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The role of respiratory electron flow in the control of excitation energy distribution in blue-green algae

P.J. Dominy * and W.P. Williams

Biochemistry Department, King's College London, London (U.K.)

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State 1/State 2 transitions in 3-(3,4-dichlorophenyl)-1,1′-dimethylurea- (DCMU)-poisoned *Anacystis* cells were monitored using modulated fluorescence techniques. Measurements of fluorescence emission spectra of cells adapted to State 1 and State 2 showed that the fate of excitation energy absorbed by Photosystem II was independent of whether it was initially absorbed by phycocyanin or chlorophyll a_{II} indicating that control of excitation energy distribution between the two photosystems is exercised at the level of chlorophyll proteins of the core complex rather than at that of the phycobilisome. Analysis of changes in the intensity dependence of State-1 adaptation in anaerobic and aerobic cells, and in aerobic cells held at different temperatures, suggested that the respiratory and photosynthetic electron-transport chains of the alga intersect at the level of the plastoquinone pool and that Photosystem I and cytochrome oxidase are in direct competition for electrons passing through this pool. This was confirmed by measurements involving the comparison of the intensity dependencies of State-1 adaptation and the light-dependent inhibition of respiration in DCMU-poisoned cells.

Introduction

Exposure of algal cells to light that preferentially stimulates PS I activity results in a transition to a state (State 1) in which the photosynthetic activity of PS II photo-processes is increased and those of PS I decreased while exposure to light that preferentially stimulates PS II activity results in a state (State 2) in which the efficiency of PS II photo-processes is lowered and those of PS I increased [1,2]. In the dark, the cells normally relax to a state that is similar, or identical, to State 2 [3–6]. This general pattern of changes appears to be common to green [1,3,4,7–14], blue-green [6,15–23] and red [2,5,24–33] algae. The only significant differences between the various groups are that the changes in the blue-green and red algae are more extensive and tend to take place much more rapidly than those seen in the green algae (see review by Williams and Allen [34]).

In the case of the green algae, State 1/State 2 changes are thought to reflect changes in the relative absorption cross-sections of PS I and PS II associated with the redistribution of chlorophyll

* Present address: Botany Department, University of Glasgow, Glasgow, U.K.

Abbreviations: DCMU, 3-(3,4-dichlorophenyl)-1,1′-dimethylurea; PQ, plastoquinone; PS I, Photosystem I; PS II, Photosystem II; LHC-II, light harvesting chlorophyll *a*/*b* protein; Chl a_I, bulk chlorophyll of Photosystem I; Chl a_{II}, bulk chlorophyll of Photosystem II.

Correspondence: W.P. Williams, Biochemistry Department, King's College London (KQC), Campden Hill, London, W7 8AH, U.K.

a/b light-harvesting protein (LHC-II). This mechanism, first proposed for higher plants [35], is based on the idea that any imbalance of the photosystems in favour of PS II results in the preferential reduction of the plastoquinone (PQ) pool lying between the two photosystems which then leads to the activation of a kinase system that phosphorylates LHC-II. Phosphorylation of LHC-II is thought to lead to its dissociation from the light-harvesting PS II apparatus and association with PS I [36]. The process is believed to be reversed by a light-independent phosphatase system when the kinase system is inactive [37].

This mechanism has been criticised on the basis of observations suggesting that LHC-II phosphorylation in *Chlamydomonas rheinhardtii* is light-independent [38] and measurements of fluorescence changes suggesting the occurrence of State 1/State 2 changes in a *Scenedesmus obliquus* mutant that lacks LHC-II [11]. More recent measurements, performed by Wollman and Delepelaire [13,14] while confirming that LHC-II is phosphorylated under both State 1 and State 2 conditions in *Chlamydomonas,* indicated that the level of phosphorylation is approx. 20% lower in State 1 than in State 2. Wollman and Delepelaire were also able to explain the phosphorylation of LHC-II, and hence State 2 formation, in the dark-adapted algae by invoking electron flow into the PQ pool via the chloro-respiration pathway identified by Bennoun [39]. The observations on *Scenedesmus* still remain to be explained but the bulk of available evidence appears to support the validity of the LHC-II phosphorylation model for State 1/State 2 adaptation in green algae [34].

Blue-green and red algae lack LHC-II; there is currently considerable debate regarding the possible existence of pigment-protein complexes in these algae that can undergo light-driven phosphorylation analogous to that seen for LHC-II. Biggins and his co-workers [30] doubt the existence of such species and have proposed a model for State 1/State 2 adaptation in the red and blue-green algae based on localised electrical changes in the thylakoid membrane associated with the over-stimulation of cyclic electron transport. A similar, but less specific, model has also been proposed by Satoh and Fork [18]. Allen and his co-workers, in contrast, believe that such species do exist and have proposed a model, based on the light-induced phosphorylation of the 18.5 kDa phycobilisome-linker protein, involving the transfer of phycobilisomes between the two photosystems [19].

