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State transitions, photosystem stoichiometry adjustment and non-photochemical quenching in cyanobacterial cells acclimated to light absorbed by photosystem I or photosystem II

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Abstract

Cells of the cyanobacterium *Synechococcus* 6301 were grown in yellow light absorbed primarily by the phycobilisome (PBS) light-harvesting antenna of photosystem II (PS II), and in red light absorbed primarily by chlorophyll and, therefore, by photosystem I (PS I). Chromatic acclimation of the cells produced a higher phycocyanin/chlorophyll ratio and higher PBS-PS II/PS I ratio in cells grown under PS I-light. State 1–state 2 transitions were demonstrated as changes in the yield of chlorophyll fluorescence in both cell types. The amplitude of state transitions was substantially lower in the PS II-light grown cells, suggesting a specific attenuation of fluorescence yield by a superimposed non-photochemical quenching of excitation. 77 K fluorescence emission spectra of each cell type in state 1 and in state 2 suggested that state transitions regulate excitation energy transfer from the phycobilisome antenna to the reaction centre of PS II and are distinct from photosystem stoichiometry adjustments. The kinetics of photosystem stoichiometry adjustment and the kinetics of the appearance of the non-photochemical quenching process were measured upon switching PS I-light grown cells to PS II-light, and vice versa. Photosystem stoichiometry adjustment was complete within about 48 h, while the non-photochemical quenching occurred within about 25 h. It is proposed that there are at least three distinct phenomena exerting specific effects on the rate of light absorption and light utilization by the two photoreactions: state transitions; photosystem stoichiometry adjustment; and non-photochemical excitation quenching. The relationship between these three distinct processses is discussed.

Abbreviations; Chl – chlorophyll, DCMU – 3-(3,4-dichlorophenyl)-1,1-dimethylurea, F_λ – relative fluorescence intensity at emission wavelength λ nm, F_0 – fluorescence intensity when all PS II traps are open, light 1 – light absorbed preferentially by PS I, light 2 – light absorbed preferentially by PS II, PBS – phycobilisome, PS – photosystem

Introduction

State 1–state 2 transitions are adaptations that control relative distribution of absorbed excitation energy between PS I and PS II (Bonaventura and Myers 1969, Murata 1969, Myers 1971, Fork and Satoh 1986, Williams and Allen 1987). In green plants and algae the transition to state 2 is generally thought to involve a decrease in the optical absorption cross-section of PS II (Horton and Black 1983, Hodges and Barber 1983, Farchaus et al. 1982, Kyle et al. 1983) which results from a phosphorylation-induced decoupling of the peripheral light-harvesting chlorophyll–protein complex (LHC-II)

from the PS II-core complex (Bennett 1983, Staehelin and Arntzen 1983, Barber 1983, Larsson and Andersson 1985). Phosphorylation of LHC-II is catalyzed by a membrane-bound protein kinase (Bennett 1977, Coughlan and Hind 1987) which is activated upon reduction of electron carriers located between the two photosystems (Allen et al. 1981, Horton et al. 1981, Allen 1983). The mobile phospho-LHC-II has been thought to couple energetically to the PS I-core complex after decoupling from PS II (Allen et al. 1981, Telfer et al. 1984, Horton 1983, Delepelaire and Wollman 1985, Allen and Holmes 1986) though the existence of a complementary increase in absorption cross-section of PS I has been called into question (Haworth and Melis 1983, Larsson et al. 1987, Allen and Melis 1988).

Recent evidence suggests that the state 2 transition in cyanobacteria also involves a decrease in the absorption cross-section of PS II (Mullineaux et al. 1986). This decrease is specific for light absorbed by the phycobilisome (Mullineaux and Allen 1988). The state 2 transition in cyanobacteria becomes activated when electron carriers between the two photosystems are reduced: this condition is attained when turnover of electrons by PS I is exceeded by the sum of electron input from PS II and net respiratory electron transport into the plastoquinone pool (Mullineaux and Allen 1986). State 1–state 2 transitions in phycobilisome-containing organisms therefore seem to have more in common with state transitions of green plants than previously thought (Biggins and Bruce 1985, Biggins et al. 1984, Fork and Satoh 1986). A role for protein phosphorylation in cyanobacterial state transitions has been proposed (Allen et al. 1985) and the identities of the phosphoproteins implicated in this process (Allen et al. 1985, Sanders and Allen, 1986) are under investigation.

