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Differential influence of dissolved oxygen on respiration and photosynthesis rates in photosynthetic bacteria wastewater bioconversion

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ABSTRACT

The use of photosynthetic bacteria (PSB) in wastewater bioconversion is a novel method that can simultaneously realize wastewater treatment and resource recovery. The metabolism of PSB is significantly influenced by dissolved oxygen (DO) conditions; however, the rates of respiration and photosynthesis in PSB metabolism remain unclear. In this study, chemical oxygen demand (COD) removal and PSB biomass were tested, then the respiration and photosynthesis rates were deeply analyzed, and related key enzymes and genes were also discussed. The results showed that COD removal increased with the increase in oxygen concentration, and reached 93% at DO > 2 mg/L. The high DO level also enhanced the growth of PSB. The maximum PSB respiration rates under DO < 0.5, 0.5–2, and >2 mg/L were 216, 237, and 226 O_2 mg/g h, respectively and the maximum photosynthesis rates were 19, 15, and 15 biomass mg/g h, respectively. Changes in respiration enzyme activity corresponded to those in the respiration rate, and phosphofructokinase and pyruvate kinase activity were higher under high DO concentrations. The respiration gene expression also corresponded to the respiration rate. The photosynthesis enzyme activity corresponded to the photosynthesis rate, and ribulose-1,5-bisphosphate carboxylase/oxygenase activity was the highest under DO < 0.5 mg/L. This study provides important basic data of PSB, which made contributions to large-scale practical application of PSB wastewater bioconversion. It also provides a unique biological sample for respiration and photosynthesis processes of biological research.

Keywords: Photosynthetic bacteria; Wastewater treatment; Resource recovery; Respiration rate; Photosynthesis rate

1. Introduction

Photosynthetic bacteria (PSB) wastewater bioconversion technology is an emerging wastewater treatment and resource recovery technology [1–4]. This technology can effectively remove pollution in wastewater and there is no problem of sludge treatment and disposal. This kind of wastewater treatment method is called resource technology, and microalgae are the same type of treatment method [5]. Moreover, the cell of PSB is regarded as valuable substances because of its high protein content and it contains many high-value substances, such as coenzyme Q_{10} [6–9]. With the rapid development of PSB wastewater bioconversion technology, the treatment of different types of wastewater, effects of environmental factors, and applications in reactors have been widely studied [10–16]. It has been reported that PSB can degrade many types of wastewater. Varied carbon sources and molecules of different sizes are metabolized by PSB, and the metabolites are essentially the same [17–21]. Environmental factors, such

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as temperature and additives, can promote or inhibit the metabolism of PSB. Temperature affects the final efficiency by influencing the changes in enzyme activity levels in PSB metabolism, while additives affect the final efficiency by stimulating the respiratory and photosynthetic reactions and the enzymatic reaction process [7,22]. The PSB technology has been reported to be performed at different scales and in light or non-light reactors. Light density and light type have been reported to affect the PSB metabolic process, and the metabolic functional substances, such as pigments, also show obvious changes [23–25]. Previous studies also found that the most important environmental factor affecting PSB metabolism is oxygen concentration dissolved oxygen (DO) [26,27]. DO is a key factor of microorganisms [28]. It has been reported that oxygen concentration affects the metabolic efficiency of PSB by affecting enzyme activity [29]. However, these studies lack research on the efficiency of respiration and photosynthesis metabolism processes in PSB, which is the key process in all conditions. Thus, this study aimed to clarify the basal respiration and photosynthesis metabolic efficiency in PSB.

The metabolism mode of PSB is unique and involves simultaneous respiration and photosynthesis. During photosynthesis, PSB absorbs light energy, synthesizes organics, and accumulates biomass. During respiration, PSB decomposes organics under the action of oxygen to reduce the chemical oxygen demand (COD). A portion of the reduced COD is converted to CO_2 and released into the atmosphere, whereas the remaining portion is used in the accumulation of biomass [17]. To clarify the basic metabolism efficiency, it is necessary to separately study the rates of respiration and photosynthesis. In biological reactions, the key factors are enzymes and the regulation of genes related to the expression of these enzymes. Therefore, enzymes and their related genes should be studied together.

In this study, the rates of respiration and photosynthesis and the genes related to these processes were investigated in PSB wastewater bioconversion under different dissolved oxygen (DO) concentrations.

