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REACTION KINETICS OF P-700, CYTOCHROME *c*-553 AND CYTOCHROME *f* IN THE CYANOBACTERIUM, *SYNECHOCOCCUS* SP.

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Absorption changes invoked by short flashes in the Soret band region were measured in the thermophilic cyanobacterium *Synechococcus* sp. and photoresponses of P-700, cytochrome *c*-553 and cytochrome *f* were resolved with the aid of a microcomputer. Cytochrome *c*-553 was oxidized very rapidly with a half-time of less than 20 μs, while the half oxidation time of cytochrome *f* was 35–45 μs. The two cytochromes were reduced monophasically with half-time of 2 ms after a lag lasting a few milliseconds. The reduction kinetics of P-700 showed three exponential phases with half-times of 40 μs, 200 μs and 2 ms, which are ascribed to electron donation from cytochrome *f*, the Rieske iron-sulfur protein and plastoquinone, respectively. The results support the following sequence and rates of linear electron transport at the physiological temperature of the cyanobacterium: P-700 $\overset{<20\ \mu s}{\leftarrow}$ cytochrome *c*-553 $\overset{40\ \mu s}{\leftarrow}$ cytochrome *f* $\overset{200\ \mu s}{\leftarrow}$ Rieske protein $\overset{2\ ms}{\leftarrow}$ plastoquinone.

Introduction

The occurrence of a soluble *c*-type cytochrome having an absorption maximum of the α-band at about 553 nm and a midpoint potential comparable to that of cytochrome *f* in green, brown and red algae as well as cyanobacteria was reported at the end of the 1950's [1], followed by crystallization of cytochrome *c*-553 from a red alga *Porphyra tenera* [2,3]. The cytochrome has an acidic protein with molecular weight of 12000 [4], is associated with chloroplasts but readily solubilized from the membranes on disruption of cells [5]. Since then, numerous reports have appeared of extraction and characterization of soluble cytochrome *c*-553 from a wide variety of algae and cyanobacteria [6–19].

Spectrophotometric studies have demonstrated that a *c*-type cytochrome with the Soret band maximum at 420 nm undergoes reversible oxidation on illumination of algal cells in a way indicating its function between PS I and II [20]. In earlier works, cytochrome *c*-553 was assumed to play a role analogous to cytochrome *f* in higher plants. Wood [11] found, however, that algae contain, besides soluble cytochrome *c*-553, a membrane-bound cytochrome equivalent to cytochrome *f*. Subsequently, the contents of cytochrome *c*-553 and plastocyanin in several algae were shown to vary inversely depending upon the copper concentrations of the growth media [13–15]. It is currently assumed that cytochrome *c*-553 and plastocyanin are functionally equivalent and thus interchangeable with each other in photosynthetic electron transport in algae and cyanobacteria.

The two soluble proteins mediate electron transfer from the cytochrome b_6- *f* complexes to the PS I reaction center complexes. Light-induced

Abbreviations: PS, photosystem; Hepes, *N*-2-hydroxyethylpiperazine-*N'*-2-ethanesulfonic acid; DBMIB, 2,5-dibromo-3-methyl-6-isopropyl-*p*-benzoquinone; DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethylurea; DCIP, 2,6-dichlorophenolindophenol; Chl, chlorophyll; Tricine, *N*-tris(hydroxymethyl)methylglycine.

absorption changes of plastocyanin are difficult to measure due to the weak and diffuse absorption bands and information on the in situ kinetics of the copper protein is still meager. Cytochrome *c*-553 having sharp and intense absorption bands is more amenable to spectrophotometric investigation. The kinetics of electron transfer between the two complexes through a soluble protein carrier can be more easily monitored by measuring the photoresponse of cytochrome *c*-553. However, the absorption spectrum of cytochrome *c*-553 largely overlaps that of cytochrome *f* and none of the earlier experiments have measured photoresponses of the two cytochromes separately.

The Rieske iron-sulfur protein is another electron carrier that is difficult to measure spectrophotometrically. Although evidence is accumulating for the functioning of the Rieske protein between plastoquinone and cytochrome *f* [21–24], the in situ kinetics of the protein remain as yet unclear.