In addition to the short-term regulation by state transitions, the photosynthetic apparatus is capable of long-term changes in photosystem stoichiometry in response to the balance of light utilization by the two photoreactions. These long-term changes appear as adjustments of the stoichiometry of PS I and PS II complexes in the thylakoid membrane, and result in optimization of light-absorption by the two photosystems (Melis et al. 1985, Glazer and Melis 1987). In cyanobacteria, adjustment of photosystem stoichiometry has been demonstrated to result from alteration in the balance of light absorption by the two photosystems (Myers et al. 1980, Fujita et al. 1985). Under light absorbed predominantly by chlorophyll (PS i-light) cyanobacterial cells develop a phycobilin-chlorophyll ratio of 1.3 and a PS II/PS I ratio of 0.7. On the other hand, cells grown under light absorbed predominantly by chlorophyll (PS I-light) antenna of PS II develop a phycobilin/chlorophyll ratio of 0.42 and a PS II/PS I ratio of 0.27. (Manodori and Melis 1986, Melis et al. 1985).

Thus, both state 1–state 2 transitions and adjustment of photosystem stoichiometry in the thylakoid membrane may result in a more balanced utilization of light by the two photoreactions. Until now, however, the interplay between the short-term state transitions and the long-term adjustments of photosystem stoichiometry has not been considered in studies of chromatic adaptation (e.g., Ley and Butler 1980). In this report, an analysis of state transitions is presented in *Synechococcus* 6301 cells grown under light absorbed predominantly by PS I (PS I-light) or by PS II (PS II-light). Cyanobacteria are particularly convenient experimental organisms for such an investigation since the phycobilin and chlorophyll light-harvesting antennae offer the possibility of defining wavelength bands highly selective for excitation of PS II and PS I, respectively. It was of interest to investigate whether PS I-light grown cells (higher phycocyanin/Chl and PS II/PS I ratios) can readily attain a state 2 condition upon PBS excitation or are permanently fixed in state 1. Conversely, PS II-light grown cells (lower phycocyanin/Chl and PS II/PS I ratios) might be fixed permanently in state 2 or be able to attain a state 1 condition promptly upon Chl excitation. The experiments were therefore directed at determining whether the two regulatory processes of state 1–state 2 transitions and chromatic acclimation to PS 1- or PS II-light have independent or closely inter-related effects on the organization and function of the two photosystems.

Materials and methods

Cells of *Synechococcus* 6301 (*Anacystis nidulans* UTEX 625) were grown photoautotrophically at 35°C in medium C (Kratz and Myers 1955) to mid-log-phase under continuous stirring and bub-

bling with 5% CO_2 in N_2. Illumination with red light, absorbed predominantly by Chl, was provided by tungsten incandescent lamps screened by one layer of Chromoid 114 "Ruby" filter (Strand Lighting Ltd., Isleworth, Middlesex, UK). This "PS I-light" had a maximum emission at 700 nm, 50% of this emission at about 650 nm and zero emission at wavelengths lower that 590 nm. Illumination with yellow light, absorbed predominantly by phycocyanin, was provided by cool-white fluorescent lamps and one layer of Cinemoid 5 "Orange" filter (Strand Lighting Ltd.) The yellow light, termed "PS II-light", had a maximum emission at 590 nm with 50% of this emission occurring at 560 nm and 620 nm. The photon flux densities of incident irradiation for the two cultures were adjusted to give similar rates of cell growth as measured by increase in A_{750}, the doubling time for which was approximately 24 h.

Absorption spectra of the cell suspensions were obtained using a Pye-Unicam SP8000 spectrophotometer, with 10 mm sample and reference cuvettes placed in holders directly against the photomultiplier to minimise signal losses caused by light scattering. Sample scattering was further reduced by the opal glass method (described by Hipkins and Baker 1986).

