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FLUORESCENCE DECAY KINETICS IN PHYCOBILISOMES ISOLATED FROM THE BLUE-GREEN ALGA *SYNECHOCOCCUS* 6301 *

GEORG W. SUTER, PAOLA MAZZOLA, JOACHIM WENDLER and ALFRED R. HOLZWARTH

Max-Planck Institut für Strahlenchemie, Stifstrasse 34–36, 4330 Mülheim an der Ruhr (F.R.G.)

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The picosecond fluorescence and energy-transfer kinetics of isolated phycobilisomes from *Synechococcus 6301* were studied under low intensity excitation. Different combinations of excitation and emission wavelengths were used in order to monitor selectively the fluorescence of the pigments phycocyanin and allophycocyanin. The relatively long overall energy-transfer time of 120 ps from the phycocyanin rods to the allophycocyanin-core is rationalized in terms of the special structure of the rods being built up of several phycocyanin hexamers in this alga species. The fluorescence lifetime of the terminal chromophores in the core was determined to be 1.8–1.9 ns depending on the excitation wavelength. A fast decay component of 20 ± 10 ps which is most prominent at short emission wavelengths is assigned to arise mainly from energy transfer within the C-phycocyanin-units from 'sensitizing' to 'fluorescing' chromophores.

1. Introduction

The light harvesting antenna system in red and blue-green algae (cyanobacteria) consists of highly organized phycobiliprotein aggregates, so-called phycobilisomes, which are linked to the outer surface of the thylakoid membrane. The primary steps of photosynthesis in these organisms involve energy-transfer processes within the phycobilisomes and from the phycobilisomes to chlorophyll *a* complexes located in the membrane [1]. Both static measurements [2–4] as well as time-resolved spectroscopy [5–14] have been applied to study these processes. They take place on a picosecond time scale, which ensures a high transfer efficiency. Parallel to the development of spectroscopic techniques providing a time-resolution of a few picoseconds, a considerable amount of work has been dedicated to the detailed analysis of the transfer kinetics and pathways.

The first picosecond measurements related to phycobilisomes have been reported by Porter et al. [14] on intact red algae. Brody et al. [5,6] have explored the energy transfer in intact cells of *Porphyridium cruentum* and *Anacystis nidulans* using a streak camera and very recently Yamazaki et al. reported time-resolved spectra from intact cells of *A. nidulans* and *P. cruentum* recorded on a single-photon-timing apparatus [7].

The fluorescence relaxation kinetics of isolated phycobilisomes from *P. cruentum* [8,9], *R. violacea* [10], *Nostoc* sp. [11], and *Mastigocladus laminosus* [12] have been investigated. The present work deals with the energy transfer kinetics in phycobilisomes isolated from *Synechococcus 6301* (formerly called *A. nidulans*) probed by the picosecond fluorescence technique. The phycobilisomes of *Synechococcus 6301* are of the hemidiscoidal type and contain no phycoerythrin, i.e., they consist only of

* Parts of these results have been presented at the Workshop on 'Molecular Structure and Function of Light-Harvesting Pigment-Protein Complexes and Photosynthetic Reaction Centers', Zürich, July, 1983.
Abbreviation: MCA, multichannel-analyzer.

the core composed of four hexameric units of allophycocyanin and, attached to it, six rods of variable length formed by C-phycocyanin hexamers [15–17]. In addition, allophycocyanin-B [18,19] and a coloured 75 kDa linker protein [20] have been identified and proposed as terminal acceptors within the energy-transfer cascade of the phycobilisomes. Both the latter pigments show strongly red-shifted absorption and emission bands with respect to allophycocyanin. On one hand from the presence of only two major types of pigments simpler kinetics are expected than in more complex phycobilisomes. On the other hand, the heterogeneity introduced by the possible variance in the length of the C-phycocyanin rods [21–23] may blur the main features of the kinetics to some extent. So far, this system has been characterized only by pump-probe experiments: Gillbro et al. [13] found double exponential decays by transient absorption with lifetimes of 13 and 84 ps, both at 600 and 620 nm monitoring wavelengths.

