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The photosynthetic and respiratory responses to temperature and nitrogen supply in the marine green macroalga *Ulva conglobata* (Chlorophyta)

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Abstract: Temperature effects on photosynthesis and respiration were investigated in the green macroalga, *Ulva conglobata*, collected from low rocky coast of Nanao Island, Shantou, China. Thalli were cultured at 15 and 25°C and at low nitrogen (LN) and high nitrogen (HN) availability. Dark respiration and light-saturating photosynthesis were measured as oxygen exchange; the characteristics of chlorophyll fluorescence were also assayed. The maximal photochemical yield (F_v/F_m) and maximum relative electron transport rates ($rETR_{max}$) remained stable with moderate fluctuations of temperature (15–30°C) in the short term. However, the values of F_v/F_m and $rETR_{max}$ declined with the high temperature ($\geq$ 35°C), and such a decline was more accentuated in 15°C- than 25°C-grown algae. Both the rates of photosynthesis and respiration were sensitive to measurement temperature, with the Q_{10} values being higher in 25°C-grown algae (HN) than 15°C-grown algae. It appeared that 25°C-grown algae displayed an optimum temperature (T_{opt}) of 30°C for photosynthesis, while 15°C-grown algae exhibited the T_{opt} of a range of 20–30°C. When measured at their respective growth temperature, the rates of photosynthesis were significant higher in 25°C- than 15°C-grown algae, while the rates of respiration were identical between 25°C- and 15°C-grown algae. Our results demonstrated that respiration displayed full acclimation; whereas, photosynthesis exhibited partial acclimation to changing growth temperatures in *U. conglobata*. Consequently, the balance between respiration and gross photosynthesis was re-established by changing growth temperature, with the ratio being lowered with warmer growth temperature. The results also showed that HN availability in culture significantly increased pigments and soluble protein contents and enhanced photosynthesis and respiration. We suggested that the acclimation potential of metabolisms in *U. conglobata* favored carbon acquisition and net carbon balance with the increasing seawater temperature resulting from climate change and/or increasing N loading from coastal eutrophication.

Key Words: Acclimation, Carbon balance, Marine macroalgae, Nitrogen, Photosynthesis, Respiration, Temperature, *Ulva conglobata*

INTRODUCTION

Temperature is a major determinant of the biogeographical distribution of marine macrophytes (Van den Hoek *et al*. 1990; Wernberg *et al*. 2003). Additionally, the significant effects of temperature on molecular movements and biochemical reactions make it a principal component among the environmental factors controlling the metabolic rates (Davison 1991). Despite the relative thermal homogeneity of the marine environment, temporal and regional variation in water temperature can be considerable. At the same time, climatic changes predicted for the next century include a continued warming of near-surface air temperatures, on the order of 2–7°C, with regional, seasonal, and diurnal heterogeneity (Christensen *et al*. 2007), which results in increasing temperature of surface ocean. Marine macroalgae may therefore experience significant changes of temperature both in the short and the long term (Davison 1991; Davison & Pearson 1996).

Temperature-mediated changes in photosynthesis and respiration are important components of coastal ecosystem responses to global climate change because a change of temperature can result in an immediate change in the rates of metabolic processes. Furthermore, marine macroalgae can usually adapt to temperature fluctuations with a high, genetically fixed potential for photosynthetic acclimation, which enables them to tune their metabolism in harmony with the prevailing temperature conditions caused by seasonal and/or latitudinal variation (e.g. Davison 1991; Terrados & Ros 1992; Stengel & Dring 1998; Campbell *et al*. 1999; Zou & Gao 2005). Marine macroalgae growing under colder environments frequently achieve their higher photosynthetic rates at lower temperatures and/or display lower optimum temperatures than those growing under warmer environments (e.g. Davison *et al*. 1991; Kübler *et al*. 1991; Kübler & Davison 1995; Eggert *et al*. 2006; Staehr & Wernberg 2009).

Because carbon and nitrogen metabolisms are closely coordinated (Turpin 1991; Huppe & Turpin 1994), the nutritional status of the algae, which may vary significantly between habitat sites and/or seasons, would markedly influence the scope of photosynthetic and respiratory processes in response to temperature changes (Raven & Geider 1988; Turpin 1991; Huppe & Turpin 1994). The concentration of inorganic nitrogen (N) is one of the factors that most frequently limits marine macroalgal productivity in natural seawater (Smith 1984; Lobban & Harrison 1997). Human agricultural and industrial activities have increased

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inorganic nutrient inputs into many coastal waters, leading to eutrophication (Druon *et al*. 2004). It has been well established that increased N availability affects the marine algal photosynthetic performances (e.g. Huppe & Turpin 1994; Gerard 1997; Andría *et al*. 1999; Gordillo *et al*. 2001, 2003; Zou *et al*. 2011). Therefore, possible effects of rising temperatures must incorporate nutrients as a prominent controlling factor (e.g. Rivers & Peckol 1995; Gerard 1997).

Here we report the responses of photosynthesis and respiration to temperature in a green macroalga, *Ulva conglobata* Kjellm (Chlorophyta), collected from the shoreline of Nanao Island, Shantou, China. *Ulva* species is commonly found along the intertidal and subtidal regions throughout the world. The species of *U. conglobata* thrives in the mid-intertidal to upper subtidal zones along the coasts of Nanao Island. The objectives of this study were to (1) examine the photosynthetic and respiratory performances regarding the changing temperature in both the short (instantaneous) and the long (growth) term and to examine the extent of acclimation of photosynthesis and respiration achieved in thalli exposed to a varied moderate growth temperatures (i.e. 15–25°C), (2) measure acclimation of photosynthesis and respiration with different amounts of N availability, and (3) determine how the balance between the respiration and photosynthesis respond to instantaneous change of temperature and address whether acclimation reestablishes the balance. We measured thalli respiratory and photosynthetic rates at seven different temperatures on the algae grown at 15 and 25°C, and at low nitrogen (LN) and high nitrogen (HN) availability. In each case, respiration rates were measured in darkness, and photosynthesis on the same algal thalli was measured at saturating irradiances and at the same temperatures.

