Minireview

The photosystem I trimer of cyanobacteria: molecular organization, excitation dynamics and physiological significance

Navassard V. Karapetyan[a,*], Alfred R. Holzwarth[b], Matthias Rögner[c]

[a] *A.N. Bakh Institute of Biochemistry, Russian Academy of Sciences, 117071 Moscow, Russia*
[b] *Max-Planck-Institut für Strahlenchemie, D-45470 Mülheim a.d. Ruhr, Germany*
[c] *Lehrstuhl für Biochemie der Pflanzen, Ruhr-Universität, D-44780 Bochum, Germany*

Received 1 September 1999

Abstract The photosystem I complex organized in cyanobacterial membranes preferentially in trimeric form participates in electron transport and is also involved in dissipation of excess energy thus protecting the complex against photodamage. A small number of longwave chlorophylls in the core antenna of photosystem I are not located in the close vicinity of P700, but at the periphery, and increase the absorption cross-section substantially. The picosecond fluorescence kinetics of trimers resolved the fastest energy transfer components reflecting the equilibration processes in the core antenna at different redox states of P700. Excitation kinetics in the photosystem I bulk antenna is nearly trap-limited, whereas excitation trapping from longwave chlorophyll pools is diffusion-limited and occurs via the bulk antenna. Charge separation in the photosystem I reaction center is the fastest of all known reaction centers.

Key words: Energy migration and trapping; Cyanobacterium; Longwave antenna chlorophyll; Photosystem I monomer; Photosystem I trimer; Reaction center

1. Organization of cyanobacterial photosystem I complex

The reaction center of photosystem I (PSI) catalyzes the oxidation of reduced plastocyanin or cytochrome c_6 and reduction of soluble ferredoxin or flavodoxin. In higher plants, algae and cyanobacteria PSI reaction centers contain the same electron carriers and carry out the same function, although the PSI complex in cyanobacteria differs in organization and content of polypeptides as compared with that of higher plants and algae [1–3]. An important difference is the existence of the PSI complex in cyanobacterial membranes in both a trimeric and monomeric form [4,5] while in higher plants and algae PSI is present only as a monomer [1]. The PSI trimer has a discoidal shape, the largest radial distance (viewed from the stromal side) being about 105 Å [6]. The PSI monomer of cyanobacteria contains only 11 polypeptides (PsaA–PsaF, PsaI–PsaM) instead of 14 polypeptides in the PSI of higher plants [1,2]. A model of the molecular organization of PSI (Fig. 1) was developed based on X-ray analysis of the crystals of PSI trimers from the thermophilic cyanobacterium *Synechococcus elongatus* [6,7]. The subunit arrangement in the cyanobacterial PSI complex was confirmed by mutational and immunological analysis of PSI polypeptides [3] and electron microscopy studies of PSI complexes of *Synechocystis* sp. [8]. The PsaA/PsaB heterodimeric (82–83 kDa) polypeptide binds the primary electron donor P700 and primary electron acceptor A_o, two molecules of accessory chlorophylls, primary electron carriers like phylloquinone, and the Fe-S cluster (F_x). The polypeptides PsaC, PsaD and PsaE are exposed to the stromal side of the complex, where PsaC binds two Fe-S terminal centers of electron transport (F_a/F_b), while PsaF is located on the lumenal side and is involved in plastocyanin docking. The polypeptide PsaL in combination with PsaI is responsible for trimerization of PSI monomers [9].

In cyanobacteria the organization of the PSI complex as monomers and trimers, and the light harvesting mainly by phycobiliproteins control other types of processes that are responsible for state transitions in photosynthetic membranes which are important for balancing the energy distribution and electron flow between the photosystems. Phycobilins supply energy mainly to PSII [10], while state transitions make it possible to redistribute energy from phycobilins partly also to PSI [11]. Preferential energy transfer from phycobilins to PSI was observed in a PSII-deficient mutant of the cyanobacterium *Synechocystis* sp. [12]. A cyanobacterial PsaL-deficient mutant containing only PSI monomers also shows state transitions indicating that there is no necessity for PSI trimers [13]. State transitions in cyanobacteria were observed even in a phycobilin-free mutant [14], which means that various mechanisms are involved in that process in cyanobacteria.

