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Energy flow in the phycobilisome core of *Nostoc* sp. (MAC): two independent terminal pigments

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Two independent terminal fluorescence emitters were resolved by second derivative spectra in phycobilisomes of *Nostoc* sp. In energetically well-coupled phycobilisomes, fluorescence maxima were 678 and 682 nm at room temperature and 682 and 685 nm at liquid nitrogen temperature, respectively. We attribute the longer-wavelength phycobilisome component to a 94 kDa molecular weight 'anchor polypeptide', because such a peptide isolated from *Nostoc* phycobilisomes has a room-temperature emission at 683 nm (684 nm; −196°C). The short-wavelength component (678 nm; 20°C and 682 nm; −196°C) is probably from the special α-allophycocyanin-B subunit. Excitation of phycobilisomes through phycocyanin produced two levels in the fluorescence polarization spectra at both temperatures. It showed a lower degree of polarization for the short wavelength component (probably α-allophycocyanin-B) and a higher degree for the 'anchor polypeptide', which indicates that energy transfer between them is not likely. Energy flow from allophycocyanin seems to occur independently to both the 'anchor polypeptide' and the presumed α-allophycocyanin-B subunit. There is a nearly parallel orientation of the dipole moment between allophycocyanin and the 'anchor polypeptide', but the angle is much greater between allophycocyanin and the presumed α-allophycocyanin-B component, thus the transfer from allophycocyanin to the 'anchor polypeptide' is probably the predominant pathway. Evidence for the presence of the 'anchor polypeptide' in thylakoids and phycobilisomes was obtained by immunoprecipitation. Energy transfer from the phycobilisome to Photosystem II through the 'anchor polypeptide' is considered a likely pathway.

Introduction

Light energy absorbed by phycobilisomes, located on the stroma side of thylakoids, is known to be efficiently transferred to Photosystem II (PS II) located in the thylakoids [1,2]. Transfer of energy within the phycobilisome follows the path from phycoerythrin (when present) to phycocyanin to allophycocyanin to the long-wavelength pigment(s) [3–5]. Two long-wavelength pigments have been previously identified both of which, according to their spectral characteristics, can serve directly in the energy transfer path from allophycocyanin to chlorophyll in the PS II antenna complex. One is: the high-molecular-weight terminal pigment ('anchor polypeptide') first identified and characterized in the red alga *Porphyridium cruentum* [6,7]; the other is a long-wavelength component from a unique α-allophycocyanin-B subunit

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Abbreviations: Hepes, 4-(2-hydroxyethyl)-1-piperazineethanesulfonic acid; PS II, Photosystem II; 'anchor polypeptide', 94 kDa molecular-weight terminal pigment; (A)PC, (allo)phycocyanin; anc, anchor polypeptide; PE, phycoerythrin.

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first found in the cyanobacterium *Synechococcus* sp. [8]. In solution this subunit, when aggregated randomly with other types of allophycocyanin subunits, had been in the past thought to be a distinct pigment (allophycocyanin-B) [9–11].

Both terminal components are in phycobilisome cores, according to detailed analyses made by Glazer and colleagues [12–14]. Interestingly, these terminal components occur in separate but adjacent discs according to the model. The energy levels of the two terminal pigments are close, but are not necessarily identical. The allophycocyanin-B is reported to have an absorption maximum in a range from 670–673 nm [9,10,13], and the 'anchor polypeptide' from 665–675 nm [6,12,15]. Variations in isolation conditions and differential affects of detergents used may account for the range in absorbance in both components.

It is well known that phycobilisomes isolated from various organisms have fluorescence emission maxima ranging from 670–680 nm at room temperature and from 678–684 nm at liquid nitrogen temperature [4,16]. The energy levels of the terminal pigments in phycobilisomes are not clear. In 1979 Leclerc et al. [17] resolved two absorbance bands, 665 and 676 nm at 24°C, and 667 and 678 nm at −196°C in *Phormidium,* and attributed the latter to allophycocyanin-B. Variation in the emission maxima have been generally attributed to the degree of phycobilisome intactness, or possibility due to species differences. However, it has generally been assumed, as above, that the longest-wavelength emission occurs from a single component, even though it was not possible to assign it specifically to either the 'anchor polypeptide' or to the α-allophycocyanin-B component. Nor has it been possible to determine the direction of the energy pathway between them. Until recently, the 'anchor polypeptide' spectra had only been made in the presence of detergents or denaturing agents [6,15,18], which complicated a reliable assignment. We recently established that the 'anchor polypeptide' has an absorption maximum at 665 nm, and a fluorescence maximum at 683 nm (684 nm, −196°C) in 100 mM phosphate buffer [19]. This has led us to undertake detailed steady-state measurements of the phycobilisome fluorescence emission.

