Science & Technology Photosynthesis
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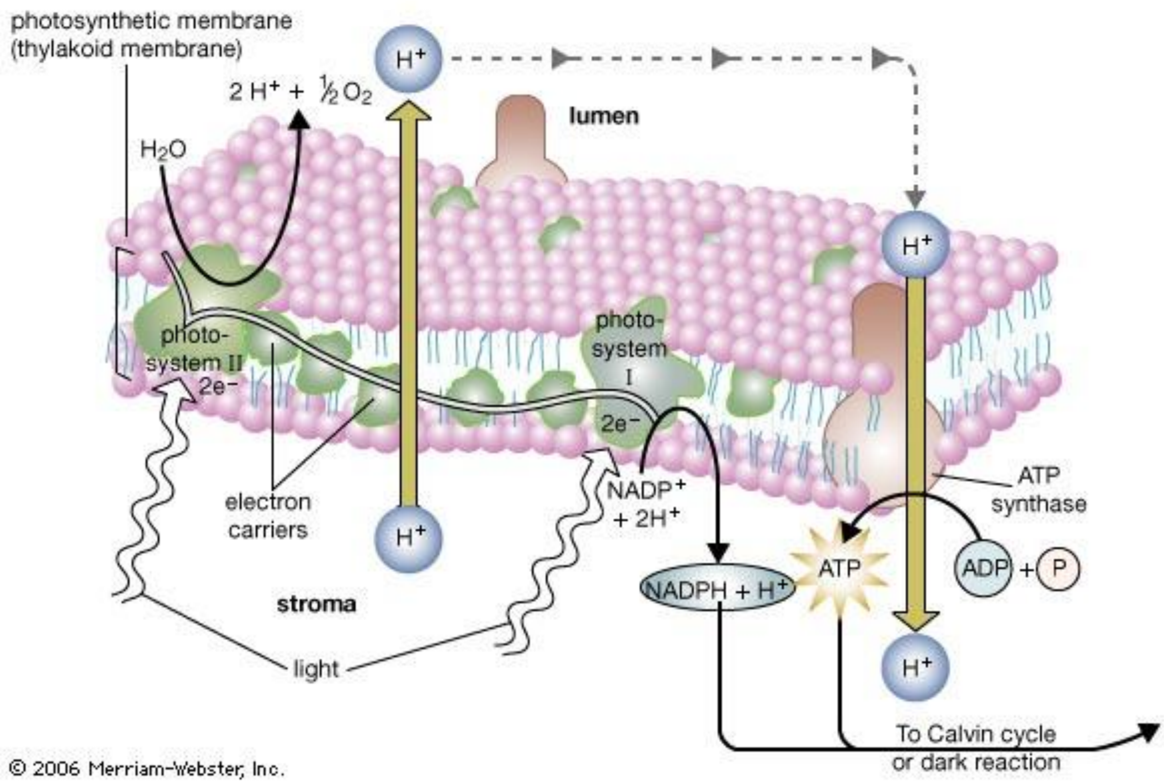

Process by which green plants and certain other organisms transform light into chemical energy.
In green plants, light energy is captured by chlorophyll in the chloroplasts of the leaves and used to convert water, carbon dioxide, and minerals into oxygen and energy-rich organic compounds (simple and complex sugars) that are the basis of both plant and animal life.
Photosynthesis consists of a number of photochemical and enzymatic reactions. It occurs in two stages.
During the light-dependent stage (light reaction), chlorophyll absorbs light energy, which excites some electrons in the pigment molecules to higher energy levels; these leave the chlorophyll and pass along a series of molecules, generating formation of NADPH (an enzyme) and high-energy ATP molecules. Oxygen, released as a by-product, passes into the atmosphere through pores in the leaves. NADPH and ATP drive the second stage, the dark reaction (or Calvin cycle, discovered by Melvin Calvin), which does not require light. During this stage glucose is generated using atmospheric carbon dioxide.
Photosynthesis is crucial for maintaining life on Earth; if it ceased, there would soon be little food or other organic matter on the planet, and most types of organisms would disappear.

Development of the idea

The study of photosynthesis began in 1771, with observations made by the English chemist Joseph Priestley. Priestley had burned a candle in a closed container until the air within the container could no longer support combustion. He then placed a sprig of mint plant in the container and discovered that after several days the mint had produced some substance (later recognized as oxygen) that enabled the confined air to again support combustion. In 1779 the Dutch physician Jan Ingenhousz expanded upon Priestley's work, showing that the plant must be exposed to light if the combustible substance (*i.e.*, oxygen) was to be restored; he also demonstrated that this process required the presence of the green tissues of the plant.

