Mechanism of photosynthetic response in *Microcystis aeruginosa* PCC7806 to low inorganic phosphorus

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Abstract

Photosynthetic response of *Microcystis aeruginosa* PCC7806 to different concentrations of phosphorus supply was studied so as to elucidate if the declining process of *Microcystis* bloom under freshwater ecosystem is related to soluble reactive phosphorus (SRP) decrease in water volume. Growth rate of *M. aeruginosa* PCC7806 was significantly reduced under P-deficient conditions, and its photosynthetic activity in terms of rETR$_{max}$ (maximum electron transport rate) decreased significantly after 48 h growth, while it kept elevating and reached to a relative stable value when supplied with rich phosphorus of 0.6 mg/L. With the increasing actinic irradiance along the rapid light curves of *M. aeruginosa* PCC7806 cultured under low-phosphorus level, qP (photochemical quenching) and rETR$_N$ (relative electron transport rate) decreased greatly, and the increase in qN (non-photochemical quenching) and F$_{PS}$ (actual photochemical efficiency of PSII) was obviously inhibited. The affinity of *M. aeruginosa* PCC7806 to inorganic carbon was reduced evidently in 0.02 mg/L P compared with in 0.6 mg/L P. When P was reduced from 0.6 to 0.02 mg/L, the decreasing rate of rETR$_{max}$ (77%) was significantly greater than that of photosynthetic carbon assimilation (22%), which indicated that down-regulation of CO$_2$ affinity caused by P-deficiency was, but not the only reason that resulted in the decline of photosynthetic efficiency. Instantaneous low-temperature significantly limited rETR$_{max}$ under rich-P condition but had no effect on it when P was insufficient, and 1% ethanol could enhance rETR$_{max}$ at low-P level but did not influence it at rich-P level. These two results proved that the decrease in thylakoid membrane fluidity caused by P-deficiency was another important reason that results in the decline of photosynthetic efficiency of *M. aeruginosa* PCC7806.

1. Introduction

In recent years, surface cyanobacterial bloom occurred frequently in most large shallow lakes in China, such as Lake Taihu (Zhang et al., 2009), Lake Dianchi (Shen et al., 2004) and Lake Chaohu (Liu, 2007), especially in summer, resulting from eutrophication caused by human activities. There are many studies on the factors that lead to water bloom and close relation between water bloom and concentration of nutrients, particularly phosphorus level was reported (Hecky and Kilham, 1988). Also, some researches indicated that the decline of cyanobacterial bloom was accompanied with the decrease in dissolved phosphorus (Chen et al., 2005).

Phosphorus is one of the most important limiting factors that determine primary productivity in water body (Valiei, 1995). Dissolved phosphorus including dissolved inorganic phosphorus can be absorbed and utilized by phytoplankton immediately (Wang et al., 2008), therefore it is usually called soluble reactive phosphorus (SRP). It plays a crucial role in determining potential productivity of bloom-forming cyanobacteria. It is well known that inorganic phosphorus is usually converted to organic phosphorus and accumulates in plant tissues during vegetation growth (Chen et al., 2002). When cyanobacterial bloom forms and continues to grow rapidly in a lake-bay, consumption rate of inorganic phosphorus is higher than regeneration rate caused by mineralization of organic phosphorus. Bloom-forming cyanobacteria such as *Microcystis* are subjected to phosphorus-deficiency stress, and there is downregulation of its growth and photosynthetic apparatus. Nutrient bottom-up has a considerable effect on *Microcystis* photosynthetic characteristics, and which is one of the important factors resulting in water-blooms declining quickly after biomass having increased greatly or being driven together in a lake-bay by wind and reached to a high density.

Phospholipids are indispensable components of biomembranes which play an important role in maintaining membrane structure intact and performing normal membrane functions (Pan, 2004). Thylakoid membrane is one of the important biomembranes and...
closely related to photosynthesis process as a carrier of photosynthetic protein complex (Simpson and Wettstein, 1989). Phospholipids in the thylakoid membrane have direct influence on membrane fluidity (Singer and Nicolson, 1972) which determine excitation energy transfer rate and light energy conversion efficiency between light-harvesting pigment and photosynthetic reaction centers due to the impact on transport rate of phycobilisomes (Huang et al., 2005).

Phosphorus-deficiency (P-deficiency) restricts photophosphorylation, and leads to a higher excited state of thylakoid membrane, lower electron transport rate and relatively inefficient operation of photosynthesis (Jacob, 1995). Long-term low-phosphorus content stress can result in a low photosynthetic efficiency and decrease in SRP in large shallow eutrophic lakes.

