



Physiological Responses of *Sargassum muticum*, a Potential Golden Tide Species, to Different Levels of Light and Nitrogen

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Sargassum golden tides have bloomed frequently in many sea areas throughout the world, and negatively impacted on the local marine ecology. *Sargassum muticum* commonly inhabits rocky shores. It is now distributed worldwide due to its invasiveness, and recently drifting individuals have been observed on the coasts of Canary Islands. However, as a potential golden tide alga, physiological, and ecological studies of this species have not been frequently explored. To investigate the responses of *S. muticum* to light and nitrogen, two key environmental factors in golden tide formation, we established three light levels (LL, low light, 10 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$; ML, medium light, 60 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, and HL, high light, 300 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) and two nitrogen levels (LN, low nitrogen, 25.0 μM of natural seawater; HN, high nitrogen, 125.0 μM), and cultivated the thalli under different conditions for 12 days before measuring the physiological properties of alga. The results showed that higher light and/or nitrogen levels enhanced the relative algal growth rate. The maximum net photosynthesis rate of alga increased with the light, while it remained unaffected by the nitrogen. The HN treatment had no effect on the apparent photosynthetic efficiency of algae in the LL culture, while increased it in the ML and HL cultures. The irradiance saturation point of photosynthesis was approximately 300 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ with no significant difference among the six treatments, except for a slight increase under HLHN in contrast to the LLHN and MLLN treatments. HL treatment decreased the maximum quantum yield of photosynthesis (F_v/F_m) in both nitrogen levels. In the HN culture, ML and HL led to lower values of photoinhibition, indicating higher survivability in the alga. The HN culture led to higher nitrogen uptake but had no effects on F_v/F_m and the contents of pigments and soluble protein, regardless of culture light level. Based on these results, we speculate that drifting individuals of *S. muticum* would be possible to form a golden tide owing to its rapid growth rate at light level of 300 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, when they encountered the sustained lower light level on the sea surface ($\leq 300 \mu\text{mol photons m}^{-2} \text{s}^{-1}$). A high nitrogen supply caused by eutrophication of seawater might facilitate this process. Our results provide an important reference for the prediction of golden tides formed by *S. muticum*.

Keywords: floating macroalgae, eutrophication, photosynthesis, photoinhibition, growth

INTRODUCTION

In recent years, there have been massive inundations of the genus *Sargassum* aggregating on the surface of sea, known as “golden tides,” in the central Atlantic Ocean, Gulf of Mexico (Smetacek and Zingone, 2013; Schell et al., 2015; Wang et al., 2019; Qi et al., 2020), East China Sea and Yellow Sea (Qi et al., 2017; Xing et al., 2017; Liu et al., 2018). When the golden tide blooms as an invasive genus, mats of floating *Sargassum* can change the ecosystem structure of the original sea area (van Tussenbroek et al., 2017; Baker et al., 2018; Caselle et al., 2018), negatively impact offshore tourism and maritime transport (Williams and Feagin, 2010; Milledge and Harvey, 2016), and lead to the deterioration of seawater quality after they sink and decay (Cruz-Rivera et al., 2015). If an episode was to occur in aquaculture areas, golden tides could cause enormous losses to the local mariculture industry, for example, blooming of *Sargassum horneri* golden tide in the Yellow Sea in December 2016, caused economic loss of 0.5 billion CNY due to the damaged local seaweed aquaculture (Xing et al., 2017).

The occurrence of golden tides has been linked to changes in marine environmental factors, such as nutrients, temperature, and light (Sfriso and Facca, 2013; Smetacek and Zingone, 2013). Satellite remote sensing monitoring data have confirmed that the formation of golden tides often occurs in eutrophic oceanic areas with the availability of upwelled (Brooks et al., 2018; Wang et al., 2019) and river (Sfriso and Facca, 2013; Louime et al., 2017; van Tussenbroek et al., 2017) plume nutrients, which provide sufficient nitrogen and phosphorus for the growth of golden tide algae. The fact that high nitrogen resulted in high growth rate has been found in several algal species known to cause golden tides, namely, *S. horneri* (Yu et al., 2019), *Sargassum natans* and *Sargassum fluitans* (Wang et al., 2019). Therefore, many scientists hypothesize that eutrophication plays an important role in inducing the formation of *Sargassum* golden tides (Sfriso and Facca, 2013; Smetacek and Zingone, 2013; Louime et al., 2017; van Tussenbroek et al., 2017; Wang et al., 2019).

Alternatively, golden tide algae drifting on the sea surface receive more light, compared with those individuals attached to the seabed, owing to the light attenuated by seawater (Kouassi and Zika, 1992; Tedetti and Sempéré, 2006; Wu et al., 2010). Typically, the majority of macroalgae manifest higher photosynthesis and growth rates at higher light levels (Xu et al., 2014; Erin Cox and Smith, 2015). However, levels of light that are too high could depress macroalgal photosynthesis, which is designated photoinhibition (Yakovleva and Titlyanov, 2001; Murata et al., 2007). However, that floating *Sargassum* receiving more light energy, may grow explosively to form a golden tide when exposed to nutrient enrichment, for example *S. natans* and *S. fluitans* (Wang et al., 2019). Moreover, the upper and lower sides of the floating *Sargassum* layer will also suffer from differing light conditions owing to the thickness of the floating layer. Unfortunately, little is known about the effects of light levels on the photosynthesis

related to growth of floating *Sargassum*, particularly when enriched by nutrients.

