

Photosynthetic Light-Harvesting Systems Organization and Function

Proceedings of an International Workshop
October 12-16, 1987
Freising, Fed. Rep. of Germany

Editors
Hugo Scheer · Siegfried Schneider



Walter de Gruyter · Berlin · New York 1988

CONTENTS

List of Participants	XIII
----------------------------	------

SECTION I. ORGANIZATION: BIOCHEMICAL METHODS

Introduction: The Biochemistry of Light-Harvesting Complexes by R.J. Cogdell	1
Phycobilisome-Thylakoid Interaction: The Nature of High Molecular Weight Polypeptides by E. Gantt C.A. Lipschultz and F.X. Cunningham Jr.	11
On the Structure of Photosystem II-Phycobilisome Complexes of Cyanobacteria by E. Mörschel and G.-H. Schatz	21
Structure of Cryptophyte Photosynthetic Membranes by W. Wehrmeyer	35
Structural and Phylogenetic Relationships of Phycoerythrins from Cyanobacteria, Red Algae and Cryptophyceae by W. Sidler and H. Zuber	49
Isolation and Characterization of the Components of the Phycobilisome from <u>Mastigocladus laminosus</u> and Cross- linking Experiments by R. Rübeli and H. Zuber	61
C-Phycocyanin from <u>Mastigocladus laminosus</u> : Chromophore Assignment in Higher Aggregates by Cystein Modification by R. Fischer, S. Siebzehrübl and H. Scheer	71
Photochromic Properties of C-Phycocyanin by G. Schmidt, S. Siebzehrübl, R. Fischer and H. Scheer	77
Concerning the Relationship of Light Harvesting Bili- proteins to Phycochromes in Cyanobacteria by W. Kufer	89
Subunit Structure and Reassembly of the Light-Harvesting Complex from <u>Rhodospirillum rubrum G9+</u> by R. Ghosh, Th. Rosatzin and R. Bachofen	93
Primary Structure Analyses of Bacterial Antenna Polypeptides - Correlation of Aromatic Amino Acids with Spectral Properties - Structural Similarities with Reaction Center Polypeptides by R.A. Brunisholz and H. Zuber	103

The Structure of the "Core" of the Purple Bacterial Photo-synthetic Unit by D.J. Dawkins, L.A. Ferguson and R.J. Cogdell	115
A Comparison of the Bacteriochlorophyll C--Binding Proteins of Chlorobium and Chloroflexus by P.D. Gerola, P. Højrup and J.M. Olson	129
Interactions between Bacteriochlorophyll c Molecules in Oligomers and in Chlorosomes of Green Photosynthetic Bacteria by D.C. Brune, G.H. King and R.E. Blankenship	141
Light-Harvesting Complexes of Chlorophyll c-Containing Algae by A.W.D. Larkum and R.G. Hiller	153
Isolation and Characterization of a Chlorophyll a/c-Hetero-xanthin/Diadinoxanthin Light-Harvesting Complex from <i>Pleurochloris meiringensis</i> (Xanthophyceae) by C. Wilhelm, C. Büchel and B. Rousseau	167
The Antenna Components of Photosystem II with Emphasis on the Major Pigment-Protein, LHC IIb by G.F. Peter and P. Thornber	175

SECTION II: ORGANIZATION: MOLECULAR GENETICS AND
CRYSTALLOGRAPHY

Molecular Biology of Antennas by G. Drews	187
High-Resolution Crystal Structure of C-Phycocyanin and Polarized Optical Spectra of Single Crystals by T. Schirmer, W. Bode and R. Huber	195
Crystallization and Spectroscopic Investigation of Purple Bacterial B800-850 and RC-B875 Complexes by W. Welte, T. Wacker and A. Becker	201
Structure of the Light-Harvesting Chlorophyll a/b-Protein Complex from Chloroplast Membranes by W. Kühlbrandt	211
Phycobilisomes of <i>Synchococcus</i> Sp. PCC 7002, <i>Pseudanabaena</i> Sp. PCC 7409, and <i>Cyanophora paradoxa</i> : An Analysis by Molecular Genetics by D.A. Bryant	217
Organization and Assembly of Bacterial Antenna Complexes by G. Drews	233

