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Light regulation of Electron Transport in N_2-fixing Cyanobacteria in Lichens

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Abstract

State 1 — state 2 transitions in the lichen *Nephroma laevigatum* containing *Nostoc* cells were monitored using photoacoustics and fluorescence induction techniques. Analysis of Emerson enhancement saturation curves showed that during transition of the cyanobacterial symbionts from state 1 to state 2, there was an increase of 15–21% in the extent of direct energy transfer (spillover) from chlorophyll of PS II to that of PS I. Similar conclusions were obtained from fluorescence induction curves of the lichen in state 1 and state 2 in the presence of 3-(3,4-dichlorophenyl)-1,1′-dimethylurea-(DCMU). Action spectra *in vivo* for PS II and PS I respectively were obtained from enhancement spectra and demonstrated that phycobiliproteins are the major light harvesting pigments for PS II, and chlorophyll for PS I, respectively, in this lichen.

Keywords: photosynthesis, state 1- state 2 transitions, photoacoustics, excitation transfer, cyanobacteria

1. Introduction

Light intensity and quality influences the development, adaptation and function of the photosynthetic apparatus in all photosynthetic organisms. Since in many environments light conditions are sometimes unfavorable, plants have the capability to adapt in order to optimize their photosynthetic performance under these conditions (Anderson, 1986). Photoregulation is exerted at the level of biosynthesis of light-harvesting pigments (Leong and

Anderson, 1983) as well as the biosynthesis of ribulose bisphosphate carboxylase/oxygenase (Tobin and Silverthorne, 1985). Light regulation occurring on the time scale of seconds to minutes, which does not involve the biosynthesis of macromolecules, takes place in all O_2 evolving organisms (for reviews see: Barber, 1986; Fork and Satoh, 1986; Williams and Allen, 1987).

In this research, the regulation of excitation energy distribution between the two photosystems is demonstrated in lichens containing cyanobacteria. Lichens are composed of fungi and algae. Usually one type of alga and/or cyanobacterium (the phycobiont) combined with one type of fungus (the mycobiont) form a new entity — the lichen — which bears little resemblance to any of its components (Galun and Bubrick, 1984). The phycobiont layer is the zone where the main physiological interplay takes place. Below this zone, is the main fungal zone, which is known as the medulla. About 40–50% of the CO_2 fixed in photosynthesis is found in the medulla within 30 min after illumination (Smith, 1974). The lichens are significantly different from other photosynthetic organisms due to their slow rate of biochemical processes, particularly in the synthesis and degradation of proteins (Smith, 1974). In free living cyanobacteria, the changes in the distribution of excitation energy, which are known as state 1-state 2 transitions, are much faster than in green algae or higher plants (Fork and Satoh, 1983). It was suggested that in red algae and cyanobacteria containing phycobilisomes the state 1- state 2 transitions are based on localized electrical changes in the thylakoid membrane associated with the over-stimulation of cyclic electron transport (Satoh and Fork, 1983; Biggins et al., 1984). On the other hand, it was proposed that reversible phosphorylation of a phycobilisome — linker protein mediates the transfer of phycobilisomes between the two photosystems (Allen et al., 1985). Further evidence for the role of protein phosphorylation for state 1 — state 2 transitions in cyanobacteria has come from photoacoustic measurements of modulated oxygen evolution in which addition of the phosphatase inhibitor NaF has been shown to block the transition to state 1 in the cyanobacterium *Nostoc* (Canaani, 1986). From a mechanistic point of view, it is still unclear if the state transitions in phycobilisome containing organisms involve a change in the absorption cross-section of each photosystem, which is implied by reversible phycobilisome transfer from PS II to PS I (Allen et al., 1985), or via a change in the quantum yield of direct energy transfer (spillover) from PS II to PS I as suggested by Williams et al. (1981) and Bruce et al. (1985). In order to try and elucidate the mechanism of light regulation in cyanobacteria, whether it involves a change in absorption cross-section or a change in

the extent of direct energy transfer, I investigated the light state transition in a lichen containing cyanobacteria. In this paper, I present photoacoustic and fluorescence measurements in *Nephroma laevigatum* which indicate that during the transition from state 1 to state 2 there is a change in the extent of direct energy transfer from chlorophyll-a light harvesting pigments of PS II to chlorophyll-a light harvesting pigments of PS I, in the cyanobacterial phycobiont. It is also shown that a more balanced distribution of excitation energy between the two photosystems (approaching state 2) is reached under anaerobic conditions in the cyanobacterial symbiont indicating that respiratory electron flow directly influences the transition to state 2 in this organism.

