Encyclopedia of
Plant Physiology

New Series Volume 19

Editors
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Photosynthesis III

Photosynthetic Membranes and Light Harvesting Systems

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Springer-Verlag
Berlin Heidelberg New York Tokyo

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With 163 Figures

ISBN 3-540-16140-6 Springer-Verlag Berlin Heidelberg New York Tokyo
ISBN 0-387-16140-6 Springer-Verlag New York Heidelberg Berlin Tokyo

Library of Congress Cataloging-in-Publication Data. (Revised for vol. 3) Main entry under title: Photosynthesis. (Encyclopedia of plant physiology; new ser., v. 5–6, 19) Includes bibliographies and indexes. Contents: 1. Photosynthetic electron transport and photophosphorylation, edited by A. Trebst and M. Avron. 2. Photosynthetic carbon metabolism and related processes, edited by M. Gibbs and E. Latzko. 3. Photosynthetic membranes and light harvesting systems, edited by L.A. Staehelin and C.J. Arntzen. 1. Photosynthesis – Collected works. I. Trebst, Achim. II. Alberte, R.S. III. Series. QK711.2.E5 vol. 5–6 581.1s [581.1'3342] 76-30357 [QK882] ISBN 0-387-07962-9 (v. 1)

Printed in Germany

Typesetting, printing and bookbinding: Universitätsdruckerei H Stürtz AG, Würzburg
2131/3130-543210

Preface

The *Encyclopedia of Plant Physiology* series has turned several times to the topic of photosynthesis. In the original series, two volumes edited by A. PIRSON and published in 1960 provided a broad overview of the entire field. Although the New Series has devoted three volumes to the same topic, the overall breadth of the coverage has had to be restricted to allow for greater in-depth treatment of three major areas of modern photosynthesis research: I. Photosynthetic Electron Transport and Photophosphorylation (Volume 5 edited by A. TREBST and M. AVRON, and published in 1977); II. Photosynthetic Carbon Metabolism and Related Processes (Volume 6 edited by M. GIBBS and E. LATZKO, and published in 1979); and III. Photosynthetic Membranes and Light-Harvesting Systems (this volume).

As we approached the organization of the current volume, we chose a set of topics for coverage that would complement the earlier volumes, as well as provide updates of areas that have seen major advances in recent years. In addition, we wanted to emphasize the following changes in the study of photosynthetic systems which have become increasingly important since 1977: the trend toward increased integration of biochemical and biophysical approaches to study photosynthetic membranes and light-harvesting systems, and a renewed appreciation of the structural parameters of membrane organization.

Due to the increased complexity of the field, we also decided to try a new format for our volume to better serve the following two purposes. First, we believe a review volume on photosynthetic membranes should serve as a reference source for nonspecialists interested in obtaining an overview of both oxygenic and anoxygenic photosynthesis. This need has been answered by the inclusion of five introductory chapters which summarize the main broad topic areas of the volume. We also recognize that a review volume should provide insight to the "state of the art" in specific research areas which have seen major recent advances. To this end, Chapters 6 through 11 have been organized such that each consists of a number of minireviews related to a common theme. All of the 43 minireviews are authored by highly regarded specialists, and focus on recent research highlights and interpretations of significant new findings. Great emphasis has been placed on the integration of the materials covered in the introductory chapters and in the minireviews. Extensive cross-referencing has been used to allow easy transitions by the reader from a general to a specialized coverage of a topic. Similarly, all minireviews contain references to the appropriate introductory chapters, as well as to other minireviews.

With students in mind, the authors of the introductory chapters have stressed integrative and comparative aspects of their topics. This type of approach is becoming more and more relevant in photosynthesis research, thanks to the convergence of information coming from structural, biophysical, and biochemical studies. Indeed, it is truly exciting to witness the progress being made toward the goal of a molecular understanding of the diverse biophysical and biochemical reactions associated with photosynthetic membranes and light-harvesting systems.

The specialized chapters in this volume begin with the topic of light harvesting by photosynthetic membranes. The minireviews of Chapter 6 summarize biochemical and structural studies of light-harvesting assemblages, with emphasis on the light-harvesting components of bacteria and algae, since higher plant chloroplast components are extensively reviewed in Chapter 3. Whereas Chapter 6 emphasizes the biochemical diversity in light-harvesting systems, Chapter 7 consists of minireviews which discuss unifying concepts governing light-harvesting events. All authors in this section are concerned with photon absorption and structural parameters of the pigment bed that determine the efficiency of excitation energy transfer to reaction centers.

The most fundamental result of photosynthetic light reactions is the conversion of excitation energy, derived from absorbed light, into stable chemical form. This occurs in the reaction center (RC). In the last 5 years there have been major advancements in the understanding of these processes – especially by those groups who have focused their work on photosynthetic bacteria. The identity of the cofactors (chlorophyll, pheophytin, quinones, etc.) involved in the initial charge separations and the events involved in charge stabilization are now highly defined. The minireviews of Chapter 8 present various aspects of this rapidly moving field, ranging from energetic considerations of the RC to discussions of similarities and differences among the different types of protein which comprise different reaction centers.

Chapter 9 makes a transition from the highly defined bacterial reaction centers into the less well understood photosystems I and II of green plants. The inclusion of several minireviews devoted to the complexity of reactions in photosystem II, for example, reflects the wide diversity in studies of a system capable of extracting electrons from water and catalyzing a stable charge separation that results in reduction of the plastoquinone pool. These studies extend from detailed understanding of the primary reactions to physiological adaptation of the process to light and chemical (herbicide) stresses.