2. Materials and methods

2.1. Selection of DO levels and enzymes and genes

2.1.1. Selection of DO levels

The concentrations of DO were determined as <0.5, 0.5–2, and >2 mg/L. The selected DO levels represent classic DO levels in conventional biological wastewater treatment, anaerobic, microaerobic, and aerobic conditions, respectively. It has been reported that COD removal and biomass of PSB are quite different under these DO levels [17,26].

2.1.2. Selection of enzymes and genes

There have been few studies on the mechanism of wastewater bioconversion by PSB; thus, the first step in this study was to select the appropriate enzymes and genes. The enzymes and genes were selected according to traditional biological wastewater treatment processes and the distinctive PSB metabolism process [29]. Phosphofructokinase (PFK), pyruvate kinase (PK), and ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) were selected as the enzymes for investigation in this study. The distribution of these enzymes in the metabolic pathway of PSB is shown in Fig. 1. PFK catalyzes the production of fructose-6-bisphosphate, which is a step in the decomposition process of glucose. It is the "gatekeeper" of the glycolysis process. The production of pyruvate and adenosine triphosphate from phosphoenolpyruvate and adenosine diphosphate, respectively, is catalyzed by PK. It plays a role in the last step of glycolysis. Both PFK and PK are key enzymes in the oxidative phosphorylation reaction. RuBisCO is the key enzyme in the Calvin cycle, which is a key step in the classical photosynthesis process. These photosynthetic enzymes were also selected because of their involvement in the photosynthetic metabolism in PSB.

Based on molecular biology, the genes that control the expression of these key enzymes are known as key genes. A gene in the respiration process and a gene in the photosynthesis process were selected. Thus, *pfk* (controlling the

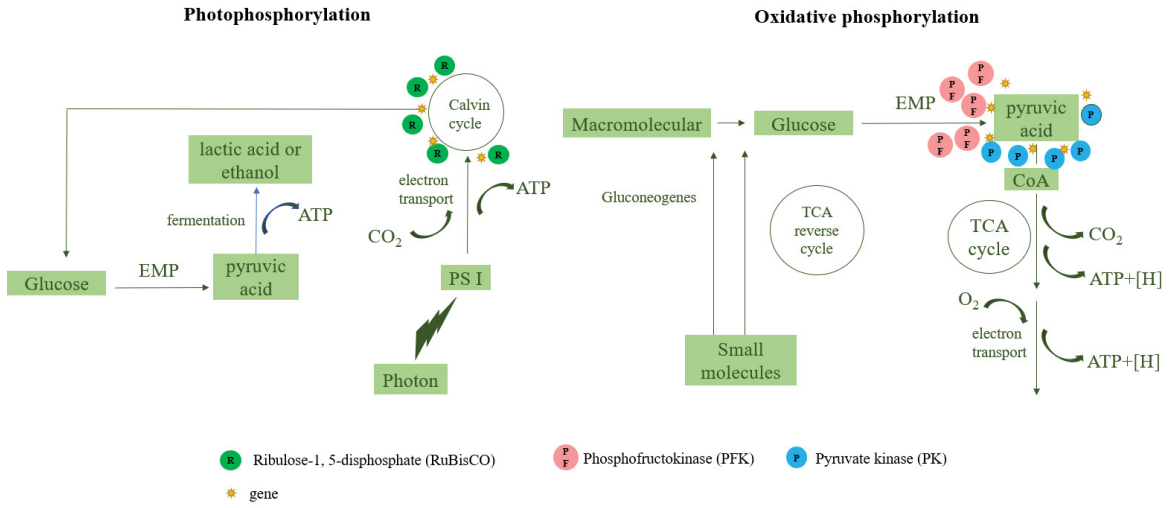

Fig. 1. Key enzymes in photosynthetic bacteria metabolism.

expression of PFK) and *cbb* (controlling the expression of RuBisCO) were evaluated.

2.2. Microorganisms and wastewater

Artificial sugar wastewater was prepared with malic acid, saccharose, potassium dihydrogen phosphate, ammonium sulfate, magnesium sulfate heptahydrate, and sodium bicarbonate. The COD concentration was 7,000 ± 200 mg/L, the NH_3–N concentration was 350 ± 20 mg/L, and the initial pH was 7.0 ± 0.2. The PSB strain used in this study was *Rhodobacter sphaeroides*.

