depth limit, such as planktonic algae, brown kelps, and crustose macroalgae (Hanelt *et al.*, 2003), and the lower depth distribution limit of macroalgae depends on their ability to maintain a positive carbon balance to build up biomass (Deregibus *et al.*, 2016). Large loads of suspended solids may constitute a constraint for benthic primary producer by reducing light penetration, and correlation between increase of turbidity and reduction of the productivity of benthic macroalgae has been established (Eriksson and Johansson, 2005; Pritchard *et al.*, 2013). Studies in Polar Regions reported that the increment of sediment into the water column reduced the light penetration, constituted a constraint for photosynthesis, exerted adverse impact on the growth of benthic algae, and eventually altered the macroalgal communities (Quartino *et al.*, 2013; Deregibus *et al.*, 2016).

Sargassum horneri (Turner) C. Agardh, one of the most common macroalgae, is endemic to the northwestern Pacific, and distributes sporadically in coastal regions of China (Zeng *et al.*, 2000). *S. horneri* is an annual brown macroalgae (Yoshida, 1983), can grow up to 3–5 m long and form a large underwater forest in the ocean, providing habits for a variety of marine invertebrates and fish (Han *et al.*, 2008). Besides, *S. horneri* can be planted for seaweed bed reconstruction and ecological restoration (Bi *et al.*, 2013). Furthermore, *S. horneri* has great economic values, which is a good bait for aquaculture and can provide a variety of biological active compounds for the treatment of a variety of diseases (Ma *et al.*, 2014; Zhao *et al.*, 2016; Sanjeeva *et al.*, 2017). The effects of various culture conditions on growth of *S. horneri* at different stages have been well studied. Compared with adult blades of *S. horneri*, the optimal growth temperature of seedlings was higher (Choi *et al.*, 2008). The optimal light parameters of seedlings were 50–90 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ and long photoperiod (18L:6D) (Zhang *et al.*, 2014). In addition, UV-A could promote its growth under low light conditions (Guan *et al.*, 2016). However, the effects of environmental factors, especially the adverse conditions on the photophysiological response was less discussed.

Many *Sargassum* forests are in decline in recent decades, and some even have disappeared. The *Sargassum* forest in Nanji Islands, Zhejiang Province, China, an important national marine ecosystem protection area, has been disappearing. Moreover, the density of *Sargassum* forest in Gouqi Island, Zhejiang Province, has been decreasing gradually (Sun *et al.*, 2008; Bi *et al.*, 2013). *Sargassum* forests have also declined markedly and could not be recovered naturally in coastal areas in other Asian countries along the northwestern Pacific (Choi *et al.*, 2008; Komatsu *et al.*, 2014). On the other hand, golden blooms caused by floating *Sargassum* seem to be in a rising trend (Smetacek and Zigone, 2013; Xu *et al.*, 2017). Komatsu *et al.* (2014) suggested that the elevated sea

surface temperature might be the cause of northward shift of the southern limit of *S. horneri* kelp distribution. Meanwhile, according to a series of study in Gouqi and Nanji Islands, re-suspension of sediment and eutrophication in coastal waters decreased the underwater light intensity, thus restricted the distribution of *S. horneri* (Bi *et al.*, 2013; Zhang *et al.*, 2013). Based on these studies, we speculate that the decline of *Sargassum* forest in these areas may be caused by the combination of high temperature and low light intensity. In this paper, physiological and biochemical response to a combination of light and temperature were studied in indoor culture experiments to understand the interactive influence of the two environmental factors on *S. horneri* growth, aiming to provide a preliminary theoretical support to the protection and recovery of *Sargassum* forest.

2 Materials and Methods

2.1 Materials

In March 8, 2019, *S. horneri* was sampled from Gouqi Island (30°42'N, 122°48'E) in the East China Sea, Zhejiang Province, China. Samples were then transferred to laboratory and cultured in water tanks until the breeding period. *S. horneri* germlings were collected on April 23 and cultured in tanks at 18°C, salinity 32, and light intensity 100 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$; the medium was sterile natural seawater with addition of 100 $\mu\text{mol L}^{-1}$ NaNO_3 and 10 $\mu\text{mol L}^{-1}$ KH_2PO_4 , and was renewed once a day. After cultured for 3 months, healthy thalli were chosen for experiment. Prior to the experiment, thalli were cleaned of debris and floc wrapped around algae, then cultured in sterile natural seawater, which was filtered by sand and sterilized by ultraviolet light, enriched by f/2 medium for 2 d at 20°C under 100 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ light condition (L:D=12:12).