Although somewhat limited in time resolution as compared to pump-probe experiments, single-photon-timing fluorescence measurements should provide important supplementary information due to the excellent sensitivity and the unsurpassed dynamic range of this technique. Moreover, our method allows to excite and detect the different pigments selectively.

2. Material and Methods

Synechococcus (Anacystis nidulans) was obtained from the Göttingen alga collection. Algae grown in continuous white fluorescent light (Osram) at 30 °C were washed and suspended in phosphate buffer solution to 120 mg wet wt. per ml. They were broken in a French press at $1.4 \cdot 10^7$ Pa and treated with 1% Triton X-100 for 30 min in 0.65 M phosphate buffer at pH 8.0. The large cell particles were removed by centrifugation (1 h at 21000 rpm, JA21 rotor). The supernatant was layered on a continuous sucrose density gradient (0.2–0.9 M; 0.75 M sodium-potassium-phosphate buffer, pH 8.0) and run in the ultracentrifuge (16 h at 24000 rpm, SW28 rotor). Different fractions of the phycobilisomes-containing band were collected to get samples with an optical density of 3–4 per cm at 622 nm. Presumably due to partial dissociation of the phycobilisomes [24,25] inconsistent and irreproducible decay curves were obtained when fractions with a high optical density, i.e., from the center of the band, were taken and diluted shortly before the measurement.

The absorption spectra were measured on a Perkin Elmer model 320 ultraviolet VIS spectrophotometer. To check the integrity of the phycobilisomes static fluorescence and excitation spectra were recorded in a 1 mm cuvette on a computer controlled Spex Fluorolog spectrometer before and after the lifetime experiments [26]. All measurements were carried out at room temperature (21–25 °C) within 12 h after the isolation. During the laser experiments the solution was passed slowly (0.3 ml/min) through a flow cell of 1.5 mm optical path length by applying air pressure on the reservoir. By this pumping technique mechanical stress exerted on the phycobilisomes could be avoided as compared to passing the solution through a peristaltic pump. Thus the stability of the phycobilisomes was significantly increased.

For the lifetime measurements, the source of the picosecond pulses was a synchronously pumped and cavity-dumped dye laser system (rhodamine 6G and DCM) with a mode-locked argon-ion laser as the pumping source (Spectra Physics). The fluorescence decay curves were recorded using the single-photon-timing technique [10,27]. The response of the single-photon-timing apparatus had a half-width of 200 ps in most cases and approx. 140 ps in some later experiments. The MCA was set to a channel-width of 10.3 ps. The photon density was below 10^{11} photons/cm^2 per pulse, i.e., low enough to avoid singlet-singlet annihilation effects [11,28,29]. The emission wavelength was selected by a double monochromator with a bandwidth of 4 nm. Anisotropic components in the fluorescence decay were eliminated by magic angle observation of the emission, i.e., the excitation beam was polarized vertically and the emission was monitored through a polarizer set at 54.7 degrees from the vertical axis. The decay curves were analyzed as sums of exponentials in an iterative convolution method. The reduced χ^2-value [30] served as a criterion for the goodness of the fits. In addition, the weighted residuals were plotted and visually checked for deviations from a random distribution. Since at least 20000 counts

were accumulated in the peak channel, the statistical errors of the decay times obtained were always smaller than the variance between different samples.

