

Photosynthetic Responses to Inorganic Carbon in *Ulva lactuca* Under Aquatic and Aerial States

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Abstract: Intertidal macroalgae experience continual alternation of photosynthesis between aquatic state at high tide and aerial state at low tide. The comparative photosynthetic responses to inorganic carbon were investigated in the common intertidal macroalga *Ulva lactuca* L. along the coast of Shantou between aquatic and aerial state. The inorganic carbon dissolved in seawater at present could fully (at 10 or 20 μM) or nearly (at 30 μM) saturate the aquatic photosynthesis of *U. lactuca*. However, the aerial photosynthesis was limited by current ambient atmospheric CO_2 level, and such a limitation was more severe at higher temperature (20 - 30 $^\circ\text{C}$) than at lower temperature (10 $^\circ\text{C}$). The carbon-saturated maximal photosynthesis of *U. lactuca* under aerial state was much greater than that under aquatic state at 10 and 20 $^\circ\text{C}$, while the maximal photosynthesis under both states was similar at 30 $^\circ\text{C}$. The aerial values of K_m (CO_2) for photosynthesis were higher than the aquatic values. On the contrary, the values of apparent photosynthetic CO_2 conductance under aerial state were considerably lower than that under aquatic state. It was concluded that the increase of atmospheric CO_2 would enhance the primary productivity of *U. lactuca* through stimulating the photosynthesis under aerial state during low tide.

Key words: *Ulva lactuca*; photosynthesis; inorganic carbon; aquatic; aerial; atmospheric CO_2 rise

Marine macroalgae occur in the intertidal and subtidal zones of the coastal waters, contributing significantly to the productivity of the marine ecosystem and playing an important role in the coastal carbon cycle (Reiskind *et al.*, 1989). Some of them are more productive than the very productive land plants and can be successfully cultivated on vast ocean surface, a great potential for CO_2 bioremediation (Gao and Mckinley, 1994).

The ecological responses of biosphere to atmospheric CO_2 concentration increase mainly since anthropogenic effects (burning of fossil fuels; deforestation) are now of general concern (Bowes, 1993; Drake *et al.*, 1997). In terrestrial ecosystems, elevated atmospheric CO_2 may have a fertilizing effect resulting in increased photosynthesis and growth (mainly C_3 plants) (Bowes, 1993; Drake *et al.*, 1997; Makino and Mae, 1999). However, such an increase seems negligible in marine systems because most algae can use bicarbonate ions rather than CO_2 as their principal source for photosynthetic substrate (Gao and Mckinley, 1994; Raven, 1997), and photosynthesis can usually be carbon-saturated in air-equilibrated seawater (Raven, 1997; Beardall *et al.*, 1998). Coralline algae even exhibit negative biological responses to elevated CO_2 due to reduced calcification rates (Cattaneo, 2000). For marine macroalgae, growth of *Gracilaria gaditana* (Andria, 1999), *Porphyra leucostica* (Mercado *et al.*, 1999) and *P. linearis* (Israel *et al.*, 1999) was not affected or reduced by CO_2 enrichment in seawater, while some other species, such as *P. yezoensis* (Gao

et al., 1991), *G. sp* and *G. chilensis* (Gao *et al.*, 1993) showed higher growth rates with aeration of elevated CO_2 .

Intertidal marine macroalgae experience continual alternation of photosynthesis between aquatic and aerial states with the change of tidal height, due to their unique habitat where a steep gradient of environmental variation occurs over a small vertical spatial scale, from marine to fully terrestrial. The total net daily carbon fixation in intertidal macroalgae consists of aquatic and aerial photosynthesis. Great interest is arisen for the amphibious characters when considering their photosynthesis in relation to the atmospheric CO_2 change. When the tide is high, the intertidal macroalgae are submerged and photosynthesize in seawater. They use the large bulk of HCO_3^- besides free CO_2 in seawater as their inorganic carbon source for photosynthesis (Gao and Mckinley, 1994; Raven, 1997). When the tide is low, they are exposed to air, being switched from an aquatic to an aerial environment. The large buffering reservoir of bicarbonate in seawater is no longer present. All of the algae tested can photosynthesize in air (Davison and Pearson, 1996; Raven, 1999; Kawamitsu *et al.*, 2000). The aerial photosynthesis of intertidal macroalgae resembles terrestrial C_3 plants, in that atmospheric CO_2 is the only exogenous carbon source for photosynthesis and the CO_2 concentration gradient is the driving force for the flux of atmospheric CO_2 into the cell (Mercado and Niell, 2000) as land plants, and carbon fixation within cells are generally solely by Rubisco