2.2 Treatments

To detect the effects of combinational temperature and light conditions on *S. horneri*, we set three temperatures (20, 25, 30°C) and three light intensities (30, 60, 120 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) with a photoperiod of 12L:12D (triplicate for each treatment) (Table 1). The chosen temperature of 25°C was about the ocean temperature during July and August in Changdao, Shandong (Yang *et al.*, 2018), and the lower and higher temperature were the optimal growth and upper threshold temperature of *S. horneri*. Although the provided light intensity was low, the lowest light intensity was higher than the light compensation point, and highest light intensity is slightly greater than the optimal light intensity (Zhang *et al.*, 2014).

Table 1 The treatment combinations

| Light ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$) | Temperature (°C) | | |
|---|------------------|---------|-------|
| | LT (20) | MT (25) | HT |
| LL (30) | LL-LT | LL-MT | LL-HT |
| ML (60) | ML-LT | ML-MT | ML-HT |
| HL (120) | HL-LT | HL-MT | HL-HT |

The *S. horneri* were blotted using filter paper to remove excess water. For each treatment, approximate 0.5 g was incubated in 500 mL sterile natural seawater enriched by f/2 medium. During the light cycle, the medium was stirred with a glass rod every half hour (Xu and Lin, 2008). The physiological performance was measured after one week.

2.3 Growth Rate and Pigments Content Analyses

The fresh weight was measured every day when renewing the culture medium. The relative growth rate (RGR) was calculated using the following formula: $RGR (\% d^{-1}) = 100 \times \ln(W_t/W_0)/t$, in which W_t and W_0 represent the fresh weight measured on the t day and the first day.

A fresh weight of 0.03 ± 0.005 g of *S. horneri* was used for determining the pigment contents. Samples were ground in methanol (3 mL) with quartz sand. The homogenate was transferred to a centrifugal tube and placed at 4°C for 24 h in darkness. The chlorophyll *a* (Chl *a*) and carotenoid (Car) concentration were calculated according to Eqs. (1)–(2) (Porra, 2002; Parsons and Strickland, 1963).

$$\text{Chl } a (\mu\text{g mL}^{-1}) = 16.29 \times (A_{665} - A_{750}) - 8.54 \times (A_{652} - A_{750}), \quad (1)$$

$$\text{Car } (\mu\text{g mL}^{-1}) = 7.6[(A_{480} - A_{750}) - 1.49 \times (A_{510} - A_{750})]. \quad (2)$$

2.4 Chlorophyll Fluorescence Parameters

The induction curves and rapid light curves (RLCs) were built at room temperature in natural seawater using a pulse amplitude modulated fluorometers (Diving-PAM, Germany). The induction curves were established after a 15-min dark adaptation, the F_o , F_m , F , and F' were determined. The actinic light was set as $104 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ and the saturating pulse was $3577 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (0.8 s). The parameter F_v/F_m and electron transport rate were calculated by using Eqs. (3)–(4).

$$F_v / F_m = \frac{F_m - F_o}{F_m}, \quad (3)$$

$$\text{ETR} = \frac{F'_m - F}{F'_m} \times \text{PAR} \times 0.84 \times 0.5, \quad (4)$$

where PAR represents the actual light intensity ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$), 0.5 is the relative ratio of absorbed PAR to photosystem II, and 0.84 is the ETR-factor representing the fraction of incident photons absorbed by the sample.

RLCs was constructed after the induction curves by exposing to eight increasing level of light. The range of light intensity was from 38 to $1189 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. The fitting formula of RLCs and calculation of photosynthetic parameters, such as the maximal electron transport rate (rETR_{max}), the half-saturation light intensity (I_k), the light harvesting efficiency (α) and the Non-chemical quenching (NPQ), were calculated according to Eqs. (5)–(8), where ETR_{mpot} represents the maximum potential light-saturated electron transport rate, β represents the

$$\text{ETR} = \text{ETR}_{\text{mpot}} \times \left(1 - e^{-\frac{\alpha \times \text{PAR}}{\text{ETR}_{\text{mpot}}}} \right) \times e^{-\frac{\beta \times \text{PAR}}{\text{ETR}_{\text{mpot}}}}, \quad (5)$$

$$\text{rETR}_{\text{max}} = \text{ETR}_{\text{mpot}} \times \frac{\alpha}{\alpha + \beta} \times \left(\frac{\beta}{\alpha + \beta} \right)^{\beta/\alpha}, \quad (6)$$

