The Reporter 294, 4-5. 24 February 1989.

Harvesting Light in a Changing Environment

Without exception, everything that happens in the living world needs energy to make it run – energy that comes ultimately from the sun. Our own lives depend on the accumulated legacy of a hundred million years of conversion of sunlight, compressed into the coal, oil and gas on which our style of civilization depends. The energy in our food was converted and stored recently, when the plants that we eat (even if at second hand) used sunlight for their growth. When you ride a bicycle, make no mistake that the wheels are driven by nuclear fusion, albeit fusion that happened some years ago and in a reactor at the safe distance of ninety three million miles. The wheels of your car go round for the same reason, but in that case the energy from the fusion reactor was accumulated and stored long ago, when ferns and amphibians by and large had things their own way on the land.

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Long before amphibians, when life originated on this planet, the first and simplest cells had to make more of themselves from the dead, raw materials around them. They produced the energy they needed from chemical reactions – reactions that would have taken place without them but which they could harness for their own use, most likely by linking them to the transport of electrically-charged particles across their own boundaries with the outside world. The supply of this chemical energy was limited, however, and the evolution of more complex and versatile forms of life could only come after one of those early cells had discovered an important trick - how to get its energy from the sun.

The heart of the green machine

In photosynthesis, light energy is converted into a chemical form to be used by a living cell for any one of its vital activities. Today we can see that the trick of photosynthesis has come a long way from its early beginnings, but we can still glimpse the essential features behind the elaborations that have come from three thousand million years or so of evolutionary change.

To store light energy, a living cell must use it to drive a photochemical reaction. The earliest chemical event in photosynthesis is in fact a photo*electro*chemical reaction of the green pigment, chlorophyll. The chlorophyll molecule, after excitation with a quantum of light, returns to its original state by way of a chemical change in which it loses an electron to a neighbouring molecule of a closely related substance called phaeophytin. The phaeophytin hands the electron on to a quinone molecule, and a series of other molecules in turn play 'pass the electron', a game in which energy is transformed again – this time from electrical potential to stored chemical energy in the making of a molecule know as ATP. This last step uses precisely the same mechanism our own cells use when we get energy from our food – in both cases the energy-rich molecule ATP is built up from its components because electrically charged particles are moved from outside to inside, across the membrane boundary of the cell.

In 1985 three German biochemists reported on a structure obtained from X-ray diffraction studies of crystals of a pure substance obtained from the photosynthetic membranes of purple bacteria. The structure showed chlorophyll, phaeophytin and quinone molecules held in a very precise symmetrical arrangement by two proteins, each of which must cross the photosynthetic membrane five times. From this structure, depicted in *figure 1*, we can see for the first time the molecular machine that carries out the crucial, early events of photosynthesis. This work earned Michel, Deisenhofer and Huber the 1988 Nobel Prize for Chemistry. One of the many delights of this work is that it shows that movement of electrical charge really does take place from one side of the boundary membrane to the other, a conjecture of the British scientist Peter Mitchell that formed part of his Nobel-prizewinning theory of how cells transform energy.

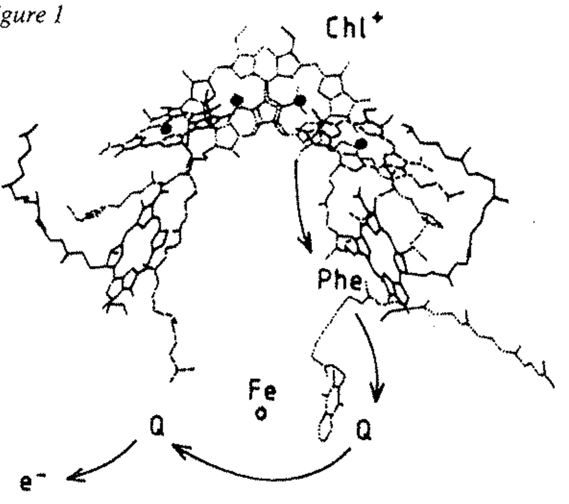
Harvesting the Sun

The beautiful structure of the reaction centre of photosynthesis is not, however, the whole story. Before the reaction centre chlorophyll molecule can be excited, the light energy must be *harvested* by a network of other chlorophyll molecules, and the energy must pass among them before it can reach the reaction centre. The light-harvesting chlorophylls must be held by protein so that they fit into the reaction centre in some way. Such chlorophylls act rather like a funnel for light energy with the reaction centre sitting under the hole at the bottom, as shown in *figure 2*.

The operation of the photosynthetic apparatus depends critically on a balance between its different components. The antenna of chlorophylls and proteins that harvest light must be large and operate at high efficiency when sunlight is in short supply – but a sudden, bright shaft of light will then dangerously overload the energy converting reaction centre unit if there is no way of matching the supply of light energy with the demand that the reaction centre can sustain. The rapid fluctuations in supply of light energy are easily seen in woodland on a sunny day, a snapshot of which is shown in *figure 3*. Plants, algae and photosynthetic bacteria clearly need to be adaptable to changes in intensity of the light they use.