The reaction centers of prokaryotic and eukaryotic photosynthetic membranes produce high energy electrons which are utilized in electron transport reactions. The energy released in these reactions is coupled to ATP synthesis. The membrane components and processes involved in the energy-coupling reactions are the topic of Chapter 10. Minireviews in this section are strongly biochemical in emphasis, with special reference to the structural organization of membranes and the protein complexes which mediate proton translocation and ATP biosynthesis. Specific enzymes involved in electron transport and inhibitors which affect them are reviewed in light of information obtained since 1977.

The last chapter of this volume (Chap. 11) deals with the use of integrative approaches to study processes associated with control of photosynthetic membrane assembly and maintenance. Chapter 11 includes subject material ranging from comparative structural analysis of photosynthetic membranes (developmental diversity) to the use of physical analysis of membranes or simulated membrane systems to characterize functional components. The minireviews of this chapter will be of increasing value as the field of membrane biosynthesis and assembly matures to use more information about physical and biochemical features of the photosynthetic membranes. We can anticipate the advent of use of genetic engineering tools to manipulate photosynthetic membranes, and the rapid expansion of knowledge in this area.

In summary, this volume is a selection of both overview chapters and numerous topical speciality reviews. It should be useful as a reference source and as a teaching aid for individuals interested in the rapidly expanding field of photosynthetic membranes.

Boulder and Wilmington, Spring 1986

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7.5 Excitation Transfer in Phycobiliproteins

H. SCHEER

1 Introduction

One of the major strategies in the competition of photosynthetic organisms for light is qualitative and quantitative adaptation in their light-harvesting apparatus (THORNBER, Chap. 3; STAEHELIN, Chap. 1; ANDERSON, Chap. 6.4, all this Vol.). This includes, in particular, the usage of pigments which harvest light efficiently in the spectral regions not covered by the chlorophylls a and b present in higher plants, e.g., the bacteriochlorophylls absorbing well beyond 700 nm (COGDELL, Chap. 6.2, this Vol.), and the phycobiliproteins and carotenoids absorbing in the "chlorophyll trough" between 470 and 630 nm (GANTT, Chap. 6.3, this Vol.). Among these, the phycobiliproteins are to date probably the best understood. They are not only the major light-harvesting pigments of cyanobacteria, red algae, and cryptophytes (see STAEHELIN, Chap. 1, this Vol., for a general characterization of these species), microorganisms which are responsible for a large fraction of the net photosynthetic production on earth, but they are also readily accessible and pleasing to the eye. Different aspects of phycobiliprotein research (GANTT 1979, 1981; GLAZER 1980, 1983; MACCOLL 1982; RÜDIGER 1979; SCHEER 1981, 1982; WEHRMEYER 1983; ZUBER 1978) and related topics (BRASLAVSKY et al. 1983; PRATT 1978, 1982; RÜDIGER 1980; RÜDIGER and SCHEER 1983) have been reviewed in the past 5 years. In this volume, GANTT (Chap. 6.3) describes the structure and function of phycobilisomes and ZUBER (Chap. 6.1) the primary structure of phycobiliproteins. This chapter provides a brief overview of the energy transfer in biliproteins. Due to space limitations, only few citations could be incorporated. They are a biased selection from a large body of work, and should be used as a source for further references.

2 Structure of Phycobiliproteins

Most phycobiliproteins contain one or both of the chromophores, phycocyanobilin (Fig. 1a) or phycoerythrobilin (Fig. 1b), but additional chromophores of yet unknown structure are present, for example, in red algae, phycoerythrins ("phycourobilin"), in phycoerythrocyanins, and in particular in biliproteins from cryptophytes. Both chromophores are linked to their apoproteins via one, and in some cases two (RAPOPORT and GLAZER 1984) stable thioether bond(s)

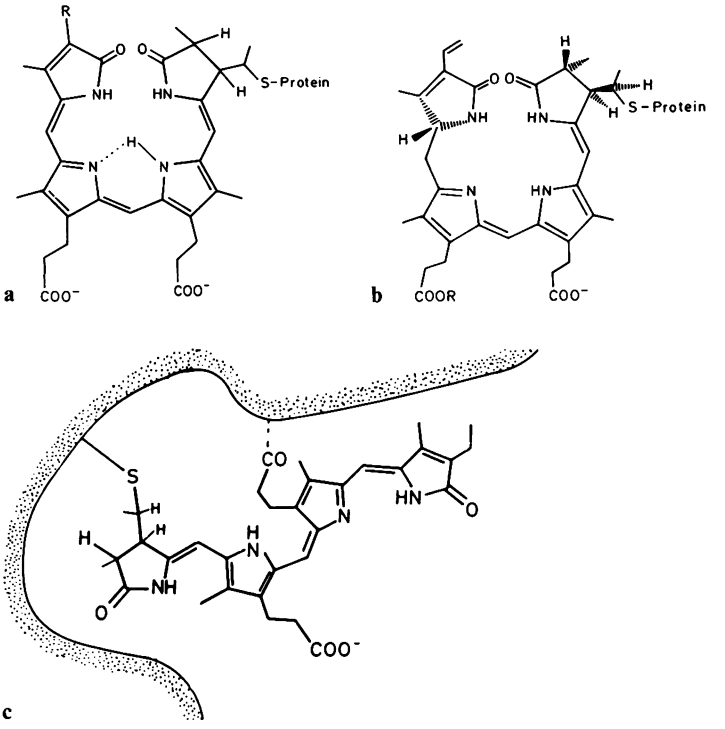

Fig. 1. Chromophores of phycobiliproteins. Molecular structures of **a** phycocyanobilin, the chromophore of PC and APC, **b** phycoerythrobilin, the main chromophore of phycoerythrins. A hypothetical conformation of the native phycocyanobilin in PC is shown in **c** (see SCHIRMER et al., 1985, for three dimensional structures of PC chromophores)

