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Mechanism of the light state transition in photosynthesis. IV. Picosecond fluorescence spectroscopy of *Anacystis nidulans* and *Porphyridium cruentum* in state 1 and state 2 at 77 K

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The sequential energy-transfer pathway through the phycobilin pigments to chlorophyll *a* was investigated as a function of the state transition in the cyanobacterium *Anacystis nidulans* and the red alga *Porphyridium cruentum*. The fluorescence decay kinetics of the phycobilin pigments and chlorophyll *a* were determined for cells frozen at 77 K in state 1 and state 2 using a single-photon timing fluorescence spectroscopy apparatus with picosecond resolution. Time-resolved 77 K fluorescence emission spectra were also obtained for both species in state 1 and state 2. In both *A. nidulans* and *P. cruentum* the transition to state 1 was accompanied by a large increase in the apparent fluorescent lifetime of chlorophyll *a* associated with PS II (emission peak at 695 nm). There were smaller increases in the lifetime of the terminal phycobilin emitter (685 nm) in both species and no change in phycocyanin (645 nm) or allophycocyanin (660 nm). Time-resolved spectra showed sequential emission from phycocyanin, allophycocyanin, the terminal phycobilin emitter and chlorophyll *a*. Spectral red shifts were observed with time for all emission peaks with the exception of the terminal phycobilin emitter. In *A. nidulans* this peak showed a small blue shift with time. The results are interpreted as evidence for an effective uncoupling of PS II chlorophyll *a* from subsequent energy transfer to PS I chlorophyll *a* upon transition to state 1. Our recently proposed model for the mechanism of the state transition in phycobilisome-containing organisms is discussed in terms of a decrease in the energy transfer overlap between PS II chlorophyll *a* and PS I chlorophyll *a* in state 1.

Introduction

The distribution of excitation energy between PS II and PS I is regulated during oxygenic photosynthesis [1–4]. Under conditions where PS II is preferentially excited, cells are converted to state 2 and are characterized by a relative decrease in fluorescence emitted by chlorophyll *a* (Chl *a*) associated with PS II and a relative increase in fluorescence emission from Chl *a* associated with PS I. When illumination conditions are altered so that PS I is preferentially excited, cells are converted to state 1, resulting in an increase in PS II fluorescence and a decrease in PS I fluorescence. Corresponding increases in the rate of PS I electron transport in state 2 and PS II activity in state 1 have been demonstrated [2,5–8].

The mechanism of the state transition in higher plants and green algae has been extensively studied and shown to involve a reversible phosphorylation of the Chl *a/b* light-harvesting complex (LHC)

Abbreviations: PS, Photosystem; LHC, light-harvesting chlorophyll *a/b* protein; Chl *a*, chlorophyll *a*.

triggered by the redox state of plastoquinone [9–12]. Transition to state 2 by phosphorylation of spinach thylakoids has been reported to decrease the yield of a 'slow phase' decay component of Chl *a* fluorescence emission and increase the yield of a 'middle phase' decay component [13]. A large-scale lateral migration of LHC in the thylakoid membrane from the appressed regions, rich in PS II, to the stroma regions, rich in PS I, is envisaged to occur following phosphorylation [14–16]. We have recently reported that no phosphorylation event occurs concomitant with the state transition in *Porphyridium cruentum* or *Anacystis nidulans* [17]. Also in contrast to the situation in higher plants and green algae is the requirement for coupled PS I cyclic electron transport for transition to state 1 in red algae and cyanobacteria [17,18]. The state transition in *P. cruentum* has previously been reported to result from a change in the rate of energy transfer from PS II associated pigments to PS I Chl *a* [4]. We have proposed that a small conformational change in the thylakoid decreases the energy-transfer rate from PS II to PS I upon transition to state 1 in phycobilisome-containing organisms [17]. We suggested this conformational change be driven by local electrostatic interactions contributed to by local gradients of protons and counterions and, or changes in redox state of charged electron carriers.

The energy-transfer pathway through the phycobilin proteins has been studied in vivo and in vitro by picosecond fluorescence determinations in both red algae and cyanobacteria [19–23]. The pathway for the transfer of excitation energy in the phycobilin-Chl *a* system has been shown to follow the pattern, phycoerythrin → phycocyanin → allophycocyanin → Chl *a*, as originally proposed by Tomita and Rabinowitch [24] and Grabowski and Gantt [25,26]. To date, there has been no report of energy-transfer characteristics on a picosecond time scale associated with the state transition in the phycobilin-Chl *a* system. The purpose of this investigation was to determine if the changes in energy transfer characteristics in *P. cruentum* and *A. nidulans* in state 1 and state 2 are compatible with the small conformational change we propose to occur during the state transition in phycobilisome-containing organisms. Our data indicate that the transition to state 1 results in an uncoupling of Chl *a* associated with PS II from energy transfer to PS I Chl *a*. Possible changes in local pigment environment between the Chl *a* associated with PS II and PS I are discussed with respect to a small conformational change accompanying the state transition. The data are consistent with the model we have recently proposed [17].