3. Results

Static measurements

The absorption spectrum, together with the fluorescence and the fluorescence excitation spectra of the phycobilisomes are shown in Fig. 1. The absorption maximum is located at 622 nm and shows a weak shoulder at 575 nm as in the phycobilisomes absorption spectrum given in Ref. 24. The A_{625} : A_{655} ratio varied from 3.1 to 3.5 in different samples. Therefore, according to Yamanaka and Glazer [21], the mean phycocyanin/ allophycocyanin ratio in our phycobilisomes was around 5, i.e., somewhat higher than in their wild-type phycobilisomes. This would correspond to about 3–4 phycocyanin hexamers per rod. The fluorescence spectra obtained upon excitation of phycocyanin or allophycocyanin at 590 nm and 640 nm, respectively, are virtually identical. The emission maximum, a parameter sensitive to dissociation [24] of phycobilisomes, is at 672 nm. Finally, the fluorescence excitation spectrum of the emission at 680 nm was very similar to the

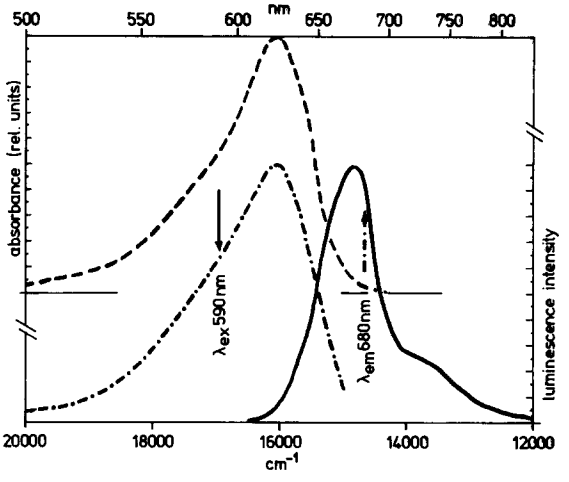

Fig. 1. Absorption (dashed), corrected fluorescence (full), and fluorescence excitation (dashed-dotted) spectra of phycobilisomes from *Synechococcus* 6301. The emission spectrum was the same when exciting at 540 nm, 590 nm and at 620 nm and the excitation spectra of the emission at 640 nm and 680 nm were identical.

TABLE I

ANALYSIS OF THE ISOTROPIC FLUORESCENCE DECAYS FROM *SYNECHOCOCCUS* 6301 IN 0.75 M PHOSPHATE BUFFER, pH = 8.0, AT ROOM TEMPERATURE *

The errors given are those obtained from the variations between several independent preparations. The statistical errors of the decay analysis are smaller than these values.

λ_{ex} (nm)	λ_{em} (nm)	τ_1 (ns)	R_1 * (%)	τ_2 (ps)	R_2 * (%)	τ_3 (ps)	R_3 * (%)
570	590	1.80±0.05	14±2	300–600	11–17	63±15	73±3
570	600	1.83±0.02	16±2	270–400	10–15	80±12	71±2
570	620	1.85±0.02	19±2	300–450	8–12	94±12	70±2
570	640	1.85±0.02	28±2	270–480	4–15	100±20	65±5
570	680	1.90±0.02	86±4	1100±200	14± 4	120±20	−45±8
580	590	1.79±0.05	13±2	650±100	11±2	70±10	76±2
600	620	1.84	17	230	18	70	65
600	640	1.84	28	370	8	101	64
600	680	1.90	88	1200	12	131	−50
620	640	1.85±0.02	28±1	280–560	6–11	104±10	64±2
620	680	1.90±0.04	90±4	1100±250	10± 4	115±20	−52±13
645	680	1.89±0.01	88±1	1000±200	12± 1	120±10	−30±8
660	680	1.84±0.01	92±1	660±100	8± 1	45±10	−21±5
675	685	1.81	100				

* Normalized relative amplitudes.

absorption spectrum of the phycobilisomes. These findings indicate that energy transfer was efficient in our samples.

Lifetime measurements

The fluorescence decays have been measured for a number of excitation and emission wavelengths. The results of the fluorescence decay analysis for all excitation-emission wavelength pairs used are summarized in Table I. The fluorescence decays observed at 590 nm and at 680 nm upon excitation at 580 nm are shown in Figs. 2 and 3, respectively. Although higher concentrations would have resulted in a better stability of the phycobilisomes, the optical density of the samples was kept below 4 per cm at 622 nm. At higher concentrations, reabsorption effects lead to distortions of the decay curves. A sum of three exponentials was required in most cases to obtain a reasonable fit of the experimental decay curves. The error bands given in Table I reflect the good reproducibility of the values obtained from several phycobilisomes samples originating from different independent preparations.