2.3. Reactors and environmental factors

Here, 80% of wastewater and 20% of PSB bacterial fluid (v/v) were put into the reactor. The DO levels of <0.5, 0.5–2, or >2 mg/L were used. The DO concentration was measured using a DO meter. The light condition was set to 2,000 lux and was supplied by an incandescent lamp. The reaction temperature of the reactor was maintained at 28°C ± 2°C. Samples (25 mL) were collected at 0, 12, 24, 48, and 72 h.

2.4. Analysis methods

2.4.1. COD and biomass

The collected samples were first centrifuged at 9,056 g (10 min). After centrifugation, the supernatant was used to test the COD using the APHA method [30]. The biomass of PSB was determined using ultraviolet spectrophotometry. The absorbance of PSB biomass was measured at 660 nm.

2.4.2. Respiration and photosynthesis rates

The respiration rate can be calculated using the oxygen consumption method [31]. The steps followed were: (a) the liquid bacteria sample (50 mL) was added into a 250 mL BOD bottle, followed by the addition of 200 mL sucrose wastewater (8,000 mg/L, aerated in advance), the DO detector probe was placed in the solution, and the mouth of the bottle was sealed with a sealing film; (b) after 10 min, the change in DO concentration was measured as an indicator of the respiration rate, which was calculated using the following formula:

$$\text{Oxygen consumption mg}/\left(\text{h}\cdot\text{g}\right)=\frac{\text{DO}_2-\text{DO}_1}{t\cdot\text{biomass}} \tag{1}$$

The photosynthesis rate can be determined by the subtraction method according to the law of biological growth. The biomass of PSB comprises organics synthesized through photosynthesis and those synthesized by respiration, and the organics consumed by endogenous respiration should be subtracted. Thus, the value can be calculated using Eqs. (2) and (3):

$$\begin{aligned}\text{Photosynthesis synthesized organics} &= \text{biomass}\\ &+\text{organics consumed by endogenous respiration}\\ &-\text{organics synthesized by respiration}\end{aligned} \tag{2}$$

$$\text{Photosynthesis rate}=\frac{\text{Photosynthesis synthesized organics}}{t} \tag{3}$$

The organics consumed by endogenous respiration can also be measured using the modified oxygen consumption method, in which 200 mL of sucrose wastewater is replaced with 200 mL of deionized water.

2.4.3. Evaluation of PFK, PK, and RuBisCO

The enzyme activities were determined using an ultraviolet spectrophotometer with corresponding assay kits (Sigma-Aldrich) [29]. Pretreatment and enzyme extraction were performed according to the manufacturer's instructions. The extracted portion was detected at 340 nm using an ultraviolet spectrophotometer. The PSB cells were rinsed with deionized water and centrifuged. PSB cells (0.1 g) were used for testing PFK and PK enzyme activity. The collected PSB cells were ultrasonicated at 200 W for 3 s at spaces of 10 s (repeated 30 times) in an ice bath. To test RuBisCO enzyme activity, PSB cells (0.1 g) were ultrasonicated at 200 W for 3 s at spaces of 7 s (repeated for 1 min) in an ice bath.

2.4.4. Quantification of pfk and cbb

The absolute levels of *pfk* and *cbb* were determined using real-time PCR (MG96+, LongGene Instruments, Hangzhou, China). The primers used for *pfk* were PFK-F(CTCTGAATTCATGGAAGACATGCGAATTGC) and PFK-R(CTCTGGATCCCTATCCAAACATTGCCTGGG). The 20 μL reaction mixture contained 2X Taq Plus Master (P211-02, Vazyme Biotech Co., Ltd., Nanjing, China), 5 μM of each primer (Sangon Biotech, Shanghai, China), and 1 μL DNA template. The reaction conditions were 5 min at 95°C (predegeneration process), followed by 30 s at 95°C (denaturation), 35 cycles of 30 s at 52°C (annealing), and 1 min at 72°C. The annealing temperature of *pfk* is 52°C; although multiple pairs of primers were used for *cbb*, the pre-experiment failed. Three technical replicates were performed for each sample. After the constructed plasmid was identified by sequencing, the OD_{260} value of the plasmid was determined using a UV spectrophotometer and converted into copy number using the formula

$$\begin{aligned}\text{Initial copy number of plasmid}\left(\text{copies}/\mu\text{L}\right)&\\ =\text{concentration}\left(\text{ng}/\mu\text{L}\right)\times 10^{-9}&\\ \times 6.02\times 10^{23}/\left(\text{molecular weight}\times 660\right)&\end{aligned} \tag{4}$$