Methods

The red alga *P. cruentum* and the cyanobacterium *A. nidulans* were grown autotrophically at a light intensity of 25 $\mu E \cdot m^{-2} \cdot s^{-1}$ on the enriched salt water medium F/2 of Guillard and Ryther [27] and medium C of Kratz and Myers [28], respectively. Cells at the late log growth phase were harvested by centrifugation and resuspended at a Chl-*a* concentration of 20 $\mu g \cdot ml^{-1}$ for *A. nidulans* and 10 $\mu g \cdot ml^{-1}$ for *P. cruentum*. The state transition was induced in *A. nidulans* by illumination of the cells in light 1 (Corning 5-60 blue filter) at 20 $\mu E \cdot m^{-2} \cdot s^{-1}$ for 5 min or light 2 (590 nm from the dye laser) at 10 $\mu E \cdot m^{-2} \cdot s^{-1}$ for 5 min. All results obtained for *A. nidulans* brought to state 2 by illumination were identical to those found with cells dark-adapted for 10 min. In *P. cruentum* the transition to state 1 was induced by the same conditions as for *A. nidulans*, and the transition to state 2 was accomplished with a combination of Corning 3-69 and Corning 4-96 filters at 50 $\mu E \cdot m^{-2} \cdot s^{-1}$. In all cases the cells were illuminated in 100 μl capillary tubes and immediately following illumination plunged into liquid N_2. We found no differences between samples frozen in the light or those frozen in the dark 1–2 s after illumination. Samples were illuminated by the measuring laser pulses for at least 2 min prior to the 2–5 min averaging process to eliminate any possible induction effects. All fluorescence determinations were performed at 77 K.

The picosecond laser system utilized a Spectra Physics 171 mode-locked argon ion laser with a Spectra Physics 375 dye laser and Spectra Physics 344 cavity dumper operated at 4 MHz. The trailing pulses were further decreased by two orders of magnitude with a Pockels cell chopper. The dye laser was operated at 590 nm for *A. nidulans* and 570 nm for *P. cruentum* and the duration of a

single pulse was less than 30 ps. The intensity of incident light at the sample was $1.5 \cdot 10^7$ photons · cm^{-2} per pulse or 1 $\mu E \cdot m^{-2} \cdot s^{-1}$ continuous.

Fluorescence emission was dispersed by a Spex Industries 3/4 m spectrometer and detected by a Hamamatsu R129U-01 microchannel plate photomultiplier cooled to −30°C. The single-photon timing apparatus utilized a Comlinear CLC100 preamplifier, a Philips Scientific 715B constant fraction discriminator, an Ortec 457 time to amplitude converter with an IBM phycocyanin based multichannel scaler. A Mitusbishi PD1302 fast avalanche photodiode was used to detect the laser pulse for the reference channel. Fig. 1 shows the equipment response at 590 nm. The equipment response has a full width at half-maximum of 160 ps. The 1/e rise-time is 37 ps and the fall time 67 ps.

The spectrometer was scanned under computer control to collect fluorescence spectra with a step size of 1 nm and a resolution of 0.5 nm. Signal averaging was used to improve the signal-to-noise ratio. Time-resolved spectra were collected with the same apparatus by summing the counts over different time windows after each laser pulse. In this way complete spectra could be collected simultaneously, precluding any instrumental or sample drifts possible in a sequential sample scheme.

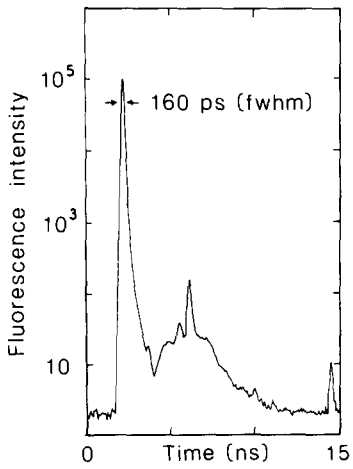

Fig. 1. Equipment response to the mode-locked dye laser pulse at 590 nm. The 1/e rise-time is 37 ps and the 1/e decay-time 67 ps. Full width at half maximum (fwhm) is 160 ps. Fluorescence intensity has been expressed as counts per channel.