and the PCR cycle (Reiskind *et al.*, 1989). It is thus assumed that varied carbon resources for photosynthesis in and out of water would result in different photosynthetic performances under aquatic and aerial states in intertidal macroalgae. However, little is known about the photosynthetic performances of them in relation to increasing atmospheric CO₂ concentration in view of the background of tidal cycles. In this study, we compared the photosynthetic responses to inorganic carbon under aquatic and aerial states in the common intertidal green macroalga *U. lactuca* along the coast of Shantou. The aim is to assess the differences of the photosynthetic carbon requirements between in and out of water, and to assess the ecological impacts of increasing atmospheric CO₂ on *U. lactuca*. This widely-distributed species occurs from the mid-intertidal to the upper subtidal zone, routinely spends a wide range of time under aerial state during low tide per day, and therefore, is a representative intertidal macroalgal species for studying the response to atmospheric CO₂ change.

1 Materials and Methods

1.1 Collection and maintenance of samples

Thalli of *U. lactuca* were collected at low tide from the middle intertidal zone during January to February, 2001 at Qianjiang bay along Shantou coast of China (23°20' N, 116°40' E). The accumulated sediments were rinsed and visible epiphytes were cleared. Only the unwounded and healthy thalli were selected. Samples were sealed in plastic bags with some seawater, and then transported to the laboratory in insulated cooler (1 - 4 °C) within 4 h. *U. lactuca* was maintained in filtered natural seawater in glass aquarium containers. The biomass density was controlled at 2.5 - 3.0 g/L. They received light of 100 μmol m⁻² s⁻¹ (PAR) from fluorescent tubes for 14 h/10 h light/dark photoperiod and at 18 - 22 °C. The seawater was aerated and renewed by half of the amount every day. To ensure that the photosynthesis of the samples had not deteriorated resulting from the laboratory maintenance, the material was tested for photosynthetic activity at the beginning of each day for experiments. When the material exhibited net photosynthetic rates > ±1 SD from established net means, the samples were discarded and fresh algal material was recollected.

1.2 Measurements of aquatic photosynthetic responses to dissolved inorganic carbon

pH-buffered (at 8.2) seawater with varied dissolved inorganic carbon (DIC) was prepared. NaOH point one mol/L HCl was added to the filtered sterile natural seawater to lower the pH to less than 4.0 following sparging for at least 1 h with high purity N₂, to remove any DIC in seawater (they escaped from the seawater by the way of CO₂ gas). A known amount of biological buffer Tris (from Sigma) was added to give a concentration of 20 mmol/L and the pH value was adjusted to 8.2 (a value representative that of natural seawater) with freshly prepared 0.1 mol/L NaOH and 0.1 mol/L HCl. All manipulations were under N₂. The pH value was measured with a pH

meter (420A, Orion) fitted with a glass/calomel combination electrode. After the pH buffered CO₂-free seawater was prepared, different aliquots of NaHCO₃ stock solution (0.044 and 0.176 mol/L) were injected into it to create varied DIC concentration in seawater. Then they were stored in stoppered glass containers at 4 °C until use.

Rates of aquatic photosynthesis of submerged thalli were measured as the uptake of DIC in seawater, using Shimadzu Total Organic Carbon Analyzer (TOC-5000A, Japan), at an irradiance level of 600 μmol · m⁻² · s⁻¹ (PAR) which could fully saturate the photosynthesis. The thalli were cut into small pieces with a sharp sterile razor blade and incubated for 2 h in the reaction medium under the light of 150 μmol · m⁻² · s⁻¹ (PAR) and the experimental temperature. This minimized the effect of damage of thalli cells on the determination of photosynthetic rate. Samples were placed in a closed Perspex chamber of a volume of 25 mL containing 20 mL reaction media of varied DIC concentrations ascribed above, which was equipped with a thermostatted water bath (three different temperatures: 10 °C, 20 °C and 30 °C were used) and was magnetically stirred. In each determination, the samples were incubated for 5 - 10 min, and then the change of DIC concentration in the medium was determined with Total Organic Carbon Analyzer. The rate of net aquatic photosynthesis (P_n) was calculated using the equation: $P_n = C \times V / (T \times DW)$, where C was the difference in concentration (mol/L) of DIC in medium before and after photosynthesis determination; V , the volume of medium (L); T , the duration of incubation (h); and DW , the amount of plant material (g).