2. Materials and Methods

The lichen *Nephroma laevigatum* was obtained as a gift from Prof. M. Galun, Tel-Aviv University, Israel. Freshly collected lichen samples were wetted and illuminated for 1 hr. Circular discs (1 cm diam.) of the thalli were cut and placed in the photoacoustic chamber, which is described elsewhere in detail (Canaani and Malkin, 1984). Light from a 450 W Xenon lamp was focused and passed through a Bausch and Lomb monochromator and modulated with a mechanical chopper. Background non-modulated saturating light was obtained from a quartz-halogen lamp. The light entered the photoacoustic cell through a bifurcated light guide (Schott) allowing simultaneous illumination by modulated and background lights. Photoacoustic signals were amplified by a preamplifier and analyzed by a lock-on amplifier (Brookdeal 9502) for their in-phase and quadrature components as described previously (Canaani et al., 1984). Fluorescence induction was measured with an exciting light produced by a d.c. projector and passed through either a 450 nm broad band or a 580 nm interference filter (10 W/m^2). Fluorescence emission was filtered through a 690 nm interference filter (Ditric Optics) and measured with a photodiode (EG&G). The resulting signal was recorded on a Tektronic 5648 storage oscilloscope. Anaerobic conditions were achieved by incubating the wetted thalli in a 100% N_2 atmosphere for 20 min prior to measurements.

3. Results

The state 1 — state 2 transitions were investigated in the lichen *N. laevigatum*. The photoacoustic oxygen evolution signal excited by modulated 560 nm light after the termination of 10 min pre-adaptation of the lichen to non-modulated far-red (710 nm) background light (L1) is shown in Fig. 1a. Addition of the 710 nm background light caused a large increase in the

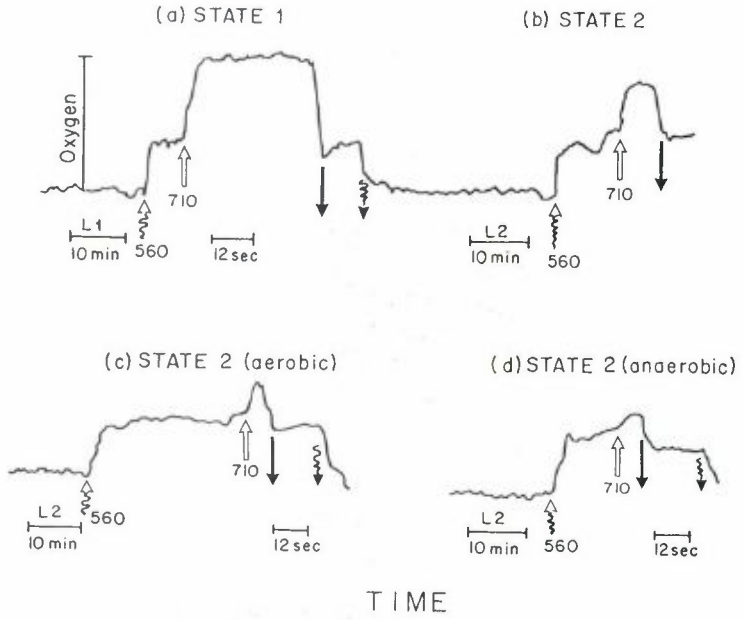

Figure 1. Emerson enhancement of oxygen evolution in *Nephroma laevigatum*. Photoacoustic oxygen signal on the quadrature mode immediately after cessation of preillumination period. (a) preillumination for 10 min with 710, 15.5 W/m^2 background light; untreated sample; (b) preillumination for 10 min with 540–620 nm, 35 W/m^2 background light; untreated sample; (c) preillumination as in (b), sample incubated in MES buffer, pH 6.2, aerobic conditions; (d) preillumination as in (c), sample in the same buffer, 20 min flushing with 100% N_2, anaerobic conditions. Modulated light wavelength: 560 nm, 6 W/m^2, modulation frequency, 12 Hz, background light: 710 nm, 14.0 W/m^2.

