Acta Oceanologica Sinica 2005, Vol. 24, No. 3, p. 105~113
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Ecophysiological characteristics of four intertidal marine macroalgae during emersion along Shantou coast of China, with a special reference to the relationship of photosynthesis and CO_2

ZOU Dinghui[1], GAO Kunshan[1,2*]

1. Marine Biology Institute, Science Center, Shantou University, Shantou 515063, China
2. Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China

Received 1 September 2004; accepted 15 March 2005

Abstract

Intertidal marine macroalgae experience periodical exposures during low tide due to their zonational distribution. The duration of such emersion leads to different exposures of the plants to light and aerial CO_2, which then affect the physiology of them to different extents. The ecophysiological responses to light and CO_2 were investigated during emersion in two red algae *Gloiopeltis furcata* and *Gigartina intermedia*, and two brown algae *Petalonia fascia* and *Sargassum hemiphyllum*, growing along the Shantou coast of China. The light-saturated net photosynthesis in *G. furcata* and *P. fascia* showed an increase followed by slightly desiccation, whereas that in *G. intermedia* and *S. hemiphyllum* exhibited a continuous decrease with water loss. In addition, the upper-zonated *G. furcata* and *P. fascia*, exhibited higher photosynthetic tolerance to desiccation and required higher light level to saturate their photosynthesis than the lower-zonated *G. intermedia* and *S. hemiphyllum*. Desiccation had less effect on dark respiration in these four algae compared with photosynthesis. The light-saturated net photosynthesis increased with increased CO_2 concentrations, being saturated at CO_2 concentrations higher than the present atmospheric level in *G. furcata*, *G. intermedia* and *S. hemiphyllum* during emersion. It was evident that the relative enhancement of photosynthesis by elevated CO_2 in those three algae increased, though the absolute values of photosynthetic enhancement owing to CO_2 increase were reduced when the desiccation statuses became more severe. However, in the case of desiccated *P. fascia* (water loss being greater than 20 %), light saturated net photosynthesis was saturated with current ambient atmospheric CO_2 level. It is proposed that increasing atmospheric CO_2 will enhance the daily photosynthetic production in intertidal macroalgae by varied extents that were related to the species and zonation.

Key words: marine macroalgae, ecophysiology, photosynthesis, CO_2, zonation

1 Introduction

Intertidal macroalgae, being an important component of coastal primary productivity, play a key role in the coastal carbon cycle (Gao and McKinley, 1994) and provide higher trophic levels for intertidal consumers via herbivory or the detrital food chain (Bustamante and Branch, 1996). They photosynthesize in air when the tide goes out, and in water at high tide, experiencing dramatic environmental changes between the aquatic and terrestrial exposures. Therefore, their ecophysiology is of general concern, especially in the changing coastal environments (Einav et al., 1995; Davison and Pearson, 1996; Raven, 1999). Many intertidal macroalgae, while submerged in seawater, use HCO_3^- as an exogenous inorganic carbon source beside CO_2 for photosynthesis (Raven, 1997). HCO_3^- utilization is either assisted by dehydration via surface-bound

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* Corresponding author, E−mail: ksgao@stu.edu.cn

carbonic anhydrase or direct transport via anion exchange (Beer, 1994; Axelsson et al., 1995; Zou et al., 2003). It is generally believed that the present day seawater dissolved inorganic carbon composition can fully or nearly saturate the photosynthesis of many marine macroalgae while submerged (Beer and Kock, 1996; Beardall et al., 1998), which has been largely explained by their efficient utilization of HCO_3^- pool in seawater (Beer, 1994), albeit enhancement of photosynthesis and/or growth by enriched CO_2 in seawater was recognized in some macroalgae, such as *Porphyra yezoensis* (Gao et al., 1991), *Gracilaria* spp. (Gao et al., 1993) and *Lomentaria articulata* (Kübler et al., 1999).