Currently, three species have been observed to form golden tides. *S. natans* and *S. fluitans* are the predominant species in golden tides that bloom in the central Atlantic Ocean and the Gulf of Mexico (Smetacek and Zingone, 2013; Schell et al., 2015; van Tussenbroek et al., 2017; Wang et al., 2019), while *S. horneri* is the only species that causes golden tides in the East China Sea and Yellow Sea (Qi et al., 2017; Xing et al., 2017; Liu et al., 2018). Although no other *Sargassum* species have been currently observed to form golden tides, whether they will do so in the case of appropriate environmental conditions in the future remains unclear. *Sargassum muticum* is widely distributed on the coast of the Western Pacific North and has recently invaded the Northern European and North American coasts (Engelen et al., 2015), resulting in significant negative impacts on local marine ecosystems (Cacabelos et al., 2013; Salvaterra et al., 2013; Sánchez and Fernández, 2018; Belattmania et al., 2020). Most seriously, many drifting alga individuals were observed on the coasts of Canary Islands (Eastern Atlantic Ocean) in March 2020 (Álvarez-Canali et al., 2021). Therefore, we suggest that more intensive study on this potential golden tide species is merited. The aim of this study was to investigate the physiological responses of *S. muticum* to light and nitrogen levels, two key factors during the formation of golden tides, which expectedly provides references for the future prediction of golden tides caused by this species.

MATERIALS AND METHODS

Materials

Samples of *S. muticum* were collected from an attached population at a depth of 2 m in Lidao Bay, Rongcheng City, Shandong Province, China (37°15' N, 122°35' E) on April 5, 2019, where temperature is 20°C, salinity is 30 PSU, NO₃⁻, 25.0 μM and dissolved inorganic phosphorus (DIP) is 1.6 μM in the natural seawater. Sporophytes of approximately 60 cm long were selected and brought to the laboratory in an insulated cooler of 4°C in 2 h. After cleaned with autoclaved seawater, segments that were approximately 5 cm long were randomly cut from several branches and pre-cultured in autoclaved natural seawater (salinity, 30 PSU; NO₃⁻, 25.0 μM; NH₄⁺, 0.8 μM and DIP, 1.6 μM) for 24 h. The temperature was set at 20°C, and the light level was 60 μmol photons m⁻² s⁻¹ with light and dark periods of 12 h:12 h. The media were continuously aerated.

Experimental Design

After preincubation for 24 h, 5–6 segments [~4.0 g of fresh weight (FW)] of the algae were cultured in a conical flask with 2 L of modified Provasoli's enriched seawater (PESI, Provasoli, 1968). The DIP concentration of 5 μM in PESI medium was obtained by the addition of NaH₂PO₄ to ensure adequate supply of P. In addition, NaNO₃ was added separately for the high nitrogen levels. According to the observation that inorganic

nitrogen concentration in golden tide bloom area increased by 3–4 times (Wang et al., 2019), two nitrogen levels were established in the experiment: low nitrogen (LN, the concentration in natural seawater, 25.0 μM) and high nitrogen (HN, 125.0 μM). The effect of NH_4^+ was ignored due to its low content of 0.8 μM in both LN and HN treatments. The media were continuously aerated and renewed every other day. The culture density was maintained at 2.0 g FW L^{-1} during the experiment by removing the excess growth part of the thalli when the media was renewed.

The containers were positioned in growth chambers (MGC-250P, Yiheng Technical Co., Ltd., Shanghai, China) with constant temperature of 20°C and 12 h:12 h light and dark periods. By regulating the light source of growth chambers, light that reached the algae was set at three levels (LL, low light, 10 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$; ML, middle light, 60 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$; HL, high light, 300 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), based on the daily mean irradiance in spring received by the attached thalli [the lowest and highest values in the distribution depths of 2–6 m, referred to Liu et al. (2021)] and the floating individuals (Rumyantseva et al., 2019), respectively. Light source was provided by LED lamps emitting white light in chambers, and the light levels were measured using a handheld optical quantum meter (QRT1, Hansatech, Norfolk, United Kingdom). The samples were cultured under different nitrogen and light conditions for 12 days, with three replicates of each treatment. At the end of 12-day culture, the growth rate, photosynthesis, contents of pigments and soluble protein, and nitrogen uptake of the algae were determined.

Determination of the Growth Rate

The growth of algae under different nitrogen and light conditions was measured during the final 2 days of culture in order to reflect acclimated physiological performance of thalli, and the relative growth rate (RGR) was calculated using the following formula:

$$\text{RGR} = 100 \times (\ln N_t - \ln N_0) / t$$

Where N_t represents the FW on day t (day 12); N_0 represents the initial FW (day 10), and t represents the time interval (2 days). The FW was determined through electronic analytical balance (ME104, Mettler-Toledo, Switzerland) after removing surface water drops of thalli by lightly blotting with tissue paper.

