

## Introduction

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This introductory chapter summarizes the 25 articles contributed by participants in the PS 2004 Light-Harvesting System Workshop for a special issue of Photosynthesis Research (Vol 86 Nos 1-2, Nov 2005) and is submitted in satisfaction of the final reporting requirement for this U.S. Department of Energy grant.

This special issue on antennas consists of 25 original peer-reviewed contributions from participants in the PS 2004 Light-Harvesting Systems Workshop (the abstract book cover is shown in on this page). Exceptionally rapid progress in the understanding of light-harvesting systems has been made in recent years, with the determination of several antenna protein structures and the maturing of ultrafast spectroscopic and molecular biological techniques for investigation and manipulation of photosynthetic systems. This is amply reflected in the special issue, which is organized into sections on antenna pigments and complexes from purple bacteria, antenna complexes of green bacteria and antenna complexes from oxygenic photosynthetic organisms.

Three articles in the section on purple bacteria deal with carotenoids. A surge of interest in carotenoid energy transfer and photoprotection mechanisms is evident, largely as a result of the convergence of new spectroscopic results with high-resolution structural information; however, a more complete picture will emerge only when the electronic excitation states of carotenoids can be precisely assigned. The important roles played by carotenoids are being investigated in model systems (Pendon et al.) and in both the LH 2 (Gall et al.) and LH 1 (Moskalenko and coworkers) light-harvesting complexes; for LH 2, the native structure could be maintained with a variety of carotenoids. Other contributions deal with the LH 1-reaction center core structure – Abresch and coworkers describe the isolation of the complete core complex of *Rhodobacter sphaeroides*, that includes the structurally and functionally important PufX protein, while the paper by Watson et al. demonstrates that a more complete picture of the thermal stability of the reaction center will only emerge when reaction center-LH 1 interactions are taken into account. The two other papers on *R. sphaeroides* LH complexes involve spectroscopic aspects – the article by Rätsep and

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coworkers assesses the high-energy electronic structure of LH 1 and LH 2 with spectrally selective techniques, while Urboniene et al. show that the spectral density function, which describes integral effects of molecular vibration modes, adequately accounts for the temperature dependence of the spectral behavior in LH 2.

Much of the section on photosynthetic green bacteria is devoted to chlorosomes, the extramembranous structure that serves as their major antenna. Frigaard et al. describes a *Chlorobium tepidum* mutant, unable to synthesize the principal chlorosome pigment BChl *c*, which forms vestigial, carotenoid-rich carenosomes instead of chlorosomes; these new structures should prove useful in chlorosome biogenesis studies. The results of a topological study of Milks and

coworkers suggest that CsmA, the most abundant chlorosome protein, may play a role in the attachment of these structures to the cytoplasmic membrane. Electron microscopy of *C. tepidum* chlorosomes is revisited in the contribution of Hohmann-Marriott et al., who by using a sequential fixation procedure, were able to visualize a contrasted chlorosome interior as well as connections to the cytoplasmic membrane. On-going electron tomography and high-pressure freezing studies may resolve whether BChl *c* forms rod-like elements within the chlorosome, as originally observed in freeze fracture, or the undulating lamellar sheets suggested from the cryo EM and wide angle X-ray scattering data presented at the Light-Harvesting Workshop by Jakub Psencik. In papers dealing with *C. vibrioforme*, Saga et al. show that the concentration of sodium sulfide in the growth medium affects the composition of BChl *c* homologs, while Harada and coworkers demonstrate that BChl *c* has a better ability than BChl *d* to deal with reactive oxygen species that damage the reaction center during illumination in the presence of oxygen. Artificial antenna systems mimicking chlorosomes were examined by Miyatake et al. who describe a zinc analog of BChl *d* that undergoes a stereochemically-dependent, autocatalytic self-aggregation via formation of small aggregates as intermediates. In the final contribution on green bacteria, Xin and coworkers characterize a B808–868 light-harvesting complex purified from the thermophilic green filamentous bacterium *Chloroflexus aurantiacus*. This protein serves as a core antenna that transfers excitation energy from chlorosomes to the reaction centers and the measured BChl *a* content suggests that a single B808–868 ring may surround two reaction centers.

A broad range of contributions on different antenna complexes are covered in the section on oxygenic phototrophs, which begins with a Mini-review by Chen and Bibby on the roles of the major prochlorophyte Chl binding protein and the closely related cyanobacterial iron-stress-induced protein in the formation of antenna-reaction center supercomplexes. A scheme for the evolutionary origin of this class of antenna proteins is also proposed. In the contribution by Loll and coworkers, the structure of the CP43 and CP47 antenna system of PS II at 3.2-Å resolution is

presented; the calculated angular orientations of the Chl *a*  $Q_y$  transition moments should prove useful for further work on excitation energy transfer in these important proteins. In the first of two papers dealing with excitation energy transfer as related to PS I, Vaitekonis and coworkers present a modified exciton model to explain the function of the red absorbing PS I Chl *a* core antenna molecules and in the second, Melkozernov et al. examines energy coupling between PS I and the associated light-harvesting complex I (LHC I) antenna in *Chlamydomonas*. Miller and coworkers report the reconstitution of the soluble antenna peridinin-Chl *a* protein with different Chls and studies by Polivka et al. support the existence of a strongly coupled intramolecular charge transfer/ $S_1$  excited state in peridinin as the donor to the various Chls. Although fucoxanthin like peridinin, is a conjugated carbonyl-group containing carotenoid, Papagiannakis and coworkers demonstrate that in the fucoxanthin-Chl protein of diatoms, efficient energy transfer occurs from the fucoxanthin  $S_2$  state to Chl *a*. In the paper by Balaban, an examination of the stereochemical features of the Chls in the recent the LHC II structure reveals that they assume two types of diastereotopic magnesium ligation. It is postulated that those with the less frequent 'special'  $\beta$ -coordination are located in positions that are of importance in excitation energy transfer and photoprotective roles. Two papers from Gyozo Garab's group further characterize the optically-induced reorganization of LHC II and the stacked thylakoid grana membranes of higher plants. The study of Cseh et al. attributes the non-Arrhenius temperature behavior of this phenomenon to both ambient temperature and local thermal transients in LHC II, the site of local energy dissipation. Holm and coworkers report that the thermo-optic changes are largely confined to the LHC II only macrodomains in pea granal thylakoids and propose that they play an important role in both light-adaptation and photoprotection. In the final paper, Santabarbara and coworkers report on a fluorescence-detected magnetic resonance study of carotenoid triplet states associated with the terminal Chl emission forms of PS II from spinach thylakoid membranes. This approach provides a window for determining the importance of the generation of carotenoid triplets as a photoprotective strategy for higher phototrophs.

This collection of papers is a good representation of the highly interdisciplinary nature of modern research on photosynthetic antenna complexes, utilizing techniques of advanced spectroscopy, biochemistry, molecular biology, synthetic chemistry and structural determination to understand these extremely diverse and elegant molecular complexes.

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