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Light 2 directed changes in the effective absorption cross-section of Photosystem II in *Synechocystis* 27170 are related to modified action on the donor side of the reaction center

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Synechocystis* 27170 was grown in green, orange and red light in order to adapt cells to light preferentially absorbed by phycoerythrin, phycocyanin and chlorophyll *a*, respectively. Chromatically adapted cells were used to study effective absorption cross-sections of RCII, σ_{eff}, in state 1 and state 2. σ_{eff} for state 1 and state 2 in orange and green light grown cells was approximately twice that for red light grown cells. Light 1 and 2 both induced increased σ_{eff} in an intensity dependent way. The effect saturated at < 10 μmol quanta m^{-2} s^{-1} for light 1 and > 40 μmol quanta m^{-2} s^{-1} of light 2. Increased σ_{eff} invoked by light 1 was related to PSI activity only, since light 1 did not close significant numbers of RCII. Light 2 also effected an increased σ_{eff}, but in an inverse relationship with the fraction of open RCII traps. These data support the model of modulated energy transfer from PSII chlorophyll *a* to PSI as the mechanism for state 1 > 2 transitions in cyanobacteria. Although matching each other in light 1, PSII fluorescence yields deviated substantially from O_2-flash yields in light 2 over a wide intensity range. Since the half-time of Q_A^- was equal in state 1 and 2, it was concluded that light 2 has a modifying effect on the RCII donor side, probably causing longer half-time of P_{680}^+, which delays the reopening of closed RCII. These results were interpreted as a feature of the RCII related to an increased half-time of an exciton in the PSII chlorophyll *a* antenna. This phenomenon is thought to be functional in facilitating energy transfer from PSII chlorophyll *a* to PSI.

Introduction

Light energy harvested in the accessory antenna of Photosystem II (PSII) can be (re)distributed over PSI and PSII. This process, the so-called state 1 > 2 transition, is controlled by the redox state of electron carriers operating between the two photosystems and is common in photosynthetic systems carrying chlorophyll *a* and *b* [1], or phycobiliproteins in the accessory antenna [1,2]. State 1 > 2 transitions are normally visualized from changes in PSII fluorescence properties, following a transfer from wavelengths preferentially absorbed in PSI (light 1) to those absorbed by PSII (light 2), although alternative methods exist [3–9]. The major source of PSII fluorescence is the reaction center (RC) II due to a charge recombination between the primary electron donor P_{680} and the primary acceptor Q_A, after the formation of $P_{680}^+Q_A^-$ or a closed RCII trap [3,5,10–12]. Consequently, PSII fluorescence yields are proportional to the apparent antenna size. Measurements of O_2-evolution and PSII fluorescence following a short, saturating flash provide simultaneous information on the donor and acceptor side of RCII. The same parameters determined at subsaturating intensities provide information on the effective absorption cross-section of RCII [10,12]. In *Chlorella* RCII absorption cross-sections determined from fluorescence yields are larger in light 2 as compared to those measured in light 1, whereas on the basis of O_2 flash yields no change could be observed [10].

In contrast to higher plants and green algae for which the molecular basis of state 1 > 2 transitions has

Abbreviations: PBS, phycobilisome; PQ, plastoquinone; PS, photosystem; RC, reaction center.