Estimates of Respiration and Photosynthesis

Dark respiration (R_d) and the rates of evolution of photosynthetic O_2 were determined using a Clarktype oxygen electrode (Chlorolab-3, Hansatech, Norfolk, United Kingdom) at 20°C. Approximately 0.15 g FW of algae harvested from the culture flask on day 12 was transferred to the oxygen electrode cuvette that contained 8 ml of autoclaved natural seawater, and the media were stirred during measurement. The dark respiration rate was measured after covering the cuvette with an opaque cloth. The photosynthetic O_2 evolution rates (E_k) were measured during 5 min under six levels of light (20, 60, 120, 200, 400,

and 600 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$). White light was provided by a metal halide lamp, and different levels of irradiance were provided by altering the distance between light source and the oxygen electrode cuvette. The light levels were measured through a handheld optical quantum meter (QRT1, Hansatech, Norfolk, United Kingdom). Therefore, the P – E curve (photosynthetic rates at different irradiance levels) was obtained using the model of Eilers and Peeters (1988) and fitting the data by iteration:

$$P = E / (a \times E^2 + b \times E + c)$$

Where P are the net photosynthesis rates ($\mu\text{mol O}_2 \text{ h}^{-1} \text{ g}^{-1}$ FW) at different irradiance levels; E is the irradiance ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), and a , b , and c are the adjustment parameters. The parameter “ a ” is the photoinhibition term. The apparent photosynthetic efficiency (α), maximum net photosynthetic rate (P_{max}) and irradiance saturation point (E_k) are expressed as a function of the parameters a , b , and c as follows:

$$\alpha = 1/c$$

$$P_{\text{max}} = 1/[b+2(a \times c)^{0.5}]$$

$$E_k = (c/a)^{0.5}$$

Determination of the Maximum Photochemical Yield of Photosystem II

The chlorophyll fluorescence yield data were measured using a plant efficiency analyzer (Handy PEA, Hansatech, Norfolk, United Kingdom) during the 6th hour of the photoperiod at end of 12 days of culture. The thalli were dark adapted for 15 min to allow all the reaction centers to open before the measurements were taken. The minimal fluorescence (F_0) was induced by low irradiation of the measuring light (approximately 0.15 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), and the maximum fluorescence (F_m) was obtained after exposed to a single saturating pulse irradiance of 5,000 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ for 800 ms. The maximum quantum yield of photosystem II (PSII) was then estimated as:

$$F_v/F_m = (F_m - F_0)/F_m$$

Measurement of Pigments and Soluble Proteins

Approximately 0.1 g FW thalli from each treatment were ground with an aqueous solution of 90% acetone. The solution was brought to 8 ml and extracted for 12 h at 4°C in the dark. After centrifugation (4,000 r min^{-1} , 15 min), the absorption spectrum of 400–700 nm of supernatant was determined using a spectrophotometer (DU 530, Beckman Coulter, Fullerton, CA, United States). The contents (mg g^{-1} FW) of chlorophyll (Chl a , Chl c) and carotenoids (Car) were calculated as described by Jeffrey and Humphrey (1975) and Parsons et al. (1984), respectively.

$$\text{Chl } a = (11.47 \times A_{664} - 0.40 \times A_{630}) \times V/M$$

$$\text{Chl } c = (24.36 \times A_{630} - 3.73 \times A_{664}) \times V/M$$

$$\text{Car} = [7.6 \times (A_{480} - 1.49 \times A_{510})] \times V/M$$

Where A was the absorbance value of supernatant at differing wavelengths; V was the volume of solution at a constant volume (8 mL), and M was the FW of algae (g).

To extract the soluble protein, approximately 0.2 g of FW thalli from each treatment were ground in a mortar, and the volume was brought to 5 mL with phosphate buffer (0.1 mol L⁻¹, pH 6.8). After centrifugation at 5,000 g for 10 min, the soluble protein was estimated from the supernatant using the Bradford (1976) assay with bovine serum albumin as the standard.

Assessment of Nitrogen Uptake

The rate of nitrogen uptake of the thalli was estimated from the decrease in rate of nitrate in the culture seawater over a 2-day interval when the medium was being renewed. The concentration of nitrate was determined as described by Strickland and Parsons (1972), and the rate of nitrogen uptake was calculated using the following equation:

$$\text{Uptake rate} = (N_0 - N_t) \times V/M/t$$

Where N_0 and N_t were the concentrations of nitrate in the medium at the initial and end of culture, respectively. V was the volume of the culture medium; M was the initial FW of the thalli (g), and t was the culture time (2 days).

Data Analysis

The results were expressed as the means of replicates \pm standard deviation. The data were analyzed using SPSS v. 21 (IBM, Inc., Armonk, NY, United States). The data under every treatment conformed to a normal distribution (Shapiro–Wilk, $P > 0.05$), and the variances can be considered equal (Levene's test, $P > 0.05$). Two-way analysis of variance (ANOVA) was conducted to assess the effects of light and N on RGR, photosynthetic parameters from the $P-E$ curves, dark respiration rate, F_v/F_m , pigments, soluble protein, and nitrate uptake rate. Tukey's honest significance difference (HSD) was conducted for a *post hoc* investigation. A confidence interval of 95% was set for all tests.

RESULTS

Growth Rate

The RGRs of *S. muticum* cultured under different light and nitrogen conditions are shown in **Figure 1**. Light and nitrogen had no interactive effect on RGR of *S. muticum* (ANOVA, $P = 0.088$), but each factor had a main effect (ANOVA, $P < 0.001$ for light; ANOVA, $P < 0.001$ for nitrogen). An increase in the light intensity enhanced the RGR at both LN and HN treatments (Tukey's HSD, $P < 0.05$). Compared with LL, treatment with ML and HL increased the RGR of algae by 55.9 and 190.6%

at LN levels, respectively, while under HN condition, the RGR were enhanced by 60.3% under ML and 168.9% under HL treatments. The enrichment of nitrogen also significantly promoted the growth of thalli under all three light conditions (Tukey's HSD, $P < 0.05$). HN increased the RGR by 11.7, 14.8, and 3.4% in LL, ML, and HL treatments, respectively, compared with LN conditions.