Intertidal macroalgae are exposed to air during low tide. Aerial exposure will result in an immediate change in the photosynthetic inorganic carbon supply (Mercado and Niell, 2000; Zou and Gao, 2002a, 2004) and availability of incident photon flux density (Dring and Lüning, 1994) for them. Varied availability of photosynthetic resources in air and in water result in distinct photosynthetic characteristics (Oaters, 1985, 1986; Gao and Aruga, 1987; Madsen and Maberly, 1990; Peña et al., 1999; Zou and Gao, 2002a, 2004). As intertidal marcroalgae cannot regulate their water status like land higher plants that posses stomata or waxy cuticules, they (except for saccate algae; Oates, 1985, 1986) are easily subject to desiccation when exposed to air at low tide. Many researchers showed that intertidal macroalgae were capable of tolerating the emersion-related environmental conditions, which would remarkably affect the photosynthetic metabolism positively or negatively (Kawamistu et al., 2000; Abe et al., 2001; Ji and Tanaka, 2002). It was believed that the carbon fixation during the periods of exposure may represent a significant contribution to the total carbon fixation budget of the intertidal macroalgae (Maberly and Madsen, 1990; Bell, 1993; Peña et al., 1999), although the time spent emersed is not more productive in terms of net carbon assimilation, which was caused mainly by decreased photosynthesis owing to desiccation during emersion (Raven, 1997). Nevertheless, more work is needed to gain a better understanding about the emersed photosynthesis of intertidal macroalgae in relation with the changing atmospheric CO_2 concentration and light intensities. In our previous work, we measured the photosynthetic responses to varied light levels, temperature, CO_2 concentration and water content of the thalli during emersion in a farmed seaweed species *Porphyra haitanensis* (Zou and Gao, 2002b). In the present study, we selected four representative intertidal macroalgae (two red algae and two brown algae) growing along the Shantou coast of China, to characterize the ecophysiological responses regarding the relationship of the photosynthesis with light intensities and CO_2 concentrations during emersion at varied water content levels, aimed at assessing the influence of aerial exposure on the macroalgae photosynthetic performances. Furthermore, the results in the present investigation may be useful for estimating the likely ecophysiological effect of atmospheric CO_2 increase on intertidal macroalgae, especially when considering the different extents of photosynthetic CO_2 limitation in the overall context of varied species, zonation and desiccation statuses.

2 Materials and methods

2.1 Plant samples

Samples of *Gloiopeltis furcata* (P.et R.) Agardh (red alga) were collected at low tide from the upper intertidal zone, *Petalonia fascia* (Muller) Kuetz (brown alga) from the middle intertidal zone, and *Gigartina intermedia* Suring (red alga) and *Sargassum hemiphyllum* (Turn.) Agardh (brown alga) from the lower intertidal zone of Nan'ao Island, Shantou, China (23°20′N, 116°40′E), rinsed and cleaned of visible epiphytes. Unwounded plants were selected, sealed in plastic bags with seawater and transported within 0.5 h to the Laboratory of the Marine Biology Station of Shantou University located in Nan'ao Island. They were maintained in filtered seawater in several glass aquaria at about 60 μmol/(m^2·s) (PAR, LD cycle 12:12) and 18~22 ℃. The seawater was aerated and renewed every day. Samples were used for experiments within 4 d of maintenance, a period during which stable photosynthetic activity was recognized. The materials were re-collected after that period.

2.2 Estimation of desiccation

To determine the effects of desiccation on photosynthetic performances, samples were desiccated under constant conditions in incubators. The light received by the algae was 200 μmol/(m^2·s) (PAR) supplied by fluorescent lamps, and the relative humidity was between 75% and 80% and temperature was controlled at 25 ℃ in the chambers. Air within the incubators was mixed at a flow rate of about 2.0 m/s. Extents of desiccation were determined as percentage of water loss from the samples. The water loss (WL) was calculated from the following equation:

$$WL=(W_0-W_t)/(W_0-W_d)\times 100,$$

where W_0 is the initial wet weight (i.e., fully-hydrated weight), which was determined after getting rid of the water drops surrounding the surface of samples by gently blotting with tissue paper; W_t is the instantaneous weight of the exposed samples; W_d is the dry weight, measured after the samples had been dried at 80 ℃ for 24 h and cooled in a desiccator.

