**The first organisms to have the ability to effect photosynthesis**, cyanobacteria, emerged in the primordial Precambrian ocean over three billion years ago. Making use of solar energy, they produced oxygen, which slowly accumulated, bringing about a veritable "evolutionary revolution." Oxygen enrichment of the primitive atmosphere led to the appearance of the ozone layer, shielding the Earth from the Sun's ultraviolet radiation, and caused changes in climate and the composition of the Earth's crust. These changes allowed the continents to be colonized by new plant and animal life forms. Plants, elaborating as they do their own organic material from mineral substances they draw from the ground or the aquatic environment, are able to grow and develop in the remotest parts of the planet, even on polluted soils.

Photosynthesis,
a green chemistry driven by solar energy

Photosynthesis and oxygen production

Antoine Gonin/CEA
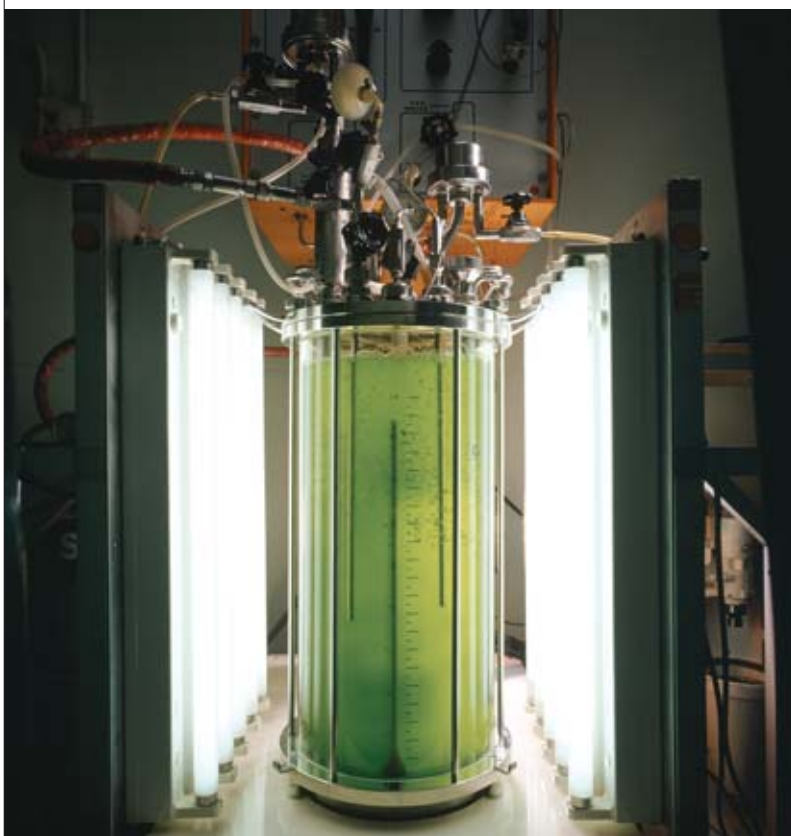
Culture fermenter for cyanobacteria used in biophysical investigations of photosynthesis. The light intensity to which these organisms are exposed increases as the growth cycle progresses. The liquid is centrifugated to recover the cells. The photosynthetic enzymes of interest are then segregated and purified through use of detergents. **Mutant** organisms may also be cultivated.

Sun, water, and carbon dioxide, these are the few ingredients with which photosynthetic organisms make do. Research efforts aimed at gaining a better understanding of the physical and chemical mechanisms underpinning the very high efficiency of photosynthesis, that green chemistry providing for the living world, have as their main goals the development of artificial photosynthetic systems and production of hydrogen, the energy of the future.

Photosynthesis is the biological process used by plants, algae and some **bacteria** to convert the energy of light into the chemical energy indispensable to living species (see Box E, ***The photosynthesis process***). The photophysical part of the process corresponds to absorption of solar energy by the **chlorophylls**, i.e. the green pigments found in plant leaves. Within the plant cell, chlorophylls are carried by membrane **proteins**, and are arrayed into harvesting networks, the **antennae**, so that, on the one hand, the greatest possible numbers of **photons** may be absorbed, and, on the other, so that the chlorophylls, electronically excited by absorption of a proton, may transfer that excitation, passing from neighbor to neighbor, to a specialized P chlorophyll (see Figure 1), whose protein environment is such as to confer to it specific properties. In its excited state, this P chlorophyll must shed

an **electron**. There thus occurs a photochemical reaction, giving birth to two **radical species** of opposite electrical signs, which are highly reactive. These radicals are then used in chemical reactions requiring input of a large amount of energy.

Life on Earth is based on the chemistry of carbon, its source being **carbon dioxide** (CO_2), also known as **carbon gas**. To become useful for biological reactions, this must be "energized," in other words it must take up electrons e^-, and **protons** H^+ to compensate for the negative charges. The high-energy electrons involved are those initially yielded by the P chlorophyll. For the system to work, it is essential that the P chlorophyll can recover every electron thus yielded. Photosynthetic organisms solved this problem very early on in the history of evolution, over 3 billion years ago, by developing a trick that changed the face of the world: *they took out electrons from water.*

