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PHYSIOLOGICAL RESPONSES OF SEAWEEDS TO ELEVATED ATMOSPHERIC CO_2 CONCENTRATIONS

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1. Introduction

The atmospheric CO_2 concentration has been rising since the industrial revolution, and will continue to rise from the present 375 to about 1,000 ppmv by 2100 (Pearson and Palmer, 2000), increasing dissolution of CO_2 from the air and altering the carbonate system of Surface Ocean (Stumm and Morgan, 1996; Takahashi et al., 1997; Riebesell et al., 2007). For example, an increase in atmospheric CO_2 from 330 to 1,000 ppmv will lead to an increase in CO_2 concentration from 12.69 to 38.46 μM in seawater (at 15°C and total alkalinity of 2.47 eq m^{-3}) and an increase in the concentration of dissolved inorganic carbon (DIC, i.e., $CO_{2(aq)}$, HCO_3^-, and CO_3^{2-}) from 2.237 to 2.412 mM, with a concurrent decrease in the pH of the surface seawater from 8.168 to 7.735 (Raven, 1991; Stumm and Morgan, 1996). Increasing atmospheric CO_2 and its associated changes in the carbonate system can influence the physiology and ecology of seaweeds.

Seaweeds (Chlorophyta, Rhodophyta, and Phaeophyta) are usually distributed in intertidal and subtidal zones of coastal waters. They play an important role in the coastal carbon cycle (Reiskind et al., 1989) and contribute remarkably to sea-farming activities. The rate of primary production of some species is comparable with those of the most productive land plants; therefore, seaweeds have a great potential for CO_2 bioremediation (Gao and Mckinley, 1994). On the other hand, increasing pCO_2 in seawater would affect physiology of seaweeds. Therefore, a number of studies have been performed to envisage the impacts of CO_2 enrichment on photosynthesis, growth, nutrients metabolism, and cell components of seaweeds. Results showed that increased CO_2 concentration may enhance, inhibit, or not affect the growth of the species investigated. This work is intended to examine how the macroalgal species respond and acclimate to elevated CO_2 levels.

2. Inorganic Carbon Limitation

The effects of elevated CO_2 concentrations on seaweeds largely depend on the degree of carbon limitation present in natural systems. Photosynthesis of seaweeds would be severely limited under current atmospheric conditions if it were dependent only on diffusional entry of CO_2 from the medium to the site of fixation via the carbon-assimilating enzyme Rubisco. There are several aspects of CO_2 limitation of carbon assimilation in seaweeds (Beardall et al., 1998): (1) rather low dissolved CO_2 concentration; (2) low diffusion rate of CO_2 in seawater, being four orders of magnitude slower than in air; (3) the slow spontaneous formation of CO_2 from HCO_3^- dehydration; and (4) the high K_m values (40–70 μM) of Rubisco of algae. Nevertheless, photosynthesis in the investigated species can be fully or nearly saturated with the current ambient dissolved inorganic carbon (Ci) composition because of the presence of CO_2-concentrating mechanisms (CCMs) that enable the algae to efficiently utilize the bulk HCO_3^- pool in seawater (Beer, 1994; Beer and Koch, 1996; Raven, 1997; Larsson and Axelsson, 1999; Zou et al., 2004; Giordano et al., 2005), which is about 150 times more abundant than free CO_2. Some species, however, exhibit Ci-limited photosynthesis in natural seawater (e.g., Johnston et al., 1992; Andría et al., 1999a; Zou et al., 2003).