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been largely unravelled [1,13,14], it remains unresolved for PBS-containing organisms (e.g., see Refs. 2,4,6,8, 15). Most of the chlorophyll *a* antenna in cyanobacteria is associated with PSI [16–18]. The PBS is anchored in the PSII core and it transfers energy directly to PSII [19–21]. Absorption characteristics of PBS allow to distinguish clearly between the effects of light 1 and light 2 [7]. Light harvesting by PBS in *Fremyella diplosiphon* accounted for 33% of total absorption by photosynthetic pigments in red light grown cells and up to 97% in green light grown cells [21]. Hence the bulk of quanta absorbed would give rise to PSII activity only. Since photosynthesis proceeds with minimal quantum requirements [21], the excitation energy must have been effectively redistributed. Modulation of RCI/RCII ratios during chromatic adaptation [21–23] may be functional in determining the extent to which excitation energy is redistributed [21]. Electron flow through the cyt b_6/f complex is functional in both state 1 > 2 transitions [15] and adaptation in RCI/RCII ratio [24,25]. The proposed mechanism for state 1 > 2 transitions in cyanobacteria is modulation of excitation energy transfer from PBS to PSI by coupling of PSI and PSII chlorophyll *a* [9]. An alternative model explains changes in PSII fluorescence yield during state 1 > 2 transitions from a dissociation of the PBS away from PSII in light 2 [6,26]. Although both models adequately explain changes in PSII fluorescence in cyanobacteria, they predict differently with respect to RCII absorption cross-sections determined from O_2-flash yields, σ_{eff}, in light 2. Upon dissociation of PBS at high intensities of light 2 σ_{eff} is expected to decrease. However, improved energy transfer from PSII to PSI chlorophyll *a* will result in increased σ_{eff} at high light 2 intensities, which act similar to light 1 [27]. σ_{eff} shows a 50% increase in light 1 for the PBS containing red alga *Porphyridium cruentum* as compared to low intensity light 2 [28]. We report here on changes in σ_{eff} in the cyanobacterium *Synechocystis* 27170 induced by (i) chromatic adaptation and (ii) by background light 1 and 2 during the O_2-flash yield measurements. σ_{eff} increased in light 1, and at higher intensities of light 2 accomodated by a modified action of the donor side of RCII. Our data confirm the model of modulated energy transfer between PSII and PSI chlorophyll *a*.

Materials and Methods

Synechocystis 27170 was grown in a mineral medium supplemented with A_5-trace metal solution [29] at a temperature of 32°C in 600 ml flat bottles with continuous aeration. The incident light intensity was 12 W m^{-2} for all cultures. Light limited cultures were kept in the late log phase of growth by daily dilution of cultures proportional to the increase in biomass as determined from turbidity measurements at 750 nm. Cells were chromatically adapted by using coloured filters that in combination with the applied light source assured broad wavelength band illumination centered around the absorption maxima of C-phycoerythrin (≈ 560 nm), C-phycocyanin (≈ 600 nm) or chlorophyll *a* (≈ 680 nm). Light intensities were measured with a YSI Kettering light meter.

For measurement of O_2-flash yields cells were harvested by centrifugation for 10 min at 10000 rpm and resuspended in fresh growth medium. Cells were allowed 15 min to settle on the platinum surface of a rate-measuring O_2-electrode as described previously [12] before applying the silver anode and the membrane. The electrode was mounted in a chamber in which fresh medium was flushed over the electrode at a constant rate. Overexcitation of PSII (light 2) was obtained by illumination with light from a Ushio 500 W xenon source passed through the following filter combinations: Toshiba y-50 + Corning 4-94, and Toshiba 0-56 + Corning 4-97 transmitting wavelengths preferentially absorbed by C-phycoerythrin and C-phycocyanin respectively. Overexcitation of PSI (light 1) was similarly obtained with light passed through a Toshiba VR-66 + Hoya HA-30 filter combination for chlorophyll *a* absorption. For the determination of effective absorption cross-sections (Results section I) cells were adapted for 10 min to the light 1 or light 2 intensity applied during the actual measurement. Maximum O_2- and fluorescence-flash yields at a given background intensity (Results section II) were determined at the moment steady state oxygen evolution rates were reached. The background light was adjusted with neutral density filters to desired intensity. Saturating light flashes were provided from a Sugawara MS-230 xenon flash lamp with sufficiently short flash duration (< 6 μ decay to 10% peak intensity). Flash intensity was adjusted with neutral density filters to obtain an intensity range from 0.1–100% of full intensity.

For the measurement of PSII fluorescence yield in addition to O_2-production we used the system described above fitted with a second xenon flash bulb. The second non saturating flash was triggered at 10 ms after the first saturating flash which synchronized all RCIIs. The fluorescence signal was detected by a Hamamatsu R-375 photomultiplier after passage through a series of neutral density filters, a HA-20 heat absorbing filter and a double line interference filter centered at 685 nm maximal transmission with a half bandwidth of 2 nm. Fluorescence yield of the second flash was registered by a Hitachi VC 6041 digital oscilloscope and signal averaged for a total of 32 flashes. O_2 signals were detected with a fast response operational amplifier. Continuous O_2 production due to the background light was registered directly on a chart recorder. During the steady state O_2 production, the state of the open reaction centers II was probed with

the saturating flashes. O_2-flash signals were digitized and stored in a Kawasaki Electronics TM 1410 transient recorder. After 32 flashes, triggered at 1 Hz, the average flash yield was obtained. Changes in the yield of O_2 production and PSII fluorescence were obtained by normalization to their respective maximum values as described previously [12].