The Use of Mutants to Investigate the Organization of the Photosynthetic Apparatus of <u>Rhodobacter sphaeroides</u> by C.N. Hunter and R. van Grondelle	247
Mechanisms of Plastid and Nuclear Gene Expression During Thylakoid Membrane Biogenesis in Higher Plants by P. Westhoff, H. Grüne, H. Schrubar, A. Oswald, M. Streubel, U. Ljungberg and R.G. Herrmann	261
SECTION III: ORGANIZATION: SPECIAL SPECTROSCOPY TECHNIQUES AND MODELS	
Assignment of Spectral Forms in the Photosynthetic Antennas to Chemically Defined Chromophores by A. Scherz	277
Linear Dichroism and Orientation of Pigments in Phycobilisomes and their Subunits by L. Juszczak, N.E. Geacintov, B.A. Zilinskas and J. Breton	281
Low Temperature Spectroscopy of Cyanobacterial Antenna Pigments by W. Köhler, J. Friedrich, R. Fischer and H. Scheer	293
Chromophore Conformations in Phycocyanin and Allophycocyanin as Studied by Resonance Raman Spectroscopy by B. Szalontai, V. Csizmadia, Z. Gombos, K. Csatorday and M. Lutz	307
Coherent Anti-Stokes Raman Spectroscopy of Phycobilisomes, Phycocyanin and Allophycocyanin from <u>Mastigocladus</u> <u>laminosus</u> by S. Schneider, F. Baumann, W. Steiner, R. Fischer, S. Siebzehrübl and H. Scheer	317
Optical Absorption and Circular Dichroism of Bacteriochlorophyll Oligomers in Triton X-100 and in the Light-Harvesting-Complex B850; A Comparative Study by V. Rozenbach-Belkin, P. Braun, P. Kovatch and A.Scherz	323
Absorption Detected Magnetic Resonance in Zero Magnetic Field on Antenna Complexes from <u>Rps. acidophila</u> 7050 - The Temperature Dependence of the Carotenoid Triplet State Properties by J. Ullrich, J.U. v. Schütz and H.C. Wolf	339
Effect of Lithium Dodecyl Sulfate on B 800-850 Antenna Complexes from <u>Rhodospseudomonas acidophila</u> : A Resonance Raman Study by B. Robert and H. Frank	349

Bacteriochlorophyll a/b in Antenna Complexes of Purple Bacteria by B. Robert, A. Vermeglio, R. Steiner, H. Scheer and M. Lutz	355
Bacteriochlorophyll c Aggregates in Carbon Tetrachloride as Models for Chlorophyll Organization in Green Photo- synthetic Bacteria by J.M. Olson and J.P. Pedersen	365
Orientation of the Pigments in the Reaction Center and the Core Antenna of Photosystem II by J. Breton, J. Durantou and K. Satoh	375
Non-Linear Absorption Spectroscopy of Antenna Chlorophyll a in Higher Plants by D. Leupold, H. Stiel and P. Hoffmann	387

SECTION IV: FUNCTION: ELECTRONIC EXCITATION AND ENERGY TRANSFER

Excitation Energy Transfer in Photosynthesis by R. van Grondelle and V. Sundström	403
Fluorescence Spectroscopy of Allophycocyanin Complexes from <u>Synechococcus 6301 Strain AN112</u> by P. Maxson, K. Sauer and A.N. Glazer	439
Picosecond Energy Transfer Kinetics in Allophycocyanin Aggregates from <u>Mastigocladus laminosus</u> by E. Bittersmann, W. Reuter, W. Wehrmeyer and A.R. Holzwarth	451
Picosecond Time-Resolved Energy Transfer Kinetics within C-Phycocyanin and Allophycocyanin Aggregates by T. Gillbro, A. Sandström, V. Sundström, R. Fischer and H. Scheer	457
Energy Transfer in "Native" and Chemically Modified C-Phyco- cyanin Trimers and the Constituent Subunits by S. Schneider, P. Geiselhart, F. Baumann, S. Siebzehnrübl, R. Fischer and H. Scheer	469
Effect of Protein Environment and Excitonic Coupling on the Excited-State Properties of the Bilinchromophores in C-Phycocyanin by S. Schneider, Ch. Scharnagl, M. Dürring, T. Schirmer and W. Bode	483
Excitation Energy Migration in C-Phycocyanin Aggregates Isolated from <u>Phormidium luridum</u> : Predictions from the Förster's Inductive Resonance Theory by J. Grabowski and G.S. Björn	491

Energy Transfer Calculations for two C-Phycocyanins Based on Refined X-Ray Crystal Structure Coordinates of Chromophores by K. Sauer and H. Scheer 507

Energy Transfer in Light-Harvesting Antenna of Purple Bacteria Studied by Picosecond Spectroscopy by V. Sundström, H. Bergström, T. Gillbro, R. van Grondelle, W. Westerhuis, R.A. Niederman and R.J. Cogdell 513

Excitation Energy Transfer in the Light-Harvesting Antenna of Photosynthetic Purple Bacteria: The Role of the Long-Wave-Length Absorbing Pigment B896 by R. van Grondelle, H. Bergström, V. Sundström, R.J. van Dorssen, M. Vos and C.N. Hunter 519

The Function of Chlorosomes in Energy Transfer in Green Photosynthetic Bacteria by R.J. van Dorssen, M. Vos and J. Amesz 531