MATERIAL AND METHODS

Thalli of *Ulva conglobata* were collected at low rocky shore along the coast of Nanao Island, Shantou, China (23°20′N, 116°40′E) and gently rinsed to remove sediments and epiphytes. Only unwounded and healthy thalli were selected. Thalli were transported to the laboratory within 4 h using an insulated cooler (4–6°C) to minimize metabolic activity. The algae were then maintained in filtered natural seawater (salinity *c*. 32) in Plexiglas aquaria under about 180 μmol photons m^{-2} s^{-1} (PAR, LD cycle 12 h:12 h) provided by cool-white fluorescent lamps and at 20 ± 0.5°C (corresponding to the ambient surface seawater temperature at the site of collection over the sampling period). The seawater was continuously aerated and renewed every other day. Thalli were used in the experimental growth treatments within 7 d of maintenance.

Thalli were cultured at 15 and 25°C, using LN and HN. Experimental treatments were started when 2.5 g of algal fresh weight (FW) were introduced into each of 12 Erlenmeyer flasks containing 5 liters of filtered seawater. The flasks were placed into two controlled environment chambers (Model EF7; Conviron, Winnipeg, Canada), operated at 15 and 25°C, respectively. The light intensity and light period were identical for all treatments as indicated above. In each chamber, three flasks contained non–N-supplemented filtered natural seawater (LN availability, total inorganic N concentration < 10 μM), and the remainder ($n = 3$) contained 200 μM NO_3 nitrogen supplemented filtered natural seawater (HN availability). For all of the treatments, the seawater was supplemented 20 μM $H_2PO_4^-$. The seawater was vigorously bubbled with ambient atmospheric air and was changed every three days because N became < 100 μM in the HN treatments.

Chlorophyll fluorescence was measured with a portable pulse modulation fluorometer (Water-PAM; Walz, Eiffeltrich, Germany). Thalli were mounted at the end of the fibre optic probe and inserted into a temperature controlled, custom-made cuvette filled with seawater. Four to six replicates were measured for each algal treatment. Before measurement, the algal samples were allowed to equilibrate for about 15 min at each measurement temperature (10, 15, 20, 25, 30, 35 and 40°C).

The photosynthetic efficiency of photosystem (PS) II (dark-adapted for 5 min) was determined as F_v/F_m (Schreiber *et al*. 1995), where F_v indicates the variable fluorescence ($F_v = F_m - F_o$). A saturating white light pulse (*c*. 6000 μmol photons m^{-2} s^{-1}) was applied to measure the maximal chlorophyll fluorescence (F_m, indicating the fluorescence yield when all the PS II reaction centers are closed), and the initial fluorescence (F_o) was attained at a pulsed measuring light of about 0.15 μmol photons m^{-2} s^{-1}. The rapid light curves, consisting of the fluorescence response to increasing actinic irradiance levels over the range of 0–2200 μmol m^{-2} s^{-1}, of the algal samples were obtained using the 'light curve' option of the Water-PAM (White & Critchley 1999; Ritchie 2008). The exposure time at each actinic irradiance was 15 s, each separated by a 0.8-s saturating flash. The maximum relative electron transport rate ($rETR_{max}$) was calculated following the model equation from Jassby and Platt (1976): $rETR = rETR_{max} \times \tanh(\alpha \times I / rETR_{max})$, where rETR is the relative electron transport rate at a given incident irradiance (I), tanh is the hyperbolic tangent function and α is the initial slope of the rapid light curves (i.e. the efficiency of the electron transport).

Photosynthetic and respiratory rates were measured as oxygen exchange using a Clark-type oxygen electrode (YSI Model 5300; YSI Inc., Yellow Springs, Ohio, USA). The oxygen electrode was held in a circulating water bath (Cooling Circulator; Cole-Parmer Inc., Vernon Hills, Illinois, USA) to keep the desired measurement temperature. Measurements were initiated after at least 2 h of photosynthesis in the growth chambers. Thalli were cut into small segments (*c*. 0.5–0.8 cm^2) with a sharp razor blade and incubated in seawater at the identical culture treatment and identical light-temperature conditions for at least 2 h. This pretreatment aimed to minimise the possible effect of cutting damage in segments cells (wound respiration) on the respiratory and/or photosynthetic measurements.

To examine temperature effects on respiratory and photosynthetic flux (the instantaneous responses of the rates to temperature), respiratory and photosynthetic rates were measured at different temperatures (10, 15, 20, 25, 30, 35 and 40°C) by adjusting the temperature in the O_2 electrode chamber. The rates were measured consecutively, commencing at the lowest and ending at the highest water temper-

Table 1. Total chlorophyll (Chl $a+b$), soluble protein (SP) and soluble carbohydrates (SC), and the Chl $a/(a+b)$ ratios for *Ulva conglobata* grown at 15°C and 25°C using LN and HN. Data are means (± s), $n = 3$–6.