In this report we analyzed the fluorescence spectra of isolated phycobilisomes from the cyanobacterium *Nostoc* under high-resolution conditions (0.5 nm and better) and together with fluorescence polarization resolved two components. Our results indicate that the two terminal pigments are independent, and that energy transfer between them is not favored. Also the orientation of the dipole moment of allophycocyanin to 'anchor polypeptide' is different from that of allophycocyanin to the presumed allophycocyanin-B component. We also provide evidence for the presence of the 'anchor polypeptide' in the thylakoids of *Nostoc* as well as in the phycobilisomes.

Materials and Methods

Algal culture and isolation of phycobilisomes

Nostoc sp. (MAC) was grown in a liquid medium at 38°C under continuous illumination with daylight fluorescent lamps (approx. 1.5 W/m^2), and supplied with air and 5% CO_2. After 10–14 days cells were harvested. Phycobilisomes were isolated by Triton treatment of broken cells and the sucrose gradient separation method routinely used in our laboratory [16]. After removal from the 1 M sucrose layer, phycobilisomes were further incubated for at least 15 h in Triton X-100 (1% v/v) at approx. 20°C. This procedure decreased possible contamination of PS II core components [20]. Following incubation, the sample was centrifuged at 43000 × *g* for 30 min, and the Triton-containing layer on top was discarded. A clear violet layer was diluted three-fold with 0.75 M potassium phosphate (pH 6.8) and phycobilisomes were pelleted by centrifugation at 254000 × *g* for 3 h.

Spectroscopic measurements

Absorption and fluorescence spectra were measured with a Cary 17 spectrophotometer and an SLM 4800 spectrofluorometer, respectively. For the fluorescence measurements, samples were dissolved in a mixture of 1 part 75% potassium glycerophosphate and 1 part 0.75 M potassium phosphate (pH 6.8). This mixture gave a transparent glass even at liquid nitrogen temperature. The calibration of the wavelengths was carried out by using several of the bright-line wavelength bands from a low-pressure mercury lamp. The

spectral sensitivity of the apparatus was corrected so that the spectra are expressed as quanta per wavelength. The excitation and emission resolution was better than 0.5 nm. For fluorescence polarization, a Glan-Thompson prism polarizer was used. Corrections of the apparatus for polarized light [21] in the wavelength region from 600 to 750 nm were made by separate measurements using a concentrated rhodamine B solution. For the data acquisition and calculations, a Hewlett-Packard 85 microcomputer was used. The program for the derivative spectrum was made based on the method of Savitzky and Golay [22,23].

Thylakoid membrane preparation and gel electrophoresis

Thylakoid membranes were twice rinsed in 10 mM Hepes/0.3 M sucrose/10 mM EDTA (pH 7.5) until phycobiliproteins were no longer detectable by absorbance. The thylakoids were solubilized for 20 min (20°C) in 1% Triton X-100/0.02 M potassium phosphate buffer/0.17 M NaCl (pH 7.0), reacted with antibodies or control serum, and IgG precipitated with protein-A, which is known to react with the IgG-precipitate complex, thus allowing removal of non-reacting components by rinsing in the same buffer. The rinsed precipitate was analyzed by SDS gel electrophoresis, according to the method of Laemmli [24] with a gradient of 8–15% acrylamide containing 0.1% SDS. The apparent molecular mass of the peptides was estimated with marker proteins in the molecular weight range of 14–200 kDa (Bio-Rad, Richmond, CA). Antisera to the 94 kDa polypeptide was produced in rabbits and was previously shown to be specific for the antigen [25]. Rabbit antiserum to the colorless linker peptide (31 kDa) and preinoculation serum were used as controls.