Results and Discussion

I. Effect of background illumination on effective absorption cross-sections of RCII in Synechocystis 27170

Light absorbed by phycocyanin (PC) and phycoerythrin (PE) preferentially excites PSII (light 2), establishing the low fluorescent state of PSII, state 2. Chlorophyll *a* (Chl *a*) absorbed light (light 1) is responsible for overexcitation of PSI relative to PSII in cyanobacteria [7,8] and leads to the high fluorescent state of PSII, state 1 [3,6,9,26]. Such situations may cause a shift in effective absorption cross-sections of RCII (σ_{eff}, as determined from O_2 yield vs. flash intensity relationships [28]. The experimental data can be conveniently described by a single hit Poisson distribution showing that σ_{eff} is determined by the background light solely [30]:

$$Y/Y_{max} = 1 - \exp(-\sigma_{eff} \cdot I) \quad (1)$$

in which Y is the yield of O_2 produced at a given flash intensity I. Estimations of σ_{eff} were obtained from non linear regression analysis fits of O_2-flash yield data to Eqn. 1. We did not attempt to quantitate flash intensities because of complicating factors such as reflection by the platinum cathode. Hence, values of σ_{eff} are given in relative units. *Synechocystis* 27170 was grown in red, orange and green light to obtain Chl *a*, PC and PE cells, respectively, differing in the PSII absorption cross-section relative to that of PSI [21]. Fig. 1, shows the flash intensity saturation curve of O_2 evolution for PE and Chl *a* cells adapted to either dark or light 1 prior to measurements. O_2-flash yields for dark adapted PE cells reached saturation at lower intensities as compared to Chl *a* cells, indicating a larger σ_{eff} for PE cells. Cells adapted for 10 min to 1 μmol quanta m^{-2} s^{-1} of continuous light 1 yielded a profile identical to the dark profile. Since the O_2-evolving state of RCII (s_3 state) decays only at flash intervals longer than 1 s [10], Y_{max} values for dark adapted cells represent the total population of active RCIIs. Light 1 at 10 μmol quanta m^{-2} s^{-1} did not alter Y_{max} and hence did not close an appreciable number of RCII. However, it effected a clear shift in flash saturation curves towards lower light intensities for both the Chl *a* and the PE cells (Fig. 1). Apparently, the dark state is state 2 as is normally found for cyanobacteria [4,5,21] due to a constant reduction of the plastoquinone pool by respiratory electron transport [5,31]. State 1 is characterized by an increase in σ_{eff} as judged from the shifted flash saturation curves, similar to what has been found for *Porphyridium cruentum* [28]. In both state 1 and state 2, σ_{eff} was 2-times larger in PE and PC cells as compared to Chl *a* cells (Table I), a result of chromatic adaptation expressed in enlarged PBS in PE and PC cells [21]. Measurements on red and green algae showed that σ_{eff} does not change with the intensity of light 2 [10,28]. In other words, the cross-section for the fraction of open RCIIs remains constant, even though an increasing number of RCII traps is closed by the background light [30]. During illumination of *Synechocystis* 27170 with bright light 2 (35 μmol quanta m^{-2} s^{-1}) clear shifts towards higher σ_{eff} were observed for all growth conditions (Fig. 2). Similar to the light 1 effect, the change in σ_{eff} was largest for PE cells. Since the shift of σ_{eff} in light 2 may result from partial closing of RCII traps, we studied the effect of light 1 and 2 intensity on σ_{eff} and the fraction of open RCII (Fig. 3). The increase in

