

# Effects of desiccation and CO<sub>2</sub> concentrations on emersed photosynthesis in *Porphyra haitanensis* (Bangiales, Rhodophyta), a species farmed in China

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The effects on photosynthesis of CO<sub>2</sub> and desiccation in *Porphyra haitanensis* were investigated to establish the effects of increased atmospheric CO<sub>2</sub> on this alga during emersion at low tides. With enhanced desiccation, net photosynthesis, dark respiration, photosynthetic efficiency, apparent carboxylating efficiency and light saturation point decreased, while the light compensation point and CO<sub>2</sub> compensation point increased. Emersed net photosynthesis was not saturated by the present atmospheric CO<sub>2</sub> level (about 350 ml m<sup>-3</sup>), and doubling the CO<sub>2</sub> concentration (700 ml m<sup>-3</sup>) increased photosynthesis by between 31% and 89% at moderate levels of desiccation. The relative enhancement of emersed net photosynthesis at 700 ml m<sup>-3</sup> CO<sub>2</sub> was greater at higher temperatures and higher levels of desiccation. The photosynthetic production of *Porphyra haitanensis* may benefit from increasing atmospheric CO<sub>2</sub> concentration during emersion.

**Key words:** CO<sub>2</sub>, desiccation, emersion, photosynthesis, *Porphyra haitanensis*, red alga, seaweed

## Introduction

Intertidal macroalgae experience alternation of photosynthesis between aquatic and terrestrial environments with the tidal cycles. When the tide is high, they are submerged in seawater, the inorganic carbon composition of which is generally regarded as not limiting the photosynthesis of marine macroalgae (Beer & Koch, 1996; Beardall *et al.*, 1998). When the tide is low, they are usually exposed to air, being switched from an aquatic to a terrestrial environment, where the large buffering reservoir of HCO<sub>3</sub><sup>-</sup> in seawater is no longer present and atmospheric CO<sub>2</sub> is the only exogenous carbon source for photosynthesis. The acquisition of CO<sub>2</sub> is less constrained in air than in seawater, through which CO<sub>2</sub> diffuses about 10000 times more slowly (Raven, 1999). However, this constraint can be offset by the abundance of HCO<sub>3</sub><sup>-</sup> (about 160-fold that of CO<sub>2</sub> at pH 8.2), as many intertidal algae can use HCO<sub>3</sub><sup>-</sup> as the exogenous inorganic carbon source for photosynthesis (Maberly, 1990; Gao & McKinley, 1994; Raven, 1997; Larsson & Axelsson, 1999). Thus, carbon limitation during photosynthesis in intertidal species may be potentially more important in air than in water. Furthermore, the advantage of using atmospheric CO<sub>2</sub> rather than

aqueous CO<sub>2</sub> is offset by the deleterious effects of desiccation during exposure (Johnston & Raven, 1986; Madsen & Maberly, 1990; Davison & Pearson, 1996; Beach & Smith, 1997; Peña *et al.*, 1999; Kawamitsu *et al.*, 2000). However, little has been documented on the relationship between photosynthesis of intertidal macroalgae and CO<sub>2</sub> concentrations in air while exposed at low tides (Gao *et al.*, 1999).

Considerable attention has been paid to the comparative rates of photosynthesis under emersed and submersed conditions. The parameters of algal photosynthetic responses to light (P–I curve) vary between air and water. Photosynthetic efficiencies that were higher in water than in air, and in which the light compensation and saturation points were higher than or similar to those in water, were reported for *Colpomenia peregrina* (Oates, 1985), *Fucus spiralis* (Madsen & Maberly, 1990), *Bostrychia calliptera* and *Caloglossa ceprieurii* (Peña *et al.*, 1999). In contrast, lower photosynthetic efficiency in water compared to air and lower light saturation point in air than water were found in *Halosaccion americanum* (Oates, 1986). However, much less attention has been paid to changes in the parameters of P–I curves in intertidal macroalgae during emersion.