at rings A or D to cystein residues, as has been inferred from several independent lines of evidence (RÜDIGER 1979; LAGARIAS et al. 1979; ZUBER 1978; KÖST-REYES and KÖST 1979; FREIDENREICH et al. 1978), including a recent X-ray structure (SCHIRMER et al. 1985). Additional, more labile bonds have been postulated to exist based on conflicting results (see SCHEER 1982). Studies with a new, mild chromophore cleavage method have recently shown the absence of a second bond in two phycocyanins (KUFER et al. 1983).

The properties of the native biliprotein chromophores are profoundly influenced by noncovalent interactions with the protein (see SCHEER 1982). Both the intense visible absorption and fluorescence of the phycobiliproteins, which are crucial for their functions, are caused by these interactions, and are absent in the denatured pigments and in free chromophores (see below). The phycobiliproteins thus present a good example of "molecular ecology", e.g., the optimization of cofactors to specific functional needs by interactions with the apoproteins (SCHEER 1982).

All biliproteins are composed of two to three chromophore-bearing subunits. To date, the primary structures are known for more than ten different subunits,

including the α- and β-subunits of all biliproteins from the cyanobacterium, *Mastigocladus laminosus* e.g. allophycocyanin (APC), phyocyanin (PC) and phycoerythrocyanin (PEC) (FÜGLISTALLER et al. 1983), and the red (?) alga, *Cyanidium caldarium* (APC and PC) (OFFNER and TROXLER 1983; see also ZUBER, Chap. 6.1, this Vol.). In the pigments from cyanobacteria and red alga, the α-subunit ($\approx$17 kDa) bearing 1–2 chromophores and a slightly larger β-subunit carrying 1–4 chromophores, are always present in a 1:1 molar ratio. Additional chromophore-carrying γ subunits of generally much larger size are known in some APC's and in red algal PE's (phycoerythrin) in $(\alpha\beta)_n\,\gamma$ stoichiometry (n = 3 or 6) (see GLAZER 1983 and SCHEER 1982). The fundamental structural units, e.g., $\alpha\alpha'\beta$ (GANTT 1979; MÖRSCHEL and WEHRMEYER 1975) of the cryptophyte biliproteins have a different composition.

The chromophore composition is most simple in the cyanobacterial biliproteins, which carry only one type of chromophore on any given subunit. Subunits bearing two different chromophores are common in the more highly evolved eukaryotic red algae and cryptophytes. The chromophore-binding sequences are known for many phycobiliproteins (see above). Together with immunochemical studies and the complete peptide sequences cited above, an evolutionary family tree has been constructed which relates all phycobiliprotein polypeptides to a common ancestral gene (see ZUBER Chapter 6.1, GLAZER 1980; WEHRMEYER 1983).

Isolated biliproteins of cyanobacteria and red algae have a strong tendency to aggregation. Trimers (=heterohexamers) $(\alpha\beta)_3$ or hexamers (=heterododecamers) $(\alpha\beta)_6$ are generally observed (see MACOLL and BERNS 1981; SCHEER 1982). The former seem to be the largest aggregates in the absence of linkers. In vivo, they are organized within complex structures, the phycobilisomes (PB'somes) (GANTT and CONTI 1966). A single PB'some can bear up to 2700 chromophores of different types (GANTT Chap. 6.3, this Vol.) and represents the functional antenna unit of these organisms. In addition to the chromophore-bearing biliproteins, PB'somes contain several, generally colorless, "linker" peptides, which play a crucial role in their organization and their attachment to the membrane (see GLAZER 1983). Much of the basic PB'some structure with an APC core and outer rods containing PC and PE (see Fig. 2 in GANTT, Chap. 6.3, this Vol. for a diagram of the different types of PB'somes) has been obtained by combining high-resolution electron microscopy with biochemical methods (MÖRSCHEL et al. 1980; GLAZER et al. 1979; SIEGELMAN and KYCIA 1982; WANNER and KÖST 1980). PB'somes are located on the outer surface of the thylakoid membrane in a dense packing, but apparently without cooperation between different PB'somes.

Very little is known about the quaternary structure of the cryptophyte biliproteins. Cryptophytes do not have PB'somes; instead their biliproteins are located on the inner surface of the thylakoids and reveal virtually no substructure in the electron microscope (see Figs. 3 and 19 in STAEHELIN Chap. 1, this Vol.). This is paralleled by a decreased tendency of the isolated pigments to aggregate (see GANTT 1979; MACCOLL and GUARD-FRIAR 1983). Preliminary X-ray results have recently been published (MORISSET et al. 1984).