Results

All fluorescence determinations were made on cells frozen into state 1 or state 2 at 77 K. In Fig. 2 fluorescence emission spectra of *A. nidulans* are shown for cells in state 1 and state 2. These cells show a typical response to the transition to state 1, with greatly increased emission at 685 and 695 nm and a very small increase at 715 nm when the spectra are normalized to the 650 nm peak. In some samples the fluorescence emission at 715 nm was slightly higher in state 2 than state 1. The pigments contributing to the observed peaks are phycocyanin and allophycocyanin at 650 nm, allophycocyanin-B, the phycobilisome core-membrane linker polypeptide and possibly some short-wavelength Chl *a* associated with PS II at 685 nm, Chl *a* associated with PS II at 695 nm and Chl *a* associated with PS I at 715 nm [19,29–31]. Fluorescence emission spectra of *P. cruentum* for cells frozen in state 1 and state 2 are shown in Fig. 3. As in *A. nidulans* the typical increase in fluorescence at 685 and 695 nm was observed on transition to state 1. The pigments contributing to the emission peaks are phycocyanin at 645 nm, allophycocyanin at 660 nm, allophycocyanin-B, the phycobilisome core-membrane linker polypeptide and possibly some short wavelength PS II Chl *a* at 685 nm, PS II Chl *a* at 695 nm and PS I Chl *a* at 715 nm [19,29,30,32,33].

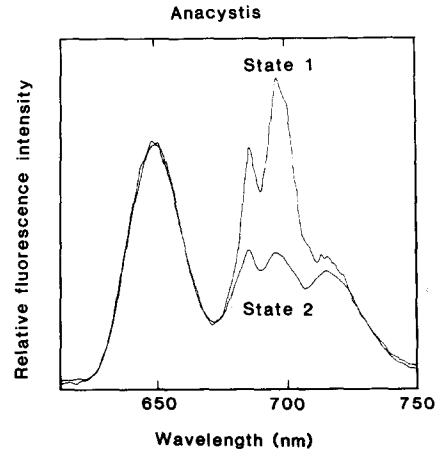

Fig. 2. 77 K fluorescence emission spectra of *A. nidulans* in state 1 and state 2. Fluorescence emission has been normalized to the 650 nm peak and is shown on a linear scale.

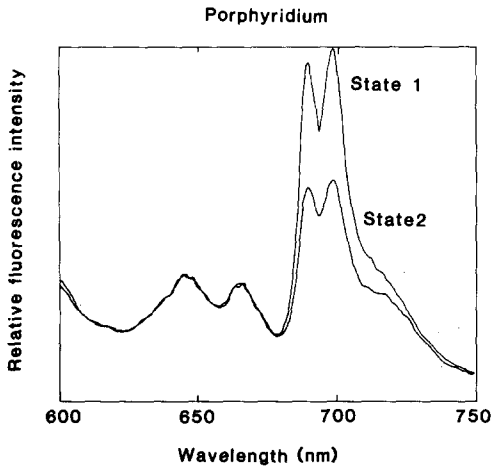

Fig. 3. 77 K fluorescence emission spectra of *P. cruentum* in state 1 and state 2. Fluorescence emission has been normalized to the 645 nm peak and is shown on a linear scale.

The fluorescence decay kinetics of the *A. nidulans* cells in Fig. 2 are shown in Fig. 4 for the peaks observed at 650 nm (trace a), 685 nm (trace b), 695 nm (trace c) and 715 nm (trace d). These curves have not been deconvolved from the equipment response shown in Fig. 1. The observed decay kinetics are the sum of individual pigment decays; however, spectral overlap at 77 K is not as large as that observed at room temperature and a relatively high degree of resolution between the 685, 695 and 715 nm emission was apparent. As previously reported for *A. nidulans* at room temperature [19,21] we found the fluorescence decay kinetics at 77 K to depend strongly on the emission wavelength. The initial decay rates decrease with increasing wavelength with the exception of the emission at 695 nm for cells in state 1, which