*Porphyra* plants are found in the upper intertidal zones of rocky shores, enduring long periods of

desiccation during emersion at low tides. The photosynthetic rates of *P. perforata* (Johnson *et al.*, 1974), *P. yezoensis* (Gao & Aruga, 1987) and *P. linearis* (Lipkin *et al.*, 1993) were higher in air than in water at moderate levels of desiccation. Their photosynthetic potential exhibits a high tolerance for many factors associated with emersion-related stresses (such as desiccation, changes of light, and temperature; Gao & Aruga, 1987; Herbert, 1990; Lipkin *et al.*, 1993; reviewed by Davison & Pearson, 1996). Recently, the mechanisms of photosynthetic inorganic carbon acquisition during submersion and the effects of different inorganic carbon levels on *Porphyra* have been extensively investigated (Gao *et al.*, 1991, 1992; Figueroa *et al.*, 1995; Mercado *et al.*, 1997, 1999; Israel *et al.*, 1999). The photosynthesis of *P. leucosticta* (Mercado *et al.*, 1997) and *P. linearis* (Israel *et al.*, 1999) appeared to be saturated at about 2.2 mM inorganic carbon (a concentration representative of that in seawater), although the growth of *P. yezoensis* was enhanced by CO<sub>2</sub> enrichment in aeration (Gao *et al.*, 1991). However, it is not known whether photosynthesis in emersed *Porphyra* plants is saturated by atmospheric CO<sub>2</sub> levels. The rise in atmospheric CO<sub>2</sub> during this century is thought likely to affect the physiological ecology of plants (Bowes, 1993). As atmospheric CO<sub>2</sub> is the exogenous carbon source for photosynthesis in intertidal macroalgae at low tides (Mercado & Niell, 2000), they may be sensitive to rising atmospheric CO<sub>2</sub>. It is therefore of interest to investigate the relationship of photosynthesis in *Porphyra* plants to CO<sub>2</sub> concentration during emersion. *Porphyra haitanensis*, an important seaweed used for sea-vegetable foods in China, is cultivated on a commercial scale in Fujian, Zhejiang and Guangdong Provinces of China, and experiences repeated desiccation during low tides. Therefore, the effects of emersion on photosynthesis of *Porphyra haitanensis* may have a major impact on aquaculture production. The present study aimed to investigate the relationship of photosynthesis to desiccation and CO<sub>2</sub> concentrations in *P. haitanensis*, and to assess its physiological responses to increased atmospheric CO<sub>2</sub> while exposed.

## Materials and methods

Thalli (12–20 cm long, about 20–28 days after the germination of conchospores released from free-living conchocelis) of *Porphyra haitanensis* T.J. Chang *et al.* B.F. Zheng were collected during November to December 1999, from a cultivation field at Nanao Island, Shantou, China (23° 20' N, 23° 20' E). The thalli were cultivated by the pole-system in a bay with a shallow sandy bottom, experiencing periodic desiccation (3–6 h) during emersion at low tides. Samples sealed in plastic bags with seawater were transported to the laboratory in darkness in a cooler

(1–4 °C) within 4 h, and were maintained in filtered seawater in several glass aquaria at about 50 μmol m<sup>-2</sup> s<sup>-1</sup> (LD cycle 12:12 h) and 18–22 °C. The seawater was aerated and half the volume was renewed every day. The samples were rinsed and cleared of visible epiphytes before use in experiments. The photosynthetic measurements were carried out within 4 days of this treatment, during which period the samples showed stable photosynthetic activities.

Photosynthesis of *P. haitanensis* while exposed to air was determined as CO<sub>2</sub> uptake by infrared gas analysis using a leaf chamber analyser (LCA4, Analytical Development Company, UK). Light was provided with a tungsten halogen lamp (220/240 V, 150 W, Hikaril-J) from above. Temperature was controlled by maintaining the leaf chamber in a temperature-controlled cabinet. Net photosynthesis ( $P_n$ ) or dark respiration ( $R_d$ ) [μmol CO<sub>2</sub> g(d.wt)<sup>-1</sup> h<sup>-1</sup>] was calculated as follows:

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

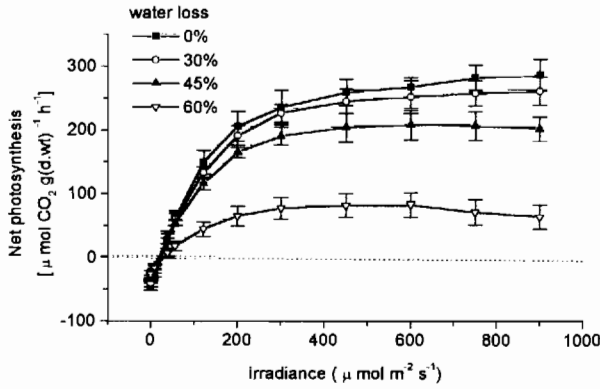
where  $\Delta C$  is the difference in CO<sub>2</sub> concentration (ml m<sup>-3</sup>) between the inlet and outlet air,  $F$  is the gas flow rate (l min<sup>-1</sup>),  $T$  is temperature (°C) and  $DW$  is dry weight (g, 80 °C, 24 h). The photosynthetic responses to light ( $P$ – $I$  curves) were determined at 20 °C. Irradiance was adjusted by altering the distance between the light source and the leaf chamber. The dark respiratory rates were determined by covering the leaf chamber with a black cloth. Photosynthetic efficiency ( $\alpha$ ) was estimated as the light-limited (below 120 μmol m<sup>-2</sup> s<sup>-1</sup>) slopes of the  $P$ – $I$  curves, light compensation point ( $I_c$ ) and light saturation point ( $I_k$ ) were estimated by  $R_d/\alpha$ , and  $(P_{max} + R_d)/\alpha$ , respectively, according to Henley (1993).

