Hydrobiologia **398/399:** 355–359, 1999.
J.M. Kain (Jones), M.T. Brown & M. Lahaye (eds), Sixteenth International Seaweed Symposium,
© 1999 *Kluwer Academic Publishers. Printed in the Netherlands.*

Relationship of CO_2 concentrations to photosynthesis of intertidal macroalgae during emersion

Kunshan Gao[1,2], Yan Ji[1,2] & Yusho Aruga[3]
[1]*Marine Biology Institute, Shantou University, Shantou, Guangdong 515063, China*
[2]*Institute of Hydrobiology, The Chinese Academy of Science, Wuhan, Hubei 430072, China;*
E-mail: ksgao@public.wh.hb.cn
[3]*Tokyo University of Fisheries, Konan-4, Minato-ku, Tokyo 108-8477, Japan*

Key words: CO_2, emersion, macroalgae, photosynthesis, seaweeds

Abstract

In order to assess the ecological impacts of the atmospheric CO_2 increase on the intertidal macroalgae during emersion, the photosynthesis of *Enteromorpha linza* (a green alga), *Ishige okamurae* (a brown alga) and *Gloiopeltis furcata* (a red alga) was investigated in air as a function of CO_2 concentrations and water loss. Their photosynthesis was not saturated at the present atmospheric CO_2 level (350 μl l^{-1} or 15.6 μM), the CO_2 compensation point and $K_{[mCO_2]}$ increased with increasing desiccation, showing that desiccation lowers the CO_2 affinity of the intertidal macroalgae. It was concluded that *E. linza*, *I. okamurae* and *G. furcata*, while exposed to air, can benefit from atmospheric CO_2 rise, especially when the algae have lost some water.

Introduction

Marine macroalgae are distributed in the intertidal and subtidal zones of the coastal areas that are most populated, playing an important role in the coastal carbon cycle. Though macroalgae contribute less than 10% of the total marine primary production (Charpy-Roubaud & Sournia, 1990), some of them are more productive than the most productive plants on land and can be successfully cultivated on vast ocean surfaces, showing a great potential for CO_2 bioremediation (Gao & McKinley, 1994). They can induce large diurnal changes in the local CO_2 partial pressure, and turn the coral reef communities to a CO_2 sink, where biogenic calcification is usually a source of CO_2 to the atmosphere (Gattuso et al., 1997).

Atmospheric CO_2 concentration is increasing mainly due to industrial combustion of fossil fuels, and its subsequent ecological impacts on photosynthesis and growth of plants are of general concern (Bowes, 1993). It has been demonstrated that atmospheric CO_2 increase can raise oceanic primary production by phytoplankton (Riebesell et al., 1993; Hein & Sand-Jensen, 1997), though phytoplankton photosynthesis can be CO_2-saturated in air-equilibrium seawater (Raven, 1997). In terms of the ecological impacts of CO_2 on macroalgae, recent studies showed that CO_2 enrichment enhanced the photosynthesis and growth of *Porphyra* and *Gracilaria* plants (Lignell & Pedersen, 1989; Gao et al., 1991, 1993a) and inhibited the calcification of *Corallina pilulifera* by lowering the pH of seawater (Gao et al., 1993b). A few studies investigated the photosynthetic CO_2 uptake by the intertidal macroalgae while exposed during emersion (Bidwell & McLachlan, 1985; Johnston & Raven, 1986; Beer & Schragge, 1987; Madsen & Maberly, 1990; Surif & Raven 1990; Raven & Johnston 1991). For the intertidal macroalgae, when the tide is low and they are exposed to air, CO_2 is the only exogenous carbon source for their photosynthesis (whereas both HCO_3^- and CO_2 are available in seawater); therefore the intertidal macroalgae may be significantly sensitive to the atmospheric CO_2 increase. Photosynthesis of the intertidal macroalgae during emersion has been studied previously (Brinkhuis et al., 1976; Quadir et al., 1979; Oates & Murray, 1983; Oates, 1985; 1986; Gao & Aruga, 1987). The emersed photosynthesis was enhanced at an early stage due to extracellular water

loss and then reduced, probably due to intracellular dehydration, in *Porphyra* spp. (Johnson et al., 1974; Gao & Aruga, 1987), *Fucus distichus* (Quadir et al., 1979) and *Ascophyllum nodosum* (Brinkhuis et al., 1976); the maximum photosynthesis during emersion was higher than that when submerged. These studies demonstrated that the intertidal macroalgae, even dehydrated to about 15% water content, do photosynthesize in the air when they are exposed during the daytime. Nevertheless, little is known about the relationship of the photosynthesis of macroalgae during emersion to CO_2 concentrations. The present study aimed to find the relationship of the emersed photosynthesis with the CO_2 concentrations, and to assess the ecological impacts of increasing atmospheric CO_2 concentration on the intertidal macroalgae.