modulated oxygen evolution signal, demonstrating Emerson enhancement in the cyanobacterial phycobiont *Nostoc*. The physiological state resulting from adaptation to far-red illumination that over-excites PS I is known as state 1 (Bonaventura and Myers, 1969). In this state, short-wavelength light (560 nm) will be initially distributed so that PS II receives excess excitation energy relative to PS I. The enhancement ratio was calculated as the ratio of the oxygen quantum yield in the presence and absence of far-red light. It was found to be equal to 3.67 when measured after additional 0.7 min of far-red adaptation in the presence of modulated light. The very high enhancement ratio observed in state 1 in the *Nostoc* symbiont, indicates a large imbalance in the distribution of excitation energy between PS II and PS I. If it is assumed that PS II and PS I do not interact energetically to a large extent in

state 1 (see later Fig. 6), then $E = \beta/\alpha$ where E is the enhancement ratio, and β and α are the fractions of the modulated exciting light distributed to PS II and PS I, respectively. In this experiment, it was calculated from the enhancement ratio, that in state 1 the fractions of short wavelength light absorbed in PS II and PS I are 79% and 21%, respectively.

State 2 occurs by adaptation of the lichen to short-wavelength light resulting in an initial over-excitation of PS II by the short-wavelength light, followed by a change leading towards a more balanced distribution. State 2 was obtained after 10 min pre-adaptation with green light (540–620 nm) (L2), and resulted in a much smaller Emerson enhancement (Fig. 1b) compared to state 1. The enhancement ratio in state 2 was 1.5. The respiratory chains of cyanobacteria are thought to intersect with their photosynthetic electron transport at the level of the plastoquinone pool (Hirano et al., 1980; Moullineaux and Allen, 1986; Dominy and Williams, 1987). Oxygen depletion inhibits the flow of electrons of the respiratory chain out of the plastoquinone pool and was shown to cause a decrease in the value of steady-state fluorescence in *Anacystis* cells adapted to state 2 (Dominy and Williams, 1987). Therefore the effect of anaerobic conditions on the transition to state 2 in the lichen *N. laevigatum* was analyzed (Fig. 1c,d). It was found that the enhancement ratio in lichen samples exposed to anaerobic conditions and adapted to green light was lower, on the average, than in lichens samples under aerobic conditions. The lowest ratio in N_2-flushed cells was 1.17 (Fig. 1d) indicating a more balanced energy distribution between PS II and PS I (close to "perfect" state 2).

Theoretical analysis of the enhancement ratio by the model of "spillover" (assuming energetic interaction between the photosystems) predicts that $E = 2\beta$ (Canaani and Malkin, 1984). Therefore, the enhancement ratio obtained in state 2 of anaerobic treated lichens, $E = 1.17$, results in a fraction of light absorbed by PS II, β, of 58%. The use of the model of "spillover" in state 2 is justified later (See Fig. 6).

In the absence of the background, far red light, the oxygen evolution quantum yield will be limited by PS I and therefore will be proportional to the fraction of light absorbed by PS I, denoted as α. The ratio of the oxygen quantum yields measured in the absence of 710 nm, in state 1 and in state 2 (Fig. 1) is directly proportional to the ratio of α in state 1 to α in state 2. From the change shown in Fig. 1, the oxygen quantum yield in state 2 increased by a factor of two compared to that of state 1. Therefore, since α in state 1 was found to be 21%, it increased to 42% in state 2. Since β in state 1

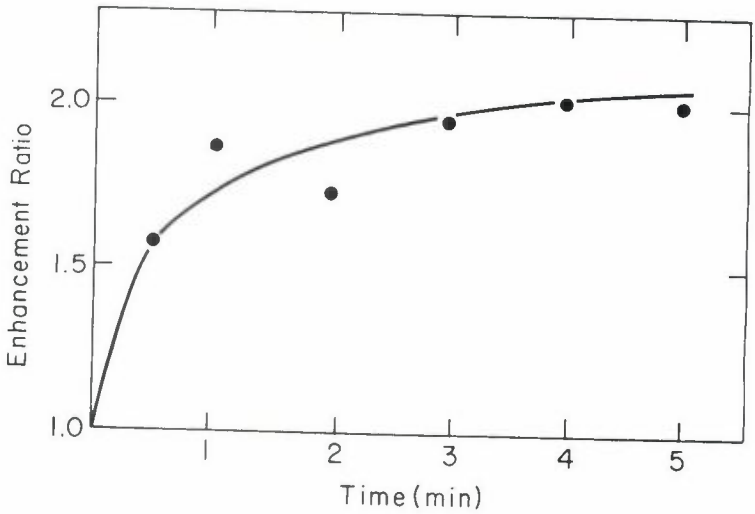

Figure 2. State 2 to state 1 kinetics in *Nephroma laevigatum*. The enhancement ratio as function of adaptation time in far-red light. Light measuring conditions as in Fig. 1.