1.3 Measurements of aerial photosynthetic responses to CO₂

Thalli were taken out of seawater and placed under constant conditions in incubators. The incident light intensity on the surface was 115 μmol · m⁻² · s⁻¹ (PAR) supplied by fluorescent lamps, and the relative humidity maintained in the incubators was between 80% - 85%. The temperature was adjusted respectively at 10 °C, 20 °C and 30 °C. The algae were then exposed to aerial state. The aerial photosynthesis was determined as CO₂ uptake with a LCA4 system (Analytical Development Company, LTD., UK). The photon flux density (PFD) received by leaf chamber came from a halogen lamp (150 W) above it and was 600 μmol · m⁻² · s⁻¹ (PAR). The temperature in the leaf chamber was maintained by a temperature-controlled cabinet. The net aerial photosynthesis (P_n) (μmol CO₂ g (d wt)⁻¹ h⁻¹) was calculated according to the equation: $P_n = C \times F \times 60 \times 273 / ((273 + T) \times 22.4 \times DW)$, where C is the difference in CO₂ concentration (mL/m³) between the inlet and outlet air; F , the gas flow rate (L/min); T , temperature (°C); DW , dry weight (g, 80 °C, 24 h).

The responses of aerial photosynthesis to varied CO₂ concentration (P-C curves) were measured respectively at three levels of temperature (10 °C, 20 °C and 30 °C).

Seven levels of CO₂ concentration (2.6, 5.2, 7.8, 15.6, 31.2, 46.8, 62.4 μmol/L) were adopted. The CO₂ concentrations were prepared either by removing CO₂ from air (the ambient air was passed through a soda lime column) or by adding pure CO₂ in an airbag before pumping air into it. Airbags were used to store the air of adjusted CO₂ concentrations. Air was directed from the airbag to the leaf chamber.

1.4 Estimation of photosynthetic parameters and the free CO₂ concentration in sea water

Half-saturation constant (*K_m*), i. e. the inorganic carbon concentration required to give half-maximal photosynthetic rate, as an indicator of the ability to extract inorganic carbon from seawater or atmosphere, and the inorganic carbon-saturated maximal rate of photosynthesis (*V_{max}*) were estimated according to Michaelis-Menten equation. The photosynthetic conductance based on the concentration of CO₂ was obtained from the initial slope of P-C curves according to Mercado *et al* (1998).

The free CO₂ concentration in seawater was estimated with the apparent dissociation constants of carbonic acid in seawater adopted from Stumm and Morgan (1996).

1.5 Data analyses

The results were expressed at the mean values ± *SD*. Statistical significance of means was tested with *t*-test or one-way ANOVA at *P* < 0.05.

2 Results

Under aquatic state, the current ambient dissolved inorganic carbon (DIC) concentration (2.2 mmol/L) in seawater could fully saturate (at 10 and 20) or nearly saturate (at 30) the photosynthesis of *U. lactuca* (Fig. 1). At 30, the photosynthetic rate at ambient DIC level was 82.2% of the inorganic carbon-saturated maximal rate. *U. lactuca* exhibited rather low *K_m* values under aquatic state. The values based on DIC (0.38 - 0.53 mmol/L) were much lower than the concentration of the ambient DIC (2.2 mmol/L) in seawater, and that based on free CO₂ (2.0 - 2.8 μmol/L) were much lower than the ambient free CO₂ (12 μmol/L) concentration in seawater.