A 10-fold gradient dilution was set up with 45 μL of diluent and 5 μL of plasmid. Dilutions ranging from 10^{-2} to 10^{-7} of the standard sample were used to prepare the standard curve by pre-experimentation.

3. Results and discussion

3.1. COD removal and biomass accumulation

The removal of COD and biomass are important indexes for PSB wastewater bioconversion. The removal of COD

resulted in the removal of organic pollutants. Biomass was expressed as PSB cell accumulation. The COD removal and PSB biomass under different DO levels are shown in Fig. 2. The COD removal increased with the increase in oxygen concentration, and reached 93% at DO > 2 mg/L. Previous studies have also reported that the COD removal by PSB wastewater bioconversion was higher under high oxygen conditions than under low oxygen conditions [17,26,32,33].

Biomass production is a key target in wastewater bioconversion using PSB. Resource recovery of the PSB biomass is a valuable aspect of this process as PSB is rich in cell proteins and can be sold as feed or fertilizer [6]. As shown in Fig. 2b, a high DO level enhanced the growth of PSB. Previous studies have reported that the cell production and growth rate of PSB is higher under high DO levels than under low DO levels [17,26,29]. It has also been reported that higher DO does not promote biomass growth [34]. This is because PSB biomass is affected by complex mechanisms of respiration and photosynthesis.

3.2. Respiration rates

For studies on respiration and photosynthesis processes, the first topic is respiration and photosynthesis rates. The respiration rates under DO levels of <0.5, 0.5–2, and >2 mg/L are shown in Fig. 3. The maximum respiration rates under DO < 0.5, 0.5–2, and >2 mg/L were 216, 237, and 226 O_2 mg/g h, respectively. As shown in Fig. 3, the respiration rates under DO of 0.5–2 and >2 mg/L were higher than those under DO < 0.5 mg/L. In addition, the values at 72 h are different because the organics were consumed under DO of 0.5–2 and >2 mg/L. The respiration rate was the highest at 12 h. The results of respiration rate showed that it was obviously affected by oxygen, similar to respiration processes in other living beings [35,36]. The respiration rate was higher than that of other organisms, which illustrates that PSB have excellent respiration efficiency. This study also provides a unique biological sample for research on respiration processes.

To further explore the respiration efficiency, the changes in key enzymes, ATP, and gene expression were determined. The changes in PFK, PK, and ATP levels under different DO concentrations are summarized in Fig. 4. As shown in Fig. 4a, PFK activity was the highest at DO > 2 mg/L. The PK activity was the highest under DO > 2 mg/L, and reached its peak the fastest (12 h). The activities of PFK and PK were both higher under DO > 2 mg/L than under DO < 0.5 or 0.5–2 mg/L. This illustrates that PFK and PK activities were also promoted by high DO concentrations. ATP was also the highest under DO > 2 mg/L and reached its highest level at 12 h. The respiration rate was also the highest at 12 h. The PFK, PK, and ATP concentrations under DO > 2 mg/L corresponded to the respiration rate. For further clarification, the respiration gene expression was studied (Fig. 5). The *pfk* gene was quantitatively analyzed after 72 h. At 72 h, the highest respiration rate was observed under DO < 0.5 mg/L, followed by that under DO > 2 and 0.5–2 mg/L. The number of *pfk* copies was the highest under DO < 0.5 mg/L, followed by DO > 2 and 0.5–2 mg/L. Thus, the number of *pfk* copies was consistent with the respiration rate.