If, State 1/State 2 transitions in red and blue-green algae do involve the light-induced phosphorylation of pigment-protein complexes, it is likely that their phosphorylation is controlled by redox-sensitive kinase systems analogous to those found in green algae and higher plants. The respiratory chains of blue-green algae are known to intersect with their photosynthetic electron-transport chains at the level of the PQ pool [40–44] and Mullineaux and Allen [22] have presented evidence, based on the comparison of State 1/State 2 changes in starved and unstarved *Synechococcus* cells, suggesting that respiratory electron flow may influence state transitions. In this paper, we present results confirming that there is a direct connection between the respiratory and electron-transport chains of the blue-green alga *Anacystis nidulans* and that respiratory electron flow has a direct effect on State 1/State 2 transitions in this organism.

Materials and Methods

Anacystis nidulans (*Synechococcus leopolensis*) TX 20, UTEX 625, Collection of Algae, University of Texas, Austin) was cultured at 40 °C in Kratz and Myers Medium C [45] bubbled with 5% CO_2 in air under an incident light intensity of 160 $\mu E \cdot m^{-2} \cdot s^{-1}$ (PAR). The medium was supplemented by the addition of 12 mg/l $Fe_2(SO_4)_3$ just prior to innoculation in order to avoid problems associated with iron deficiency. Under these conditions, the optical density of the cell suspensions doubles approx. every 3.5 h during the log phase. The cell suspensions used in this study were normally harvested in early log phase and had optical densities at 675 nm in the range 0.2–0.5 and a ratio of absorption at 625 nm to that at 675 nm of about 1.2–1.3. When measurements were made using older cultures, they were diluted with growth medium just prior to use so as to yield optical densities in the same range.

Most of the fluorescence measurements described in this paper were made using a Perkin-Elmer MPF-44A spectro-fluorimeter modified by

the incorporation of a stirrer and a fibre-optic to deliver a high-intensity actinic beam to the sample. Measurements involving the comparison of the intensity dependencies of fluorescence emission and O_2-uptake, however, were made using a fluorimeter constructed in this laboratory [16] fitted with a Hansatech (U.K.) oxygen electrode in the sample cuvette position. Both instruments were operated in an a.c. mode using a weak modulated measuring beam to monitor sample fluorescence and a strong non-modulated actinic beam to drive State 1/State 2 changes. In both cases, the measuring beam was isolated using a monochromator while the actinic beam was isolated from a 150 W quartz-halogen lamp using a combination of Schott broad-band blue glass filters. Unless otherwise stated, the intensity and wavelength of the measuring beam were 5.5 $\mu E \cdot m^{-2} \cdot s^{-1}$ and 570 nm, respectively, and the intensity of the actinic beam was 80 $\mu E \cdot m^{-2} \cdot s^{-1}$. Measuring and actinic beam intensities were reduced when required by the use of Balzer neutral-density filters and light intensities were measured using a Li-Cor (Lincoln, NE, U.S.A.) LI-1905B quantum sensor.

Results

Measurement of State 1 / State 2 changes

State 1/State 2 transitions in algal cells can be conveniently measured by comparing the fluorescence yields of dark-adapted cells (State 2) and cells illuminated in the presence of DCMU (40 μM) to block PS II activity (State 1) using modulated fluorescence techniques [1,4]. The fluorescence yield of the cells is monitored using a relatively low intensity modulated beam (the measuring beam) that is sufficiently intense to keep all PS II traps closed, but too weak to influence the state of the cells. The state transitions are then driven by a more intense beam (the actinic beam). The detection system is arranged so that the unmodulated component of fluorescence emission, stimulated by the actinic beam, is rejected. Under these conditions changes in the quantum yield of fluorescence associated with state transitions are directly reflected in changes in the intensity of the modulated component of emission associated with the measuring beam.

A typical trace obtained for DCMU-poisoned *Anacystis* cells is shown in Fig. 1. The cells are in the dark-adapted state (State 2) prior to exposure to the actinic beam. Exposure to the actinic beam results in a large increase in the yield of fluorescence excited by the measuring beam reflecting the transition of the cells to State 1. The relative increase in fluorescence $\Delta F/F_2$ (where $\Delta F = F_1 - F_2$ and F_1 and F_2 are the fluorescence yields in State 1 and State 2, respectively) varies with the intensity of the actinic light. Under saturating light conditions, however, the increase is usually about 0.6–0.8, but can be appreciably higher. The rate of the transition from State 2 to State 1, as discussed below, is dependent on light intensity, temperature and the metabolic status of the algae. Log-phase cells measured at their growth temperature (40 °C) under light saturating conditions, however, typically show transitions with half-times of 1–5 s.

Changes in emission spectra

Typical emission spectra of State-1 and State-2 adapted cells excited at 430 and 570 nm are shown in Fig. 2. At 430 nm, most of the exciting light absorbed by PS II is absorbed directly into Chl

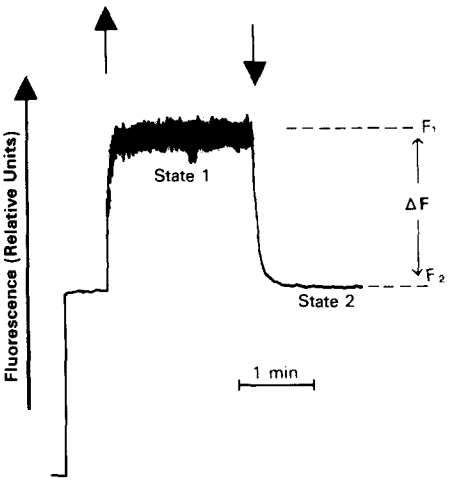

Fig. 1. Typical trace showing the fluorescence increases associated with the State-1 adaptation of DCMU-poisoned *Anacystis*. The fluorescence yield of the sample is monitored by the modulated beam and the points at which the unmodulated actinic beam is switched on and off are indicated by the arrows. The fluorescence yield of the cells in State 1 (F_1) and State 2 (F_2), and the light-induced increase in fluorescence (ΔF), are as indicated.