HCO_3^- is usually dehydrated extracellularly as mediated by periplasmic carbonic anhydrase (CA) to release CO_2, which is then taken up into the cell. Another important approach for Ci acquisition of algae is the active uptake of HCO_3^- through the plasma membrane facilitated by an anion exchange protein (Drechsler et al., 1993, 1994; Axelsson et al., 1995). Additionally, H^+-ATPase-driven HCO_3^- uptake has also been recognized in several marine seaweeds (Choo et al., 2002; Snoeijs et al., 2002). Seaweeds show different capacities to take advantage of the HCO_3^- pool in seawater (Axelsson and Uusitalo, 1988; Maberly, 1990; Mercado et al., 1998). Therefore, they can exhibit heterogeneous, often species-specific responses to elevated CO_2. Their physiological responses to elevated CO_2 levels can also depend on their acclimation strategies and the environmental constraints under which CO_2 enrichment is imposed.

3. Growth

When juveniles of *Porphyra yezoensis* germinated from the chonchospores were grown at enriched CO_2 levels of 1,000 or 1,600 ppmv for 20 days, their growth was significantly enhanced (Gao et al., 1991; Fig. 1). Similar findings were reported in *Gracilaria* sp., *Gracilaria chilensis*, and *Hizikia fusiforme* (Gao et al., 1993a; Zou, 2005). Although these species are capable of using bicarbonate, they still showed carbon-limited photosynthetic rates in natural seawater. Growth of a nonbicarbonate-user, the red alga *Lomentaria articulata*, was stimulated by enriched CO_2 (Kübler et al., 1999). The enhancement could be attributed to the accelerated photosynthetic carbon fixation by increasing Ci availability or the depression of photorespiration by elevating the ratio of CO_2 to O_2 in the culture medium. It was interesting that growth of a green alga, *Ulva rigida*, which showed efficient ability of HCO_3^- utilization and
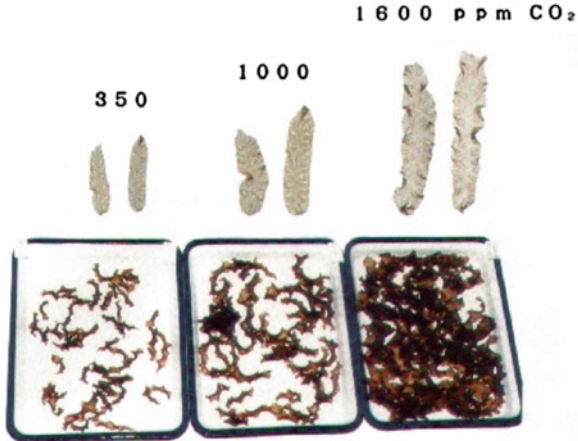
Figure 1. Enhanced growth of *Porphyra yezoensis* when 50 juveniles each (germinated from the same bunch of chonchospores released from the same chonchocelis, about 5 mm long at the beginning of the culture) were grown at different CO_2 concentrations in aeration. The photo images were taken after 20 days culture (Gao et al., 1991).

saturated photosynthesis at the current Ci concentration of seawater (Björk et al., 1993; Mercado et al., 1998), was also enhanced at high CO_2 concentrations (Björk et al., 1993; Gordillo et al., 2001). Such an enhancement of growth was suggested to be caused by the enhanced N-assimilation (Gordillo et al., 2001), but could also be attributed to downregulation of HCO_3^- uptake and consequent energy saving for its operation. On the other hand, a decrease in growth rate caused by elevated CO_2 has been reported in *G. tenuistipitata* (Garcìa-Sánchez et al., 1994), *P. leucostica* (Mercado et al., 1999), and *P. linearis* (Israel et al., 1999). Such an inhibition of growth was associated with lowered photosynthetic activity even measured at high CO_2 concentrations (Garcìa-Sánchez et al., 1994). However, such a negative effect could also be caused by acidification of the medium (Israel et al., 1999). A more recent study by Israel and Hophy (2002) reported that the growth rates of 13 species (representing Chlorophyta, Rhodophyta, and Phaeophyta) cultivated in normal seawater were comparable with their growth in CO_2-enriched seawater. The authors ascribed such nonresponsive behavior to the presence of CCMs that rely on the utilization of HCO_3^-. Obviously, researches show that enrichment of CO_2 in seawater may affect, positively, neutrally, or negatively, the growth of seaweeds in direct or indirect ways.