$$I_k = \frac{\text{ETR}_m}{\alpha}, \quad (7)$$

$$\text{NPQ} = \frac{F_m - F'_m}{F'_m}. \quad (8)$$

2.5 Photosynthetic Oxygen Evolution

A fresh weight 0.03 ± 0.005 g of thalli were weighed and put into a sample beaker containing 2 mL of natural seawater. The net photosynthetic rate (P_n) was measured using a Clark-type oxygen electrode (Hansatech Instruments Ltd, UK) at each cultured temperature and light intensity, and the dark respiration rate (R_d) was measured under dark condition. At least three replicates were evaluated for each treatment.

2.6 Data Analysis

Origin 7.0 and SPSS 18.0 were used for plotting and statistical analysis. A two-way ANOVA was used to test the effects of temperature and irradiance on the RGR, pigments content, and photosynthesis. Prior to the data analyses, the homogeneity of variances was verified with Levene's test ($P > 0.05$). A Tukey post hoc test (Tukey HSD) was performed to detect the differences between different temperature and light treatments. $P < 0.05$ was considered as statistically significant.

3 Results

3.1 Effect of Light and Temperature on the Growth and Pigments Content

The two-way ANOVA showed that the temperature and light had significant interactive effects, and both exerted a

Table 2 Two-way analysis of variance for the effects of temperature and light intensity on different parameters

| | Source | df | F | Sig. |
|-------------------|-------------------|----|--------|-------|
| RGR | Temperature | 2 | 21.176 | 0.000 |
| | Light | 2 | 21.667 | 0.000 |
| | Temperature×Light | 4 | 1.261 | 0.033 |
| Chl <i>a</i> | Temperature | 2 | 2.410 | 0.118 |
| | Light | 2 | 1.427 | 0.266 |
| | Temperature×Light | 4 | 2.971 | 0.048 |
| Car | Temperature | 2 | 0.651 | 0.533 |
| | Light | 2 | 1.904 | 0.178 |
| | Temperature×Light | 4 | 2.063 | 0.128 |
| Chl <i>a</i> /Car | Temperature | 2 | 2.287 | 0.130 |
| | Light | 2 | 0.349 | 0.710 |
| | Temperature×Light | 4 | 1.294 | 0.310 |

Notes: df, degrees of freedom; F, the value of the F statistic.

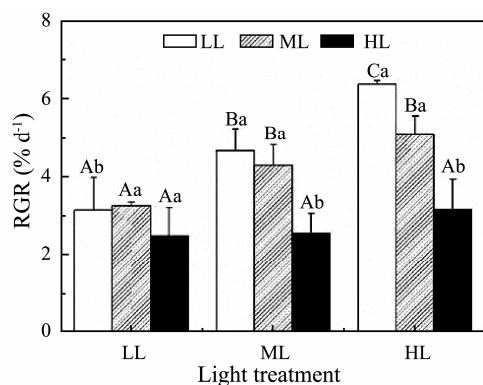


Fig.1 The relative growth rate (RGR) of *S. horneri* grown at different treatment. Values were mean \pm SD ($n=3$). Different uppercase letters indicate significant differences between different temperature treatments under the same light intensity; different lowercase letters indicate significant differences between different light treatments under the same temperature ($P < 0.05$).

