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The Efficiency of Non-Photochemical Fluorescence Quenching of Phycobilisomes by the Orange Carotenoid Protein

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Abstract—We report on the theoretical efficiency of non-photochemical fluorescence quenching of phycobilisomes by the orange carotenoid protein. The created 3D computer model of the three-cylindrical phycobilisome core allowed us to determine the distances between the centers of mass of all of the phycobilin chromophores of the core and calculate the time and the average number of energy migration steps for the resulting non-radiative excitation transfer from the phycobilisomes to photosystem II. The obtained kinetic scheme equations for the path of the energy transfer confirm the incomplete interception of energy flow in the phycobilisome core by the orange carotenoid protein. The theoretical estimation of the rate of phycobilisome quenching is in good agreement with experimental data.

Keywords: allophycocyanin, non-photochemical quenching, orange carotenoid protein, energy migration, phycobilisome, fluorescence

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Phycobilisomes (PBSs) are giant pigment-protein complexes of phycobiliproteins, that weigh several million Daltons and serve as a photosynthetic antenna for cyanobacteria. The polypeptides of phycobiliproteins stereotypical form discoid aggregates–trimers, which are joined into cylinders as a part of PBS by minor linker proteins. The structure of PBSs is divided into two parts: the central part (core), consisting of three cylinders of allophycocyanin (APC), which fluoresces at 660 nm, and six side cylinders, which are fan shaped adjacent to the core and formed by more shortwave phycobiliproteins [1, 2]. Like other phycobiliproteins, APC consists of α- and β-polypeptide subunits in a molar ratio of 1 : 1. Each subunit contains one phycobilin chromophore that is bound covalently to the apoprotein. In addition to the APC subunits, the PBS core has three minor polypeptides with longwave chromophores, namely, L_{CM} (ArcE), β^{18} (ApcF) and ApcD. In gaining energy due to migration from the shortwave APC chromophores, these polypeptides fluoresce at 680 nm, which is the reason that they are called terminal emitters. In a cyanobacterial cell, energy is transferred from a PBS through the terminal emitters to chlorophyll with almost 100% efficiency [3]. According to electron microscopy [4], unlike the side cylinders, the PBS core has a fixed number of discs–trimers (four discs on each one, consisting of three parallel cylinders) and, accordingly, a certain number of chromophores (72), including 66 APC chromophore molecules and 6 terminal emitters. Being intermediaries in the energy transfer from a PBS to chlorophyll photosystem II (PS II), the terminal emitters are located in the lower cylinders of the PBS core. Due to the biochemical procedures of controlled dissociation, immunoprecipitation, and limited proteolysis of PBS proteins (see reviews [1, 2]) it was found that ApcD is a part of the extreme trimer, L_{CM} and β^{18} are parts of the second adjacent one. The third and fourth trimers of the lower cylinders, as well as the entire upper cylinder of the PBS core, are free from terminal emitters. Furthermore, the two lower cylinders are antiparallel, so that the terminal emitters are arranged in them starting from the opposite end surfaces. In hybrid trimers (APC + terminal emitter), each terminal emitter replaces one of the α- and β-subunits of the APC. The supramolecular structure of phycobilisome's core is shown in Fig. 1.

The molecular protective mechanism called non-photochemical quenching of fluorescence activates in a PBS under intensive light in order to intercept the excess absorbed energy with its possible photodamaging action in the cells of cyanobacteria. It belongs to the fast light adaptive responses that reduce the energy transfer from the antenna to the reaction centers of photosynthesis. Quenching is realized through the addition of orange carotenoid protein (OCP) to the L_{CM}-polypeptide in the PBS core [5, 6]. The caro-

Abbreviations: PBS, phycobilisome; APS, allophycocyanin; TE, terminal emitters; OCP, orange carotenoid protein; PS II, photosystem II.