	15°C		25°C	
	Low N	High N	LN	HN
Total Chl (μg g^{-1} FW)	241.7 ± 32.3	951.2 ± 42.9	191.0 ± 5.9	1536.6 ± 109.9
Chl $a/(a+b)$ ratio	0.53 ± 0.03	0.55 ± 0.01	0.51 ± 0.01	0.57 ± 0.01
SP (mg g^{-1} FW)	2.00 ± 0.15	3.44 ± 0.76	2.14 ± 0.35	3.77 ± 0.55
SC(mg g^{-1} FW)	43.67 ± 1.41	37.25 ± 1.88	45.23 ± 0.29	41.54 ± 4.35

ature.The algal samples were allowed to equilibrate for about 15 min at each measurement temperature before the respiratory and photosynthetic rates were taken. Moreover, the O_2 electrode was recalibrated for each measurement temperature. About 0.2 g algal FW was transferred to the O_2 electrode cuvette containing 8 ml of reaction medium that was magnetically stirred. Respiration was recorded at darkness when the O_2 uptake stabilized, usually within 4–8 min. Immediately following the respiration measurement, the irradiance-saturated net photosynthetic rates were determined (within 4–6 min) at the irradiance of 500 μmol photons m^{-2} s^{-1} and the same temperature as R_d measurement. Preliminary experiments showed that the photosynthesis was sufficiently saturated, and no photoinhibition occurred.

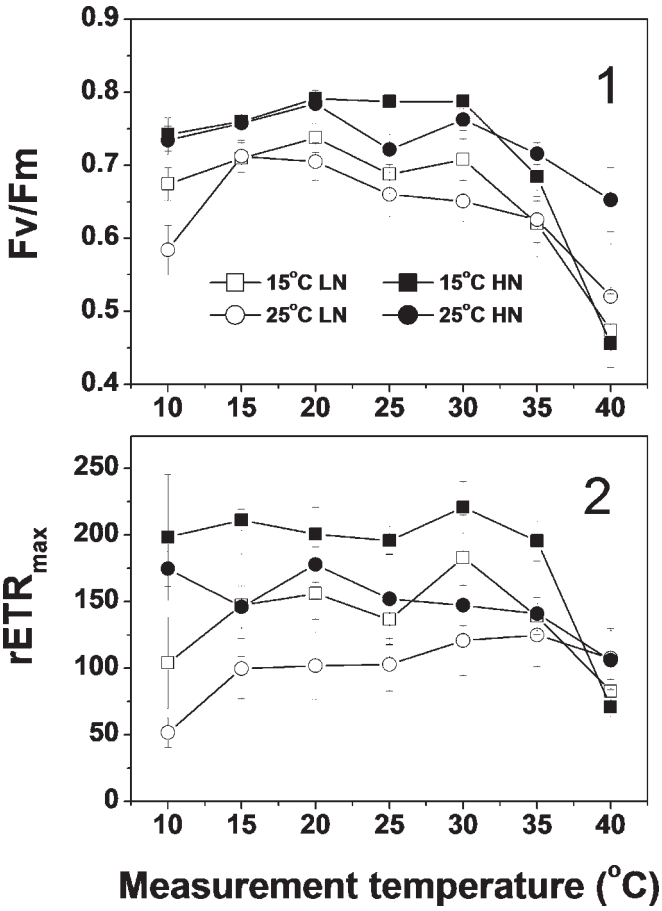
To determine chlorophyll concentrations (Chl *a* and *b*), about 0.2 g FW per sample was extracted in 100% acetone. The concentration of Chl *a* and *b* was calculated spectrophotometrically using the equation given by Jensen (1978). For soluble protein (SP) determination, samples of about 0.2 g algal FW were placed in 5 ml of 0.1 M phosphate buffer (pH 6.8), homogenized at 4°C using a mortar and pestle (with a little acid-washed sand) and rinsed with 5 ml of buffer. The extracts were then centrifuged at 5000 × *g* for 20 min. The supernatants were used for the spectrophotometrical measurement of SP contents using the Coomassie Blue G-250 method (Bradford 1976). Soluble carbohydrates (SC) contents were measured colorimetrically according to Kochert (1978) using the phenol sulphuric acid method for color development and glucose as standard.

Q_{10} values, that is, the proportional change in the rate of respiration per 10°C rise, were calculated using the following equation according to Atkin and Tjoelker (2003): $Q_{10} = 10^{(\text{slope}-10)}$, where the slope is the regression slope of a $\log_{10}$-transformed respiratory (or photosynthetic) rates vs temperatures plot. Apparent activation energy (E_a) for photosynthesis and respiration were calculated from the slopes of the linear potions of the Arrhenius plots ($\log_{10}$ photosynthetic or respiratory rates against the reciprocal of the absolute temperature).