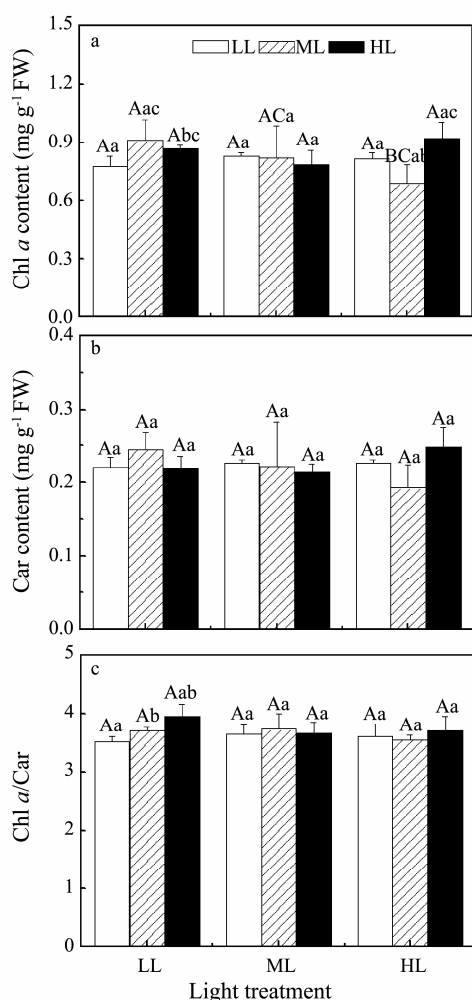


Fig.2 The Chl *a* (a), Car (b) content, and the ration of Chl *a* and Car (c) of *S. horneri* grown at different treatments. Values were mean \pm SD ($n=3$). Different uppercase letters indicate significant differences between different temperature treatments under the same light intensity; different lowercase letters indicate significant differences between different light treatments under the same temperature ($P < 0.05$).

main effect on the relative growth rate (RGR) (Table 2, $P < 0.05$). The RGR of *S. horneri* increased with the increasing light intensity under all the temperatures. Under the low temperature condition (20°C), the effect of light on the growth rate was significant ($P < 0.05$), the RGR of high light treatments (120 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) was about 2-fold higher than low light treatments (30 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$). However, under the high temperature (30°C), the difference of RGR between different light was not significant ($P > 0.05$). The highest RGR was observed at high light and low temperature treatments (Figs.1, 2). Besides, these results show that all treatments had the similar contents of Chl *a* and Car; both temperature and light had no obvious effect on the contents of Chl *a* and Car (Table 2, $P > 0.05$), and showed no interactive effect on the contents of Car (Table 2, $P > 0.05$).

3.2 Effect of Light and Temperature on the Chlorophyll Fluorescence Parameters

As for F_v/F_m and electron transport rate (ETR) at the end of induction curve, there were no significant differences among all the treatments, and the interactive effects of light and temperature were not significant (Fig.3, Table 4, $P > 0.05$). However, the light had a main effect on ETR (Table 3, $P < 0.05$), the highest ETR occurred at the high light treatment (120 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$).

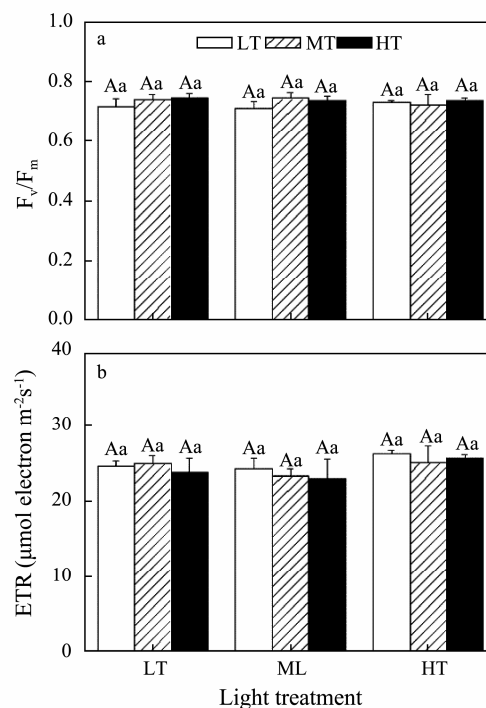


Fig.3 F_v/F_m and ETR of *S. horneri* grown at different treatment. Values were mean \pm SD ($n=3$). Different uppercase letters indicate significant differences between different temperature treatments under the same light intensity; different lowercase letters indicate significant differences between different light treatments under the same temperature ($P < 0.05$).

In relation to rapid light curves, the electron transport rate (ETR) of *S. horneri* increased gradually at first and then decreased after reaching the maximum value with

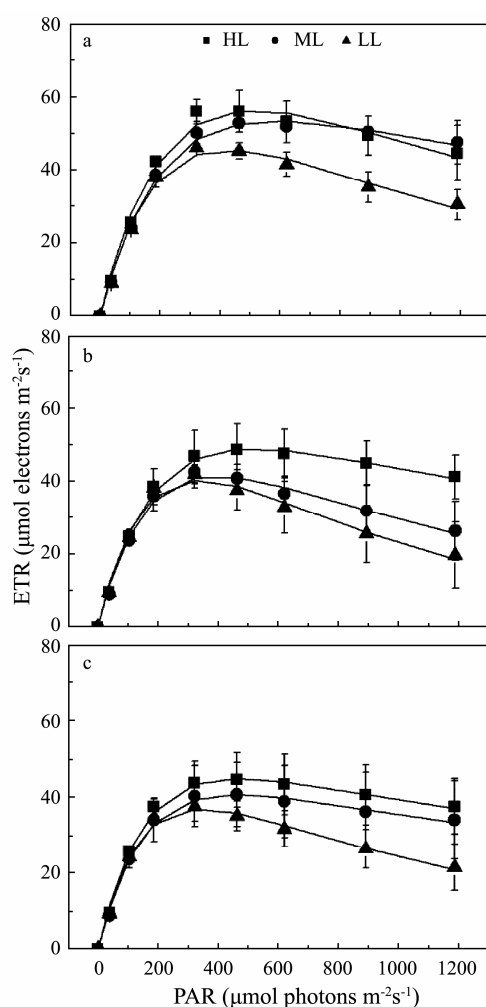
Table 3 Two-way analysis of variance for the effects of temperature and light intensity on different parameters