In the present work, absorption changes invoked by short flashes in the cyanobacterium *Synechococcus* sp. have been studied. Photoresponses of cytochrome *c*-553 and cytochrome *f* in the Soret band region were isolated by correcting for overlapping absorption changes by the means of computer subtraction. Reaction kinetics of the two cytochromes and P-700 will be discussed in terms of a linear electron transport. The results also suggest the functioning of the Rieske iron-sulfur protein between cytochrome *f* and plastoquinone.

Materials and Methods

The unicellular thermophilic cyanobacterium *Synechococcus* sp. was cultured at 55°C as described previously [25,26]. Cells grown for 24 h were employed throughout the present work. The contents of electron carriers and reaction centers in the 24-h-grown cells have recently been determined [27]. For spectrophotometric measurements, the cells were suspended in fresh culture medium containing 25 mM Hepes-NaOH (pH 7.5) to give a final Chl *a* concentration of about 10 μg/ml. The suspension was kept under illumination with white light of 1000 lx at 22–24°C prior to measurement. Otherwise, reduction kinetics of cytochromes and P-700 were gradually slowed down during the course of experiments due to respiratory consumption of endogenous substrates [26]. To eliminate the fast electrochromic absorption changes, 5 μM gramicidin D and 50 mM KCl were added before measurement [28]. The thylakoid membranes were prepared as described by Takahashi et al. [29].

Absorption changes were measured with a Union Giken single-beam spectrophotometer as described previously [26,30], except that a narrower bandwidth of the measuring beam (1.4 nm) was used. Cells were illuminated with red flashes (longer than 650 nm) which preferentially excite PS I. The flash duration was 5 μs at its half-peak height but had a long tailing of about 80 μs. The photomultiplier was protected against the actinic light with two Corning 4-96 filters. Unless otherwise stated, flashes were fired at 3 Hz and 500–1000 signals were averaged. Signal averaging and data processing were carried out with a microcomputer (Sord M223 mark II) connected to the spectrophotometer. The time resolution of absorption changes was limited by the flash used. All experiments were carried out at 55°C, except those shown in Fig. 2.

Amounts of P-700, cytochrome *c*-553 and cytochrome *f* oxidized were estimated from magnitudes of absorption changes by taking the flattening effect of intact cells into consideration [31,32]. The flattening of absorption bands in the Soret region was estimated by comparing the size of the P-700 signal at 434 nm in intact cells with that in the spheroplasts which had been solubilized with Triton X-100. The complete reduction and oxidation of P-700 were ensured by adding suitable reductants prior to illumination and by the use of a continuous actinic light of a sufficient intensity, respectively. The signal size of P-700 in solubilized spheroplasts was 1.6-times larger than that in intact cells. This value was also employed for estimation of cytochromes from photoresponses in the Soret band region.

Chlorophyll was determined as described by Mackinney [33].

Results

Separation of photoresponses

On flash excitation, *Synechococcus* cells showed a rapid bleaching of an absorption band centered

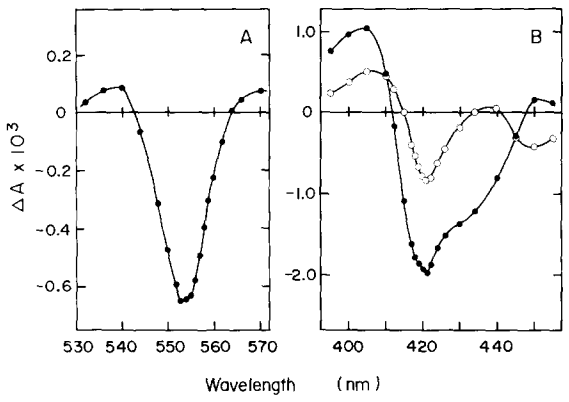

Fig. 1. Difference spectra of flash-induced absorption changes in the α-band region (A) and in the Soret band region (B). Cells were suspended in fresh growth medium containing 25 mM Hepes-NaOH (pH 7.5), 5 μM gramicidin D and 50 mM KCl. Chlorophyll concentration was 7 μg/ml. Flashes were fired at 3 Hz and 1000 signals were averaged. (B) (●———●) Difference spectrum for total absorption changes; (○———○) difference spectrum of cytochrome *f* oxidation obtained by subtracting the photoresponses of cytochrome *c*-553 and P-700 from the total absorption changes as described in the text.