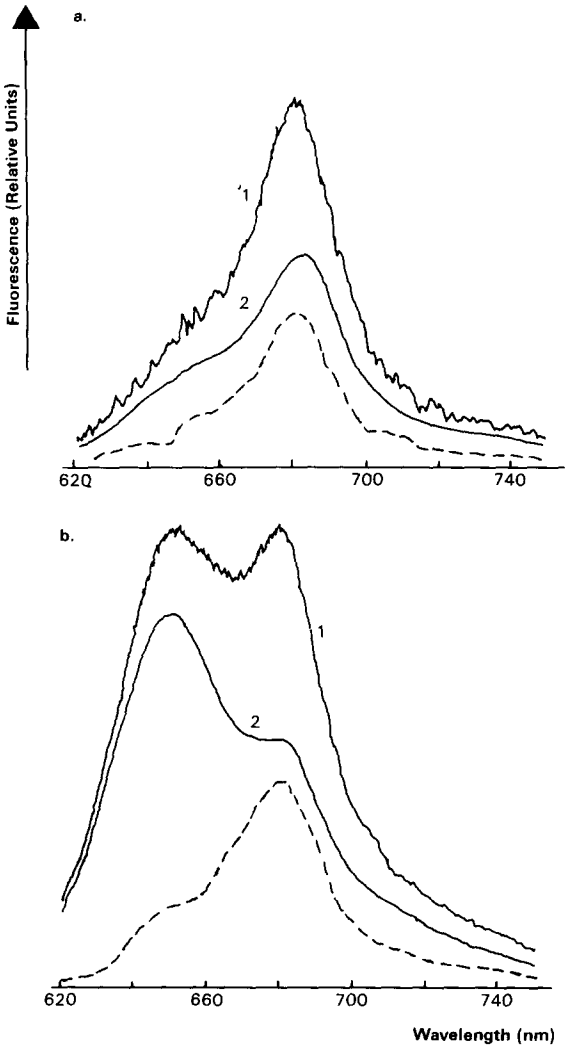

Fig. 2. Emission spectra of DCMU-poisoned *Anacystis* cells adapted to State 1 (1) and State 2 (2) measured (a) using a 430 nm modulated measuring beam and (b) a 570 nm measuring beam. The corresponding difference spectra are indicated by the dashed lines.

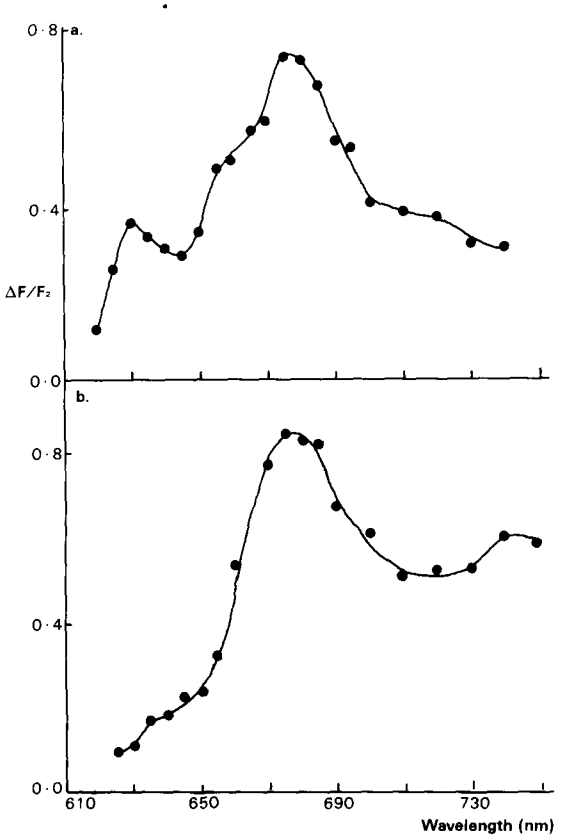

Fig. 3. Plot of the wavelength dependence of $\Delta F/F_2$ calculated from the spectra shown in Fig. 2 for (a) excitation at 430 nm, (b) excitation at 570 nm.

a_{II}, while at 570 nm most of the light is absorbed by phycocyanin and then passed on to Chl a_{II} by energy transfer. Difference spectra calculated by subtraction of the emission spectrum of State-2-adapted algae from that of the corresponding State-1-adapted sample are included in Fig. 2 and plots of the variation in the values of $\Delta F/F_2$ with detection wavelength are presented in Fig. 3. In both cases, State 1 adaptation appears to lead to an about 80% increase in emission at 680–685 nm. Lower increases are seen at 650 nm, the emission maximum of phycocyanin. Overlap of the emission peaks of Chl a_{II} and phycocyanin make an exact estimation of their relative contributions to the fluorescence increase occurring on State 1 adaptation difficult. Comparison of the two sets of emission spectra suggests, however, that fluorescence from Chl a_{II} is approximately doubled while that from phycocyanin increases by only about 10–20% for both excitation wavelengths. There appears to be little or no difference in the fate of excitation energy absorbed directly by Chl a_{II} and that reaching Chl a_{II} via the phycobilisome.