Results

Phycobilisomes are energetically well coupled as is evident by the small emission peak of phycoerythrin (581 nm) and large peaks at longer wavelengths (above 670 nm) (Figs. 1A and 2A). Most of the energy was transferred to allophycocyanin (660 nm) and to longer-wavelength components. Two distinct long-wavelength maxima were resolved in second derivative spectra both at 20°C (Fig. 1B) and at −196°C (Fig. 2B). One maximum was at 678 nm, and the other at 683 nm at room temperature, and shifted to 682 and 685 nm, respectively, at −196°C. We attribute the 683 nm (685 nm, −196°C) emission to the 'anchor polypeptide', i.e., the high molecular weight 94 kDa terminal pigment, because it corresponds to the fluorescence emission of the isolated polypeptide from the same organism [19]. The 678 nm emission (682 nm, −196°C) is believed to emanate from α-allophycocyanin-B [10,13], although α-allophycocyanin-B was not isolated from *Nostoc* sp. in our study.

The existence of two long-wavelength emission bands was further confirmed by fluorescence polarization spectra at room and liquid nitrogen temperatures (Fig. 3) when phycobilisomes were excited at 610 nm, which is preferentially absorbed by phycocyanin. At −196°C the polarization degree around 640 nm was high (+0.35), and decreased (+0.18) at approx. 650 nm, whereas at 660 nm the polarization degree decreased further to a negative value (−0.01) at 680 nm, and after a 'plateauing' increased again at approx. 687 nm (Fig. 3B). Clearly two components are present between 680 and 695 nm, with the shorter-wavelength component having a lower degree of polarization and a negative value, and the longer-wavelength component a higher degree of polarization and a positive value which is very close to the degree of polarization of allophycocyanin. Fluorescence polarization spectra made at room temperature (Fig. 3A) support the above conclusions (see Discussion).

We further attempted to resolve the origin of the absorption bands which contribute to the long-wavelength emission by examining excitation spectra. Two new bands were clearly resolved at 668 and 678 nm at −196°C (Fig. 4A), but they were not seen at room temperature. Bands at 550 and 575 nm arising from phycoerythrin, 625 and 635 nm from phycocyanin, and 649 nm from allophycocyanin were also evident. In excitation polarization spectra the degree of polarization was nearly zero from 600 to 650 nm (not shown) because of energy transfer to the terminal pigments. However, beyond 650 nm (Fig. 4B) the degree of polarization increased from the level of allophycocyanin (0.03), between 665 and 675 nm

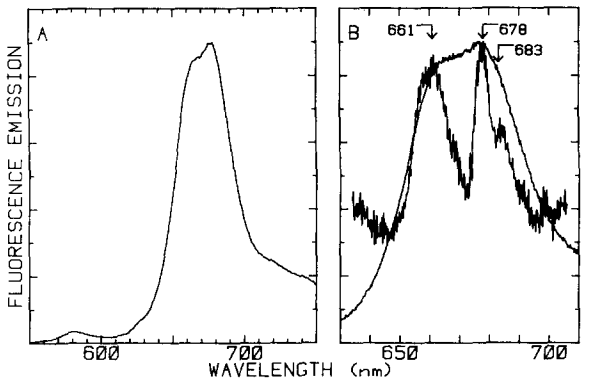

Fig. 1. Fluorescence spectrum (A), and the second derivative spectrum (B) of *Nostoc* phycobilisomes (20°C) in a 1:1 mixture of 75% potassium glycerophosphate/0.75 M potassium phosphate (pH 6.8) (λ_{exc} = 520 nm). (Half bandwidth of excitation = 4 nm; emission = 2 nm and scanning interval = 1 nm in (A); and 2 nm, 0.5 nm, 0.25 nm in (B), respectively).