Photosynthetic responses of the algae to desiccation were measured during exposures of varied time intervals that resulted in different degrees of percent water loss.

2.3 Measurements of emersed photosynthesis

The rates of net photosynthesis (P_n) or dark respiration (R_d) of the macroalgae while exposed to air were measured as CO_2 uptake or evolution by infrared gas analysis using a leaf chamber analyzer (LCA4, Analytical Development Company LTD, UK). The photon flux density received by the leaf chamber came from a halogen lamp (150 W) above it. The chamber was covered completely with a black cloth for the measurement of dark respiration. Temperature in the leaf chamber was maintained at 25 ℃ by keeping it in a temperature-controlled cabinet. P_n or R_d[μmol/(g·h)] was calculated as follows:

$$P_n \text{ or } R_d=\Delta C\times F\times 60\times 273/[(273+T)\times 22.4W_d],$$

where ΔC is the difference in CO_2 concentration (μmol/mol) between the inlet and outlet air from the leaf chamber; F is the gas flow rate (dm^3/min); T is the temperature in the chamber (℃); W_d is dry weight (g) (80 ℃, 24 h).

Net photosynthetic rates were measured at varied levels of light or CO_2 to determine photosynthesis versus irradiance or CO_2 behavior (P–I or P–C curve). Determination of the P–I curve was manipulated at the ambient atmospheric CO_2 concentration. Varied incident light intensities were obtained by altering the distance between the light resource and the leaf chamber, and sometimes by using the neutral filters screening. The dark respiratory was measured by closing the light source and hiding the leaf chamber with a black cloth. Apparent photosynthetic efficiency (APE) was estimated as the slope of the initial linear portion [light intensity lower than 100 μmol/(m^2·s)] in a P–I curve. Light compensation point (I_c, the light intensity at which the net photosynthesis is zero) and light saturation point (I_k, the light intensity which marks the transition from light limitation to light saturation for net photosynthesis) were calculated as R_d/APE and $(P_{max}+R_d)/APE$, respectively, according to Henley (1993), where P_{max} is the light-saturated net photosynthetic rate (i.e., photosynthetic capacity), which is calculated from the mean of 3~5 values in the asymptote region of the P–I curve. APE is the apparent photosynthetic efficiency.

Determination of the P–C curve was carried out at 600 μmol/(m^2·s) (PAR, 400~700 nm) that resulted in the saturated net photosynthesis of those species (none of them showed photoinhibition at that irradiance intensity). Six levels of CO_2 concentration (60, 120, 180, 360, 720, 1 080 μmol/mol) were adopted.

The varied CO_2 concentrations were prepared either by removing CO_2 from the ambient air that was passed through a soda lime column or by adding pure CO_2 in an airbag before pumping air into it. Airbags (1 m^3) were used to store the air of adjusted CO_2 concentrations. Air was directed from the airbag to the leaf chamber. The apparent carboxylating efficiency (ACE) of Rubisco (ribulose −1, 5-bisphosphate carboxylase/oxygenase) was calculated by the initial slope of a P−C curve according to von Caemmerer and Farquhar (1981). CO_2 compensation point (CCP, a CO_2 concentration bringing about net zero CO_2 uptake by the sample) was estimated from the point of intersection of initial parts of net photosynthesis (Y axis) and the CO_2 concentration (X axis) in a P−C curve.

All the data plotted on graphs were values with standard deviations, and they were analyzed by t-test or analysis of variance (ANOVA) at $P<0.05$ to test the differences for significance between means if necessary.