Energy Transfer in *Chloroflexus aurantiacus*: Effects of Temperature and Anaerobic Conditions by B.P. Wittmershaus, D.C. Brune and R.E. Blankenship 543

Interpretation of Optical Spectra of Bacteriochlorophyll Antenna Complexes by R.M. Pearlstein 555

Time Resolution and Kinetics of "F680" at Low Temperatures in Spinach Chloroplasts by R. Knox and S. Lin 567

Picosecond Studies of Fluorescence and Absorbance Changes in Photosystem II Particles from *Synechococcus* Sp. by A.R. Holzwarth, G.H. Schatz and H. Brock 579

Analysis of Excitation Energy Transfer in Thylakoid Membranes by the Time-Resolved Fluorescence Spectra by M. Mimuro 589

V. CONCLUDING REMARKS

Future Problems on Antenna Systems and Summary Remarks by E. Gantt 601

Author Index 605

Subject Index 609

ENERGY TRANSFER IN "NATIVE" AND CHEMICALLY MODIFIED
C-PHYCOCYANIN TRIMERS AND THE CONSTITUENT SUBUNITS

S. Schneider, P. Geiselhart, F. Baumann

Institut für Physikalische und Theoretische Chemie der
Technischen Universität München,
Lichtenbergstraße 4, D-8046 Garching

S. Siebzeührübl, R. Fischer, H. Scheer

Botanisches Institut der Ludwig-Maximilians-Universität
Menzingerstraße 67, D-8000 München 19

Introduction

The light-harvesting complexes of blue-green and red algae, called phycobilisomes, are highly organized assemblies of the biliproteins allophycocyanin (APC) and phycocyanin (PC), often containing also phycoerythrin (PE) or phycoerythrocyanin (PEC) [1,2]. These biliproteins carry one or several tetrapyrrol chromophores bound covalently to polypeptides. In case of PC, which is discussed here, the monomeric unit consists of the α -polypeptide chain with one chromophore (A84) and the β -chain with two phycocyanobilin chromophores attached to it (B84 and B155) [3,4].

From X-ray work [5,6] on PC from two different organisms, the crystal structure of the chromoprotein, the conformations, distances and the approximate relative orientations of the chromophores have become known recently. Very similar results have been obtained for a trimer $(\alpha\beta)_3$ from Mastigocladus laminosus and a hexamer $(\alpha\beta)_6$ from Agmenellum quadruplicatum, which is composed of two trimeric units aggregated face-to-face. For the understanding of the energy transfer process within these units and in the whole phyc-

bilisome, three features deduced from this analysis are important.

- (i) The chromophore arrangement exhibits a 3-fold symmetry around the central axis orthogonal to the plane of the trimeric unit.
- (ii) The shortest distance is found between the 1A84 chromophore of one monomeric unit and the 2B84 chromophore of the neighbouring monomer; it is only about 21 Å center to center.
- (iii) All three chromophores adopt an extended geometry; they exhibit hydrogen bonds to a conserved aspartate residue (A87, B87, B39, resp.) and are subject to strong coulombic interaction with the net charges localized on the surrounding amino acids.

If the threefold symmetry established in the crystal structure is also present in the native trimeric unit (i.e., there are only three types of non-equivalent chromophores), then theory predicts that any measurement, which monitors the time course of the excited state population, should be fittable by a sum of three exponentials provided that the evolution of the system can be described by a set of linear differential equations (radiative and intramolecular radiationless decay, energy transfer by dipole-dipole interaction (Förster transfer)).

Because of the short distance between pairs of chromophores, like 1A84 and 2B84, it was concluded that the energy transfer rate between these chromophores should be very high and/or the coupling so strong that Förster theory may not be applicable anymore [7]. Alternatively the model of localized excitonic states should then be used for the description of the energy transfer kinetics (see fig. 1). Besides of the very fast

(and eventually unresolvable) internal conversion process, only two decay times should then be observed in a picosecond time-resolved experiment: one related to the transfer between the s-chromophore and the excitonically coupled state of chromophores A84/B84 (devoted C^+ or C^- in fig.1) and intramolecular decay of the corresponding state (C^+). Since the important factors in excitonic coupling are the energy difference of the unperturbed states and their interaction energy, a modification of one of the chromophores by a distinct perturbation could result in an intermediate situation between the two above described limiting cases and therefore help to elucidate the situation in PC-trimers.