| Source | df | F | Sig. |
|----------------------------|----|-------|-------|
| F_v/F_m | | | |
| Temperature | 2 | 2.495 | 0.111 |
| Light | 2 | 0.096 | 0.909 |
| Temperature \times Light | 4 | 1.035 | 0.416 |
| ETR | | | |
| Temperature | 2 | 0.895 | 0.426 |
| Light | 2 | 4.528 | 0.026 |
| Temperature \times Light | 4 | 0.334 | 0.851 |

Notes: df, degrees of freedom; F, the value of the F statistic.

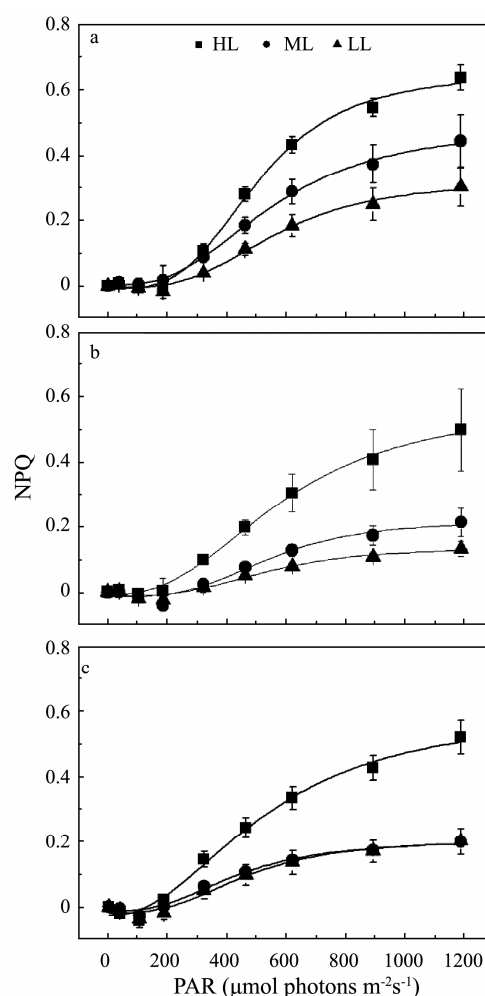
Table 4 The photosynthetic parameters of *S. horneri* grown at different treatments

| Treatment | α | I_k | rETRmax |
|-----------|------------------------|-----------------------------|---------------------------|
| HL-LT | 0.353 ± 0.007^{Aa} | 160.029 ± 17.255^{Aa} | 56.427 ± 5.063^{Aa} |
| ML-LT | 0.320 ± 0.022^{Aa} | $168.828 \pm 6.830^{Aa,b}$ | $53.912 \pm 3.099^{Aa,c}$ |
| LL-LT | 0.344 ± 0.017^{Aa} | $134.379 \pm 10.621^{Aa,c}$ | 46.157 ± 2.426^{Abc} |
| HL-MT | 0.336 ± 0.027^{Aa} | 145.855 ± 17.651^{Aa} | 49.045 ± 7.341^{Aa} |
| ML-MT | 0.332 ± 0.020^{Aa} | 126.262 ± 10.343^{Ba} | 41.824 ± 3.650^{Aa} |
| LL-MT | 0.361 ± 0.016^{Aa} | 112.848 ± 10.753^{ACa} | 40.635 ± 3.445^{ACa} |
| HL-HT | 0.358 ± 0.024^{Aa} | 126.871 ± 28.240^{Aa} | 45.043 ± 7.297^{Aa} |
| ML-HT | 0.329 ± 0.023^{Aa} | 121.524 ± 21.625^{Ba} | 40.381 ± 9.629^{Aa} |
| LL-HT | 0.352 ± 0.016^{Aa} | 105.076 ± 7.528^{BCa} | 36.979 ± 3.405^{BCa} |