Six levels of CO<sub>2</sub> concentrations (50, 100, 150, 200, 350, 700 ml m<sup>-3</sup>) were adopted to determine the relationship of  $P_n$  with CO<sub>2</sub> ( $P$ – $C$  curve) during emersion. CO<sub>2</sub> in the ambient air was removed to different extents by pumping it through a soda lime column to obtain lower concentrations of CO<sub>2</sub>. A concentration of 700 ml m<sup>-3</sup> CO<sub>2</sub> was obtained by injecting pure CO<sub>2</sub> before pumping outdoor air into an air bag (1 m<sup>3</sup>). The air bags were used for all measurements to maintain constant CO<sub>2</sub> concentrations. Measurements were carried out at 20, 25 and 30 °C and 600 μmol m<sup>-2</sup> s<sup>-1</sup> (PAR, 400–700 nm), an irradiance that saturated  $P_n$  of the species. The apparent carboxylating efficiency (ACE) of Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) was estimated from the initial slope of the  $P$ – $C$  curves according to Von Caemmerer & Farquhar (1981). The CO<sub>2</sub> compensation point (CCP; a CO<sub>2</sub> concentration resulting in equal CO<sub>2</sub> uptake and evolution) was estimated from the intersection of a  $P$ – $C$  curve and the  $x$ -axis.

Samples were desiccated in an incubator at 100 μmol m<sup>-2</sup> s<sup>-1</sup>, 75% relative humidity and the same temperatures as used for the photosynthetic determinations. The desired levels of desiccation were obtained by varying the duration of the exposures. Degree of desiccation was expressed as percentage of water loss from the thalli. The water loss (WL, %) was estimated as follows:

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

where  $W_o$  is the initial wet weight (i.e. fully hydrated weight), measured after removing surface water drops by lightly blotting with tissue paper,  $W_t$  is the desiccated weight after a known time interval and  $W_d$  is the dry



**Fig. 1.** Net photosynthetic rates of *Porphyra haitanensis* while exposed as a function of irradiance at different levels of desiccation (water loss), measured at ambient  $\text{CO}_2$  concentration ( $350 \text{ ml m}^{-3}$ ) and  $20^\circ\text{C}$ . Vertical bars represent  $\pm \text{SE}$  of the means ( $n = 9-16$ ).

**Table 1.** Photosynthetic parameters of *Porphyra haitanensis* under different degrees of water loss, derived from the P-I curves in Fig. 1

Parameters	Water loss			
	0	30%	45%	60%
$P_{\text{max}}$	$286.5 \pm 25.1^{\text{a}}$	$261.4 \pm 21.8^{\text{a}}$	$202.1 \pm 18.8^{\text{b}}$	$82.7 \pm 19.3^{\text{c}}$
$R_{\text{d}}$	$46.3 \pm 5.0^{\text{a}}$	$40.7 \pm 6.1^{\text{a}}$	$33.0 \pm 4.7^{\text{b}}$	$27.1 \pm 5.8^{\text{b}}$
$\alpha$	$1.6 \pm 0.1^{\text{a}}$	$1.4 \pm 0.1^{\text{b}}$	$1.2 \pm 0.1^{\text{b}}$	$0.8 \pm 0.2^{\text{c}}$
$I_c$	$29.2 \pm 4.7^{\text{a}}$	$29.0 \pm 4.8^{\text{a}}$	$27.4 \pm 5.2^{\text{a}}$	$37.0 \pm 5.9^{\text{b}}$
$I_k$	$209.1 \pm 10.1^{\text{a}}$	$214.2 \pm 11.2^{\text{a}}$	$199.1 \pm 6.7^{\text{a}}$	$133.7 \pm 36.9^{\text{b}}$