In a previous publication [8] it was shown that titration of solutions of biliproteins in various states of aggregation with the mercury salt p-chloromercurbenzenesulfonate (PCMS)

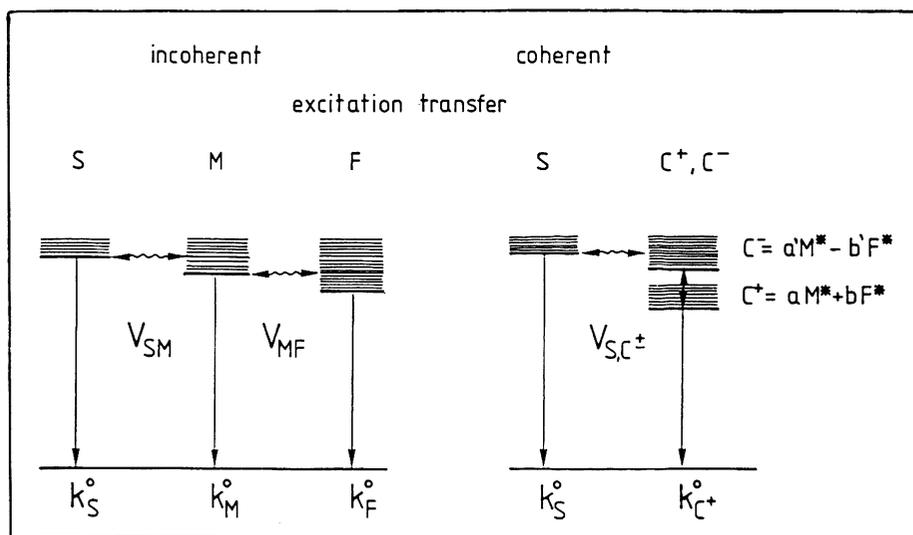


Fig. 1: Left : Förster type energy transfer
Right: Excitonic interaction between M and F chromophores

leads to a binding of this compound to the free cystein B111, and concomitantly to a selective change in the absorption and circular dichroism spectra of the close-by chromophore B84. Resonance-enhanced CARS spectra (Coherent Anti-Stokes Raman Scattering) of such modified PC-trimers confirm the evidence for a change in geometry of B84, which was deduced from the X-ray data [9]. In this contribution the effects of PCMS-binding on CARS spectra (structural information) and excited state kinetics are compared. It is concluded that in smaller aggregates (up to trimers) a microheterogeneity of the chromophore-protein arrangement exists, which produces a rather complex fluorescence decay pattern.

Materials and Methods

PC-trimers without linker peptides were prepared according to published procedures [10]. β -subunits were isolated by a modified flat-bed gel electrofocusing technique [11]. In particular, care was taken to avoid oxidative bleaching of the chromophores by gassing with Argon and work under subdued light. The pigment is present as a dimer (β_2). Both types of samples were titrated with PCMS in approximately 1.1 fold excess with respect to the number of free cysteines to assure complete modification.

The fluorescence decay curves were recorded by means of a Hamamatsu synchroscan streak camera using interference filters for spectral narrowing of the monitored emission. Excitation was performed under magic angle conditions at low average intensity (≈ 10 mW or 10^{13} photons pulse⁻¹cm⁻²) by the output of a synchronously pumped mode-locked dye laser (pulse repetition rate 84 MHz). The decay curves were analysed by applying a least-squares fit routine and assuming a 3-exponential decay law (More details are given in references 12-14).

Resonance-enhanced Coherent Anti-Stokes Raman Scattering (CARS) was measured with an apparatus described in detail in references 15 and 16. Two eximer laser-pumped dye lasers generate the so-called pump- and Stokes-beams, with wavelengths λ_p (fixed) and λ_s (variable), which are focused in the sample under a small angle. Recording the intensity of the generated anti-Stokes radiation as a function of the wavenumber difference $\tilde{\nu}_p - \tilde{\nu}_s$ yields a vibrational spectrum. Since λ_p coincides with an electronic transition (absorption band) of the chromophore, only the chromophore's vibrations are resonance-enhanced and, therefore, dominate the spectrum.

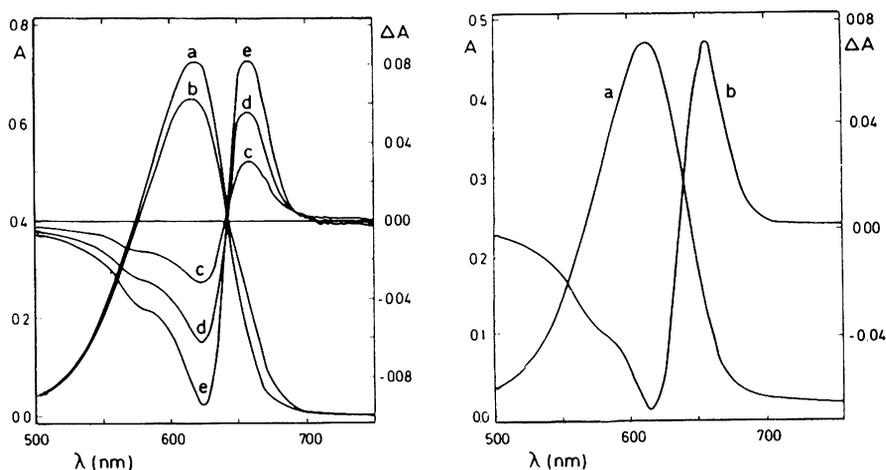


Fig. 2: Left: Absorption spectra of PC trimers before (a) and after titration with PCMS (b). Difference spectra recorded 30 (c), 60 (d) and 100 min. (e, final absorption) after PCMS addition. Right: Absorption spectrum of β -subunit (a) and final difference spectrum after PCMS titration (b).