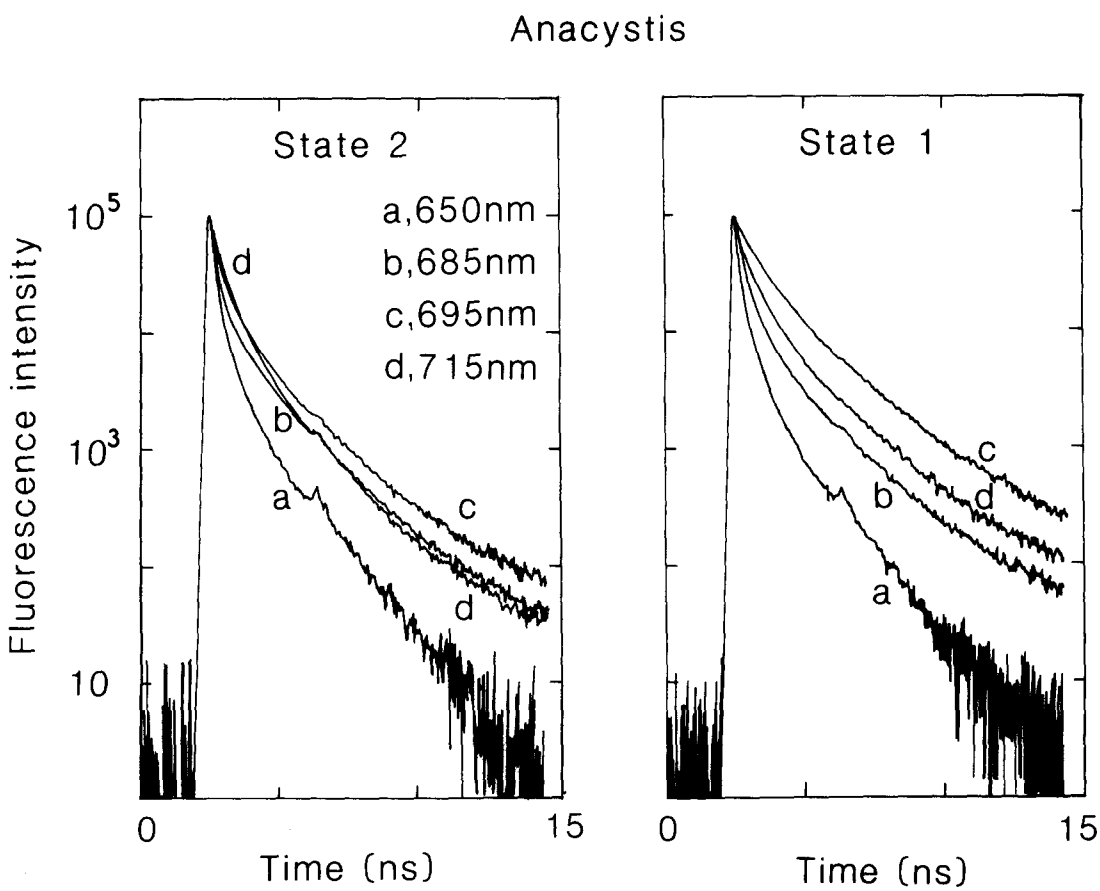

Fig. 4. 77 K fluorescence decay transients of *A nidulans* for cells in state 1 and state 2. Traces labelled 'a' are for emission at 650 nm (phycocyanin and allophycocyanin), traces 'b' for 685 nm (terminal phycobilin emitter), traces 'c' for 695 nm (PS II Chl-*a*) and traces 'd' for 715 nm (PS I Chl *a*). Fluorescence intensity has been expressed as counts per channel, curves have been normalized to a maximum of $1 \cdot 10^5$ counts.

had the slowest initial decay rate. At 650 and 685 nm the decay appeared predominantly biphasic becoming increasingly complex at 695 and 715 nm. Although the initial decay rate at 715 nm in state 2 was slower than that at 695 and 685 nm, longer lived components had faster decay rates and trace d (715 nm) is seen to cross both trace c (695 nm) and trace b (685 nm).

Decay kinetics for *P. cruentum* are shown in Fig. 5 for emission at 660, 685, 695 and 715 nm for cells in state 1 and state 2. As for *A. nidulans* the initial decay rates decrease with increasing emission wavelength. The decays at shorter wavelengths appear predominantly biphasic and increase in complexity at 695 and 715 nm. The decay at 645 (not shown) was very similar to that at 660 nm with a slightly faster initial decay rate. The decays at wavelengths shorter than 660 nm (not shown) show increasing yields of a slow component which had a simple exponential decay with a 1/e lifetime of 2.5 ns. This was also observed by Yamazaki et al. [19] in *P. cruentum* at room temperature and attributed to phycoerythrin which was not participating in energy transfer to other biliproteins. The lifetimes of the phycobilin peaks we observed at 77 K are close to the spectrally deconvolved lifetimes reported by Yamazaki et al. for both *P. cruentum* and *A. nidulans* at room temperature [19].