All molecules of chlorophyll *a* (Chl) in the cyanobacterial PSI monomer are located in the core antenna with an antenna size of about 100 Chl/P700 [15]; cyanobacteria are devoid of Chl-containing light-harvesting complexes (LHC). The PSI monomeric complex of higher plants contains LHCI that surrounds each core complex thereby increasing the Chl/P700 ratio up to 200; the eight LHCI complexes surrounding each PsaA/PsaB heterodimer [16] prevent the formation of PSI trimers in higher plants. In contrast to PSII and bacterial reaction centers, the main feature of PSI is a tight binding of P700 along with about 100 molecules of core antenna Chls on the same polypeptides [17] which allows and possibly requires special mechanisms of energy utilization and dissipation. Eighty-three of the about 100 Chl molecules have been resolved in PsaA/PsaB (Fig. 1); the main part of those Chls is randomly positioned among the walls of an oval bowl with a distance of 8–15 Å from each other [6]. The short center-to-center distances between Chls allow very fast energy transfer. The average distance of Chls from P700 is about 14–19 Å, although some Chls are localized at a distance of 30–40 Å

*Correspondence author. Fax: (7) (095) 9542732.
E-mail: inbio@glas.apc.org

PII: S0014-5793(99)01352-6

from P700 [6]. The PsaA/PsaB polypeptide also binds β-carotenes (about 10 molecules per P700) that serve as efficient light harvesters; interestingly, no β-carotene molecule is located in close proximity to P700 to prevent the interaction with the P700 triplet state [18,19]. The location of β-carotenes on the PsaA/PsaB protein was revealed by X-ray analysis with 2.5 Å resolution (Petra Fromme, personal communication).

Despite variations in the details, reaction centers of PSI, PSII and purple bacteria show a high degree of structural similarity that demonstrates a close evolutionary link between these centers [20,21]. As compared with other pigment-protein complexes, the PSI complex remains active for a long time and shows the highest structural stability of all reaction center complexes. The cyanobacterial PSI trimer is particularly stable since cyanobacteria, the most evolutionarily old photosynthetic organisms, are very well adapted to growth under stress conditions. The knowledge of the molecular organization of the reaction center complex of PSI trimers and the kinetics of ultrafast energy transfer and electron transport help in understanding how this complex is built for efficient conversion of light energy.

The composition, organization and electron transfer in the PSI complex have been described in several reviews [1–3,22–24]. This review updates the latest data on the molecular organization of cyanobacterial PSI complexes, the excitation dynamics among Chls of the PSI core antenna and the charge separation in the reaction center. Photosynthetic complexes were studied in detail for unicellular cyanobacteria that are easily manipulated genetically [2,3]. Molecular genetics of the filamentous cyanobacteria is not yet developed. However, the presence of PSI trimers in the filamentous cyanobacterium *Spirulina platensis* with an unusual longwave Chl absorbing at 735 nm (Chl735), also showing P700-dependent fluorescence emission at 760 nm [25], makes that system very useful to learn about the excitation dynamics at different redox states of P700. Therefore, most of the data discussed in this review pertain to PSI trimers of the cyanobacterium *Spirulina*.

Monomeric and trimeric PSI complexes of the cyanobacterium *Spirulina* are characterized by a similar pigment and polypeptide composition and Chl/P700 ratio [25,26] and have the same dimensions [5] as the unicellular cyanobacteria *Synechocystis* sp. and *S. elongatus* [2,4]. In contrast to the PSI of other cyanobacteria, the PsaL protein of *Spirulina* is extremely stable [26]; this may be the reason for the pronounced stability of the PSI trimers of that cyanobacterium. There are strong indications that PSI trimers pre-exist in all cyanobacterial membranes and are not an artifact of the isolation procedure: the 77 K fluorescence band at 760 nm (F760) which is emitted by the longwave Chl735 was found in PSI trimers and *Spirulina* cells but not in monomers [5]. Moreover, the main part of the PSI complexes in cyanobacterial membranes are present in trimeric form: the F760 intensity of *Spirulina* cells is only slightly less than that of purified PSI trimers [26]. Thus PSI trimers of *Spirulina* are organized in the same manner and have a similar antenna size as trimers in other cyanobacteria.

2. Longwave chlorophylls of photosystem I core antenna

The core antenna of cyanobacterial PSI complexes contains a relatively high amount of the long wavelength, or so called red Chls absorbing in the spectral region above P700 [27–33]. The longwave Chls function as terminal energy acceptors at the final stages of energy migration and could be important for energy distribution in the antenna. The most longwave Chl735 emitting at 760 nm was found in the cyanobacterium *Spirulina platensis* [34]. The 77 K fluorescence spectrum of *Spirulina* cells and isolated membranes shows distinct bands at 685, 695, 725 and 760 nm (F685, F695, F725, F760, respectively). F685 and F695 bands are emitted by antenna Chls of PSII subunits, the F725 band was ascribed to the emission of Chl710 in the PSI monomer, and F760 to the emission of Chl735 in the PSI trimer [25]. Since Chl735 is present only in PSI trimers, the 77 K fluorescence band at 760 nm can be used as an internal marker for PSI trimers. The very intense fluorescence at 730–740 nm of PSI trimers and membranes of *Spirulina* at room temperature indicates that the longwave Chl735 exists in PSI antenna also at physiological conditions and is not a freezing artefact [35–37].