The appearance of oxygen on Earth: an ecological cataclysm

Taking electrons from water (H_2O) resulted in production of dioxygen (O_2) and protons. For a long time, after the emergence of photosynthesis, O_2 concentration in the atmosphere remained very low, owing to the high capacity to trap it, found in minerals. This event in the Earth's history is clearly recorded in geological strata, iron-oxide (Fe_2O_3) rich up to around -2.5 billion years. [1] Once minerals became saturated in oxygen, it then seeped out into the atmosphere, with major consequences. Up till that time, the amount of oxygen encountered by living species had been very low. The amounts issuing from photosynthesis were of an altogether different order of magnitude, to the point of becoming a poison to the living species coming into contact with it. For those that survived, the presence of O_2 was put to advantage in a new energy process: a type of **respiration**, using O_2 as end acceptor of the electrons. The energy-rich carbon-based molecules produced through photosynthesis became the fuel, the O_2 waste being used as the oxidant. This type of respiration, exhibiting as it does good energy efficiency, favored the rise of multicellular organisms, and further on of more complex life forms. Through action of **ultraviolet** (**UV**) **radiation** from the Sun, the emergence of O_2 resulted in accumulation of **ozone** in the upper layers of the atmosphere, thus shielding living species from the damaging effects of the free radicals generated by UV radiation. This natural anti-UV filter allowed life, for the first time, to "come out into the open." Thus it was photosynthetic species that were responsible for creating, and sustaining, the conditions necessary for life on Earth, as we know it. Such a success may be attributed to the paucity of resources required: Sun, water, and carbon dioxide.

It may be said, with no exaggeration, that the emergence of photosynthetic **oxidation** of water is the most important event our planet has experienced. It generated, and goes on generating, the oxygen we breathe. It allowed multicelled life forms to develop, and altered the physical–chemical characteristics of the Earth.

(1) On this topic, see the site at:
http://www.ac-montpellier.fr/ressources/99/99en0328.html.

Antoine Gonin/CEA

High-magnetic field electronic paramagnetic resonance (EPR) experiment to investigate free radicals in photosynthesis and biology. This allows very precise determination of the radical species formed during the photochemical reactions occurring in the core of photosystem II, the oxygen-evolving enzyme.

The contribution of photosynthesis energy to human development

Photosynthesis still stands as the main source of energy for humans. Our food comes from agriculture, of which only photosynthesis allows the development, whether directly (vegetable foodstuffs) or indirectly (meat from herbivores). **Fossil energy** is wholly derived from former photosynthetic organisms. The biomass also forms a major source of energy. Understanding the physical and chemical mechanisms underpinning the very high efficiency of photosynthesis will allow efficient artificial photo-**catalytic** systems to be devised.

The mechanisms at the core of the enzyme

Chlorophyll photochemistry, electron transport and water oxidation all take place in the same **enzyme**: the oxygen-evolving enzyme, a **complex** known as **photosystem II**, or **PSII reaction center**, also known as water–plastoquinone oxidoreductase (see Box 1). This green enzyme consists in the association of over twenty proteins, embedded in a **lipid** membrane. All the important photochemical reactions take place in two of these proteins, where the specialized chlorophylls and **pigments** required for charge separation are to be found (see Figure 1).

The mechanism unfolds as follows. Chlorophyll is excited by light, and, in the few million-millionths (10^{-12}) of a second that follow, charge separation occurs. The chlorophyll thus excited has yielded one of its electrons
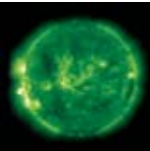
to another molecule, a **pheophytin**, this being a chlorophyll having no magnesium atom at its center. The pair thus formed, i.e. the pigment with an extra electron and the chlorophyll that has shed its electron, carries practically all of the light energy. If these charged species were in isolation, they would enter into a reaction together. The electron would be returned to the chlorophyll, and the light energy absorbed would be reemit-

ted in the form of heat, or light of lower energy, i.e. light that is redder: this is the phenomenon of fluorescence. In contrast to this, however, the electron-donor and -acceptor pigments are sited in the protein in such a way as to ensure that the positive and negative charges migrate in opposite directions all along the chain of electron transporters. In the few millionths (10^{-6}) of a second that follow charge separation, elec-

Cyanobacteria, privileged organisms for photosynthesis research

1

Cyanobacteria are the originators of the planet's oxygen. They are exemplars of the extreme adaptability shown by **photosynthetic** organisms. The thermophile bacterium *Thermosynechococcus elongatus (T. elongatus)* is of particular interest. It was discovered at Beppu, in Japan, in a hot spring. In this species, the oxygen-evolving **enzyme** (photosystem II, **PSII**) is far more stable than that found in plants, even though it is practically identical to it. Quite recently, its **genome** was fully **sequenced**. This cyanobacterium is deemed to be similar to the first organisms to have acquired the ability to **oxidize** water. The enzyme has changed little over the course of evolution.
This cyanobacterium can be dish-grown, and its **DNA** may be manipulated. Appropriate protein-engineering techniques have enabled a purification protocol to be arrived at for the PSII enzyme. This is a membrane **complex** of about 300 kDa (1 dalton = $1.66 \cdot 10^{-27}$ kg), comprising at least 17 subunits. It contains at least 13 cofactors [1] active in **electron** transport, and over 35 **chlorophylls**. The stability of the purified PSII means it is wholly suited for the carrying out of enzymology experiments in which extreme biochemical constraints may be used, to trap intermediate states in the key water-oxidation reactions. This enzyme's three-dimensional structure has recently been elucidated.
Thus, because its genome is known, because its PSII enzyme is easily manipulated, and because the latter's three-dimensional structure is known, the *T. elongatus* cyanobacterium is a privileged organism for photosynthesis research.

(1) Cofactors: small organic molecules or inorganic ions bound to a protein, acting as part of its structure, and in most cases required for its activity. In photosystem II, the main cofactors involved, directly or indirectly, in electron transport are chlorophylls, pheophytins, plastoquinones, and manganese and calcium ions.