2.1. Strain and culture conditions

M. aeruginosa PCC 7806 was originally obtained from the Pasteur Culture Collection of Cyanobacteria in France and kindly provided by the Freshwater Algae Culture Collection of the Chinese Academy of Sciences. The culture was centrifuged at 4000 rpm for 8 min, and the pelleted cells were washed three times with phosphorus-free BG11 medium (Rippka et al., 1979). Subsequently, cultures were phosphorus starved for 72 h under a 12:12 LD cycle with an intensity of 60 µmol photons m⁻² s⁻¹ provided by cool white fluorescent tubes at 25 ± 1 °C. After phosphorus starvation, the cells were re-inoculated into 150 mL glass flask filled with 100 mL BG11 medium which contained four different concentrations of phosphorus: 0.005, 0.02, 0.1 and 0.6 mg/L. Potassium ion in four concentrations was calculated using formula

\[ \text{K} = \frac{\text{C} - \text{C}_0}{\text{m}} \]

where C is the final concentration of 5, 10, 25, 50, 100 or 200 mg/L. Cells cultured with different P concentrations for 48 h were water bathed at a lower temperature of 15 °C for 5 min, and then their F₀/Fₘ and rETRmax were measured. Chlorophyll fluorescence parameters were measured with a pulse-amplitude-modulated fluorescence monitoring system (Phyto-PAM, Walz, Effeltrich, Germany). Cells cultured with various P concentrations for 48 h were used to plot rapid light curves (RLC). After dark-adapted for 15 min, F₀ (original fluorescence) and Fₘ (maximum fluorescence) were measured under a low measuring light of 0.15 µmol photons m⁻² s⁻¹ and a saturation light pulse of about 3000 µmol photons m⁻² s⁻¹ for 0.8 s, respectively. F₀ (minimal fluorescence of light-adapted) instead of Fₘ due to qN of cyanobacteria was lower than 0.4 (cited from the Operation Manual of Phyto-PAM). Fₘ (instantaneous steady state fluorescence at every step of actinic light, sometimes was called as Fₘ) and Fₘ (maximum fluorescence) were measured under different intensities of actinic light when plotting RLC. RLC including 10 steps of actinic irradiance: 1, 32, 64, 96, 192, 320, 448, 576, 707, 1216 µmol photons m⁻² s⁻¹, and a saturation light pulse (about 3000 µmol photons m⁻² s⁻¹) with a 10-s interval time between any two adjacent steps is applied to determine Fₘ (Ralph and Gademann, 2005). The maximum photochemical efficiency of PSII (F₀/Fₘ), qPSII, rETR, photochemical quenching (qP) and non-photochemical quenching (qN) were calculated as:

\[ q_P = (F_{max} - F_0) / F_{max} \]

(Genty et al., 1989); The relative electron transport rate (rETR) was calculated as:

\[ \text{rETR} = (F_{max} - F_0) / F_{max} \times 0.4 \times \text{PPFD} \]

where rETRmax is the maximum relative electron transport rate.

2.4. Photosynthetic oxygen evolution

After being cultured in various P levels for 48 h, M. aeruginosa PCC7806 was sampled and centrifuged for 8 min at 4000 rpm, the pelleted cells were washed with a DIC and P-free tris-BG₁₁ buffer solution (pH 7.8) for three times, finally resuspended in the same buffer. Oxygen evolution rate was measured with a Clark-type oxygen electrode at 25 °C. Illumination of 500 µmol photons m⁻² s⁻¹ was provided by a halogen lamp, which was measured with a quantum sensor (LI-185B, Li-Cor Inc., USA). When oxygen evolution rate approached to 0 (CO₂ evolution), a NaHCO₃ solution with known concentration was added to the DIC-free reaction medium to a final concentration of 5, 10, 25, 50, 100 or 200 µmol/L. Parameters of photosynthetic responses to DIC were obtained by fitting net photosynthetic rates at various DIC concentrations with the Michaelis–Menten formula:

\[ \frac{v}{V_{max}} = \frac{K_{DIC}}{[DIC]} \times \frac{1}{1 + \frac{[DIC]}{V_{max}}} \]

where v, photosynthetic rate; Vmax, DIC saturated photosynthetic rate; [DIC], concentration of DIC; K₅, DIC concentration where photosynthetic activity is the half of the maximum value.