Spectral forms of PSI longwave Chls have been resolved by deconvolution of absorption spectra of PSI complexes (the number of Chl molecules in each spectral form is shown in parentheses in the following). The only longwave Chl form of PSI of *Synechocystis* PCC6803, Chl708, is most likely a dimer [32]. PSI trimers and monomers of *S. elongatus* contain similar longwave Chl forms differing only in the number of Chl molecules: Chl719 (4–6) in trimer and Chl719 (2) in monomers, while Chl708 in monomers and trimers contains 6 Chls each [33]. Four longwave Chl forms (about 6% of all Chls) were found for PSI trimers of *Spirulina*: Chl705 (2), Chl714 (1), Chl726 (1), Chl738 (2), and three longwave Chl forms (about 5% of Chls) in PSI monomers: Chl703 (3), 715 (1) and 725 (1) [35].

The unique feature of the fluorescence band at 760 nm of *Spirulina* PSI trimers is the dependence of its intensity on the redox state of P700: it is maximal when P700 is reduced, and strongly quenched when P700 is oxidized [5,35]. The fluorescence of the longwave Chls in the PSI complex of the unicellular cyanobacteria is independent of the P700 redox state: this could be due to some different nature and location of these Chls. The strong quenching of F760 by the cation radical of P700 ($P700^+$) was ascribed to energy migration from Chl735 to $P700^+$ [28,34,38]. The action spectrum of F760 quenching in *Spirulina* PSI trimers was similar to that of P700 oxidation [28] providing additional evidence that F760 quenching is determined by energy migration from Chl735 to $P700^+$. The rate constants calculated from the overlap integral of the absorption band of reduced and oxidized P700 with the fluorescence band at 760 nm have indicated that $P700^+$ in PSI trimers of *Spirulina* is a much stronger quencher (by at least two orders of magnitude) of F760 than is P700 [28,39]. Both P700 and $P700^+$ in PSI monomers of *Spirulina* and higher plants are about equal quenchers which explains the absence of pronounced variable fluorescence in PSI monomers [28,40]. The distance between Chl735 and P700 in PSI trimers of *Spirulina* was calculated to be about 42 Å [39], but the high overlap between Chl735 emission and $P700^+$ absorption determines the strong quenching effect of $P700^+$.

Several lines of evidence show that the longwave Chl735 in PSI trimers of *Spirulina* originates from the interaction of the Chl molecules located on the surface of the PsaA/B polypeptide of monomers forming the trimer [41] (Fig. 2). First, modifying the ratio of PSI trimer/monomer within the cyanobacterial detergent-free membranes by salt concentration [42] decreases the F760/F730 ratio at high salt concentrations be-