At (a), hot spring at Beppu, in Japan, where cyanobacterium *T. elongatus* was discovered. It cells may be grown on a Petri dish or in a liquid medium (b). At (c), cross-sectional and longitudinal views of a cell, in electron microcopy. Highly elongated in shape, it is replete with lipid membranes carrying chlorophyll-containing proteins together with the other proteins involved in the energy machinery (see Box E, *The photosynthesis process*). At (d), structure of the PSII core, obtained by X-ray crystallography. The oxygen-evolving enzyme contains over twenty different proteins. The two central subunits (D_1 and D_2) hold all the important cofactors, and are host to the photochemical and catalytic reactions.

1 µm

10 nm
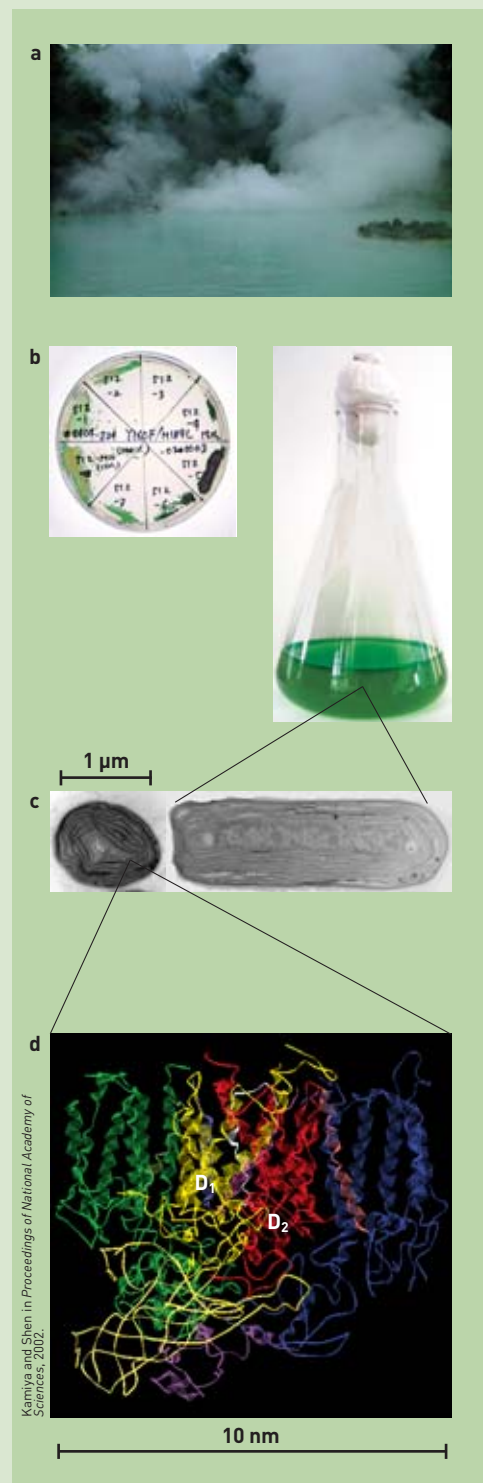
Kamiya and Shen in *Proceedings of National Academy of Sciences, 2002.*

tron-transfer reactions occur, and the two charges (negative and positive) end up located in distant regions of the protein, at opposite ends. This state is stable for a few seconds, and still carries half of the excitation light energy. This energy amounts to about 1 **electronvolt** stored per photon. Astonishingly, most of these reactions still occur at the temperature of liquid **helium**, −269 °C, almost the coldest temperature achievable. This ability, exhibited by part of the system, to function at such extreme temperature is of no consequence in nature, however it has proved crucially helpful to the physicist and the chemist, in investigations of the enzyme.

The percentage of solar energy stored by the enzyme is not bad, for a **photovoltaic cell** working both chemistry and solid-state electronics. Water oxidation requires extraction of four electrons from two molecules of water, yielding four protons and one molecule of gaseous oxygen. Now, photo-induced charge separation generates but a single positive charge, having the ability, in principle, to strip just one electron from the water molecule. For water oxidation to take place, four charge separations are thus required, to yield the four positive charges. Photosystem II evolved to store these four positive charges. For that purpose, it makes use of a cluster of four manganese **ions**, associated to a calcium ion (Mn_4Ca) (see Figure 2). These metals also form the binding site for the two water molecules: this is the catalytic site of the enzyme. The reaction mechanism at work in the **active site** remains very much unknown, and many research efforts are currently directed at elucidating it.

Achieving deeper understanding of the catalytic stage

Decades of research work in biology, chemistry and physics, carried out in dozens of universities and research centers, including many numbering among the most prestigious world-wide, have yielded a detailed vision of the oxygen-evolving enzyme. Identification of the various partners involved, from proteins to pigments, required investigations in the fields of biochemistry, molecular biology, and spectroscopy. These same disciplines, availing themselves of the assistance of **molecular modeling**, considerations on evolution and, more recently, three-dimensional **X-ray** crystallography, have supplied structural information. The mechanistic model for electron transfer and water oxidation is the outcome of detailed spectroscopic investigations and biophysical measurements, and, as regards the Mn_4Ca complex, contributions from inorganic chemistry.

