

Nature's Solar Cell

Structure of the Light Harvesting Complex

Stephen Suresh and Gautham Nadig

The sun is the principal source of energy for all life on earth. Yet, only green plants and certain bacteria can directly use solar energy by converting the light energy into chemical energy. They do this by photosynthesis in specialised organelles called chloroplasts. The energy then trickles down to all the other organisms through the food chain. Ever since 1842, when Mayer discovered that plants convert solar energy to chemical free energy, scientists have been attempting to understand this fundamental process. Photosystem I, Photosystem II and the Cytochrome bf complex mediate the photosynthetic process. The molecular mechanism of photosynthesis is finally being unravelled by a combination of powerful techniques that include spectroscopy, molecular biology, X-ray crystallography and electron microscopy.

The key players in photosynthesis are two membrane-bound protein complexes in the

chloroplasts, the 'light harvesting complex' (also called the antenna complex) and the 'reaction centre'. The light harvesting complex captures the light energy and transfers it to the reaction centre, which acts as a light-driven electron pump across the photosynthetic membrane.

The three-dimensional structure of the reaction centre from purple photosynthetic bacteria was determined by Harmut Michel and his colleagues at the Max Planck Institute in Germany. This was a landmark achievement in understanding photosynthesis and was recognized by the award of the Nobel prize for Chemistry in 1989. The recent determination of the structure of the plant light harvesting complex by Werner Kuhlbrant and his group at the European Molecular Biology Laboratories, and that of the bacterial light harvesting complex by N W Isaacs and his group at the University of Glasgow in 1995 marks yet another major step in the understanding of the molecular basis of photosynthesis. The structure of the light harvesting complex LHC II associated with photosystem II of green plants was solved by electron microscopy, while the corresponding complex LH2 from the purple

Photosystem I Assembly of about 13 polypeptide chains which catalyze the formation of NADPH, a strong reductant. It absorbs light of wavelength shorter than 700 nm.

Photosystem II Assembly of more than 10 polypeptide chains which catalyze the light driven transfer of electrons from water to plastoquinone. It can absorb light of wavelength shorter than 680 nm.

Cytochrome bf Complex A membrane bound protein complex that links Photosystem I and Photosystem II. It is responsible for the transport of electrons from Photosystem II to Photosystem I. Both Photosystems are composed of the light harvesting complex and a reaction centre.



photosynthetic bacteria was elucidated by X-ray crystallography. With the knowledge of the three-dimensional structure, we are in a position to understand at the atomic level how photons are collected and funnelled to the reaction centre where photosynthesis takes place.

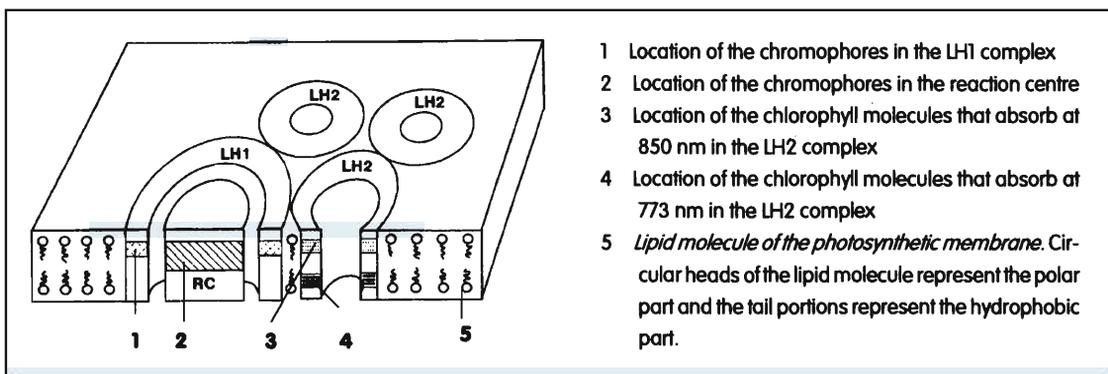
In bacteria, the photosynthetic machinery is embedded in small vesicles which are spherical structures made up of lipid bilayers. The light harvesting complexes with associated chlorophylls, carotenoid molecules and other chromophores and the all-important reaction centre are present in these vesicles. Most photosynthetic bacteria have two light harvesting complexes, LH1 and LH2. The omnipresent LH1 surrounds the reaction centre and has a number of LH2 complexes at its periphery. The number and the properties of the LH2 vary depending on the available light and growth conditions.