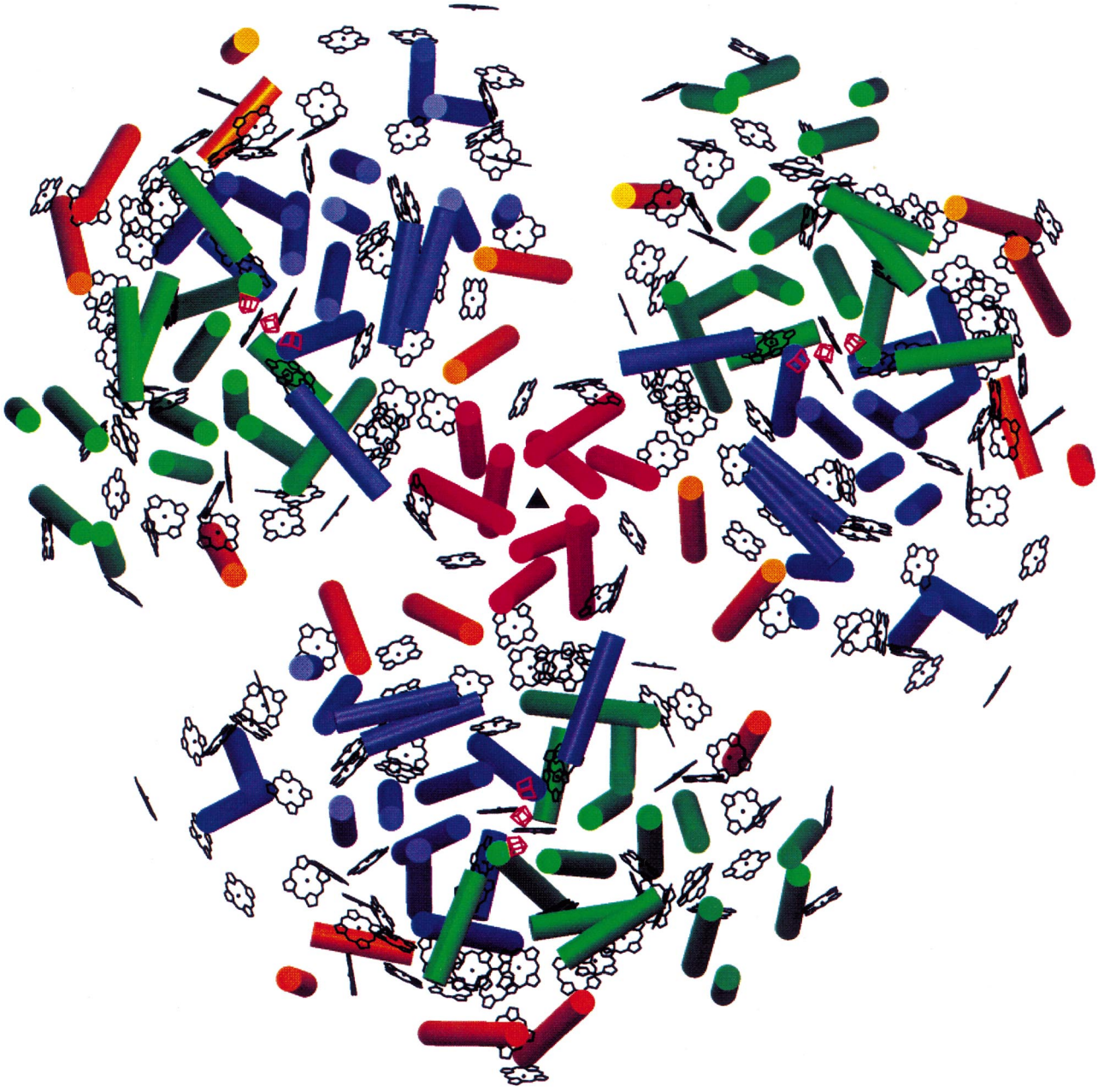

Fig. 1. 4 Å structure of PSI trimeric complex of the cyanobacterium *S. elongatus* including identified α-helices, core antenna Chls (porphyrin rings), P700 (central part of monomers) and primary electron transport carriers. Peripheral location of some Chls is visible in the region of the PsaL polypeptides (red cylinders in the central part of the trimer). The scheme reproduces the data of Schubert et al. [6] and is presented with permission of the authors.

cause monomerization leads to deaggregation of Chl735; in contrast, that ratio increases at low salt concentration due to the formation of Chl735 during reversible trimerization [35]. Second, reconstitution of the isolated and purified *Spirulina* monomeric PSI complexes into liposomes causes the formation of trimers, which is accompanied by the appearance of F760 that is lacking in PSI monomers [26]. Reconstitution of trimers in vitro was highly efficient: up to 40% of monomers were assembled into trimers. Finally, each PSI monomer within a trimer of *Spirulina* contains two molecules of Chl735 per P700 [35]. Thus pigment-pigment interaction of Chl molecules peripherally located on the surface of monomers and contacting each other within the trimer determines the red shift of Chl735 formed as a result of that interaction. The peripheral location of some antenna Chls (porphyrin rings in the central part of PSI trimer, Fig. 1) was confirmed by X-ray analysis of PSI trimers of *S. elongatus* [6]. Longwave Chl719 in PSI trimers of *S. elongatus* was suggested to be associated in part with the connection domain of the monomeric PSI subunits within the trimer [43], and limited energy exchange was expected between those subunits [6]. Trimerization of PSI monomeric complexes may change the state not only of antenna Chls (resulting in the appearance of Chl735) but also of some β-carotene molecules. This can be concluded from the

high circular dichroism (CD) signal at 512 nm of PSI trimers and isolated membranes that contain mainly PSI trimers, while that CD signal in PSI monomers is much lower [5]. A relatively high CD signal at 711 nm in PSI monomers indicates a strong coupling of the Chls forming Chl710, whereas the extremely longwave Chl does not contribute to the CD spectrum suggesting a weaker coupling of Chls forming Chl735.

3. Role of the longwave chlorophylls in photosystem I trimers

Within cyanobacterial PSI trimers, the monomers contribute individually to the electron transport from PSII to NADP since each monomer is capable of crosslinking with soluble ferredoxin and flavodoxin indicating their affinity to electron acceptors [44,45]. The photochemical activity of PSI trimers and monomers isolated from *Spirulina* measured as the rate of oxygen consumption was found to be similar, i.e. no deficiency of electrons was observed in vitro. Such deficiency of electron flow from PSII to PSI occurs in cyanobacterial cells and leads to overoxidation of P700 since the PSI/PSII ratio in cells is above unity [46]. The lower intensity of F760 in the 77 K fluorescence spectrum of previously illuminated *Spirulina* cells as compared with dark-incubated ones indicates the accumulation of $P700^+$ [26].