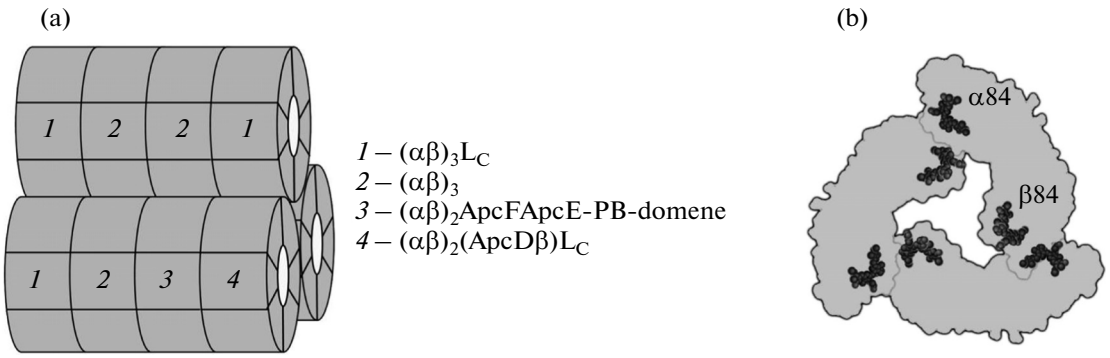

Fig. 1. (a), The scheme of the PBS core structure, consisting of three parallel cylinders. Each cylinder contains four APC trimers as the basic elements, designated as $(\alpha\beta)_3$. Edge trimers have the additional small non-chromophoric L_C polypeptide in the central cavity, which terminates the growth of the cylinders. The third and fourth trimers of the bottom cylinder contain terminal emitters designated as ApcD, ApcE, and ApcF. The numbering of the trimers in the cylinder on the background is opposite to the front cylinder. (b), The frontal image of the APC trimer. Chromophores, which are clearly seen as assembled pairs, are indicated.

tenoid chromophore, OCP, is a hydroxyechinenone that intercepts the energy that is absorbed by a phycobilisome and transforms it quickly into heat, concurrently reducing the PBS fluorescence. A decrease in fluorescence is easy to observe, which gave rise to the name of the non-photochemical quenching of PBSs. According to the experimental data [7, 8], OCP enables one on average to halve the energy transfer from a PBS to chlorophyll.

The aim of this work is a theoretical analysis of the changes in the intensity of PBS fluorescence during non-photochemical quenching caused by the orange carotenoid protein.

Construction of Three-dimensional Model of the Phycobilisome Core

The structure of the crystals that are formed by trimers of allophycocyanin and that have a resolution of approximately 2 Å, allows one to distinguish the sizes and arrangement of the chromophores (see, e.g., [9]). In contrast to the individual phycobiliproteins, crystallization of a phycobilisome or even just its core is impossible today because of the huge molecular mass and amorphous linker proteins that are included in the PBS structure. At the same time, the sizes and shape of APC trimers in the PBS core, which are distinguishable on electron micrographs [4], are similar to parameters that are known from crystallographic structures. Therefore, we used the information that is contained in the APC crystals for the reconstruction of the PBS core. The resulting structure is a component model, which is based on the APC structure of *Rorrhyra yezoensys* (1NK1), *Arthrosrira rlatensis* (1ALL), and *Thermosyneshososus vulsanus* (3DBJ). By combining the known three-dimensional structures in the space, we were able to determine the relative positions of all 12 trimers of allophycocyanin that form the core and to calculate the distance between the chromophores in the core, as well as the most probable paths of migration of the absorbed energy to the terminal emitters.

According to X-ray data, APC trimers are characterized by a fixed position of chromophores in the three-dimensional structure [9]. Six chromophores in the trimer are divided into three pairs; each of them consists of two chromophores that are located in adjacent α- and β-subunits at a distance of 20.6 Å. The distance between the chromophores of adjacent pairs is 34.5 Å (Fig. 2). The 3D-model helped us to determine that the minimal distance between the chromophores that are located on discs that are in contact with each other and adjacent cylinders in the PBS core is also close to 35 Å (Fig. 2).

The analysis of the structure of the 3D model (Fig. 2) has led to speculation that the chromophores in the apoprotein frame of a phycobilisome are structured in such a way that they form a functional system that is optimal for energy-exchange processes. The model of this functional structure is shown in Fig. 3, each circle, which is called a PBS node, denotes the above-mentioned pair of α/β-chromophores. Combination of such α/β-chromophores (or nodes) into a single system is caused by the fact that the energy transfer between chromophores within the node is very fast, viz., 1–2 ps [10–12]; it is at least an order of magnitude faster than the rate of energy transfer between the other PBS chromophores (see below).