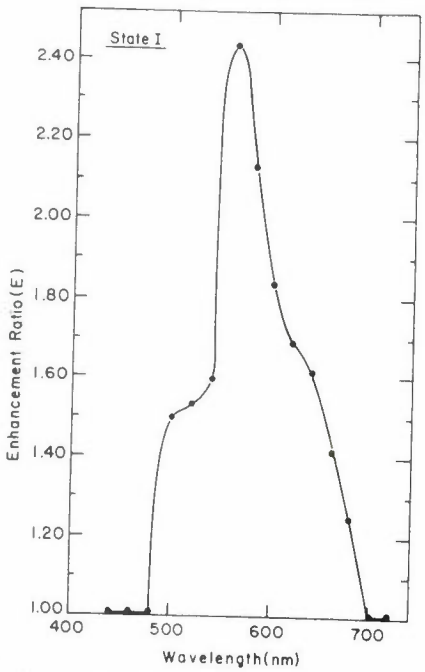

Figure 3. Enhancement ratio as function of wavelength of modulated light, in state 1. Background light, 710 nm, 14 W/m^2.

was found to be 79% and in state 2 it was 58% respectively, β has decreased by 21% during the state 1 to state 2 transitions. The above considerations show that during the transition from state 1 to state 2, in this cyanobacterial lichen under anaerobic conditions, the change in the enhancement ratios from $E = 3.67$ to $E = 1.17$ corresponds to an increase of 21% in the fraction of light absorbed by PS I, and a similar decrease in that of PS II. However, typical values of enhancement ratios of this lichen under aerobic conditions show that in the transition from state 1 to state 2, a smaller change of 9–15% occurs in the fractions of light absorbed in PS II and PS I, respectively.

The kinetics of the state 2 to state 1 transitions was followed by monitoring the enhancement ratio E as function of the adaptation time in far-red light. It was found that the transition from state 2 to state 1 occurred in less than 1 min (Fig. 2). The observed half time of 25 sec for this transition is in agreement with previous studies in free-living cyanobacteria (Moullineaux and Allen, 1986).

The enhancement spectrum of *Nostoc* in *N. laevigatum* reflecting the action spectrum of PS II, showed a maximum at 560 nm, and a shoulder at 620 nm corresponding to the absorption of phycobiliproteins (Fig. 3). Very small contribution of chlorophyll to the PS II action spectrum was observed. In Fig. 4, the slope of enhancement ratio as function of the wavelength of the background light, reflecting the action spectrum of PS I in the lichen is shown. The slope of the enhancement ratio showed 2 maxima at 440 nm and 710 nm corresponding to the absorption of chlorophyll a. No contribution of phycobiliproteins to PS I action spectrum was observed. Therefore it is concluded that chlorophyll a is the major light harvesting pigment of PS I in *N. laevigatum* in contrast to PS II which is shown to be composed of phycobiliproteins.

The saturation curve of the enhancement effect with addition of 710 nm background light is depicted in Fig. 5. Saturation of the enhancement effect in these cyanobacteria was observed already at low light intensity of 3 W/m^2. Analysis of the saturation curves for the enhancement effect in state 1 and state 2 is shown in Fig. 6. From the maximal enhancement ratio obtained in state 1 of $E = 3.67$ (Fig. 1), the fractions of light distributed to PS II and PS I were calculated to be $\beta = 0.79$ and $\alpha = 0.21$, respectively. The ratio of the quantum yields of oxygen evolution obtained at 710 nm and at 560 nm was found to be 0.29 (not shown). At 710 nm the electron-transport rate is limited by PS II. Therefore, the quantum yield of oxygen evolution at 710 nm is proportional to the distribution of this light to PS II, denoted by