Photosynthesis and Respiration

The irradiance saturation point (E_k), photoinhibition term (a), apparent photosynthetic efficiency (α), and maximum net photosynthesis rate (P_{max}) are presented in **Table 1**. The irradiance saturation point (E_k) was approximately 300 photons m⁻² s⁻¹, with no significant difference between the six treatments (Tukey's HSD, $P > 0.05$), with the exception of a slight increase under HLHN in contrast to the LLHN and MLLN treatments (Tukey's HSD, $P < 0.05$). Light and nitrogen had an interactive effect on P_{max} (ANOVA, $P < 0.001$), α (ANOVA, $P < 0.001$) and the photoinhibition term " a " (ANOVA, $P < 0.05$). In all six treatments of different light and nitrogen levels, the thalli cultured in MLHN and HLHN expressed lower " a " values (Tukey's HSD, $P < 0.05$), suggesting that algae that had adapted to HN and HL conditions were more tolerant of strong light inhibition. Regardless of the nitrogen concentration, P_{max} increased with the light level of culture, with the exception of an insignificant difference between MLHN and HLHN (Tukey's HSD, $P > 0.05$). At the ML and HL levels, the nitrogen level insignificantly affected P_{max} (Tukey's HSD, $P > 0.05$), while in LL treatments, HN enhanced the P_{max} of thalli by 28.3%, compared with LN (Tukey's HSD, $P < 0.05$). In the LN culture, the light level had no effect on the α of algae (Tukey's HSD, $P > 0.05$). However, in HN culture, the value of α differed significantly between the three light levels (Tukey's HSD, $P < 0.05$). The highest (0.169 ± 0.005) and lowest (0.105 ± 0.012) values of α occurred at ML and LL, respectively.

In the LL and ML culture, the dark respiration rate (R_d) of thalli remained unaffected interactively by different levels of culture light and nitrogen (ANOVA, $P > 0.05$, **Figure 2**). However, HL culture ($300 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$) remarkably increased R_d in both nitrogen concentrations, compared with the LL and ML treatments (Tukey's HSD, $P < 0.05$). In addition, in HL culture, HN enhanced the R_d by 24.6%, in contrast to that in LN culture (Tukey's HSD, $P < 0.05$).

The Maximum Photochemical Yield

The maximum photochemical yields (F_v/F_m) of the algae cultured at different light and nitrogen levels are shown in **Figure 3**. Light and nitrogen had no interactive effect on F_v/F_m of algae (ANOVA, $P > 0.05$). The nitrogen levels had an insignificant effect on F_v/F_m regardless of the culture light levels (ANOVA, $P > 0.05$). In both LN and HN cultures, the values of F_v/F_m expressed insignificant differences between the LL and ML conditions (Tukey's HSD, $P > 0.05$), while it decreased remarkably in the HL treatment

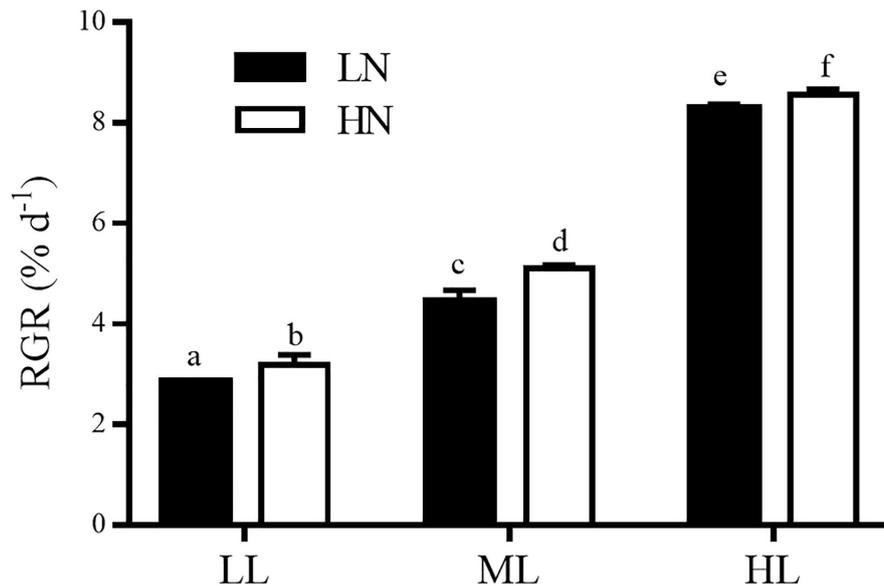


FIGURE 1 | Relative growth rates (RGRs) in *Sargassum muticum* grown at different light and nitrogen levels, which were determined during 2 days at the end of 12 days of incubation. Significant ($P < 0.05$) differences among the treatments are indicated by different lowercase letters. Vertical bars represent \pm SD for the means of three samples.

TABLE 1 | Photosynthetic parameters from the $P-E$ curves of *Sargassum muticum* cultured under different light and nitrogen conditions.