State 1–state 2 transitions were monitored at 30°C using a Perkin-Elmer LS 5 fluorescence spectrometer with a single-sample room temperature housing holding a 10 mm fluorescence cuvette mounted above an electronic stirrer-head (Rank Bros., Bottisham, Cambridge, UK). Excitation was modulated at 50 Hz. The excitation wavelength was 600 nm (15 nm slit width) and the emission wavelength 685 nm (20 nm slit width). Continuous actinic illumination was provided from the top of the cuvette by a fibre-optic light-guide. The transmission band of the actinic beam was that of a combination of Corning 5-60 and 4-96 broad-band blue filters (maximum transmittance at 425 nm) giving light absorbed primarily by Chl and therefore by PS I. This actinic illumination is therefore referred to as "light 1". Similar results (not shown) were obtained using an actinic light 1 defined by an Ealing 709 nm interference filter.

Fluorescence emission spectra at 77 K were obtained using the Perkin-Elmer LS 5 fluorescence spectrometer with the low-temperature sample housing. Prior to freezing, cells at 5 μg Chl *a* ml^{-1} in growth medium were incubated in the dark to establish state 2 (Mullineaux and Allen 1986) or for 5 min in 709 nm light (defined as above) at approximately 30 W m^{-2} to establish state 1. Fluorescence emission at 77 K was scanned from 630 to 800 nm (5 nm slit width) with excitation (2.5 nm slit width) at either 600 nm (for phycobilin excitation) or 435 nm (for Chl excitation). In both cases spectra were normalized to fluorescence emission at 655 nm upon 600 nm excitation, that is, to the emission maximum arising from phycocyanin. This normalization was applied even for emission spectra obtained at 435 nm excitation (Fig. 6), and differences in fluorescence emission at 655 nm with 435 nm excitation are not therefore inconsistent with normalization to fluorescence emission at 655 nm with 600 nm excitation.

Results

Figure 1 shows absorption spectra of suspensions of cells of *Synechococcus* 6301 grown in PS I-light and in PS II-light, normalized to the Chl long-wave absorption maximum at 678 nm. The absorption at 625 nm relative to that at 678 nm is larger in PS I-light grown cells than in PS II-light grown cells: for PS I-light grown cells A_{625}/A_{678} = 2.20 and for PS II-light grown cells A_{625}/A_{678} = 1.26. The absorption maximum of phycocyanin is at 625 nm and so these spectra (Fig. 1) show clearly that the

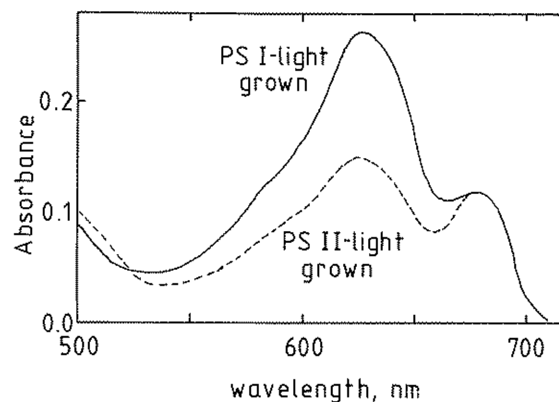

Fig. 1. Absorbance spectra of cell suspensions of *Synechococcus* 6301 after acclimation to PS I-light or PS II-light. The spectra are shown normalized to the Chl maximum at 678 nm. Note the higher absorption at the phycocyanin maximum (at 625 nm) in PS I-light grown cells.