The functional scheme (Fig. 3) consists of four equilateral triangles (energy exchange PBS layer) that are located in parallel planes and thus contain nine nodes. The distances between any adjacent nodes in the layer are the same and are approximately 35 Å (Fig. 2). The three lateral distances between the nearest chromophores of the adjacent planes (layers) were 29, 26, and again 29 Å according to the 3D-model (Fig. 3). The nodes of the two lower cylinders that contain terminal emitters are in grey: ApcD for the outer layers (first and fourth) and L_{CM} and ApcF for

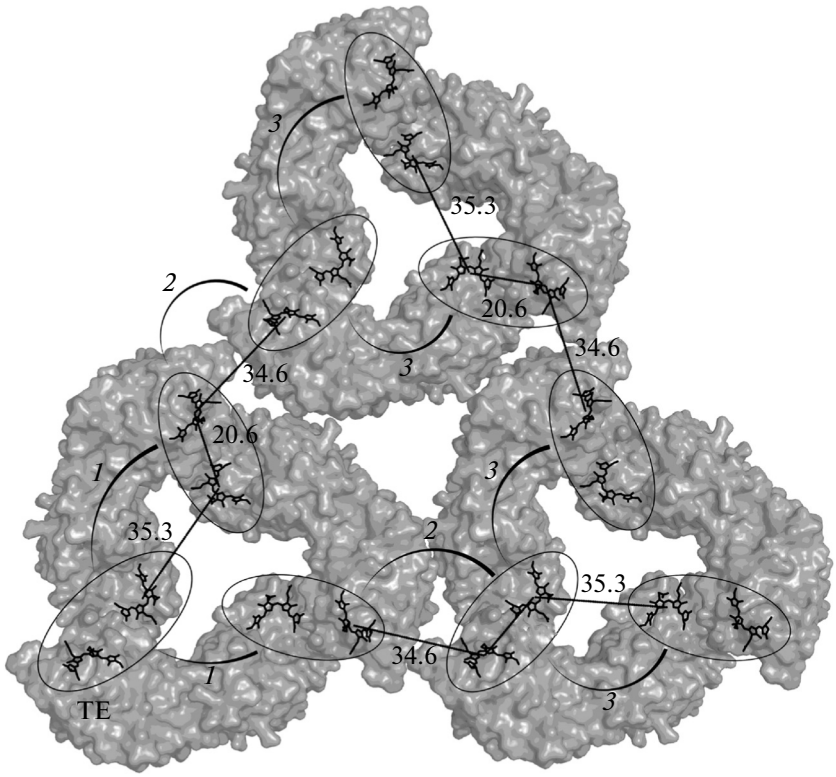

Fig. 2. The model of the PBS core that was built in the PyMOL program. The model is assembled on the basis of crystallographic data for APC trimers taken from the RDB database (code 1ALL). The front surfaces of three contiguous core cylinders are shown and the distances between the mass centers of the adjacent chromophores are measured. All chromophores, which constitute pairs with an interchromophoric distance of 20.6 Å, are enclosed in an oval. It is clearly seen that the distance between the pair chromophores within each APC trimer (35.3 Å) are almost identical to the same distances between adjacent trimers (34.6 Å).

the inner layers (second and third). Thus, each of the four layers in a phycobilisome core comprises one node with a terminal emitter, which receives the energy that is absorbed by the chromophores of each layer with its subsequent transfer to PS II. The binding of OCP occurs in the case of intensive light flow to the L_{CM}-polypeptide, which leads to a redistribution of the energy flow and to efficient quenching of fluorescence in a phycobilisome.

The Kinetic Scheme of Energy Migration in the Core of a Phycobilisome

Kinetic analysis of the energy migration process was conducted on the basis of the model of the functional structure of a phycobilisome, as shown in Fig. 3; the key timing parameters of the model were initially identified to perform it. Energy exchange between the α- and β-chromophores of each node occurs, as already mentioned, very quickly, in a time of approximately 2 ps [10] (there are also data that indicate times of 0.4 ps [11] and 1.3 ps [12]). This energy transfer can occur by both exciton and inductive resonance (Forster) mechanisms (see review [13]). Energy transfer to the distance between the nodes of the PBS core and further from a PBS to PS II is carried out by the Forster mechanism [11], while energy transfer from a PBS to the OCP occurs via the exciton mechanism [5]. The particular mechanism of individual acts of migration is not, however, essential for further kinetic analysis, the only important parameter is the rate of the energy exchange processes.