3 Results

Figure 1 illustrates the photosynthetic capacity and dark respiratory responses to desiccation. Light-saturated net photosynthesis increased ($P<0.05$) with process of initial desiccation to about 13% water loss in *G. furcata* or with water loss between 20% and 35% in *P. fascia.* The rates decreased thereafter with further water loss and approached zero at about 80% water loss in *G. furcata* or 66% in *P. fascia.* In *G. intermedia* and *S. hemiphyllum*, net photosynthetic rates decreased almost linearly with water loss to zero at 57% in *G. intermedia* or 55% water loss in *S. hemiphyllum.* The water loss levels at which photosynthetic rates decreased to half of their initial values in *G. furcata, G. intermedia, P. fascia and S. hemiphyllum*, were 49%, 34%, 50% and 36%, respectively. The dark respiration decreased straightly with water loss in *G. furcata, G. intermedia* and *P. fascia*, except for *S. hemiphyllum*, that of which was enhanced by 14% compared with the initial value when 26% of water was lost from the thalli. The water loss resulting in decreased respiration to half of its initial rates was 60%, 75% and 68% respectively, in *G. furcata, G. intermedia* and *P. fascia.*

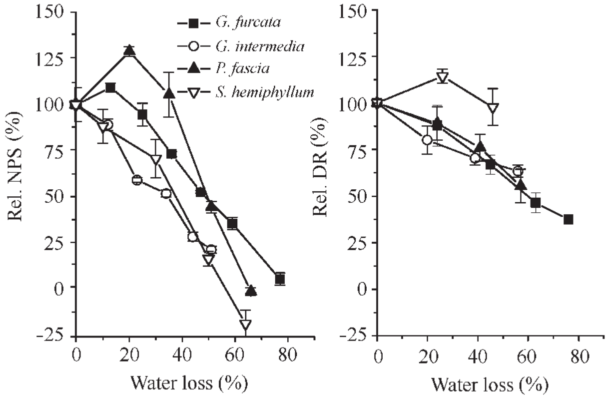

Fig. 1. Changes of relative light-saturated net photosynthetic rates (NPS) and relative dark respiratory rates (DR) with water loss in *Gloiopeltis furcata, Gigartina intermedia, Petalonia fascia* and *Sargassum hemiphyllum* while exposed, the initial net photosynthetic rates of which were (77.7 ±5.8), (52.9 ±2.6), (144.1 ±8.7) and (42.0 ±3.8) μmol /(g·h), respectively; and the initial dark respiratory rates were (23.7±2.9), (26.7±4.0), (97.9±4.4) and (22.9±1.4) μmol/(g·h), respectively (n = 6~9).

The parameters of photosynthesis versus light in *G. furcata, G. intermedia, P. fascia* and *S. hemiphyllum* while exposed and desiccated are shown in Fig. 2. Marked differences ($P<0.01$) in the initial values of apparent photosynthetic efficiency, light compensation and light saturation point were observed between species, and the values of I_k in *G. furcata* and *P. fascia* were much higher ($P<0.01$) than those in *G. intermedia* and *S. hemiphyllum* in the course of desiccation. Differences in the functional morphology and habitat of these algae might be responsible for this effect. It appeared that APE and I_k decreased, while I_c increased with enhanced desiccation in all these four species, although they displayed species−specific differences in their change patterns with progress of desiccation.

The light-saturated net photosynthetic rates (NPS) as a function of CO_2 concentrations at different emersed phases are shown in Fig. 3. In *G. furcata, G.*

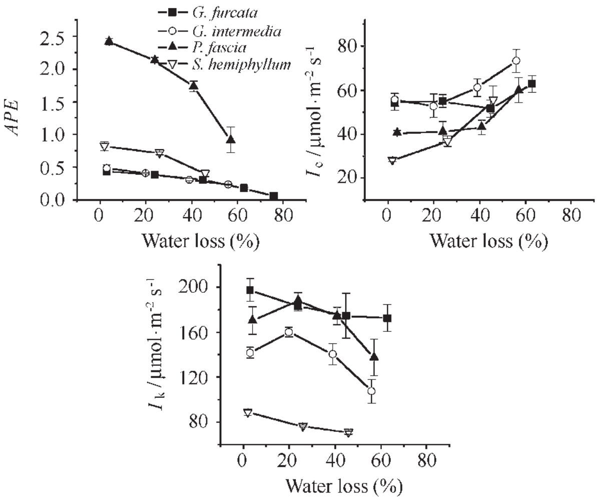

Fig. 2. Apparent photosynthetic efficiency{[μmol/(g·h)]/[μmol/(m^2·s)]}, light compensation point and light saturation point as a function of water loss in *Gloiopeltis furcata, Gigartina intermedia, Petalonia fascia* and *Sargassum hemiphyllum* while exposed ($n = 6 \sim 9$).