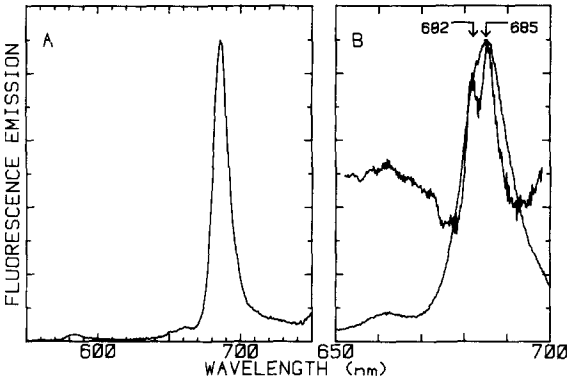

Fig. 2. Fluorescence emission spectrum (−196°C) of phycobilisomes (A), and the second derivative spectrum (B). Measuring conditions were as in Fig. 1A.

to 0.13 and increased again, finally reaching the theoretical maximum (0.5). The 678 nm band probably corresponds to both terminal pigments (see Discussion), although it was not possible to resolve two peaks in excitation polarization spectra. The 668 nm component is not attributed to a terminal pigment, but may arise from an 18 kD polypeptide [19] in the phycobilisome core [12].

Location in or near the thylakoid membrane of α-allohycocyanin-B and 'anchor polypeptide' would enhance energy transfer to the photosystems, especially Photosystem II. Evidence for location of the 'anchor polypeptide' in the thylakoid was obtained from thylakoids from which phycobilisomes had been removed by rinsing them under dissociation conditions. The immunoprecipitates of thylakoids with anti-94 kDa (phycobilisome) antiserum is shown in Fig. 5 (lane A). A 94 kDa polypeptide was clearly present in the immunoprecipitates in thylakoids (lanes A and D) which was comparable to that in phycobilisomes (lanes E and F). Interestingly, two additional polypeptides (approx. 92 kDa, approx. 38 kDa) were observed in the immunoprecipitate from thylakoids, but not from phycobilisomes. The nature of these is not known, but polypeptides of corre-

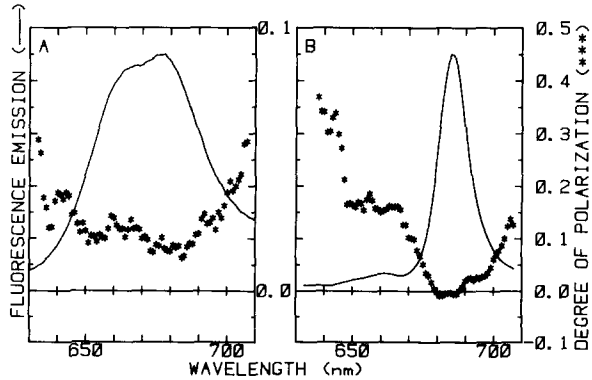

Fig. 3. Fluorescence polarization spectrum of phycobilisomes at 20°C (A), and −196°C (B). (λ_{exc} = 610 nm, measuring conditions as in Fig. 1A).

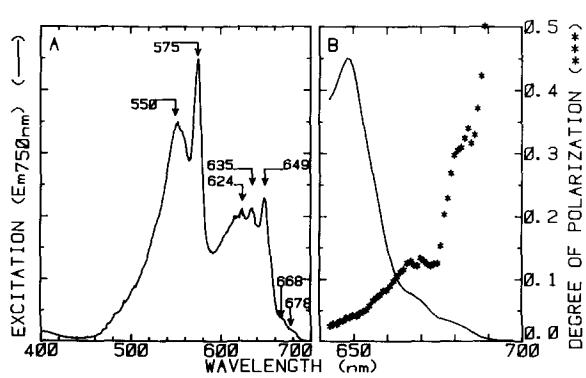

Fig. 4. Excitation spectrum (A), and excitation polarization spectrum of phycobilisomes (−196°C). (λ_{em} = 750 nm, excitation half bandwidth = 2 nm, and 1 nm scanning interval).