Notes: Different uppercase letters indicate significant differences between different temperature treatments under the same light intensity; different lowercase letters indicate significant differences between different light treatments under the same temperature ($P < 0.05$).Fig.4 Rapid light curve (P-L curves) of *S. horneri* grown

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the increasing light. Compared with those at medium- (25°C) and high temperature (30°C) treatments, the low temperature treatments (20°C) had higher half-saturation light intensity (I_k) and maximal electron transport rate (rETR_{max}). I_k and rETR_{max} basically increased with the light intensity under the same temperature, but under the low temperature, I_k at medium light was a little higher than low light although the difference was not obviously ($P > 0.05$). However, the light harvesting efficiency (α) did not change significantly under all the treatments (Fig.4, Table 4, $P > 0.05$).

Fig.5 Non-photochemical quenching (NPQ) vs. the light intensity (PAR) of *S. horneri* grown under different treat-

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The non-photochemical quenching (NPQ) increased gradually with the increasing light. The maximum NPQ occurred at high light ($120 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) treatments, and the medium light ($60 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) treatments was little higher than that of the low light ($30 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) treatment under all the temperatures. Under high light treatments, the fast and obvious increase of NPQ was observed at each temperature. However, under the medium and low light treatments, the increment of NPQ was smaller with increasing light, and particularly at the high temperature (30°C) treatments the curves showed barely upward trend (Fig.5).

3.3 Effect of Light and Temperature on the Photo Synthetic Oxygen Evolution

The net photosynthetic rate (P_n) increased significantly with the increasing light at all temperature treatments (Fig. 6a, $P < 0.05$), and the highest P_n occurred at HL-LT ($120 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, 20°C). P_n show no obvious difference among different temperature treatments at LL, but

the P_n at HT was significantly lower than those of LT and MT at HL. HL increased P_n to $73.3 \pm 1.37 \mu\text{mol O}_2 \text{g}^{-1} \text{FW h}^{-1}$ compared to LC's ($17.5 \pm 0.47 \mu\text{mol O}_2 \text{g}^{-1} \text{FW h}^{-1}$) at LT. However, HL only increased P_n to $43.2 \pm 1.15 \mu\text{mol O}_2 \text{g}^{-1} \text{FW h}^{-1}$ compared to the LC's ($19.2 \pm 1.86 \mu\text{mol O}_2 \text{g}^{-1} \text{FW h}^{-1}$) at HT. Besides, the P_n increased with temperature decreasing. However, under the low light condition, the medium temperature present the highest P_n in all temperature treatments, which is consistent with the RGR, but had no significant difference between them (Fig.6a, $P > 0.05$). With the decrease of temperature and light, the dark respiratory rate (R_d) decreased; the high temperature (30°C) and high light treatment showed the maximum R_d (Fig.6b). In addition, the ratio of P_n and R_d (P_n/R_d) shows a similar pattern to that of P_n (Fig.6c). Results of two-way ANOVA show that temperature and light had significant interactive effects on P_n and P_n/R_d , and both exerted main effects (Table 5, $P < 0.05$). Additionally, significant effects of temperature and light on the R_d were also observed, but there were no significant interactive effects between these two factors.