	α	P_{max}	α	E_k
LLLN	$(1.23 \pm 0.11) \times 10^{-4a}$	84.11 ± 8.44^a	0.085 ± 0.010^a	310.48 ± 4.28^{ab}
LLHN	$(1.09 \pm 0.15) \times 10^{-4a}$	107.91 ± 3.40^b	0.105 ± 0.012^a	297.88 ± 5.17^a
MLLN	$(1.23 \pm 0.04) \times 10^{-4a}$	123.91 ± 3.89^c	0.093 ± 0.003^a	295.53 ± 1.00^a
MLHN	$(0.65 \pm 0.01) \times 10^{-4b}$	135.43 ± 3.80^{cd}	0.169 ± 0.005^b	303.38 ± 4.69^{ab}
HLLN	$(1.17 \pm 0.11) \times 10^{-4ac}$	152.73 ± 3.32^e	0.107 ± 0.007^a	309.92 ± 10.76^{ab}
HLHN	$(0.80 \pm 0.14) \times 10^{-4bc}$	146.52 ± 2.46^{de}	0.129 ± 0.008^c	314.67 ± 2.00^b

α , the photoinhibition term; P_{max} ($\mu\text{mol O}_2 \text{ h}^{-1} \text{ g}^{-1} \text{ FW}$), the maximum net photosynthesis rate; α [$(\mu\text{mol O}_2 \text{ h}^{-1} \text{ g}^{-1} \text{ FW})/(\mu\text{mol photons m}^{-2} \text{ s}^{-1})$], the apparent photosynthetic efficiency; E_k ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), the irradiance saturation point. Different superscript letters indicate significant differences in one parameter between the treatments ($P < 0.05$).

compared with the LL and ML treatments (Tukey's HSD, $P < 0.05$).

Photosynthetic Pigments

The contents of photosynthetic pigments (Chl a, Chl c, and Car) of the thalli that had adapted to different light and nitrogen conditions are shown in **Figure 4**. Light and nitrogen had no interactive effect on the contents of all three pigments (ANOVA, $P = 0.671$ for Chl a, $P = 0.419$ for Chl c, and $P = 0.512$ for Car). Regardless of the culture light levels, the contents of Chl a, Chl c, and Car were not affected by the nitrogen level in cultures (ANOVA, $P = 0.057$ for Chl a, $P = 0.417$ for Chl c, and $P = 0.148$ for Car). However, light had main effects on three pigments (ANOVA, $P < 0.001$ for Chl a, $P < 0.001$ for Chl c, and $P < 0.01$ for Car). In the LN or HN treatment, HL treatment reduced the contents of all three photosynthetic pigments by approximately 30–45% compared with the LL and ML conditions (Tukey's HSD, $P < 0.05$), while no significant difference was observed between the LL and ML culture (Tukey's HSD, $P > 0.05$).

Soluble Proteins and Nitrogen Uptake

Light and nitrogen had no interactive effect on the content of soluble proteins (ANOVA, $P > 0.05$, **Figure 5**). The culture nitrogen levels had no impact on the content of soluble proteins at LL, ML, or HL treatment (ANOVA, $P > 0.05$). However, light had a main effect on it (ANOVA, $P < 0.001$). The LL culture markedly enhanced the content of soluble protein in thalli grown under LN or HN conditions (Tukey's HSD, $P < 0.05$), despite no significant difference was observed between the ML and HL cultures (Tukey's HSD, $P > 0.05$).

Light and nitrogen had an interactive effect on the nitrogen uptake rates of algae (ANOVA, $P < 0.001$, **Figure 6**), and each factor had a main effect (ANOVA, $P < 0.001$ for light; ANOVA, $P < 0.001$ for nitrogen). Compared with the LN treatment, HN culture increased the rate of uptake of nitrogen by 7.6 times at low light, 1.3 times in ML treatment, and 0.8 times in HL treatment. In LN cultures, ML and HL improved the rate of nitrogen uptake of algae by 3.0 and 8.5 times, respectively, compared with the

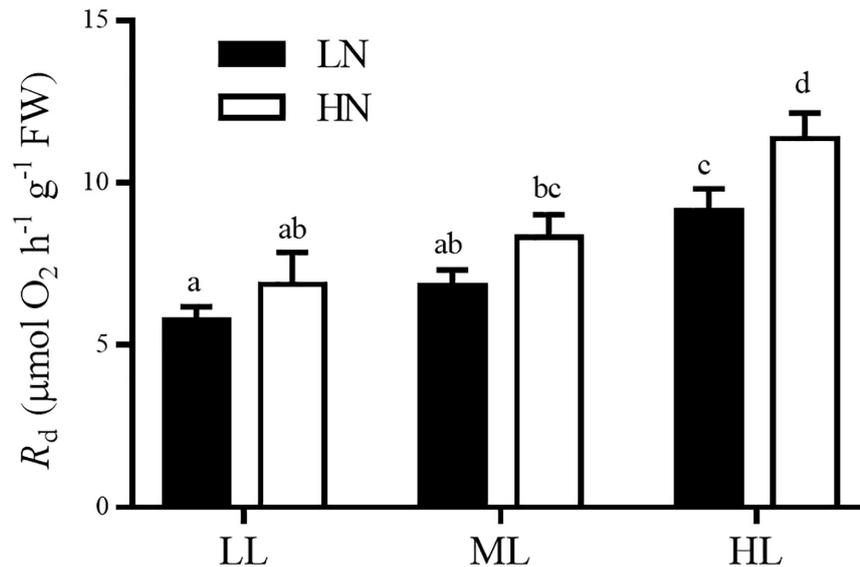


FIGURE 2 | Dark respiration rates of *S. muticum* grown at different light and nitrogen levels for 12 days. Significant ($P < 0.05$) differences among the treatments are indicated by different lowercase letters. Vertical bars represent \pm SD for the means of three samples.