Role of respiratory electron transport

As discussed above, the extent of State-1 and State-2 adaptation in higher plants and green algae is believed to be strongly influenced by the redox state of their PQ pools. Wollman and Delepelaire [13,14] have shown that in the case of the green alga *Chlamydomonas,* the fluorescence yield of PS II is lowered, and the overall magnitude of State 2 to State 1 transition increased, in anaerobic as opposed to aerobic cells. These changes were interpreted in terms of an increased reduction of PQ by chloro-respiration following the inhibition of electron-flow out of the PQ pool to O_2. Given that the respiratory electron-transport chains of blue-green algae are also thought to intersect with their photosynthetic electron-transport chains at the level of PQ [40–44], we decided to examine the effects of using glucose/glucose oxidase to remove O_2 from our *Anacystis* samples.

Addition of glucose (20 mM) has no effect on State 1/State 2 transitions in DCMU-poisoned cells. Following the addition of glucose oxidase, however, the fluorescence yield of algae in State 2 decreases (Fig. 4). Little or no change occurs in the fluorescence yield of State-1-adapted algae, indicating that the reduction in yield seen for the State-2-adapted algae is not due to a non-specific quenching of chlorophyll *a* fluorescence. The extent of the decrease in the value of F_2 on O_2 depletion was found to depend on the metabolic state of the cells. Cells from older cultures tended to show larger changes in F_2 on going anaerobic than those from younger cultures.

Cells from early log-phase cultures are usually characterised by much more rapid State 1/State 2 transitions than cells from cultures close to the stationary phase (see results set out in Table I). The fact that the rates of the State 2 to State 1 and the State 1 to State 2 transitions are both decreased in the cells from older cultures suggests that it is probably the rate of conformational changes at the level of the thylakoid membrane that is the limiting rather than metabolic changes per se. This view is supported by measurements (not detailed) showing that the two sets of cells exhibit similar rates of dark respiration and photosynthesis under saturating white light. The slower kinetics exhibited by older cultures mean that it is often difficult to be certain that the cells are fully equilibrated to State 2 on removal of the actinic beam. This problem is exacerbated by an increased sensitivity of older cultures to perturbation by the modualted measuring beam. In general, the measuring beam tends to oppose the restoration of State 2 on switching off the measuring beam. This is reflected in the increased values

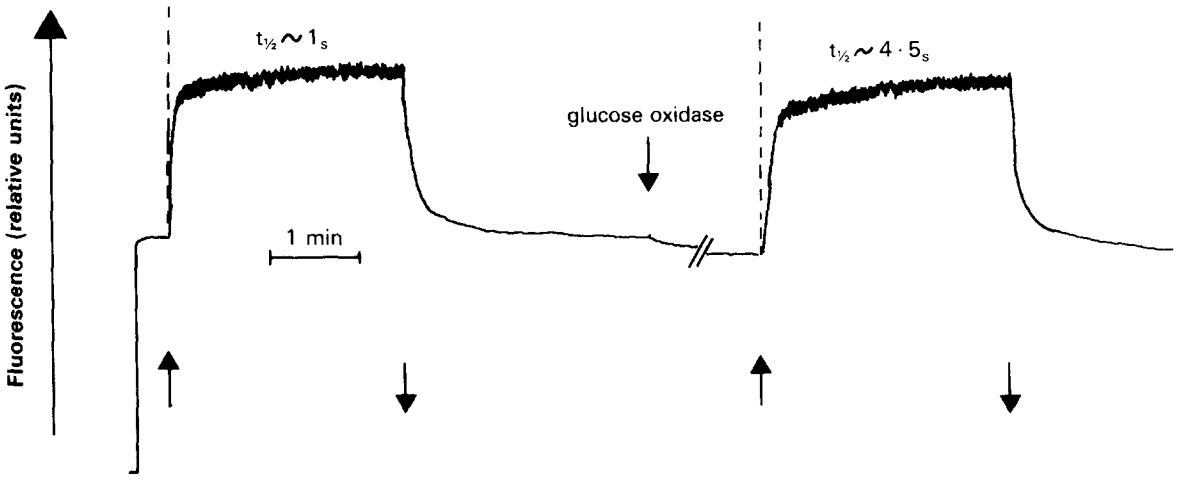

Fig. 4. Typical traces showing the effects on the fluorescence yield of DCMU-poisoned *Anacystis* cells of rendering the cells anaerobic. The suspension contained 20 mM glucose and 120 I.U. untis of glucose oxidase were added as indicated. The measuring conditions are as described in the caption to Fig. 1.