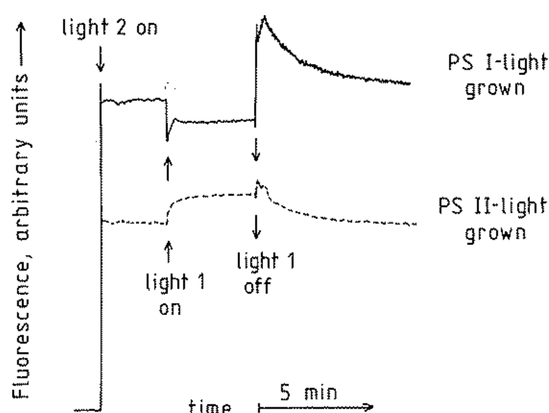

Fig. 2. State 1–state 2 transitions in *Synechococcus* 6301 after acclimation to PS I-light or PS II-light. Fluorescence emission at 685 nm was excited by modulated, actinic light 2 at 600 nm. A broad-band continuous light 1 centred at 425 nm was superimposed where indicated. The two fluorescence traces are presented on the same scale: note that the fluorescence emission of the PS II-light grown cells is closer to F_0 than that of the PS I-light grown cells.

ratio of phycocyanin to Chl is greater in PS I-light grown cells than in PS II-light grown cells. Using the equation of Myers et al. (1980) the data of Fig. 1 give phycocyanobilin/Chl ratios of 1.4 for PS I-light grown cells and 0.7 for PS II-light grown cells. It has been demonstrated previously that differences in the A_{625}/A_{678} absorbance ratio reflect different PBS-PS II/PS I ratios in the thylakoid membrane of *Synechococcus* 6301 (Myers et al. 1980; Manodori and Melis 1986, Fujita and Murakami 19870. Thus, the PS I-light grown cells have a greater PBS-PS II/PS I ratio than the PS II-light grown cells. This adjustment in photosystem stoichiometry in *Synechococcus* 6301 is essentially a compensation response that enables the cells to maintain approximately equal utilization of light by the two photoreactions (Melis et al. 1985, Manodori and Melis 1986).

Figure 2 shows state 1–state 2 transitions in cells grown under PS I-light and PS II-light with the fluorescence traces superimposed on the same scale. In addition of actinic light 1, cells grown under PS I-light show a fast fluorescence decrease that can be attributed to photochemical quenching of PS II fluorescence on opening of PS II traps by increased turnover of PS I. A subsequent, slow rising phase is observed that can be attributed to a combination of increased absorption cross-section of PS II and to relaxation of photochemical quenching of PS II fluorescence as relative PS II turnover increases: this change is characteristic of the state 1 transition (Murata 1969). On extinction of the actinic light 1, a fast fluorescence increase occurs as a result of relaxation of photochemical quenching of PS II fluorescence as PS II traps close. There follows a phase of decreasing fluorescence as the PS II absorption cross-section decreases and PS II traps re-open. This approximately single-exponential decay phase is interrupted by a transient secondary rise characteristic of the induction phase of photosynthesis and attributable to a short-lived closure of traps that occurs before carbon assimilation begins to regenerate the PS I acceptor $NADP^+$ (Krause and Weiss 1984). This combination of a rapid rise followed by a slow decay-phase is characteristic of the state 2 transition (Murata 1969, Chow et al. 1981).

On addition of actinic light 1 to cells grown under PS II-light the slow rising phase of the state 1 transition was observed without the fast initial decrease (Fig. 2). For PS II-light grown cells the amplitude of the fluorescence rise on extinction of the actinic light 1 is smaller than for PS I-light grown cells. The transient interruption of the slow decay-phase during the state 2 transition was less marked in PS II-light grown cells than in PS I-light grown cells (Fig. 2). The lower amplitude of the fluorescence changes upon state transitions in PS II-light grown cells is attributed directly to the fact that the fluorescence yield established upon phycocyanin excitation at 600 nm was much closer to the F_0 than that of the PS I-light grown cells (Fig. 2). Since a higher proportion of PS II traps would then be open for PS II-light grown cells in the presence of the 600 nm excitation beam alone, this would provide an explanation for the lack of a fast fluorescence dcrease on addition of light 1. The same consideration would also help to explain both the smaller amplitude of the rapid fluorescence rise on extinction of light 1, and the smaller secondary fluorescence maximum during the state 2 transition.