3 Photophysics and Photochemistry of the Chromophores

Denatured biliproteins, in which the chromophores are uncoupled from the protein, as well as free bile pigments of similar structures, have flexible chromophores which are predominantly present in solution in a cyclic-helical conformation (SCHEER 1982; BRASLAVSKY et al. 1983). These conformers have absorptions of moderate intensity in the visible range ($\varepsilon \approx 17{,}000\ M^{-1}\ cm^{-1}$ at neutral pH) (see BRANDLMEIER et al. 1981), low fluorescence yields ($\Phi \leq 10^{-3}$ see BRASLAVSKY et al. 1983) with corresponding fast excitation decays (SCHNEIDER, unpublished) and low phosphorescence intensities (LAND 1979). The deexcitation is governed by internal conversion, which is promoted by one or more of the following mechanisms: proton transfer (FALK and NEUFINGERL 1979; FRIEDRICH et al. 1981), vibrations, or rotations around single bonds (KUFER et al. 1983), and by photoreactions, e.g., to the labile 10 E isomers (BRASLAVSKY et al. 1983). This deactivation is only hindered if the above mechanisms are blocked, e.g., by a rigid fixation (KUFER et al. 1983), distortion of the chromophores (FALK and THIRRING 1980), or (photo)selection of more rigid and extended conformers (BRASLAVSKY et al. 1983). In these cases, the lifetimes of the excited states are increased to allow high yields of fluorescence, or photochemical reactions to products like the 4 E– or 15 E isomers which are stable at ambient temperatures.

In the biliproteins, such conformers are predominant. The chromophores are probably rigidly fixed in an extended and twisted conformation near the surface of the protein (SCHEER 1982). This rather general picture has been detailed recently by the current X-ray analysis of a PC (SCHIRMER et al. 1985). The energetically unfavorable conformations must be stabilized by noncovalent interactions with the polypeptide chains (SCHEER 1982). The absorption in the visible range is thus increased by a factor of ≈ 5, and fluorescence by several orders of magnitude to $\Phi \geq 0.5$ (see GRABOWSKI and GANTT 1978a). The phycobiliproteins are photochemically stable at ambient temperatures. It is, however, of interest to note that the photoreactive, light-sensing plant pigment phytochrome has a chromophore structure and protein interaction that resembles PC, and that partial denaturation renders phycobiliproteins to a certain extent photoreactive by partial uncoupling from the protein (BJÖRN 1979; BRASLAVSKY et al. 1983).

In spite of the large number of chromophores present in phycobiliproteins, there are generally only moderate interchromophore interactions. Strong coupling between chromophores has been established for the pigments in cryptophytes (HOLZWARTH et al. 1983; JUNG et al. 1980; KOBAYASHI et al. 1979), and may also be present in some of the cyanobacterial and red algal ones, but many of the isolated phycobiliproteins do not show good evidence of such coupling as judged from their CD spectra. However, aggregation is often paralleled by the rise of S-shaped CD signals which are indicative of strong coupling. Since the chromophores are probably located at or near the surface of the native biliproteins, this would mean that the nearest neighbors in situ may not be the chromophores on the same subunits or heterodimers, but rather on different ones [see STAEHELIN, Chap. 1, this Vol. for a discussion of phycobilisome packing in vivo and the recent x-ray results of SCHIRMER et al. (1985)].

4 The Energy Transfer Chain

The participation of phycobiliproteins in photosynthesis and, in particular, their association with photosystem II was originally recognized by action spectroscopy (EMERSON 1958). Energy transfer from biliproteins to chlorophylls has also been demonstrated in solution (FRACKOWIAK et al. 1979; KRASNOVSKII and EROKHINA 1969). The discovery of PB'somes (GANTT and CONTI 1966) marks the beginning of an understanding of phycobiliprotein function in cyanobacteria and red alga on a molecular basis. PB'somes collect light efficiently in the wavelength range between 480 and 630 nm, but their fluorescence is emitted almost exclusively ($\geq 95\%$) by a small fraction of a minor constituent, e.g., APC (λ_{max}, absorption ≈ 665 nm, λ_{max}, emission ≈ 680 nm). If attached to the photosynthetic membrane, the energy is transferred further to the chlorophyll-containing reaction centers in the membrane, preferentially to PS II (GANTT 1981).

In the original PB'some model derived from electron microscopic and biochemical studies of the red alga, *Porphyridium cruentum*, a phycobilisome somewhat resembles an onion cut in half: a core, made up of APC, is surrounded by layers of PC and, further out, PE. Although this model has been considerably refined by applying improved techniques and working with organisms having less complex phycobilisomes (see above), the basic elements have remained unchanged: there is a morphological ordering from PE to PC to APC when going from the periphery to the center of the PB'some (see Fig. 2 in GANTT, Chap. 6.3, this Vol.).

This sequence corresponds perfectly to the decrease in excitation energy among the three pigments, which can thus form an energy transfer chain in which the fluorescence of any preceding member overlaps reasonably well with the absorption of the next one (Fig. 2). This model was refined by fluorescence polarization experiments first undertaken by TEALE and DALE (1970), which suggested part of an energy transfer chain to be present already within each individual biliprotein. The absorptions of PC's and PE's can be resolved into components of slightly different energies. These are assigned to individual chromophores of often the same molecular structure, but with slightly different absorption energies due to different interactions with the protein. The ones absorbing at shorter wavelengths act as sensitizers (s) to the ones absorbing and fluorescing at longer wavelengths (f chromophores), which provides an efficient fine-tuning of the energy transfer.

In cyanobacteria, each individual pigment represents only a rather short fragment of such an energy transfer chain. PC has, for example, one s chromophore on the β- and one f chromophore on both the α- and β-subunits. The full transfer chain is completed by the aggregation with APC and PE in the PB'some. The cryptophytes represent the other extreme. They do not have PB'somes, instead they have biliproteins which carry sufficiently different types of chromophores to establish an energy transfer over the full absorption spectrum of biliproteins. The red algae, finally, use a combination of both. They have PB'somes in which the major biliproteins already span a wide absorption range.