In the emission region from 590 to 640 nm, a short-lived component (60–110 ps) and a component with a lifetime between 1.8 and 1.9 ns were observed in all measurements. The lifetimes of the middle component varied over a range of 230–600 ps. With increasing wavelength the relative amplitude of the component in the nanosecond range

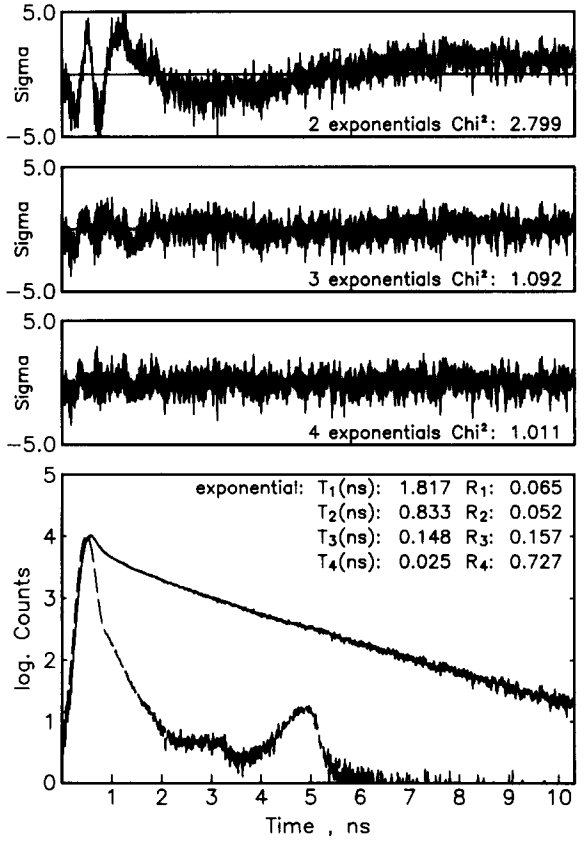

Fig. 2. Fluorescence decay of phycobilisomes from *Synechococcus* 6301 at 590 nm upon excitation at 580 nm. The decay is dominated by short-lived components which are assigned to energy-transfer processes within the C-phycocyanin subunits and from C-phycocyanin to allophycocyanin. Note (Figs. 2 and 3): superimposed on the experimental decay is the fluorescence decay (coincident with the noisy experimental curve) calculated from the best-fit kinetic parameters. Also shown is the semilogarithmic representation of the exciting pulse (- - - - - -). Furthermore, the lifetimes (τ_n) and the relative amplitudes (R_n) of the decay components are given. On top of the decay curve plots of the weighted residuals indicating deviations between fitted and experimental values are shown for four-, three and double-exponential fits.

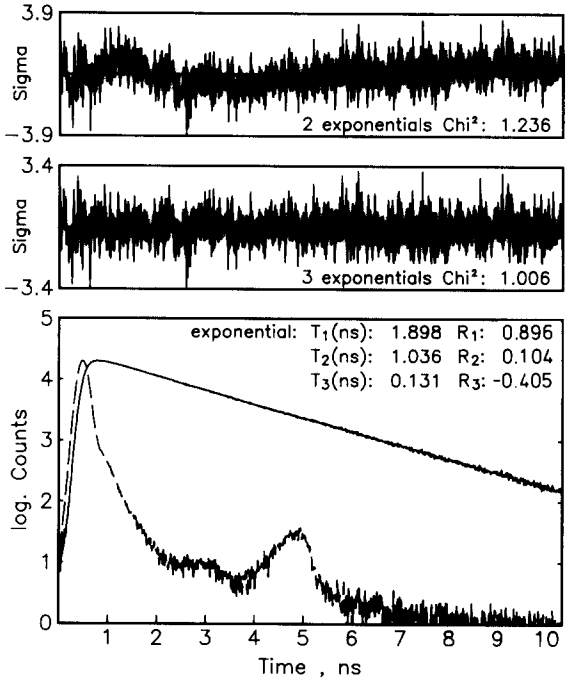

Fig. 3. Fluorescence decay of phycobilisomes from *Synechococcus* 6301 at 680 nm, i.e., near the emission maximum. Excitation at 580 nm (cf. Note Fig. 2).