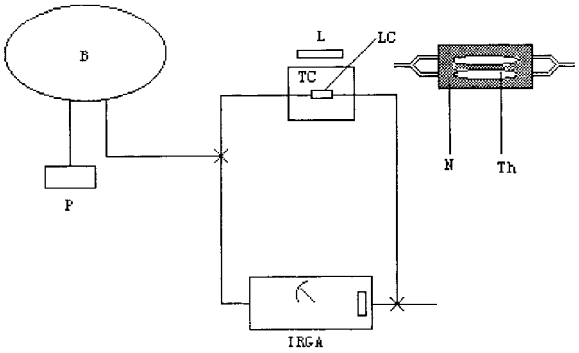

Figure 1. Outline of the system for measuring the photosynthesis. B, air bag; IRGA, infrared gas analyzer; L, fluorescent light source; LC, assimilation chamber; N, polyethylene monofilament net; P, pump; Th, thallus; TC, temperature-controlling cabinet.

Materials and methods

Three species, *Enteromorpha linza* (L.) J. Ag. (a green alga), *Ishige okamurae* Yendo (a brown alga) and *Gloiopeltis furcata* (P. et. R.) J. Ag. (a red alga) were used for the experiments. All the species are distributed in the middle to upper parts of the intertidal zone and were collected from the coast of Ibaraki Prefecture of Japan during the period from May 16 to June 10, 1997. Samples with seawater in plastic bags were transported by cooled icebox in 2–3 h to the laboratory. Wounded or unhealthy individuals were rejected, and only healthy samples were maintained in a water tank (0.1 m^3) with filtered seawater under dim light at 18–20 °C. Half of the seawater was renewed every day. Six to fifteen individuals were used for each measurement. Photosynthesis was measured at 20, 25 and 30 °C and 300 μmol photons m^{-2} s^{-1}. Photosynthesis of *E. linza*, *G. furcata* and *I. okamurae* in air was saturated at this light level.

The rates of photosynthetic CO_2 uptake by the algae exposed to air were determined by infrared gas analysis. The system for measuring photosynthesis consists of an infrared gas analyzer (IRGA) (Horiba ASSA-1100), a Plexiglas assimilation chamber (16.5 × 8.5 × 3 cm), light source, temperature-controlled cabinet, air bag and connecting tubes (Figure 1). The assimilation chamber with algal thalli in it was maintained in the temperature-controlled cabinet; air of known CO_2 concentration was supplied from the air bag and flushed through the assimilation chamber before the system was closed. The CO_2 concentration in the air bag was obtained by injecting pure CO_2 before pumping outdoor air into it. In the closed system, CO_2 concentration was reduced due to photosynthesis, and the photosynthetic rates changed as a function of changing CO_2 concentrations, which was recorded with time. Net photosynthetic rates were calculated with the following formula:

$$P_{\mathrm{n}} = \frac{(C_j - C_i) \times V \times 60 \times 273}{(t_j - t_i) \times W \times 22.4 \times (273 + T)}, \qquad (1)$$

where P_{n} [μmol CO_2 g(f. wt)$^{-1}$ h^{-1}] is the net photosynthetic rate at CO_2 concentration of (C_j + C_i)/2, C_j and C_i are the CO_2 concentrations at time t_j and t_i (min), W is the initial fresh weight (g) of samples used, V_l is the volume of the closed system, V, including the inner part of the IRGA, was determined provided that the CO_2-saturated photosynthetic rate in the closed system is consistent with that in the open system under the same conditions. It was estimated as:

$$V = \frac{(X_{\mathrm{o}} - X_{\mathrm{i}}) \times F \times (t_j - t_i)}{(C_j - C_i)}, \qquad (2)$$

where X_{i} and X_{o} indicate the CO_2 concentrations of inlet and outlet air through the assimilation chamber at flow rate of F (l min^{-1}), determined in the open system with the same amount of samples as in the closed system; other symbols for the closed system are the same as in Equation (1).