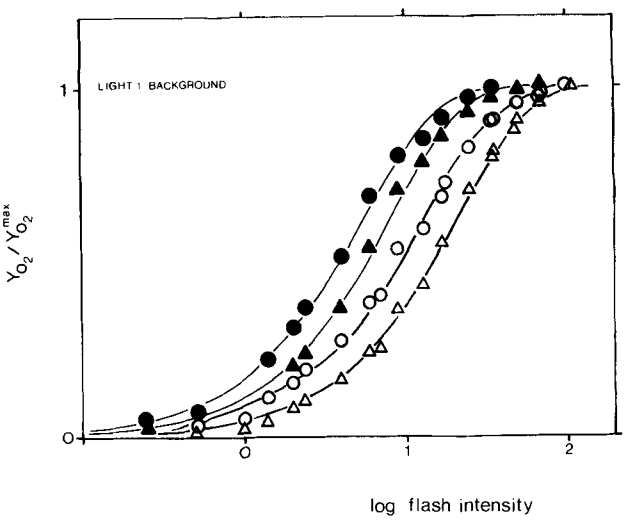

Fig. 1. Profiles of O_2-flash yield versus flash intensity for *Synechocystis* 27170 grown in red light (open symbols) and green light (closed symbols). Cells were preadapted for 10 min to dark (triangles) or 10 μmol quanta m^{-2} s^{-1} 435 nm light 1 (circles).

TABLE I

Effective absorption cross-sections of Synechocystis 27170 (σ_{eff}) grown in broad band monochromatic light absorbed by phycoerythrin (PE), phycocyanin (PC) and chlorophyll a (Chl a)

σ_{eff} was determined on cells incubated in the dark for 5 min (state 2) or illumination for 10 min with 10 μmol quanta m^{-2} s^{-1} of 435 nm light (state 1)

Growth condition	σ_{eff}	
	state 2	state 1
PE	0.105 ± 0.005	0.177 ± 0.010
PC	0.099 ± 0.005	0.153 ± 0.015
Chl *a*	0.043 ± 0.003	0.081 ± 0.009

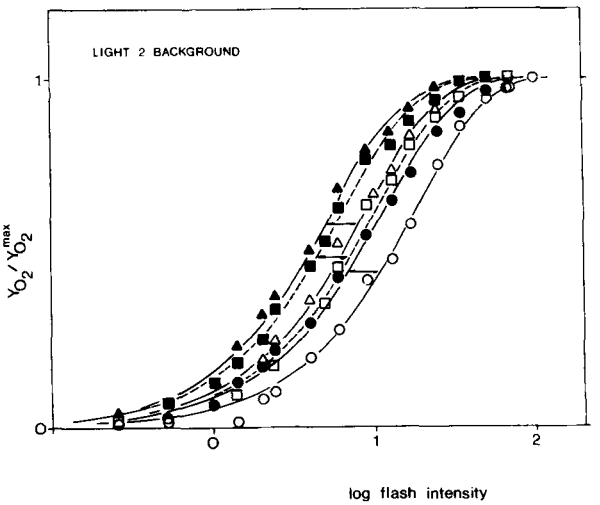

Fig. 2. Profiles of O_2-flash yield versus flash intensity for *Synechocystis* 27170 grown in red (circles), orange (rectangles) and green light (triangles). Cells were preadapted to dark (open symbols) or 10 μmol quanta m^{-2} s^{-1} of 620 nm light 2 background (closed symbols). Arrows indicate shifts in effective absorption cross-section at each growth condition.