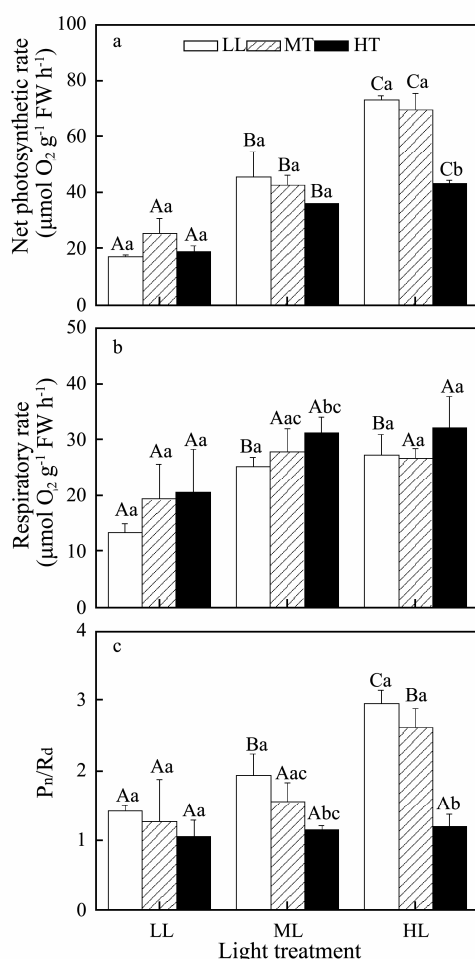


Fig.6 The net photosynthetic rate (P_n) (a), respiratory rate (R_d) (b) and P_n/R_d (c) of *S. horneri* grown at different treatment. Values were mean \pm SD ($n=3$). Different uppercase letters indicate significant differences between different temperature treatments under the same light intensity; different lowercase letters indicate significant differences between different light treatments under the same temperature ($P < 0.05$).

Table 5 Two-way analysis of variance for the effects of temperature and light intensity on the photosynthetic oxygen evolution

| Source | df | F | Sig. |
|----------------------------|----|---------|-------|
| P_n | | | |
| Temperature | 2 | 22.547 | 0.000 |
| Light | 2 | 173.965 | 0.000 |
| Temperature \times Light | 4 | 9.885 | 0.000 |
| R_d | | | |
| Temperature | 2 | 4.171 | 0.032 |
| Light | 2 | 17.396 | 0.000 |
| Temperature \times Light | 4 | 0.422 | 0.791 |
| P_n/R_d | | | |
| Temperature | 2 | 27.495 | 0.000 |
| Light | 2 | 30.051 | 0.000 |
| Temperature \times Light | 4 | 5.917 | 0.003 |

Notes: df, degrees of freedom; F, the value of the F statistic.

4 Discussion

Sargassum horneri distributes normally in intertidal and subtidal zones, and easily suffers from environmental stresses (temperature, light, salinity, desiccation) (Zhang *et al.*, 2008). Among them, temperature and light are two main factors influencing the growth of *S. horneri* (Zeng and Wang, 2011). In the present study, we find that the suitable growth condition for *S. horneri* was the lowest temperature (20°C) and highest light ($120 \mu\text{mol photons m}^{-2} \text{s}^{-1}$), while the highest temperature (30°C) seriously inhibited the growth, especially at lowest light ($30 \mu\text{mol photons m}^{-2} \text{s}^{-1}$). As reported by Zhang *et al.* (2014), the suitable growth temperature for *S. horneri* was between 20 and 25°C , while 30°C significantly inhibited the growth, and the optimal light was about $90 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, which is consistent with our results. By affecting the main functional proteins, membranes, and other cellular components, temperature and light determine the growth of macroalgae (Eggert, 2012; Su *et al.*, 2014). At

optimum temperature and light, the growth of macroalgae will be promoted; otherwise, it would be inhibited under supra- or sub-optimum conditions (Lideman *et al.*, 2012; Wu *et al.*, 2018). An elevated water temperature may be the main factor causing the decline of *S. horneri* beds (Zhang *et al.*, 2008; Komatsu *et al.*, 2014). The decreased transparency of water caused by re-suspension of amount sediments load in Nanji and Gouqi Islands enhanced the inhibition of high temperature on the growth of *S. horneri* (Sun *et al.*, 2008; Bi and Wang, 2016). This is because the low light limited the photosynthesis, thus less energy was not strong enough to mitigate the negative effects of high temperature (Zeng *et al.*, 2020).

Photosynthesis is easily affected by environmental stress. In our study, the photosynthetic oxygen evolution and chlorophyll fluorescence parameters were measured at the growth temperature and light in the culture under different temperatures and light intensities for 7 d. These results show that the net photosynthetic rate (P_n) increased significantly with the light in regardless of temperature, while high temperature (30°C) obviously inhibited the P_n , and had a synergistic effect with light; low light (30 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) promoted the inhibitive effects of high temperature on the P_n . High temperature affects the photosynthetic oxygen evolution by reducing the chloroplast electron transport, decreasing the photosynthetic pigments contents, and influencing the enzyme activity (Feller *et al.*, 1998; Eggert, 2012). However, it was unusual that the photosynthetic pigments contents and the electron transport rates (ETR) at the end of induction curve were not significantly affected by temperature and light, indicating that the factors affecting P_n other than temperature and light. As shown in Fig.6b, the dark respiration rate (R_d) increased with increasing temperature, and higher light enhanced the effects of temperature on R_d . In this case, the increased metabolic rate caused by high temperature consumed more energy and resulted in the reduction of growth (Wang and Wang, 2008). Moreover, high light could promote the accumulation of Rubisco, while high temperature could reduce the Rubisco activity by inactivating the Rubisco activase (Koch *et al.*, 2013; Beer *et al.*, 2014). However, our results show that high temperature and high light led to a lower P_n , indicating that the high temperature (30°C) was the main limiting factor to P_n . In addition, the P_n/R_d increased with increasing light at 20 and 25°C, while under high temperature (30°C), no significant change was observed between light treatments. On the other hand, the P_n/R_d decreased with the increasing temperature. These results indicate that the photosynthetic performance and accumulation of photosynthetic products were inhibited by high temperature and low light, and the high temperature (30°C) was the primary factor (Li *et al.*, 2000; Zhong *et al.*, 2016).