at 553 nm, which can be ascribed to oxidation of cytochrome *c*-553 or cytochrome *f*, or both [26,28]. The negative peak at 553 nm was, however, significantly distorted by overlapping fast electrochromic band shifts of a carotenoid [28]. In the present work, therefore, we have measured photoresponses in the presence of gramicidin D at a concentration sufficient to eliminate the fast electrochromic band shift. The spectral resolution was also improved by the use of the measuring beam of a narrower bandwidth. Fig. 1A depicts the difference spectrum for the flash-induced absorption changes thus determined. In agreement with previous results [26,28], the bleaching was maximal at 553 nm and there was no peak or shoulder attributable to cytochrome *b*-563. However, the difference spectrum determined in the present work revealed a noticeable shoulder on the long-wavelength side of the maximum, at about 555 nm. This suggests that flashes caused oxidation of both cytochrome *c*-553 and cytochrome *f* which have the α-band maxima at 553 and 555 nm, respectively [19,27,34].

The photooxidation of the two cytochromes was also seen in the difference spectrum in the Soret band region (Fig. 1B, closed circles). Cytochrome *c*-553 and cytochrome *f* have the Soret band maxima at 415–417 and 421–422 nm, respectively [11,12]. Correspondingly, the difference spectrum showed a shoulder at 418 nm and a maximum at 421 nm. A large shoulder at 435 nm and a positive band at 450 nm are ascribed to P-700 photooxidation.

Photoresponses of cytochrome *c*-553 and cytochrome *f* largely overlap each other both in the α-band and in the Soret band regions. In order to observe the kinetics of cytochrome *c*-553, it is necessary to correct flash-induced absorption changes for the contribution of cytochrome *f*. This could be accomplished with the aid of a microcomputer in the Soret band region where the spectral overlapping of the two cytochromes is less than that in the α-band region. In addition, the photoresponses of cytochromes were much larger in size and the interference of the gramicidin-insensitive blue shift of carotenoid [28] was less significant in the Soret band than in the α-band region. P-700 showed a large photoresponse in the blue region. We have also isolated the P-700 response, because its reduction kinetics are important for the understanding of functions of the cytochromes on the electron-donating side of the PS I.

Accurate oxidized minus reduced difference spectra of components contributing to absorption changes in the Soret band region are needed for the resolution of individual photoresponses from the total absorption transients. Cytochrome *c*-553 has previously been isolated from *Synechococcus* [19]. The oxidized minus reduced difference spectrum of the cytochrome shows a negative peak at 417 nm and isosbestic points at 410 and 434 nm (Fig. 2A). Cytochrome *f* has not yet been isolated from the cyanobacterium employed here. Böhme et al. [34] have reported that the oxidized minus reduced difference spectrum of cytochrome *f* purified form *Spirulina platensis* has a maximum at 423 nm and isosbestic points at 415 and 434 nm. The spectral features of *Synechococcus* cytochrome *f* were assumed to be identical to those of *Spirulina* cytochrome *f*.

The difference spectrum of P-700 was measured in thylakoid membranes prepared with a hypotonic medium [29]. The membranes show only P-700 photooxidation because they lost cyto-

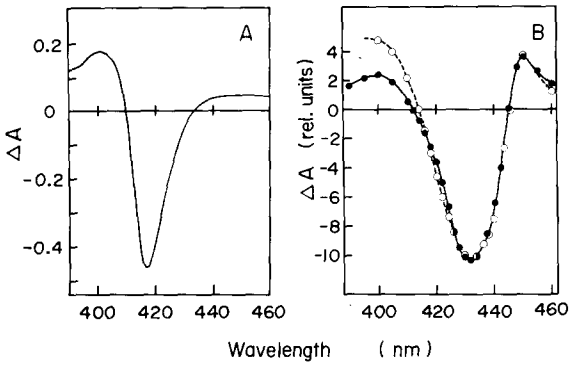

Fig. 2. Oxidized minus reduced spectra of cytochrome *c*-553 (A) and P-700 (B) in the Soret band region. (A) Cytochrome *c*-553 was reduced with ascorbate and then passed through a small column of DEAE-cellulose to remove the reductant. The absorption spectrum of the reduced cytochrome was recorded, then the cytochrome was oxidized with ammonium persulfate and its spectrum was determined. Recording, digitizing and subtraction of spectra were carried out with a Hitachi-320 spectrophotometer. (B) (●———●) Thylakoid membranes were suspended in 50 mM Tricine-NaOH (pH7.5), 1 mM methyl viologen, 2 mM ascorbate and 10 μM DCIP and illuminated with continuous red light (longer than 650 nm, $6.2 \cdot 10^5$ erg·$cm^{-2} \cdot s^{-1}$). Absorption changes were determined with a Hitachi-356 spectrophotometer at 25°C. (○- - -○) Difference spectra for flash-induced absorption changes in cells at 8°C. Flashes were fired at 0.5 Hz and 250 signals were averaged. The two curves were normalized at 434 nm.

