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Impacts of increased atmospheric CO_2 concentration on photosynthesis and growth of micro- and macro-algae

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Marine photosynthesis drives the oceanic biological CO_2 pump to absorb CO_2 from the atmosphere, which sinks more than one third of the industry-originated CO_2 into the ocean. The increasing atmospheric CO_2 and subsequent rise of pCO_2 in seawater, which alters the carbonate system and related chemical reactions and results in lower pH and higher HCO_3^- concentration, affect photosynthetic CO_2 fixation processes of phytoplanktonic and macroalgal species in direct and/or indirect ways. Although many unicellular and multicellular species can operate CO_2-concentrating mechanisms (CCMs) to utilize the large HCO_3^- pool in seawater, enriched CO_2 up to several times the present atmospheric level has been shown to enhance photosynthesis and growth of both phytoplanktonic and macro-species that have less capacity of CCMs. Even for species that operate active CCMs and those whose photosynthesis is not limited by CO_2 in seawater, increased CO_2 levels can down-regulate their CCMs and therefore enhance their growth under light-limiting conditions (at higher CO_2 levels, less light energy is required to drive CCM). Altered physiological performances under high-CO_2 conditions may cause genetic alteration in view of adaptation over long time scale. Marine algae may adapt to a high CO_2 oceanic environment so that the evolved communities in future are likely to be genetically different from the contemporary communities. However, most of the previous studies have been carried out under indoor conditions without considering the acidifying effects on seawater by increased CO_2 and other interacting environmental factors, and little has been documented so far to explain how physiology of marine primary producers performs in a high-CO_2 and low-pH ocean.

CO_2, photosynthesis, growth, phytoplankton, macroalgae

Ecological effects of increasing atmospheric CO_2 concentration have been well studied in terrestrial plants[1,2]. Growth and photosynthesis are known to be enhanced by increased atmospheric CO_2 concentrations in most of the investigated terrestrial plants, which take up CO_2 via diffusion[3,4]. Algae (phytoplanktonic and macroalgal species), being distributed in a variety of environments and carboxylating CO_2 with the same enzyme (Rubisco) as in higher plants, play an important role as primary producers in aquatic ecosystems. However, their responses to increased atmospheric CO_2 concentrations have been understood to much less extent[5] in contrast to the higher plants. CO_2 acquisition processes are more complicated in algae than in higher plants; the $K_{1/2}$ for CO_2 of algal Rubisco ranges from 20 to 70 μmol·L^{-1}, varying with species[6]. Dissolved inorganic carbon exists in the form of CO_2, HCO_3^- and CO_3^{2-}, with the CO_2 concentration as low as 10—20 μmol·L^{-1}. In addition, the diffusion of CO_2 in water is about 10 thousand times slower than that in the air. Therefore, CO_2 concentrations in aquatic environments are usually not enough to saturate the carboxylation process. Although many algal species investigated so far possess CO_2-concentrating

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mechanisms (CCMs), which can raise intracellular CO_2 concentrations, their photosynthesis and growth are likely to be enhanced by increasing atmospheric CO_2 concentration.

1 Ocean and CO_2

When CO_2 is dissolved in waters, it combines with water to form carbonic acid, which disassociates to bicarbonate, then to carbonate ions to reach an equilibrium:

$$CO_2+H_2O = H_2CO_3; \quad (1)$$

$$H_2CO_3 = H^++HCO_3^-; \quad (2)$$

$$HCO_3^- = H^++CO_3^{2-}. \quad (3)$$

The coefficients K_0, K_1, K_2 respectively for the above reactions depend on temperature, salinity and pressure.