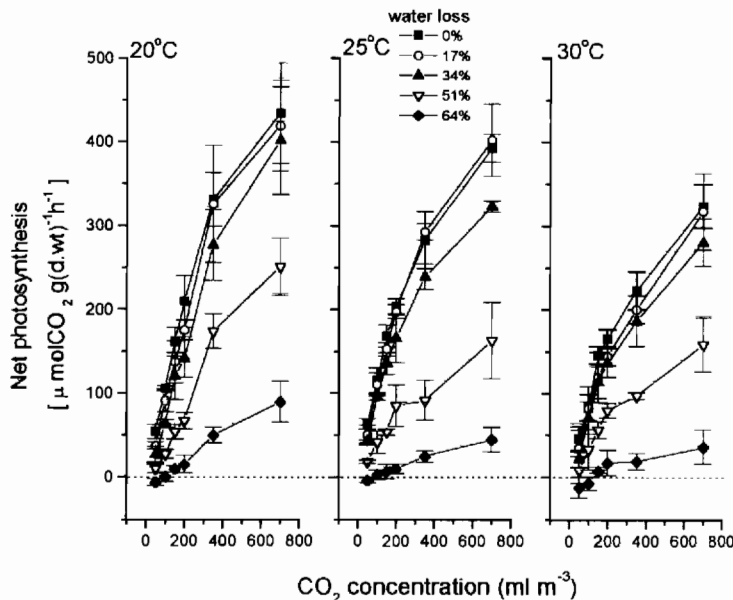
$P_{\text{max}}$ , maximum net photosynthetic rate [ $\mu\text{mol CO}_2 \text{ g(d.wt)}^{-1} \text{ h}^{-1}$ ];  $R_{\text{d}}$ , dark respiration rate [ $\mu\text{mol CO}_2 \text{ g(d.wt)}^{-1} \text{ h}^{-1}$ ];  $\alpha$ , photosynthetic efficiency [ $(\mu\text{mol CO}_2 \text{ g(d.wt)}^{-1} \text{ h}^{-1}) / (\mu\text{mol m}^{-2} \text{ s}^{-1})$ ];  $I_c$ , light compensation point ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ );  $I_k$ , light saturation point ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ). All values are mean  $\pm \text{SE}$  ( $n = 9-16$ ); within each row, values with different superscripts are significantly different at  $p = 0.05$ .

weight ( $80^\circ\text{C}$ , 24 h). Data were analysed by  $t$ -test or one-way analysis of variance (ANOVA).

**Results**

Light-saturated net photosynthesis of *P. haitanensis* was not significantly affected by desiccation up to 30% water loss ( $p > 0.05$ ), but was significantly reduced with further desiccation ( $p < 0.01$ ). Rates were lowered by 29% and 71% at 45% and 60% water loss, respectively (Fig. 1, Table 1). Dark respiration decreased with increased desiccation. A water loss of 60% resulted in a 41% decline in dark respiratory rate. Photosynthetic efficiency ( $\alpha$ ) decreased with more severe desiccation ( $p < 0.01$ ; Table 1), being reduced by about 50% at a water loss of 60%. Light compensation point ( $I_c$ ) increased ( $p < 0.05$ ), while light saturation point ( $I_k$ ) decreased ( $p < 0.05$ ) at 60% water loss.  $I_c$  and  $I_k$  were not significantly affected ( $p > 0.05$ ) by desiccation at water loss levels lower than 45% (Table 1).

Fig. 2 shows the relationship between net photosynthesis ( $P_n$ ) and  $\text{CO}_2$  concentrations in air at different temperatures and levels of desiccation in *P. haitanensis*. Increased temperature had a negative effect on emersed net photosynthesis within the range of  $20-30^\circ\text{C}$ , especially under conditions of enhanced desiccation. The  $P_n$  rates in ambient  $\text{CO}_2$  concentrations at 25 and  $30^\circ\text{C}$  were reduced by 15% and 33%, respectively, compared with  $20^\circ\text{C}$  in fully hydrated thalli, and by 49% and 61%, respectively, when the tissues had lost 64% of their water. The change in  $P_n$  at doubled  $\text{CO}_2$  concentration ( $700 \text{ ml m}^{-3}$ ) with temperature showed the same pattern as that at ambient  $\text{CO}_2$  con-