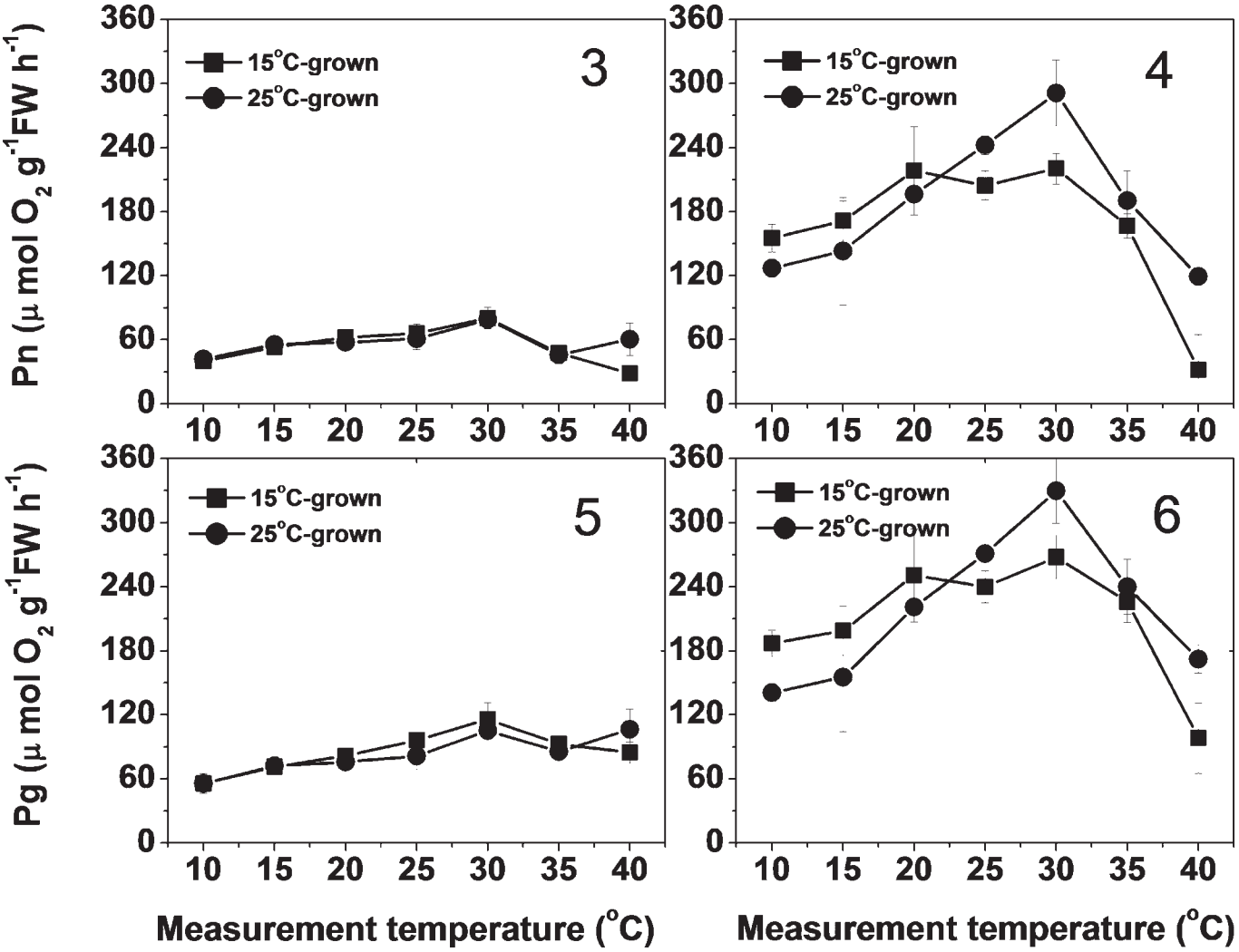
The data plotted on graphs were mean values with standard deviations (s; $n \geq 3$). Statistical tests were conducted with SPSS for Windows version 13.0 with the significance level being set at $P < 0.05$. Data were analysed using analysis of variance and linear and stepwise regression. To compare means, Fisher's least significant difference *post hoc* test and Student's *t* test were used if necessary.

RESULTS

Growth temperature displayed a less pronounced effect on the biochemical components in *Ulva conglobata* thalli than the N supply level (Table 1). SP and SC content were not significantly different at the two growth temperatures ($P > 0.05$). Warmer growth conditions decreased cellular chlorophyll (Chl $a+b$) in LN-grown algae ($P < 0.05$) but increased Chl contents in HN algae ($P < 0.01$). The addition of N significantly increased the contents of Chl and SP ($P < 0.01$);



Figs 1, 2. *Ulva conglobata*.
Fig. 1. Maximum photochemical yield (F_v/F_m) as a function of measuring temperature at 15°C and 25°C and at LN and HN. Vertical bars represent ± s ($n = 6$).
Fig. 2. Maximum relative electron transport rates ($rETR_{max}$) as a function of measuring temperature in thalli grown at 15°C and 25°C and at LN and HN. Vertical bars represent ± s ($n = 6$).