Only a part ($\sim$30%) of the energy absorbed by PSI bulk Chls (Chl680) migrates to Chl735 and it contributes to P700 photooxidation [28,35] thus indicating the efficient uphill energy transfer from Chl735 to P700 under physiological conditions (Fig. 2, dashed arrows). Photooxidation of P700 in PSI complexes of the cyanobacterium *S. elongatus* was observed under excitation with actinic light in the spectral region up to 750 nm [43] but the mechanism of that uphill energy transfer is not clear. It was proposed that longwave Chls in PSI complexes may concentrate energy near P700 [28,29,47] or in addition increase the absorption cross-section [48]. Mechanisms of energy migration within PSI antenna were discussed earlier [29,47,49,50]. The longwave Chls in PSI trimers significantly increase the absorption cross-section [38,48] and promote energy exchange between monomers within a trimer [51].

The peripheral location of some Chls on the monomers forming the PSI trimer of *Spirulina* enables the interaction of their antennae. The linear dependence of the rate of P700 photooxidation on the relative content of $P700^+$ indicates no energy exchange between the antennae of monomers within a trimer that gives a gain in photochemistry [27]. However, a non-linear dependence between the rate of F760 quenching and the relative P700 content ($P700/P700+P700^+$) in PSI trimers indicates such an energy exchange between monomers: although only $P700^+$ is responsible for F760 quenching, the rate of F760 quenching is faster than the rate of $P700^+$ accumulation [51]. Thus the antennae of monomers within a trimer may exchange energy which then dissipates into heat. When P700 in one of the monomers is oxidized, energy from monomers with reduced P700 migrates via the longwave Chl735 to the antenna of a monomer with oxidized P700 and is quenched by $P700^+$ (Fig. 2, bold arrow). Dissipation of the excess energy may protect the PSI complex against photodestruction, thus increasing its stability. This protection mechanism, found for PSI trimers of *Spirulina,* living in alkaline lakes with high light intensity, may also appear in other cyanobacteria as an answer to growth at stress conditions

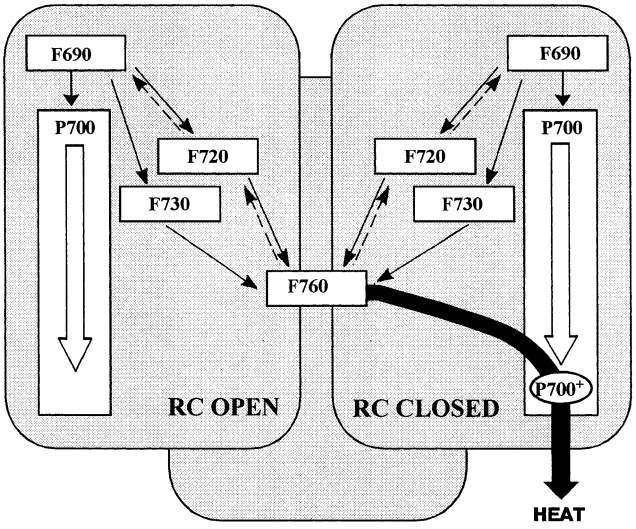

Fig. 2. Scheme of energy migration within Chl pools of the core antenna of monomers in the PSI trimer of *Spirulina,* and energy exchange between the antennae of the monomers with open (left) and closed (right) reaction center (RC). The pigment pools of the core antenna are represented as corresponding fluorescence bands: F690, emission of the bulk Chl; F720 and F730, emission of the intermediately longwave Chls; F760, emission of the extremely longwave Chl735 that originates from interaction of Chl molecules located on different monomers and therefore makes possible energy exchange between them. Arrows indicate downhill (solid arrow) and uphill (dashed arrow) energy transfer between the pigment pools, the bold arrow indicates the dissipation of energy into heat by $P700^+$.

such as high light intensity, high salt and pH, varying nutrient availability, etc. Non-radiative energy quenching as observed also in aggregates of LHCII [52,53] indicates that the ability to dissipate energy could be a general feature of trimeric pigment-protein complexes.

4. Excitation dynamics in photosystem I trimers

Although the position of most antenna Chls within the cyanobacterial PSI complex is now known [6], the exciton kinetics in the PSI antenna and the time of charge separation in the reaction center remain unclear. The detailed kinetics of energy migration and trapping could be determined by means of ultrafast optical spectroscopy in the femtosecond to nanosecond time range. Improvement of time resolution made it possible to resolve the fastest components of the kinetics reflecting the energy equilibration in the bulk antenna and energy migration to and from the longwave Chls. Time-resolved fluorescence as a function of the emission wavelength (decay-associated spectra, or DAS) is a very sensitive method for probing the antenna equilibration process [54]. The DAS of PSI trimers and monomers of unicellular cyanobacteria at room temperature showed only small differences [30,31] while the DAS of *Spirulina* PSI trimers and monomers indicated a clear contribution of the extremely longwave Chl735 in PSI trimers [35,38]. The dependence of the F760 intensity on the redox state of P700 at 77 K suggests substantially different kinetics of energy migration in the PSI core antenna of *Spirulina* with P700 being reduced or oxidized. However, no effect of the P700 redox state was observed on the fluorescence decays at room temperature, in accordance with steady-state