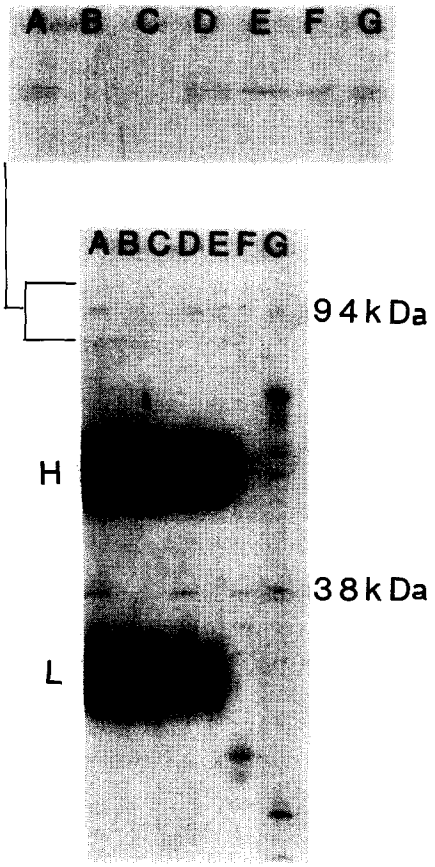

Fig. 5. Immunoprecipitate patterns on SDS-polyacrylamide gel stained with Coomasie blue; enlargement from top of gels reveals polypeptide pattern in the 94 kD region. Heavy (H) and light (L) of the IgG subunits are heavily stained by Coomassie blue (A–E). (A) Thylakoids (solubilized in Triton) treated with antiserum to anchor 'polypeptide'. (B) Thylakoids (solubilized in Triton treated with antiserum to 31 kDa linker polypeptide. (C) Thylakoids (solubilized in Triton) treated with control serum (pre-bleed). (D) Thylakoids (solubilized in Triton) treated with IgG fraction of anti 'anchor peptide'. (E) Phycobilisomes (dissociated) treated with antiserum to 'anchor polypeptide'. (F) Phycobilisomes, untreated. (G) Thylakoids, untreated.

sponding molecular weights were present in thylakoids (lane G). 'Anchor polypeptide' was not immunoprecipitated with control serum (prebleed) (lane C), or with antiserum to a 31 kDa phycobilisome linker peptide (lane B). It is possible that the 94 and 92 kD polypeptides are distinct and are released only upon detergent solubilization of the thylakoid membrane, but proteolytic degradation cannot be ruled out. A close parallel may exist in the red alga *P. cruentum* where evidence for two high-molecular-weight polypeptides has been presented [7].

Discussion

The existence of two long-wavelength emitting pigments in phycobilisomes has been known ever since they were isolated from dissociated phycobilisomes (cf. Ref. 4,5). According to Glazer's analysis both occur in the phycobilisome core in one hexamer pair, but on separate trimers [5]. This is the first report, to our knowledge, in which two distinct long-wavelength emission components have been resolved in spectra of intact phycobilisomes. According to our results we assume that the 685 nm (−196°C) long-wavelength emitter corresponds to the 684 nm emission of the 94 kDa peptide, which we have recently purified from *Nostoc* phycobilisomes [19], and we suggest that the 682 nm (−196°C) peak arises from α-allophycocyanin-B because the fluorescence emission of isolated allophycocyanin-B components have emission at approx. 680 nm [9–14].

Circular dichroism spectra of *Nostoc* phycobilisomes had a maximum at 680 nm (−196°C), which is attributable to the trimer containing the 'anchor polypeptide', but not to that containing allophycocyanin-B [11]. We observed two bands around 668 and 678 nm in the fluorescence excitation spectrum at liquid nitrogen temperature (Fig. 4A). The 678 nm band we assigned to both terminal pigments, although the α-allophycocyanin-B might have a slightly shorter maximum, because the fluorescence maximum is located at shorter wavelength by 3 nm than that of the anchor polypeptide. In fact, we estimated the location of the absorption band as 677 and 678 nm by the Stepanov equation [26,27] from the 682 and 685 nm (−196°C) fluorescence bands. These locations agree well with the observed data. At room temperature, the absorption maximum is shifted to a shorter wavelength.

