The Efficient Functioning of Photosynthesis and Respiration in *Synechocystis* sp. PCC 6803 Strictly Requires the Presence of either Cytochrome *c*$_6$ or Plastocyanin*

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In cyanobacteria, cytochrome *c*$_6$ and plastocyanin are able to replace each other as redox carriers in the photosynthetic and respiratory electron transport chains with the synthesis of one or another protein being regulated by the copper concentration in the culture medium. However, the presence of a third unidentified electron carrier has been suggested. To address this point, we have constructed two deletion mutants of the cyanobacterium *Synechocystis* sp. PCC 6803, each variant lacking either the petE or petJ gene, which respectively codes for the copper or heme protein. The photosynthetic and heterotrophic growth rate of the two mutants in copper-free and copper-supplemented medium as well as their photosystem I reduction kinetics *in vivo* were compared with those of wild-type cells. The two mutant strains grow at equivalent rates and show similar in vivo photosystem I reduction kinetics as wild-type cells when cultured in media that allow the expression of just one of the two electron donor proteins, but their ability to grow and reduce photosystem I is much lower when neither cytochrome *c*$_6$ nor plastocyanin is expressed. These findings indicate that the normal functioning of the cyanobacterial photosynthetic and respiratory chains obligatorily depends on the presence of either cytochrome *c*$_6$ or plastocyanin.

In eukaryotic organisms, the components of the photosynthetic and respiratory electron transfer chains are well identified and located in chloroplasts and mitochondria, respectively, but in cyanobacteria, the two redox pathways occur in the same membrane and share a number of components such as the plastoquinone pool and cytochrome *b*$_{6f}$ (1, 2). Because respiratory cytochrome *c* is lacking in cyanobacteria, it has been proposed that these organisms use the same *c*-type cytochrome, in particular cytochrome *c*$_6$ (Cyt), to serve both in photosynthesis and respiration (3).

Cyt is a well known electron carrier between cytochrome *b*$_{6f}$ and photosystem I (PSI) in cyanobacteria and some algae, but it can be replaced by plastocyanin (Pc) when the cells are grown in the presence of copper (cf. Ref. 4 for a recent review). In those species that are able to synthesize either Cyt or Pc, the expression level of the corresponding genes is controlled by the copper concentration in the growth medium (5, 6).

Despite their intrinsic different conformations, Cyt and Pc share a number of similar physicochemical and structural features that allow them to interact with the same redox partners with equivalent kinetic efficiency and replace each other inside the cells (7, 8). The two metalloproteins are thus presented as an excellent case study of biological evolution, which is not only convergent (two structures playing the same role) but also parallel (two proteins varying in a concerted way from one organism to another) (9). Such an interchangeability between Cyt and Pc in photosynthesis has also been proposed for the respiratory chain in which the two metalloproteins could act as alternative donors of electrons to cytochrome *c* oxidase (1, 10).

The observations by Zhang et al. (11) with Cyt- or Pc-deficient mutant strains of the cyanobacterium *Synechocystis* sp. PCC 6803 led these authors to conclude that electrons can be transferred from the cytochrome *b*$_{6f}$ complex to PSI in the absence of both Cyt and Pc and that Cyt is not obligatorily required for respiratory electron transport. Metzger et al. (12) indeed proposed the presence of a third electron carrier as the mutant strains of *Synechocystis* were able to grow photoautotrophically and sustain normal rates of oxygen evolution and dark respiration in the absence of both Cyt and Pc. These authors also measured the kinetics of *in vivo* PSI reduction and found that the electron transfer rates only occurred 4–6 times slower in the mutants than in the wild-type (WT) cells.

The challenge is thus to understand how photosynthetic and respiratory electron transport chains operate in cyanobacterial cells in the absence of both Cyt and Pc. To answer this question, we herein report the construction of mutant strains of *Synechocystis* cells that lack either Cyt or Pc to further analyze their photoautotrophic and heterotrophic growth along with their *in vivo* PSI reduction kinetics. In contrast to previous proposals, our findings allow us to conclude that the normal functioning of the cyanobacterial photosynthetic and respiratory chains obligatorily depends on the presence of one of these proteins, thus discarding the existence of any third efficient electron carrier.