spectra. The same lifetimes (~9, ~30, ~65 and ~1400–2200 ps) were found for both types of PSI complexes of *Spirulina* [35]. The spectrum of the fastest component was ascribed to the slowest component of the energy transfer from the bulk antenna to the red pigments which is comparable with that of PSI complexes from *Synechocystis* sp. [31]. Slow components with maxima at 720 nm (30 ps) and 740 nm (65 ps) reflect energy transfer to and from longwave Chls, i.e. the equilibration among the small pools of longwave Chls takes a relatively long time.

The trapping in PSI occurs only via the bulk Chls: upon excitation of the bulk antenna charge separation takes place with a high yield and only part of the excitation reaches the longwave Chls [35]. Calculated rate constants indicate that charge separation from the bulk is more trap-limited than diffusion-limited but the excitation dynamics of the longwave Chls is extremely diffusion-limited [38]. An important feature of PSI is that the red pigment pools are not in close contact with each other as reflected by an almost negligible rate constant of transfer among red pools, and the fact that excitation trapping from red pools occurs almost exclusively via the bulk antenna. The indirect connection of the red pools to P700 proves that they are located at the periphery of the complex, and none of the red pools may serve as a pre-trap.

A unique dependence of fluorescence kinetics of PSI trimers of *Spirulina* on the redox state of P700 was found in measurements of DAS at 77 K [39]. In the DAS of trimers with reduced P700 three zero-crossing energy transfer components (~9, ~190, ~450 ps) have been resolved, reflecting downhill energy migration (Fig. 2) from bulk Chls (F690) and shorter longwave Chls (F720, F730) to the most longwave Chl735 (F760) from which the excitation leaves the antenna as ns fluorescence. In addition, two all-positive components (~1.3 and ~3.5 ns) were discovered in fluorescence DAS spectra of PSI trimers with P700 reduced. For PSI trimers with P700 oxidized the shortest component remained the same, while the other lifetimes became shorter: the 190 ps component decreased to 100 ps, and the 1.3 ns component decreased to 585 ps. If P700 in PSI trimers is oxidized, the fluorescence of extremely longwave Chl735 is quenched efficiently by the P700 oxidation due to the energy migration from Chl735 to the cation radical of P700. Although Chl735 is not located in the direct vicinity of P700 – the distance between Chl735 and P700 is about 42 Å – the extreme red pool (F760 in Fig. 2) is quenched by $P700^+$ most efficiently due to optimal overlap: a lifetime of about 100 ps was calculated for efficient Förster transfer [38,39].

A special spatial arrangement of the spectrally different pigment pools may explain the data obtained for the PSI trimer. A kinetic model was developed describing two parallel ways of energy migration in the core antenna of PSI trimers from the bulk to the longwave Chls with emission peaks at 720 or 730 nm (F720 and F730, respectively), and then to Chl735 [39]. The quenching of the red pigment pools occurs directly via energy transfer from Chl735 to $P700^+$. All rate constants of energy transfer and charge separation were found to be similar in both P700 redox situations, only the quenching rate constants to the ground state differed between PSI trimers with oxidized and reduced P700. The scheme in Fig. 2 combines the pathways of energy migration among Chl pools within the core antenna [38] with the process of energy exchange between the monomers [51].

The detailed kinetics of the energy migration in the antenna and of the charge separation in the PSI reaction center were followed as absorption transients of cyanobacterial complexes with picosecond resolution [29,55,56]. The most advanced absorption transients measured for *Spirulina* PSI trimers (P700 reduced) with 60 fs resolution show only a small number of lifetimes. Energy transfer and equilibration within the bulk antenna occurs in the range of 100 fs to 1 ps; two lifetime components in the range of 1–10 ps reflect a large part of charge separation that occurs from bulk Chls [38]. The 10 ps component also reflects energy transfer to the red pools, where components of about 20–30 ps and 70 ps reflect the energy trapping from red pools. The PSI reaction center is the fastest one known so far: 300–500 fs for the intrinsic charge separation as compared with 3 ps for other reaction centers. The proposed kinetic model for the excitation trapping from the bulk antenna and the processes in the PSI reaction center confirm this extremely high rate of charge separation.

