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 → $(CH_2O)_n$ (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. Ultimately, 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) → 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

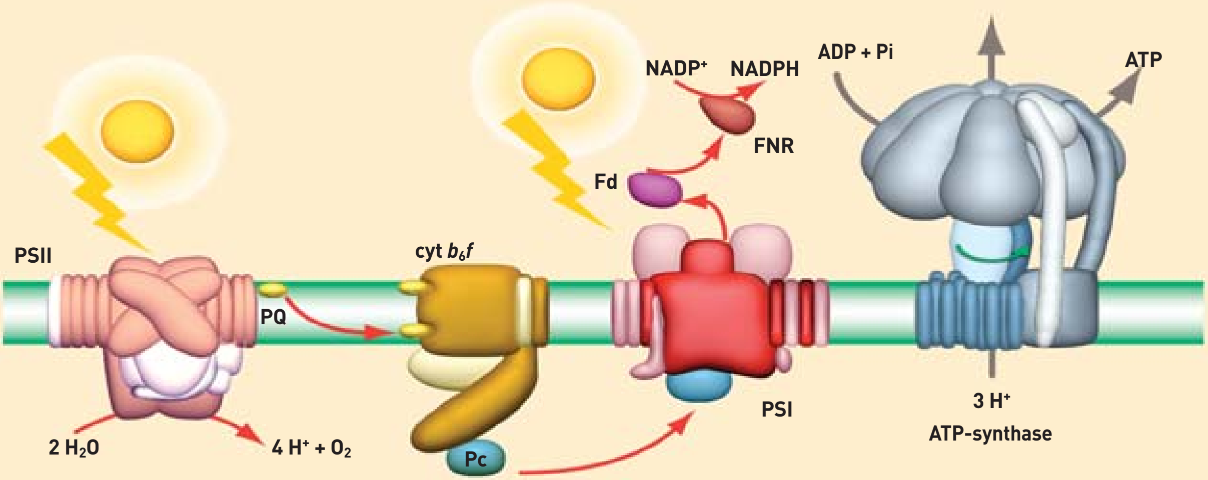


Figure.
Les étapes membranaires du processus de photosynthèse se déroulant chez les plantes vertes, les algues et les cyanobactéries.

E (next)

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:

$3\,CO_2 + 9\,ATP + 6\,NADPH + \text{water} \rightarrow$ 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.

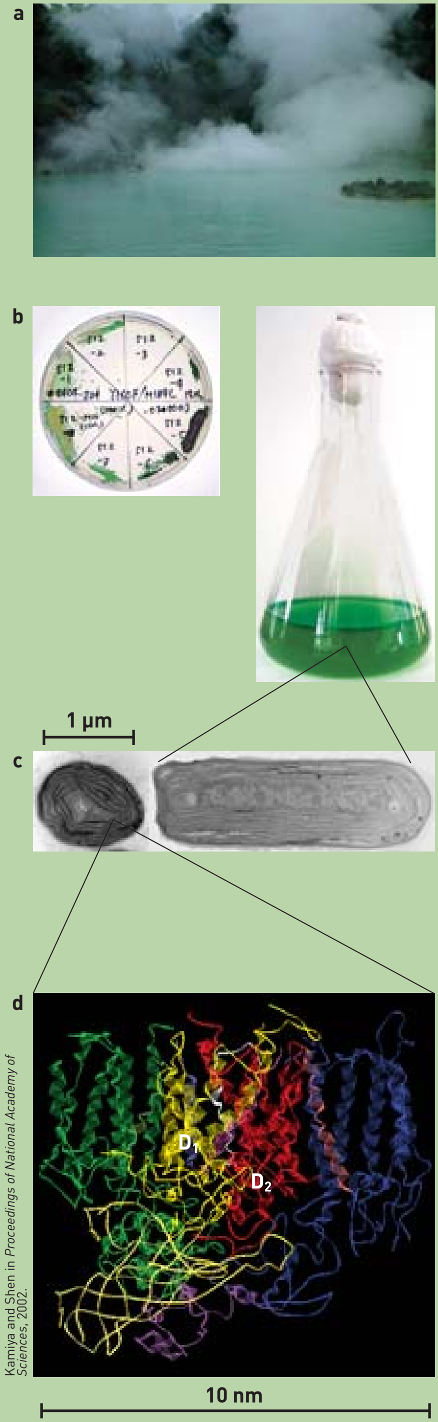
Cyanobacteria, privileged organisms for photosynthesis research

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.

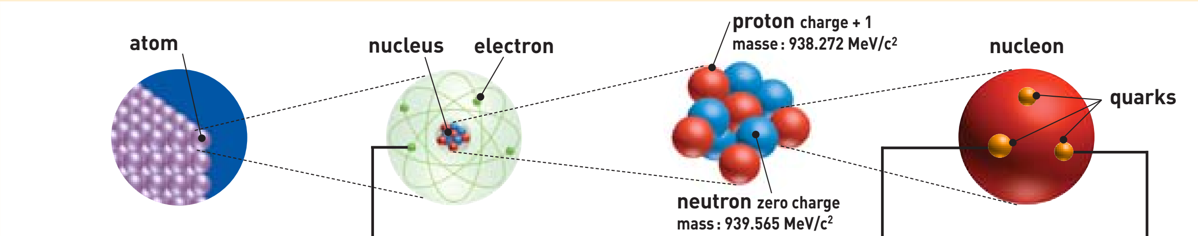


Kamiya and Shen in *Proceedings of National Academy of Sciences*, 2002.

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.

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 ν_μ, 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** (W^+, W^-, Z^0) 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 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 **Z^0** 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.

(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).

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^-, Z^0	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.