**EXPERIMENTAL PROCEDURES**

Strains and Culture Conditions—*Synechocystis* sp. PCC 6803 was grown photoautotrophically in liquid or solid mineral BG-11 medium (13) either in the presence or absence of copper under continuous white fluorescent illumination (50 microEinsteins m$^{-2}$ s$^{-1}$) at 30 °C. Liquid cultures were bubbled with air supplemented with 1% (v/v) CO$_2$. Whenever necessary, copper was added at 1 μM, whereas copper-depleted medium (BG-11-C) was supplemented with 300 μM bathocuproinedisulfonic acid as a chelating agent to eliminate any traces of copper (14). Cell cultures with or without copper were pre-adapted to the new conditions by growth for 4 days in the new medium.
medium with increasing amounts of kanamycin from 50 to 500 mg l⁻¹ (22), and the transformants were selected and segregated in solid medium. WT cells were transformed with this plasmid by standard procedures. The CK1 plasmid was tested by restriction analysis.

The SPE plasmid was tested by restriction analysis. The ClaI-EcoRV fragment of the [³²P]dCTP-labeled pCytF plasmid (right). The band length is expressed in number of bp. See "Experimental Procedures" for details.

Cloning and Deletional Inactivation of petE and petJ Genes—To amplify the petE gene (coding for Pc) and its flanking regions by PCR, the following two oligonucleotides were designed from the genomic sequence of Synechocystis (19) (NCBI accession number NC_000911): RPC001A (ctgaggcggccatcctct) as the direct primer and RPC001B (atgcccctgccgat) as the reverse primer. Genomic DNA from Synechocystis was used as a template (Fig. 1) (20). A 2.6-kb band resulting from PCR was purified by electrophoresis in 1% agarose gel and cloned into the pGEMT commercial vector (Promega) to obtain the pPlaF plasmid.

The SmaI-CelII fragment from pPlaF was replaced by a C.K1 kanamycin resistance cassette from pRL-SPE plasmid, which contains theaadA gene that confers spectinomycin resistance as follows. pCytF was digested with NheI and EcoRV, and the resulting pCytF plasmid (left) was used to transform the pRL-SPE plasmid. The PvuII fragment from pRL-SPE corresponding to the pPlaF plasmid.

The Smal-Cell fragment from pPlaF was replaced by a C.K1 kanamycin resistance cassette from pRL161 plasmid (21). A 5.2-kb band was obtained after pPlaF digestion with Smal and Cell, and its ends were blunt-end ligated with Klenow polymerase and ligated with a 1.2-kb fragment obtained after pRL161 digestion with HinCII. The resulting pPlaFK1 plasmid was tested by restriction analysis. Synechocystis WT cells were transformed with this plasmid by standard procedures (22), and the transformants were selected and segregated in solid medium with increasing amounts of kanamycin from 50 to 500 µg ml⁻¹. The correct integration and segregation of the deleted copies was tested by Southern blot as follows. Genomic DNA of isolated mutants was digested with XmnI and separated in 0.7% agarose electrophoretic gels. The ends of this band were blunted with Klenow polymerase. The PvuII fragment from pRL-SPE corresponding to the pPlaF plasmid.

FIG. 1. Strategy designed to delete the petE (upper) and petJ (lower) genes in Synechocystis cells. Solid arrows denote open reading frames; open segments stand for probes used in Southern blot analysis; and closed segments correspond to primers for PCR cloning.

FIG. 2. Southern hybridization of petE and petJ deletional mutants compared with the WT species. Genomic DNAs were digested with appropriate restriction enzymes and hybridized with either the NheI-Smal fragment of the [³²P]dCTP-labeled pPlaF plasmid (left) or the ClaI-EcoRV fragment of the [³²P]dCTP-labeled pCytF plasmid (right). The band length is expressed in number of bp. See “Experimental Procedures” for details.