Macroalgae have evolved in a series of protective mechanisms under environmental adversity (Mata *et al.*, 2009), among which nonphotochemical quenching (NPQ) is an important protective mechanism. By NPQ, the excess absorbed energy can be harmlessly dissipated

quickly via thermal dissipation to avoid damage generated by light stress to plants. NPQ is often regarded as an indicator to a physiological stress (Niyogi, 2000), which has been proved in studies on algae (Gao *et al.*, 2017, 2018b). In the present study, NPQ of higher light cultured algae was induced faster by increasing light under 20 and 25°C. Especially at 30°C, the effect of high light (120 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) on NPQ was obvious, while the difference between 30 and 60 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ was not significant (Fig.5). The higher NPQ might be related to the accumulation of zeaxanthin, which is directly associated with NPQ in brown algae (Garcia-Mendoza *et al.*, 2011; Pang, 2018). These results suggested that high light can provide more energy to synthesize zeaxanthin, thus to enhance the photo-protective ability of *S. horneri*. However, high temperature had antagonistic effect to high light thus weaker photo-protective ability. Besides, the maximal electron transport rate ($rETR_{\text{max}}$) and half-saturation light intensity (I_k) were used to characterize the photo-acclimation ability (Behrenfeld *et al.*, 2004; Ralph and Gademann, 2005; Serôdio *et al.*, 2005; Pniewski *et al.*, 2018). The higher values of $rETR_{\text{max}}$ and I_k indicated the higher light acclimation. As shown in Fig.4 and Table 4, the low temperature (20°C) and high light (120 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) treatments produced greater I_k and $rETR_{\text{max}}$, respectively. The reason might be that low temperature and high light cultured algae have enough energy for the synthesis of photosynthetic enzymes, electron chain components as well as the operation of photo-protective and energy-dissipating mechanisms (Hanelt and Figueroa, 2012), thus the thalli had higher light-saturation point, higher maximal photosynthetic rates at light saturation and increased effective photo-protection. As a result, under the low temperature and high light conditions, *S. horneri* displayed higher potential photosynthetic performance and could tolerate higher light, which had been proved by Pang (2018). On the contrary, under high temperature and low light conditions, *S. horneri* had weaker resistance to high light.

In conclusion, our study provided evidence that a high temperature could inhibit the growth, photosynthetic performance, and photo-protective ability of *S. horneri*, and low light further aggravated the adverse effects. Komatsu (2014) predicted that the southern limit *S. horneri* is gradually replaced by tropical species due to the impact of ocean warming. The annual sea surface temperatures (SST) in South China Sea is approaching to 28°C in recent years (Pang *et al.*, 2018), and the ocean temperature will be elevating in the future (Zhu *et al.*, 2019), thus the southern boundary may shift northward constantly and the decline of *S. horneri* beds in China may continue. Moreover, the negative effect would be magnified by low light. As been proved that the increasing of sediments load could restrict the adhesive ability and development of fertilized eggs, and re-suspension of the increment of sediments load decreased the transparency of seawater, lower the light intensity (Bi *et al.*, 2014; Bi and Wang, 2016). Therefore, if the nearshore sediments load could not be reduced, the phenomenon of decline of *S. horneri*

will continue. As a consequence, the decline of *S. horneri* would be accelerated in the future.

Acknowledgements

This work was financially supported by the National Key Research and Development Program of China (No. 2016YFC1402106), the Technology Innovation Development Program of Yantai (No. 2020MSGY058), the National Natural Science Foundation of China (No. 31700327), the Shandong Provincial Natural Science Foundation, China (No. ZR2019QD017), the Key R & D Projects in Shandong Province (International Scientific and Technical Cooperation) (No. 2019GHZ026), and the Technology Innovation Development Program of Yantai (No. 2020MSGY068).

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(Edited by Ji Dechun)