It is apparent that the photochemical part of the enzyme is better known than the chemistry carried out by the catalytic site. The structural configuration of the metals forming it has only just been published, in February 2004. This is a major advance, which, however, does not settle the issue, since **resolution** is not perfect, and there are many strong arguments militating in favor of a structural modification of the Mn_4Ca complex during storage of the four positive charges. Considerable work thus still remains to be done, before the structures of the Mn_4Ca complex are known for its various **oxidation states**. Nevertheless, with publication of this first structure for the active site, the topic has entered a new era: one where spectroscopists and molecular
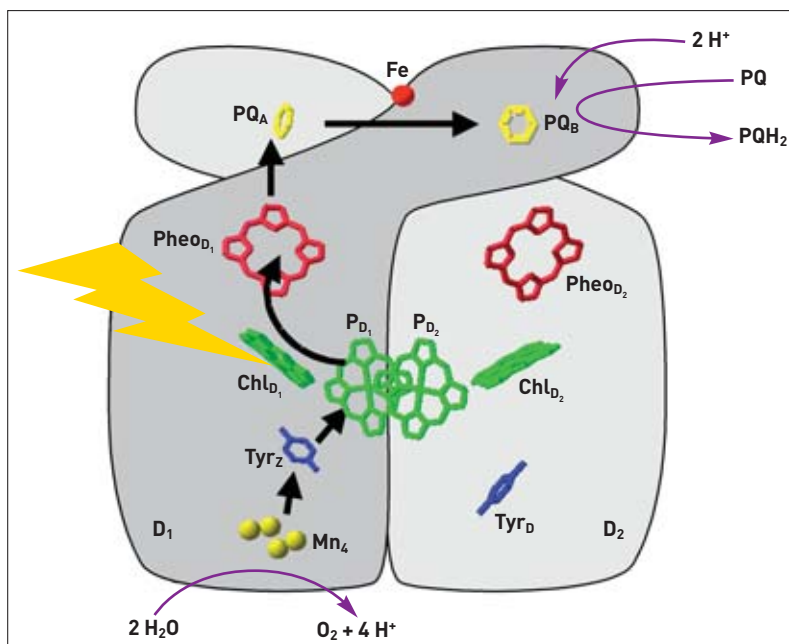

Figure 1.

Photochemical and catalytic reactions occurring in the core of photosystem II. Light is absorbed by the chlorophylls (Chl and P in proteins D_1 and D_2). One of these, Chl_{D_1}, yields one electron to a pheophytin, Pheo, resulting in a pair of radicals of opposite charges (Chl^+, $Pheo^-$). The pair of P chlorophylls yields one electron to the Chl^+, and $Pheo^-$ transfers one to plastoquinone PQ_A. The subsequent electron transfers lead to oxidation of the Mn_4Ca complex, and reduction of the second plastoquinone, PQ_B. It should be noted that a tyrosine, one of the twenty amino acids that make up proteins, plays a role as electron transporter in this sequence: indeed, tyrosine Tyr_Z yields an electron to P^+, going on to oxidize the Mn_4Ca complex. Ending the sequence, the doubly-reduced plastoquinone PQ_B binds two H^+ ions, and exits PSII to diffuse into the membrane, in the PQH_2 form.
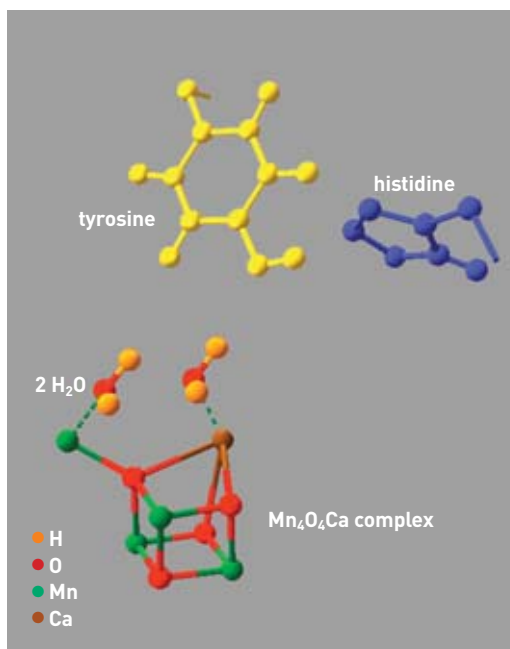

Figure 2.

Crystallographic structure of the tyrosine Tyr_Z and oxidized Mn_4Ca catalytic site of the enzyme (Ferreira *et al., Science*, 2004). While this structure represents a remarkable breakthrough as regards knowledge of photosystem II, it allows neither the way water is oxidized to be accounted for, nor the determination of the positions of the two water molecules before oxidation. This figure illustrates one hypothesis, whereby the water molecules are able to bind to the adjacent calcium and manganese. This assumption entails that tyrosine Tyr_Z can strip the electrons and protons from the water during the catalytic stage. Tyrosine oxidation can only take place if it ejects its proton. It is the neighboring histidine (an amino acid) that captures it.
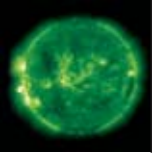
E The photosynthesis process