The observed fluorescence decay time is $\tau_F \approx 1750$ ps for the PBS solution, and the quantum yield $\varphi_{ex} \approx 0.6$ [14]. The time of the energy migration from the terminal emitter to PS II $\tau_{PS\ II} \approx 200$ ps [10] and time of the energy migration from a PBS to OCP at quenching $\tau_{OCP} \approx 36$ ps [5]; data showing 16 ps also occur [15]). The observed time of the fluorescence decay for the PBS solution with the binding of OCP $\tau_F^{ex}(\text{OCP}) \approx 1300$ ps [16]. Estimates exist of 50 Å [9] and 68 Å [11] for the Forster radius, R_0, of the chromophores from the PBS core.

Let us denote the parameters that are required for further analysis: the radiation lifetime of the excited state of PBS chromophores τ_R (rate constant $k_R = \tau_R^{-1}$) and the characteristic time of nonradiative excitation relaxation τ_Q (rate constant $k_Q = \tau_Q^{-1}$). According to the definition [17], the fluorescence quantum yield in

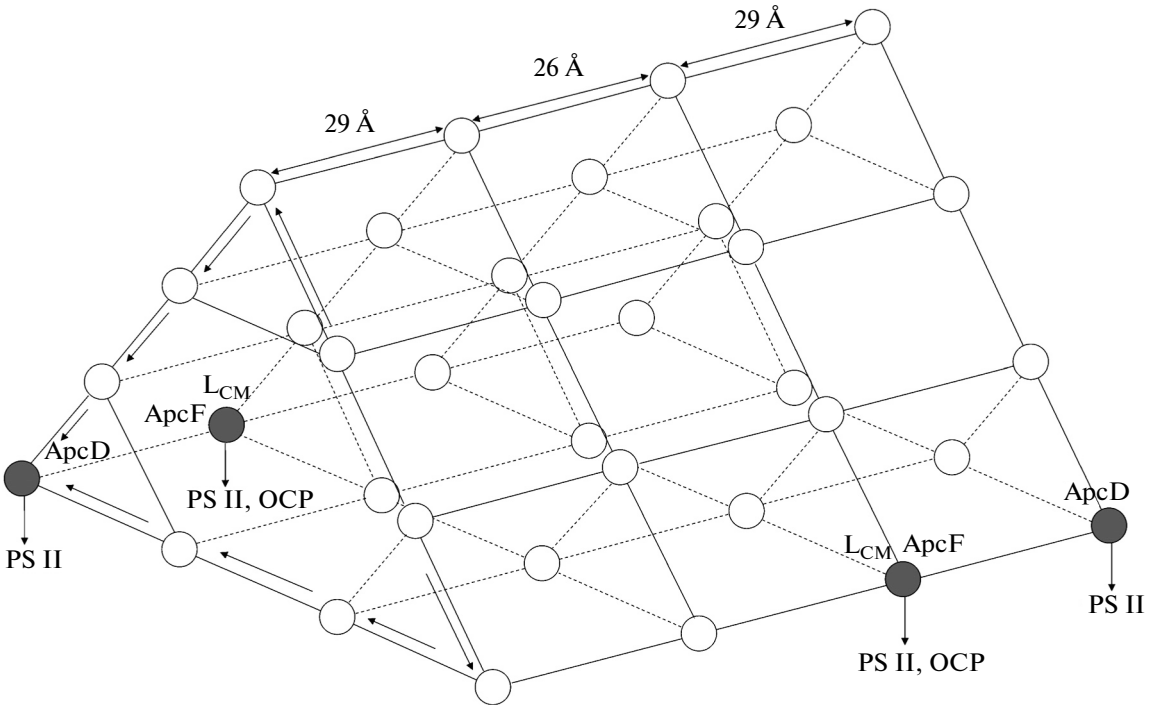

Fig. 3. The scheme of the PBS core reduced by combining closely spaced pair α/β-chromophores. Combined chromophores were called nodes and are denoted by circles. There are 36 nodes divided into four nine-node layers that correspond to the contacting APC trimers (see Fig. 2) of the three core cylinders. Four nodes, which are highlighted in gray, belong to the terminal emitters (indicated as ApcD and L_{CM}). The energy in the cyanobacterial cell is transferred from each of the four terminal emitters to PS II and from L_{CM} to OCP simultaneously with PS II during the development of non-photochemical quenching under intensive light. It can be seen that each of the four layers must contain one of the terminal emitters to which the energy flows are directed eventually in a PBS; they are shown by arrows on the front nine-node layer. The distances between the chromophores in each node and between the nodes of a layer refer to those designated in Fig. 2. The lateral gaps between the first and second and third and fourth layers, according to PyMOL model, are 29 Å and they are 26 Å between the second and third layers.