σ_{eff} for Chl *a* cells saturated at approx. 10 μmol quanta m^{-2} s^{-1} of light 1. For PC and PE cells saturation was reached at 5 μmol quanta m^{-2} s^{-1} and the increase in σ_{eff} was much more pronounced. There were no conditions at which light 1 closed appreciable numbers of RCII. Higher intensities of light 2 led to increased σ_{eff} for all growth conditions, most pronounced in PE cells. Since the effect saturated at 50 μmol quanta m^{-2} s^{-1} for all conditions, both the slope of σ_{eff} vs. intensity and the overall increase in σ_{eff} was largest for PE cells (Table II). This pattern coincided with a sharp decline in the fraction of open RCII traps as compared to PC and Chl *a* cells. We recognize that changes in σ_{eff} in cyanobacteria with light 2 background contrast with the virtually constant σ_{eff} in green and red algae [10,28]. An increased σ_{eff} in light 1 has been observed in the red alga *Porphyridium cruentum* [28] and is in good agreement with the high PSII fluorescence yield (state 1) observed in cyanobacteria [2–9,21]. If lower PSII fluorescence yields of cyanobacteria in light 2 (state 2) are explained from increased sharing of the PSII antenna with PSI, one would intuitively have expected a low σ_{eff} at all light 2 intensities. We hypothesize that low σ_{eff} values at low light 2 intensities are related to insufficient PSI activity due to the poor absorption of light 2 by PSI Chl *a*. Energy transfer from PSII to PSI at higher intensities of light 2 enhances PSI action and thus establishes an increase in σ_{eff}. This is consistent with the low minimal quantum requirements observed during photosynthesis in monochromatic light 2 [21] and the account of high light 2 intensities acting as light 1 [27]. Higher PSI/PSII ratios in PE cells as opposed to Chl *a* cells [21–23] may increase the chance of energy transfer to PSI, thereby explaining the steeper increase in σ_{eff} in the former. Increased σ_{eff} in light 2 seems to agree with the model of modulated energy transfer from PSII to PSI [9] rather than with the model of dissociation of PBS away from PSII [6,26].

TABLE II

Minimal (dark) and maximal σ_{eff} in light 1 (20 μmol quanta m^{-2} s^{-1}) and in light 2 (50 μmol quanta m^{-2} s^{-1}) for Synechocystis 27170 grown under conditions as described in Table I

Growth condition	σ_{eff}		
	dark	light 1	light 2
PE	0.105 ± 0.005	0.177 ± 0.003	0.313 ± 0.022
PC	0.099 ± 0.005	0.154 ± 0.009	> 0.171
Chl *a*	0.043 ± 0.003	0.083 ± 0.009	0.095 ± 0.026

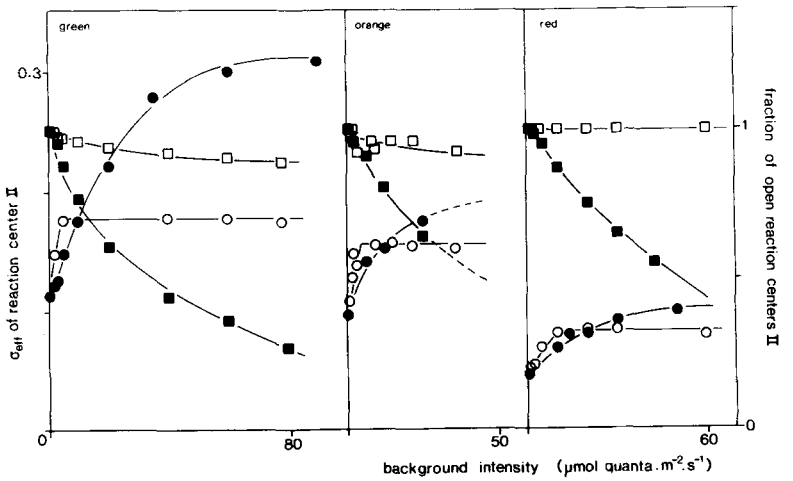

Fig. 3. Effective absorption cross-sections, σ_{eff} (circles), and changes in the fraction of open reaction centers II (rectangles) as a function of intensity of the background light 1 (open symbols) or light 2 (closed symbols) for *Synechocystis* 27170 grown in green, orange and red light. The fraction of open RCII was determined from Y_{max} assuming that Y_{max} in dark adapted cells represents 100% open RCII.