Thus PSI trimers in cyanobacteria are involved in photosynthetic electron transport and in dissipation of the excess energy. Longwave Chls of PSI trimers are located not in the close vicinity of P700, but are active in P700 photooxidation and rather increase the absorption cross-section than concentrate energy near P700. Charge separation in the PSI reaction center is the fastest as compared with other centers. The extremely longwave Chl735 in PSI trimers of *Spirulina* makes possible energy exchange between monomers promoting dissipation of the excess energy into heat by $P700^+$. The longwave Chls of *Spirulina* PSI trimer that permit the inter-monomer energy exchange, and therefore protect that complex, may also be formed in PSI trimers of other cyanobacteria as an answer to growth under stress conditions.

Acknowledgements: We thank Dr. P. Fromme and colleagues for permission to use a scheme of the cyanobacterial PSI trimer in our review. This work was supported by grants of NATO Scientific Affairs Division (LST.CLG 975955, N.K. and M.R.), the Russian Foundation of Basic Research (99-04-41180, N.K.), and the Deutsche Forschungsgemeinschaft (SFB 189, A.R.H. and SFB 480, M.R.).

References

[1] Golbeck, J.H. (1992) Annu. Rev. Plant Physiol. Plant Mol. Biol. 43, 293–324.
[2] Golbeck, J.H. (1994) in: The Molecular Biology of Cyanobacteria (Bryant, D.A., Ed.), pp. 319–360, Kluwer Academic, Dordrecht.
[3] Chitnis, P.R. (1996) Plant Physiol. 111, 661–669.
[4] Rögner, M., Mühlendorf, U., Boekema, E.J. and Witt, H.T. (1990) Biochim. Biophys. Acta 1015, 415–424.
[5] Shubin, V.V., Tsuprun, V.L., Bezsmertnaya, I.N. and Karapetyan, N.V. (1993) FEBS Lett. 334, 79–82.
[6] Schubert, W.-D., Klukas, O., Krauss, N., Saenger, W., Fromme, P. and Witt, H.T. (1997) J. Mol. Biol. 272, 741–769.
[7] Krauss, N., Hinrichs, W., Witt, I., Fromme, P., Pritzkow, W., Dauter, Z., Betzel, C., Wilson, K.S. and Witt, H.T. (1993) Nature 361, 326–331.
[8] Kruip, J., Chitnis, P.R., Lagoutte, B., Rögner, M. and Boekema, E.J. (1997) J. Biol. Chem. 272, 17061–17069.
[9] Chitnis, V.P. and Chitnis, P.R. (1993) FEBS Lett. 336, 330–334.
[10] Biggins, J. and Bruce, D. (1984) Photosynth. Res. 20, 1–34.
[11] Mullineaux, C. (1992) Biochim. Biophys. Acta 1100, 285–292.
[12] Mullineaux, C. (1994) Biochim. Biophys. Acta 1184, 71–77.
[13] Schluchter, W.M., Shen, G., Zhao, J. and Bryant, D.A. (1996) Photochem. Photobiol. 64, 53–66.