3.3. Photosynthesis rates

The photosynthesis rate, key enzymes, and genes were also investigated. Photosynthesis rates under different DO

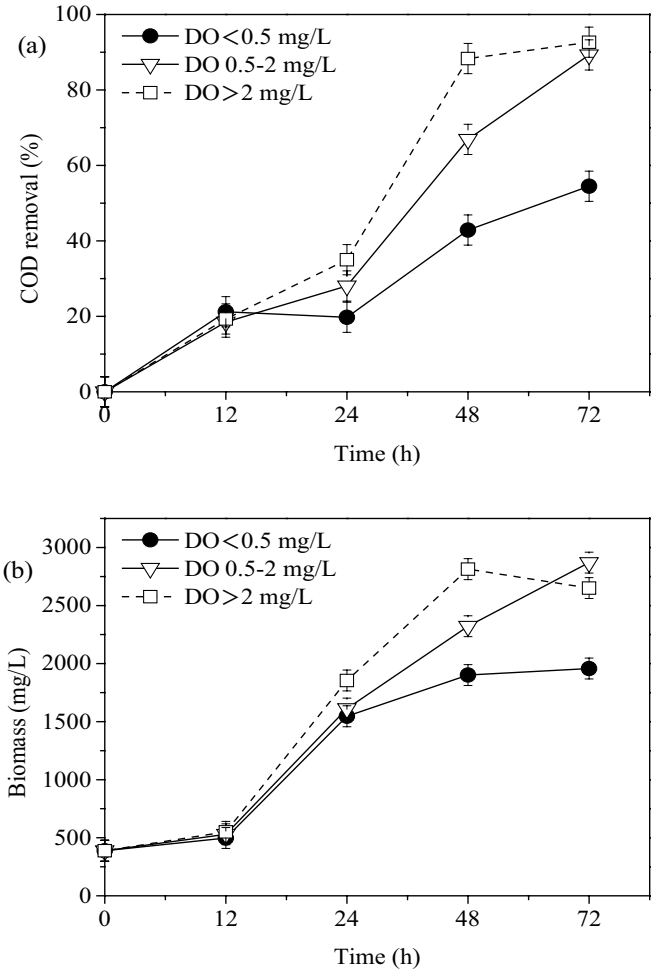

Fig. 2. (a) COD removal and (b) biomass of photosynthetic bacteria under different dissolved oxygen (DO) concentrations.

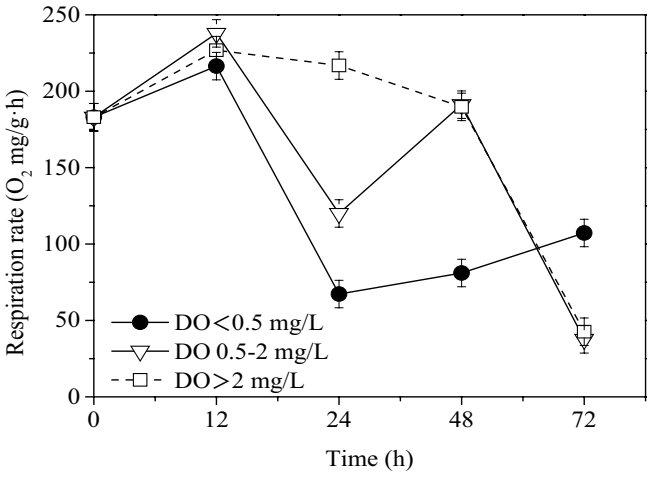

Fig. 3. Respiration rate of photosynthetic bacteria under different dissolved oxygen (DO) concentrations.