Results and Discussion

In figure 2, the effect of PCMS titration (binding) on the absorption spectra of β -subunits (present as dimers β_2) and trimeric PC are shown. In both cases the absorbance at the long-wavelength side of the absorption maximum ($\lambda_{max} = 604 \text{ nm}$ and 616 nm , resp.) is reduced by about 10 % and there is a concomitant increase in the long wavelength slope of this band (wavelength of maximum absorbance increase is $\approx 655 \text{ nm}$).

Figure 3 displays the CARS spectra recorded for the four samples in the fingerprint region. At first glance it is already apparent that the band centered at 1247 cm^{-1} in native PC-trimers disappears upon addition of PCMS, whereas the other bands remain essentially unchanged. The spectrum of β_2 , on the other hand, exhibits no change which is beyond experimental uncertainty. Furthermore it is interesting to

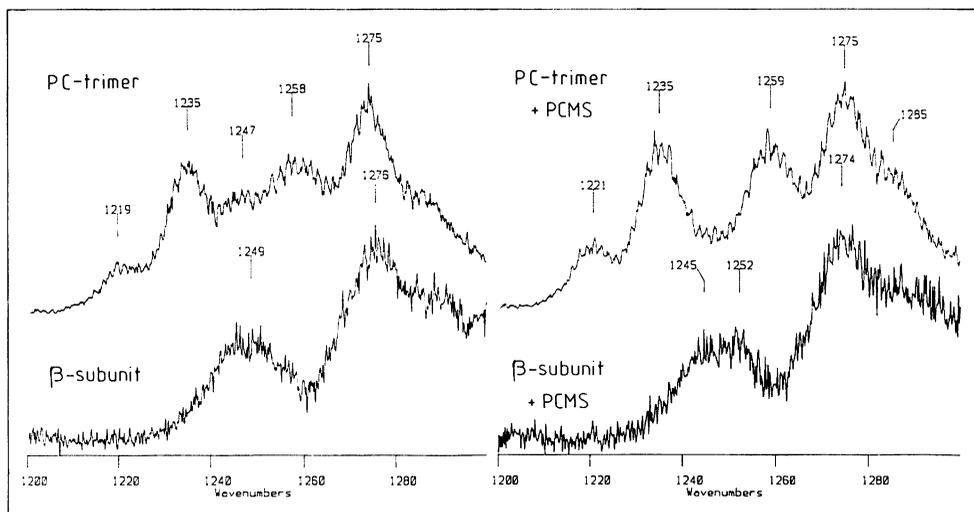


Fig. 3: Resonance-enhanced CARS spectra of PC trimers (left, top), PC β -subunits (left, bottom), PC trimers titrated with PCMS (right, top), PC β -subunits titrated with PCMS (right, bottom). Pumpwavelength 640 nm.

note that PC trimers, which have only one additional type of non-equivalent chromophore, show at least 3 more bands, namely at 1221, 1235 and 1259 cm^{-1} . The band which appears in both spectra (1245 - 1252 cm^{-1}) disappears upon PCMS binding in the trimer spectrum. This fact can be taken as additional evidence that it is the chromophore B84, whose geometry is changed predominantly upon PCMS binding. In the double bond stretching region (1550 - 1700 cm^{-1}) no changes upon PCMS titration have been observed for β_2 and only small, but significant ones are observed for PC trimers [16].

In order to demonstrate the large change induced in the fluorescence decay of PC trimers upon PCMS binding, the decay curves recorded with 600 nm excitation, but different observation wavelengths are shown in fig.4. Even without analysis it is obvious that the wavelength, above which a delayed onset of the fluorescence is observed, is increased from about 620 nm to 670 nm. Furthermore, it is apparent that the contribution of the long-lived component is much larger in the native system and this effect is increasingly pronounced at shorter wavelengths. In contrast to the pronounced effect found in PC-trimers, however, only a minor effect is observed for β_2 (small reduction in the lifetime of the terminal emitter). In figures 5 to 8, the results (lifetimes deduced from a 3-exp. fit) are summarized for easier comparison. The following conclusions can be drawn:

In case of dimers of the β -subunit the lifetime of the long-lived component shows a slight reduction upon PCMS binding. Its apparent value varies with observation wavelength, but appears to be fairly independent of the excitation wavelength. A similar statement holds for the intermediate component. For the short-lived component, the situation is quite different. With increasing observation wavelength, the apparent decay time of the fast fluorescence increases by more than a factor of 2 up to 60 ps. In the red part of the emission,

the derived rise times are generally speaking below 20 ps. In the measurements close to the "turning" wavelength, an excitation wavelength dependence is apparent.