Photosynthesis is the biological process by means of which solar energy is used by living cells for their own energy requirements. This highly complex process is carried out by plants, but equally by algae and numerous bacteria. Among the latter, cyanobacteria (see Box 1, p. 88) make use of the same kind of photosynthesis as plants and algae, enabling them to oxidize water and release oxygen. These photosynthetic organisms are autotrophic: they synthesize their own organic material from the mineral substances they draw from the ground or the aquatic environment (water and mineral salts). In symbolic representation, formulation of this so-called oxygen photosynthesis goes as follows:
n [CO_2 (carbon dioxide) + H_2O (water)] + solar energy $\rightarrow$ $(CH_2O)_n$ (carbohydrate) + n O_2 (oxygen).
All the stages of photosynthesis take place in the chloroplasts, which are internal organelles in plant cells. The chloroplasts, just as the cyanobacteria, contain specialized membranes in which are found all the molecular structures required for the initial steps of photosynthesis. These membranes are organized to form closed structures (a form of flat vesicle, these are known as thylakoids in chloroplasts).
Visible light from the Sun is absorbed by colored molecules: mainly chlorophylls, the universal photosynthesis pigment, and a variety of molecules, which differ according to the organism (carotenoids, phycobilins, phycocyanins...). These photoreceptor pigments are bound to proteins, which are in

turn, in most cases, embedded in the photosynthetic membrane. These proteins, together with their pigments, are associated into vast arrays comprising around 300 chlorophylls, known as photosystems. Each photosystem is structured round a central region, the reaction center, the core of which is formed by a specialized pair of chlorophyll molecules. Only this pair is chemically reactive. It receives, in the form of electronic excitation, the energy from the solar photons captured by all of the pigments in the photosystem. The latter thus have a function as harvesting antenna elements, also carrying out an electron-energy transfer function. Thus excited, the "special" chlorophyll pair has the ability to transfer an electron to a succession of electron-acceptor and -donor sites present in the reaction center. It is consequently termed the "primary electron donor."
Electron transfers follow a precise organization within the photosynthetic membrane, to achieve, on the one hand, chemical reduction of one compound, nicotinamide adenine dinucleotide phosphate ($NADP^+$), by an enzyme, NADP-reductase (also known as **FNR**, or ferredoxin–NADP-reductase), and, on the other, storage of protons H^+ in the thylakoids' internal space. The chemical energy potential resulting from this difference in proton concentration on either face of the photosynthetic membrane is used by a membrane protein, ATP-synthase, to synthesize adenosine triphosphate (ATP), subsequent hydrolysis of which will release, in controlled fashion, the chemical energy thus stored. Ulti-

mately, the energy from solar photons is converted into two forms of chemical energy, in reduced $NADP^+$ (NADPH) and in ATP.
Photosynthetic organisms having the ability to release oxygen have two quite distinct types of photosystems, designated as I and II. Associated within the same photosynthetic membrane, they work to couple the energy from their two photochemical reactions into the electron-transfer chain going from oxidation of water into oxygen through to NADPH and ATP synthesis. They thus work in series, in energy terms (see Figure).
Photosystem II, PSII, has a primary electron donor designated as P680 (as this pair of chlorophylls absorbs light at 680 nm). Photo-induced departure of one electron leaves P680 bearing a positive charge, i.e. in an oxidized state. In order to return the P680$^+$ to its neutral state, and allow a new photochemical cycle to occur, a major step of photosynthesis now takes place within PSII, photolysis of water:
$2\ H_2O$ (water) $\rightarrow O_2$ (oxygen) + $4\ H^+$ (protons) + $4\ e^-$ (electrons).
The electrons originating in water photolysis are transferred through to P680, and gaseous oxygen is released. The electrons stripped from P680 travel through to photosystem I, PSI, by way of a sequence of oxidation–reduction reactions involving electron transporters bound to the PSII core (see *Photosynthesis and oxygen production*). They exit PSII in the guise of doubly-reduced plastoquinones, PQH_2, that diffuse in the membrane, and transfer this reduction potential to a membrane cytochrome (cyt b_6f), and
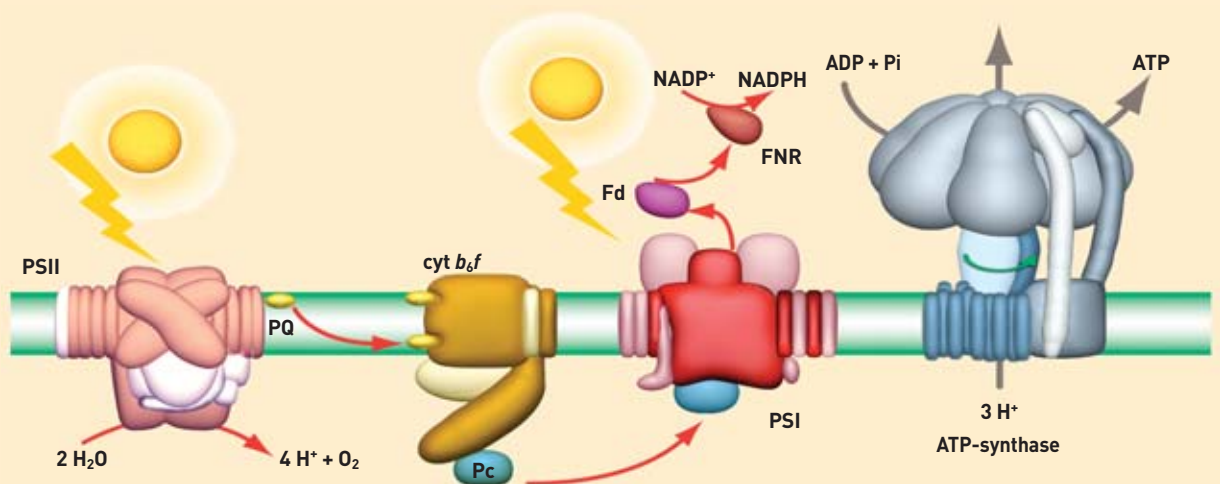

Figure.
Membrane-based stages of the photosynthesis process occurring in green plants, algae and cyanobacteria.

subsequently to a plastocyanin, **Pc**, a small, copper-containing soluble molecule.