As indicated in the above reactions, H^+ concentration increases when CO_2 dissolves in water. However, adequate H^+ can reverse reaction (3) toward the left side, resulting in reduction of carbonate ions. The pH of the surface oceanic seawaters has been reduced by 0.1 U[7] due to the increased atmospheric CO_2 since industrial revolution, corresponding to 30% increase in the H^+ concentration. With further increase of CO_2 concentration in the atmosphere to 1000 ppmv (before 2100), pH of oceanic surface seawater will decrease by 0.3 0.4 U[7,8], which means an increase of H^+ by 100% 150%. The exchange of CO_2 between the sea and atmosphere depends on the dynamics of mixing. The dissolved CO_2 stays in the surface seawater (up to 100 m deep)for about 6 years on average. The mixing of seawater from surface to deep layers (1000 4000 m) usually occurs slowly, taking hundreds to thousands of years. This implies that CO_2 absorbed by the surface ocean will take hundreds to thousands of years to diffuse to deep layers. Studies show that 50% of the CO_2 taken up by the oceans since the industrial revolution still stays in the seawater up to 400 m deep[9]. Obviously, organisms in the surface ocean are exposed to a high-CO_2 environment. All of the photosynthetic organisms live in euphotic zones, their physiology may respond to the increased CO_2 as well as chemical changes related to the altered carbonate system and lowered pH. It is of general interests to know how marine algae as the primary producer of oceans respond to the increasing atmospheric CO_2 concentration.

2 Phytoplanktonic species

Marine phytoplankton contributes to about half of the global primary productivity[10]. The "biological CO_2 pump" driven by photosynthetic carbon fixation in seawater leads to continuous decrease of CO_2 concentration in seawater, thus promotes the absorption of CO_2 from atmosphere[11–13]. Although the concentration of dissolved inorganic carbon (DIC) is high (about 2 mmol/L) in seawater, its predominant form is HCO_3^-, and CO_2 accounts for less than 1% of it. In addition, CO_2 in seawater diffuses about 10 thousands times slower in water than in air, its availability is limited for photosynthetic carbon fixation[14–16]. Elevated atmospheric CO_2 concentrations have been considered to enhance the primary production by phytoplankton[17,18]. On the other hand, the extent of enhanced primary productivity at elevated atmospheric CO_2 levels has been questioned since most of the species investigated so far possess CCMs[19,20]. Effects of high concentration of CO_2 on photosynthetic characteristics and carbon acquisition mechanisms of phytoplankton have been studied extensively[21–26]. These studies demonstrated the physiological changes under high concentration of CO_2, such as decreased CO_2 affinity or increased CO_2 requirement for photosynthesis, inhibited carbonic anhydrase activity and depressed HCO_3^- transportation.

Recent studies showed that elevated CO_2 concentrations enhanced growth of some terrestrial cyanobacteria, freshwater green algae and some marine microalgae[15,18,26–28]. Riebesell et al.[29] demonstrated that CO_2 enrichment could increase the growth of several marine diatoms. Hein and Sand-Jensen[17] also showed that the phytoplankton primary production in open ocean was stimulated by increased concentrations of CO_2. However, some other researchers consider that atmospheric CO_2 rise and consequently elevated seawater pCO_2 would not stimulate phytoplankton primary productivity as previously reported, the enhancement should be less than 10%[19], since the operation of CCMs can compensate for low CO_2 concentrations[20]. However, enhancement of photosynthesis or growth under CO_2-enriched conditions can be species-specific, depending on their physiological characteristics, such as capability to actively take up HCO_3^- or CO_2 and different strategies for CCMs[26,30,31]. In *Skeletonema costatum*, photosynthesis becomes saturated at the present atmospheric CO_2 concentration (about 15 μmol)[30], while in coccolithophores like *Emiliania huxleyi*, photosynthesis increased with increased CO_2 concentrations[26]. Nevertheless, the acidification of seawater resulted from high CO_2 led to less calcification in the *Emiliania huxleyi*[32]. The balance between production of organic matter and calcification (sediment of inorganic matter) in such calcifying phytoplankton species could be affected by elevated CO_2 levels, thus influencing growth and species competition capability. In view of biochemical components, elevated CO_2 concentrations did not affect the contents of photosynthetic pigments[33], but reduced the activity of both extracellular (periplasmic) and intracellular carbonic anhydrase (which plays an important role in utilization of HCO_3^- in algae)[34,35], and altered C∶N∶P ratio[36–38].