Water loss was estimated as follows: WL (%) = (W_{i} – W_{t})/W_{i} × 100, where W_{i} is the initial wet weight that was determined after removing excessive water drops on the algal surface by tapping or shaking the samples; W_{t} the instantaneous weight determined at certain time intervals during the measurement.

Results

Photosynthesis of *E. linza, G. furcata* and *I. okamurae* was not saturated at the present atmospheric CO_2 level (15.6 μM), and tended to be saturated at CO_2 concentrations above 30 μM CO_2 when the algae were wet (Figure 2). However, more CO_2 was required for the photosynthesis to be saturated when the algae were dehydrated: $K_{[mCO_2]}$ increased with increasing desiccation, showing that increased water loss lowers the algae CO_2 affinity. At the present level of CO_2 concentration, when the algae were wet, relative photosynthesis was 65%, 74% and 61% saturated in *E. linza, G. furcata* and *I. okamurae*, respectively. In *E. linza*, 70% water loss reduced the photosynthesis by 49–55%, 90% water loss resulted in CO_2 evolution at the present CO_2 level and only left 9% of the CO_2 uptake rate at doubled CO_2 concentration. In *G. furcata*, 30% water loss did not affect the photosynthesis while 60% water loss reduced it by 50–55%. Photosynthesis of *I. okamurae* also decreased with increased water loss, 40% water loss reduced it by 30% at the present CO_2 level and by 54% at doubled concentration; 60% water loss gave rise to negative and slightly positive photosynthesis at present and doubled CO_2 concentrations respectively.

Figure 3 shows the relationship of CO_2 compensation point (CO_2 CPP) to water loss. The CO_2 CPP increased with increased water loss, indicating that higher CO_2 concentrations are needed for dehydrated than for fully hydrated *E. linza, G. furcata* and *I. okamurae* to maintain photosynthesis positive. Fifty percent water loss did not result in negative photosynthesis at the present CO_2 level in any of the species at the temperature range of 20–30 °C except *G. furcata* at 30 °C . For *G. furcata* at 30 °C, 50% water loss brought the CO_2 CPP to 22 μM, indicating such a level of water loss at the temperature results in negative photosynthesis at the present CO_2 level. Effects of temperature on the CO_2 CPP were not obvious in *E. linza* and *I. okamurae*; however, increased temperature raised the CO_2 CPP in *G. furcata*, the CO_2 CPP at 50% water loss was 4, 8 and 22 μM, respectively, at 20, 25 and 30 °C.

Discussion

The present study showed that photosynthesis in air of *E. linza, G. furcata* and *I. okamurae* is CO_2-limited at the present atmospheric CO_2 concentration; higher CO_2 concentrations were needed to saturate the photosynthesis when the algae were desiccated. The CO_2 concentration for saturating photosynthesis, the CO_2 compensation point and $K_{[mCO_2]}$ increased with increasing desiccation, showing that increased water loss lowers the algae's CO_2 affinity. This pattern was true for all of the species, though they showed specific differences in the way their responses were affected by the level of water loss and temperature. Elevation of CO_2 from the present level (15.6 μM) to its doubled concentration (31.2 μM), which has been assumed to happen in the next century, brought about 25–40% increase in the photosynthesis of the three species at moderate levels of water loss while exposed. Relationship of CO_2 compensation point to water loss shows a trend that increased water loss would lead to negative photosynthetic production at the present day CO_2 level. *E. linza, I. okamurae* and *G. furcata* are usually exposed daily for 3 to 5 h at low tide, and their photosynthesis is subject to environmental constraints in air different from those in water, which can result in reduced or even negative production during the emersion period by the macroalgae at the present day CO_2 concentration.