2.5. The fluidity of thylakoid membrane

Samples of M. aeruginosa PCC 7806 grown under 0.02 and 0.6 mg/L P levels for 48 h were water bathed at a lower temperature of 15 °C for 5 min, and then their F₀/Fₘ and rETRmax were measured. Chlorophyll fluorescence parameters at 25 °C were taken as control, and the limiting degree of thylakoid membrane fluidity was estimated with the ETR differences between the two temperatures.

Tadeusz (1974) proposed that lipids (α-tocopherol, phytol and tocol) played a structural role in restoration of the thylakoid membrane. And all these lipids belonged to organic solvent. Also Mi et al. (1997) reported that low concentration organic solvent, 1%
ethanol, could enhance the fluidity of membrane lipid. Based on above two reports, 1% ethanol was used for the testing of the thylakoid membrane fluidity. *M. aeruginosa* PCC 7806 which had grown under 0.02 and 0.6 mg/L P levels for 48 h were sampled, and absolute ethanol was added to a final concentration of 1%, then fluorescence parameters of $\Phi_{PSII}$, $\alpha$, rETR and $I_d$ were measured under exciting light of 256 $\mu$mol photons m$^{-2}$ s$^{-1}$ after treating for 5 min. Chlorophyll fluorescence parameters of two cultures without ethanol added were respectively taken as control. The enhancing effect of low concentration ethanol on the thylakoid membrane fluidity was estimated with the difference of $\Phi_{PSII}$, $\alpha$, rETR and $I_d$ between the two treatments of with and without ethanol added.

2.6. Statistical analysis

All experiments were performed in three replicates. SAS Statistical software was applied to analyze the data. A T-test was used to examine whether there is difference in chlorophyll fluorescence parameter or the rate of photosynthetic carbon assimilation between the two concentrations of DIP (0.02 and 0.6 mg/L). Differences were considered to be significant at $P < 0.05$.

3. Result and discussion

3.1. Changes of growth rates and rETR$_{max}$

Calculated from Fig. 1 (left), the specific growth rates ($\mu$) of *M. aeruginosa* PCC7806 which were grown under P concentration of 0.005, 0.02, 0.1 and 0.6 mg/L were 0.030 ± 0.014, 0.095 ± 0.064, 0.433 ± 0.019 and 0.917 ± 0.093, respectively. The $\mu$ values of *M. aeruginosa* PCC7806 cultured under rich-P concentration (more than 0.1 mg/L) were significantly higher than those of cultures under low P level (T-test, $P < 0.05$). It suggested that the growth of *M. aeruginosa* PCC7806 was obviously inhibited by low P status.

The rETR$_{max}$ of *M. aeruginosa* PCC7806 cultured under P concentrations of 0.005 and 0.02 mg/L showed a similar trend (Fig. 2, right). They maintained steady values (37.93 and 41.73, respectively) in initial two days followed by a rapid decrease to 12.03 and 19.24 respectively, and finally declined to 11.72 and 11.57 respectively after a slight increase. Under the condition of 0.1 mg/L P, rETR$_{max}$ increased to 61.21 at the second day, and then decreased slowly to 16.03 at 14th day. The rETR$_{max}$ under 0.6 mg/L P level kept elevated with time and finally was stabilized on a large average value (96.2). Under lower levels of P supply (<0.1 mg/L), rETR$_{max}$ decreased rapidly, which suggested that rETR$_{max}$ was a sensitive monitoring indicator of environmental stress. But at rich-P level, the curve of rETR$_{max}$ was a typical sigmoid shape (Fig. 2). In the curve, rETR$_{max}$ was limited by low level of P-in-cell content in the early days of experiment period, and then it increased rapidly with the elevation of P-in-cell and finally reached to a plateau, where the photosynthetic pathway might be limited (Ralph and Gademann, 2005).

3.2. Changes of rETR and $\Phi_{PSII}$

Fig. 2a–d showed RLC of the actual photochemical efficiency of PSII ($\Phi_{PSII}$) and the rETR as functions of PPFD. The shapes of the two curves were almost opposite. At low-P level of 0.005 and 0.02 mg/L, $\Phi_{PSII}$ decreased 66.3% and 61.6% of initial values respectively over the first three actinic light steps, and gradually reached to a relatively stable status. Previous study proposed that a linear rise of rETR was accompanied with the increase in actinic light intensities, and then followed by a plateau where photosynthetic carbon assimilation became limited (Ralph and Gademann, 2005), with which our result was consistent. Under condition of 0.1 mg/L P, rETR increased more quickly and $\Phi_{PSII}$ decreased slower compared with those of lower-P level (0.005 and 0.02 mg/L P). $\Phi_{PSII}$ only decreased by 29.0% and rETR increased from 0.17 to 7.92 over the first three actinic light steps. At 0.6 mg/L P level, maximum relative ETR (rETR$_{max}$) was 76.77, which was obviously higher than those at low-P levels, and the decrease of $\Phi_{PSII}$ at P 0.6 showed a slower decrease among the four P concentrations. When P concentration dropped from 0.6 to 0.02 mg/L, the rETR$_{max}$ decreased by 76.99 ± 5.29%.