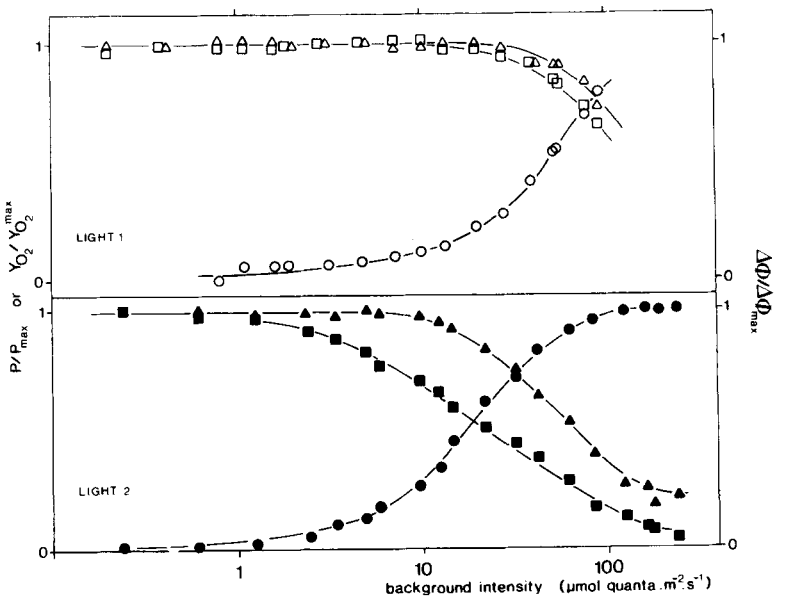

Fig. 4. Continuous O_2-production, P/P_{max} (dots), O_2-flash yields, $Y_{O_2}/Y_{O_2,max}$ (rectangles) and fluorescence yields, $\Delta\phi/\Delta\phi_{max}$ (triangles) as a function of the intensity of light 1 (upper graph) and light 2 (lower graph). Normalization to P_{max} in light 1 conditions was to P_{max} measured in light 2.

II. Effect of background illumination on donor and acceptor side of RCII in Synechocystis 27170

Whatever the mechanism is behind modulation of energy transfer from PSII to PSI and adjustment of the effective absorption cross-section of RCII, it inevitably implies a competition for excitons with processes like fluorescence emission and energy trapping in RCII. There are a number of possible hypotheses relating to the molecular/physical basis of the mechanism allowing light 2 directed enhancement of σ_{eff} in *Synechocystis* 27170: (i) PBS funnel excitation energy to more than one RCII, so that closing of RCII traps would enlarge the absorption cross-section of the remaining open ones. (ii) Excitation energy can escape from closed RCII traps and be efficiently transferred to open RCII. (iii) The energy transfer from the PBS to PSII can be modulated. (iv) Cyclic electron flow around PSII [11,12]. (v) Modification or destabilization of either donor or acceptor side of RCII.

Although they cannot be excluded out of hand, options i and ii seem less likely. Whereas, in red algae and some cyanobacteria multiple RCII share one hemispheroidal PBS [28,32], there is a controversial situation concerning cyanobacteria with hemidiscoidal PBS [2,16]. Numerous reports have appeared claiming PSII/PBS ratios ranging from 1.4 to 2 (e.g., Refs. 33–35), but an extensive research by Ohki et al. [32] showed a ratio of 1 for a number of cyanobacteria under a variety of growth conditions. There is a low propability of energy transfer among cyanobacterial RCIIs [19]. Dissociation of PBS [6,26,33] from PSII is hard to envisage considering that PBS is tightly bound to PSII [20] and the above observed increase in σ_{eff} in light 2. Cyclic electron flow around PSII was posed as a mechanism to avoid photoinhibition at high light intensities [11,12]. Since changes in σ_{eff} of *Synechocystis* did occur at relatively low intensities of light 2, we consider this explanation as unlikely. We studied effects of background light on donor and acceptor side of RCII by probing the O_2-flash yield and the fluorescence yield with pump and probe flash trains triggered at 1 Hz. Fig. 4 shows that O_2-flash yield and continuous oxygen evolution were mirror imaged in light 2, but not in light 1. Since the open/closed state of RCII in light 1 is expected to reflect the maximal rate of electron donation from H_2O to PQ, it follows this rate was decreased in light 2 as judged from O_2-flash yields. PSII fluorescence yields matched the O_2-flash yields closely for all but the highest intensities of light 1. With light 2 there was a distinct deviation between O_2-flash yields and fluorescence yields starting at light intensities less than 10 μmol quanta m^{-2} s^{-1}. This suggested that in light 2 the reopening of RCII traps occurs slower on the donor side than on the acceptor side. Identical patterns were observed for *Synechocystis* 27170 grown in orange and in red light, thus prompting a study of relaxation time of the acceptor side of RCII. Inhibiting electron transfer to Q_B with 10^{-6} M DCMU left Q_A^- as the only species present after a saturating flash irrespective of the delay time between the pump and the probe flash (Fig. 5). The half-time for reopening of the acceptor side of RCII (reoxidation of Q_A^- by electron transfer to Q_B) was determined to be 0.3 ms, identical to the half-time reported for the marine diatom *Thalassiosira weisflogii* [11]. This time constant did not change with either light 1 or light 2 back-