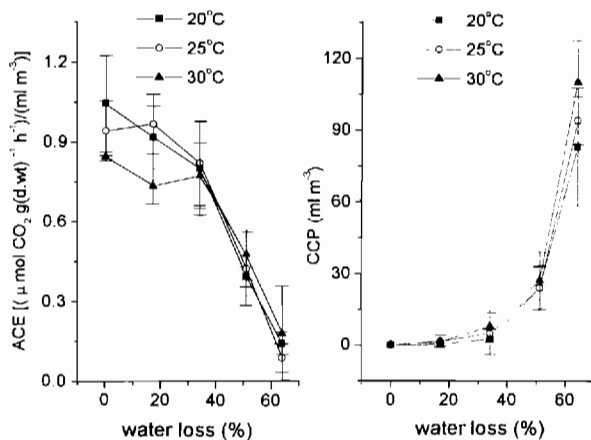


**Fig. 2.** Net photosynthetic rates of *Porphyra haitanensis* while exposed as a function of  $\text{CO}_2$  concentration in air at different levels of desiccation (water loss) and temperature. Irradiance for all measurements  $600 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . Vertical bars as in Fig. 1.

**Table 2.** Percentage increase in light-saturated net photosynthesis of *Porphyra haitanensis* at doubled atmospheric CO<sub>2</sub> concentration

Temperature (°C)	Water loss				
	0	17%	34%	51%	64%
20	31	29	45	44	80
25	33	37	35	78	79
30	45	58	50	63	89

Values are based on Fig. 2.

**Fig. 3.** Relationship of apparent carboxylating efficiency (ACE) and CO<sub>2</sub> compensation point (CCP) to desiccation (water loss) in *Porphyra haitanensis* at 20, 25 and 30 °C. Vertical bars represent  $\pm$  SE of the means ( $n = 9-12$ ).

centration (350 ml m<sup>-3</sup>). The  $P_n$  increased ( $p < 0.01$ ) with CO<sub>2</sub> concentrations within the tested range (50–700 ml m<sup>-3</sup>) at all the desiccation states tested. Doubling the CO<sub>2</sub> level of the ambient air enhanced  $P_n$  by 31–89% within the ranges of temperature and water loss tested (Table 2). The relative increase in photosynthesis at 700 ml m<sup>-3</sup> CO<sub>2</sub> was greater at higher levels of temperature as well as desiccation.

Desiccation did not significantly affect ( $p > 0.05$ ) apparent carboxylating efficiency (ACE) or CO<sub>2</sub> compensation points (CCP) of *P. haitanensis* at water loss levels below 34%. However, ACE was reduced while CCP increased significantly ( $p < 0.01$ ) with further water loss (Fig. 3). Temperature (over the range of 20–30 °C) did not affect the patterns of the relationship of ACE or CCP with water loss ( $p > 0.05$ ).

## Discussion

This study showed that elevation of CO<sub>2</sub> concentration to double that in the air brought about a 31–89% enhancement in the net photosynthesis of *P. haitanensis* while the alga was exposed and desiccated, indicating that CO<sub>2</sub> is limiting for

photosynthesis of the alga during emersion at present atmospheric CO<sub>2</sub> concentration. Emerged photosynthesis of many other intertidal macroalgae – *Fucus serratus* (Bidwell & McLachlan, 1985), *Ascophyllum nodosum* (Johnston & Raven, 1986), *Chondrus crispus* (Smith & Bidwell, 1987), *Fucus spiralis* (Madsen & Maberly, 1990), *Enteromorpha linza*, *Ishige okamurae* and *Gloiopeltis furcata* (Gao *et al.*, 1999) – was also reported to be CO<sub>2</sub>-limited at the present atmospheric CO<sub>2</sub> concentration, and Gao *et al.* (1999) suggested that higher CO<sub>2</sub> concentrations were needed to saturate photosynthesis when these species were desiccated. However, emerged photosynthesis in *Enteromorpha compressa* (Becr & Shrage, 1987) and *Prasiola stipitata* (Raven & Johnston, 1991) was saturated by the ambient CO<sub>2</sub> concentration. Our results show that the relative enhancement in net photosynthesis of *P. haitanensis* due to the elevation of CO<sub>2</sub> increased with increased desiccation or temperature, implying that any rise in atmospheric CO<sub>2</sub> would have more beneficial effects on the photosynthesis of the alga at higher levels of desiccation and temperature. Our results indicate that doubling of the atmospheric CO<sub>2</sub> concentration, which has been predicted to occur in the next few decades (King *et al.*, 1992), will increase the carbon gain of *P. haitanensis* during periods of emersion at low tides (when farmed thalli could lose up to 80% of their water), and therefore enhance their growth.