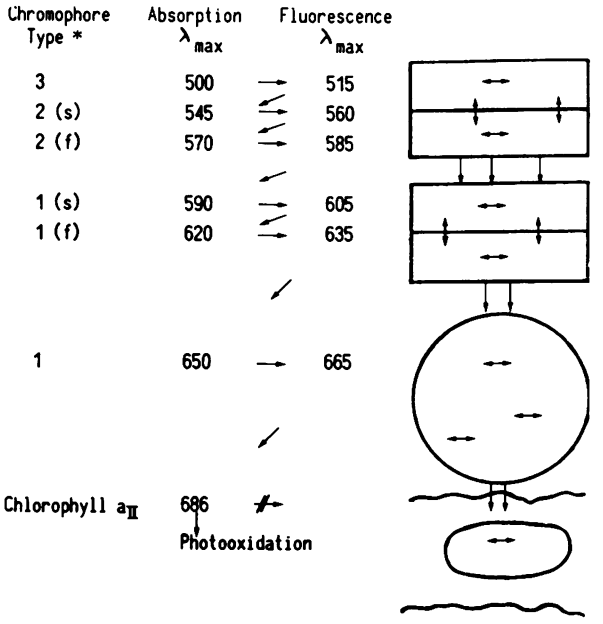

Fig. 2. Energy transfer scheme of a phycobilisome. *Right* a diagramatic representation of a PB'some with only one outer rod containing B-PE (*top double disk*) and C-PC (*lower double disk*). *Vertical arrows* correspond to longitudinal energy transfer, with the downward direction strongly favored due to a larger overlap integral; *horizontal arrows* to transversal energy transfer within the disks. *Left* approximate absorption and fluorescence maxima of the chromophores. *: 1 = phycocyanobilin, 2 = phycoerythrobilin, 3 = phycourobilin

The energy transfer chain is completed by the transfer to the chlorophylls within the photosynthetic membrane. Both the final donor in the PB'some and the acceptor in the membrane have not yet been firmly established. At present, the best candidates seem to be a large chromopeptide of the APC core (GINGRICH et al. 1983; REDLINGER and GANTT 1982; RUSCHKOWSKI and ZILINSKAS 1982) and a chlorophyll protein close to or even identical with P-680, respectively (CLEMENT-METRAL and GANTT 1983, see also GANTT, Chap. 6.3, this Vol.).

5 Dynamics of Energy Transfer

A large fraction of the energy transfer in phycobiliproteins proceeds probably via a FÖRSTER type process (see SAUER, Chap. 2; KNOX, Chap. 7.1, both this Vol.). This has been deduced from the efficiency of the energy transfer on one hand, and the low occurrence of strong couplings on the other. GRABOWSKI and GANTT (1978a, b) have critically investigated a series of biliproteins and calculated FÖRSTER's critical distances, which are mostly in the range of 40–60 Å,

well beyond the diameter of the phycobiliprotein subunits (≈ 30 Å). The formalism of FÖRSTER (1949) has been developed for a randomly ordered and fluctuating system with high acceptor and low donor concentrations. Since probably none of these criteria applies to the phycobiliproteins (see above), a concise theoretical treatment of the process is not yet possible (BLUMEN and MANZ 1979; PEARLSTEIN 1982), but the critical radius is expected to be even larger based on still incomplete data on the chromophore orientations (see e.g., ZICKENDRAHT et al. 1980; SCHIRMER et al. 1985; GILLBRO et al. 1983). The second critical factor, i.e., the overlap integral between the donor fluorescence and the acceptor absorption, is also fine-tuned in the biliproteins (see above).

Recent applications of picosecond time-resolved techniques to the energy transfer process in biliproteins have principally verified this concept. The first detailed investigations by SEARLE et al. (1978) established in *Porphyridium cruentum* a sequential flow of excitation energy from PE via PC and APC to chlorophyll. The observed rates of excitation energy transfer could be fit by the $\exp(t^{-1/2})$ decay law characteristic for the classical FÖRSTER tansfer. Although the actual kinetics can be fit well with a concise set of rise and decay times for the PB'somes of this organism (WENDLER et al. 1984), the physical laws governing the decay have been questioned. The better signal-to-noise ratios of the current experiments still do not allow an unequivocal discrimination between multi-exponential $[\sum A \cdot \exp(kt)]$ and non-exponential decay laws, but generally favor the former. This is in particular supported by the observation of corresponding decay and rise time constants in pairs of donors and acceptors, respectively (WENDLER et al. 1984).

Qualitatively similar results have been obtained with entire PB'somes, as well as with isolated phycobiliproteins and their subunits from several cyanobacteria and red algae (HEFFERLE et al. 1984a, b; HOLZWARTH et al. 1982; KOBAYASHI et al. 1979; PELLEGRINO et al. 1981; SUTER et al. 1984; SWITALSKI and SAUER 1984; WONG et al. 1981; YAMAZAKI et al. 1984).

Photosynthetic antenna systems are optimized for high absorption cross-sections and cooperativity. They thus present a problem for the interpretation of time-resolved measurements, because $^1S - {}^1S$ annihilation can compete efficiently with energy transfer (see BRETON and GEACINTOV 1980; GEACINTOV and BRETON, Chapter 7.4). This process has been demonstrated in phycobiliproteins and investigated in detail by ALFANO's group (ALFANO 1982; PELLEGRINO et al. 1981; WONG et al. 1981). It can be distinguished from conventional excitation energy transfer ($^1S - {}^0S$) by its dependence on the intensity of the exciting light. More recent studies have thus focused on techniques which use only low photon fluxes, e.g., repetitive streak cameras (HEFFERLE et al. 1984a, b) or single-photon timing (HOLZWARTH et al. 1982; WENDLER et al. 1984; YAMAZAKI et al. 1984; HOLZWARTH, Chap. 7.3, this Vol.). An advantage of the former is the ready availability of polarized data, whereas the latter has an exceptionally high dynamic range and can thus detect even minor contributions.