a PBS solution looks like $\varphi_{ex} = k_R(k_R + k_Q)^{-1} = k_R\tau_F$, where $\tau_F = (k_R + k_Q)^{-1}$. Expressing here $\tau_R = \varphi_{ex}^{-1}\tau_F$ and substituting numerical values, one will receive $\tau_R \approx 2900$ ps ($k_R \approx 3.5 \cdot 10^8$ s^{-1}). Expressing $\tau_Q \approx \tau_R\tau_F(\tau_R - \tau_F)^{-1}$ and substituting the numerical values, one will receive the estimation $\tau_Q \approx 4400$ ps ($k_Q \approx 2.3 \cdot 10^8$ s^{-1}). Thus, the radiative time and the time of non-radiative deactivation of the excitation of chromophores lie in the nanosecond range of the time scale.

Let us estimate the amount of the energy migration time between the nodes of a functional lattice, which we denote as τ_{in} ($k_{in} = \tau_m^{-1}$, the rate constant). To do this, first we estimate the value of the Forster radius, R_0, for the chromophores of phycobilisomes according to the known formula $R_0 = R_{\alpha\beta}(\tau_R/\tau_{\alpha\beta})^{1/6}$, where $R_{\alpha\beta}$ is the distance between the chromophores and $\tau_{\alpha\beta}$ is the typical time of the energy migration between them. Using data for the α/β-pair of chromophores in a node $R_{\alpha\beta} = 20.6$ Å and $\tau_{\alpha\beta} \approx 2$ ps, we obtain the estimate $R_0 \approx 69.3$ Å, which is consistent with the data [11] (with $\tau_{\alpha\beta} \approx 1.3$ ps we obtain $R_0 \approx 74.5$ Å, with $\tau_{\alpha\beta} \approx 0.4$ ps $R_0 \approx 90.6$ Å, respectively). Taking the distance between lattice nodes $R \approx 35$ Å and using the formula $\tau_m = \tau_R(R/R_0)^6$, we obtain an estimate for the time of energy migration between the nodes at $R_0 \approx 69.3$ Å $\tau_m \approx 48$ ps. This value is used in further calculations (at $R_0 \approx 74.5$ Å for this time we obtain 31 ps, and at $R_0 \approx 90.6$ Å – 10 ps only, which is unlikely, in our opinion). These estimates imply that the value τ_{in}, as well as $\tau_{PS\ II}$ and τ_{OCP}, lies in the picosecond range of the time scale and τ_{in} is approximately four times smaller than $\tau_{PS\ II}$ and approximately 1.3 times greater than τ_{OSR}.

Kinetic Analysis of the Energy Migration in One Node Layer of Phycobilisomes

An important conclusion follows from the conducted evaluations, viz., the rate of energy exchange processes between the chromophores within a PBS significantly exceeds (by 1–2 orders of magnitude) the rate of the processes of their own deactivation of the excited state of the chromophore. This means that in the absence of an efficient flow the excitation energy will wander between the chromophores within a PBS for a long period of time. Based on these data, we pro-