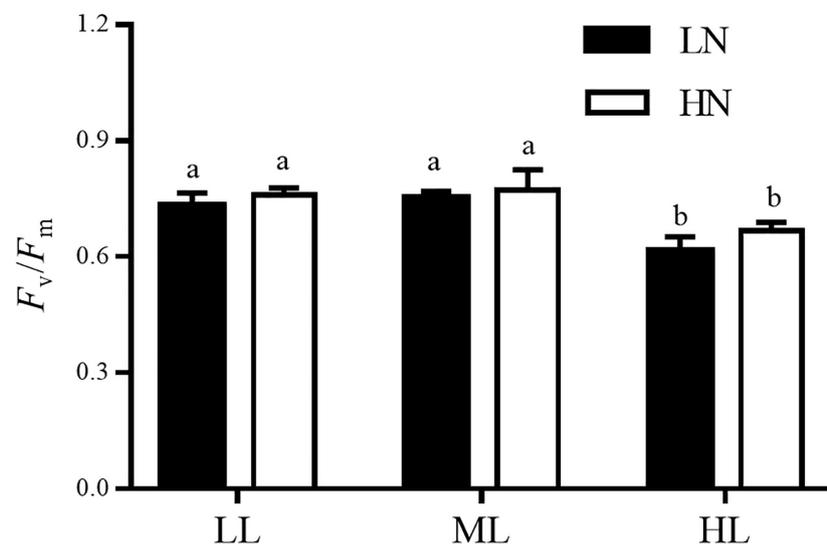


FIGURE 3 | The maximum quantum yield of photosystem II (F_v/F_m) in *S. muticum* grown at different light and nitrogen levels for 12 days. Significant ($P < 0.05$) differences among the treatments are indicated by different lowercase letters. Vertical bars represent \pm SD for the means of three samples.

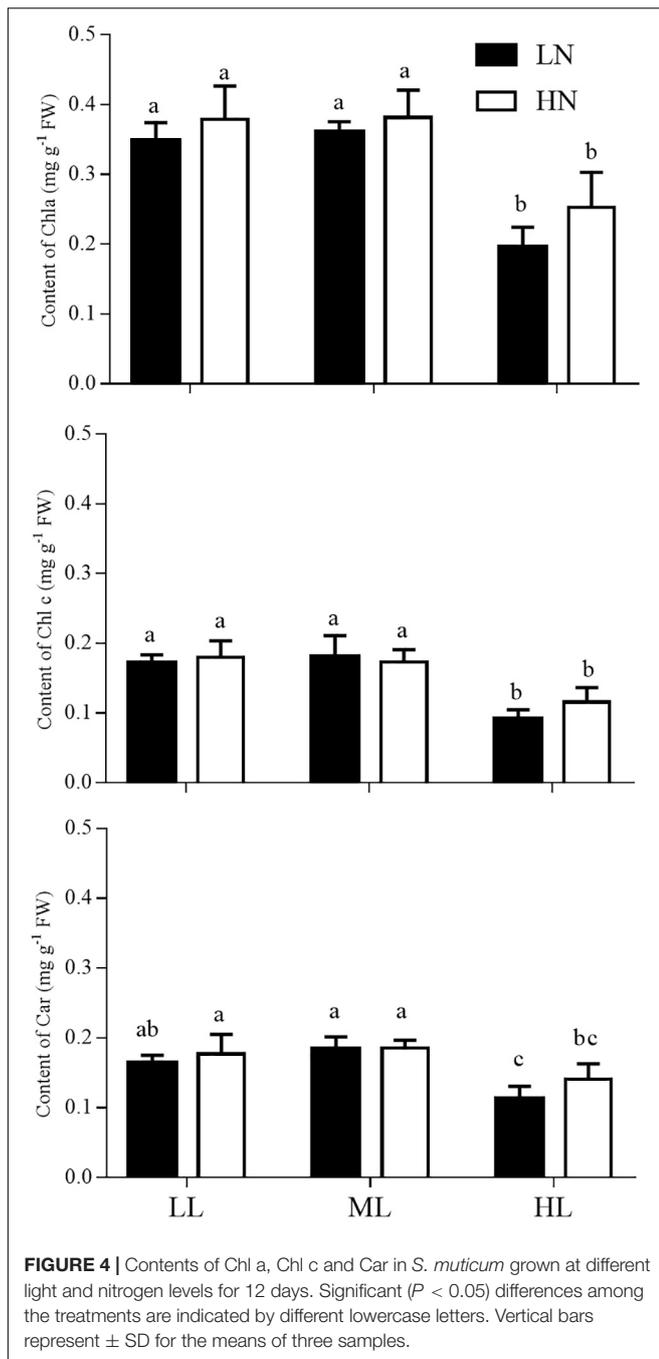
LL culture, while ML and HL improved it by 9.0 and 96.0%, respectively, when cultured in HN treatment.

DISCUSSION

In this study, higher light culture led to a higher RGR in *S. muticum*. The growth of macroalgae is closely related to algal photosynthesis (Lobban et al., 1985; Xu and Gao, 2009). Light provides the initial energy for photosynthesis, and the increase in culture light level can usually promote the photosynthesis

of macroalgae by affecting electron transfer, pigment synthesis, and/or the activity of enzymes associated with carbon utilization (Xu et al., 2014; Wu et al., 2018; Dudgeon and Kübler, 2020; Eismann et al., 2020). In this study, a higher culture light level induced a greater maximum net photosynthesis rate, which indicated a higher photosynthetic capacity, and ultimately contributed to the higher growth rate of *S. muticum*.