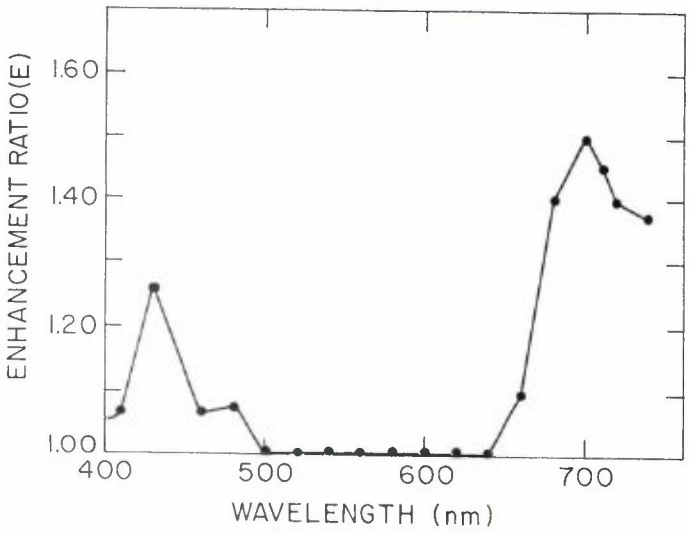

Figure 4. Relative quantum yield spectrum of the Enhancement effect, calculated from the initial slope of the far-red saturation curves. Modulated light, 560 nm, 6 W/m^2. Modulation frequency 12 Hz.

β'. On the other hand, the quantum yield of oxygen evolution at 560 nm is proportional to the distribution of this short-wavelength light to PS I, which is denoted by α, since PS I is limiting the electron transport rate in this case. Therefore, the ratio of the quantum yields of oxygen evolution at 710 nm and at 560 nm is equal to the ratio of the corresponding light fractions and results in $\beta' = 0.061$. Furthermore, knowing β' and assuming that $\alpha' + \beta' = 1$, it is found that $\alpha' = 0.939$, where β' and α' are the fractions of 710 nm light distributed to PS II and PS I, respectively. It is clear from these results that most of the far-red light (94%) is distributed to PS I.

According to the model of "separate package", which assumes no energetic interaction between PS II and PS I, the theoretical initial slope of the enhancement saturation curve is given by the equation $S = \alpha'/\alpha - \beta'/\beta$ as already reported (Canaani and Malkin, 1984). In state 1, the predicted theoretical slope is equal to $S = (0.939/0.21) - (0.061/0.79) = 4.4$. If, on the other hand, the "spillover" model is assumed, the predicted theoretical slope is equal to $S = (\alpha' - \alpha\beta'/\beta) = (0.939 - 0.21 \times 0.061/0.79) = 0.923$. The experimentally measured slope in state 1 is 3.125 (Fig. 6). The experimental value found in state 1 is much closer to the theoretical slope obtained for the "separate package" model rather than with the "spillover" model. However, a certain extent of direct energy transfer from PS II to PS I in

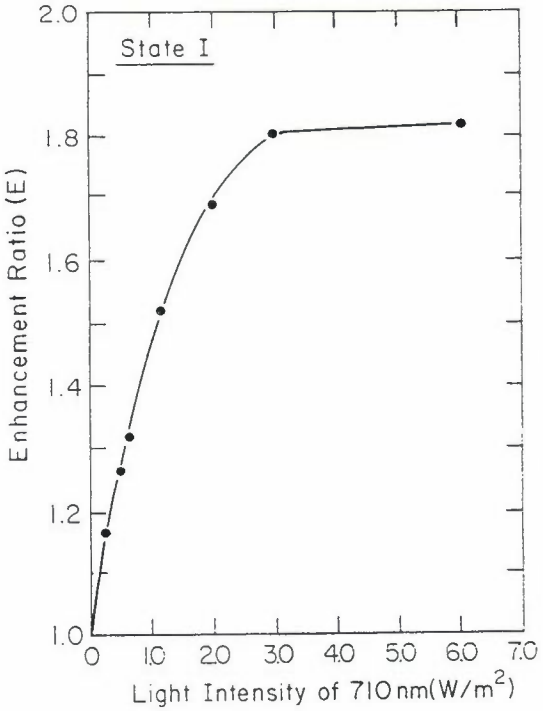

Figure 5. Saturation curve of Emerson enhancement ratio at state 1 with far-red (710 nm) background light in *Nephroma laevigatum*. Modulated light as in Fig. 4.