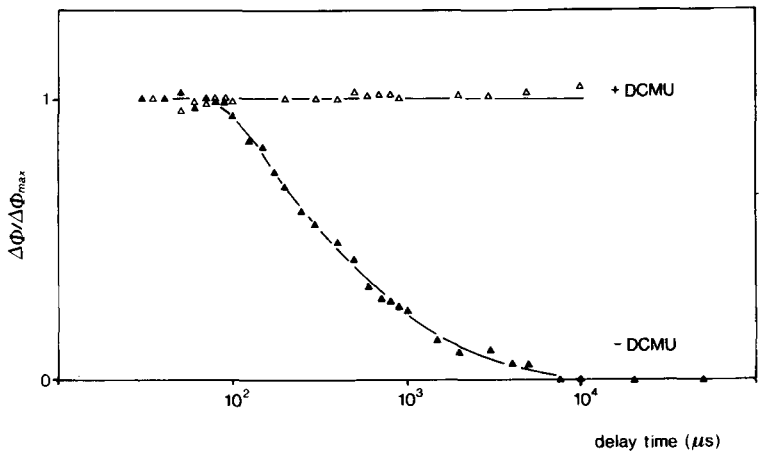

Fig. 5. Changes in fluorescence yield as a function of the delay time between the saturating 'pump' flash and the low intensity 'probe' flash for *Synechocystis* 27170. Reopening of RCII (reoxidation of Q_A^-) was measured with DCMU (open symbols) and without DCMU (closed symbols).

ground. The deviation between O_2-flash yields and fluorescence yields was not a result of the chromatic adaptation of the cells but a property of RCII itself expressed in light 2 (Fig. 6). When donor and acceptor side of RCII operate in a coordinated way one would theoretically expect that at each intensity as many RCII traps are closed on the donor side as there are on the acceptor side (dashed line). In our measuring system we could not obtain light 1 intensities strong enough to close all RCII traps, but it appeared that measured values were close to the theoretically predicted line. With light 2 there was a strong deviation from the theoretical line starting at low light intensities. The relationship between the open state of donor and acceptor side of RCII was identical in light 1 and light 2 for cells grown under different light qualities. It thus follows that we observed here a basic property of the cyanobacterial RCII expressed in light 2 only. We interpret this phenomenon as a delayed rereduction of P_{680}^+ by Z or the oxygen evolving complex. Overexcitation of PSII in *Chlamydomonas* prolonged the half-time of P_{680}^+ from 0.3 ms in the control (identical to Q_A^- relaxation in *Synechocystis* 27170 (this paper) and in *T. weisflogii* [11]) up to 3 ms [36].

Although we have not identified the site of action of this light 2 directed effect, we can speculate on a possible function. Whereas, in red light grown cyanobacteria there is a balance in PSII and PSI absorption cross-sections, green light grown cells are characterized by a large absorption cross-section of PSII and PBS together, 97% of total absorption [21]. Under these conditions cyanobacteria maintain high PSI/PSII ratios [21,23,24], which is suggested to enhance direct energy transfer in light 2 [21]. Direct energy transfer occurs between the PSII and PSI Chl *a* antenna [4,9]. Fig. 7 shows a simplified model of the different energetic states of RCII following excitation with light 1 or 2. During overexcitation of PSI quanta harvested in