When the electron transmitted by PSII by way of the plastocyanin reaches PSI, it replaces the electron lost by that photosystem's primary donor, **P700**, this also having been indirectly excited by a second photon. The electron yielded by PSI follows a chain of transporters within the reaction center, ultimately being transferred to a ferredoxin, **Fd**, a small iron-containing molecule. The electron is then transferred on to the NADP-reductase, this reducing $NADP^+$ into NADPH.

The chemical energy thus generated by the membrane-located photosynthesis processes just described allows reactions of organic molecule synthesis (including carbohydrate synthesis) to occur inside the cell. These reactions, which require input of energy, and take place in the aqueous phase, constitute the *Calvin cycle*.

This final stage of photosynthesis involves the ATP and NADPH generated by the in-membrane reactions. The main carbon-fixation reaction, whereby an atom of inorganic carbon is converted into organic carbon, unfolds as follows: atmospheric CO_2 reacts with a sugar, ribulose 1,5-bisphosphate, or RuBP, and water, to yield two molecules of 3-phosphoglycerate. This carbon-fixation reaction is catalyzed by a large enzyme, ribulose bisphosphate carboxylase, or **Rubisco**. The remaining steps in the cycle result in regeneration of RuBP. For every molecule of CO_2 converted into a carbohydrate, three molecules of ATP and two molecules of NADPH are consumed. The overall equation for the Calvin cycle may thus be set out as follows:

$3 CO_2 + 9 ATP + 6 NADPH + water \rightarrow$ glyceraldehyde 3-phosphate + 8 Pi (inorganic phosphate) + 9 ADP (adenosine diphosphate) + 6 $NADP^+$.

The glyceraldehyde 3-phosphate goes on to be transformed into saccharose (sucrose), and starch, these constituting the energy reserves of plant cells.

Rubisco is a bifunctional enzyme, being equally able to effect fixation of oxygen O_2. This reaction yields 2-phosphoglycolate, which is not involved in the Calvin cycle. It would thus seem to be of no use to the plant. It sets off a complex process, known as **photorespiration**, for the purposes of consuming the 2-phosphoglycolate. Some plants, such as corn (maize), have developed leaf structures and biochemical pathways that concentrate CO_2 in the vicinity of Rubisco, thus restricting its utilization of oxygen.

biologists can focus on understanding the chemical mechanism, on the basis of the three-dimensional structure. Further, with this structure on hand, chemists seeking to develop **biomimetic** catalysts will find a new source of inspiration.

Optimizing research work, with two major goals

Why should investigations on photosynthesis go forward? First of all, photosynthesis plays the leading role as far as creation and sustenance of the **biosphere** is concerned. This is also where energy input, for the living world, originates. Further, investigations in this area represent a driving force for biophysics as a whole (see Box 2). Moreover, this field has provided a paradigm for membrane proteins (yielding a Nobel Prize in 1988), electron-transfer theory (with a Nobel Prize in 1992), the chemistry of **amino acids** in the radical state, the chemistry of manganese-based multinuclear complexes, and catalysis of water oxidation. The significance of photosynthesis for agriculture does not only arise on a fundamental level, it equally concerns the effects of herbicides. The photosystem II enzyme forms the target of numerous commercial herbicides, and its functioning may represent a limiting stage in plant growth. Further, photosynthesis is at the heart of such issues of ecological concern as carbon wells [2] or coral bleaching owing to warming of the oceans. And these are just a few examples.

(2) Carbon well: occurring as it does in our environment in a variety of forms, carbon is stored in the atmosphere, the ocean, soils, vegetation and animals. It is subject to many exchanges between these compartments. The biomass and ocean, being absorbers of carbon, are known as carbon wells.

Antoine Gonin/CEA

Illumination of a sample of photosystem II, the oxygen-evolving enzyme. Use of low temperature allows trapping of an intermediate state of the photochemical reaction.
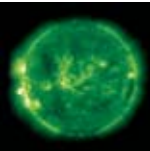
A multidisciplinary research effort   2

The world over, development of new biophysical methods has often been associated to research work on **photosynthesis**. This is particularly true of fast kinetic laser-flash absorption spectroscopy, some infrared spectroscopy techniques and vibrational spectroscopy as a whole, and magnetic-resonance spectroscopy techniques. The Bioenergetics Service at Saclay has played a major part in the investigation of the biophysics of photosynthesis, and has gained international renown for all of these methods. Its strength lies, on the one hand, in the synergetic utilization of the entire range of biophysical techniques to focus on a particular problem, and, on the other, in its mastering both the "bio" and the "physical" in the "biophysical" term. Indeed, it brings together not only physicists but also physical chemists, biochemists, molecular biologists, and physiologists. Along with researchers from CEA, research workers from CNRS (National Scientific Research Council: Centre national de la recherche scientifique), from INRA (National Agronomics Research Institute: Institut national de la recherche agronomique), academic researchers, as well as many researchers from abroad, are all working together on this fascinating topic.

The new spectroscopy techniques developed in conjunction with photosynthesis research have been extensively used, to good advantage, in other research programs. Investigations carried out at the Saclay Center, on such themes as DNA repair, hydrogen production, oxidizing stresses, and processes involved in aging and some illnesses have all benefited from the expertise gained in the photosynthesis field. Notwithstanding the diversification that has occurred, over the past few years, as regards research topics, some of which have seen remarkable successes, photosynthesis remains the main driving force for biophysical research at Saclay.

At CEA, interest centers more particularly on photosynthesis as a source of energy, with two major goals: "photobiohydrogen," i.e. the production of hydrogen by photosynthetic organisms, and development of artificial photosynthetic systems.