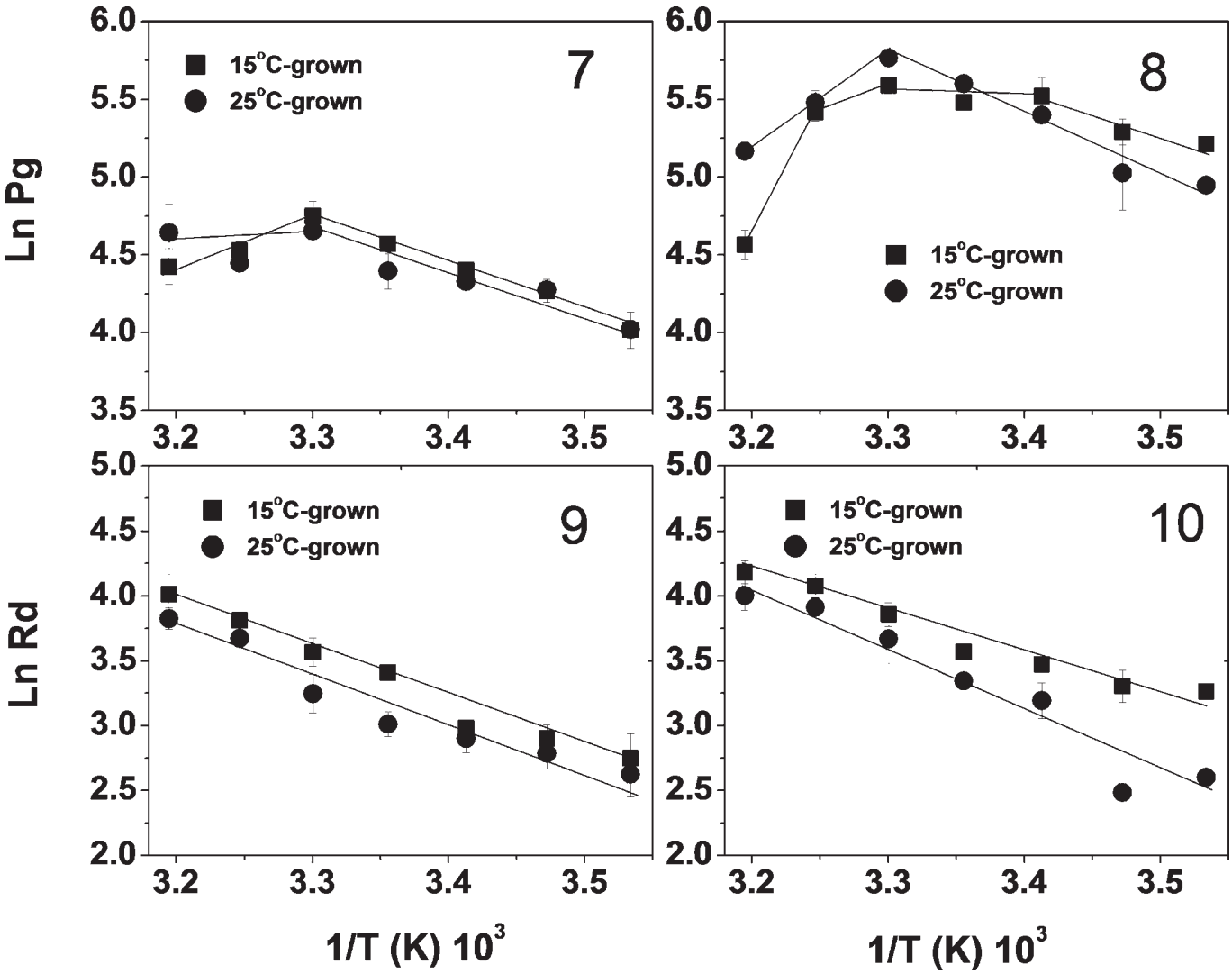
Figs 3–6. *Ulva conglobata*.
Fig. 3. Net photosynthesis (P_n) as a function of measuring temperature grown at 15°C and 25°C and at LN. Vertical bars represent ± *s* ($n = 3$).
Fig. 4. Net photosynthesis (P_n) as a function of measuring temperature at 15°C and 25°C and at HN. Vertical bars represent ± *s* ($n = 3$).
Fig. 5. Gross photosynthesis (P_g; i.e. P_n plus dark respiration) as a function of measuring temperature at 15°C and 25°C and at LN. Vertical bars represent ± *s* ($n = 3$).
Fig. 6. Gross photosynthesis (P_g; i.e. P_n plus dark respiration) as a function of measuring temperature at 15°C and 25°C and at HN. Vertical bars represent ± *s* ($n = 3$).

whereas, it decreased the contents of SC for 15°C-grown algae ($P < 0.01$).

Figures 1 and 2 illustrated the maximal photochemical yield (F_v/F_m) and maximum relative electron transport rates ($rETR_{max}$) as a function of measuring temperature for *U. conglobata* grown at different treatments. Compared with 15°C-grown algae, algae grown at 25°C exhibited lower values of both F_v/F_m and $rETR_{max}$ at their respective growth temperature ($P < 0.05$). By contrast, F_v/F_m and $rETR_{max}$ were significantly greater in HN algae than LN algae ($P < 0.01$). Overall, the values of both F_v/F_m and $rETR_{max}$ remained relatively unchanged with the measuring temperatures, except that F_v/F_m and $rETR_{max}$ displayed low values at a measurement temperature of 10°C for the LN algae. The values of F_v/F_m and $rETR_{max}$ declined with the high temperature (35–40°C), and such a decline was more accentuated in 15°C-grown algae with respect to 25°C-grown algae (Figs 1, 2).

Growth temperature, N supply and measurement temperatures significantly affected net photosynthesis (Figs 3, 4) and gross photosynthesis (Figs 5, 6). N additions strongly increased photosynthesis. The rate of P_n was increased by 2.2 times at 15°C and by 3.0 times at 25°C for HN relative to LN (Figs 3, 4).

Under LN, photosynthetic rates (either P_n or P_g; i.e. P_n plus dark respiration) were similar at 15°C and 25°C ($P > 0.05$; Figs 3, 5). Photosynthetic rates increased gradually with increasing temperature until they reached a maximum at an optimum temperature (T_{opt}) of 30°C, after which rates declined. The respective Arrhenius plot of the rates of P_g was generally linear over the temperature range of 10–30°C; however, thalli grown at 15°C and HN had an Arrhenius



Figs 7–10. *Ulva conglobata*.
Fig. 7. Arrhenius plots for gross photosynthesis (P_g; Ln P_g rates vs reciprocal of absolute temperature) at 15°C and 25°C and at LN. Vertical bars represent ± *s* ($n = 3$).
Fig. 8. Arrhenius plots for gross photosynthesis (P_g; Ln P_g rates vs reciprocal of absolute temperature) at 15°C and 25°C and at HN. Vertical bars represent ± *s* ($n = 3$).
Fig. 9. Arrhenius plots for respiration (R_d; Ln R_d rates vs reciprocal of absolute temperature) 15°C and 25°C and at LN. Vertical bars represent ± *s* ($n = 3$).
Fig. 10. Arrhenius plots for respiration (R_d; Ln R_d rates vs reciprocal of absolute temperature) at 15°C and 25°C and at HN. Vertical bars represent ± *s* ($n = 3$).

plot with a break at 20°C (Figs 7–10). The calculated apparent E_a values of P_g were similar between 15°C- and 25°C-grown algae under LN growth conditions ($P > 0.05$); however, the apparent E_a values were significantly higher at 25°C than 15°C under HN conditions ($P < 0.01$; Table 2).