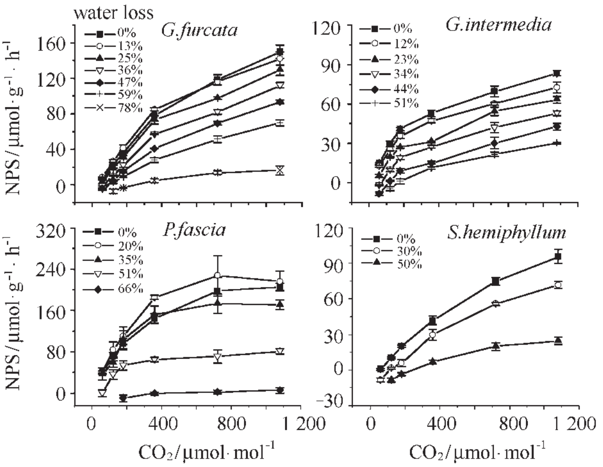

Fig. 3. Effects of CO$_2$ concentrations on net photosynthesis of *Gloiopeltis furcata, Gigartina intermedia, Petalonia fascia* and *Sargassum hemiphyllum* while exposed to varied levels of water loss (n = 6~9).

intermedia and *S. hemiphyllum*, photosynthesis increased with the increase of CO$_2$ concentration within the tested ranges (60~1 080 μmol/mol) at all levels of desiccation, indicating CO$_2$-limited photosynthesis during emersion. Elevation of CO$_2$ in air from 360 to 720 μmol/mol, that is, doubled atmospheric CO$_2$ concentration, enhanced the emersed NPS by 33%~196% in *G. furcata* with water loss of 0%~78%, by 28%~99% in *G. intermedia* with 0%~51% water loss, and by 78%~180% in *S. hemiphyllum* with 0%~50% water loss, respectively. It showed that the relative photosynthetic enhancement by elevated CO$_2$ concentration increased with increased extents of desiccation, although the absolute photosynthetic enhancement by CO$_2$ enrichment exhibited the contrary trend. In *P. fascia*, NPS increased to level off at 720 and 360 μmol/mol CO$_2$ with desiccation of less or higher than 20% water loss, respectively.

Figure 4 shows the apparent carboxylating efficiency (ACE) and CO$_2$ compensation point (CCP) as a function of desiccation in *G. furcata, G. intermedia, P. fascia* and *S. hemiphyllum*. ACE showed similar patterns to NPS with regard to the effects of water loss. ACE increased till water was lost by 30% from *G. furcata* and *P. fascia*, and thereafter decreased with further desiccation. However, it showed a steady decline with water loss in *G. intermedia* and *S. hemiphyllum*. CCP was not affected, P>0.1) by desiccation with water loss no more than 12% in *G. furcata* and *G. intermedia*, and with it less than 35% in *P. fascia*, but soared with further increased desiccation. In *S. hemiphyllum*, CCP showed a steady increase with water loss. Fifty water loss brought CCP to 90, 136, 40 and

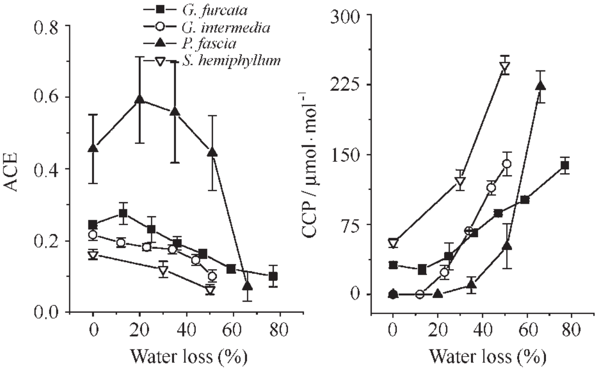

Fig. 4. Apparent carboxylating efficiency {[μmol/(g·h)]/[μmol/mol)]}and CO$_2$ compensation point as a function of water loss in *Gloiopeltis furcata, Gigartina intermedia, Petalonia fascia* and *Sargassum hemiphyllum* while exposed (n = 6~9).