TABLE I

VARIATION IN MEASURED VALUES OF $\Delta F/F_2$ FOR AEROBIC AND ANAEROBIC CELLS AND CELLS MEASURED USING A HIGH INTENSITY (22 $\mu E \cdot m^{-2} \cdot s^{-1}$) AND AN ATTENUATED MEASURING BEAM

Measuring conditions	$\Delta F/F_2$	$t_{1/2(2\rightarrow1)}$ (s)	$t_{1/2(1\rightarrow2)}$ (s)
Early log-phase cells			
Full measuring beam (aerobic)	0.61	1.0	3.0
Full measuring beam (anaerobic)	0.64	1.5	3.4
10% measuring beam	0.66	<1.0	1.5
Late log-phase cells [a]			
Full measuring beam (aerobic)	0.87	7	20
Full measuring beam (anaerobic)	0.90	10	20
10% measuring beam	0.97	5	11.0

[a] Diluted 4-fold prior to measurement.

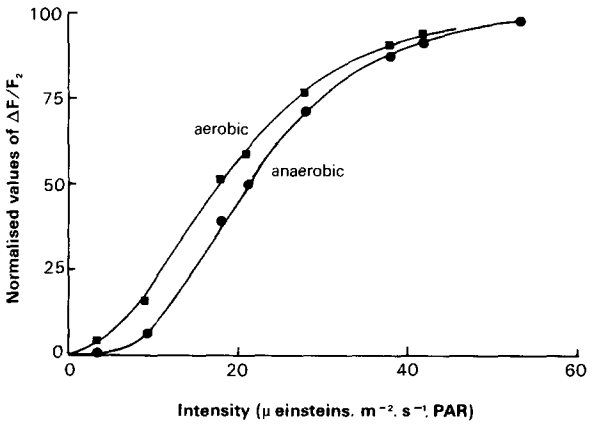

Fig. 5. Plot showing the dependence of normalised values of $\Delta F/F_2$ on the intensity of the actinic beam for aerobic (■) and anaerobic (■) DCMU-poisoned *Anacystis*. The measured values for $\Delta F/F_2$ under saturating light conditions were 1.02 and 1.12 for aerobic and anaerobic cells, respectively.

of $t_{1/2}$ for State-1-to-State-2 transitions measured using a strong as opposed to a weak measuring beam presented in Table I. O_2 depletion, which inhibits the flow of respiratory electrons out of the PQ pool, tends to facilitate the relaxation of the cells to State 2 and hence to bring about reductions in the value of F_2 in such samples.

While the effects of O_2 depletion on State-2-to-State-1 adaptation are seen mostly in older cultures, its effects on State 1 adaptation can easily be seen even in younger cells. Under anaerobic conditions, increased turn-over of PS I is required to deplete the PQ pool of electrons that would normally have gone to O_2 before State 1 can be

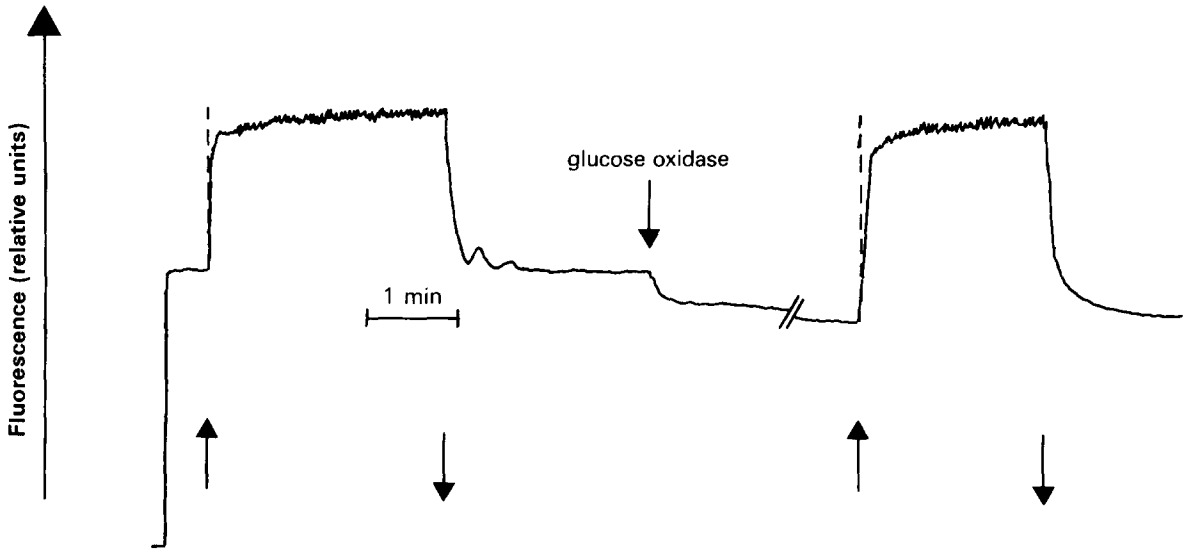

Fig. 6. Trace showing oscillations in the fluorescence yield of DCMU-poisoned *Anacystis* cells associated with the transition of the cells from State 1 to State 2 and the effects of anaerobosis on such oscillations. Experimental conditions as described in the caption to Fig. 4.

established. This is reflected in the slower rates of State-2-to-State-1 transitions seen in anaerobic as opposed to aerobic cells (see Fig. 4 and Table I). It is also apparent in measurements of the dependence of the extent of such transitions on the intensity of the actinic beam. Removal of O_2, as illustrated by the results presented in Fig. 5, decreases the ability of the actinic beam to drive the cells from State 2 to State 1 under light-limiting conditions.