In some photosynthetic species, the electrons extracted from water, which are normally used to **reduce** CO_2 into sugars, can be used to reduce H^+ ions into *gaseous hydrogen* (H_2). At Grenoble, in the Jean-Pierre Ebel Structural Biology Institute (CEA–CNRS–Joseph-Fourier University), experts of world renown are working on the hydrogen-evolving enzyme. The Bioenergetics Service at Saclay has specialized on the water-oxidizing enzyme, and all processes involved in the migration of energy-rich electrons to the site where they will be used by the hydrogen-evolving enzyme. CEA's Cadarache Center is home to experts on plant **metabolism** and other physiological aspects of these processes. A drive is being mounted to coordinate and optimize research efforts, to gain a better understanding of the way photosynthetic species make use of the energy of light to generate hydrogen and oxygen from water. The Bioenergetics Service at Saclay is also collaborating with an inorganic-chemistry laboratory at Orsay University nearby, a correspondent research laboratory (LRC: *laboratoire de recherche correspondant*) of CEA, on the development of *artificial photosynthetic systems* mimicking the biological system. The ultimate aim is development of "photoactivatable" catalysts, carrying out water oxidation and hydrogen generation. Concurrent investigation of the biological model and chemical systems, implementing new physical approaches, is the most valuable asset for this research effort. It is now conceivable that the biological process that provides the living world with its energy, and stands as the origin of fossil energies, may be used as a source of hydrogen, the energy of the future.

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Bioenergetics Service
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Positioning a sample for electronic paramagnetic resonance (EPR) investigation of the Mn_4Ca complex of photosystem II. The sample is held in the EPR spectrometer at a temperature of – 269 °C, the temperature of liquid helium.

C Elementary particles and fundamental interactions

Neutrinos are the stealthiest particles in the **standard model of particle physics**, the theoretical framework describing all known **elementary particles** and the **fundamental interactions** they mediate (see Table).

The basic constituents of matter, **fermions**, are partitioned into two main categories: **leptons**, which do not respond to **strong interaction**, and **quarks**, which are subject to all of the interactions. The six quarks form three pairs (up/down, charmed/strange, beauty/top). In the lepton category, the **charged leptons (electron** e⁻, **muon** μ, **tau** τ) are involved in the **electromagnetic interaction** and the **weak interaction**, while **neutral leptons** (**electron neutrino** ν_e, **muon neutrino** $\nu\mu$, **tau neutrino** ν_τ) are only subject to weak interaction. In the standard model, neutrinos have zero mass, however experiments have shown they do have some mass, though very small, the exact value of which is as yet unknown. Involvement

		leptons able to move freely		**quarks** held captive in larger particles, they are not observed separately	
Fermions Common matter is made up of particles from this group.	**first family**	**electron** Responsible for electricity and chemical reactions. Charge: – 1. mass: 0.511 MeV/c²	**electron neutrino** Has no electric charge, and interacts very seldom with the ambient medium.	**down** Electric charge: – 1/3. The proton holds one, the neutron two. mass: 5 – 8,5 MeV/c²	**up** Electric charge: + 2/3. The proton holds two, the neutron one. mass: 1,5 – 4,5 MeV/c²
Most of these particles were around just after the Big Bang. Presently only to be found in cosmic rays, and around accelerators.	**second family**	**muon** A more massive companion to the electron. mass: 105,658 MeV/c²	**muon neutrino** Properties similar to those of the electron neutrino.	**strange** A heavier companion to "up." mass: 80 – 155 MeV/c²	**charmed** A heavier companion to "down." mass: 1 000 – 1 400 MeV/c²
	third family	**tau** Heavier still. mass: 1 777 MeV/c²	**tau neutrino** Properties similar to those of the electron neutrino.	**beauty** Heavier still. mass: 4 000 – 4 500 MeV/c²	**top** Heaviest in the family (observed in 1985): 180 times the proton mass. mass: 174 300 ± 5 100 MeV/c²
Vector Bosons Fundamental particles carrying out transmission of all natural forces.		**photon** Elementary grain of light, vector for the electromagnetic force.	**gluon** Bearer of the strong force between quarks.	**W±, Z⁰** Bearers of the weak force, responsible for some forms of radioactive decay.	
Higgs Boson?		Responsible for "electroweak symmetry breaking."			

Tableau.
Constituants élémentaires.

of the various elementary constituents in the fundamental interactions is governed by their quantum numbers, or interaction charges (electric charge, color charge [1]...). To every constituent of matter is associated its **antiparticle**, a particle having the same mass and opposite charges. The **gravitational force**, which is not included in the standard model, acts on all fermions in proportion to their mass. The table of elementary constituents of matter manifests another classification – independently from their involvement in fundamental interactions – into three generations, or families. From one family to the next, charged quarks and leptons having the same charges only differ by their mass. The electron, up quark and down quark, which all belong to the first family, are the lightest massive particles. They are stable particles, and the constituents of common matter. For instance, the **proton** is made up of two up quarks and one down quark; the **neutron**, of two down quarks and one up quark. Particles in the other two families are unstable, and rapidly decay into

(1) Color charge: a quantum number that determines whether a particle is involved in strong interaction. The color charge can take on three values: "red," "green," or "blue" – such colors bearing no relation to visible colors. Every quark bears one of the three color charges, every antiquark one of the three anticolor charges. Gluons bear double color–anticolor charges (eight possible combinations).

stable first-generation particles. This is why all the stable matter in the Universe is made up from constituents from the first family.