When light is in short supply, photosynthesis must operate at maximum efficiency. This means that the wasted light energy must be reduced to a minimum. In order to do this, the light energy needs to be distributed between the energy-converting reaction centres in direct proportion to how fast each centre can work. This depends on

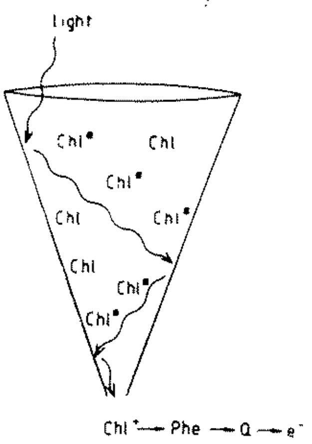
Figure 1



The structure of the main components of the photosynthetic reaction centre of the purple bacterium Rhodopseudomonas viridis, *as first indicated by the work of Deisenhofer and co-workers. There are four chlorophyll molecules (Chl) (the dot at the centre of each chlorophyll ring is an atom of magnesium), two phaeophytin molecules (Phe), two quinone molecules (Q) (one not shown), and an iron atom (Fe). The first and fundamental step of energy conversion in photosynthesis is the movement of an electron (e−) from one of the chlorophylls to the adjacent phaeophytin. This takes several millionths of a millionth of a second. The electron then moves first to one (in just less than a millionth of a second) then the other (in just less than a thousandth of a second) of the quinone molecules. For the hard-line reductionist the rest – life, history, Beethoven quartets, the UFC – is then just a question of more time and a little genetics. The structure shows that the electron must move across the boundary of the cell, from outside to inside, just as Peter Mitchell's theory predicted.*

the colour (spectral composition) of the light, because different reaction centres obtain their light energy from different sets of lightharvesting chlorophyll pigments. Plants, algae and photosynthetic bacteria must also be able to adapt to changes in spectral composition of the light they use.

Figure 2



The reaction centre is just one part of the whole photosynthetic unit and is supplied with light energy ready for conversion by an antenna of light-harvesting chlorophyll molecules, which collect light for the reaction centre rather like a funnel collects water.

Adapt or perish

Green plants can regulate the way light-harvesting and reaction centre units work together by carrying out a subtle chemical modification of their protein molecules. This chemical modification of the protein is *phosphorylation* of one of the protein's amino acid building blocks. Phosphorylation of light-harvesting proteins was discovered by John Bennett at Warwick University in the late 1970s, and the function of the process has been uncovered by a number of research groups around the world, including our own. The effect of phosphorylation is to detach a portion of the major light-harvesting complex of the photosynthetic membrane from its neighbouring reaction centre, thereby decreasing the amount of light energy presented to the reaction centre for conversion.

How the detached, phosphorylated light-harvesting complex disposes of its absorbed light energy is currently a controversial question. Some groups (including that of Tasso Melis, a sabbatical visitor to our Leeds laboratory last year from Berkeley, California) believe that the energy is converted wastefully to heat, and that phosphorylation is a device that prevents overburdening the reaction centre at high light intensities. Other groups believe that the detached, phosphorylated light-harvesting complex reattaches instead to a different kind of reaction centre, in which case energy may be saved by making sure that each reaction centre is correctly supplied with its appropriate share of the absorbed light energy. In either case, it is clear that phosphorylation causes proteins that are near neighbours in the photosynthetic membrane to move apart from each other. This process is illustrated in *figure 4*.

Other adaptations of photosynthesis involve radical alterations in the relative numbers of the different components of the photosynthetic machine – a subtle modification of existing proteins is not enough to explain the great differences between plants or cells grown in sunny and shady environments. In my research group we think that the switch that controls phosphorylation also controls the activity of the genes that carry the genetic information for individual light-harvesting and reaction centre components. We need to know how these genes can be turned on and off by light before we will understand the way in which development can be steered by the environment. The tools of molecular genetics must be used on photosynthesis before these problems can be solved.

We need to know the structure of light-harvesting complexes in order to understand how they fit together with reaction centres. We need to know how these things fit together in order to understand how the green machine of photosynthesis works and adapts. We also need to know how photosynthesis is able to switch genes for its own components on and off during development. The answers should tell us how proteins interact with each other in a controlled way in all biological membranes, including the membranes of vision, smell, hormone action, and nerve signal transmission.

Leeds University today possesses some of the brightest people and sharpest tools found anywhere in modern biology. The future is bleak for those who haven't learnt from Nature that you have to adapt, though may be the amphibians are still happy in a small way. But in photosynthesis as elsewhere, the future is bright for those who can muster the interests and resources residing in different departments and specialist fields – and who are willing to learn.

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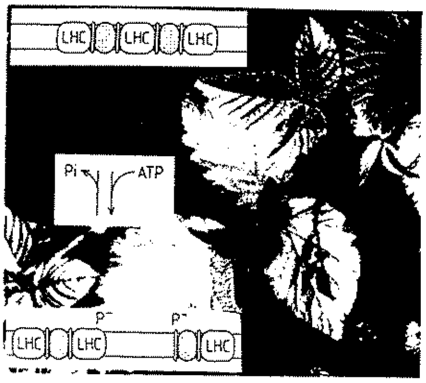
Figure 4



In shade or in dim light, light-harvesting units (LHC) fit together tightly with reaction centres (dotted area) in photosynthetic membranes of plants, as shown in the upper part of the figure. In bright, direct sunlight, a reaction is switched on that adds a phosphate group (P−) to the proteins of the LHC and of the reaction centre itself. This causes them to move apart. The phosphate group is added from ATP, the energy storage molecule of biology. On return to shade, the phosphate group is removed and released (Pi), and the LHC and reaction centre molecules then recognize each other again and so reconnect. SERC-supported work currently carried out by Michael Harrison, Alan Cox and Nicholas Tsinoremas in my laboratory now suggests that this process happens in green plants, algae and bacteria – implying that this kind of control of light-harvesting is universal in photosynthesis. With the help of Dr John Findlay and his research group in the Biochemistry Department, we are finding out precisely which proteins are affected, and where. The changes in protein structure are unknown, and understanding these effects in the same way that we now understand the reaction centre (figure 1) *is a major challenge for the future.*

Figure 3

Light-harvesting is not a job for a machine that likes a steady and predictable workload. Roundhay Park on sunny June day shows how changes in the supply of light can be large and rapid – with a moderate breeze the flecks of sunlight can dance across any leaf near the woodland floor several times a second.