An explanation for the unexpected behaviour of the PS II-light grown cells in comparison with the PS I-light grown cells (Fig. 2) cannot be provided solely on the basis of their smaller phycocyanin absorption cross-section relative to that of Chl. Upon deconvolution of the absorption spectra

shown in Fig. 1, by the method of Glazer and Melis (1987), we estimate that phycocyanin absorbs 80% of the 600 nm excitation in the PS II-light grown cells and 90% in the PS I-light grown cells. Clearly, this difference alone is not sufficient to explain why PS II-light cells remain with most PS II traps open even under a predominantly PS II excitation. A more likely explanation for this phenomenon is the operation in PS II-light grown cells of a non-photochemical quenching of phycobilisome excitation already noted in cyanobacteria (Manodori and Melis 1986, Melis et al. submitted). A non-photochemical quenching process has also been described for higher plant chloroplasts (Krause et al. 1983, Weiss and Berry 1987, Oxborough and Horton 1983) and is apparently activated under conditions of persistent PS II overexcitation.

Figure 3 shows the reversibility of chromatic acclimation in *Synechococcus* 6301. The ratio A_{625}/A_{678} decreases from 2.0 to 1.4 within 44 h upon transfer of PS I-light grown cells to PS II-light and increases from 1.3 to 1.9 within 44 h of transfer of PS II-light grown cells to PS I-light. This well-defined reversibility of the photosystem stoichiometry in the thylakoid membrane of *Synechococcus* 6301, as measured by the A_{625}/A_{678} change, led us to address the question of the reversibility of the changes in state transitions upon reacclimation of PS I-light grown cells to PS II-light.

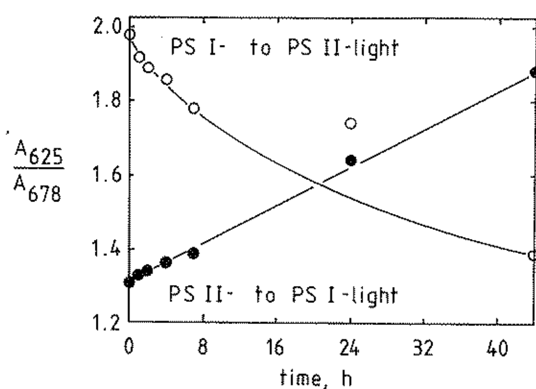

Fig. 3. Chromatic acclimation of *Synechococcus* 6301 cells following transfer of PS I-light grown cells to PS II-light and of PS II-light grown cells to PS I-light. Cells fully acclimated as in Fig. 1 were transferred to the opposite light regime at 0 h and absorbance spectra were measured at intervals during the re-acclimation. A_{625}/A_{678} was measured as the ratio of the absorption maxima shown in Fig. 1

In order to test whether the differences in state transitions between the two cell types were dependent on their acclimation to PS I- or PS II-light, a number of state transition measurements were performed on PS I-light grown cells at intervals after they had been transferred to PS II-light. The results of these measurements are shown in Fig. 4 where fluorescence traces are presented on the same scale but offset on both axes to facilitate comparison. It is seen that the amplitudes of the two fast phases (attributed purely to effects on trap closure) decrease as PS I-light grown cells become acclimated to PS II-light. After 7 h growth in PS II-light the initial fluorescence decrease on addition of light 1 is brief and smaller in amplitude than the rise caused by the state 1 transition. Furthermore, the interruption of the decay phase on extinction of light 1 is either absent or so fast as to be indistinguishable from the initial rise.

After 24 h growth in PS II-light the modulated fluorescnece yield changes of the PS I-light grown cells (Fig. 4) are identical to those of the cells originally grown in PS II-light (Fig. 2), despite the fact that change in the ratio A_{625}/A_{678} is only about