According to quantum mechanics, for an interaction to take place, at least one elementary particle, a **boson**, must be emitted, absorbed or exchanged. The **photon** is the vector for the electromagnetic interaction, the **W⁺**, **W⁻** and **Z⁰** mediate the weak interaction, and **gluons** act as messengers for the strong interaction. Quarks and charged leptons exchange photons, but conserve their electric charge after the exchange, the photon having no electric charge. Since the photon's mass is zero, the electromagnetic interaction's range is infinite. Having no electric charge, neutrinos are the only elementary fermions that are not subject to electromagnetic interaction.

In the electroweak theory (a unification of the weak and electromagnetic interactions), the weak interaction has two aspects: charged-current weak interaction, for which the interaction vectors are the W^+ and W^-; and neutral-current weak interaction, for which the mediator is Z^0. These two forms of weak interaction are active between all elementary fermions (quarks, charged leptons and neutrinos). The mass of these bosons being very large (80,000 MeV/c^2 for $W^\pm$, 91,180 MeV/c^2 for Z^0), the range of the weak interaction is tiny – of the order of

10^{-18} m. Since $W^\pm$ bosons have a non-zero electric charge, fermions exchanging such bosons undergo a change in electric charge, as of nature (flavor). Conversely, since the Z^0 boson has no electric charge, fermions exchanging one undergo no change in nature. In effect, neutral-current weak interaction is somewhat akin to exchanging a photon. As a general rule, if two fermions are able to exchange a photon, they can also exchange a Z^0. On the other hand, a neutrino has the ability to exchange a Z^0 with another particle, though not a photon. Only those quarks that have a color charge exchange gluons, these in turn being bearers of a color charge. Thus, when a gluon exchange takes place between quarks, the latter exchange their respective colors. Gluons have zero mass, however, since they do bear a color charge, they are able to interact. The range of the strong interaction is consequently very restricted – of the order of 10^{-15} m.

The graviton, the vector for gravitational interaction, has not so far been observed.

Theory predicts that another fundamental interaction mechanism exists, responsible for the mass of elementary particles, for which the messenger is the Higgs boson, which remains as yet undiscovered. This boson makes it possible to assign a mass to elementary fermions of zero mass that interact with it.

| fundamental interaction	messenger	actions
gravitational	graviton?	responsible for the mutual attraction of any two masses and for the law of falling bodies
electromagnetic	photon	responsible for the attraction between electrons and atomic nuclei, hence for the cohesion of atoms and molecules
weak	W⁺, W⁻, Z⁰	the root cause of **thermonuclear fusion** inside the Sun, ensuring its longevity. β⁻ and β⁺ radioactivity, and reactions involving neutrinos are weak interactions
strong	gluons	ensures the cohesion of the atomic nucleus

Table.
Fundamental interaction and elementary constituents.

F How is solar energy turned into electricity?

The **photovoltaic effect** used in **solar cells** (which are further assembled into **modules**, then into **panels**) for the direct conversion of the rays of sunlight into electricity involves the generation and transport of positive and negative electric charges through the action of light in a **semiconducting** material.

Silicon was selected for its electronic properties, characterized by presence of four **electrons** in its outermost shell (column IV of the Mendeleyev periodic table). In solid silicon, each **atom** is bound to four neighbors, and all the electrons in the outermost shell participate in the bonds. If a silicon atom is substituted for by an atom from column V (a phosphorus atom, for instance), one of the electrons is not involved in the bonds; it is thus free to move through the lattice. There is electron conduction, and the semiconductor is designated as an n-*type doped*

contact on *n* region

absorption of photons

n-doped region

p-doped region

contact on *p* region

carrier generation

generation collection

I

semiconductor. If, on the other hand, a **silicon** atom is substituted for by an atom from column III (boron, for instance), one electron is missing if all bonds are to be maintained , and an electron can move in to fill this gap. One then speaks of hole conduction, and the semiconductor is said to be a *p*-type doped semiconductor. Atoms of elements such as boron or phosphorus are **doping agents** in silicon.
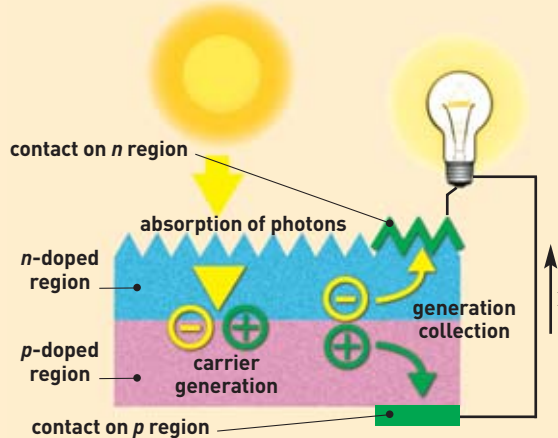
When an *n*-type semiconductor is brought into contact with a *p*-type semiconductor, the excess electrons from the *n* material diffuse into the p material. The initially *n*-doped region becomes positively charged, while the initially *p*-doped region takes on a negative charge. An electric field is thus set up between the *n* and *p* regions, tending to force electrons back into the *n* region, and equilibrium arises. A **junction** has been set up, and, if metallic contacts are placed onto the n and p regions, a **diode** is obtained.

When this diode is illuminated, **photons** are absorbed by the material, and every photon gives rise to an electron and a hole (this is termed an **electron-hole pair**). The diode junction keeps apart the electrons and the holes, giving rise to a potential difference between the *n* and *p* contacts, and a current passes, if a resistance is inserted between the diode contacts (see Figure).