The rapid changes in electron flux occurring on the addition or removal of the actinic beam can, for reasons discussed below, give rise to oscillations in the redox state of the PQ pool that are reflected in the fluorescence changes associated with state transitions (see Figs. 6 and 7 for examples). These oscillations are most commonly seen in the course of the State-1-to-State-2 transition, but can also occur during the State-2-to-State-1 transition. They too are normally suppressed by the changes occurring as the cells go anaerobic.

Decreasing the rate of respiratory electron flow into the PQ pool by lowering the temperature of the algal cells gives rise to a set of changes that are closely related to those seen in anaerobic cells. As the temperature is lowered, the rate of the state transitions decreases (Fig. 7). At the same time, the value of F_2 tends to increase and that of $\Delta F/F_2$ to decrease (Table II). The slower transitions seen at low temperatures appear to be reflections of purely kinetic factors [16,18,46]. The changes in the value of $\Delta F/F_2$, however, are again due to increases in the value of F_2 brought about by the interference of the measuring beam. The true value of F_2, corresponding to the fully dark-adapted state, can readily be determined either by adding glucose/glucose oxidase to the samples to block electron flow to cytochrome oxidase, and hence accelerate the reduction of PQ, or by equilibration in the absence of the measuring beam (not shown). Measurements of the intensity dependence of State-1 adaptation at different temperatures presented in Fig. 8 clearly indicate that much lower light intensities are required to compensate for the reduced respiratory electron flow into the PQ pool at low temperatures explaining

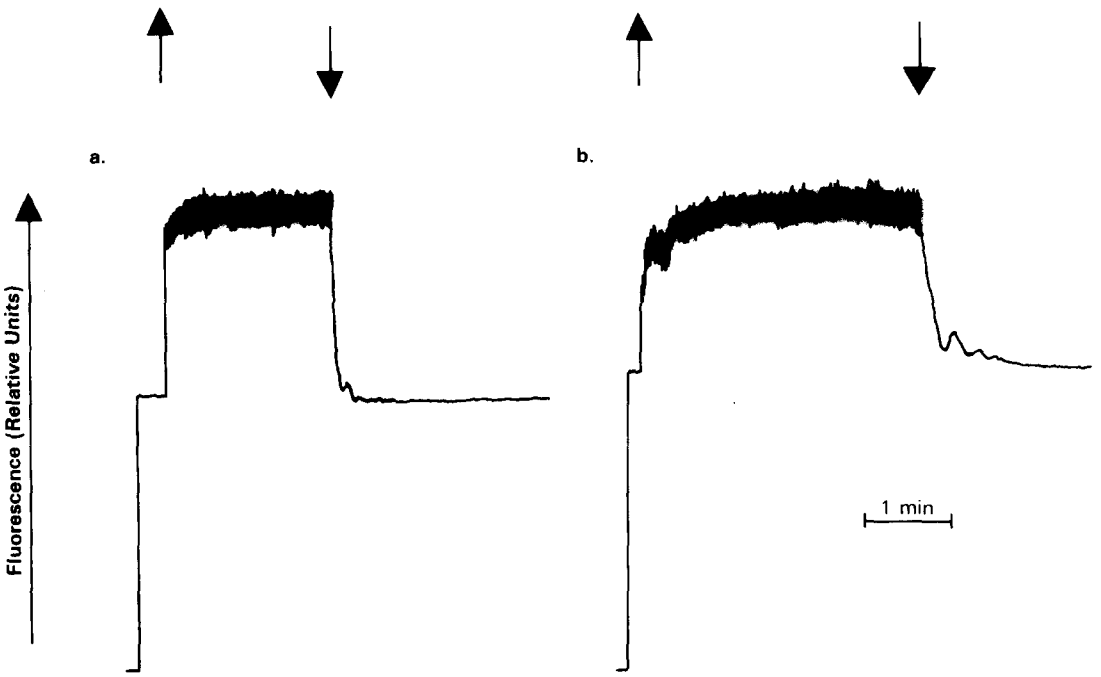

Fig. 7. Traces showing the effect on the fluorescence transients associated with State 1/State 2 transitions of lowering the measuring temperature of the samples from (a) 40 °C to (b) 27 °C.

TABLE II

VARIATION IN MEASURED VALUE OF $\Delta F/F_2$ WITH DECREASING TEMPERATURE

Temperature	F_1	F_2	$\Delta F/F_2$
40	61.0	36.0	0.694
34	61.5	37.5	0.640
27	60.5	40.0	0.513

the enhanced sensitivity of the samples to the measuring beam under these conditions.

Light-dependent inhibition of respiration

Respiratory electron flow in DCMU-poisoned blue-green algae is inhibited by exposure to light [47]. This inhibition is thought to reflect competition between PS I and cytochrome oxidase for electrons passing through the PQ pool. If this is the case, exposure of the algae to the actinic beam is itself likely to alter the pattern of electron flow through the PQ pool. In order to check this point, we compared the intensity dependencies of the light-induced inhibtion of respiratory electron flow and the extent of State-1 adaptation in our samples under similar conditions. The results of these measurements are presented in Fig. 9. They indicate that the intensity dependence of the two phenomena are almost identical confirming the view that there is competition for electrons between O_2 and PS I and that State 1/State 2 transitions in blue-green algae are directly influenced by the redox state of the PQ pool.