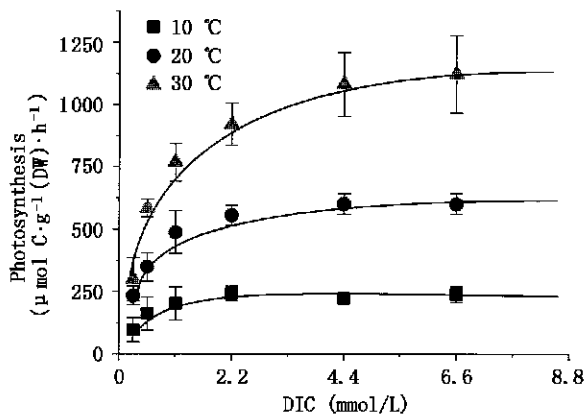


Fig. 1. Photosynthetic responses of *Ulva lactuca* to dissolved inorganic carbon (DIC) concentrations under aquatic state at different temperatures (10, 20, and 30).

Figure 2 shows that the current ambient atmospheric CO₂ level (15.6 μmol/L) could not saturate the aerial photosynthesis of *U. lactuca* during low tide. The rates of photosynthesis increased with increasing CO₂ concentration within the tested range (2.6 - 62.4 μmol/L) at higher temperature (20 and 30), while the rates were saturated with doubled atmospheric CO₂ concentration (31.2 μmol/L) at 10. The rates of aerial photosynthesis at current ambient CO₂ level were 58.1%, 31.4% and 33.7% of the CO₂-saturated maximal rates when the temperature was 10, 20 and 30, respectively. This phenomenon was in accordance with the high *K_m* (CO₂) values under aerial state. The value of *K_m* (CO₂) was at the ambient atmospheric CO₂ level (at 10) or higher (at 20 and 30), indicating that CO₂ was limiting for photosynthesis of *U. lactuca* under aerial state.

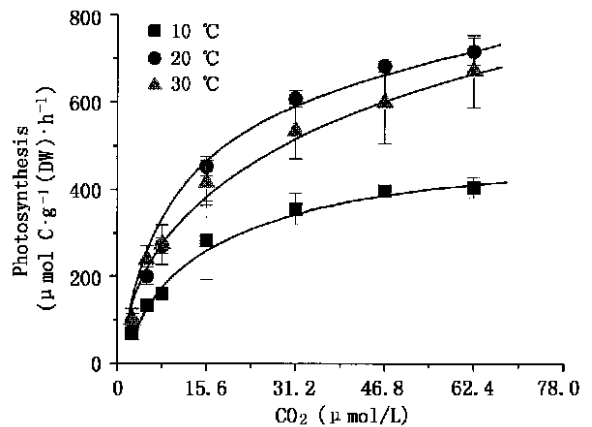


Fig. 2. Photosynthetic responses of *Ulva lactuca* to CO₂ concentrations under aerial state at different temperatures (10, 20, and 30).

At lower temperature (10) no significant differences were observed between the aquatic and aerial rates of photosynthesis at ambient inorganic carbon level, whereas the aquatic rates were markedly greater than the aerial rates at higher temperature (20 or 30). The aquatic photosynthetic rates at ambient DIC level significantly increased with increasing temperature at the tested range of 10 - 30, with a Q₁₀ of 2.3 from 10 to 20, and of 1.7 from 20 to 30. This suggested that the temperature optimum for aquatic photosynthesis was not lower than 30. Compared to aquatic photosynthesis, the aerial photosynthesis was less affected by temperature, with a Q₁₀ of 1.6 from 10 to 20, and an insignificant difference at 20 and 30. For the carbon-saturated maximal photosynthesis, the aerial rates were considerably higher than the aquatic rates at 10 and 20, but both showed no significant difference at 30 (Fig. 3). On the other hand, the values of *K_m* (CO₂) under aquatic state were reduced by one order of magnitude compared with that under aerial state, while the values of apparent photosynthetic CO₂ conductance (APC) under aquatic state increased by two orders of magnitude than that under aerial state. Temperature had insignificant

effects on the K_m (CO_2) under aquatic state, but had positive marked effects on APC. Under aerial state, the values of K_m (CO_2) or APC were significantly lower at 10 than that at 20 or 30 (Fig. 3).