Repeated incubation cycles, and cell growth was monitored by spectrophotometrically measuring the chlorophyll content (15). Total protein concentration was determined as described elsewhere (16).

Light-activated heterotrophic growth experiments were carried out by adding 10 mM glucose to the standard BG-11 or BG-11-C solid medium. Cell cultures were incubated in darkness with 5-min pulses of white light (50 microeinsteins m⁻² s⁻¹) every 24 h (17). Other conditions were as for the photoautotrophic growth.

Escherichia coli DH5α was grown in Luria-Bertani liquid or solid medium (18) supplemented, when required, with kanamycin (50 µg ml⁻¹, spectinomycin (100 µg ml⁻¹), or ampicillin (100 µg ml⁻¹).

FIG. 3. Immunodetection of Pc and Cyt. WT, ΔpetE, and ΔpetJ Synechocystis cells were grown in the presence or absence of copper as indicated. 100 µg of total protein from cells were loaded into each gel lane with 0.1 µg of purified Cyt and Pc as controls. Polyclonal antibodies against Pc (A) and Cyt (B) were used.

FIG. 4. Photoautotrophic growth of WT, ΔpetE, and ΔpetJ Synechocystis strains. In each case, the cells were cultured either in the presence (ΔpetJ) or absence (ΔpetE) of copper. See “Experimental Procedures” for further details.

For the Southern blot analysis, genomic DNA was digested with BstEII using enzymes from the NheI-Smal fragment of the pRL161 plasmid, which contains theaadA gene that confers spectinomycin resistance as follows. pCytF was digested with NheI and EcoRV, and the resulting 5.0-kb band was isolated by 1% agarose gel electrophoresis. The ends of this band were blunted with Klenow polymerase. The PvuII fragment from pRL-SPE corresponding to the pPlaF plasmid.

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![Image](image_url)

**Fig. 5. Kinetic traces showing in vivo PSI reduction in WT, ΔpetE, and ΔpetJ Synechocystis cells.** The cells were previously cultured in the presence or absence of copper as indicated. The reaction cell contained an amount of Synechocystis cells equivalent to total chlorophyll content of 150–300 μg ml⁻¹. Absorbance changes were recorded at 820 nm. The continuous lines correspond to theoretical fittings to monoeponential or biexponential kinetics. Other conditions were as described under “Experimental Procedures.”

**Table 1**

|          | +Cu  | −Cu  |
|----------|------|------|
| kM × 10⁻³ |      |      |
| kF × 10⁻⁴ |      |      |
| kS × 10⁻⁴ |      |      |
| WT       | 2.7 ± 0.2 | 4.5 ± 0.6 | 2.0 ± 0.2 |
| ΔpetE    | <0.01 | 4.0 ± 0.3 | 3.1 ± 0.2 |
| ΔpetJ    | 3.6 ± 0.2 | ND     | <0.01 |

ND, not detected.

inoculating purified proteins (24, 25) into rabbits followed by extraction of serum blood at the Centro de Producción y Experimentación Animal (Seville, Spain). Binding of antibodies was visualized with peroxidase-conjugated antibodies and the commercial ECL-Plus kit (Amersham (Seville, Spain). Binding of antibodies was visualized with peroxidase-conjugated antibodies and the commercial ECL-Plus kit (Amersham Biosciences).

**Kinetics Analysis of In Vivo PSI Reduction—**WT and mutant cells of Synechocystis were harvested by centrifugation at different growing phases and suspended in 20 mM Tricine-KOH buffer, pH 7.0, supplemented with 10% (w/v) Ficoll to avoid cell aggregation. The in vivo kinetics for electron transfer from either Pc (in copper-supplemented cultures) or Cyt (in copper-depleted cultures) to PSI were followed by laser flash absorption spectroscopy as previously described (26). The reaction cell (optical path length, 1 mm) contained whole Synechocystis cells at 150–300 μg ml⁻¹ chlorophyll concentration and 1 mM ascorbate. The kinetics were recorded after excitation by laser flash both in the presence and absence of 20 μM phenazine methasulfate, which is a well-known efficient donor of electrons to PSI. Interferences arising from photosystem II (PSII) were avoided by pre-illumination of the samples with white light in the presence of 10 μM DCMU (3-(3',4'-dichlorophenyl)-1,1-dimethyleurea) and 10 mM hydroxylamine (27).