Many intertidal macroalgae exhibit an increase in emerged photosynthetic rate following moderate desiccation compared with the fully hydrated emerged state (Quadir *et al.*, 1979; Johnston & Raven, 1986; Gao & Aruga, 1987; Madsen & Maberly, 1990; Lipkin *et al.*, 1993; Peña *et al.*, 1999), and this has been attributed to the removal of the surface layer of water on the thallus, which lowers the diffusive resistance to atmospheric CO<sub>2</sub>. However, such a phenomenon was not found in *P. haitanensis* in the present study. This might be related to the species or to differences in the amounts of water on the surface of the algae when initiating measurements of emerged photosynthesis. Intertidal red macroalgae such as *Gastroclonium coulteri* (Hodgson, 1981) and *Caloglossa leprieuera* (Peña *et al.*, 1999) also failed to show enhanced photosynthesis during moderate desiccation.

Desiccation decreased the rates of both photosynthesis and dark respiration in emerged *P. haitanensis*, but respiration was less affected than photosynthesis. This implies that the photosynthetic processes, such as electron transfer and the enzymatic reactions of the Calvin cycle, are more water-dependent than respiratory processes. The data of Kawamistu *et al.* (2000) suggest that the capacity of intertidal macroalgae to tolerate desiccation during emersion is influenced by the mol-

ecular environment around the photosynthetic enzymes which may prevent membrane breakage and promote the retention of small amounts of water that are critical for viability. Direct physiological studies are required to characterize the biochemical reactions or enzyme activities in the tissue of *P. haitanensis* during exposure to air.

It is known that photosynthetic efficiency reflects the activities of photochemical reactions (light-harvesting efficiency and photosynthetic energy conversion efficiency) of plants (Henley, 1993), and the apparent carboxylating efficiency of Rubisco (Von Caemmerer & Farquhar, 1981). Our results show that the photosynthetic and carboxylating efficiency decreased with desiccation in *P. haitanensis* during emersion, and this suggests that desiccation has negatively affected photochemical reactions and carboxylation. On the other hand, the light and CO<sub>2</sub> compensation points increased with enhanced desiccation, showing that more CO<sub>2</sub> and light were required to maintain positive photosynthesis when *P. haitanensis* was highly desiccated. Kroon *et al.* (1993) reported that the predominant fluorescence quenching mechanism at irradiances less than the light saturation point for O<sub>2</sub> evolution is photochemical, i.e. photosynthetic, whereas above the light saturation point, it is non-photochemical, involving thermal dissipation, proton gradient formation and exciton spillover. Thus, the reduction of light saturation points by desiccation in *P. haitanensis* indicated not only the inefficient use of photosynthetically active radiation, but also the tendency for photodamage to occur under high light (e.g. midday on sunny days).

The CO<sub>2</sub> compensation point of *P. haitanensis* increased substantially with increased desiccation, probably due to enhanced photorespiration, which was demonstrated to be very active in *P. yezoensis* (Gao *et al.*, 1992). Furthermore, the K<sub>m</sub> of Rubisco for O<sub>2</sub> increases more slowly with increasing temperature than that for CO<sub>2</sub>, so that the potential for photorespiration increases with increasing temperature (Davison, 1991). In fact, carboxylation activity declined with enhanced desiccation in *P. haitanensis*. All these factors could affect the response of emersed photosynthesis in *P. haitanensis* to temperature. The present study indicated that higher temperatures lowered the net photosynthesis of *P. haitanensis* to a greater extent as the desiccation increased, but had no obvious effects on the apparent carboxylating efficiencies. It appeared, therefore, that temperature had less effect than desiccation on the Rubisco carboxylating activity in *P. haitanensis* during emersion. The CO<sub>2</sub> compensation point of emersed photosynthesis in *P. haitanensis* was also insensitive to temperature, as previously reported for *Ulva lactuca* (Colman, 1984), *Enteromorpha linza* and *Ishige okamurae* (Gao *et al.*, 1999).

It is concluded that the photosynthesis of *P. haitanensis* is CO<sub>2</sub>-limited during emersion under present atmospheric CO<sub>2</sub> concentrations, and that photosynthetic light utilization and CO<sub>2</sub> carboxylating efficiencies are reduced with increasing desiccation. Therefore, *P. haitanensis* will benefit from an increase in atmospheric CO<sub>2</sub> when exposed to air at low tide, and this will enhance the production of this species in aquaculture.

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