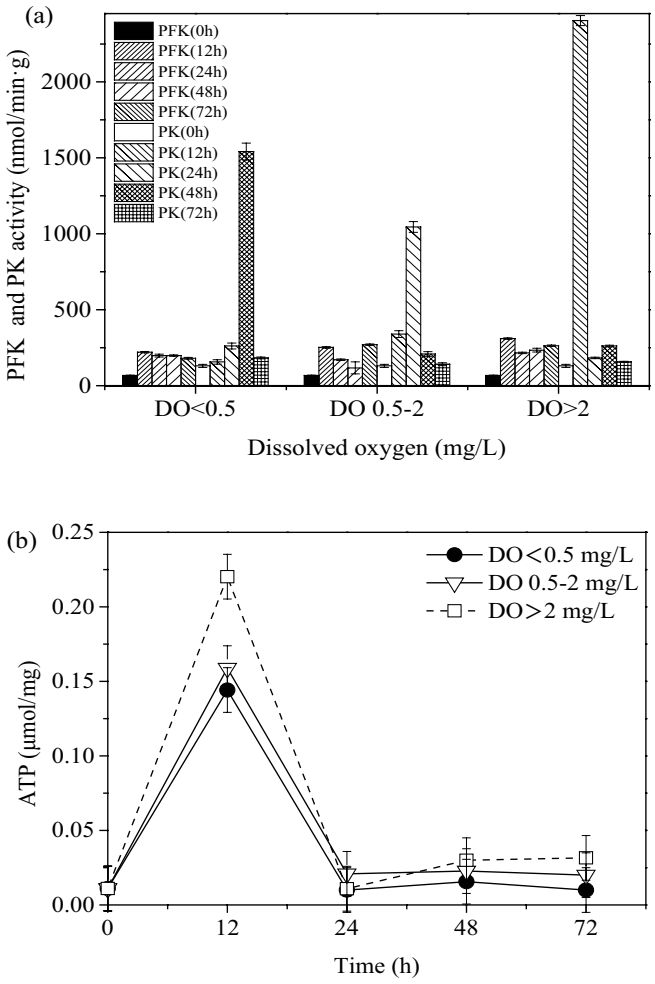

Fig. 4. (a) PFK and PK activity, and (b) ATP of photosynthetic bacteria under different dissolved oxygen (DO) concentrations.

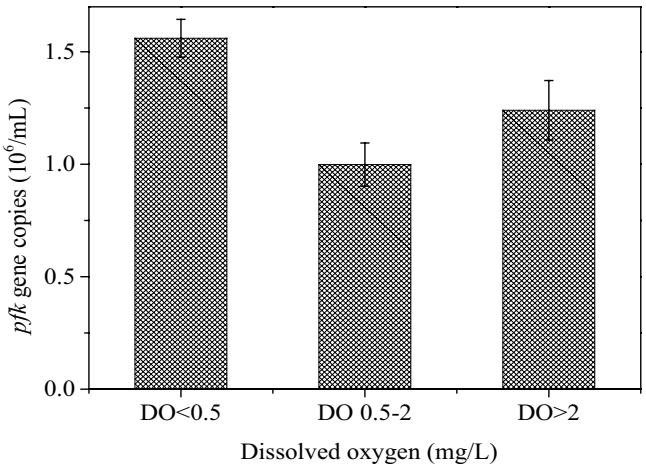

Fig. 5. Respiration gene *pfk* copies at 72 h of photosynthetic bacteria activity under different dissolved oxygen (DO) concentrations.

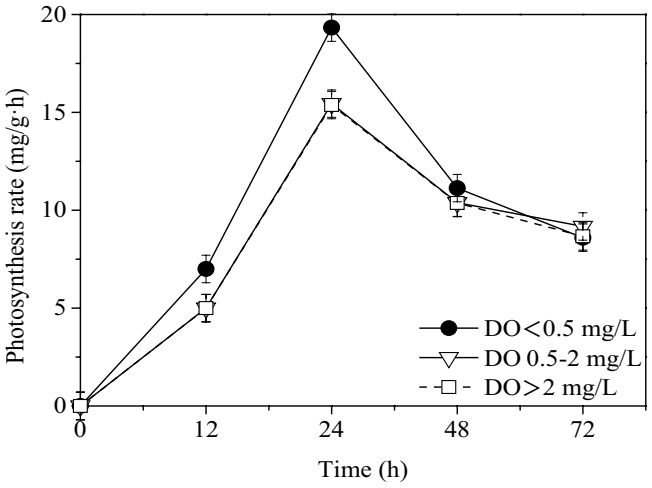

Fig. 6. Photosynthesis rate of photosynthetic bacteria under different dissolved oxygen (DO) concentrations.

concentrations are summarized in Fig. 6. The photosynthesis rates under DO < 0.5, 0.5–2, and >2 mg/L were 19, 15, and 15 biomass mg/g h, respectively. As shown in Fig. 6, the photosynthesis rates under DO < 0.5 mg/L were higher than those under DO of 0.5–2 and >2 mg/L. The photosynthesis rate was the highest at 24 h. The results show that photosynthesis rate was clearly affected by oxygen concentration. Oxygen affects photosynthesis efficiency by affecting the unique PSB mechanism. This study also provided a unique biological sample for photosynthesis research.