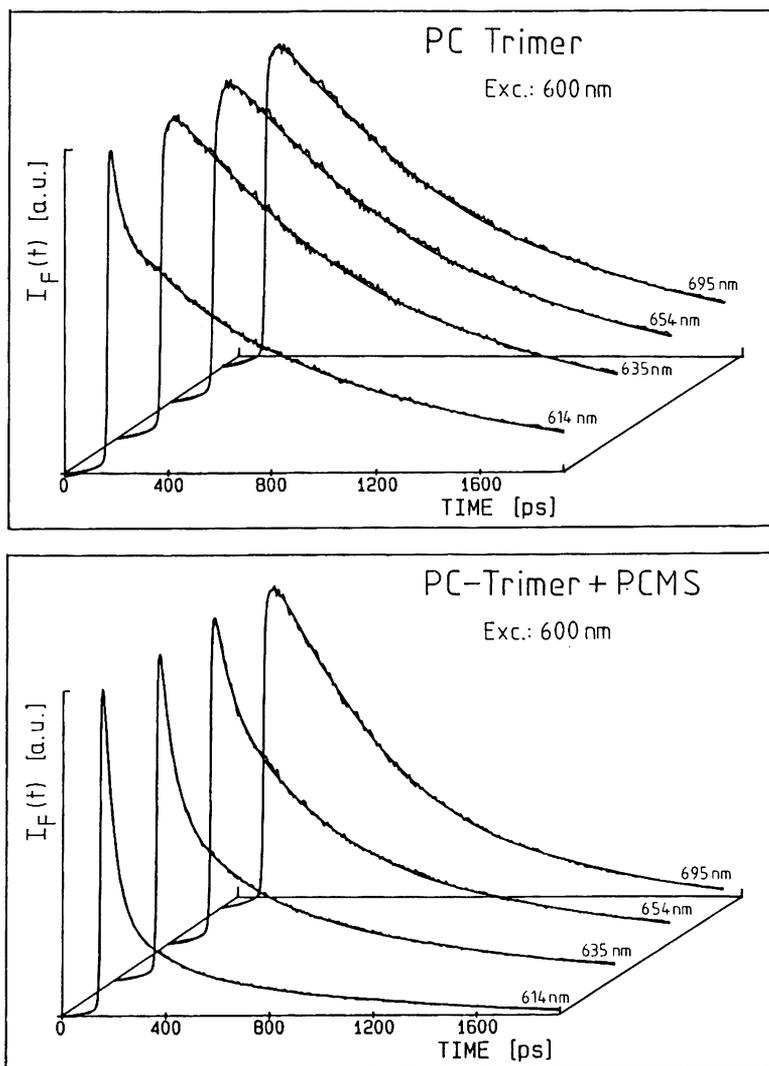


Fig. 4: Fluorescence decay of PC trimers and PC trimers titrated with PCMS.