With the increase in irradiation, more photons can reach to reactive centre of PSII and drive primary charge separation at a higher level. This resulted in more electron flux via the electron transport chain, subsequently primary electron acceptor (QA) is reduced when get an electron, and loss the function as an effective transporter before it was reoxidized. In this circumstance, excessive excitation energy at PSII is dissipated via a charge-recombination reaction, and such non-assimilatory dissipation of excitation generates singlet oxygen that would lead to photodamage of PSII reaction centers (Melis, 1999). The actual photochemical efficiency of PSII ($\Phi_{PSII}$) is calculated with the formula ($F_{mv} - F_{o}$)/$F_{mv}$ (Genty et al., 1989), where $F_o$ is linked to PSII reaction center closure. Therefore, $\Phi_{PSII}$ in low P concentration...
dropping quickly could be attributed to the rapidly decreasing $F_{m}$ and/or the increasing proportion of closed PSII reaction center.

Relative electron transport rate ($rETR$) can be derived by the product of $F_{PSII}$ and PPDF followed $rETR = (F_{m} - F_{s}) \times 0.42 \times PPDF$ (Schreiber et al., 1998), and its RLC curve was composed of a linear rise phase and a plateau phase. The relative value of the plateau phase in RLC is called $rETR_{max}$, which is closely associated with carbon assimilation activity in photosynthesis process. By comparing the four curves of $rETR$ in Fig. 2, we can conclude that $rETR_{max}$ rises significantly with the increase of inorganic phosphorus level and P-deficiency limited $rETR_{max}$.

However, under the condition of high inorganic P level (0.6 mg/L), the curve did not always keep at a stable level after reaching to a plateau at saturated light. When the irradiance further elevated (in supersaturated phase of 1216 m mol photons m$^{-2}$ s$^{-1}$), the curve of ETR slightly declined, which could be attributed to dynamic down-regulation of PSII (Schreiber, 2004).

3.3. Photochemical quenching ($qP$) and non-photochemical quenching ($qN$)

Fig. 3a–d showed RLC of $qP$ and $qN$ versus increasing irradiance in M. aeruginosa PCC7806 cultured under various P concentrations. Under low-P level of 0.005 and 0.02 mg/L, $qP$ decreased quickly dropped to 36.0% and 41.0% of corresponding initial values respectively over the first three actinic light steps, while $qN$ elevated rapidly at the first step of unsaturated illumination and gradually reached to a relatively stable value (both are 0.21). When in 0.1 and 0.6 mg/L P, $qP$ declined at relatively slower speeds than those in 0.005 and 0.02 mg/L P and reached to 78.0% and 88.0% of corresponding initial values respectively over the first three actinic light steps; $qN$ also elevated at a slower speed and reached to higher values of 0.32 and 0.27 respectively than those under low-P conditions.

Chlorophyll molecules of cyanobacteria can absorb light directly or accept excited energy from phycobilisomes, and subsequently transit rapidly from ground state to unstable excited state (Mullineaux, 1992). Excited chlorophyll molecules could return to stable ground state by means of three ways (Campbell et al., 1998; Roháček and Bartáek, 1999), namely emitting fluorescence ($F_t$), heat dissipation ($qN$ and NPQ) and/or driving photochemical process in PSII interaction centers ($qP$) after a series of energy transfer among chlorophyll molecules. These three kinds of fluorescence quenching compete with each other and as one rises, others might fall.

In Fig. 3, with the increasing of irradiance, $Q_A$ would be accumulated at acceptor side, and $qP$ decreased quickly due to the closure of PSII interaction centers. When light is high enough to be saturating, the declining rate of $qP$ is very low because of most interaction centers are closed and functionally inactivated. Compared with those cultured under sufficient phosphorus conditions, M. aeruginosa PCC7806 which was grown under lower phosphorus concentrations showed a slower descending rate of $qP$, which associated with distribution of excitation energy by state transitions in photosynthesis (Yang et al., 2001) and the starting of photosynthetic carbon assimilation shown in slow chlorophyll fluorescence induction kinetics (Roháček and Bartáek, 1999). The results suggested that inorganic phosphorus plays an important role in enhancing light use efficiency.