In both organisms we found the largest change in initial decay rate as a function of the state transition to occur at 695 nm. The two traces are compared in Fig. 6 for both *A. nidulans* and *P. cruentum*. The initial decay rate changes 1/e decay

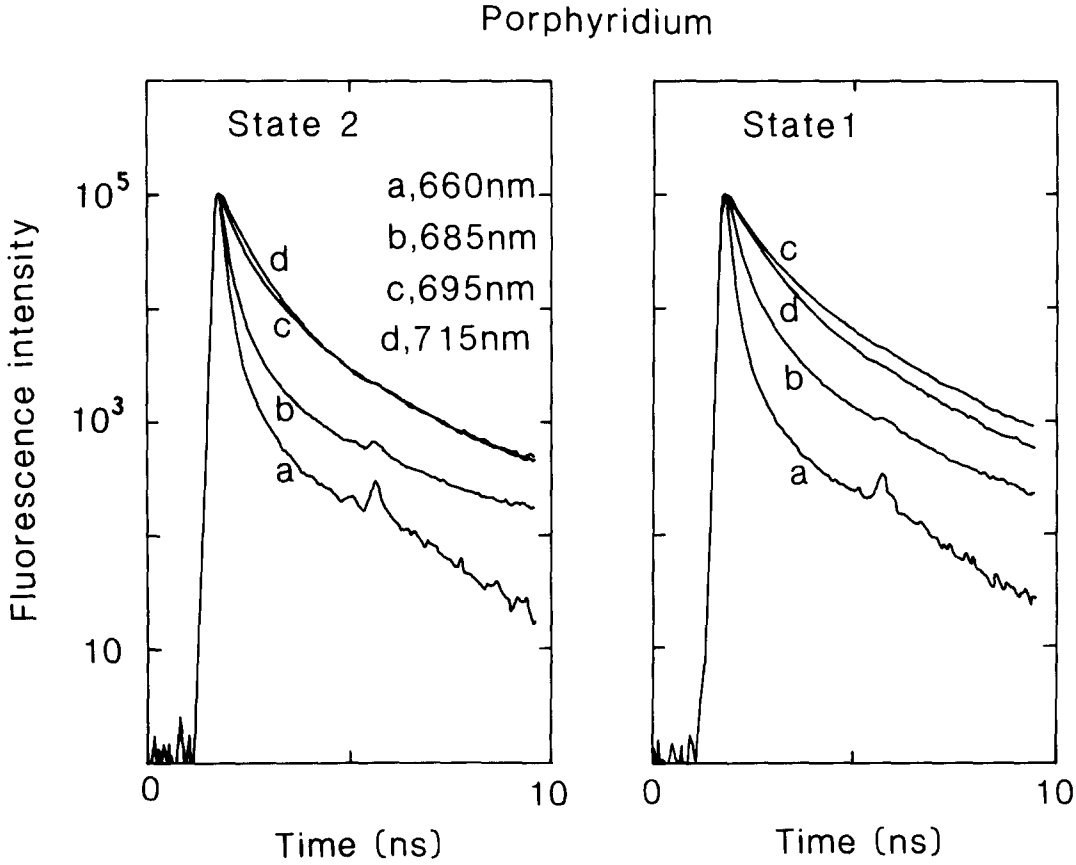

Fig. 5. 77 K fluorescence decay transients of *P. cruentum* for cells in state 1 and state 2. Traces labelled 'a' are for emission at 660 nm (allophycocyanin), traces 'b' for 685 nm (terminal phycobilin emitter) traces 'c' for 695 nm (PS II Chl *a*) and traces 'd' for 715 nm (PS I Chl *a*). Data presentation as in Fig. 4.