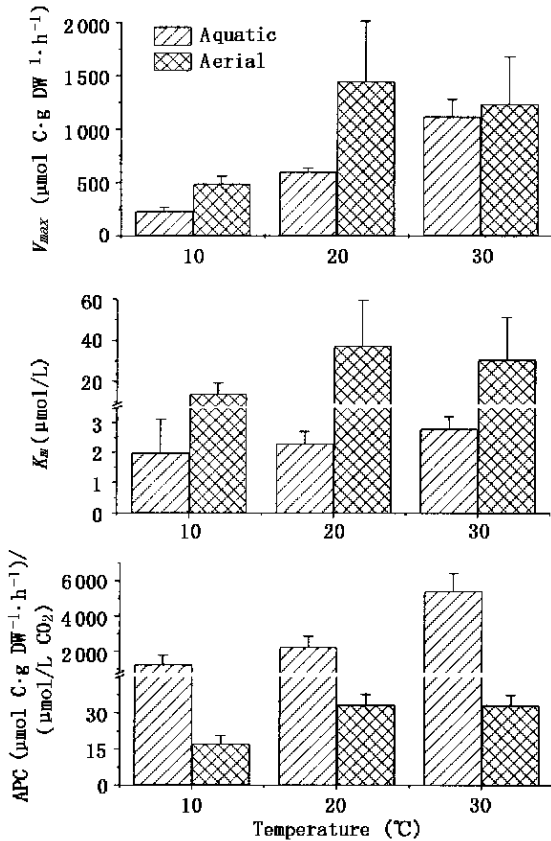


Fig. 3. The carbon-saturated maximal photosynthesis (V_{max}), K_m (the CO_2 concentration at half of V_{max}) and the apparent photosynthetic conductance (APC) in *Ulva lactuca* under aquatic and aerial states and different temperatures.

3 Discussion

Although the total dissolved inorganic carbon (DIC) concentration is much higher in seawater, 2.2 mmol/L compared to 15.6 $\mu\text{mol/L}$ in air, the majority of DIC is bicarbonate (HCO_3^-) due to high pH (8.2) in seawater, and the concentration of free CO_2 (about 10 - 15 $\mu\text{mol/L}$) is similar to that in air. As the rate of supply of CO_2 to macroalgae underwater is much lower than in air resulting from an 10 000-fold lower diffusion coefficient in seawater (Falkowski and Raven, 1997), the acquisition of CO_2 for macroalgae might be much restricted potentially in water compared to air. Nevertheless, the results in the present study showed that the intertidal macroalga *U. lactuca* exhibited the carbon-saturated photosynthesis underwater, but CO_2 -limited photosynthesis under aerial state. In addition, the photosynthetic conductance based on CO_2 was much greater in water than out of water. This suggested that the inorganic carbon affinities in *U. lactuca* were much higher under aquatic state than under aerial state. The primary cause for these phenomena was associated with the mechanism of inorganic carbon utilization in wa-

ter differing from that in air. Under aerial state, *U. lactuca* use only the atmospheric CO_2 through diffusion for photosynthesis. When submerged, *Ulva* plants have rather high abilities to use the external pool of HCO_3^- in seawater as the source of inorganic carbon for photosynthesis (Axelsson *et al.*, 1995; Zou and Gao, 2001). They can directly uptake HCO_3^- from seawater by anion exchange and even their operations are independent of external carbonic anhydrase activity which is usually involved in HCO_3^- utilization in most other macroalgae (Axelsson *et al.*, 1995; Raven, 1997; Zou and Gao, 2001). Our results of high photosynthetic conductance for CO_2 of *U. lactuca* also suggested the high ability to extract inorganic carbon from seawater. Consequently, the constraint on CO_2 supply in *U. lactuca* underwater could be more than offset by the high ability of HCO_3^- use from seawater.