As shown in Fig. 3, non-photochemical quenching was increasing with the rise of irradiance. $Q_A$ was obviously increased at the low-P concentrations of 0.002, 0.05 and 0.1 mg/L in comparison with those of higher level of 0.6 mg/L P supply. Combined with the changes of $qP$ it suggests there are two ways to promoting solar utilization efficiency for M. aeruginosa PCC7806 in environment with sufficient DIP (Dissolved Inorganic Phosphorus) supply. One is the increased $qP$, and the other is realized by enhanced $qN$.

$qN$ of the 0.6 mg/L P cultured cells was not higher, but lower than that of 0.1 mg/L P cultured cells (Fig. 3). This phenomenon might be caused by effective operation of photosynthetic carbon assimilation (Calvin cycle) in cells under rich-P condition. Calvin
cycle could remove most of the electrons which accumulated at the acceptor side of PSI reaction centers, leading to Qₐ reoxidation and a higher qP, which further resulted in a lower qN due to the mutual competition effects among qP, qN and Fₗ.

3.4. The response of photosynthetic carbon assimilation to low P level

Table 1 shows the differences of several photosynthetic parameters between *M. aeruginosa* PCC7806 cultured under different P concentrations of 0.02 and 0.6 mg/L. Compared with cells cultured under 0.6 mg/L rich-P level, the photosynthetic carbon assimilation ability had declined significantly in cells cultured under 0.02 mg/L P (*t*-test, *P* < 0.05). When cultured under 0.02 mg/L P condition, its *Kₗ₅* (DIC) elevated by 22.24%, CE decreased by 42.25%, the value of CO₂ compensation point increased by 98.44%, and the maximum oxygen evolution rate (*V*ₘₐₓ) decreased by 49.02% in comparison with cells cultured under 0.6 mg/L P condition.

Previous studies showed that phosphorus was an activation agent of Rubisco (*Bhagwat, 1981*) and low phosphorus level led to a decrease in ATP/ADP ratio, and furthermore resulted in a down-regulated activity of Rubisco (Ribulose-1.5-bisphosphate carboxylase/oxygenase) and restricted process of photosynthetic carbon assimilation (Portis, 1992). Under this condition, electron transfer chain was blocked and electrons were accumulated in acceptor side. Therefore photochemical quenching coefficient was decreased, while non-photochemical quenching coefficient rose as shown in Fig. 3, further resulted in a limiting of photosynthetic carbon assimilation as described in Table 1.

When P concentration in medium reduced from 0.6 to 0.02 mg/L, photosynthetic activity of *M. aeruginosa* PCC7806 declined significantly, and photosynthetic CO₂ affinity (1/*Kₗ₅* (DIC)) decreased by 22.24% (Table 1) while rETRₘₐₓ decreased by 76.99 ± 5.29% (Fig. 2). If we assumed that the decrease in rETRₘₐₓ was caused only by the down-regulation of CO₂ affinity, both of which would have the same decreasing degree or be not significantly different. But the result showed that the former was higher than the latter with respect to decreasing degree. This indicated that the limitation of photosynthetic carbon assimilation is an important, but not the unique reason which caused the lowering of photosynthetic activity under low P level (0.02 mg P/L). Since carbon assimilation is a final electrons’ deposition in the electron transport chain, the inhibition of photosynthetic carbon assimilation inevitably results in feedback regulation of photosynthetic efficiency (*Yuan and Xu, 2001*), and further cause the decrease in rETR and Φₚₛᵢᵢ in rapid light curve (RLC).

3.5. The responding mechanism of *M. aeruginosa* PCC7806 to low-phosphorus

*Fₗ/Fₘ* is a useful parameter to monitor whether some stress factors exist in ambient environment since when plants were subjected to environment stress, *Fₗ/Fₘ* would decrease (*Xu et al., 1992*). As shown in Fig. 4 a, *Fₗ/Fₘ* decreased with the decreasing P concentrations in culture medium. Instantaneous low-temperature treatment (ILTT) had no significant effect on *Fₗ/Fₘ* in various P concentrations. Compared with those cells cultured under rich-P level (0.6 mg/L), the ETR values were markedly decreased when *M. aeruginosa* PCC7806 was cultured under low-P conditions (0.005, 0.02 mg/L).