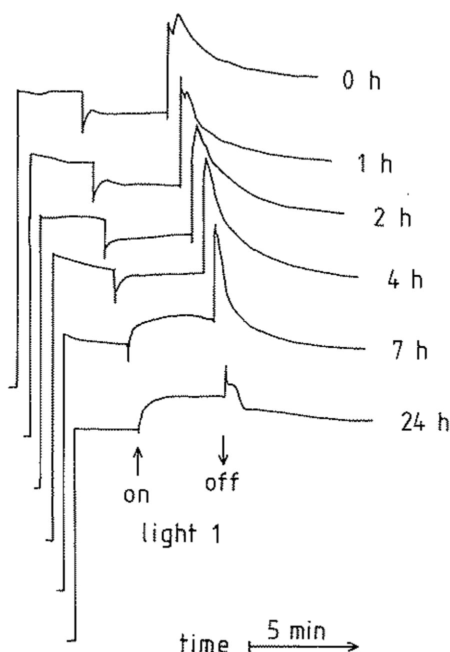

Fig. 4. State 1–state 2 transitions of *Synechococcus* 6301 at time intervals following transfer of PS I-light grown cells to PS II-light. Fluorescence traces were obtained as in Fig. 2 at times shown after transfer of cells to PS II-light.

50% completed (Fig. 3). The results of Fig. 4 suggest that within 24 h of cell growth under PS II-light, the response of the photochemical apparatus to state transitions is limited, presumably because of the operation of the non-photochemical quenching. This difference between the time-course of chromatic acclimation and the appearance of the non-photochemical quenching indicates that chromatic acclimation and non-photochemical quenching are complementary but independent phenomena occurring on a time-scale considerably longer than that of state transitions.

The results of Figs. 2 and 4 together certainly indicate that both PS I-light grown cells and PS II-light grown cells are capable of undergoing state 1–state 2 transitions, and therefore show conclusively that alteration in the relative distribution of excitation energy between PS I and PS II by state transitions can be superimposed on chromatic acclimation and on the non-photochemical quenching. State 1–state 2 transitions, non-photochemical quenching and chromatic acclimation during cell growth are therefore distinct phenomena even though they each serve apparently to equalize light-utilization by the two photosystems.

Further analysis of the characteristics of the photochemical apparatus in PS I-light grown and PS II-light grown cells was undertaken by fluorescence emission spectroscopy at 77 K. Figure 5 shows fluorescence emission spectra obtained with an excitation wavelength (600 nm) which is selectively absorbed by phycocyanin. Four fluorescence emission maxima can be seen (Butler 1978); F_{655} from phycocyanin and to which the spectra are normalized; F_{687} from PBS core components and PS II Chl *a*; F_{697} from PS II Chl *a*; and F_{720} from PS I Chl *a*, the latter observed as a distinct band only in the spectrum of PS II-light grown cells in state 2 and as a shoulder in those of the other samples. A further shoulder is seen at 760 nm in state 1 in both cell types.

Figure 5(a) shows fluoresence emission spectra obtained with PS I-light grown cells and Fig. 5(b) shows spectra obtained with PS I-light grown cells, with the spectrum from cells in state 2 being shown as a broken line and that from cells in state 1 as a continuous line in each case. It is observed that the apparent PS II/PS I fluorescence emission ratio is substantially lower in state 2 than in state 1 in both cell types. This result arises entirely from the decreased F_{687} and F_{697} in state 2: the amplitude of the F_{720} remained apparently independent of state transitions in both cell types. This result therefore suggests that state transitions affect the absorption cross-section of PS II without having a pronounced affect on the absorption cross-section of PS I (Mullineaux and Allen 1988). Differences in the fluorescence emission spectra between PS I-light grown cells and PS II-light grown cells include a more pronounced F_{720} in the latter (Fig. 5b) than in the former (Fig. 5(a)). This may come about because of greater excitation of PS I Chl by 600 nm light in the PS II-light grown cells as a result of their lower PBS-PS II/PS I ratio.

Figure 6 shows fluorescence emission spectra

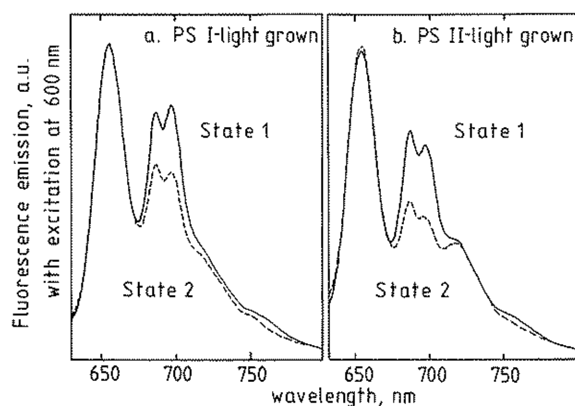

Fig. 5. Fluorescence emission spectra at 77 K of *Synechococcus* 6301 cells acclimated either to PS I-light or to PS II-light. Excitation was at 600 nm in order to sensitize primarily the phycobilisome.