4. Photosynthesis

4.1. PHOTOSYNTHETIC Ci UTILIZATION

The response of macroalgal photosynthesis to elevated pCO_2 in seawater is species-specific. When cultured in high CO_2, the light-saturated photosynthetic rate was reduced in *Fucus serratus* (Johnston and Raven, 1990), *G. tenuistipitata*

(Garcìa-Sánchez et al., 1994), and *P. yezoensis* (Gao, unpublished data) when measured at normal Ci of seawater. When the photosynthetic rate was measured at elevated DIC levels, it was significantly higher in the thalli grown at enriched CO_2 levels in *P. yezoensis* (Gao et al., 1991) and *Gracilaria* sp. (Andría et al., 1999b). In *P. leucostica*, Mercado et al. (1999) found no significant difference between the maximal gross photosynthetic rates of the thalli grown at enriched and current inorganic carbon concentrations.

The photosynthetic affinity for Ci and the capacity of HCO_3^- utilization are usually lowered in seaweeds following exposures to high CO_2 (Johnston and Raven, 1990; Björk et al., 1993; Mercado et al., 1997; Andría et al., 1999a, b; Zou et al., 2003). Growing the cells at high CO_2 levels decreased activity of the external (periplasmic) or total CA activity in *Ulva* sp. (Björk et al., 1993), *G. tenuistipitata* (Garcìa-Sánchez et al., 1994), *P. leucosticta* (Mercado et al., 1997), and *H. fusimorme* (Zou et al., 2003). Such a decrease reflects a decline in the capacity of HCO_3^- utilization. Israel and Hophy (2002) showed that the enzymatic features of Rubisco did not differ in the seaweeds when compared between the CO_2-enriched and control cultures, though enrichment of CO_2 was reported to decrease the content of Rubisco in *G. tenuistipitata* (Garcìa-Sánchez et al., 1994), *Gracilaria* sp. (Andría et al., 1999a), and *P. leucosticta* (Mercado et al., 1997).

4.2. PHOTOCHEMICAL EFFICIENCY

Photosynthetic acclimation in seaweeds to high levels of Ci generally resembles their responses to high irradiances, resulting in a decrease in pigment contents. For example, the phycobiliprotein (phycoerythrin and phycocyanin) and Chl *a* contents were reduced in *Gracilaria* sp. (Andría et al., 1999b, 2001), *G. tenuistipitata* (Garcìa-Sánchez et al., 1994), and *P. leucosticta* (Mercado et al., 1999) grown at high levels of Ci than those at normal Ci level. On the other hand, both maximum quantum yield and effective quantum yield were downregulated in *P. leucostica* when grown under high Ci conditions (Mercado et al., 1999), suggesting that enriched CO_2 lowered the demand of energy for the HCO_3^- utilization mechanism.

4.3. EMERSED PHOTOSYNTHESIS OF INTERTIDAL SEAWEEDS

Intertidal seaweeds experience continual alternation of living in air and in water as the tidal level changes. Their photosynthesis undergoes dramatic environmental changes between the aquatic and terrestrial exposures. When the tide is high, they are submerged in seawater, where HCO_3^- pool is available for their photosynthesis (Beer and Koch, 1996; Beardall et al., 1998). When the tide is low, intertidal seaweeds are exposed to air, large buffering reservoir of HCO_3^- in seawater is no longer present, and atmospheric CO_2 becomes the only exogenous carbon resource for their photosynthesis. The acquisition of CO_2 is less constrained in air than in seawater, through which CO_2 diffuses about 10,000 times slower (Raven, 1999). However, this constraint can be offset by the abundance of HCO_3^-, as many intertidal algae can

use HCO_3^- as the exogenous inorganic carbon source for photosynthesis (Maberly, 1990; Gao and McKinley, 1994). Thus, carbon limitation during photosynthesis in intertidal species may be potentially more important in air than in water.