240 μmol/mol in *G. furcata*, *G. intermedia*, *P. fascia* and *S. hemiphyllum*, respectively, indicating that higher CO_2 concentrations were required for highly dehydrated than for hydrated thalli to maintain photosynthesis positive.

4 Discussion

The ecphysiological differences among photosynthetic performances in *G. furcata*, *G. intermedia*, *P. fascia* and *S. hemiphyllum* during emersion might be correlated with vertical zonation patterns of these species observed in the field, as suggested by Einav et al. (1995), Harker et al. (1999) and Peña et al. (1999). *G. furcata* and *P. fascia*, which distributed in the higher intertidal zone, were exposed for longer duration to air during low tide than *G. intermedia* and *S. hemiphyllum* did. It could be seen that *G. furcata* and *P. fascia* not only exhibited an increase of photosynthetic rates and carboxylating efficiencies following some water loss, but also showed the higher abilities of the positive photosynthetic activities to resist the water loss than *G. intermedia* and *S. hemiphyllum*. Additionally, light saturation points were higher in *G. furcata* and *P. fascia* than those in *G. intermedia* and *S. hemiphyllum* during emersion, suggesting the adaptation to the higher light conditions in higher intertidal algae.

Many intertidal macroalgae were reported to photosynthesize during emersion at maximal rates when moderately desiccated, presumably due to reduced aqueous diffusion barrier on the surface of their thalli for CO_2 (Davison and Pearson, 1996; Peña et al., 1999; Raven, 1999). In the present study, *G. furcata* and *P. fascia* showed an increase of photosynthesis, as well as carboxylating efficiency, following 10%~20% water loss. An increase of carboxylating efficiency indicates increased activity of the carboxylating enzyme, Rubisco (von Caemmerer and Farquhar, 1981), which results in enhanced CO_2 uptake. Therefore, that the emersed photosynthesis increased following mild water loss from the thalli could be attributed to the enhanced activity of carboxylation, which might be associated with reduced CO_2 diffusion barrier. Photosynthesis enhanced with moderate desiccation has been also recognized in numerous lichen species (Coxsen et al., 1983) and a terrestrial blue-green alga *Nostoc flagelliforme* (Qiu and Gao, 2001). Activity of some photosynthetic enzymes in these species might be similarly stimulated as in intertidal macroalgae.

With advanced desiccation, *G. intermedia* and *S. hemiphyllum* exhibited constantly decreased photosynthesis, while *G. furcata* and *P. fascia* showed reduced rates after their photosynthesis has increased to a maximum. It was evident that severe desiccation negatively affected both photosynthetic and dark respiratory activities. The mechanisms that emersed photosynthesis declined with desiccation had been variously speculated: (1) a reduction in the ability of electron transport between photosystems (Wiltens et al., 1978); (2) a decrease in the turgor pressure of cells or an increase in the ions concentrations within cells (Davison and Pearson, 1996); (3) a change of molecular environment around the photosynthetic enzymes (Kawamistu et al., 2000; Burritt et al., 2002). This study showed that the decreased photosynthesis was closely associated with the declines in efficiencies of photosynthetic light utilization and CO_2 carboxylation in *G. furcata*, *G. intermedia*, *P. fascia* and *S. hemiphyllum* during emersion. Additionally, that CO_2 compensation points increased sharply in highly desiccated thalli of the species implied a decline of the ratio of carboxylase to oxygenase activity of Rubisco and a potential increase of photorespiration. Thus, desiccation must have negatively affected the photochemical properties and carboxylase activity of Rubisco in these algae, which can supply the physiological mechanism causing the reduced net photosynthesis in highly dehydrated algae. At the same time, light saturation points decreased while light compensation points increased in advanced desiccated algae, indicating a reduction of capacity to utilize light energy. It is likely that severe desiccated intertidal macroalgae exhibit the tendency of photodamage or chronic photoinhibition (loss of functional D1-proterin) under high irradiance.