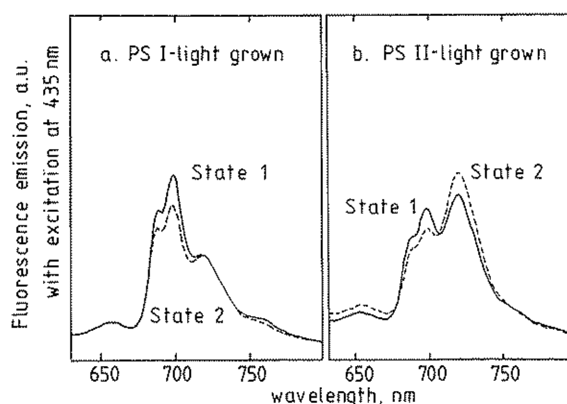

Fig. 6. Fluorescence emission spectra at 77 K of *Synechococcus* 6301 cells acclimated to either PS I-light or PS II-light. Excitation was at 435 nm in order to sensitize primarily chlorophyll.

obtained with excitation at 435 nm, favouring absorption by Chl. Here the phycocyanin emission maximum, F_{655}, is very small. To facilitate comparison, the spectra in Fig. 6 have been normalized to F_{655} with excitation at 600 nm. The spectra in Fig. 6 are therefore presented on a fluorescence scale proportional to that of the spectra in Fig. 5.

Figure 6(a) shows spectra of PS I-light grown cells and Fig. 6(b) shows spectra of PS II-light grown cells. It is observed that in PS I-light grown cells F_{687} and F_{697} are greater than F_{720}. In PS II-light grown cells F_{720} is greater than F_{687} and F_{697}. This difference is a direct reflection of the different photosystem stoichiometries between the two cell types, and is therefore is agreement with the proposal that PS I-light grown cells (Fig. 6(a)) have a higher PS II/PS I ratio than PS II-light grown cells (Fig 6(b)). With Chl excitation, the minor emission shoulder at 760 nm appears to be greater in PS I-light grown cells than in PS II-light grown cells, irrespective of light-state.

With PS I-light grown cells it is also apparent that the state 2 transition decreases PS II emission without appreciably affecting PS I emission (Fig. 6(a)). However, in PS II-light grown cells (Fig. 6(b)) the state 2 transition produces a measurable increase in F_{720} and a decrease in F_{687} and F_{698} similar to results previously described (Allen et al. 1985, Sanders and Allen 1987).

Discussion

The present work examines the interplay between state transitions, non-photochemical quenching and photosystem stoichiometry adjustments in the regulation of light-utilization by the two photoreactions of oxygenic photosynthesis. In the cyanobacterium *Synechococcus* 6301, state transitions occur on a time-scale of a few minutes and modulate the absorption cross-section of PS II for PBS excitation. The absorption cross-section of PS I appears to remain fairly constant during state transitions. The existence of a mechanism for the non-photochemical quenching of excitation energy in cyanobacteria was indicated in earlier work (Manodori and Melis 1986, Melis et al. submitted). The non-photochemical quenching in cyanobacteria is analogous to that of higher plant chloroplasts (Krause et al. 1983, Weiss and Berry 1987, Oxborough and Horton 1988) and in manifested under conditions of overexcitation of the photosynthetic apparatus and especially of PS II. In this work, the non-photochemical quenching operates in the PS II-light grown cells where a lower PS II/PS I ratio is necessary but not quite sufficient to balance light utilization by the two photoreactions (Manodori and Melis 1986, Melis et al. submitted). Thus, upon a 600 nm excitation, PS II-light grown cells show a fluorescence yield near F_o, corresponding to a situation where most PS II centres are open (Fig. 2). The non-photochemical quenching is fully expressed within 24 h upon transfer of PS I-light grown cells to PS II-light conditions (Fig. 4). The adjustment in photosystem stoichiometry during the chromatic acclimation occurs within 44 h (Fig. 3) and it is therefore the slowest of the three responses of the thylakoid membrane to imbalance in light utilization by the two photoreactions. This slowest response affects the relative concentration of PBS-PS II and PS I complexes in the thylakoid membrane of *Synechococcus* 6301 and does not affect directly the absorption cross-section of individual complexes.