Structurally, the LH2 complex is ring shaped and is made up of 9 identical units, each consisting of 2 polypeptide chains named alpha and beta with 53 and 41 amino acid resi-

dues respectively. To each unit, 3 'bacteriochlorophyll a' (*Bchl a*) molecules and a carotenoid molecule are bound. It is interesting that, of these chromophores 2 of the 3 *Bchl a* molecules absorb light of a longer wavelength than the third, due to differences in their chemical environment. These 9 pairs of chlorophyll molecules that absorb at 850 nm (1 nanometer = 10^{-9} m) are arranged in a ring close to the periplasmic surface. Each molecule in the ring is in van der Waals contact with its neighbours on either side. The other 9 chlorophyll molecules that absorb at 773 nm form a ring in a plane 18\AA directly below.

When a photon hits one of the chlorophyll molecules the absorbed energy spreads in about 200-300 femtoseconds (1 femtosecond = 10^{-15} seconds) to the other chlorophyll molecules in the ring through a mechanism called the exciton coupling. This mode of energy transfer is

Figure 1 *The membrane bound light harvesting complexes (LH1 and LH2) and the reaction centre (RC) in purple photosynthetic bacteria (Rhodospseudomonas acidophila). LH1 = light harvesting complex 1; LH2 = light harvesting complex 2; RC = reaction centre.*



- 1 Location of the chromophores in the LH1 complex
- 2 Location of the chromophores in the reaction centre
- 3 Location of the chlorophyll molecules that absorb at 850 nm in the LH2 complex
- 4 Location of the chlorophyll molecules that absorb at 773 nm in the LH2 complex
- 5 Lipid molecule of the photosynthetic membrane. Circular heads of the lipid molecule represent the polar part and the tail portions represent the hydrophobic part.

When a photon hits one of the chlorophyll molecules the absorbed energy spreads in about 200-300 femtoseconds to the other chlorophyll molecules in the ring through a mechanism called the exciton coupling.

made possible by the appropriate disposition and close arrangement of the chromophores within the ring. The energy is then transferred from one LH2 complex to another till it reaches the chromophores of an LH1 complex, which absorb at a longer wavelength. The LH1 complex then transfers the energy to the chromophores in its associated reaction centre (*Figure 1*). This extremely quick transfer of energy from LH2 to LH1 and to the reaction centre is facilitated by the positioning of the chromophores in each of the complexes at the same height. The photosynthetic process begins when the photon strikes a pair of chlorophyll molecules called the 'special pair' situated at the end of the reaction centre. An electron within the special pair absorbs energy from the photon and moves to a neighbouring molecule of pheophytin, a chlorophyll-like accessory pigment, leaving the special pair with an excess positive charge. This electron travels from one quinone molecule to a second quinone molecule on the periplasmic side of the membrane. The positive charge on the special pair of chlorophyll molecules is neutralised by an electron from a cytochrome C molecule permitting the special pair to absorb another photon and repeat

the process over again. This results in the second quinone molecule having 2 extra units of negative charge. These quinone molecules now dissociate from the reaction centre to participate in the later stages of photosynthesis which take place at the outer surface of the membrane. Thus the reaction centre serves as a solar cell using light energy to bring about charge separation across the membrane. Nature's solar cell is highly efficient; it captures 98 -100 % of the incident photons. Half this energy is used in driving the electrons along the pathways of the photosynthetic pigments; while the other half gets stored as electrical potential energy across the membrane. Such depth of understanding of this fundamental process has been made possible only by the elucidation of the atomic structure.

Suggested Reading

Lubert Styer. *Biochemistry*, WH Freeman and Company, San Francisco. 1988.

J Deisenhofer, W Michel. The Photosynthetic Reaction Centre from Purple Bacteria, *Rhodospseudomonas viridis*, *EMBO J.* 8:2149-2169. 1989.

W Kuhlbrant et al. Atomic Model of Plant Light Harvesting Complex by Electron Crystallography. *Nature* 367: 614-621. 1994.

Mc Dermott et al. Crystal Structure of an Integral Membrane Light Harvesting Complex from Photosynthetic Bacteria. *Nature* 374: 517-521. 1995.

Stephen Suresh and Gautham Nadig are with the Molecular Biophysics Unit, Indian Institute of Science, Bangalore 560 012. Stephen Suresh obtained his Ph.D degree from the Unit in 1995, while Gautham Nadig is working for his Ph.D degree at the Unit. Their interests are in the structures function relationships of macromolecules.