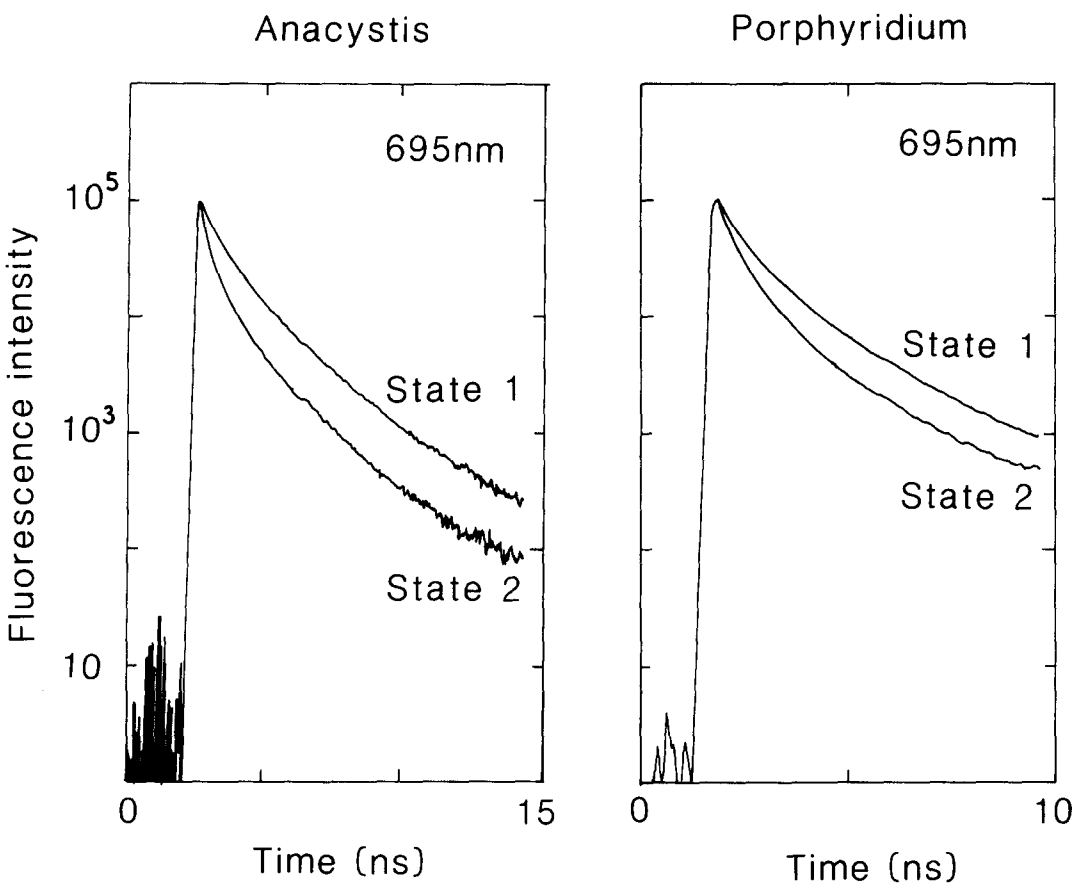

Fig. 6. A comparison of the 77 K fluorescence decay transients of *A. nidulans* and *P. cruentum* in state 1 and state 2 at 695 nm (PS II Chl *a*). Data presentation as in Fig. 4.

time from 330 ps in state 2 to 910 ps in state 1 in *A. nidulans* and from 450 to 720 ps in *P. cruentum*. Longer-liver components of the decay were not affected by the state transition. A smaller change in initial apparent lifetime was also observed at 685, from 220 to 320 ps on transition from state 2 to state 1 in *A. nidulans* and from 200 to 280 ps in *P. cruentum*. The initial decay lifetimes for all of the peaks are summarized in Table I where it is seen that no other emission peaks undergo large changes in either organism as a function of the state transition. All reported lifetimes in Table I have been deconvolved from the equipment decay which has a lifetime of 67 ps.

In Fig. 7 time-resolved fluorescence emission spectra for *A. nidulans* in state 1 and state 2 are shown for the time windows, 0–0.49, 0.49–0.99, 0.99–1.49, 1.49–2.47 and 3.46–4.45 ns. The spectra are normalized to peak emission. In both states emission from the short wavelength peaks (approx. 650 and 685 nm) predominates in the early time intervals and emission from the longer-wavelength peaks predominate at later intervals. The major difference between states being the complete dominance of the 695 nm peak at later intervals for cells in state 1. The emission maximum of the short wavelength peak was red shifted at later intervals from an initial maximum near 650 nm to a final maximum at 657 nm in both states. In the initial time interval (0–0.49 ns) a shoulder is detectable on the sort wavelength side of this peak which would correspond to the peak emission of phycocyanin at 645 nm. The maximum at later time intervals corresponds to the peak emission of allophycocyanin at 660 nm. The Chl-*a* emission peaks at 695 and 715 nm also exhibit red shifts at

TABLE I

LIFETIME (1/e) OF THE INITIAL DECAY COMPONENTS OF THE FLUORESCENCE EMISSION PEAKS IN *A. NIDULANS* AND *P. CRUENTUM*

The decay times are accurate to within ±10%.

Maximal emission (nm)	Pigment	Lifetime (1/e) (ps)			
		A. nidulans		*P. cruentum*	
		State 2	State 1	State 2	State 1
645	phycocyanin			100	105
650	phycocyanin + allophycocyanin	180	170		
660	allophycocyanin			110	115
685	terminal phycobilin emitter	220	320	200	280
695	PS II Chl *a*	330	910	450	720
715	PS I Chl *a*	500	500	600	730

later time intervals in both states indicating inhomogeneity in the Chl *a* population of both PS II and PS I. In contrast, the 685 nm peak shows a small blue shift at later time intervals in state 2. In state 1 the 685 nm peak appears stationary; however, the small blue shift would be masked by the concomitantly large increase in the 695 nm peak at later intervals. Although spectral shifts occur with time, there was no indication of a spectral shift resulting from the state transition.