This study indicated that the photosynthesis of desiccated *P. fascia* (water loss higher than 20%) was saturated at the current ambient atmospheric CO_2 levels, while the emersed photosynthesis of *G. furcata*, *G. intermedia* and *S. hemiphyllum* was not saturated by the ambient CO_2 levels in air. It displayed a trend that the relative photosynthetic enhancement by the elevated CO_2 increased with desiccation, although the absolute values of photosynthetic enhancement by the atmospheric CO_2 rise were reduced due to the decreased photosynthetic capacities in those algae with further water loss. According to Rubisco kinetics, doubling CO_2 concentration in air will stimulate the carboxylation rate by about two-times (von Caemmerer and Farquhar, 1981; Makino and Mae, 1999). However, the actual relative enhancements of photosynthesis observed were much less than 100% in *G. furcata* (within 0%~59% water loss), *G. intermedia* (within 0%~51% water loss), and in *S. hemiphyllum* (within 0%~30% water loss). This implied that photosynthesis of those algae with moderate desiccation during emersion under elevated CO_2 levels might be limited by other factors, i.e., the capacities of electron transport or inorganic phosphate regeneration. Additionally, the likely intracellular inorganic carbon accumulation resulting from the carbon concentrating mechanisms of many marine macroalgae (e.g., Axelsson et al., 1995; Raven, 1997) may also cause lower percentage of photosynthetic enhancements by elevated atmospheric CO_2 concentration during the initial emersed phase.On the other hand, the observed relative photosynthetic enhancements by the doubled CO_2 levels in air were greater than 100% in highly desiccated algae, *G. furcata* (78% water loss) and *S. hemiphyllum* (50% water loss). This suggested that the primary components limiting photosynthesis switched to Rubisco–catalyzed carboxylation.

Whether the photosynthesis of intertidal algae is saturated by the current ambient CO_2 levels or not is of general concern in a view of the ecological impacts of the atmospheric CO_2 rise, which is caused mainly by anthropogenic effects (such as burning of fossil fuels and deforestation).The constraints on inorganic carbon acquisition from water for the submerged macroalgae might be negligible. This is because submerged macroalgae might possess the ability of directly or indirectly catalyzing bicarbonate use (Raven, 1997). Moreover, the reflection of the seawater surface and attenuation within the water column would result in a relatively low availability of light level for them. As a result of that, the submersed photosynthesis might be non-sensitive to the increasing atmospheric CO_2. However, this study together with our previous works (Gao et al., 1999; Zou and Gao, 2002a, b, 2004) showed that elevated atmospheric CO_2 might have a fertilizing effect resulted in increasing photosynthesis in intertidal macroalgae while exposed to air at low tide. It appeared that the degree of carbon limitation of photosynthesis at ambient CO_2 in air differs among species and varied levels of desiccation statuses owing to their tidal heights and exposure duration (this study). Additionally, intertidal macroalgae are prone to suffer from photoinhibition resulting from full sunlight during the period of emersion (e.g., Hanelt, 1992; Häder and Figueroa, 1997), thus decreasing their primary productivity. As a limitation of photochemistry is often caused by lack of CO_2, a CO_2 increase may decrease the level of photoinhibition. Therefore, the actual enhancement of daily photosynthetic production by elevated atmospheric CO_2 in intertidal macroalgae during emersion will differ among species and among a range of tidal heights. However, the long-term photosynthetic response to elevated CO_2 might be lower than the short-term responses determined here, which have been shown frequently for land plants (Drake et al., 1997; Makino and Mae, 1999). Thus, further investigations on shores are required to better describe the long-term photosynthetic and growth responses of intertidal macroalgae to the increase of atmospheric CO_2.

Acknowledgements

This study was funded by the National Natural Science Foundation of China under contract Nos 30470343, 30300050 and 39830060 and the Guangdong Natural Science Foundation under contract No. 04010990.

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