Oxygenic photosynthesis is the main process that produces oxygen and organic matter on earth [1]. During this oxygenic process, water molecules act as electron donors to produce oxygen and protons through the activity of Photosystem II (PSII) [2]. The electrons produced in PSII are transferred to Photosystem I (PSI) via quinones, cytochrome b6f, cytochrome c or plastocyanin [2]. PSI then transfers these electrons to the Ferredoxin-NADP+ reductase (FNR) enzyme through Ferredoxin for the reduction of nicotinamide adenine dinucleotide phosphate (NADPH) [3]. Similarly, protons are transferred by the ATP synthase across the thylakoid membrane to generate ATP. These two high energy products (ATP and NADPH) are used later on in the light-free synthesis of sugars from carbon dioxide by the action of the enzyme complex Rubisco.

Most of the protein structures involved in photosynthesis are resolved at high resolution from different photosynthetic species that includes cyanobacteria, algae and plants (spinach) [4]. Resolving the X-ray crystallographic structure of PSII has always been difficult for structural biologists due to its instability. In photosynthesis, PSII produces free radicals during water splitting that damages the PD1 subunit, therefore it disassembles itself to repair the subunit. This process of damage and repair is continuous during the lifetime of PSII. The benefit of Cryo-electron microscopy is that images are taken from the intact form of PSII, whereas during X-ray crystallography the PSII gets damaged due to high radiation.

The availability of the structure of plant photosystem II bound to its light harvesting complex II (PSII-LHCII) at high resolution is another landmark in photosynthesis studies. It is a scientific breakthrough of immense importance that will be helpful not only in terms of the biophysics of photosynthesis, but also will help with the understanding of the evolutionary progress of oxygenic photosynthesis [5-7]. Wei et al. of the Chinese Academy of Sciences published a paper in Nature in which they showed the resolution of 1.1-megadalton spinach photosystem II–LHCII supercomplex at 3.2 Å resolution using single-particle cryo-electron microscopy (cryo-EM) [Figure 1] [8].

In this homodimeric structure, each monomer contains 25 polypeptide subunits, 105 chlorophylls, 28 carotenoids and some other important cofactors [8]. In each of the PSII monomeric units, Wei et al. showed that the core complex is made of four large intrinsic subunits D1, D2, CP43 and CP47, along with twelve low-molecular-mass membrane bound subunits: PsbE, PsbF, PsbH, PsbI, PsbJ, PsbK, PsbL, PsbM, PsbTc, PsbW, PsbX and PsbZ. In addition, four extrinsic subunits are present on the luminal side: PsbO, PsbP, PsbQ and PsbTn [8].

The amino acid sequence similarity between cyanobacteria PSII and that of spinach is quite high and ranges from 77% to 90% for the main subunits. This close similarity is also established when this cryo-electron microscopic structure is superimposed on that of the cyanobacteria PSII crystal structure of Umea et al. [9], with a Cα-root mean square deviation of 0.57 to 0.69 Å for the main subunits. These close similarities result in almost the same binding sites for cofactors inside the two PSII structures. The small subunits are also similar between the two PSII structures with the exception of PsbW subunit which is absent in cyanobacteria. These small units help in stability, dimerization, association of the peripheral antenna to the core, and protection from photodamage. The four core subunits (CP43, CP47, D1 and D2) contain only Chl a and β-carotenes, while LHCII, CP29 and CP26 have both Chl a and Chl b along with three different xanthophyll molecules [8].

In this cryo-EM structure, there are four extrinsic subunits (PsbO, PsbP, PsbQ and PsbTn) on the luminal side. The subunits PsbO, PsbP and PsbQ are arranged in the form of a triangle around the luminal region of CP43...
and the C-terminus of the D1 subunits [8]. Thus, these three extrinsic subunits protect the CP43 and D1 areas that cover the oxygen evolving complex. Indirectly, these three extrinsic subunits protect and increase the efficiency of the water splitting machinery of PSII.

PSII contains two types of external antenna, the major one is the light harvesting complex II while the smaller ones are the chlorophyll binding proteins: CP29, CP26 and CP24 [10-13]. These minor antennae are present around the core of PSII where they absorb the incoming photons and convert them into excitations that are transferred to the reaction center (RC) where charge separation (CS) occurs [14]. Although crystal structures of plant LHCII have previously been available at a better resolution [14, 15], here the intact structure shows the exact binding modes between PSII and LHCII. The intact structure also shows how the absorbed solar energy in the form of excitons is transferred from the antenna to the core PSII. Each of the peripheral antenna, both CP29 and CP26, contains three carotenoids and thirteen chlorophyll binding pockets. Other differences, such as the 87 amino acid residues that had not been previously resolved, have also been observed for CP29 in the cryo-EM structure. This previously unstructured part forms two motifs, but Wei et al. were not able to exactly assign the carotenoid types to their binding pockets for CP29. A new chlorophyll \( \text{a} \) molecule was also observed at the interface that is possibly involved in energy transfer between two LHCs. For CP26, there is now more information regarding the ligands for the chlorophylls and the exact types of carotenoids.

Based on the cryo-EM structure and previous mutant studies, Wei et al. provide a detailed description of the interaction between the antenna and the core of PSII. They discuss the role of the PsbW subunit in the interaction of LHCII with the PSII core. The role of specific chlorophylls and protein domains in different types of interactions is also thoroughly discussed. Similarly to the CP26 and CP29 antenna chlorophylls, certain lipids molecules are likewise involved in different types of interactions that help in joining the outer antenna to the central core complex. The helix A and C of LHCII forms an AC loop that makes several different kinds of important interactions with CP29 and CP26 and helps in recognition.

One of the interesting things about the Wei et al. structure, which was also pointed out by Croce and Xu in Nature News and Views, is the location of Chlorophyll \( \text{b} \) in the LHCs interfaces [16]. These chlorophyll \( \text{b} \) molecules are distant from one another at the interfaces between LHCs. Thus the excitons are directly moved from each LHCII monomer to the central complex and there is no transfer of energy between chlorophyll \( \text{b} \) molecules. However, the binding and release of the LHCII to the core complex of PSII is a transient process and depends upon the light intensity conditions. These LHCII antenna move between PSII and PSI depending upon the light intensity [17], and give excitation energy to PSI during low light conditions – a phenomenon called state transition [18-21]. PSI has a quantum efficiency of 100% and both branches of the reaction center are active in electron transfer [22-24].

In the near future, it will be possible to unlock the mystery of the exact mechanism of water splitting in PSII. Furthermore, the high resolution structure of both photosystems from cyanobacteria, green algae, and plants will show a comparative evolutionary modification.
in these proteins, and based on this information better artificial photosynthetic machineries can be developed.

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