In Fig. 8 time resolved spectra for *P. cruentum* in state 1 and state 2 are shown for the time windows 165–330, 330–500, 500–660, 660–990 and 1490–4600 ps. As in *A. nidulans*, a progressive shift towards emission of longer wavelengths at later time intervals was seen. The major difference occurring as a function of the state transition was

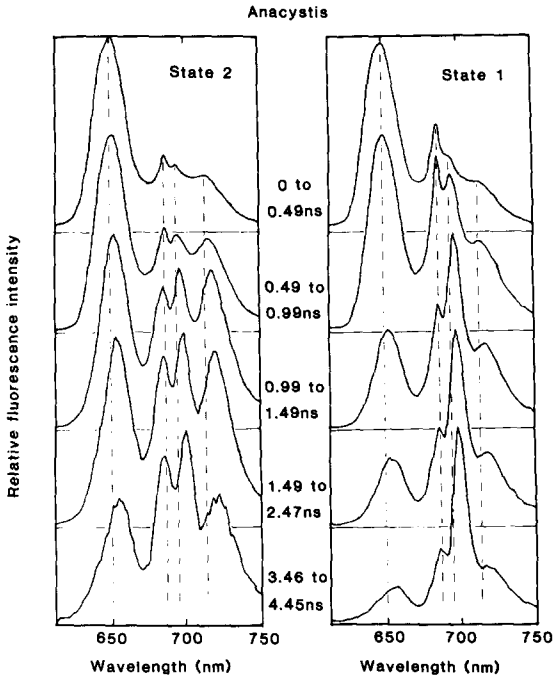

Fig. 7 Time-resolved 77 K fluorescence emission spectra of *A. nidulans* in state 1 and state 2. The curves have been normalized to the peak emission and are shown on a relative linear scale.

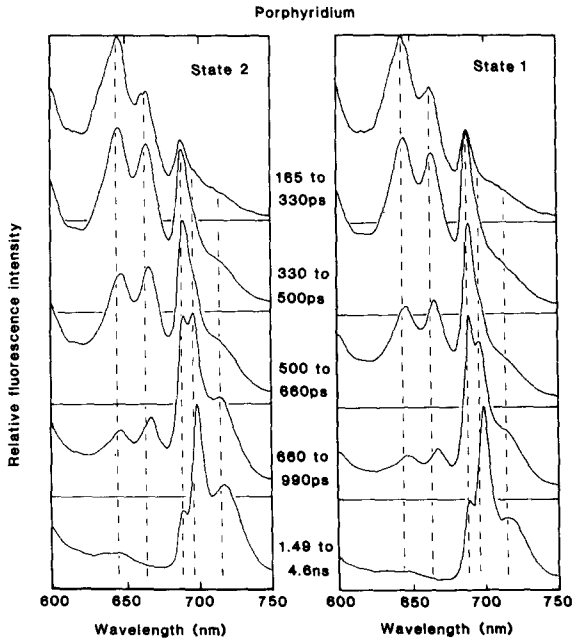

Fig. 8. Time resolved 77 K fluorescence emission spectra of *P. cruentum* in state 1 and state 2. Data presentation as in Fig. 7.

the predominance of the 685 and 695 peaks with respect to the 645, 660 and 715 nm peaks at later time intervals in state 1. The separation of the 695 nm peak emission at later time intervals was not as striking as in *A. nidulans*. The emission peaks at 645 and 660 nm red shift, as does the 695 nm peak. A slight red shift was also indicated at 715 nm, but due to overlap with PS II Chl *a* emission it is hard to determine the extent. The 685 nm peak did not shift appreciably. There were no spectral shifts induced by the state transition.