Several criteria have been used to identify energy transfer in biliprotein antenna systems. The first is the analysis of time-resolved depolarization. Due to their rigid binding to proteins, rotational depolarization is generally thought to be absent on the subnanosecond time scale, and depolarization is thus be-

lieved to be due to energy transfer among chromophores (GILLBRO et al. 1983; HEFFERLE et al. 1983, 1984a, b). It should be noted, however, that segmental movements of the chromophores (HEFFERLE et al. 1984b) and nonparallel excitation and emission dipoles (SWITALSKI and SAUER 1984) have been implicated to rationalize the kinetics of some isolated biliproteins and their subunits. It is also not trivial to obtain energy transfer time from the raw data (HEFFERLE et al. 1984a). The second criterion is the correspondence of decay time constants in the donors with rise time constants in the acceptors, which are separated by wavelength selective excitation and emission (HOLZWARTH et al. 1982; WENDLER et al. 1984; YAMAZAKI et al. 1984).

The following conclusions can be drawn from the results obtained until now: the energy transfer from PE to the terminal APC chromophore proceeds at a time scale ≤ 100 ps (e.g., 60–70 ps in *Porphyridium cruentum*, WENDLER et al. 1984; YAMAZAKI et al. 1984). It follows the pigment sequence expected from their energetic and morphological ordering within the PB'somes. The energy transfer from PE to PC appears to be faster than that from PC to the APC core (SUTER et al. 1984). In isolated biliproteins, the transfer times increase with decreasing aggregation, e.g., from 70 ps in the trimer $(\alpha\beta)_3$ to ≈ 500 ps in monomeric $(\alpha\beta)_1$ PC from *Mastigocladus laminosus* (HEFFERLE et al. 1984b). The transfer times are also dependent on the species, the isolation procedure and temperature. An intriguing conclusion might be drawn from the comparison of isolated biliproteins with phycobilisomes, e.g., that the physiologically important longitudinal energy transfer toward the APC core is faster than the potentially wasteful transversal transfer within the platelets of the phycobilisome.

Currently, kinetic data are only available for a single cryptophytan pigment, i.e., PC-645 from *Chroomonas* sp. (HOLZWARTH et al. 1983; KOBAYASHI et al. 1979). The findings support again a somewhat different behavior of the cryptophytan pigments compared to the PB'some-forming biliproteins. Differences between the absorption and fluorescence excitation spectra have been discussed in terms of a heterogeneous population of f chromophores, albeit with the same decay kinetics, and the results support the presence of strongly coupled chromophores (JUNG et al. 1980).

6 Physiological Status

Photosynthetic organisms are dynamic systems with the capacity to react to environmental changes. These changes include the structure of the phycobilisomes, and their light-harvesting and energy-transfer capacities. The best investigated feature is the chromatic adaptation of many cyanobacteria, which involves changes in the composition and structure of the phycobilisomes in response to changes in the qualitity of light (BJÖRN 1979; GANTT 1981; GLAZER 1983). Other important factors are the nutritional and developmental status of the organisms (CSATORDAY 1978). Considerably less is known about the changes in the energy transfer kinetics in these systems. Using fluorescence spectroscopy CSATORDAY (1978) has followed the repigmentation of *Anacystis*

nidulans cells after nitrogen starvation. This approach allows for the detection of particular biliproteins before they have been incorporated into the antenna system. HARNISCHFEGER and CODD (1978) have observed a decrease in biliprotein fluorescence after illumination of dark-adapted cells of the same organism, which was correlated with an increased chlorophyll fluorescence. Changes of the fluorescence yields (FORK et al. 1982) and kinetics (KARUKSTIS and SAUER 1984) upon treatment of algal cells with DCMU or desiccation, indicate the involvement of different chlorophyll containing antennas, and possibly also different PS II populations. This changed coupling between phycobilisomes and membrane-bound pigments probably contributes to the chromatic transients in cyanobacteria as well. These few examples have been chosen to illustrate that the physiological status of the cells (as well as the isolation procedures of PB'somes and their components) may produce significant changes in energy transfer reactions, which must be considered in the interpretation of the physicochemical data.

Acknowledgements. The cited work of the author was supported by the Deutsche Forschungsgemeinschaft. I thank Drs. A.R. HOLZWARTH and S. SCHNEIDER for critically reading the manuscript.

Notes Added in Proof: The field has been advancing rapidly after finishing the manuscript for this mini review. Important aspects should be referenced.

The crystal structure has been determined for a second phycocyanin, viz. from *Agmenellum quadruplicatum*, which is hexameric instead of trimeric, but otherwise very similar to that of *M. laminosus* (T. SCHIRMER, W. BODE, M. SCHNEIDER, W. BODE, M. MILLER, M.L. HACKERT, J. Mol. Biol., in press). The details of chromophore structures and the linkage to the apoprotein have been determined by chemical methods, including the high-resolution NMR of bilipeptides (J.O. NAGY, J.E. BISHOP, A.V. KLOTZ, A.N. GLAZER, H. RAPOPORT, J. Biol. Chem. 260, 4864–4868 (1985)), milder degradation methods (W. KUFER, G. SCHMIDT, O. SCHMID, H. SCHEER, Z. Naturforsch., in press) and sequencing studies (W. SIDLER, B. KUMPF, H. ZUBER, W. RÜDIGER, Abstr. Vth. Int. Symp. on Photosynthetic Procaryotes (ed. H. ZUBER, p. 303, 1985, ETH Zürich). The results include the structure of the phycourobilin chromophore in R-PE and the characterization of singly and doubly bound chromophores, depending on the species and the chromophore attachment site.