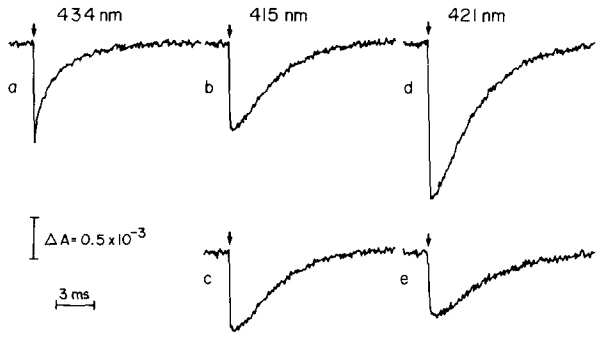

Fig. 3. Separation of flash-induced absorption changes of P-700, cytochrome *c*-553 and cytochrome *f* in the Soret band region. a,b and d are the uncorrected absorption changes at 434, 415 and 421 nm, and c and e the corrected absorption changes at 415 and 421 nm, respectively. Measurements were carried out as in Fig. 1. Downward arrows mark flash illumination. For details, see text.

chrome *c*-553 and the electrochromic carotenoid band shift. The light minus dark difference spectrum showed bleaching of a band with a maximum at 432 nm and isosbestic points at 411 and 445 nm (Fig. 2B). In order to examine the contribution of the electrochromic absorption changes in the Soret band region, the difference spectrum of P-700 oxidation was also measured in intact cells at 8°C. Hirano and Katoh [28] have shown that flash excitation of cells causes P-700 photooxidation and electrochromic absorption changes but little oxidation of cytochromes at temperature below 10°C, where rereduction of cytochromes was too slow to accumulate the reduced form during the flash intervals. Comparison of the two spectra indicates that the contribution of electrochromic absorption changes is slight or negligible between 415 and 450 nm and becomes significant only below 410 nm. A small difference between the two spectra at 420 nm may be ascribed to residual changes of cytochromes at the low temperature.

Since cytochrome *c*-553 and cytochrome *f* share a common isosbestic point at 434 nm, absorption changes observed at this wavelength can be ascribed to P-700 alone. The flash illumination induced a rapid absorption decrease at 434 nm which quickly returned to the original level (Fig. 3, trace a).

Absorption changes at 415 nm, an isosbestic point of cytochrome *f*, are attributed to both cytochrome *c*-553 and P-700 (trace b). The photoresponse of cytochrome *c*-553 was isolated by subtracting P-700 response at this wavelength from observed absorption transients. The P-700 response at 415 nm was estimated by multiplying the time course recorded at 434 nm (trace a) by a factor of 0.12, which is the ratio of the signal amplitude of P-700 at 415 nm to that at 434 nm determined from the difference spectra of P-700 shown in Fig. 2B. Since the contribution of P-700 is relatively small at 415 nm, the resulting trace (trace c) is not much different from trace b.

The photoresponse of cytochrome *f* was isolated by correcting the absorption changes at 421 nm for the contributions of cytochrome *c*-553 and P-700 (trace e). Responses of P-700 and cytochrome *c*-553 at this wavelength were obtained by multiplying their absorption transients at 434 and 415 nm by factors of 0.43 and 0.81, respectively. Thus, the correction results in a considerable diminution in the signal size. The validity of the

computer manipulations is indicated by a spectrum obtained by plotting magnitudes of corrected absorption changes against wavelength (Fig. 1B, open circles). The spectrum having a negative peak at 421 nm and a positive band at 410 nm clearly indicates cytochrome *f* oxidation. Note, however, that the spectrum is somewhat displaced upward, suggesting an overlapping positive absorption change. The spectrum also shows a negative band at 450 nm. The absorption decrease at 450 nm was faster than photooxidation of cytochrome *c*-553 or *f* and was totally insensitive to DCMU. Although the nature of the absorption change was not further studied, the 450 nm band may be ascribed to a reaction related to the primary photochemistry of PS I.