Discussion

The data presented show the initial decay lifetime of fluorescence emission from PS II Chl *a* to be 2.8 times longer for cells in state 1 than those in state 2 in *A. nidulans* and 1.6-times longer in *P. cruentum*. In comparison to this difference exhibited at 695 nm the decay lifetime was only 1.4-times longer in state 1 for the terminal phycobilin emitter at 685 nm in both species. The change at 685 nm may be contributed to by spectral overlap with the 695 nm peak or the presence of some short wavelength PS II Chl *a*. No difference was observed in the decay kinetics at 650 nm in *A. nidulans*, where both phycocyanin and allophycocyanin contribute to fluorescence emission, or at 645 nm (phycocyanin) and 660 nm (allophycocyanin) in *P. cruentum*. These results show that PS II Chl *a* is actively involved in the mechanism of energy redistribution accompanying the state transition in *A. nidulans* and *P. cruentum*. In state 1 the long initial decay lifetime at 695 nm may indicate that much of PS II Chl *a* is uncoupled from any further energy transfer to PS I Chl *a*. An increase in the energy transfer rate from PS II Chl *a* to PS I Chl *a* in state 2 would be expected to cause a delay in the rise of PS I Chl *a* fluorescence in state 2. A delay in the rise of emission at 715 nm directly corresponding to the decay at 695 nm was not observed. However, it was not possible with our apparatus to determine confidently if a change in rise-time less than 30 ps occurred.

The time-resolved 77 K fluorescence emission spectra support previously reported results for *A. nidulans* and *P. cruentum* at room temperature that show a successive emission from phycocyanin, allophycocyanin and Chl *a* [19,21]. This and the similarities in decay rates reported at room temperature [19] to those in the present study at 77 K indicate that rapid freezing of the cells to 77 K does not significantly alter the energy-transfer characteristics from the phycobilins to Chl *a*. By using very low intensity excitation light at 77 K in the present study, it was possible to observe differences in energy-transfer characteristics as a function of the state transition without interference from any electron-transport-dependent quenching state of the reaction centers.

With the resolution obtained at 77 K it was possible to detect red shifts in the peaks at 695 and 715 nm in both species and red shifts at 645 and 660 nm in *P. cruentum* as well as the previously reported shift at 650 nm in *A. nidulans* [19]. The shifts at 695 and 715 nm indicate an inhomogeneity in the Chl *a* associated with both PS II and PS I which may be due to subpopulations of Chl *a* involved in energy transfer from PS II to PS I. The red shifts observed for the phycocyanin and allophycocyanin peaks in *P. cruentum* are not surprising as the local environment of any particular phycocyanin or allophycocyanin will depend on its location in the phycobilisome super structure [30]. This is exemplified by the shift of the 650 nm peak in *A. nidulans*. The rod structures of the *A. nidulans* phycobilisomes have been shown to contain three different phycocyanin proteins with fluorescence emission maxima at 643, 648 and 652 nm, and the phycobilisome core contains two different allophycocyanin proteins with emission maxima at 660 and 662 nm [30]. The observed red shift of the 650 nm peak must result from energy transfer through these pigments. Most interesting was the slight blue shift observed at 685 nm in *A. nidulans*, indicating the presence of some short-wavelength component contributing to this peak that is apparently not involved in the main energy-transfer pathway. This supports the suggestion that some far-emitting allophycocyanin is not involved in the main energy-transfer pathway in *A. nidulans* [19,21]. Both allophycocyanin-B and the 75 kDa core-membrane linker protein have reported emission peaks at 680 nm [30,34], so it is not readily apparent which of these two pigments is causing the blue shift of our 685 nm peak, or if the situation is complicated by the presence of some short-wavelength Chl *a* associated with PS

II. In *P. cruentum* the 685 nm peak remained stationary. Although spectral overlap between the 685 and 695 nm peaks is somewhat greater in *P. cruentum* than in *A. nidulans* and may account for the observed differences between the species, it is possible that these changes reflect differences in energy-transfer characteristics from allophycocyanin-B and the phycobilisome core-membrane linker polypeptide to PS II Chl *a*, with a tighter coupling apparent between these pigments in *P. cruentum* [19].

In summary, the data presented support our recently proposed model [17] for the mechanism of the state transition in phycobilisome-containing organisms. The transformation to state 1 in both *A. nidulans* and *P. cruentum* decreases the efficiency of energy transfer from PS II to PS I associated Chl *a*. We believe this to be accomplished by a small conformational change of the thylakoid membrane. It is not necessary to invoke large-scale changes in membrane topography to explain the increase in initial decay rate of PS II Chl *a* observed in state 1. The energy-transfer efficiency is dependent on intrinsic fluorescence lifetime, the overlap integral, orientation and distance between the pigment molecules. The distance dependence for the excitation-transfer rate is $1/R^6$ for the weak intermolecular coupling [35,36], believed predominant in antennae Chl *a* resonant energy transfer. Thus, a small change in distance between PS II Chl *a* and PS I Chl *a* would greatly affect energy transfer efficiency. A change in bulk orientation of PS II Chl *a* or PS I Chl *a* could also effect such a change. The latter possibility is presently under investigation.

Acknowledgements

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