increased at the cost of the shortest-lived component. Upon excitation in the range from 570 to 645 nm, the 'middle' lifetime at 680 nm was in the range 0.8–1.3 ns and the shortest-lived component appeared as rising term, i.e., with negative amplitude.

4. Discussion

For the analysis of the fluorescence decays of phycobilisomes it is important to keep in mind the complexity of these systems: a typical phycobilisome of *Synechococcus* [15,22] made up of four hexamers of APC and six rods each consisting of three C-phycocyanin hexamers contains more than 300 tetrapyrrole chromophores. Although the conformational variety typical for these chromophores [31] is reduced in the rigid protein surrounding, a considerable heterogeneity within the spectrum of one and the same chromoprotein may be expected: variations in the protein-chromophore interaction may influence the spectroscopic properties of individual chromophores. Additional inhomogeneities may originate from energy-transfer processes: the transfer capability of a particular chromophore is influenced by its spectral properties and its relative position, both to the chromophores of the same protein subunit and to those of the neighbouring units. From these considerations, it is obvious that a sum of a few exponentials may only be an approximate description of the real fluorescence decay of phycobilisomes. However, the general features of the decay curves readily appear in a multiexponential analysis, and the dominating components may be assigned to distinct processes. It should be pointed out, however, that an $\exp(-2At^{1/2})$-function as a kinetic model [14] again did not result in acceptable fits, as has been discussed extensively in an earlier paper [9].

The long-lived nanosecond component

The decay time of the longest-lived component slightly increases with increasing wavelength. Different types of chromophores contributing to this component are responsible for this variation: below 640 nm only C-phycocyanin emits. We therefore ascribe the lifetime of 1.83 ± 0.02 ns to C-phycocyanin which is not involved in energy transfer (i.e., free phycocyanin or otherwise energetically uncoupled phycocyanin). This lifetime is in good agreement with the value of 1.77 ns obtained from phycobilisomes of *Rhodella* [10] upon selective monitoring of the C-phycocyanin emission. It is, however, significantly lower than the lifetime of 2.11 ± 0.08 ns reported for free C-phycocyanin from *Nostoc* sp. [28]. Preliminary results from our laboratory on isolated hexameric C-phycocyanin from Synechococcus indicate a fluorescence lifetime of 1.7 ± 0.1 ns. In our phycobilisomes preparations, the relative amplitude of this long-lived component depends on the concentration and history of the sample. Presence of various amounts of energetically uncoupled pigments have first been reported by us for phycobilisomes of *R. violacea* [10], and more recently in phycobilisomes of *P. cruentum* [9].

At 680 nm, i.e., near the emission maximum of the phycobilisomes, the lifetime of the longest-lived component reaches 1.90 ± 0.02 ns. This lifetime for the terminal acceptor has also been observed in phycobilisomes from *Rhodella* (1.9–2.0 ns [10]) and from *P. cruentum* (1.81–1.89 ns [9]) and it also matches well the values of 1.81–1.93 ns reported for free allophycocyanin from *Nostoc* [28]. When exciting at 660 and at 675 nm, the lifetime of the longest-lived component decreases again. This might reflect the inhomogeneity of the allophycocyanin-emission due to the various constituent allophycocyanin-complexes present in the phycobilisome core [15].