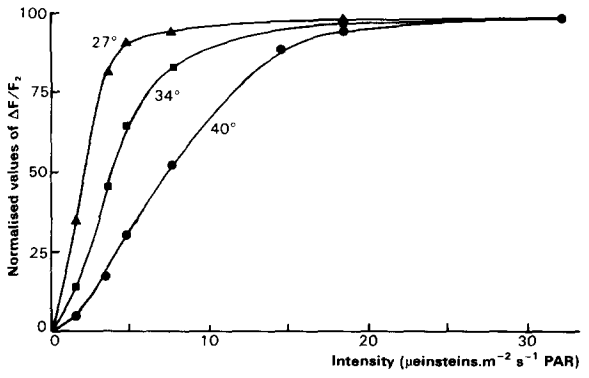

Fig. 8. Plot showing the dependence of the normalised values of $\Delta F/F_2$ on the intensity of the actinic beam for DCMU-poisoned *Anacystis* measured at 40 °C (●), 34 °C (■) and 27 °C (▲).

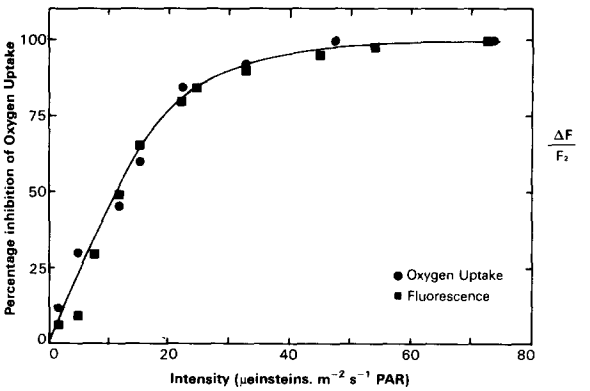

Fig. 9. Comparison of the dependencies of the inhibition of oxygen uptake, and values of $\Delta F/F_2$, on the intensity of the actinic beam for a sample of DCMU-poisoned *Anacystis*.

Discussion

Two main areas of discussion arise from the results reported in this investigation. The first concerns the changes in the pathway of excitation energy distribution associated with State 1/State 2 transitions and the second the intersection of the respiratory and photosynthetic pathways in blue-green algae and its consequences in terms of State 1/State 2 adaptation. These will be dealt with in turn.

Low-temperature emission spectra measurements performed on red and blue-green algae adapted to State 1 and State 2 prior to freezing indicate that an increased fraction of absorbed light reaches PS I in State-2-adapted as compared to State-1-adapted cells [2,6,9,27,29]. Two very different models have been proposed to account for these changes. Biggins et al. [30] are of the opinion that they reflect a decreased spillover of excitation energy from PS II to PS I in State 1 following conformational changes in the thylakoid membrane associated with localised electrical changes brought about by proton fluxes generated by cyclic electron transport. Allen et al. [19], in contrast, favour the idea that it reflects a direct exchange of phycobilisomes between the two photosystems.

If State 1/State 2 transitions were to involve a re-distribution of phycobilisomes, this should be reflected in differences in the fate of excitation energy absorbed in the phycobilisomes and the chlorophyll cores of PS II. Depending on the state of the algae, energy absorbed within the phycobilisome would be expected to be diverted to the PS I or PS II reaction centre, while energy absorbed in Chl a_{II} would be expected to be passed to the PS II reaction centre independent of the state of the algae. The room temperature emission spectra for State 1 and State 2 measured for excitation at 430 and 570 nm presented in Fig. 2 indicate that similar fluorescence yield changes occur for absorption by phycocyanin and Chl a_{II} confirming our earlier report [16] that any re-direction of excitation energy from PS II to PS I must be occurring at the level of Chl a_{II} rather than phycocyanin. Analyses of time-resolved fluorescence emission spectra [32] and linear dichroism [33] performed by Biggins and his co-workers agree with this conclusion. The origins of the small changes in phycocyanin fluorescence that accompany State 1/State 2 adaptation are, however, still unclear and the possibility that these are associated with the light-driven phosphorylation of the 18.5 kDa polypeptide reported by Allen and his collaborators [19] cannot be excluded.

The interaction of the respiratory and photosynthetic electron-transport chains of *Anacystis* is clearly demonstrated in the competition that occurs between PS I and cytochrome oxidase for respiratory electrons in DCMU-poisoned cells. This is reflected in the changes in intensity dependence of State-1 adaptation exhibited by anaerobic cells as opposed to aerobic ones (Fig. 5) and cells held at low temperatures as opposed to cells at high temperatures (Fig. 8). The origin of these changes can be readily appreciated by reference to Fig. 10 which illustrates the intersection of the respiratory and photosynthetic electron-transport pathways in blue-green algae.