It is known that intertidal seaweeds can tolerate the emersed conditions, and the photosynthesis during emersion contributes significantly to their total carbon fixation budget (e.g., Gao and Aruga, 1987; Maberly and Madsen, 1990). Our previous works (Gao et al., 1999; Zou and Gao, 2002; Zou and Gao, 2004a, b, 2005; Zou et al., 2007) showed that elevated atmospheric CO_2 might have a fertilizing effect increasing photosynthesis while exposed to air at low tide in most of the tested species, i.e. the red seaweeds *P. haitanensis, Gloiopeltis furcata*, and *Gigartina intermedia*, the brown seaweeds *Ishige okamura*, *H. fusiformis*, and *Sargassum hemiphyllum*, and the green seaweeds *Enteromopha linza* and *Ulva lactuca*. The relative photosynthetic enhancement by the elevated CO_2 levels increased with desiccation, although the absolute photosynthetic rate decreased with desiccation. The enhancement of daily photosynthetic production by elevated CO_2 concentration during emersion differs among species owing to their zonational depths and exposure durations and the daily timing of emersion (Gao et al., 1999; Zou and Gao, 2005; Zou et al., 2007). Additionally, the CO_2 compensation points increased with enhanced desiccation, with higher CO_2 concentrations required to maintain positive photosynthesis (Gao et al., 1999; Zou and Gao, 2002, 2005).

5. Calcification

It is estimated from more than two million surveys that the oceans have absorbed more than one third of the anthropogenic CO_2 released to the atmosphere (Sabine et al., 2004). With increasing atmospheric CO_2 concentration, CO_2 dissolves in seawater to reach new equilibrium in the carbonate system. This leads to an increase in the concentrations of HCO_3^- and H^+ and a decrease in the concentration of CO_3^{2-} and of saturation state of calcium carbonate (Gattuso et al., 1999; Gattuso and Buddemeier, 2000; Caldeira and Wickett, 2003; Orr et al., 2005). The surface water of the ocean is known to have been acidified by 0.1 pH unit (corresponding to a 30% increase of H^+) since 1800 (Orr et al., 2005), and will be further acidified by another 0.3–0.4 unit (about 100–150% increase of H^+) by 2100 (Brewer, 1997; Caldeira and Wickett, 2003). Such an ocean-acidifying process has been suggested to harm marine-calcifying organisms by reducing the rate of calcification of their skeletons or shells (e.g., Gao et al., 1993b; Gattuso et al., 1999; Riebesell et al., 2000; Orr et al., 2005).

In the coastal waters where seaweeds are distributed, pH of seawater fluctuates within a larger range than pelagic waters because of inputs from terrestrial systems and fisheries. Nevertheless, additional CO_2 input can still affect the biological activities in coastal waters, because ocean acidification will lower the pH regimes, shifting the pH range to a lower one. Therefore, increased pCO_2 and decreased pH and CO_3^{2-} will affect calcifying seaweeds. Gao et al. (1993b) showed that enrichment of CO_2 to 1,000 and 1,600 ppmv in aeration inhibited the calcification in the

articulated coralline alga *Corallina pilulifera*. It has also been shown that the increase in CO_2 concentrations significantly slowed down calcification of temperate and tropical corals and coralline macroalgae (Gattuso et al., 1998; Langdon et al., 2000). For the marine-calcifying phytoplankton *Emiliania huxleyi*, calcification was reported to be reduced by the enriched CO_2 (Riebesell et al., 2000), while a recent study showed that its calcification increased with elevated CO_2 (Iglesias-Rodriguez et al., 2008). On the other hand, when pH was controlled at a constant level, elevated concentrations of DIC enhanced the calcification of *Bossiela orbigniana* (Smith and Roth, 1979) and *C. pilulifera* (Gao et al., 1993b).