An assignment of spectrally distinct chromophores to the different chromophore sites of PC from *M. laminosus* has been suggested on the basis of fluorescence polarization, circular dichroism and photochemical reactivities (M. MIMURO, P. FÜGLISTALLER, R. RÜMBELI, H. ZUBER, Abstr. Vth. Int. Symp. on Photosynthetic Procaryotes (ed. H. ZUBER, 1985, p. 276, ETH Zürich; W. JOHN, R. FISCHER, S. SIEBZEHNRÜBL, H. SCHEER, in Antennas and Reaction Centers of Photosynthetic Bacteria – Structure, Interactions and Dynamics (eds. M.E. MICHEL-BEYERLE, H. SCHEER, S. FISCHER, Springer, Berlin – Heidelberg – New York, in press).

Several new results have been presented on the excited state dynamics in biliproteins. Fast (7–10 ps) decay times of the short-wavelength fluorescence and a corresponding rise-term of the longer wavelength fluorescence has been demonstrated for PC 612 from the cryptophyte, *Hemiselmis virescens* (C.A. HANZLIK, L.E. HANCOCK, R.S. KNOX, D. GUARD-FRIAR, R. MACCOLL, J. Luminescence 34, 99–106 (1985). All groups have adopted the multi-exponential decay analysis, at least as a phenomenological approach, requiring up to 5 components depending on the system and on the signal-to-noise ratios of the data. The physical correctness of this approach has been supported by a global analysis of data sets obtained at different excitation and emission wavelengths with a single set of components (A.R. HOLZWARTH, in Antennas and Reaction Centers of Photosynthetic Bacteria – Structure, Interactions and Dynamics (eds. M.E. MICHEL-BEYERLE, H. SCHEER,

S. SCHNEIDER), Springer Verlag, Heidelberg, Berlin, New York, 1985, in press). This method allows at the same time the extraction of time-resolved spectral information. First data on the influence of linker peptides have shown only relatively small changes in the excited state dynamics of an R- and a C-PC (S. SWITALSKI, K. SAUER, pers. communication, J. WENDLER, W. JOHN, H. SCHEER, A.R. HOLZWARTH, unpublished results). The spectra of the individual components contributing to the emission have been studied in a chromatically adapting cyanobacterium, *Fremyella diplosiphon* (M. MIMURO, I. YAMAZAKI, T. YAMAZAKI, Y. FUJITA, Photochem. Photobiol. 41, 597–603 (1985). Particular attention has been paid to the relative importance of lateral and vertical energy transfer, with the latter being favored in green-light adapted cells containing PE, PC and APC. The uncoupling of phycobilisomes from the PSII-related chlorophylls has been induced by heat stress in *Anacystis nidulans* (P. MOHANTY, S. HOSHINA, D.C. FORK, Photochem. Photobiol. 41, 589–596 (1985). In an interesting application, tandem phycobiliprotein conjugates have been used as immunofluorescent probes with an unusually large Stoke's shift due to the energy transfer from PE to APC (A.N. GLAZER, J. STRYER, Biophys. J. 43, 383–386 (1983)).

References

Alfano RR (ed) (1982) Biological events probed by ultrafast laser spectroscopy. Academic Press, London New York (See in particular chaps 6: Breton J, Geacintov N; 17: Doukas et al.; 18: Shank and Greene)
Björn LO (1979) Q Rev Biophys 12:1–25
Blumen A, Manz J (1979) J Chem Phys 71:46–94
Brandlmeier T, Scheer H, Rüdiger W (1981) Z Naturforsch 36c:431–439
Braslavsky SE, Holzwarth AR, Schaffner K (1983) Angew Chem 22:670–689, Angew Chem Int Ed 20:656–674
Breton J, Geacintov NE (1980) Biochim Biophys Acta 594:1–32
Bryant DA (1982) J Gen Microbiol 128:835–844
Clement-Metral JD, Gantt E (1983) FEBS Lett 156:185–188
Csatorday K (1978) Biochim Biophys Acta 504:341–343
Emerson R (1958) Annu Rev Plant Physiol 9:1–24
Falk H, Neufingerl F (1979) Monatsh Chem 110:987–1001
Falk H, Thirring K (1980) Z Naturforsch 35b:376–380
Förster T (1949) Z Naturforsch 4A:321–327
Fork DC, Öquist G, Hoch GE (1982) Plant Sci Lett 24:249–254
Frackowiak D, Erokhina LG, Fiksinski K (1979) Photosynthetica 13:245–253
Freidenreich P, Apell GS, Glazer AN (1978) J Biol Chem 253:212–219
Friedrich J, Scheer H, Zickendraht-Wendelstadt B, Haarer D (1981) J Am Chem Soc 103:1030–1035
Füglistaller P, Suter F, Zuber H (1983) Hoppe-Seyler's Z Physiol Chem 364:691–712
Gantt E (1979) Biochem Physiol Protozoa 1:121–137
Gantt E (1981) Annu Rev Plant Physiol 32:327–347
Gantt E, Conti SF (1966) J Cell Biol 29:423–434
Gillbro T, Sundström A, Sundström V, Holzwarth AR (1983) FEBS Lett 162:64–68
Gingrich JC, Lundell DJ, Glazer AN (1983) J Cell Biochem 22:1–14
Glazer AN (1980) In: Sigman D, Brazier MAB (eds) The evolution of protein structure and function. Academic Press, London New York, pp 221–244
Glazer AN (1983) Annu Rev Biochem 52:125–157
Glazer AN, Williams RC, Yamanaka G, Schachman HK (1979) Proc Natl Acad Sci USA 76:6162–6166
Grabowski J, Gantt E (1978a) Photochem Photobiol 28:39–45
Grabowski J, Gantt E (1978b) Photochem Photobiol 28:47–54
Harnischfeger G, Codd GA (1978) Biochim Biophys Acta 502:507–513