To further explore photosynthetic efficiency, the changes in photosynthetic pigments, key enzymes, and genes were determined. RuBisCO is an important enzyme involved in photosynthesis process. It catalyzes the reaction process of CO_2 fixation and contributes to cell accumulation. Therefore, RuBisCO is a crucial enzyme in PSB photosynthesis. As shown in Fig. 7a, RuBisCO activity reached its highest level at DO < 0.5 mg/L. This illustrated that low DO levels were beneficial to photophosphorylation activity, whereas high DO levels were inhibitory. It is clear that photophosphorylation and oxidative phosphorylation in PSB are competitive processes. The photosynthesis rate was also the highest at 24 h. The maximum RuBisCO concentration corresponded to the photosynthesis rate. Pigments are essential for phosphorylation. The pigments in PSB cells are carotenoids and bacteriochlorophyll. Fig. 7b shows that the levels of both pigments peaked at 24 h under most DO conditions. Bacteriochlorophyll and carotenoid production were both high at higher DO concentrations. This might be because a lower photosynthetic rate stimulated the production of pigments. The key gene of photosynthesis was not detected, possibly because the photosynthetic reaction center of PSB is different from that of other photosynthetic organisms. It was also reported that the gene for photosynthesis of PSB is different from that of other photosynthetic organisms [37–40].

4. Conclusions

The respiration and photosynthesis rates of PSB under different oxygen conditions were studied, leading to the following conclusions:

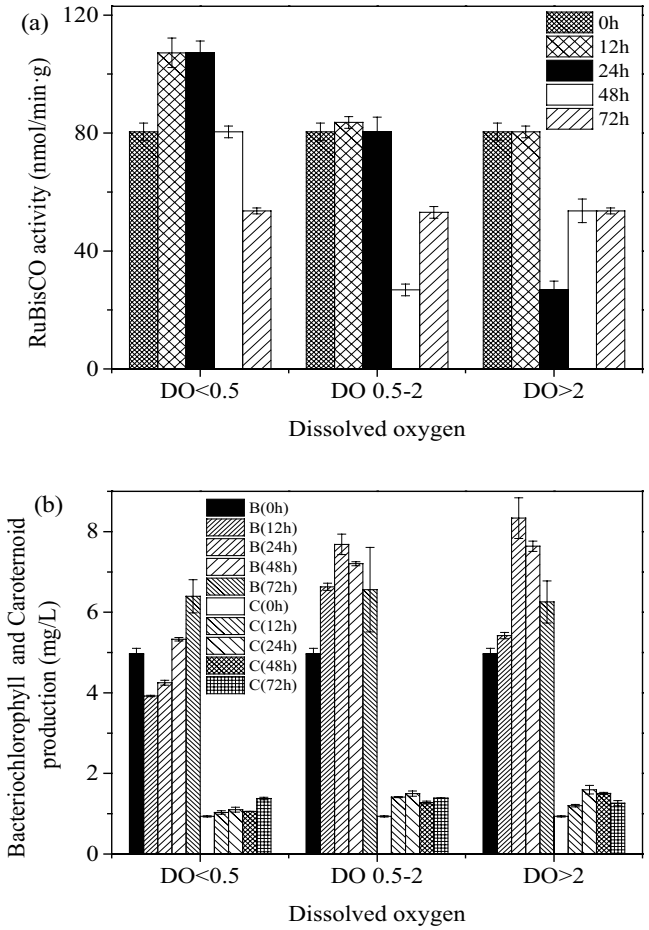

Fig. 7. (a) RuBisCO activity and (b) pigment concentrations of photosynthetic bacteria under different dissolved oxygen (DO) concentrations.

- The maximum respiration rates under DO < 0.5, 0.5–2, and >2 mg/L were 216, 237, and 226 O_2 mg/g h, respectively. The levels of PFK, PK, and ATP were higher under high DO concentrations, which corresponded to the respiration rate. The number of *pfk* copies was consistent with the respiration rate.
- The photosynthesis rates under DO < 0.5, 0.5–2, and >2 mg/L were 19, 15, and 15 biomass mg/g h. RuBisCO was the highest under DO < 0.5 mg/L. Pigments were stimulated when the photosynthesis rate was low.
- Oxygen promoted the respiration rate and inhibited the photosynthesis rate.

Acknowledgements

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