When atmospheric CO_2 increases to doubled concentration, the HCO_3^- in surface seawater would rise only 6%, from 2.2 to 2.34 mmol/L, due to a decline of pH in seawater resulting from dissolution of CO_2 (Bowes, 1993; Stumm and Morgan, 1996). Furthermore, the present day inorganic carbon composition of seawater can saturate the photosynthesis of marine macroalgae when submerged (Beer and Koch, 1996; Beardall *et al.*, 1998), whereas under aerial state, marine macroalgae usually show the CO_2 -limited photosynthesis at current ambient atmospheric CO_2 (Gao *et al.*, 1999). Therefore, increasing atmospheric CO_2 will enhance the photosynthetic productivity of intertidal macroalgae like *U. lactuca* through stimulating the aerial photosynthesis during low tide but not the aquatic photosynthesis during high tide. As the submerged macroalgae are concerned, many of them use HCO_3^- besides free CO_2 in seawater and exhibit carbon-saturated photosynthesis. Some other use free CO_2 alone in seawater and show potential carbon-limited photosynthesis (Raven, 1997; Falkowski and Raven, 1997). However, as the submerged algae photosynthesize in an environment with a relatively low availability of light level due to reflection of the seawater surface and attenuation within the water column (Falkowski and Raven, 1997), it is likely that the constraints of carbon acquisition for these macroalgae using CO_2 alone would also be negligible. Thus, among marine macroalgae, we propose that the intertidal macroalgae may be the primary beneficiaries for the atmospheric CO_2 concentration increase. However, the long-term growth response to elevated CO_2 is usually much lower than the short-term photosynthetic responses measured in this work, which had been shown frequently for land plants (Bowes, 1993; Drake *et al.*, 1997; Makino and Mae, 1999). When cultured in seawater with CO_2 enrichment, many macroalgae such as *G. chilensis*, *P. leucosticta* and *G. gaditana* exhibited reduction of photosynthetic capacities (Andria *et al.*, 1999; Mercado *et al.*, 1999; Israel *et al.*, 1999), which might be associated with the decreased utilizing abilities for HCO_3^- in seawater and the activities of Rubisco.

Therefore, further studies are needed for the understanding of the long-term effect of elevated atmospheric CO₂ on aquatic and aerial photosynthesis of *U. lactuca*.

This study showed that photosynthetic performances of *U. lactuca* under aquatic state differed from that under aerial state, and such difference was temperature-dependent. Temperature had a much greater stimulating effect on the rates of photosynthesis at ambient inorganic carbon level under aquatic state than under aerial state. Consequently, the difference between aquatic and aerial rates at ambient inorganic carbon level increased substantially with increasing temperature. However, reverse results were found for such difference under inorganic carbon-saturated conditions. In addition, the aquatic photosynthesis optima of temperature (no less than 30 °C) was higher than the aerial one (20 - 30 °C). The primary causes of the above phenomena could be attributed to the different limiting factors for aquatic and aerial photosynthesis and the difference between effects of temperature on such factors under aquatic and aerial states. According to the characteristics of photosynthetic responses to inorganic carbon in *U. lactuca* under aquatic and aerial states, the photosynthetic rates in aquatic state were limited primarily by Pi regeneration or electron transport capacity, whereas both of Rubisco activity and electron transport capacity co-limited the rates in aerial state (Makino and Mae, 1999). On the other hand, temperature affected the rate of photosynthesis by affecting potentially many physiological and physical factors, such as the photosynthesis rate-limiting enzymes, carbonic anhydrase activity, the diffusion of inorganic carbon, cellular pH, the active transport of CO₂ or HCO₃⁻ across the plasmalemma and/or chloroplast membranes, and so on (Davison, 1991). Additionally, the extent for effects of temperature on the above factors in aquatic state might differ from that in aerial state. It will be interesting to directly measure the change of related biochemical and physical processes in *U. lactuca* alternating from aquatic to aerial states for better understanding of the mechanistic basis and ecological significance.

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在水生与气生状态下石莼光合作用对无机碳的响应

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摘要: 潮间带海藻光合作用总是处于水生(高潮时)与气生(低潮时)两种连续变化的环境状态下进行。对汕头沿岸常见的潮间带海藻石莼(*Ulva lactuca* L.)在水生和气生不同状态下光合作用对无机碳的响应特性进行了比较研究。在水生状态下,现有海水中溶解性无机碳浓度能充分饱和(10 和 20 时)或接近饱和(30 时)石莼的光合作用;而在气生状态下,石莼光合作用受大气 CO₂ 浓度的限制,且这种限制作用在较高温度(20 - 30)下比在低温(10)下更严重。在 10 和 20 时,石莼在气生状态下比在水生状态下具有更高的碳饱和和最大光合速率;而在 30 时,石莼在这两种状态下的碳饱和和光合速率相似。石莼光合作用的 $K_m(\text{CO}_2)$ 值在气生状态下比在水生状态下高;而在气生状态下石莼对 CO₂ 的表观光合导度远小于其在水生状态下的值。认为大气 CO₂ 浓度升高将通过促进石莼在气生状态下的光合作用而增加其初级生产力。

关键词: 石莼; 光合作用; 无机碳; 水生; 气生; 大气 CO₂ 浓度升高

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