That little, if any, energy transfer occurs between the terminal pigments is suggested by the presence of two independent fluorescence bands at −196°C (Fig. 2B) at a temperature where

transfer efficiency is enhanced. Also, results from the polarization spectra do not support transfer between the two terminal components. When the data on degree of polarization was converted to anisotropy (according to Refs. 28 and 29), it was possible to assess the relative angles between allophycocyanin and the terminal pigments. If energy transfer occurred from allophycocyanin to the 'anchor polypeptide' through the allophycocyanin-B component, then the anisotropy of the 'anchor polypeptide' would be written as:

$$r_{anc} = r_{APC} \frac{3\cos^2\theta_1 - 1}{2} \frac{3\cos^2\theta_2 - 1}{2}$$

where displacement of the absorption and emission dipole is expressed by a factor of $\frac{1}{2}(3\cos^2\theta - 1)$ [30], with θ_1 and θ_2 being the respective angles of the dipole moment between allophycocyanin and α-allophycocyanin-B, and between α-allophycocyanin-B and the 'anchor polypeptide' (anc). When we consider the values $r(\mathrm{APC}) = 0.105$ ($p = 0.15$) and $r(\mathrm{anc}) = 0.083$ ($p = 0.12$) (cf. Fig. 3B), we can expect 0.793 as the products of the second and third terms. The second term must be negative, because r(APB) is a negative value. This indicates that the third term should be negative. However, the maximum product of the two negative terms is 0.25, because each term is in a range from -0.5 to 1.0. This is not the case, thus indicating that the energy transfer does not occur from the α-allophycocyanin-B to the 'anchor polypeptide'. The same rationale applies to the spectrum at room temperature (Fig. 3A), where the degree of polarization, i.e., the anisotropy, is higher at the longer wavelength. If the energy were transferred from the α-allophycocyanin-B to the 'anchor polypeptide' then the anisotropy at the longer-wavelength region would be lower than that at the α-allophycocyanin-B level. This is also not the case. It can be concluded, therefore, that the two terminal pigments function independently in phycobilisomes, and that energy is separately transferred from allophycocyanin to each terminal pigment. Furthermore, since the decrease in the anisotropy is very small in the energy flow from allophycocyanin to the 'anchor polypeptide', it indicates that the dipole moment between them is nearly parallel. On the other hand, the α-allophycocyanin-B has a large difference in anisotropy, suggesting a greater angle of the dipole moment between allophycocyanin and α-allophycocyanin-B, and hence a lesser chance of energy transfer.

Two independent terminal emitters have also been postulated from analysis of the decay kinetics of isolated phycobilisomes in the picosecond range. Short (1.0–1.3 ns) and long (1.8–1.95 ns) components have been found around 680 nm in all phycobilisomes thus far examined [31–33]. Whereas it has been postulated that they may correspond to the terminal emitters, it is not known which corresponds to the 'anchor polypeptide' and which to α-allophycocyanin-B. In the case of *P. cruentum* [33], the longer lifetime component (1.8 ns) had a higher amplitude at the shorter wavelength region (670 nm), while at 685 nm the amplitude of the short-lifetime component (1.18 ns) was nearly equal to that of the long-lifetime component. This indicates a higher fluorescence intensity at the shorter wavelength which is in agreement with our observations, and thus we suggest that the short-lifetime component probably corresponds to the 'anchor polypeptide' and the long-lifetime component to α-allophycocyanin-B. The presence of two decay components is consistent with the lack of energy transfer between the two terminal pigments as suggested by our calculations above.

The spectral observations of steady-state measurements presented here are an initial step in the illucidation of the transfer pathway between the phycobilisome antennae and the photosystems. According to our present evidence, and assuming little or no reverse energy flow, we suggest below an energy-transfer pathway in *Nostoc* which is a modification of an earlier proposal [25]. This pathway differs from the previous one by disallowing energy transfer between the terminal emitters, and emphasizes the transfer through the 'anchor polypeptide' as a preferred pathway.

PE ⇉ PC ⇉ APC ⇉ 'anchor polypeptide' ⇉ PS II antenna Chl
↓
APB

This pathway is justified by the observation that (a) energy transfer from allophycocyanin to the 'anchor polypeptide' is favored, since orientation

of the dipole moment is nearly parallel, (b) the 'anchor polypeptide' is in the thylakoid and (c) that PS II is directly bound to the phycobilisome [20,34]. The α-allophycocyanin-B might be part of a by-pass as indicated from our kinetic analysis on intact cells [3,35]. It could participate, possibly in conjunction with other core components, in energy regulation within the phycobilisomes and between the photosystems under special conditions.

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