It is generally accepted that increased atmospheric CO_2 concentrations can stimulate growth of many microalgal species, especially those with less ability of CCM. The enhanced growth rate could be achieved in two ways: (1) when the photosynthetic CO_2 fixation is limited by the availability of free CO_2 and dissolved inorganic carbon in water, elevated CO_2 levels in air could increase the concentration of CO_2 and DIC in water, thus promotes the photosynthesis; (2) the enriched CO_2 in water can lower the requirement of light energy for CCMs or HCO_3^- transportation, thus stimulates the growth under light-limited conditions[30]. For some CCM-species, high CO_2 might increase their photosynthetic sensitivity to high light (enhanced photoinhibition at high CO_2)[39]. At high CO_2 levels, the CCM does not function efficiently and requires less light energy for its operation, thus more energy goes to cause photoinhibition when light is at levels oversaturating photosynthesis. Since high CO_2 can reduce the activity of CCM-related enzymes, such as carbonic anhydrase, it is expected to down-regulate the capacity of CCMs if cells become acclimated to the high CO_2 level. Therefore, it is interesting to know if the enhanced photoinhibition at high CO_2 levels still function when the cells have acclimated to the CO_2-enriched conditions and when their CCMs become down-regulated.

3 Macroalgae

Marine macroaglae (Chlorophyta, Rhodophyta and Phaeophyta) occur commonly in the intertidal and subtidal zones of the coastal waters, playing an important role in the coastal carbon cycle[40]. Their primary productivity per unit of biomass or vegetation area is comparable to that of the most productive land plants and can be successfully cultivated on vast ocean surface, a great potential for CO_2 bioremdiation[5].

The effects of increased CO_2 concentrations on marine macroalgae largely depend on the degree of carbon limitation in natural systems. Photosynthesis of them would be severely limited under current atmospheric conditions if it were dependent only on the diffusional entry of CO_2 from the medium to the site of carboxylation, considersing the low CO_2 availability in seawater and the high K_m value (40—70 μmol/L) of Rubisco in macroalgae. However, photosynthesis in many macroalgae would be fully or nearly saturated with the current ambient dissolved inorganic carbon composition, because many of them investigated so far possess CCMs like terrestrial C_4 plants, being able to utilize, directly or indirectly, the bulk HCO_3^- pool in seawater[41–44]. Macroalgae species capable of using HCO_3^- might have an adaptive advantage over those only restricted to dissolved CO_2 when other essential nutrients are not limiting. HCO_3^- can be dehydrated extracellularly as mediated by membrane-bound carbonic anhydrase (CA) to produce CO_2, which is then taken up into the cell. Another important way is the direct HCO_3^- uptake through the plasma membrane facilitated by an anion exchange protein[45–47]. Marine macroalgae show variety of capacities and strategies to utilize external HCO_3^- pool in seawater, and thereby show different degrees of carbon limitation for photosynthesis in natural seawater. Therefore, they are anticipated to have heterogeneous, often species-specific responses to elevated CO_2.

Growth of some species, such as *Porphyra yezoensis*[48], *Gracilaria* sp., *G. chilensis*[49] and *Hizikia fusiforme*[50], was enhanced when grown at CO_2 levels 2—3 times the present atmospheric CO_2 concentration. These species were capable of using HCO_3^-, yet they showed carbon-limited photosynthesis in natural seawater. Growth of the red alga *Lomentaria articulata*, a non-bicarbonate-user, was stimulated by enriched CO_2 in aeration[51]. The growth enhancement in these algae by elevated CO_2 can be attributed to accelerated photosynthetic carbon fixation at increased Ci availability and/or depression of photorespiration at higher ratios of CO_2 to O_2 in the medium as well as within the cells. A green seaweed, *Ulva rigida*, which has efficient ability of HCO_3^- utilization, was found to have its photosynthesis saturated at the current Ci concentration of seawater[52,53], but its growth was still enhanced at enriched CO_2 levels[52,54]. Such an enhancement was attributed to stimulated N-assimilation rates at the high CO_2 level[54]. On the other hand, a decrease of growth rate caused by elevated CO_2 has also been reported, in *Gracilaria tenuistipitata*[55], *Porphyra leucostica*[56] and *Porphyra linearis*[57]. Such an inhibition of growth was considered due to the acidification of seawater[57]. A more recent study[58] examined growth rates of a large number of macroalgal species (representing Chlorophyta, Rhodophyta and Phaeophyta) under normal and CO_2-enriched conditions. Their growth responses depend on presence of CCMs. Consequently, the enrichment of CO_2 in seawater may affect positively, neutrally or negatively the growth of macroalgae in direct or indirect ways.