Hefferle P, Nies M, Wehrmeyer W, Schneider S (1983) Photobiochem Photobiophys 5:325–334
Hefferle P, John W, Scheer H, Schneider S (1984a) Photochem Photobiol 39:221–232
Hefferle P, Geiselhart P, Mindl T, Schneider S, John W, Scheer H (1984b) Z Naturforsch 39c:606–616
Holzwarth AR, Wendler W, Wehrmeyer W (1982) Photochem Photobiol 36:479–487
Holzwarth AR, Wendler W, Wehrmeyer W (1983) Biochim Biophys Acta 724:388–395
Jung J, Song PS, Paxton RJ, Edelstein MS, Swanson R, Hazen Jr EE (1980) Biochemistry 19:24–32
Karukstis KK, Sauer K (1984) Biochim Biophys Acta 766:141–147
Kobayashi T, Degenkolb EO, Behrson R, Rentzepis PM, MacColl R, Berns DS (1979) Biochemistry 18:5073–5078
Köst-Reyes E, Köst HP (1979) Eur J Biochem 102:83–91
Krasnovskii AA, Erokhina LG (1969) Dokl Acad Nauk SSSR 186:957–960
Kufer W, Scheer H, Holzwarth AR (1983) Isr J Chem 23:233–240
Lagarias JC, Glazer AN, Rapoport H (1979) J Am Chem Soc 101:5030–5037
Land EJ (1979) Photochem Photobiol 29:483–487
MacColl R (1982) Photochem Photobiol 35:899–904
MacColl R, Berns DS (1981) Isr J Chem 21:296–300
MacColl R, Guard-Friar D (1983) Biochemistry 22:5568–5572
Mörschel E, Wehrmeyer W (1975) Arch Microbiol 105:153–158
Mörschel E, Koller K, Wehrmeyer W (1980) Arch Microbiol 125:43–51
Morisset W, Wehrmeyer W, Schirmer T, Bode W (1984) Arch Microbiol 140:202–205
Offner GD, Troxler RF (1983) J Biol Chem 258:9931–9940
Pearlstein RM (1982) Photochem Photobiol 35:835–844
Pellegrino F, Wong D, Alfano RR, Zilinskas B (1981) Photochem Photobiol 34:691–696
Pratt LH (1978) Photochem Photobiol 27:81–105
Pratt LH (1982) Annu Rev Plant 33:557–582
Rapoport H, Glazer AN (1984) In: Blauer G, Sund H (eds) Optical properties and structure of tetrapyrroles. De Gruyter, Berlin, pp 411–423
Redlinger T, Gantt E (1982) Proc Natl Acad Sci USA 79:5542–5546
Rüdiger W (1979) Ber Dtsch Bot Ges 92:414–426
Rüdiger W (1980) Struct Bond 40:101–140
Rüdiger W, Scheer H (1983) In: Shropshire W, Mohr H (eds) Photomorphogenesis. Encyclopedia of Plant Physiology Vol 16. Springer, Berlin Heidelberg New York, pp 119–151
Rusckowski M, Zilinskas BA (1982) Plant Physiol 70:1055–1059
Scheer H (1981) Angew Chem 93:230–250, Angew Chem Int Ed 20:241–261
Scheer H (1982) In: Fong FK (ed) Light reaction path of photosynthesis. Springer, Berlin Heidelberg New York, pp 7–45
Schirmer T, Bode W, Huber R, Sidler W, Zuber H (1985) J Mol Biol 184:257–277
Searle GFW, Barber J, Porter G, Tredwell CJ (1978) Biochim Biophys Acta 501:246–256
Siegelman HW, Kycia H (1982) Plant Physiol 70: 887–897
Suter GW, Mazzola P, Wendler J, Holzwarth AR (1984) Biochim Biophys Acta 766:269–276
Switalski SC, Sauer K (1984) Photochem Photobiol 40:423–427
Teale FWJ, Dale RE (1970) Biochem J 116:161–169
Wanner G, Köst HP (1980) Protoplasma 102:97–109
Wehrmeyer W (1983) In: Jensen U, Fairbrothers DE (eds) Proteins and nucleic acids in plant systematics. Springer, Berlin Heidelberg New York, pp 143–167
Wendler J, Holzwarth AR, Wehrmeyer W (1984) Biochim Biophys Acta 765:58–67
Wong D, Pellegrino F, Alfano RR, Zilinskas BA (1981) Photochem Photobiol 33:651–662
Yamazaki I, Mimuro M, Murao T, Yamazaki K, Yoshihara K, Fujita Y (1984) Photochem Photobiol 39:233–240
Zickendraht-Wendelstadt B, Friedrich J, Rüdiger W (1980) Photochem Photobiol 31:367–376
Zuber H (1978) Ber Dtsch Bot Ges 91:459–474

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