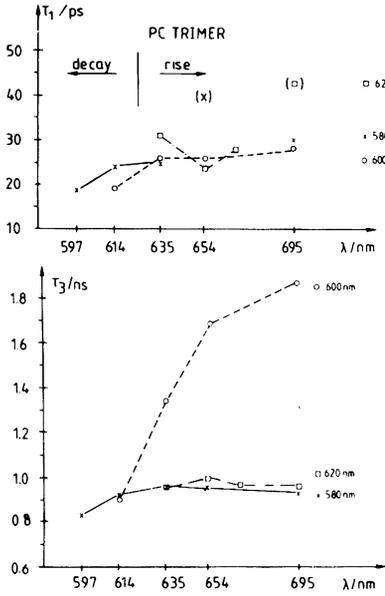


Fig. 5

Fig. 7

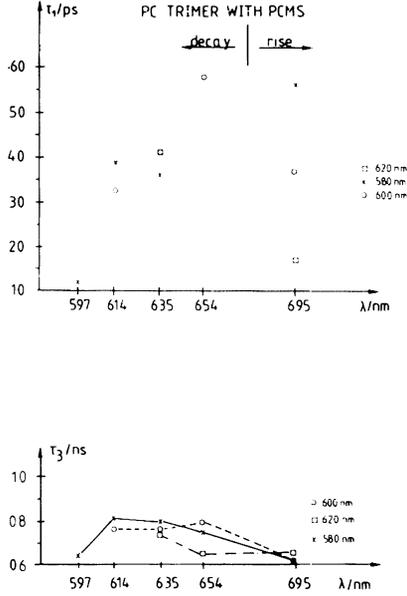


Fig. 6

Fig. 8

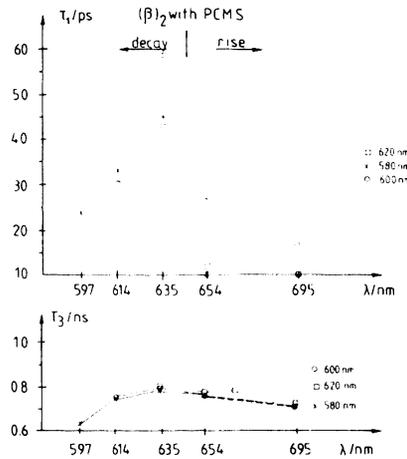
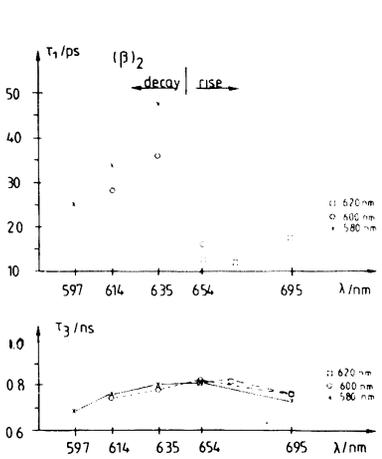


Fig. 5-8: Observed fluorescence lifetimes τ_1 and τ_3 of PC trimers in dependence of excitation ($x=580\text{nm}$, $o=600\text{nm}$, $\square=620\text{nm}$) and detection wavelength (absciss).

Fig. 5: PC trimers. Fig. 6: PC trimers titrated with PCMS.

Fig. 7: Dimers of β -subunits from PC.

Fig. 8: Dimers of β -subunits from PC titrated with PCMS.

As one might already expect from the behaviour of the CARS spectra, the effects of PCMS binding are substantially different in case of trimers. In the "native" system, excitation around 600 nm seems to preferentially select a chromophore-protein moiety, which is characterised by a very long fluorescence decay time (1.8 ns). By PCMS-binding the formation of this species must be prevented, because no such long time constant is observed for any of the excitation wavelengths (600, 580 or 620 nm).

The apparent lifetime of the predominant terminal emitter is reduced upon PCMS binding from about 0.9 to about 0.7 ns. Similarly, the decay time of the intermediate component is reduced from approx. 200 ps to approx. 100 ps.

The lifetime of the shortest-lived component experiences an interesting PCMS-effect. In the "native" system the decay times derived from the emission on the short-wavelength side of the fluorescence spectrum (20-30 ps) agree fairly well with the rise times found in the emission on the long-wavelength side. However, a situation similar to that described for β_2 is found in the PCMS treated trimers. There is an increase of the decay time with observation wavelength and a dependence of the rise time on excitation wavelength.

Because of the change in sign of its amplitude with increasing observation wavelength and the appearance of similar values in the decay of the β -subunit (in monomeric β -subunits prepared by application of detergent, a very similar decay pattern as in β_2 is observed) the 20 - 30 ps lifetime is assigned to the decay of the excited state population of B155 (in agreement with other authors [18, 19]).

The observed decrease in the lifetime of the terminal emitters upon PCMS binding could also be due to changes in radiationless decay rates, caused by the reduced energy gap ΔE ($S_1 \rightarrow S_0$). It can not be taken as unambiguous indication for strong coupling between 1A84 and 2B84 chromophores.

The intermediate lifetime has been related in the past [20, 21, 22] to the energy transfer between 1A84 and 2B84 chromophores. Our present results do not support this interpretation for several reasons:

- (i) A component exhibiting a lifetime of around 200 ps was found not only in the trimers, but also in monomers and both α - and β -subunits.
- (ii) This component was always detected as a decaying component. Representing a transfer time, its amplitude should change sign for long wavelength detection similar to the one of the fast component or at least decrease in amplitude at long wavelength detection.
- (iii) The amplitude was always above 10%. If it were related to a transfer between two chromophores with similar absorption and emission characteristics, the amplitude should be very small (it is expected to be proportional to the difference of the spectral properties, i.e. emission or absorption in case of pump-probe experiments).

We therefore believe that the intermediate component is connected with a modified chromophore-protein arrangement. E.g., we have found a lifetime in the 200 - 300 ps time domain in chromopeptides, where it is suspected that the chromophore adopts a ZZE configuration.

Before entering the discussion about the coupling of the 1A84 - 2B84 pair, it should be mentioned that, when pump-probe experiments were performed on PC trimers [14], all absorption recovery curves could be fit very well by assuming a biexponential decay law. The derived long lifetime varied around 950 ps, the shorter one between 20 and 100 ps, depending on wavelength of pump and probe beam.