state 1 cannot be excluded. The same experiment was carried out in state 2. If a separate package is assumed, then for $E = 1.4$ in state 2, it is calculated that $\beta = 0.58, \alpha = 0.42, \beta' = 0.12$ and $\alpha' = 0.88$, yielding a slope of $S = (0.88/0.42 - 0.12/0.58) = 1.9$. On the other hand, if a "spillover" model is assumed in state 2, then for $E = 1.4$ and assuming $E = 2\beta$, it is calculated that the slope will be equal to $S = (0.91 - 0.30 \times 0.09/0.70) = 0.91$. The experimental slope measured in state 2 is 0.75 (Fig. 6). It is in a good quantitative agreement with the "spillover" model and does not fit at all the "separate-package" model. Therefore, it is concluded that in state 1 the two photosystems do not interact energetically to a large extent. On the other hand, a similar analysis shows that in state 2 a considerable change has occurred in the interaction between the 2 photosystems leading to an increased extent of energy transfer from PS II to PS I by 21% under anaerobic conditions and by 9–15% under aerobic conditions respectively.

State 1 — state 2 transitions were also monitored by fluorescence induction *in vivo* in *N. laevigatum* as already reported for free living cyanobacteria (Fork and Satoh, 1983). When the lichen was pre-illuminated for 10 min

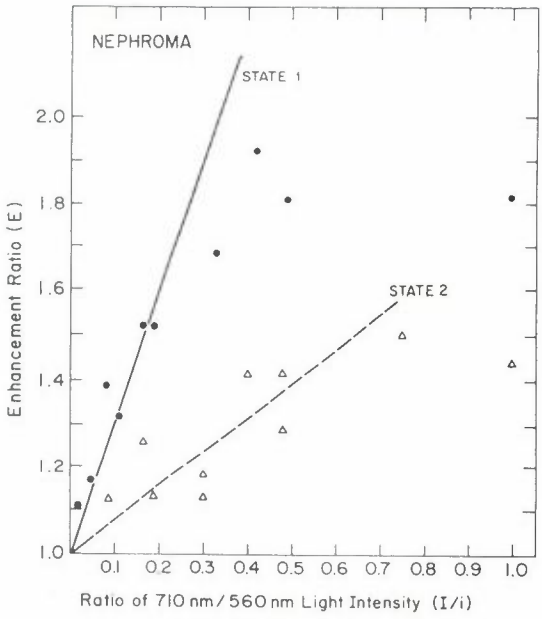

Figure 6. Saturation curves of Emerson enhancement effect at state 1 and at state 2 as function of the ratio of far-red light (710 nm) intensity (I) to the modulated exciting light (560 nm) intensity (i). Light conditions as in Fig. 1. The lines are theoretical calculations corresponding to a separate package (•) and spillover (▵) models.

at 710 nm and following the addition of DCMU the fluorescence induction showed a much faster increase (Fig. 7a) compared to the control (Fig. 8a). In the presence of DCMU (10^{-5} M) there was no O_2 evolution detected by photoacoustics, since Q_A oxidation in PS II was blocked. Therefore, besides thermal deactivation, the only PS II fluorescence quencher is energy spillover. The *Nostoc* cells in the lichen were in state 1 after far-red illumination in the presence of DCMU as already reported for free living cyanobacteria (Dominy and Williams, 1987). The lichen was preilluminated for 10 min with green light (560–620 nm) and following the addition of DCMU, the fluorescence induction was monitored and showed the same rapid kinetic increase due to the reduction of Q_A. However, the F_m, maximal fluorescence value obtained after green light treatment (Fig. 7b), was lower following the far-red light illumination (Fig. 7a), since the *Nostoc* cells have adapted to state 2. The variable fluorescence yields in state 1, ϕ_I, and in state 2, ϕ_{II}, were measured