**RESULTS AND DISCUSSION**

**Deletion of the petE and petJ Genes in Synechocystis Cells—**The cyanobacterial cells were transformed with the pPiaFΔCK1 or pCytFASPE plasmids, and the resulting ΔpetE and ΔpetJ strains were selected as transformants corresponding to petE and petJ null mutants, respectively. ΔpetE was selected in BG-11-C medium with 300 μM bathocuproinedisulfonic acid to ensure the complete removal of copper and kanamycin (500 μg ml⁻¹). ΔpetJ was selected in BG-11 medium supplemented with 1 μM copper in the presence of both spectinomycin and streptomycin (20 μg ml⁻¹ each). The correct integration and segregation of both mutants were checked by Southern blot (Fig. 2) with the length of resulting bands and the absence of other bands being as expected for completely segregated mutants (see “Experimental Procedures”). Several attempts to segregate the double mutant were unsuccessful.

In agreement with the copper-dependent regulation of Pc and Cyt expression levels (see Introduction), WT Synechocystis cells synthesize either Pc or Cyt when cultured in the presence or absence of copper, respectively (Fig. 3). Accordingly, the ΔpetE strain produces Cyt when growing in copper-depleted medium but is completely unable to synthesize even traces of Cyt and/or Pc when the medium is supplemented with this metal. In a similar way, the ΔpetJ strain forms Pc in copper-supplemented medium but no detectable levels of Cyt and/or Pc were yielded in cells cultured in the absence of copper (Fig. 3).

**Photoautotrophic Growth of WT and Mutant Strains—**The ability of the ΔpetE and ΔpetJ mutants to grow under photoautotrophic conditions was determined in cultures with and without copper. As previous studies in the absence of a copper-chelating agent had led to controversial results (28) and we had
observed by Western blot analysis that residual copper levels (nanomolar range) in the culture medium were enough to induce Pc expression (data not shown), the copper-chelating agent bathocuproinedisulfonic acid was added to the cell cultures to completely remove metal traces and abolish residual Pc expression.

Growth curves show not only that the WT strain similarly grows either with or without added copper but also that the two deletion mutants grow at rates equivalent to that of WT when cultured in media that allow them to express one of the two electron donor proteins (Fig. 4). In fact, ΔpetE is only able to grow at a standard rate in the absence of copper, i.e. when Cyt is produced, whereas ΔpetJ grows normally when Pc is synthesized because of copper induction. When the ΔpetE and ΔpetJ strains are under conditions at which the expression levels of both Pc and Cyt are not detectable, their respective growth rate is much lower than that of WT cells.

In contrast to such a drastic decrease in the growth rates of the two mutant strains, Zhang et al. (11) reported a slightly diminished growth rate and a normal steady-state photosynthetic electron transport for their Pc- and Cyt-deficient mutants under similar phototrophic conditions. In view of these discrepancies, the kinetics for PSI reduction in whole cells of ΔpetE and ΔpetJ were analyzed by laser flash absorption spectroscopy.

In Vivo Reduction of PSI in WT, ΔpetE, and ΔpetJ Cells—In vitro PSI reduction by Cyt and Pc has been extensively investigated in a wide variety of photosynthetic organisms such as cyanobacteria (including Synechocystis), green algae, and plants (7, 25, 29). However, little is known on the kinetic behavior of the two metalloproteins serving as electron donors to PSI in vivo (30). In this work, the kinetics of in vivo PSI reduction by Cyt or Pc in Synechocystis were analyzed in whole cells by following the absorbance changes at 820 nm after flash-induced P700 photoxidation. From the resulting kinetics, the values for the observed rate constants of PSI reduction by either Pc or Cyt were estimated.