6. Nitrogen Metabolism

Zou (2005) reported that both the nitrate uptake rate and the activity of nitrate reductase (NR) in the brown algae *H. fusiforme* were increased following cultures at high CO_2 levels. It was also shown that elevated CO_2 concentrations in culture stimulated the uptake of NO_3^- in *Gracilaria* sp. and *G. chilensis* (Gao et al., 1993a), *Ulva lactuca* (Zou et al., 2001), and *U. rigida* (Gordillo et al., 2001), and enhanced the activity of NR in *P. leucosticta* (Mercado et al., 1999) and *U. rigida* (Gordillo et al., 2001, 2003). This indicates that elevated CO_2 concentrations can enhance nitrogen assimilation, as more nitrogen is required to support higher growth rate. The regulation of NR activity in seaweed by CO_2 might be through a direct action on de novo synthesis of the enzyme, rather than through physiological consequences in carbon metabolism as occurring in terrestrial higher plants (Gordillo et al., 2001, 2003). Contrarily, decreased uptake rate of NO_3^- by high CO_2 in *G. tenuistipitata* (Garcìa-Sánchez et al., 1994) and *G. gaditana* (Andría et al., 1999b) was also reported. Mercado et al. (1999) stated that NO_3^- uptake and reduction might be uncoupled when algae are grown at high CO_2. Responses of macroalgal nitrogen assimilation to elevated CO_2 could be species-specific; however, the results from different studies might be also generated from different culture systems or methods.

7. C/N Ratio

Growth under enrichment of CO_2 would alter the cellular components of seaweeds. Contents of soluble proteins and phycobiliprotein were decreased in *Graciaria tenuisitipitata* (García-Sánchez et al., 1994), *Gracilaria* sp. (Andría et al., 1999b), and *P. leucosticta* (Mercado et al., 1999) when they were grown at high DIC levels. In contrast, the content of soluble carbohydrate was increased in *Gracilaria* sp. (Andría et al., 1999b). As a result of these changes, C/N ratios were increased in the seaweeds grown at elevated CO_2 levels (García-Sánchez et al., 1994; Kübler et al., 1999; Mercado et al., 1999). Although phycobiliprotein, soluble proteins, and Rubisco contents were found to decrease under DIC-enriched conditions, internal N content was not significantly affected by the DIC levels. Andría et al. (1999b)

thereby suggested that the exposure and acclimation to high CO_2 would involve the reallocation of resources, such as N, away from Rubisco and other limiting components (electron transport) towards carbohydrate synthesis and nonphotosynthetic processes.

8. Summary

Atmospheric CO_2 rise leads to a proportional increase in pCO_2 of seawater and alters the carbonate chemistry, reducing the carbonate ions and pH while increasing that of bicarbonate. Physiological responses of seaweeds to elevated CO_2 concentrations are highly variable, depending on the species, growing conditions, and duration of CO_2 enrichment. In the species investigated, growth was enhanced, inhibited, or not affected by enrichment of CO_2, while photosynthetic performance varied according to Ci acquisition mechanisms or the acclimation strategies. Usually, net photosynthesis was enhanced in elevated DIC levels for the species with less efficiency in bicarbonate utilization or CCMs. Growing the seaweeds in high CO_2 downregulated their CCMs and possibly the electron transport demanded for its operation. On the other hand, calcification of calcifying seaweeds is negatively affected; nitrogen metabolism and the cellular C/N ratio would be increased in high-CO_2-grown cells. For the intertidal species, large buffering reservoir of HCO_3^- in seawater is no longer present and atmospheric CO_2 becomes the only exogenous carbon resource for their photosynthesis at low tide, elevation of atmospheric CO_2 might have a fertilizing effect, increasing their photosynthesis during emersion. More research efforts on biochemical and molecular aspects for a wider range of species grown at high CO_2/low pH conditions are needed to further evaluate the impacts of increasing atmospheric CO_2 concentrations on seaweeds. At the same time, physiological approaches are required to distinguish the effects of high CO_2 from that of lowered pH.

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10. References

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