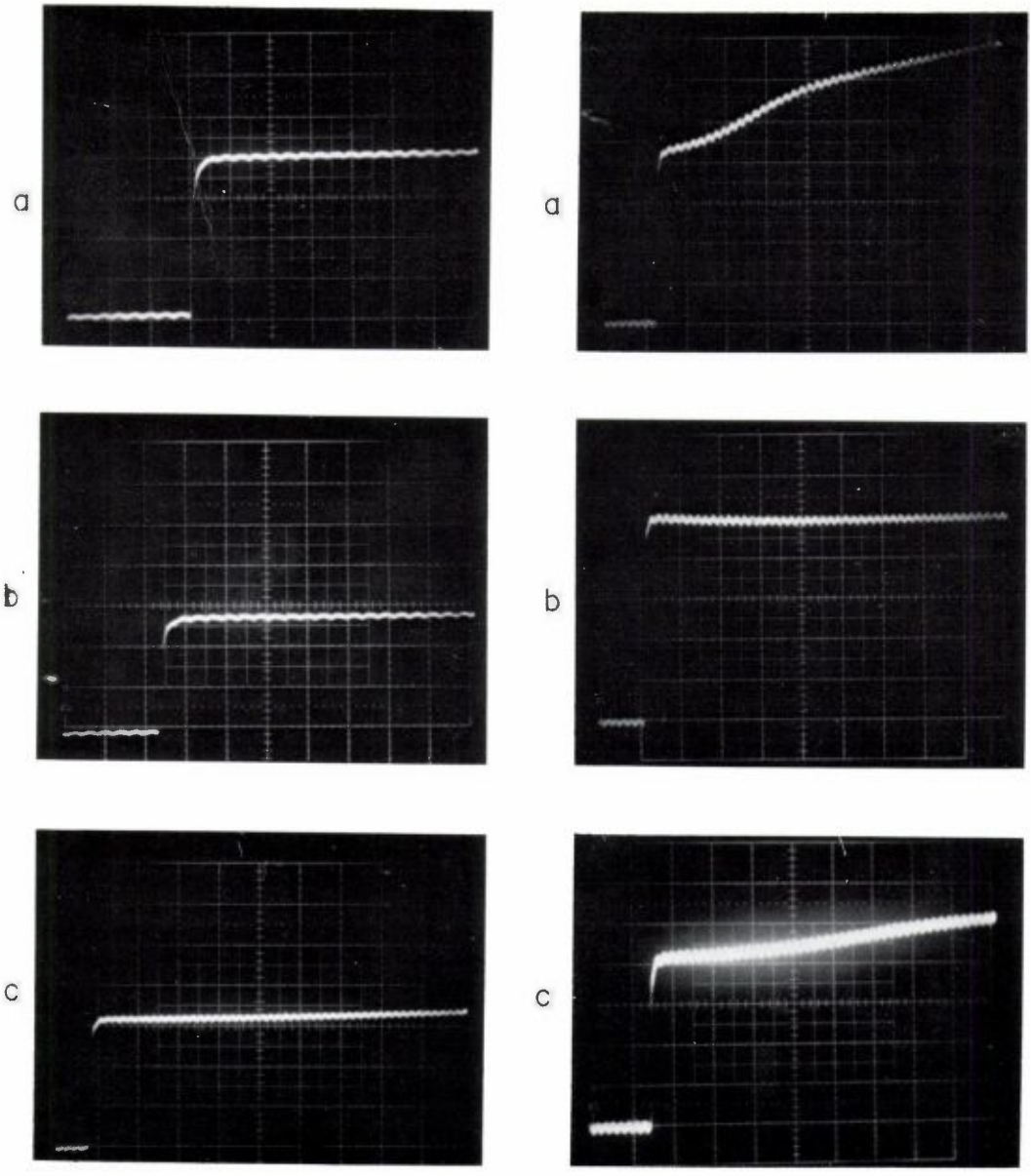

Figure 7. Fluorescence induction curves of *Nephroma laevigatum* in the presence of DCMU (10^{-5} M). The time scale on the oscilloscope was 50 ms/division. (a) 10′ pre-illumination with far-red (10 nm, 15.5 W/m^2) light; (b) 10′ pre-illumination with green (540–620 nm, 35 W/m^2) light; (c) 10′ dark adaptation.

Figure 8. Fluorescence induction curves of untreated *Nephroma laevigatum* pre-illumination with: (a) 10′ far-red; (b) 10′ green light; (c) 10′ dark. Light conditions as in Fig. 7.