In addition to growth and photosynthesis, increasing CO_2 levels enhanced the activity of nitrogen reductase (NR) in *Porphyra leucosticta*[56], *Ulva rigida*[54] and *Hizikia fusiforme*[50] . The enhanced NR would support enhanced growth rate by providing adequate N required for the metabolism under the high CO_2 level. Elevated CO_2 to 1600 ppmv did stimulate the uptake of NO_3^- in *Gracilaria* sp. and *G. chilensis*[49] and *Hizikia fusiforme*[50]. Such a stimulation was also found in *Ulva lacuca*[59] and *U. rigida*[54]. Nevertheless, decreased uptake rate of NO_3^- at high CO_2 in *Gracilaria tenuistipitata*[55] and *G. gaditana*[60] was reported. Additionally, it was reported that increasing CO_2 levels inhibited calcification of coralline algae[61] and coral reefs, though net production was not affected in a coral reef dominated by macroalgae under natural, nutrient-limited conditions[62].

Macroalgal species that are distributed in intertidal zones are exposed to air periodically at low tides. These species photosynthesize in air when the tide is low, and in water at high tide, experiencing dramatic environmental changes between the aquatic and terrestrial exposures. Intertidal macroalgae have evolved to tolerate desiccation, high solar radiation and temperature extremes during the emersion[63,64]. Their photosynthetic performance may be significantly sensitive to the atmospheric CO_2 rise, since the gaseous CO_2 is the only carbon source for their photosynthesis while emersed at low tide[65,66]. Elevated CO_2 concentrations in air enhanced photosynthesis of the intertidal species in the gena of *Porphyra*, *Ulva, Ishige*, *Gloipeltis* and *Enteromorphra* [67-69]. Increased atmospheric CO_2 concentration to about 700 ppmv stimulated the photosynthesis by 30%—40% during the emersion. The relative photosynthetic enhancement by the elevated CO_2 increased with increased extent of desiccation[68–70]. Obviously, intertidal macroalgal species would benefit the most among the marine primary producers from increasing atmospheric CO_2 concentration.

4 Interaction of increasing atmospheric CO_2 concentration with other environmental factors

The ecological impacts of increasing CO_2 level depend on nutrients availability and other environmental factors, such as temperature and solar radiation. Nitrogen, phosphorus and iron are usually considered as key elements that limit marine primary production. The concentrations of these elements vary in different oceanic waters, therefore, may affect the physiological responses of phytoplankton to increased CO_2 levels. Global warming due to atmospheric CO_2 rise raises the surface seawater temperature, consequently enhances stratification and diminishes mixing in surface oceans. Promoted stratification will limit the transport of nutrients from deep layers to surface layer. On the other hand, in the waters where mixing is active, light can be the limiting factor for photosynthetic apparatus[20]. Most of the studies so far have been conducted under indoor-controlled conditions without considering the interactive effects of other factors, therefore, their results can hardly reflect the “real” CO_2 effects under changing solar radiation and nutrients-limited conditions. Nutrient limitation is a well known phenomenon in oceanic environments. Therefore, future studies need to focus on the impacts of elevated CO_2 levels under different concentrations or ratios of nutrients, such as N, P and Fe. Additionally, effects of solar UV radiation (280—400 nm) have not been considered in indoor-controlled experiments due to UV-free light sources or UV-opaque vessels. Our recent findings show that solar UVR, depending on the incident levels of solar radiation, can be either harmful or useful for photosynthetic carbon fixation by phytoplankton assemblages and its presence definitely raises the daily production in the coastal water columns[71,72]. Solar UVR can also alter the morphology and damage DNA of the economically important blue-green alga *Arthrospira platensis*[73,74]. Accordingly, ecological and physiological impacts of increased CO_2 concentrations need to be carried out under solar radiation because (1) cells may respond differently to solar UV radiation in high-CO_2 seawater; (2) presence of UVR may result in different physiological responses to changes in CO_2 concentrations.

Marine autotraphs possess different strategies to acquire inorganic carbon, increased pCO_2 and altered carbonate system in oceanic environments can affect competitions among species[75]. Phytoplankton population may adapt to the changing oceanic carbonate system associated with increasing atmospheric CO_2 rise, so that the evolved phytoplankton communities in future are likely to be genetically different from contemporary communities[76].

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