[14] Bruce, D., Brimble, S. and Bryant, D.A. (1989) Biochim. Biophys. Acta 974, 66–73.
[15] Rögner, M., Boekema, E.J. and Barber, J. (1996) Trends Biochem. Sci. 21, 44–49.
[16] Jansson, S. (1994) Biochim. Biophys. Acta 1184, 1–19.
[17] Shubin, V.V., Karapetyan, N.V. and Krasnovsky, A.A. (1986) Photosynth. Res 9, 3–12.
[18] Takahashi, Y., Hirota, K. and Katoh, A. (1985) Photosynth. Res. 6, 183–192.
[19] Karapetyan, N.V. (1998) Membr. Cell Biol. 12, 571–584.
[20] Schubert, W.-D., Klukas, O., Saenger, W., Witt, H.T., Fromme, P. and Krauss, N. (1998) J. Mol. Biol. 280, 297–314.
[21] Rhee, K-H., Morris, E.P., Barber, J. and Kühlbrandt, W. (1998) Nature 396, 283–286.
[22] Chitnis, P.R., Xu, Q., Chitnis, V.P. and Nechushtai, R. (1995) Photosynth. Res. 44, 23–40.
[23] Brettel, K. (1997) Biochim. Biophys. Acta 1318, 322–373.
[24] Scheller, H.V., Naver, H. and Moller, B.L. (1997) Physiol. Plant. 100, 842–851.
[25] Shubin, V.V., Bezsmertnaya, I.N. and Karapetyan, N.V. (1992) FEBS Lett. 309, 340–342.
[26] Kruip, J., Karapetyan, N.V., Terekhova, I.V. and Rögner, M. (1999) J. Biol. Chem. 274, 18181–18188.
[27] Duval, J.C., Thomas, J.C. and Choquet, Y. (1986) Biochim. Biophys. Acta 848, 352–358.
[28] Shubin, V.V., Bezsmertnaya, I.N. and Karapetyan, N.V. (1995) J. Photochem. Photobiol. 30B, 153–160.
[29] Holzwarth, A.R., Schatz, G., Brock, H. and Bittersmann, E. (1993) Biophys. J. 64, 1813–1826.
[30] Turconi, S., Schweitzer, G. and Holzwarth, A.R. (1993) Photochem. Photobiol. 57, 113–119.
[31] Turconi, S., Kruip, J., Schweitzer, G., Roegner, M. and Holzwarth, A.R. (1996) Photosynth. Res. 49, 263–268.
[32] Gobets, B., van Amerongen, H., Monshower, R., Kruip, J., Rögner, M., van Grondelle, R. and Dekker, J.P. (1994) Biochim. Biophys. Acta 1188, 75–85.
[33] Pålsson, L.-O., Dekker, J.P., Schlodder, E., Monshouwer, R. and van Grondelle, R. (1996) Photosynth Res. 48, 239–246.
[34] Shubin, V.V., Murthy, S.D.S., Karapetyan, N.V. and Mohanty, P. (1991) Biochim. Biophys. Acta 1060, 28–36.
[35] Karapetyan, N.V., Dorra, D., Schweitzer, G., Bezsmertnaya, I.N. and Holzwarth, A.R. (1997) Biochemistry 36, 13830–13837.
[36] Koehne, B. and Trissl, H.-W. (1998) Biochemistry 37, 5494–5500.
[37] Garlashi, F.M., Karapetyan, N.V., Cametta, A., Zucchelli, G. and Jennings, R.C. (1998) in: Photosynthwsis: Mechanisms and Effects (Garab, G., Ed.), Vol. 1, pp. 417–420, Kluwer Academic, Dordrecht.
[38] Holzwarth, A.R., Dorra, D., Müller, M. and Karapetyan, N.V. (1998) in: Photosynthesis: Mechanisms and Effects (Garab, G., Ed.), Vol. 1, pp. 497–502, Kluwer Academic, Dordrecht.
[39] Dorra, D., Fromme, P., Karapetyan, N.V. and Holzwarth, A.R. (1998) in: Photosynthesis: Mechanisms and Effects (Garab, G., Ed.), Vol. 1, pp. 587–590, Kluwer Academic, Dordrecht.
[40] Butler, W.L. (1978) Annu. Rev. Plant Physiol. 22, 345–378.
[41] Karapetyan, N.V., Dorra, D., Holzwarth, A.R., Kruip, J. and Rögner, M. (1998) in: Photosynthesis: Mechanisms and Effects (Garab, G., Ed.), Vol. 1, pp. 583–586, Kluwer Academic, Dordrecht.
[42] Kruip, J., Bald, D., Boekema, E.J. and Rögner, M. (1994) Photosynth. Res. 40, 279–286.
[43] Pålsson, L.O., Flemming, C., Gobets, B., van Grondelle, R., Dekker, J.P. and Schlodder, E. (1998) Biophys. J. 74, 2611–2622.
[44] Mühlendorf, U., Kruip, J., Bryant, D.A., Rögner, M., Setif, P. and Boekema, E.J. (1996) EMBO J. 15, 488–497.
[45] Lelong, C., Boekema, E.J., Kruip, J., Bottin, H., Rögner, M. and Setif, P. (1996) EMBO J. 15, 2160–2168.
[46] Fujita, Y. (1997) Photosynth. Res. 53, 83–93.
[47] van Grondelle, R., Dekker, J.P., Gilbro, T. and Sundström, V. (1994) Biochim. Biophys. Acta 1187, 1–65.
[48] Trissl, H.-W. (1993) Photosynth. Res. 35, 247–263.
[49] Valkunas, L., Liuolia, V., Dekker, J.P. and van Grondelle, R. (1995) Photosynth. Res. 43, 149–154.
[50] Croce, R., Zucchelli, G., Garlashi, F.M., Bassi, R. and Jennings, R.C. (1996) Biochemistry 35, 8572–8579.
[51] Karapetyan, N.V., Shubin, V.V. and Strasser, R.J. (1999) Photosynth. Res. (in press).
[52] Mulleneaux, C.W., Pascal, A.R., Horton, P. and Holzwarth, A.R. (1993) Biochim. Biophys. Acta 1141, 23–28.
[53] Ruban, A.V., Young, A.J. and Horton, P. (1996) Biochemistry 35, 674–678.
[54] Holzwarth, A.R. and Roelofs, T.A. (1992) J. Photochem. Photobiol. 15B, 45–62.
[55] Hastings, G., Kleinherenbrink, F.A.M., Lin, S. and Blankenship, R.E. (1994) Biochemistry 33, 3185–3192.
[56] Hastings, G., Hoshina, S., Webber, A.N. and Blankenship, R.E. (1995) Biochemistry 34, 15512–15522.