**Table 1**

<table>
<thead>
<tr>
<th>P concentration (mg/L)</th>
<th>CE (μmol O₂ mg⁻¹ Chla h⁻¹)</th>
<th>Fₗ (μmol/L)</th>
<th>Vₘₐₓ (μmol O₂ g⁻¹ Chla h⁻¹)</th>
<th><em>Kₗ₅</em> (DIC) (μmol/L)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.02</td>
<td>1.49 ± 0.12</td>
<td>1.27 ± 0.42</td>
<td>198.69 ± 2.26</td>
<td>44.35 ± 3.81</td>
</tr>
<tr>
<td>0.6</td>
<td>2.58 ± 0.26</td>
<td>0.64 ± 0.26</td>
<td>389.74 ± 8.88</td>
<td>36.28 ± 3.11</td>
</tr>
</tbody>
</table>

0.02 mg/L), and no significant decline occurred after the ILTT (Fig. 4b). But when under rich-P conditions of 0.1 and 0.6 mg/L, the values of \( rETR_{\text{max}} \) dropped rapidly by 36.6% and 34.0%, respectively after the ILTT.

Cyanobacteria also possess a thylakoid membrane, but not as intact as that in high plants. Four kinds of protein complexes were found in thylakoid membrane (Han et al., 2003): Cytb6/f, ATP synthase, PSI and PSII, whose activities of photosynthetic carbon assimilation are associated with the fluidity of thylakoid membrane. It is well known that the fluidity of biomembrane lipid can be lowered by low-temperature treatment (Wang et al., 2006) and thus led to reduced rates of substance transportation and information transmission which occurred on the surface of membrane. ILTT made no significant change in \( F_{v}/F_{m} \) suggesting that low-temperature did not damage photosynthetic apparatus in a short time. \( rETR_{\text{max}} \) of low-P cultures (0.005 and 0.02 mg/L) were not significantly changed by ILTT while it was obviously affected in rich-P (0.1 and 0.6 mg/L) cultures, it suggested P-deficiency led to a very low fluidity of thylakoid membrane in \( M. \) aeruginosa PCC7806.

Chlorophyll fluorescence parameters, namely \( \Phi_{\text{PSII}}, rETR_{\text{max}} \) and \( I_{o} \) of \( M. \) aeruginosa PCC 7806 cultured under low-P condition (0.2 mg/L) could be enhanced significantly by 1% ethanol after 5 min treatment (Table 2), while those of rich-P (0.6 mg/L) cultures only showed a slight increase of 0.78%, 4.83% and 9.92%, respectively. No significant differences were observed between the treatment and the control.

Previous report showed that the fluidity of membrane lipid and the electron transport rate of PSII cyanobacterium Synechocystis PCC 6803 could be enhanced by 1% ethanol (Mi et al., 1997). When cultured under P-deficient conditions, \( M. \) aeruginosa PCC 7806 showed a low rate of photosynthetic carbon assimilation as shown by low \( rETR_{\text{max}} \) and \( \Phi_{\text{PSII}} \) values (Table 2). However, they increased markedly after being treated with 1% ethanol. This phenomenon was not found in P-sufficient cultures. The results proved again that P-deficiency can result in low fluidity of thylakoid membrane in \( M. \) aeruginosa PCC 7806, hence it showed a low photosynthetic performance.

**4. Conclusion**

In conclusion, the growth rate of \( M. \) aeruginosa PCC7806 was inhibited under P-deficient conditions, and it showed a lower photosynthetic activity indicated by lower \( \Phi_{\text{PSII}}, rETR_{\text{max}}, \) carboxylation efficiency (CE), maximum oxygen evolution rate (\( V_{\text{max}} \)) and affinity of DIC (expressed as a higher CO₂ compensation point and a higher half-saturated DIC concentration) compared with those of P-rich cultures. The decrease in photosynthetic activity was assumed to be caused by the poor fluidity of thylakoid membrane in \( M. \) aeruginosa PCC7806 when P-deficiency occurred, and it was proven by means of instantaneous low-temperature and 1% ethanol treatments. Thus we speculated that P-deficiency is one of the important factors resulting in cyanobacterial blooms which decline rapidly due to decrease in photosynthetic activity in freshwater ecosystem where P-deficiency occurs after biomass increases greatly or is driven together by wind and reach a high density. However, other factors (such as nitrogen, pH, water temperature, etc.) might have synergistic effects with phosphorus. The synergistic effects of some ecological factors should be further studied.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.hal.2010.04.012.

References