Photosynthesis vs temperature responses at HN revealed a different response than at LH. Under HN, the rates of P_n or P_g were greater at 15°C than at 25°C at a low measurement temperature of 10°C (Figs 4, 6). There was no significant difference in the rates of photosynthesis between the algae grown at 15°C and 25°C when the measurement temperature rose to 15–20°C. At higher measuring temperatures (≥ 25°C), 25°C-grown algae revealed higher photosynthetic rates than 15°C-grown algae. It appeared that 25°C-grown algae displayed a T_{opt} of 30°C for photosynthesis, while 15°C-grown algae exhibited the T_{opt} of a range of 20–30°C (Figs 4, 6).

When photosynthesis was measured at its respective growth temperature (i.e. *in situ* temperature), the rates of P_n (or P_g) were similar between the 15°C- and 25°C-grown algae under LN growth condition ($P > 0.05$); whereas, under the HN growth condition, the rates were dramatically greater in 25°C-grown algae than 15°C-grown algae ($P < 0.01$; Figs 3–6).

The instantaneous temperature responses of R_d for all the growth treatments revealed a characteristic exponential increase with increasing temperature over the tested range of 10–40°C (Figs 11, 12). The Q_{10} values of R_d were generally

Table 2. The calculated apparent activation energy (E_a expressed as KJ mol^{-1}) and Q_{10} value (the rate increase caused by raising temperature 10°C) for dark respiration (R_d) and gross photosynthesis (P_g) in *Ulva conglobata* grown at 15°C and 25°C using LN and HN. Values are means ± *s* ($n = 3$).

	R_d		P_g	
Growth conditions	E_a	Q_{10}	E_a	Q_{10}
LN, 15°C	32.5 ± 4.9[1]	1.56 ± 0.14[1]	25.2 ± 4.4[2]	1.43 ± 0.12[2]
LN, 25°C	29.9 ± 4.6[1]	1.51 ± 0.13[1]	19.8 ± 1.0[2]	1.32 ± 0.03[2]
HN, 15°C	24.6 ± 1.1[1]	1.40 ± 0.03[1]	21.2 ± 5.6[3]	1.37 ± 0.16[3]
HN, 25°C	39.7 ± 1.9[1]	1.72 ± 0.06[1]	31.6 ± 4.1[2]	1.55 ± 0.13[2]

[1] 10–40°C temperature range.
[2] 10–30°C temperature range.
[3] 10–20°C temperature range.

around 1.5 for all the growth treatments; however, the HN algae grown at 25°C had a $Q_{10} = 1.7$ (Table 2). The Arrhenius plots of the rates of R_d were linear (Figs 7–10). Like P_g, under HN growth conditions, the apparent E_a of R_d was significantly higher at 25°C than 15°C ($P < 0.01$; Table 2).

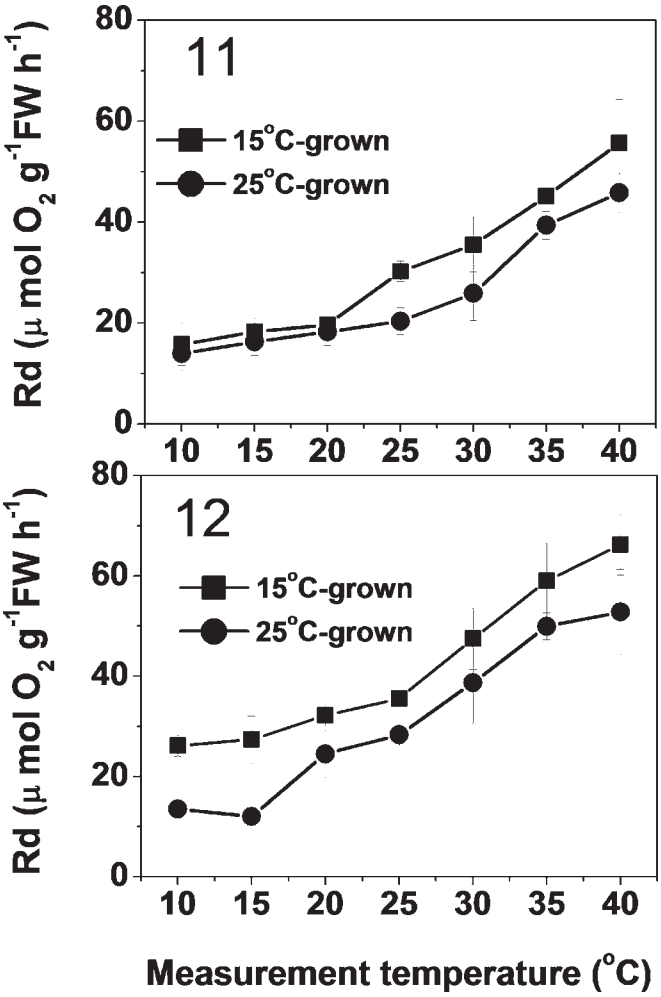
Generally, the rates of R_d were higher at 15°C than at 25°C for both N growth conditions (Figs 11, 12); however, under LN, little difference in the rates of R_d was observed. The addition of N significantly enhanced respiration at 15°C and 25°C ($P < 0.01$). Comparing HN and LN, the rate of R_d increased by 50% for 15°C-grown algae and by 39.1% for 25°C-grown algae under HN (Figs 11, 12).

As a consequence of temperature elevation from 15°C to 25°C, the instantaneous temperature responses of R_d showed that the rate was increased by 65.8% (for LN), or by 29.8% (for HN). However, when R_d was measured at its respective growth temperature (i.e. *in situ* temperature), the rates of R_d were similar between 15°C and 25°C regardless of the N growth condition ($P > 0.1$; Figs 11, 12). This strongly indicated the full acclimation of R_d (thermal homeostasis) across the 15–25°C range, and N status did not affect the thermal acclimation potential of R_d.