Oxidation-reduction kinetics

Semilogarithmic plots of the reduction kinetics of P-700, cytochrome *c*-553 and cytochrome *f* are presented in Fig. 4. The P-700 reduction was approximated by two first-order components with half-times of 0.2 and 1.7 ms at the recording time used (but see below for a faster time scale). We shall refer to the two reduction components as the 0.2 and 2 ms components, although the actual half-times of the fast and slow components varied to some extent with cultures. The size of the 0.2 ms components was about one-third of the total P-700 reduction.

The reduction kinetics of the two cytochromes agree with that of the 2 ms component of the P-700 reduction, indicating that reduction of the three electron carriers share a common rate-limiting reaction, i.e., plastoquinol oxidation. Note that the reduction of cytochromes *c*-553 and *f* started after a significant lag during which a considerable portion of P-700 had been reduced. This indicates that electrons equilibrate rapidly among P-700 and the two cytochromes according to their midpoint potentials.

Fig. 5 illustrates photoresponses recorded at a faster time scale. The P-700 photooxidation was too fast to be determined. Cytochrome *c*-553 was rapidly oxidized with a half-time of less than 20 μs. Note that the reduction kinetics of P-700 had no rapid phase corresponding to the oxidation of cytochrome *c*-553. Instead, it showed a lag, during which cytochrome *c*-553 was mostly oxidized.

The half oxidation time of cytochrome *f* was in the range 35–45 μs. It is seen that cytochrome *f* oxidation proceeded halfway during the lag of P-700 reduction. Correspondingly, the P-700 reduction kinetics showed a rapid phase indicating

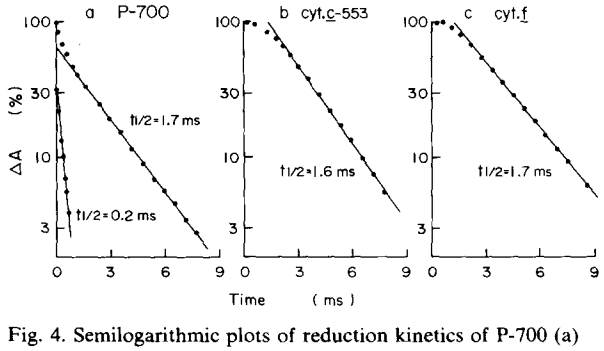

Fig. 4. Semilogarithmic plots of reduction kinetics of P-700 (a) cytochrome *c*-553 (b) and cytochrome *f* (c).

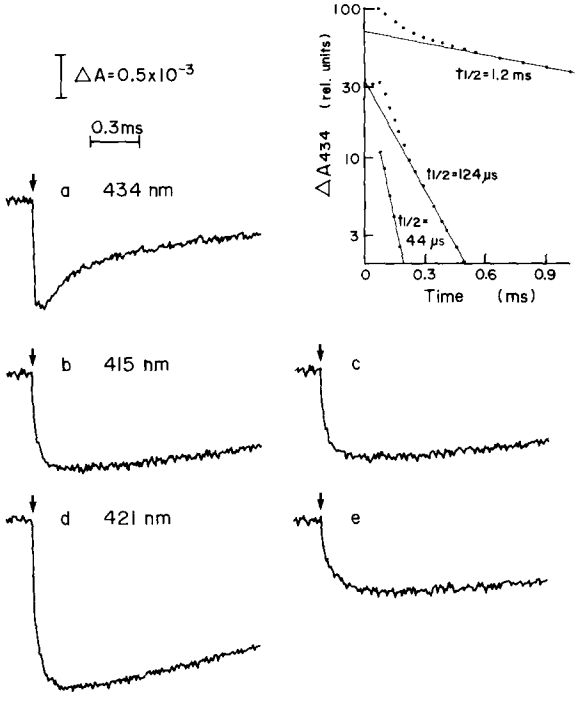

Fig. 5. Separation of flash-induced absorption changes of P-700, cytochrome *c*-553 and cytochrome *f* at a fast recording time. Experimental manipulations were as described in Fig. 3, except that a 10-times faster recording time was used. a,b and d are the uncorrected absorption changes at 434, 415 and 421 nm, and c and e the corrected absorption changes at 415 and 421 nm, respectively. The inset shows a semilogarithmic plot of the reduction kinetics of P-700.

electron donation from cytochrome *f*: A semilogarithmic plot revealed that about 10% of P-700 was reduced with a half-time of 44 μs (Fig. 5, inset).

