Chapter 2

Distal and Extrinsic Photosystem II Antennas

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Summary

The distal and extrinsic light-harvesting antennas of Photosystem II (PS II) provide the capability to match electron flow through Photosystem I thus allowing for regulated responses to environmental changes. In this chapter we provide a concise up-to-date description of these antenna complexes and discuss what is known about their function. The cyanobacteria and red algal PS II antennas are phycobiliproteins organized into complex membrane-extrinsic structures called phycobilisomes. A small group of cyanobacteria lack phycobilisomes and instead use the membrane-intrinsic prochlorophyte chlorophyll (Chl) a/b proteins. PS II of eukaryotes is

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primarily served by members of the light-harvesting complex (LHC) superfamily which has become widely diversified into Chl a/b and Chl a/c antennas. As members of the LHC superfamily, cryptophyte algae also have novel phycobilins in the thylakoid lumen, and dinoflagellate algae have a unique peridinin-Chl a protein. Atomic resolution structures of these two antennas and the major plant LHC are opening up a new era in understanding energy transfer.

I. Introduction

Light-harvesting antennas are the pigment-protein complexes that serve to absorb light energy and transfer it to the photosynthetic reaction centers of Photosystem I (PS I) and Photosystem II (PS II). The core antennas are the antennas that bind only chlorophyll (Chl) a and are most intimately associated with the photosystems. PS I has a combined core antenna-reaction center, where about 90 additional Chl a molecules are bound to the same two membrane-intrinsic proteins (PsA and PsB) as the reaction center chromophores. An interesting exception is the PS I core antenna of Acaryochloris with 180 Chl d per 1 Chl a (Hu et al., 1998). In contrast, PS II has two separate Chl a-proteins, CP47 and CP43, that bind only 16 and 14 Chl a respectively (Table 1). The core Chl a antennas are discussed in Chapter 3 (Eaton-Rye and Putnam-Evans).

The fact that the PS II core antennas bind only one-third the number of Chls as the PS I core means that PS II requires additional light-harvesting capacity in order to maintain linear electron flow. The distal and extrinsic antennas provide that capacity. The ‘distal’ antenna complexes are defined as those that are membrane-bound but not part of the core antenna, and the ‘extrinsic’ antennas are those that are attached to the surface of the thylakoid membrane (Green and Durmford, 1996). Both kinds of antenna are regulated qualitatively and quantitatively in response to physiological status and environmental signals. This provides the flexibility required for acclimation to different light, temperature and nutrient regimes, as well as to short-term changes in the redox state of the electron transport chain.

In spite of the great variety of light-harvesting antennas, only three major types of light-absorbing chromophores and only four protein families are employed in all the antennas of PS II (Table 1). Open-chain tetrapyroles called phycobilins are attached to members of the phycobiliprotein family: they are generally found in complex membrane-extrinsic structures called phycobilisomes (PBS). Several groups of cyanobacteria lack PBSs but have a unique membrane-bound Chl a/b antenna using proteins related to the core antenna. The chloroplasts of photosynthetic eukaryotes employ members of the light-harvesting complex (LHC) superfamily, which bind Chl b or c in addition to Chl a and have three trans-membrane helices. Members of this well-studied family transfer energy to either or both photosystems, and have an important role in photoprotection as well as light-gathering. The peridinin-Chl a antenna is unique to dinoflagellates; because the carotenoid peridinin rather than Chl plays the major role in light-harvesting, it is being extensively studied as a model system in energy transfer (Ilagan et al., 2004).

Many aspects of light-harvesting antennas were extensively covered in a recent book in this same series (Green and Parson, 2003), and in individual chapters in two other books (Frank et al., 1999; Larkum et al., 2003). This chapter is restricted to the antennas of PS II, and our aim is to provide a concise introduction and update of material in the above volumes.

II. Phycobiliproteins and Phycobilisomes

A. Phycobiliprotein types

Phycobiliproteins are the predominant antenna pigments in cyanobacteria, rhodophytes, glaucophytes, and in many cryptophytes. They are water soluble pigments that are readily released upon cell breakage and produce vibrant blue- or orange to red-colored solutions. Chemically, the chromophores are linear

Abbreviations: B-PE, R-PE – phycerythrin of red algae (Banchynchronium, Rhodophyceae); Chl – chlorophyll; CP24, CP26, CP29 – minor internal Chl a/b antennas that connect the external antennas with the PS II core; CP43, CP47 – antennas of the PS II core complex; FCP – fucoxanthin-Chl a/c protein; IsIA – Chl a protein induced by Fe limitation (CP43); LHC – member of light-harvesting complex superfamily; LHCII – major LHC antenna of PS II in higher plants; PBS – phycobilisome; Pch – prochlorophyte Chl a/b protein; PS I, PS II – Photosystem I, Photosystem II; PsA, PsB – PS I reaction center-core antenna proteins; RC1, RC2 – reaction centers of PS I, PS II; RP-HPLC – reversed-phase high performance liquid chromatography; SDS-PAGE – sodium dodecyl sulfate-polyacrylamide gel electrophoresis