The picosecond components

The shortest-lived component dominates the fluorescence decay between 590 and 640 nm. The average lifetime value of about 85 ps is very close to the C-phycocyanin → allophycocyanin transfer time reported by Gillbro et al. [13]. Despite the variations of up to approx. 20 ps in the lifetime values obtained from different samples a significant increase of these values from 60 to 100 ps was observed with increasing emission wavelengths in each of the samples (cf. Table I). This finding suggests that the shortest-lived component of our analysis is in fact not a single exponential. It might rather reflect more than one photophysical process. By fitting these decays with four exponentials we were able to further resolve the 85 ps-component (cf. Fig. 2). As shown in Fig. 2, these four-ex-

ponential analyses yielded some improvement of the χ^2-values and, more important so, of the residuals plots. It will be shown that these data indeed facilitate the interpretation of the shortest-lived component(s) as compared to the three-exponential analysis. In the four-exponential analysis this component split into components with lifetimes of 20 ± 10 ps and 130 ± 10 ps. The ratio of their two amplitudes decreased from 4 : 1 at $\lambda_{em} = 590$ nm to about 0.5 : 1 at $\lambda_{em} = 640$ nm, which reflects the increase of the lifetime of the (unresolved) shortest component with increasing emission wavelength in the three-exponential analysis mentioned above (cf. Table I). This means that the 20 ± 10 ps component has an emission spectrum that peaks at shorter wavelength than the spectrum of the 130 ps decay component.

Based on this spectral dependence we assign the 20 ps component mainly to the energy transfer from the sensitizing ('s'-) to the fluorescing ('f'-) chromophores [32] within the phycocyanin-units. The transfer time of 20 ps is probably only an upper limit for the real 's' to 'f' transfer time, whereas the value of 10 ps observed by Gillbro et al. [13] for the anisotropy decay measured by the pump-probe technique might represent a lower bound. The corresponding isotropic decay component in that work had a value of 13 ps. So far, various 's' to 'f' transfer times in this range have been reported for phycobiliproteins: 32 ps have been found by Kobayashi et al. [33] for hexameric C-phycocyanin of *Phormidium luridum* and the corresponding values observed by us in B-phycoerythrin from *Porphyridium cruentum* [9] and in phycocyanin 645 from *Chroomonas* [27] were 13 and 15 ps, respectively.

The 130 ps component is assigned to the overall energy transfer from C-phycocyanin to the core, since in the fluorescence decay at 680 nm a rising term (negative amplitude) with a similar time-constant of $(120 \pm 10$ ps) appears. The relative amplitude of this rising term decreases when exciting at 645 nm due to the decrease of the C-phycocyanin absorption relative to the allophycocyanin absorption.

A four-exponential analysis of the C-phycocyanin decay at short emission wavelengths is rather critical as viewed by statistical arguments. For this reason, the error in the short decay component is rather large (20 ± 10 ps). The appearance of two short-lived fluorescence components, however, is in full agreement with the results of our pump-probe measurements [13]. Furthermore, the second decay component (130 ± 10 ps) obtained in four-exponential fits excellently agrees with the rising term (120 ± 20 ps) observed for indirect excitation of the allophycocyanin fluorescence with $\lambda_{exc} = 570$–645 nm (cf. also Fig. 3 and Table I).

The overall phycocyanin → allophycocyanin transfer time of 120 ps is definitely longer than those reported for phycobilisomes from *Porphyridium cruentum* [9] and from *Rhodella violacea* [10] of about 40 ps. We attribute this to the special structure of the phycobilisomes from *Synechococcus*, which have about three to four phycocyanin hexamers per rod, compared to only one in those from *R. violacea* [10] and other blue-green and red alga [9]. This assumption is supported by a recent analysis of the fluorescence decay kinetics of the phycobilisomes from a mutant with only one C-phycocyanin per rod (Gillbro, T., Sandström, A., Sundström, V., Wendler, J. and Holzwarth, A.R., unpublished data) which shows a considerably shorter C-phycocyanin → allophycocyanin transfer time than the wild type. Furthermore, such an increase of the apparent rod/core transfer time may be expected qualitatively from the following very simple kinetic model for the energy transfer in phycobilisomes: taking into account only energy transfer between nearest-neighbour trimers along the rods and a final transfer step from the innermost C-phycocyanin (C-PC) trimer to the core:

$$(\text{C-PC}^3)_1 \underset{\tau^-}{\overset{\tau^+}{\rightleftarrows}} (\text{C-PC}^3)_2 \underset{\tau^-}{\overset{\tau^+}{\rightleftarrows}} \dots \underset{\tau^-}{\overset{\tau^+}{\rightleftarrows}} (\text{C-PC}^3)_n \xrightarrow{\tau_C} \text{Core}$$

one obtains for the observed rod-core transfer time τ_{obs} in the case of symmetrical transfer in the rods (i.e., $\tau^+ = \tau^-$):

$$\tau_{obs} > n\tau_C \qquad \text{if } \tau_C \approx (\tau^+ = \tau^-)$$

and

$$\tau_{obs} = n\tau_C \qquad \text{if } \tau_C \gg (\tau^+ = \tau^-)$$

However, since the spectra of the C-phycocyanin

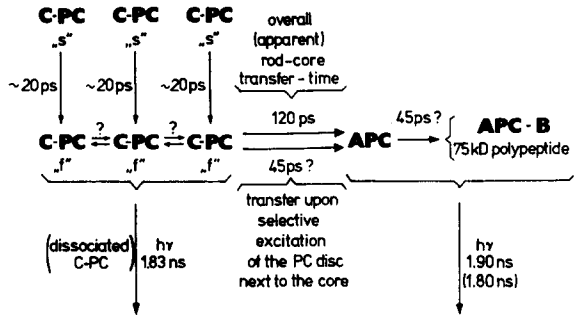

Fig. 4. Schematic diagram of the photophysical processes in phycobilisomes from Synechococcus as observed by single-photon-timing measurements. PC, phycocyanin; APC, allophycocyanin.

units close to the core are somewhat red-shifted with respect to those of the outer discs, energy transfer within the rods is expected to be directed preferentially towards the core [15], i.e., in a more quantitative model τ^+ has to be chosen smaller than τ^- and probably variations of these values along the rod should be considered.

The time constant (45 ps) of the rising term in the fluorescence decay at 680 nm upon excitiaton at 660 nm is significantly smaller than those observed when exciting at shorter wavelengths. So far, it is not clear whether this component has to be assigned to an intracore energy transfer or to a transfer step from the innermost C-phycocyanin disc to the core. Such special phycocyanin-units might have been excited selectively at 660 nm [15].

The relative amplitude of the 'middle' component is always below 20% and the lifetimes are only poorly defined. One might attribute this component to somewhat distorted phycobilisomes in which the various protein complexes are only loosely bound to each other, thus allowing only slow energy transfer. Due to the inefficiency of these transfer steps, the corresponding risetime may not be observed at 680 nm. However, in view of the aforesaid complexity of the phycobilisomes it is also possible that this component accounts for the systematic errors occurring when a decay curve which is basically multiexponential is fitted by a model function with a limited number of parameters, such as a sum of only three or four exponentials. Nevertheless, it is interesting to note that upon excitation below 645 nm the lifetime of this intermediate component at 680 nm is significantly longer than at $\lambda_{em} = 640$ nm or below. It varies in the range of 0.8–1.3 ns, and we would like to refer to a similar, still unidentified component observed in the fluorescence decay of phycobilisomes from *P. cruentum* at $\lambda_{em} = 680$ nm [9].

The assignment of the various components observed in the fluorescence decay of phycobilisomes from *Synechococcus* 6301 is summarized in the energy transfer scheme shown in Fig. 4.

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We should like to emphasize the fact that we observe two different terminal emitters (lifetimes of 1.8 ns and approx. 1.0 ns) both in *Synechococcus phycobilisomes* (cf. Table I) as well as in those from *P. cruentum* [9]. This finding may be intimately related to the energetic coupling of phycobilisomes to the two photosystems in intact cells.

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