The apparent photosynthetic efficiency (α) is regarded as the indication of efficiency of the alga to utilize light energy under limited light intensity (Eilers and Peeters, 1988). In this study, α showed the highest value in middle light culture of



60 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ and comparatively decreased in high light culture of 300 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. Moreover, the value of F_v/F_m also decreased in high light culture, suggesting that *S. muticum* thalli suffered from light stress in the high light culture of 300 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. Such findings may be explained by the reduction of photosynthetic pigments in the high light culture compared with low and middle light culture. Algae can alter the contents of reaction center and light-harvesting pigments to adapt to different culture light intensities (Makarov, 2012). Previous studies have shown that high light

intensity may reduce the photosynthetic pigment yields of algae in minutes [reviewed by Eismann et al. (2020)]. Photopigments, particularly light-harvesting pigments, usually play an important role in photoprotection and are damaged first under the high light stress, resulting in the reduction of contents (Xu and Gao, 2012; Quintano et al., 2019). However, in this study, the decrease induced by high light was not found in the growth rate and P_{max} of *S. muticum*. The possible explanation could be that the light stress at 300 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ did not damage the reaction center protein owing to the protection by its pigments, or the improved repair rate was enough to alleviate such photodamage to the reaction center (Murata et al., 2007; Zhang et al., 2020). As indirect evidence, the elevated dark respiration rate in the high light culture at 300 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ is likely to provide sufficient energy to repair the damage of photosynthetic reaction center in *S. muticum* (Xu and Gao, 2009, 2012).

Excessive light energy generally leads to the damage of photosynthesis reaction center of algae, and such a deleterious effect is often counteracted by the protective strategies of algae, such as the accumulation of photoprotective compounds, repair mechanisms, and the removal of reactive oxygen species (Bonomi-Barufi et al., 2020; Zhang et al., 2020). In the case that damage exceeds protection, the algae will reduce their evolution of photosynthetic oxygen, which is designated “photoinhibition” (Murata et al., 2007). In this study, the irradiance saturation point of oxygen E_k was $\sim 300 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ with no significant difference in all six treatments of different light and nitrogen levels. Beyond this irradiance point, the rate of evolution of photosynthetic oxygen of algae decreased drastically with the increase in light intensity, i.e., photoinhibition was induced in *S. muticum*. In contrast, many species of macroalgae have light saturation points at $\sim 600 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Xu and Gao, 2012; Xu et al., 2014). Especially, *S. horneri*, a golden tide species, did not exhibit photoinhibition even at a light level of 600 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, and it maintained enhanced photosynthetic and growth rates with the increase in light intensity (Liu et al., 2019). In the north temperate zone, which is inhabited by *S. muticum* and *S. horneri*, the daily mean irradiance of sea surface is approximately 300–800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ during the spring, summer, and autumn (Rumyantseva et al., 2019), the seasons in which golden tides have been observed. At such light levels, compared with *S. horneri*, drifting *S. muticum* is not prone to form a golden tide owing to the induction of photoinhibition.

Nitrogen is an essential nutrient for the survival and growth of algae, and an increased supply of nitrogen generally results in the promotion of growth rate in algae, owing to enhanced photosynthesis (Gao et al., 2018; Liu et al., 2019; Jiang et al., 2020). Such enhanced growth rates by N were also found in three golden tide species: *S. horneri* (Yu et al., 2019), *S. natans* and *S. fluitans* (Wang et al., 2019). The fact that enhanced photosynthesis induced by high nitrogen is usually attributed to an enhanced electron transfer rate, pigment content, or enzyme activity associated with carbon fixation (e.g., RUBISCO and carbonic anhydrase among others) in the photosynthetic system of algae (Giordano et al., 2005; Xu et al., 2014; Gao et al., 2018; Liu et al., 2019; Rugiu et al., 2020). In this study, high nitrogen enhanced the growth rate of *S. muticum* cultured at

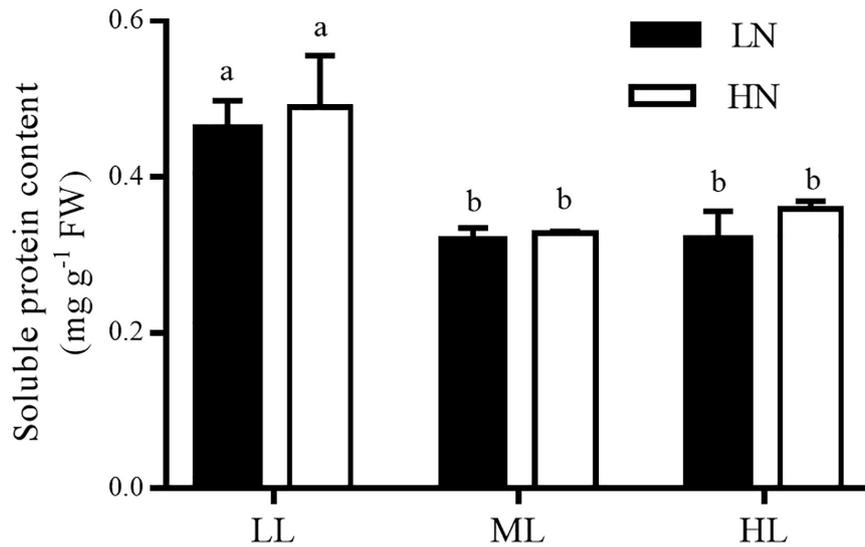


FIGURE 5 | Content of soluble proteins in *S. muticum* grown at different light and nitrogen levels for 12 days. Significant ($P < 0.05$) differences among the treatments are indicated by different lowercase letters. Vertical bars represent \pm SD for the means of three samples.