as $\phi_I = (F_{m1} - F_{01})/F_{01}$ and $\phi_{II} = (F_{m2} - F_{02})/F_{02}$, where F_{m1} and F_{m2} are the maximal levels of fluorescence and F_{01} and and F_{02} are the initial fluorescence levels, in state 1 and state 2, respectively. An increase in spillover to PS I would preferentially decrease variable fluorescence and would not affect F_0 (Horton and Black, 1983; Hodges and Barber, 1983). F_0 increased by about 15% however F_m increase by about 33% during the transition from state 1 to state 2. This observation is in agreement with the data reported by Fork and Satoh (1983) and indicates that the antennae of PS II and, therefore, the absorption cross-section of PS II, did not change to a large extent. The variable fluorescence level decreased in the transition from state 1 to state 2 indicating a decrease of the rate constant of fluorescence most probably due to an increase in the rate constant of energy transfer from PS II to PS I, in state 2. Therefore, the change in the variable fluorescence yields in the presence of DCMU was attributed to a change in spillover from PS II to PS I. An estimate of the spillover fraction S_p, was obtained by the relation $S_p = (1 - \phi_{II}/\phi_I)$ where ϕ_I and ϕ_{II} are the fluorescence yields for state 1 and state 2, respectively (Post, 1987). Using the values of fluorescence parameters from Fig. 7a,b resulted in a spillover fraction, S_p, of 0.17. This result suggests that during the transition from state 1 to state 2, the extent of direct energy transfer increased by 17%. The maximal fluorescence level in a sample that was dark adapted in the presence of DCMU, was found to be an intermediate between state 1 and state 2. For example, in Fig. 7c the fluorescence parameters of the dark state were closer to those in state 2.

Fluorescence induction curves in the absence of DCMU of samples adapted to state 1, state 2 and dark, are shown Fig. 8 (a–c). Pre-illumination (10 min) with 710 nm light resulted in a higher F_m (Fig. 8a) than pre-illumination with 10 min of green light (Fig. 8b), with $F_m/F_0 = 2.0$ and $F_m/F_0 = 1.43$ for state 1 and state 2, respectively. The dark state in the absence of DCMU was between state 1 and state 2 (Fig. 8c).

4. Discussion

In free living cyanobacteria, changes of 10–15% in the distribution of excitation energy were found during state 1 — state 2 transition (Canaani, 1986). However, it was not possible then to distinguish between a mechanism involving a change in the rate of energy transfer from PS II to PS I or actual redistribution of antenna components between PS I and PS II (Canaani, 1986). In this report, it was shown that during state 1 — state 2 transitions, the change in the distribution of excitation energy, occurs *via* a 15% change

in the extent of direct energy transfer from PS II reaction centers to PS I reaction centers as calculated by the photoacoustic method. A similar change of 17% in the extent of energy transfer during state 1 — state 2 transition was found by the fluorescence induction method. These conclusions are in agreement with the studies of Ley and Butler (1980) and Bruce et al. (1985) in the red algae *Porphyridium cruentum.* The latter suggested that state 1 — state 2 transitions in phycobilisome containing organisms result from a change in the extent of energy transfer between PS II and PS I. However, in contrast to Biggins et al. (1984) the triggering mechanism for the light state transitions is thought to be due to a light-dependent reversible phosphorylation of phycobiliprotein polypeptides (Allen et al., 1985; Canaani, 1986). From the results presented in this report and from previous work (Canaani, 1986) it is suggested that light-dependent protein phosphorylation may lead to a conformational change in PS II allowing an increase in the quantum yield of energy transfer from PS II toPS I, in state 2. This change may involve a small displacement of PS II so that their distance from PS I would be smaller than 100Å , or a modified orientation of the PS II chlorophyll molecular planes. Both would allow more efficient inductive resonance energy transfer from the reaction centers of PS II to PS I, in state 2. The conclusion presented here for cyanobacteria are in contrast to the conclusion reported for intact leaves (Canaani and Malkin, 1984). The latter involved changes in absorption cross-sections of PS II and PS I. The difference between the regulatory mechanism of energy distribution in the cyanobacteria, which is based on direct changes in energy transfer and that of higher plants, which involves changes in absorption cross-sections of PS II and PS I caused by diffusion of phosphorylated light-harvesting chlorophyll a/b protein in the membrane, stems from the difference in their membranal organization. In cyanobacteria, the thylakoid membranes are unappressed, PS I and PS II are thought to be more homogenously distributed. (Williams and Allen, 1987), and therefore changes in energy distribution can occur through changes in direct energy transfer. In higher plants, PS II is found mostly in the granal thylakoids and PS I is found in the stromal thylakolids, and therefore changes in distribution of excitation energy occur through reversible migration of phosphorylated LHC from grana to stroma (Bennett et al., 1980; Andersson and Anderson, 1980; Staehelin and Arntzen, 1983; Barber, 1986). This protein diffusion is probably the rate limiting step in the state transitions in higher plants and therefore, the transitions are slower (7 min)in higher plants compared to cyanobacteria (30 sec).

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