It is of general concern whether the photosynthesis of the intertidal macroalgae is also CO_2-limited while submerged when the tide is high. The present day inorganic carbon composition of seawater has been regarded as not limiting the photosynthesis of marine macroalgae when submerged (Beer & Kock, 1996), albeit growth enhancement by enriched CO_2 has been reported for some red algae (Gao et al., 1991, 1993a). Most macroalgae use both HCO_3^- and CO_2 (Maberly et al., 1992; Gao & McKinley, 1994), utilization of HCO_3^- is either assisted by the dehydration via surface-bound carbonic anhydrase or HCO_3^- transport via anion exchange in some species (Larsson et al., 1997). However, for the periods of emersion at low tide when CO_2 is the only carbon source, the intertidal species may use only CO_2 when they photosynthesize in air. Maximal length of such an exposure can be as long as 5–7 h, during this period the algae lose extracellular and then intracellular water due to desiccation. Increasing atmospheric CO_2 will enhance CO_2-limited photosynthesis during such a period.

With an increase in CO_2 plants would differ in growth and competitive interactions (Bowes, 1993). We propose that CO_2 rise can benefit macroalgae, especially those suffering longer desiccation at low tide. The influence of CO_2 combined with that of sea-level rise associated with global warming can be expected

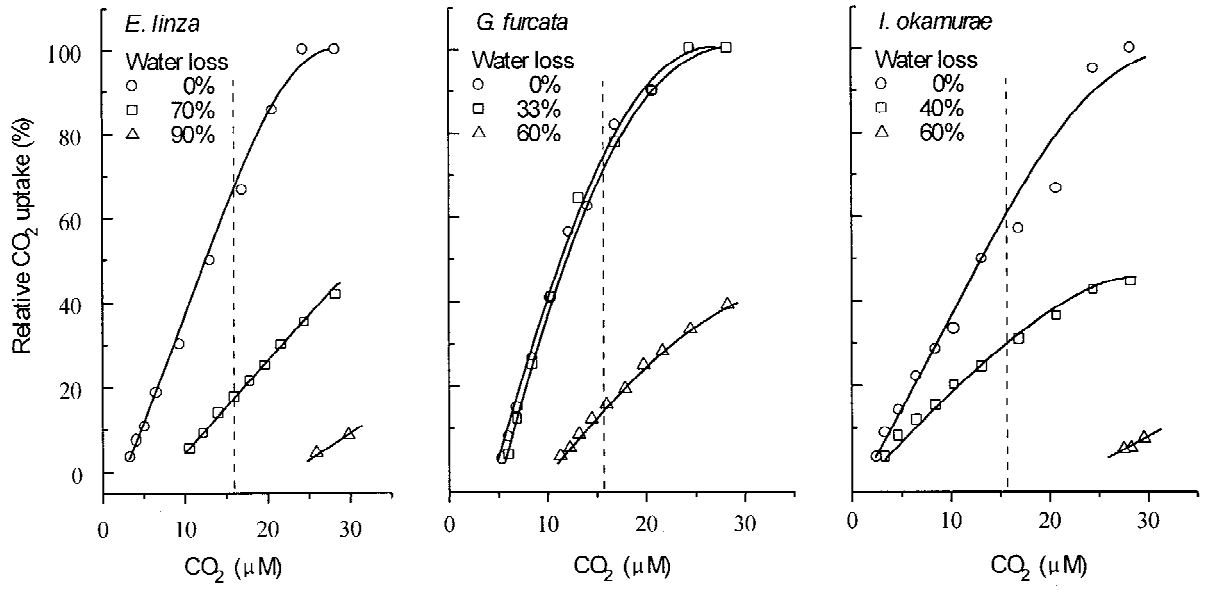

Figure 2. Photosynthetic CO_2 uptake as a function of CO_2 concentrations and desiccation (water loss) when *E. linza*, *G. furcata* and *I. okamurae* photosynthesized in air at 25°C; the maximal rates of photosynthetic CO_2 uptake were 112.6, 7.8 and 17.3 μmol CO_2 g (f.wt)$^{-1}$h^{-1} for *E. linza*, *G. furcata* and *I. okamura*, respectively. Six to fifteen individuals were used for each measurement. The dashed lines indicate the present day CO_2 level.