Combining the results of transient absorption and fluorescence experiments we conclude that the energy transfer time between the 1A84 - 2B84 pair is on the order of or faster than the measured fast component. Then, the fast component is actually a superposition describing two processes (i.e. a s-to-f transfer from B155 and a f-to-f transfer A84/B84). Since the coupling strength between the A84 - B84 pair is sensitive to variations in the electronic properties of the chromophores, the pronounced wavelength dependence could be understood. That is to say we relate the observed dependence of the short lifetime on excitation and detection wavelength to the existence of a microheterogeneity in chromophore-protein arrangement which effects mainly the coupling between A84 and B84 of neighbouring monomers. Model calculations [23] have shown that small changes in the protein environment (e.g. formation of tautomeric forms of amino acid residues) are sufficient to shift the excitation energy of one chromophore by 10 nm.

Preliminary experiments using the CARS technique suggest that the microheterogeneity postulated here for the smaller aggregates is reduced when linker peptides are present as in phyco-bilisomes [24]. Deviations from exact threefold symmetry seem nevertheless to occur even in the larger systems. Because of the overall arrangement of the chromophores in the light-harvesting complexes a few "defects" should not reduce significantly the efficiency of energy transfer to the reaction center.

Acknowledgement

Financial support by Deutsche Forschungsgemeinschaft (SFB 143 and Forschergruppe 'Pflanzliche Tetrapyrrole') und Fonds der Chemie is gratefully acknowledged. Thanks are also due to Hamamatsu Photonics Europe for loan of the streak camera.

References

- [1] Gant, E., 1981. *Ann. Rev. Plant Physiol.* 32, 327 - 347
- [2] Mörschel E. and E. Riehl, 1987. In: *Electron Microscopy of Proteins (vol 6): Membraneous Structures.* (J. R. Harris, W. Home, eds.). Academic Press, London. 209-254.
- [3] Scheer, H., 1982. In: *Light Reaction Path of Photosynthesis.* (F.K. Fong, ed.). Springer-Verlag, Berlin. 7 - 45.
- [4] Frank G., W. Sidler, H. Widmer and H. Zuber, 1978. *Hoppe-Seyler's Z. Physiol. Chem.* 359, 1499 - 1507.
- [5] Schirmer, T., W. Bode, R. Huber, W. Sidler and H. Zuber, 1985. *J. Mol. Biol.* 184, 257 - 277
- [6] Schirmer, T., W. Bode, R. Huber, 1987. *J. Mol. Biol.*, 196, 677-695.
- [7] Sauer, K. and H. Scheer, 1987. Contribution in this volume.
- [8] Siebzehrübl, S., R. Fischer and H. Scheer, 1987. *Z. Naturforsch.* 42c, 258 - 262
- [9] Duerring M. and R. Huber. Private communication.
- [10] Füglistaller, P., H. Widmer, G. Frank and H. Zuber, 1981. *Arch. Microbiol.* 129, 268 - 274.
- [11] Köst-Reyes E., S. Schneider, W. John, R. Fischer, H. Scheer, H.-P. Köst, 1987. *Electrophoresis* 8, 335-336.
- [12] Hefferle, P, P. Geiselhart, T. Mindl, S. Schneider, W. John, and H. Scheer, 1984. *Z. Naturforsch.* 39c, 606 - 616.
- [13] Geiselhart, P, 1987. PhD thesis, Techn. University Munich.
- [14] Schneider, S., P. Geiselhart, S. Siebzehrübl, R. Fischer and H. Scheer, 1987. *Z. Naturforsch.* c, in press.
- [15] Klüter, U., 1986. PhD thesis, Techn. University Munich.
- [16] Schneider, S, F. Baumann, U. Klüter, 1987. *Z. Naturforsch.* 42c(11/12).

- [17] Schneider, S., P. Geiselhart, F. Baumann, H. Falk and W. Medinger, 1987. *J. Photochem. Photobiol.*, (submitted).
- [18] Holzwarth A.R., J. Wendler and G.W. Suter, 1987. *Biophys. J.* 51, 1 - 12.
- [19] Gillbro T., A. Sandström, V. Sundström, R. Fischer and H. Scheer, 1987. Contribution in this volume.
- [20] Holzwarth, A.R., 1986. In: *Topics in Photosynthesis* (J. Barber, ed.). Elsevier, Amsterdam.
- [21] Hefferle, P., W. John, H. Scheer and S. Schneider, 1984. *Photochem. Photobiol.* 39, 221 - 232.
- [22] Wendler, J., W. John, H. Scheer and A.R. Holzwarth, 1986. *Photochem. Photobiol.* 44, 79 - 86.
- [23] Schneider S., Ch. Scharnagl, M. Duerring, T. Schirmer and W. Bode, 1987. Contribution in this volume.
- [24] Schneider S., F. Baumann, W. Steiner, S. Siebzehrübl, R. Fischer and H. Scheer, 1987. Contribution in this volume.