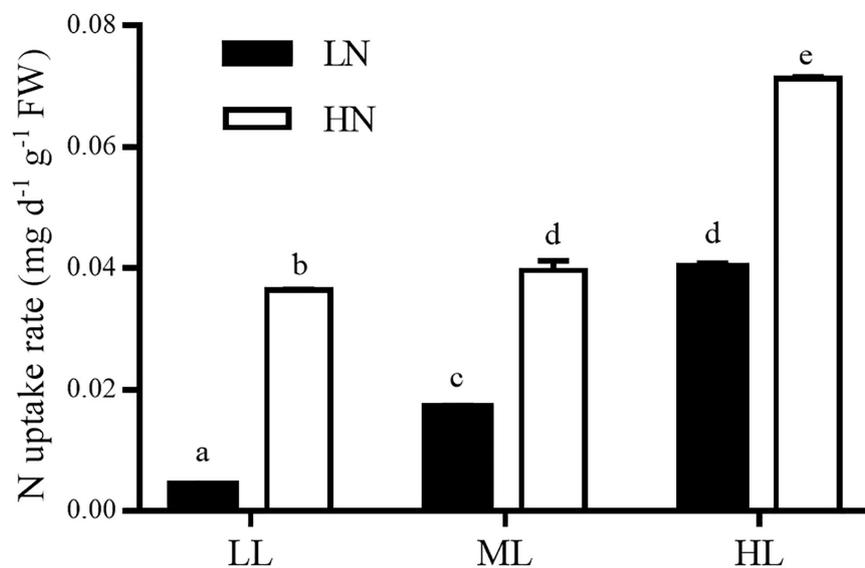


FIGURE 6 | Nitrogen uptake rates of *S. muticum* grown at different light and nitrogen levels, which were determined during 2 days at the end of 12 days of incubation. Significant ($P < 0.05$) differences among the treatments are indicated by different lowercase letters. Vertical bars represent \pm SD for the means of three samples.

three light levels. Correspondingly, the photosynthesis of thalli was increased by culture in high nitrogen, reflected by the increased “ P_{max} ” at low light and increased “ α ” at middle and high light levels. Such findings were consistent with previous reports in other species of macroalgae, including *Ulva prolifera*, *S. horneri*, *Gracilariopsis lemaneiformis*, *Saccharina latissima*, etc., (Xu et al., 2014; Liu et al., 2019; Yu et al., 2019; Jiang et al., 2020; Rugiu et al., 2020). Moreover, in the case of an adequate supply of nitrogen, the macroalgae can rapidly absorb it to supply the demand for nitrogen for growth and other physiological

processes (Xu and Gao, 2012; Jiang et al., 2020), and excessive nitrogen may be stored in cells as nitrogen pools in the forms of pigments, soluble proteins, and/or amino acids (Teichberg et al., 2010; Yu et al., 2019; Jiang et al., 2020). In this study, a high supply of nitrogen induced a high rate of nitrogen uptake in *S. muticum*, while neither the contents of pigments nor soluble proteins were affected by the high nitrogen treatment. Therefore, we hypothesized that the greater amounts of nitrogen absorbed in the high nitrogen culture contributed to the higher rates of photosynthesis and growth in *S. muticum*. In addition, a higher

acquisition of nitrogen may be used to improve the capability of the algae to endure high light stress (Murata et al., 2007; Xu and Gao, 2012), which was reflected by the lower “*a*” value of the photoinhibition term in *S. muticum* cultured under high nitrogen conditions.

CONCLUSION

Sargassum muticum is naturally distributed in the rocky shores of the Western Pacific North and has been colonized to the Northern European and North American coasts as an invasive species (Sánchez and Fernández, 2018; Belattmania et al., 2020). Owing to the concern that this species could form a golden tide (Álvarez-Canali et al., 2021), we investigated its physiological responses to different light and nitrogen levels in this study. Our results showed that higher light and/or nitrogen levels generally promoted the photosynthesis and growth of the algae. However, when the intensity of light exceeded 300 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, its photosynthesis was inhibited, regardless of nitrogen conditions set in this study. Based on these findings, we hypothesized that the lower value of irradiance saturation point resulted in drifting individuals of *S. muticum* that were unable to tolerate the light intensity of sea surface on sunny days (Rumyantseva et al., 2019). Therefore, for this *Sargassum* species, it would not easily form a golden tide, compared with *S. horneri*. However, when encountered a sustained suitable light level ($\leq 300 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$), it would also be possible for the drifting individuals of *S. muticum* to form a golden tide due to its

rapid growth rate ($\sim 8\% \text{ d}^{-1}$ at light level of 300 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$). And a high supply of nitrogen might facilitate this process.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding authors.

AUTHOR CONTRIBUTIONS

FY and LL conceived and designed the experiment with help from ZX and HW. FY carried out the experiment, with help from LL and DY. FY and LL performed the data analyses, with help from DY, CC, and SZ. FY wrote the manuscript with contributions from LL, DY, CC, SZ, ZX, and HW. All authors reviewed and gave their approval for the final manuscript.

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