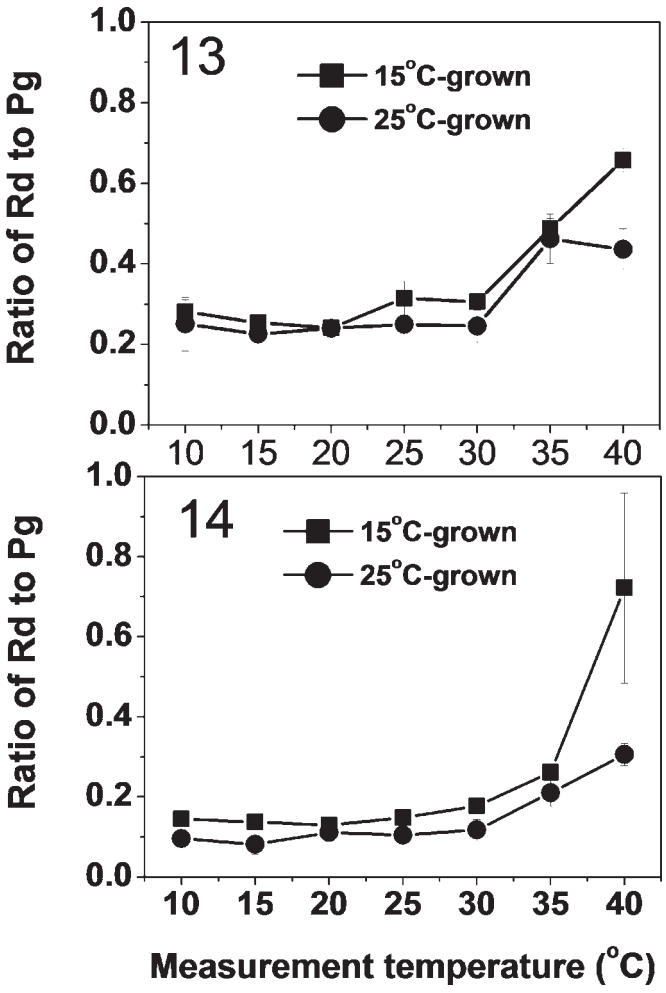
The R_d was mostly between 0.10 and 0.25 of P_g across the different growth conditions and temperatures. Overall, the R_d/P_g ratios remained unchanged with the increasing temperature within 10–30°C (Figs 13, 14), but the ratios increased dramatically at above 35°C. This was the consequence of increased R_d and, simultaneously, declining P_g at a high measuring temperature. There was no significant difference in the R_d/P_g ratio between the algae grown at 15°C and 25°C ($P > 0.05$). However, HN algae exhibited a considerable decline in the R_d/P_g ratio relative to LN algae ($P < 0.01$; *c*. 0.11 vs *c*. 0.25; Figs 13, 14). Although N enhanced both photosynthesis and respiration, photosynthesis was much more pronounced.

DISCUSSION

Nitrogen stress affects photosynthesis through impacts on pigment synthesis, thylakoid stacking and absorbtivity, and Calvin cycle enzymes (Turpin 1991; Huppe &Turpin 1994). Our results showed that, compared to LN experiments, HN-grown *U*. *conglobata* exhibited higher pigment and protein content, higher F_v/F_m and $rETR_{max}$ values and higher photosynthetic rates, which are consistent with many previous studies (e.g. García-Sânchez *et al*. 1993; Jimenez del Rio *et al*. 1995; Gerard 1997; Andría *et al*. 1999; Gordillo *et al*. 2001, 2003; Zou *et al*. 2011). Additionally, the respiratory rate was higher in HN algae than LN algae,



Figs 11, 12. *Ulva conglobata*
Fig. 11. Dark respiration (R_d) as a function of measuring temperature at 15°C and 25°C and at LN. Vertical bars represent ± *s* ($n = 3$).
Fig. 12. Dark respiration (R_d) as a function of measuring temperature at 15°C and 25°C and at HN. Vertical bars represent ± *s* ($n = 3$).



Figs 13, 14. *Ulva conglobata*

Fig. 13. The ratios of dark respiration (R_d) to gross photosynthesis (P_g) as a function of measuring temperature at 15°C and 25°C and LN. Vertical bars represent ± *s* ($n = 3$).

Fig. 14. The ratios of dark respiration (R_d) to gross photosynthesis (P_g) as a function of measuring temperature at 15°C and 25°C and at HN. Vertical bars represent ± *s* ($n = 3$).

perhaps necessary to support higher maintenance demands (e.g. increased RuBisCO contents) and greater uptake and assimilation of extra N.

Moderate temperature change (from 15°C to 30°C) had no influence on the maximal quantum yield of PSII (F_v/F_m) and $rETR_{max}$, which suggests that *U. conglobata* temporarily accommodates excessive light energy, probably by adopting energy-dissipating mechanisms. In contrast, high temperatures ($\geq$ 35°C) resulted in a significant decrease of F_v/F_m and $rETR_{max}$, suggesting a high temperature-induced photoinhibition, a decrease in Calvin cycle activity and/or an enhancement of nonradiative dissipation of excitation energy. The decrease of F_v/F_m and $rETR_{max}$ at high temperatures indicates that 25°C -grown algae were less susceptible to high temperature–induced impairment of the photosynthetic apparatus.

Our results showed that both photosynthesis and respiration were very sensitive to the instantaneous change of temperature. This may suggest that under eutrophication and climate change scenarios, the metabolic rates of *U. conglobata* would be temperature sensitive. These results contrasted with terrestrial plant studies (Covey-Crump *et al.* 2002; Atkin & Tjoelker 2003) and phytoplankton, where exposure to a higher temperatures lowered the values of Q_{10} (Staehr & Birkeland 2006). However, our results agreed with other terrestrial plant studies (Loveys et al. (2003) and studies that showed that growth temperature has no systematic effect on the Q_{10} (Tjoelker *et al.* 2001).