In the case of anaerobic cells, restriction of electron flow from PQ to O_2 leaves a surplus of electrons in the PQ pool which has to be removed before State-1 adaptation can commence, thus leading to an increase in the threshold level for full adaptation to State 1. The reverse situation prevails for cells held at low temperatures. Lowering the temperature of the cells decreases the rate of respiratory electron flow into their PQ pools, resulting in a decrease in the number of electrons to be removed before adaptation to State 1 can occur. The changes seen for low-temperature cells

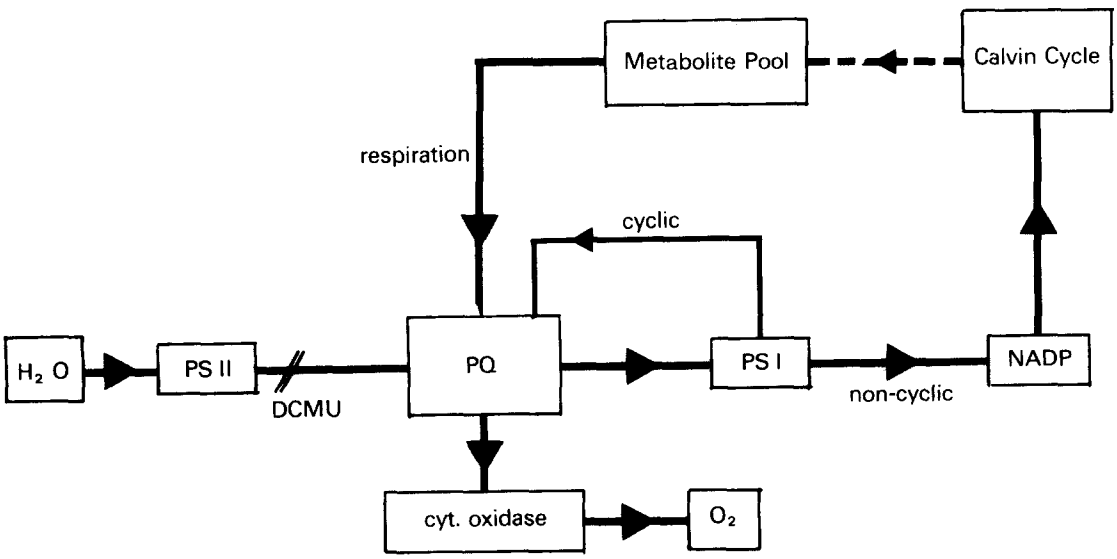

Fig. 10. Diagrammatic representation of the intersection of the respiratory and photosynthetic electron transport pathways of blue-green algae.

are directly analogous to those reported by Mullineaux and Allen [23] following the starvation of *Synechococcus* cells. In their experiments, they showed that decreases in the rate of respiratory electron flow into the PQ pool brought about by exhaustion of the metabolite pool resulted in a decreased capacity of the cells to perform State 1/State 2 transitions. This, as they point out, is due to a partial State-1 adaptation of the starved cells of the type that we have described for older cells, brought about by their measuring beam.

The competitive relationship between PS I and cytochrome oxidase for respiratory electrons flowing through the PQ pool is further underlined by the similarities of the intensity dependence of light-induced inhibition of respiratory O_2 uptake and State-1 adaptation presented in Fig. 9. It is also illustrated in the oscillatory components seen in some of our traces (Fig. 6). The presence of such oscillations appears to be dependent on the relative rates of electron flow into, and out of, the PQ pool. They are abolished on decreasing the rate of electron flow from the PQ pool to O_2 by anaerobosis, but seem to be largely independent of decreases of electron flow into the pool brought about by low temperatures (Fig. 7), suggesting that they probably arise from feed-back of electrons into the PQ pool via cyclic electron transport.

Given the interaction of the respiratory and photosynthetic electron pathways, the observed changes in the intensity dependence of State 1 adaptation can, in principle, be equally well explained in terms of the pigment-protein phosphorylation model of Allen et al. [19] or the cyclic electron-transport models of Biggins et al. [30] and Satoh and Fork [18].

In terms of the phosphorylation model, the explanation is analogous to that adopted by Wollman and Delepelaire [13,14] for explaining their results with anaerobic *Chlamydomonas* cells. Namely, respiratory flow drives the PQ pool to a reduced state in the dark resulting in an increased phosphorylation of a pigment-protein complex that acts in a way akin to that of LHC-II in green algae. Increased turn-over of PS I is then required in order to reset the redox state of the PQ pool to a more oxidised state before State-1 adaptation can occur. Conversely, at lower temperatures, the flow of electrons through the PQ pool is decreased and lower PS I turn-over rates are required to re-set the pool to an oxidised state. The alternative explanation, in terms of the cyclic electron-transport model, is that electrons from the respiratory chain can be used by PS I for non-cyclic electron transport and that, consequently, a smaller fraction of PS I turn-over is associated with cyclic electron transport, and hence State-1 adaptation, in anaerobic cells. At low temperatures, or in starved cells, where respiration rates are low, a correspondingly larger fraction is available for cyclic electron transport.

In conclusion, the results presented in this paper strongly support the idea that State 1/State 2 transitions in blue-green algae are influenced by respiratory electron flow. Our observations do not allow us at this stage to determine whether this is due to changes in the redox level of the PQ pool per se or to changes in the balance between cyclic and non-cyclic electron transport. Measurements of fluorescence emission changes indicate that excitation energy distribution is controlled at the level of the chlorophyll *a* cores of the two photosystems, but the basis of this control remains uncertain.

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