The result presented in this work also support the proposition that the three phenomena (state transitions, non-photochemical quenching and photosystem stoichiometry adjustments) operate independently of one-another. Moreover, their effects can be superimposed. Thus, under our experimental conditions, PS II-light grown cells have a relatively low PS II/PS I ratio, they manifest non-photochemical quenching of the excess PS II excitation, and they are capable of undergoing state transitions. The amplitude of state transitions in these cells, however, is severely limited because of the superimposed non-photochemical quenching of excitation in the pigment bed of the PBS-PS II complex. Furthermore, the three regulatory processes appear to operate on different time-scales as well as bringing about different effects on the photosynthetic apparatus.

Why should it be necessary for a photosynthetic organism to have three apparently independent processes for the regulation of light utilization by PS I and PS II centres? We propose that each of the three regulatory processes has distinct effects, as follows:

a) *State transitions* are effective in the fine adjustment of the rate of light utilization by PS II

under light-limiting conditions. They provide a fine control of the absorption cross-section of this photosystem (Allen et al. 1985, Mullineaux and Allen 1988). However, we suggest that it would be wasteful for the cell to maintain a state 2 condition for a prolonged period of time since this condition renders a sizable portion of the auxiliary PS II antenna (PBS or LHC II) useless.

b) *Non-photochemical (or energy-dependent) quenching* of excitation in the pigment bed of PS II provides protection against overexcitation of this photosystem but it results in the substantial lowering of the quantum yield of photosynthesis (Krause et al. 1983, Weiss and Berry 1987, Oxborough and Horton 1988). As such, the non-photochemical quenching mechanism affords protection against photodamage and it can operate both under conditions of imbalance in the rate of light utilization by the two photoreactions (Manodori and Melis 1986) and under saturating light conditions when the rate-limiting step is defined by the dark reactions of photosynthesis (Weiss and Berry 1987).

c) *Chromatic acclimation by photosystem stoichiometry adjustment* in the thylakoid membrane clearly provides the cell with the greatest flexibility for the long term optimization of the electron-transport function in the thylakoid membrane. Thus, the existence of a feedback-control mechanism for the adjustment of photosystem stoichiometry (Melis et al. 1985) allows the cell, through the process of selective protein turnover and regulation of gene expression, to modify the composition and function of its photosynthetic apparatus in a relatively permanent manner. Conversely, chromatic acclimation of photosystem stoichiometry would seem to be a rather unsuitable mechanism for the regulation of light absorption in response to rapid environmental light fluctuations since the breakdown and *de novo* synthesis of protein complexes is both slow and metabolically expensive.

Viewed in this way there is a clear role for each of the three processes in the regulation of light utilization by PS II and PS I centres in oxygenic photosynthesis, and the three processes together comprise a repertoire of control mechanisms from which can be drawn the most appropriate strategy for a given set of environmental and metabolic circumstances.

It has been proposed that two of these regulatory processes, state transitions (Murata 1969, Duysens 1972, Mullineaux and Allen 1986) and chromatic acclimation of the thylakoid membrane (Melis et al. 1985, Fujita et al. 1987), are controlled by the redox state of an electron-carrier located between the two photosystems. If this is the case then it is possible that changes in protein phosphorylation are responsible for the control of gene expression that results in alteration of photosystem stoichiometry, as well as for the decoupling of the peripheral light-harvesting system during the state 2 transition. Changes in protein phosphorylation during chromatic acclimation are currently under investigation.

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