Ulva conglobata thalli grown for longer periods at contrasting temperatures (15°C and 25°C) had identical rates of respiration when measured at their respective growth temperatures. In contrast to instantaneous temperature changes, long-term temperatures resulted in acclimation (or respiratory homeostasis). The net effect was an essentially flat response over a moderate range of temperatures (15–25°C). An increase in SC was previously suggested to be directly responsible for the subsequent recovery of respiration associated with acclimation to lower temperature through increased substrate availability (Atkin & Tjoelker 2003). However, our results showed that SC content was similar between cooler-grown and warmer-grown algae. An explanation for these findings could be that respiration was not substrate limited in cooler-grown algae. On the other hand, increases in respiration in cold-acclimated tissues may reflect reductions in the adenylate restriction of respiratory metabolism via increased rates of ATP turnover, increased ADP concentrations and/or uncoupling of electron transport from proton translocation across the inner mitochondrial membrane (Campbell *et al.* 2007).

The T_{opt} for P_g is usually used as an indicator for the degree of thermal acclimation (Berry & Björkman 1980; Li & Morris 1982; Sage & Kubien 2007; Stæhr & Wernberg 2009). In our study, the growth temperature affected the instantaneous response shape of photosynthesis to temperature such that P_g at 15°C reached a plateau (20–30 ° C); whereas, P_g at 25°C continued to increase up to a single T_{opt} point (30°C). The lower T_{opt} for cooler-grown algae reflected the photosynthetic acclimation to temperature.

Our results showed that realized rates of photosynthesis (measured at the respective growth temperature) became less temperature dependent than predicted from the instantaneous responses of photosynthesis to temperature over the moderate temperature range (15–25°C), suggesting the partial compensation by acclimation. For example, the rate of P_g at 25°C (HN) was reduced by 42.7% as a result of temperature decrease from 25°C to 15°C; alternatively, the rate was reduced by only 26.6% with prolonged growth at 15°C. Additionally, the rate of P_g at 15°C (LN) was increased by 35.0% as a result of elevation of temperature from 15°C to 25°C; however, the rate was increased by only 13.8% with prolonged growth at 25°C. This was in contrast with respiration, which was completely independent of growth temperature. The acclimation potential of photosynthesis has also been documented in many other macroalgal species (e.g. Davison 1991; Davison *et al.* 1991; Kübler & Davison 1995; Campbell *et al.* 1999; Zou *et al.* 2005; Stæhr and Wernberg 2009).

The Arrhenius plots displayed no break from 10°C to 40°C, suggesting the same rate-limiting steps for respiration at different temperatures. However, the break occurring in

the Arrhenius plots of P_g implied that photosynthesis suffered changes in temperature dependence of rate-limiting steps. Additionally, the results showed that the break in the Arrhenius plots of P_g occurred at 20°C in 15°C-grown algae, while that occurred at 30°C in 25°C-grown algae (HN). Previous studies suggested that growth at lower temperature might result in changes in thylakoid membrane fatty acid composition (Davison 1987, 1991; Vona *et al*. 2004). Changes in lipid composition might explain the break in the Arrhenius plots of the photosynthesis vs temperature relationship and also adjust the apparent activation energy (E_a) of the metabolic reactions (Laczko-Dobos & Szalontai 2009). Such changes in the E_a of potentially rate-limiting aspects of photosynthesis might also explain the differences in the Q_{10} of photosynthesis and/or respiration in *U. conglobata*.

The balance between respiration and photosynthesis is crucial for the carbon budget of individual algae. Our results showed that the R_d/P_g ratio was unchanged over the low to moderate temperature range. Our interpretation is that respiration and photosynthesis have similar temperature sensitivities (i.e. both processes had a similar value of Q_{10}). However, our results showed that R_d/P_g values increased substantially when the algae were exposed temperatures greater than those normally experienced in their natural environment ($\geq$ 35°C), with the increase in R_d/P_g being most pronounced at 15°C.

As consequence of the different acclimation responses of respiration and photosynthesis (i.e. full acclimation in respiration but partial acclimation in photosynthesis, with prolonged exposure to a new growth temperature), the balance between R_d/P_g was re-established, with the ratio being lowered in warmer growth temperature than cooler temperature. Additionally, our results showed R_d/P_g declined with HN and not LN growth conditions. These results suggest that, as temperatures increase over a moderate range and N increases, photosynthetic carbon fixation of *U. conglobata* will increase more rapidly than the rate of respiratory carbon loss. The lowered R_d/P_g ratio suggests that algae growing under higher temperatures and N will use less photosynthate as a respiratory substrate, which will lead to higher growth rates.

In summary, our results show that growth temperature changes might elicit an adjustment (partial acclimation response) of photosynthesis. Importantly, we demonstrated that respiration would display full acclimation to changing growth temperatures in *U. conglobata*. This indicates that respiration probably will not be stimulated significantly if moderate seawater temperature increases occur. In contrast, the photosynthetic carbon uptake would be enhanced by moderately increased temperatures. While high N availability significantly enhanced the rates of both photosynthesis and respiration, our results show that it did not affect the acclimation potential for both metabolisms. *Ulva conglobata* thalli grown under the combined higher temperature (25°C) and HN exhibited a higher temperature sensitivity (i.e. higher Q_{10} value). We suggest that the acclimation potential in *U. conglobata* will favor carbon acquisition and net carbon balance with increasing seawater temperature and/or increasing N levels.

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