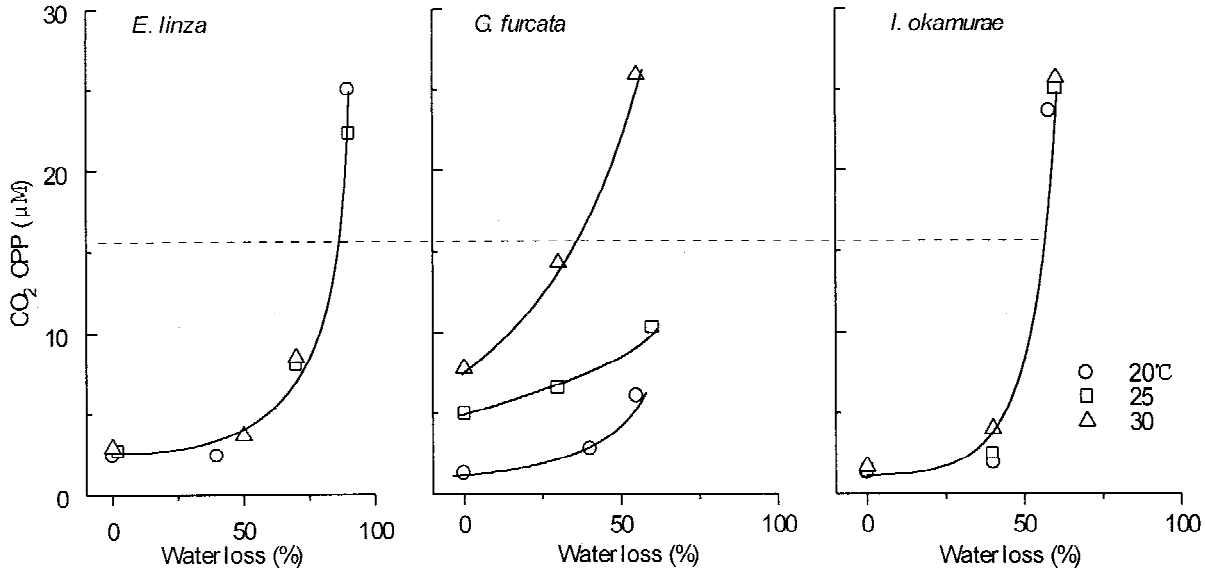

Figure 3. Relationship of CO_2 compensation point (CO_2 CPP) of *E. linza*, *G. furcata* and *I. Okamura* with desiccation (water loss), determined at 20, 25 and 30 °C. Six to fifteen individuals were used for each measurement. The dashed lines indicate the present day CO_2 level.

to bring about changes in succession and zonation of intertidal macroalgae.

Acknowledgements

This study was funded by the Natural Science Foundation of China (No. 39830060 and No. 39625002), by The Chinese Academy of Sciences ('BAIREN JIHUA', One Hundred Talents Program) and by the Research Fund for the Centennial Anniversary, Tokyo University of Fisheries of Japan. We thank Ms K. Matsuyama for her assistance in sampling.

References

Beer, S. & E. Koch, 1996. Photosynthesis of marine macroalgae and seagrasses in globally changing CO_2 environments. Mar. Ecol. Prog. Ser. 141: 199–204.

Beer, S. & B. Schragge, 1987. Photosynthetic carbon metabolism in *Enteromorpha compressa* (Chlorophyta). J. Phycol. 23: 580–584.

Bidwell, R. G. S. & J. McLachlan, 1985. Carbon nutrition of seaweeds: photosynthesis, photorespiration and respiration. J. exp. mar. Biol. Ecol. 97: 287–294.

Bowes, G., 1993. Facing the inevitable: plants and increasing atmospheric CO_2. Annu. Rev. Plant Physiol. Plant mol. Biol. 44: 309–332.

Brinkhuis, B. H., N. R. Tempel & R F. Jones, 1976. Photosynthesis and respiration of exposed salt-marsh fucoids. Mar. Biol. 34: 349–359.

Charpy-Roubaud, C. & A. Sournia, 1990. The comparative estimation of phytoplanktonic, microphytobenthic and macrophytobenthic primary production in the oceans. Mar. Microb. Food Webs 4: 31–57.

Gao, K. & Y. Aruga, 1987. Preliminary studies on the photosynthesis and respiration of *Porphyra yezoensis* under emersed conditions. J. Tokyo Univ. Fish. 47: 51–65.