In WT Synechocystis cells growing in culture media supplemented with copper, PSI reduction was only ascribed to Pc because Cyt synthesis was repressed and the kinetics were well fitted to monoeponential curves (Fig. 5). The value for the observed rate constant of such a monoeponential kinetic (kM) was 

\[
\text{~2,700 s}^{-1} \text{ (t} 20 \text{, 250 \mu s)}
\]

(Table I). In WT Synechocystis cells growing in copper-depleted cultures in which Pc synthesis was repressed, Cyt-dependent PSI reduction followed a biphasic kinetic (Fig. 5): the first, fast phase yielded a rate constant (kF) of 

\[
\text{~45,000 s}^{-1} \text{ (t} 20 \text{, 16 \mu m)}
\]

and the second, slower phase exhibited a rate constant (kS) of 

\[
\text{~2,000 s}^{-1} \text{ (t} 350 \text{, 350 \mu s)}
\]

(Table I). The fast and slow phases accounted for 37 and 63%, respectively, of the total signal amplitude. These values for kM, kF, and kS remained constant at the different culture stages but significantly increase when phenazine methasulfate, a well known artificial electron donor to PSI, was added to the reaction cell (not shown).

In vivo PSI reduction in both ΔpetE and ΔpetJ cells growing under conditions that allow the expression of one of the two electron donor proteins follows kinetics similar to those observed in the WT strain (Fig. 5). In fact, the kinetics with the ΔpetE mutant in the absence of copper and with the ΔpetJ mutant in the presence of copper were, respectively, biphasic and monophasic and their observed rate constants were equivalent to those attained with the WT cells (Table I), but no PSI reduction was detected in mutant cells in which neither Pc nor Cyt was expressed (Fig. 5).

These data not only explain our experimental observations on the photoautotrophic growth of WT and mutant Synechocystis strains (see above) but also suggest that either Cyt or Pc is obligatorily required for the efficient reduction of PSI. In contrast, Metzger et al. (12) observed in vivo PSI reduction even in the absence of Pc or Cyt, a finding that can be ascribed to one (or both) of the following facts: (i) optical interferences derived from PSI excitation, or (ii) Pc expression because of residual copper levels.

To avoid these difficulties and assure that the observed kinetic signals can only be assigned to changes in the oxidation state of PSI, we have used a 694-nm laser flash to specifically favor the excitation of PSI over PSII, have added DCMU-hydroxylamine to the reaction cell to block electron transfer from PSI, have confirmed that the kinetic signals are ascribed to PSI by adding phenazine methasulfate, and have completely removed copper from copper-free culture media by adding an efficient chelating agent.

Light-activated Heterotrophic Growth of WT and Mutant Cells—Taking into account that the cyanobacterial respiratory and photosynthetic electron transfer chains share a number of redox components like Cyt and Pc (1, 10), the ability of the WT, ΔpetE, and ΔpetJ strains to grow in glucose-supplemented culture media was investigated. Under such heterotrophic conditions, glucose was used as an organic carbon source (17) and the electrons were transported from the sugar molecule to dioxygen throughout the respiratory pathway.

Fig. 6 shows that none of the cell strains (including the WT) can grow in copper-free medium. This is as expected from the specific requirement for copper of cytochrome c oxidase to be correctly assembled and able to function (10). However, in copper-containing media, the WT and ΔpetJ strains synthesized Pc and showed a normal growth level but the ΔpetE strain produced neither Cyt nor Pc and was thus unable to grow because of the absence of a donor of electrons to cytochrome c oxidase.

Taken together, all of these data indicate that there is no any other alternative redox mediator as efficient as Cyt and Pc in the photosynthetic and respiratory electron transport chains and therefore Synechocystis cells strictly depend on the synthesis of either Cyt or Pc to grow not only photoautotrophically but also heterotrophically.

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