Cells grown for 24 h contain 7.4 mol P-700, 4.0 mol cytochrome *c*-553 and 3.0 mol cytochrome *f* per 1000 mol Chl *a* [27]. Taking the flattening effect into account, we estimated from the magnitude of the photoresponses that 77, 87 and 65% of P-700, cytochrome *c*-553 and cytochrome *f* present in the cells were oxidized by the flash illumination, respectively. The extent of oxidation of cytochrome *f* would be an underestimate due to the above-mentioned overlapping absorption change (see Fig. 1B). The incomplete oxidation of P-700, as well as the absence of a rapid phase corresponding to cytochrome *c*-553 oxidation from the P-700 reduction kinetics, may be explained by assuming that cytochrome *c*-553 donates electrons to P-700 so rapidly that P-700 is again oxidized during the illumination with the flash having a long tailing. To examine this assumption, the numbers of electrons transferred through PS I by a single flash excitation were estimated. The sum of P-700, cytochromes *c*-553 and *f* oxidized during the lag of P-700 reduction was 0.19 nequiv. in the sample containing 0.13 nmol P-700. This indicates that every P-700 present in the cells was oxidized on average 1.5-times during the single flash illumination.

Discussion

The kinetic data obtained in the present work suggest the following sequence and rates of photosynthetic electron transport from plastoquinone to P-700 in *Synechococcus*,

$$\text{P-700} \overset{<20\,\mu s}{\leftarrow} \text{cyt. } c\text{-553} \overset{40\,\mu s}{\leftarrow} \text{cyt. } f \overset{200\,\mu s}{\leftarrow} \text{Rieske protein}$$

$$\overset{2\,ms}{\leftarrow} \text{plastoquinone}$$

Photoresponses of cytochrome *c*-553 and cytochrome *f* were measured separately for the first time. Cytochrome *c*-553 was photooxidized too rapidly to be determined by the instrument used, whereas photooxidation of cytochrome *f* proceeded with half-times of 35–45 μs. The oxidation kinetics of the cytochromes are compatible with a linear sequence of cytochrome *f* → cytochrome *c*-553 → P-700, although they do not necessarily exclude a parallel electron donation from the two cytochromes to PS I. A direct oxidation of cytochrome *f* by P-700 may, however, be ruled out by the observation that only P-700 oxidation, but no cytochrome *f* oxidation, occurred in the thylakoid membranes, from which cytochrome *c*-553 had been solubilized (Fig. 2B)

Hirano and Katoh [28] have previously measured the temperature dependence of photooxidation of a cytochrome at 553 nm in *Synechococcus* cells. The photoresponse measured by them has a half-time of 50 μs at 55°C and, in the light of the present findings, is ascribed to cytochrome *f* oxidation. Then, their data imply that cytochrome *f* oxidation proceeds independently of changes in membrane fluidity due to phase separation of the membrane lipids. This is incompatible with the view that electron transfer from cytochrome *f* to P-700 is supported by the lateral diffusion of the cytochrome b_6- *f* complexes and PS I reaction center complexes localized in the membranes [35].

The previous works have shown that the cytochrome photoresponse determined at 553 nm relaxed with a half-time of 2 ms [28] and that the dark relaxation was strongly suppressed either in the presence of DBMIB which blocks electron flow from plastoquinone, or when plastoquinone had been oxidized through the respiratory chain [26]. The 2-ms reduction phase of cytochrome *c*-553, cytochrome *f* and P-700 observed in the present work is therefore ascribed to electron transfer from plastoquinone. Detailed effects of DBMIB on these photoresponses will be described elsewhere.

The reduction kinetics of P-700 did not show a rapid phase corresponding to the oxidation of cytochrome *c*-553. Instead, a lag of the P-700 reduction lasting several tens of microseconds occurred. During the lag, every P-700 was estimated to be oxidized 1.5-times on average. It should be noted that no equimolar stoichiometry exists between P-700 and cytochrome *c*-553 in *Synechococcus* cells: The cytochrome *c*-553 content is about half that of P-700 [27]. We suggest, therefore, that electron transfer from cytochrome *c*-553 to P-700 is so rapid that P-700 is oxidized twice during the flash excitation in about half of the PS I reaction centers.