Gao, K. & K. McKinley, 1994. Use of macroalgae for marine biomass production and CO_2 remediation: a review. J. appl. Phycol. 6: 45–60.

Gao, K., Y. Aruga, K. Asada & M. Kiyohara, 1993a. Influence of enhanced CO_2 on growth and photosynthesis of the red algae *Gracilaria* sp. and *G. chilensis*. J. appl. Phycol. 5: 563–571.

Gao, K., Y. Aruga, K. Asada & M. Kiyohara, 1993b. Calcification in the articulated coralline alga *Corallina pilulifera*, with special reference to the effect of elevated atmospheric CO_2. Mar. Biol. 117: 129–132.

Gao, K., Y. Aruga, K. Asada, T. Ishihara, T. Akano & M. Kiyohara, 1991. Enhanced growth of the red alga *Porphyra yezoensis* Ueda in high CO_2 concentrations. J. appl. Phycol. 3: 355–362.

Gattuso, J. P., C. E. Payri, M. Pichon, B. Delesalle & M. Frankignoulle, 1997. Primary production, calcification, and air-sea CO_2 fluxes of a macroalgal-dominated coral reef community (Moorea, French Polynesia). J. Phycol. 33: 729–738.

Hein, M. & K. Sand-Jensen, 1997. CO_2 increases oceanic primary production. Nature 388: 526–527.

Johnson, W. S., A. Gison, S. L. Gulmon and H A. Mooney, 1974. Comparative photosynthetic capacities of intertidal algae under exposed and submerged conditions. Ecology 55: 450–453.

Johnston, A. M. & J. A. Raven, 1986. The analysis of photosynthesis in air and water in *Ascophyllum nodosum* (L.) Le Jolis. Oecologia 69: 288–295.

Larsson, C., L. Axelsson, H. Ryberg & S. Beer, 1997. Photosynthetic carbon utilization by *Enteromorpha intestinalis* (Chlorophyta) from a Swedish rockpool. Eur. J. Phycol. 32: 49–54.

Lignell, A. & M. Pedersén, 1989. Effects of pH and inorganic carbon concentration on growth of *Gracilaria secundata*. Br. phycol. J. 24: 83–89.

Maberly, S. C., J. A. Raven & A. M. Johnston, 1992. Discrimination between ^{12}C and ^{13}C by marine plants. Oecologia 91: 481–492.

Madsen, T. V. & S. C. Maberly, 1990. A comparison of air and water as environments for photosynthesis by the intertidal alga *Fucus spiralis* (Phaeophyta). J. Phycol. 26: 24–30.

Oates, B. R., 1985. Photosynthesis and amelioration of desiccation in the intertidal saccate alga *Colpomenia peregrina*. Mar. Biol. 89: 109–119.

Oates, B. R., 1986. Components of photosynthesis in the intertidal saccate alga *Halosaccion americanum* (Rhodophyta, Palmariales). J. Phycol. 22: 217–223.

Oates, B. R. & S. N. Murray, 1983. Photosynthesis, dark respiration and desiccation resistance of the intertidal seaweeds *Hesperophycus harveyanus* and *Pelvetia fastigiata* f. *gracilis*. J. Phycol. 19: 371–380.

Quadir, A., P. J. Harrison & R. E. DeWreede, 1979. The effects of emergence and submergence on the photosynthesis and respiration of marine macrophytes. Phycologia 18: 83–88.

Raven, J. A., 1997. Inorganic carbon aquisition by marine autotraphs. Adv. bot. Res. 27: 85–209.

Raven, J. A. & A. M. Johnston, 1991. Photosynthetic inorganic carbon acquisition by Prasiola *stipitata* (Prasiales, Chlorophyta) under emersed and submersed conditions: relationship to the taxonomy of *Prasiola*. Br. Phycol. J. 26: 24–25.

Riebesell, U., D. A. Wolf-Gladrow & V. Smetacek, 1993. Carbon dioxide limitation of marine phytoplankton growth rates. Nature 361: 249–251.

Surif, M. B. & J. A. Raven, 1990. Photosynthetic gas exchange under emersed conditions in eulittoral and normally submerged members of the Fucales and Laminariales: interpretation in relation to C isotope ratio and N and water use efficiency. Oecologia 82: 68–80.