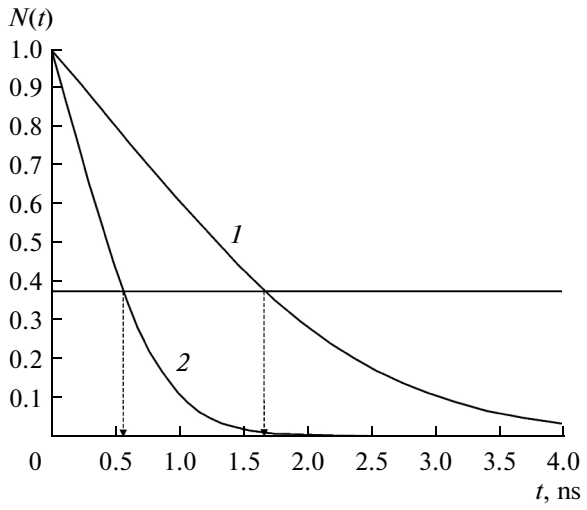

Fig. 4. The effective population of the excited state of PBS chromophores (nodes), calculated according to formula (3) for $\beta = 2 \cdot 10^9\ s^{-1}$ (curve *1*) and $\beta = 5.9 \cdot 10^9\ s^{-1}$ (curve *2*), depending on the time of the beginning of excitation. The horizontal line identifies the level of the reduction of the population by 2.7 times. The dashed arrows indicate the values $t = \tau_P(\text{PS II}) \approx 1700$ ps (curve *1*) and $t = \tau_P(\text{OCP}) \approx 600$ ps (curve *2*) (see text).

pose a simplified kinetic scheme of the energy migration process in the node layer. In fact, due to the fact that the energy release to PS II occurs in one point of each node layer (see Fig. 3), the average energy flow (drift) will be forwarded to it on the background of the random walking of energy between the nodes that are considered to be the same. There are two equivalent energy channels that connect the release point with the periphery (indicated by arrows in Fig. 3), due to the spatial distribution of the nodes in the layer of phycobilisomes. The drift rate of the energy transfer in these streams, each of which contains five nodes, will be determined by some effective time of transfer between the nodes, which can be taken as $\tau_{eff} = \tau_M + \tau_m$, where $\tau_M = \tau_{PS\ II}$ or $\tau_M = \tau_{OCP}$. This time is the same for all adjacent nodes of a layer and determines the average flow rate. Thus, there is a system of two equivalent parallel channels, by which the energy flows to the same release point. Therefore, it is possible to combine the two streams into one common one with half of the flow rate compared to each of the separate streams. Then, the effective time of the energy migration between the nodes in the combined stream is equal to $2\tau_{eff}$ and the effective rate of energy transfer will be $\beta = (2\tau_{eff})^{-1}$. Thus, a chain of five effective nodes (tanks) is formed, in which the energy flows, moving consistently from the most remote node to the node effluent. Introducing the parameter of filling, $n_j(t)$, with the energy (resource) of each effective node, we obtain a system of equations that describe the energy output from the node layer (the common tank):

$$\begin{aligned} \dot{n}_1 &= -\beta(n_1 - n_2), \quad \dot{n}_2 = -\beta(n_2 - n_3), \\ \dot{n}_3 &= -\beta(n_3 - n_4), \quad \dot{n}_4 = -\beta(n_4 - n_5), \\ \dot{n}_5 &= -\beta n_5. \end{aligned} \tag{1}$$

Here, the first node is a point of release and the fifth node is the farthest from the first one. The initial condition: $n_1(0) = n_2(0) = n_3(0) = n_4(0) = n_5(0) = 1$, i.e., all nodes are filled at the initial moment of time, i.e., all chromophores are in an excited state. The solution of system (1) is as follows:

$$\begin{aligned} n_5(t) &= e^{-\beta t}, \quad n_4(t) = (1 + \beta t)e^{-\beta t}, \\ n_3(t) &= \left(1 + \beta t + \frac{1}{2}(\beta t)^2\right)e^{-\beta t}, \\ n_2(t) &= \left(1 + \beta t + \frac{1}{2}(\beta t)^2 + \frac{1}{6}(\beta t)^3\right)e^{-\beta t}, \\ n_1(t) &= \left(1 + \beta t + \frac{1}{2}(\beta t)^2 + \frac{1}{6}(\beta t)^3 + \frac{1}{24}(\beta t)^4\right)e^{-\beta t}. \end{aligned} \tag{2}$$

The integral indicator, $N(t)$, which characterizes the portion of the node layer filling with energy after time, t, from the start of the process, is determined by the sum $n_j(t)$ normalized per unit and provided by the system of equations in (2):

$$\begin{aligned} N(t) &= \frac{1}{5}\sum_1^5 n_j(t) \\ &= \frac{1}{5}\left(5 + 4\beta t + \frac{3}{2}(\beta t)^2 + \frac{1}{3}(\beta t)^3 + \frac{1}{24}(\beta t)^4\right)e^{-\beta t}. \end{aligned} \tag{3}$$