Cytochrome *c*-553 is mostly oxidized during the lag of P-700 reduction and remains in the oxidized state for a few milliseconds. Thus, P-700 reduction observed immediately after the lag should be ascribed to electrons from carriers located on the PS II side of cytochrome *c*-553. A small fraction of P-700 was found to be reduced with a half-time of 44 μs. This can be attributed to cytochrome *f* because cytochrome *f* oxidation proceeds at a comparable rate and over a corresponding time period.

Several lines of indirect evidence suggest functioning of the Rieske iron-sulfur protein between cytochrome *f* and plastoquinone [21,23,24]. The in situ reaction kinetics of the protein are, however, very difficult to measure spectrophotometrically. Koike et al. [22] showed that DBMIB increases the extent of cytochrome *f* oxidation mainly by inducing a slow extra oxidation in spinach chloroplasts and suggested that the poison blocks electron transfer from the Rieske protein to cytochrome *f*. The observation suggests that the Rieske protein reduces cytochrome *f* at a rate comparable to or faster than that of the slow cytochrome *f* oxidation induced by the inhibitor. The biphasic kinetics of cytochrome *f* oxidation observed in the presence of DBMIB may be related to a heterogeneity of electron transport, such as the heterogeneous distribution of the PS I reaction centers and the cytochrome b_6-*f* complexes in different membrane regions [36,37]. Another electron-transport inhibitor, 5-(*n*-undecyl)-6-hydroxy-4,7-dioxobenzothiazole (UHDBT), seems to act like DBMIB because the inhibitor, at 15 μM, not only increased the extent of cytochrome *f* oxidation but also induced biphasic kinetics in cytochrome *f* oxidation (Fig. 4 of Ref. 38).

The 44-μs phase of P-700 reduction kinetics was followed by a reduction phase with a half-time of 0.2 ms. This suggests the presence of an electron carrier which transfers its electrons to P-700 after electrons in the cytochrome *f* molecules are exhausted. We interpret the 0.2-ms reduction phase as being due to electron transfer from the Rieske protein. Then, the protein is oxidized by cytochrome *f* and, in turn, is reduced by plastoquinone with half-times of 0.2 and 2 ms, respectively.

Cytochrome b_6 is currently assumed to play an important role in electron transport from plastoquinone to the Rieske protein [39]. We could not detect, however, a photoresponse attributable to cytochrome b_6 under the present experimental conditions. Studies on the function of cytochrome b_6 in the cyanobacterium are in progress.

Two important features of photosynthetic electron transport in *Synechococcus* are worthy of mention. First, because electron transfer from cytochrome *f* to P-700 is much faster than plastoquinol oxidation, equilibrium can be assumed to be maintained among P-700, cytochrome *c*-553 and cytochrome *f* during the reduction period. In higher plants and green algae, however, a lag of cytochrome *f* reduction that is expected from the potential difference between the cytochrome and P-700 is absent, or small if it occurs, demonstrating the lack of equilibrium between them [40–42]. Such an anomaly is not seen in photosynthetic electron transport of the cyanobacterium. The reduction kinetics of cytochrome *c*-553 and cytochrome *f* both showed lags of comparable magnitudes. This suggests that electrons equilibrate rapidly among P-700, cytochrome *c*-553 and cytochrome *f* according to their redox potentials and that the midpoint potential of cytochrome *f* is close to that of cytochrome *c*-553, which was estimated as 315 mV at 55°C [19].

The second feature is that electron transport in *Synechococcus* is about one order of magnitude faster than those in higher plants and green algae, where the rates of the limiting step and cytochrome *f* oxidation are 10–20 ms and about 200 μs, respectively. This may be related to the high assay temperature used, or to the thermophilic character of the cyanobacterium. However, the rate of cytochrome *f* oxidation in a mesophilic cyanobacterium, *Plectonema boryanum*, is comparable to that in *Synechococcus* [43]. Some photosynthetic bacteria also show very rapid photooxidation of cytochrome *c* [44]. In particular, the rates estimated for individual steps of electron transport from ubiquinone to the reaction center chlorophyll via the Rieske protein, a membrane-bound and a soluble cytochrome *c* in *Rhodopseudomonas sphaeroides* [45] are comparable to those of the corresponding steps of electron transport from plastoquinone to P-700 in *Synechococcus*. It seems, therefore, that fast electron transport is a characteristic of some primative photosynthetic organisms.

Acknowledgements

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