Summary

Photosystems I and II are remarkable membrane-bound pigment-protein complexes that together produce NADPH, oxidize water and energize the thylakoid membrane, all using light energy. The polypeptides provide an environment in the membrane in which cofactors are placed at optimum distance and orientation, ensuring a rapid efficient trapping and conversion of light energy. The polypeptide core modifies the redox potentials of cofactors to provide fast forward electron transfer and to minimize recombination. The electron transfer pathways use a variety of both common and unusual cofactors. This chapter sets out some of the current ideas and data on the cofactors and polypeptides of photosystems I and II with special emphasis on research in algae and cyanobacteria.

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I. Introduction

The objective of this chapter is to overview our current knowledge of the structure and function of Photosystem I (PS I) and Photosystem II (PS II). These two reaction center complexes are responsible for the initial steps in the conversion of light energy into biochemical products by oxygenic photosynthetic organisms. Two outstanding properties of these complexes are the use of water by PS II as a terminal electron donor thereby producing molecular oxygen and protons, and the direct reduction of NADP by PS I. The review will concentrate on the recent work on these complexes. We refer the reader to the books (Hall and Rao, 1999; Ke, 2001) and reviews referenced to find many of the original papers and details of techniques used.

II. Overview of Photosystems I and II

PS I and PS II consist of membrane-bound pigment-protein complexes. They can each be divided into two parts, the light harvesting complex (LHC) (Chapters 4 (Durnford) and 13 (Larkum)) and the core complex. The light harvesting complex binds light-absorbing pigments. The most important pigments in oxygenic photosynthesis are chlorophyll (Chl) and carotenoids. In cyanobacteria and red algae, phycobilins are also important pigments in the LHC (Chapter 14, Toole and Alnutt). The core complex is responsible for the photochemical reaction and forward electron transfer.

Abbreviations: A₃ – PS I chlorophyll electron acceptor; A₁ – PS I phylloquinone electron acceptor; Chl – chlorophyll; Cyt – cytochrome; Eₚ – midpoint redox potential; Eₚ₀ – midpoint redox potential at pH 7; EPQ – electron paramagnetic resonance; Fd – ferredoxin; Fe-S – iron-sulfur center; kDa – kilodalton; LHC – light harvesting complex; mV – millivolt; NADP – nicotinamide adenine dinucleotide phosphate; P₆₈₀ – PS II primary electron donor; P₇₀₀ – PS I primary electron donor; PC – plastocyanin; Pheo₁ – PS II phaeophytin electron acceptor I; PS I – Photosystem I; PS II – Photosystem II; QA – the first PS II plastoquinone electron acceptor; QB – the second PS II plastoquinone electron acceptor; WOC – water oxidizing complex; Y₀ – tyrosine D2161 (Y₀ when oxidized); Y₂ – tyrosine D1161 (Y₂ when oxidized)

This initial event must be stabilized by a further separation of the charges using an electron transfer chain. It is the optimized organization of the light harvesting pigment-protein and the cofactors in the reaction center which allows high photon trapping efficiency and limits loss of energy by other singlet relaxation mechanisms. The LHC also allows the system to cope with a wide variety of light intensities and wavelengths, thereby increasing the overall efficiency. The essential step for energy trapping is the light driven charge separation between the primary donor (P) and the primary acceptor. In both PS I and PS II, the primary donors are Chl molecules. On excitation by light energy, P becomes a powerful reactant (P*) and interacts with the primary acceptor resulting in the primary electron transfer event. The reaction center Chl of PS II, termed P₆₈₀ due to its bleaching near 680 nm, is photo-oxidized and the electron transferred to the membrane pool of plastoquinone. P₆₈₀ is re-reduced by the water oxidizing complex (WOC) resulting in oxygen evolution. PS II can therefore be termed a water-plastoquinone oxidoreductase. Analogous events with similar rates of forward electron transfer occur in PS I, the net result being the reduction via ferredoxin (Fd) or flavodoxin of NADP and oxidation of plastocyanin (PC) or cytochrome (Cyt) c by the reaction center Chl, P₇₀₀.

The initial part of each electron transfer chain is specifically bound to the core complex and allows fast activationless electron transfer. Following this, mobile electron carriers allow protonation reactions and transfer of reductant out of the reaction center complex. PS I and PS II are linked by the Cyt b₆f complex, which is a membrane-bound protein complex containing cytochromes and a Rieske iron-sulfur center (Chapter 35 in Ke, 2001). The Cyt b₆f complex catalyzes the oxidation of plastoquinol and the reduction of plastocyanin or Cyt c. This complex is also involved in cyclic electron flow around PS I (Bendall and Manasse, 1995).

An important feature of the electron transfer chain is the organization of cofactors to produce vectorial electron transfer across the membrane. Linked to proton transfer, this generates an electrochemical potential across the membrane, which drives processes such as ATP synthesis (Chapter 36 in Ke, 2001). Turnover of PS I and PS II is regulated to prevent imbalances in light energy transfer and electron flow. PS II possesses several photoprotection mechanisms designed to protect it from the harmful effects of