Figure 4 shows two $N(t)$ curves: *1* characterizes the energy release on PS II ($2\tau_{eff} = 500$ ps, $\beta = 2 \cdot 10^9\ s^{-1}$) and *2* characterizes the energy release on OCP ($2\tau_{eff} = 170$ ps, $\beta = 5.9 \cdot 10^9\ s^{-1}$). These graphs allow one to determine the characteristic time of the fluorescence quenching due to the energy release on PS II at $\tau_P(\text{PS II}) \approx 1700$ ps or on OCP at $\tau_P(\text{OCP}) \approx 600$ ps, using the standard approach of reducing the amplitude e by 2.7 times (this level is indicated by the horizontal line in Fig. 4); the corresponding rate constants are $k_P(\text{PS II}) \approx 6 \cdot 10^8\ s^{-1}$ and $k_P(\text{OCP}) \approx 17 \cdot 10^8\ s^{-1}$.

According to definition [17], the observed fluorescence decay time is calculated by the formula $\tau_F = (k_R + k_Q + k_P)^{-1}$. Consequently, when the energy is reset to PS II for a single layer of chromophores of PS II $\tau_F(\text{PS II}) \approx 850$ ps for a single layer of chromophores of PS II, and when the release is on OCP, $\tau_F(\text{OCP}) \approx 440$ ps, and the corresponding values of the PBS fluorescence quantum yield are $\varphi(\text{PS II}) \approx 0.3$ and $\varphi(\text{OCP}) \approx 0.15$.

We obtained estimates for the parameters of fluorescence and its quenching in a single layer of a phycobilisome's core. If we neglect the energy migration between the layers (i.e., consider them as isolated from

each other) then the fluorescence characteristics of PBS can be assessed in general by the average quantum yield. In the case of the binding of one OCP molecule to a PBS isolated in solution, i.e., isolated from PS II, the mean quantum yield will be 0.49 and the observed fluorescence decay time $\tau_F^{(1)} \approx 1420$ ps. If two OCP molecules bind to PBS, the average quantum yield is approximately 0.38 and the time $\tau_F^{(2)} \approx 1100$ ps. In a real experiment, obviously, both cases occur, so they can also be averaged. The overall average quantum yield is then approximately 0.44, and the mean observed time of fluorescence decay of a phycobilisome's core is $\bar{\tau}_F \approx 1280$ ps, which coincides almost perfectly with the experimental value $\tau_F^{ex}(OCP)$, which is equal to 1300 ps [16]. This result can be interpreted as an indirect indication of the fact that the lateral energy migration, in comparison to migration within each layer, has no great significance on the functioning of the core of a phycobilisome.

A Kinetic Analysis that Takes the Lateral Energy Migration in Phycobilisomes into Account

The distances between the nearest chromophores of adjacent layers of the PBS core are 29, 26, and 29 Å, respectively (Fig. 3), and the characteristic time of energy transfer between the nearest nodes of adjacent layers is 15.6 and 8.1 ps, respectively. These values are significantly lower than not only the radiative lifetime of the chromophores (2900 ps) and the time of energy migration among nodes within a layer (48 ps), but also than the time of the energy release from a phycobilisome to OCP (36 ps). Hence, it would seem that we can conclude that the chromophores of the PBS core constitute a single system in which balance is maintained in the filling of the node layers with energy in the process of PBS functioning. It should be taken into account, however, that the nearest nodes of adjacent layers may be in four states: 0–0, 0–1, 1–0, and 1–1, where 0 is an "empty" node (unexcited) and 1 is a "full" assembly (excited). Small transfer times are referred to the situation where the nearest two nodes of adjacent layers are in the 0–1 or 1–0 state and the favorable situation is that where the energy is transferred to the node layer with an attached OCP molecule. Considering these states of nodes as equally probable, we obtain a fourfold increase in the time for a favorable energy transfer between the layers, viz., 62.4 and 32.4 ps, respectively. Thus, the energy transfer from the external layer (first and fourth) on the inner layer (second and third, respectively) is approximately 1.3 times higher than that for the nodes within the layer. Then, to a first approximation, we can neglect the lateral energy transfer between these layers and consider the outer layers as relatively isolated. The two inner layers, which contain L_{CM} and to which OCP molecules can bind, form a more intimate contact, since the average rate of energy transfer between them is approximately 1.5 times higher than the rate of energy exchange between nodes within a layer. In the first approximation, we can combine the two inner layers in a single system and believe that a rapid alignment occurs of the populations of nodes of these layers during the process of PBS core functioning. In other words, one can imagine these two layers in the form of two communicating vessels, where the role of the fluid is played by the excitation energy.