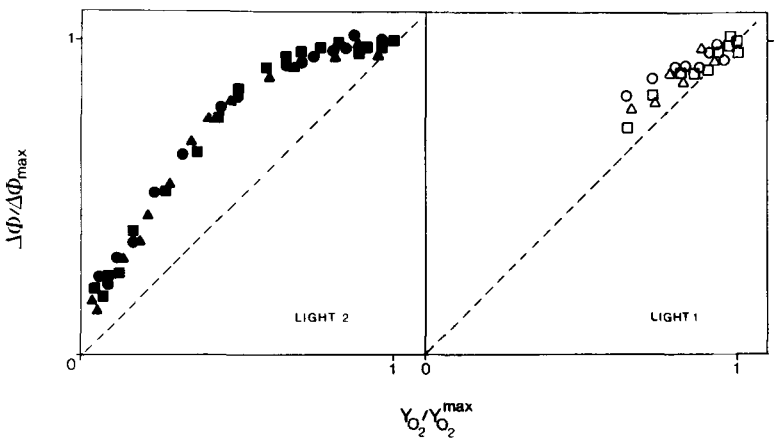

Fig. 6. Correlation between O_2-flash yields, $Y_{O_2}/Y_{O_2,max}$ and PSII fluorescence yields, $\Delta\phi/\Delta\phi_{max}$ for *Synechocystis* 27170 grown in green (triangles), orange (rectangles) and red (circles) at different intensities of light 2 (left hand) and light 1 (right hand) background illumination.

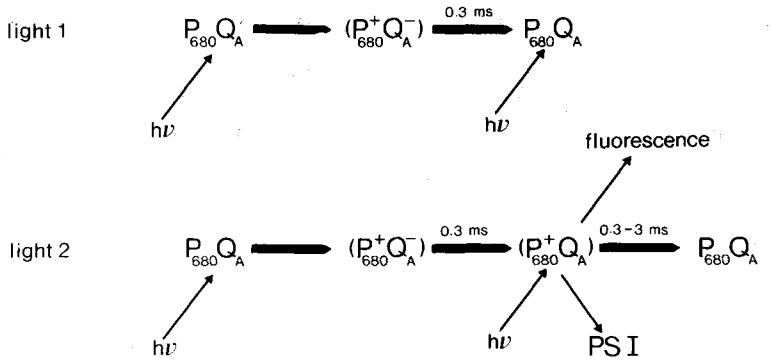

Fig. 7. A simplified model of photochemical events in cyanobacterial RCII in vivo under illumination with light 1 and light 2. An exciton arriving in the PSII antenna is trapped in RCII which is subsequently closed ($(P^+_{680}Q^-_A)$). Relaxation to the ground state for the whole RCII complex ($(P_{680}Q_A)$) is attained with a half-time of 300 μs in light 1, whereas in light 2 RCII remains closed for a much longer timespan due to a longer half-time of P^+_{680} ($(P^+_{680}Q_A)$). During this time an incoming exciton in the PSII antenna cannot be trapped in RCII and is either dissipated as fluorescence or 'spilled over' to PSI.

PSII are processed efficiently with identical relaxation times for P^+_{680} and Q^-_A. Light 2 quanta arriving in the PSII Chl *a* antenna are preferentially funneled to a RCII. If in a continuous light 2 flux, reopening of RCII is delayed due to a longer half-time of P^+_{680}, it may somehow lead to an increased half-time of an exciton in the PSII antenna. This may facilitate direct energy transfer to PSI or alternatively enhance PSII fluorescence. The PSI/PSII ratio then determines if direct energy transfer takes place or not by 'setting the physical proximity' of PSI to PSII [15,21]. We could not resolve relaxation times for the donor side due to the relatively slow response time of the O_2-detection system (> 1 ms). Since the acceptor side of RCII relaxes with a half-time of 300 μs, it follows that longer relaxation times for the donor side may amount to sufficient time for an exciton to escape to the PSI antenna (Fig. 7). Assuming a PBS cross-section of 50 nm^2 [21,28] we calculated that on average every 30 μs an exciton arrives at a RCII at a light intensity range of 100 μmol quanta m^{-2} s^{-1}. Such a 'photon arrival time' would account for a significant amount of excitons arriving at closed RCII traps at non-saturating intensities. The proposed model for enhanced energy spillover to the PSI antenna is consistent with the observation that bright light acts as light 1 [27]. Increased σ_{eff} in light 2 as observed here for *Synechocystis* 27170 would be an obvious result due to the balanced activities obtained for PSI and PSII.

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