Obviously, if the power of the flows from all of the layers is the same then the observed decay time and the quantum yield of PBS fluorescence will be generally the same as the above-defined fluorescence parameters of one layer. Some difference should be observed apparently only in the case of OCP molecule binding, when the power of a flow of one of the inner layers will increase. Based on the analogy of liquid flowing out of a vessel and assuming that the capacity of one of the two flows from this vessel increases by three times (this follows from the ratio $\tau_F/\tau_P(OCP) \approx 3$), we find that the time of the emptying of the vessel will be $0.5\tau_F \approx$ 875 ps. This time has the same meaning as the above-introduced time $\tau_P(OCP)$. The fluorescence quantum yield of the two inner PBS layers will be 0.2 and the observed time of the PBS fluorescence decay as a whole will be 1160 ps, which is, as expected, close to the value $\tau_F^{(2)}$ and slightly smaller than the experimental value of 1300 ps. If two OCP molecules bind to a PBS, the situation will be almost the same as that in the case of neglecting the energy exchange between the layers (see above). Thus, the intensive energy exchange between the inner layers of a PBS leads to a small dependence of the fluorescence quenching effect on the binding of one or two OCP molecules to a PBS.

DISCUSSION

In this work, we were able to show for the first time that the consideration of the energy transfer in a complex system of 72 chromophores that constitute the PBS core can be significantly simplified due to the regular repeating structural elements. First, the twinning incorporation of chromophores in the APC trimers leads to a very rapid energy exchange inside the pair and allows one to consider it as a single "chromophoric node." Second, this is due to the determination on the basis of the constructed PBS three-dimensional model (Figs. 2 and 3) of interchromophoric distances for the adjacent nodes in the APC trimers and between the nearest trimers of contacting cylinders that are virtually identical and equal to 35 Å. Third, it is due to the division of the three cylinder PBS core into four layers with equivalent structures and 18 chromophores in each one. Fourth, this is due to the presence of one terminal emitter in each such layer, where the final energy migration from APC

chromophores occurs. The latter issue allowed us to sharply reduce the calculations, to set up a system of kinetic equations, and to obtain data on the time and other spectral parameters that are associated with the final energy transfer to the terminal emitters in the energy exchange layer. In particular, the assumption was justified due to the Forster mechanism, according to which interchromophoric migration in a PBS actually takes place only between the adjacent chromophoric nodes. The remaining migration variants are also possible, but the time of migration becomes so large because of the increased distance between the chromophores that they can reasonably be disregarded.

In fact, let us consider the minimal theoretically possible scheme that reflects the energy interception from a PBS to PS II. Since L_{CM} serves as a binding site between OCP and the PBS core [5, 6] it is clear that only three components are sufficient for such a scheme: OCP, PS II, and just one L_{CM} protein instead of PBS, since the energy flows simultaneously from it, as from the terminal emitter, to both PS II and OCP. We use experimental data for the analysis: the L_{CM} fluorescence lifetime in a solution (approximately 1600 ps) is very close to that of a PBS (1750 ps), which once again confirms that the PBS fluorescence is mainly conducted by L_{CM}. The time of the energy migration from L_{CM} to PS II in the cyanobacterial cell does not exceed 200 ps, as mentioned, while that to OCP is less than 40 ps. From these data it is easy to estimate the amount of energy that can reach OCP during quenching: it is 5/6 of the entire flow, i.e., more than 80%. At the same time, according to numerous experiments, the quenching of PBS via OCP reaches 50% in the cells of cyanobacteria. In this regard, we succeeded in theoretically substantiating a lesser degree of the OCP quenching effect on a PBS, which is never complete. A lesser degree of quenching is associated with the fact that the binding of OCP to the PBS core maintains one more channel of the energy flow to PS II through the second terminal emitter, ApcD (Fig. 3). Therefore, the energy flux from a PBS to PS II is not interrupted after the binding of OCP, but it is only redistributed due to the greater rate of transfer to OCP, as well as due to a very rapid subsequent thermal relaxation of excited states that is typical for the carotenoid molecules. This allows one to adjust the amount of energy that is transferred to PS II more finely, since the regulation occurs not to interrupt photosynthesis, but to prevent the potentially damaging effects of excessive light.

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