In 1782 it was demonstrated that the combustion-supporting gas (oxygen) was formed at the expense of another gas, or “fixed air,” which had been identified the year before as carbon dioxide. Gas-exchange experiments in 1804 showed that the gain in weight of a plant grown in a carefully weighed pot was the sum of carbon, which came entirely from absorbed carbon dioxide, and water taken up by plant roots. Almost half a century passed before the concept of chemical energy developed sufficiently to permit the discovery (in 1845) that light energy from the sun is stored as chemical energy in products formed during photosynthesis.

Overall reaction of photosynthesis

In chemical terms, photosynthesis is a light-energized oxidation–reduction process. (Oxidation refers to the removal of electrons from a molecule; reduction refers to the gain of electrons by a molecule.) In plant photosynthesis, the energy of light is used to drive the oxidation of water (H_2O), producing oxygen gas (O_2), hydrogen ions (H^+), and electrons. Most of the removed electrons and hydrogen ions ultimately are transferred to carbon dioxide (CO_2), which is reduced to organic products. Other electrons and hydrogen ions are used to reduce nitrate and sulfate to amino and sulfhydryl groups in amino acids, which are the building blocks of proteins. In most green cells, carbohydrates—especially starch and the sugar sucrose—are the major direct organic products of photosynthesis. The overall reaction in which carbohydrates—represented by the general formula (CH_2O)—are formed during plant photosynthesis can be indicated by the following equation:

$$CO_2 + 2H_2O \xrightarrow[\text{green plants}]{\text{light}} (CH_2O) + O_2 + H_2O.$$

This equation is merely a summary statement, for the process of photosynthesis actually involves numerous complex reactions. These reactions occur in two stages: the “light” stage, consisting of photochemical (*i.e.*, light-dependent) reactions; and the “dark” stage, comprising chemical reactions controlled by enzymes (organic catalysts). During the first stage, the energy of light is absorbed and used to drive a series of electron transfers, resulting in the synthesis of the energy-rich compound adenosine triphosphate (ATP) and the electron donor reduced nicotine adenine dinucleotide phosphate (NADPH). During the dark stage, the ATP and NADPH formed in the light reactions are used to reduce carbon dioxide to organic carbon compounds.
This assimilation of inorganic carbon into organic compounds is called carbon fixation.
During the 20th century, comparisons between photosynthetic processes in green plants and in certain photosynthetic sulfur bacteria provided important information about the photosynthetic mechanism. Sulfur bacteria use hydrogen sulfide (H_2S) as a source of hydrogen atoms and produce sulfur instead of oxygen during photosynthesis. The overall reaction is:

$$CO_2 + 2H_2S \xrightarrow[\substack{\text{sulfur}\\ \text{bacteria}}]{\text{light}} (CH_2O) + S_2 + H_2O.$$

In the 1930s Dutch biologist Cornelis van Niel recognized that the utilization of carbon dioxide to form organic compounds was similar in the two types of photosynthetic organisms. Suggesting that differences existed in the light-dependent stage and in the nature of the compounds used as a source of hydrogen atoms, he proposed that hydrogen was transferred from hydrogen sulfide (in bacteria) or water (in green plants) to an unknown acceptor (called A), which was reduced to H_2A. During the dark reactions, which are similar in both bacteria and green plants, the reduced acceptor (H_2A) reacted with carbon dioxide (CO_2) to form carbohydrate (CH_2O) and to oxidize the unknown acceptor to A. This putative reaction can be represented as:

$$CO_2 + 2H_2A \xrightarrow{\text{light}} (CH_2O) + 2A + H_2O.$$

Van Niel's proposal was important because the popular (but incorrect) theory had been that oxygen was removed from carbon dioxide (rather than hydrogen from water) and that carbon then combined with water to form carbohydrate (rather than the hydrogen from water combining with CO_2 to form CH_2O).

By 1940 chemists were using heavy isotopes to follow the reactions of photosynthesis. Water marked with an isotope of oxygen (^{18}O) was used in early experiments. Plants that photosynthesized in the presence of water containing $H_2{}^{18}O$ produced oxygen gas containing ^{18}O; those that photosynthesized in the presence of normal water produced normal oxygen gas. These results provided strong support for van Niel's theory that the oxygen gas produced during photosynthesis is derived from water.

Factors that influence the rate of photosynthesis

The rate of photosynthesis is defined in terms of the rate of oxygen production either per unit mass (or area) of green plant tissues or per unit weight of total chlorophyll. The amount of light, the carbon dioxide supply, the temperature, the water supply, and the availability of minerals are the most important environmental factors that directly affect the rate of photosynthesis in land plants. The rate of photosynthesis also is determined by the plant species and its physiological state—*e.g.*, its health, its maturity, and whether or not it is in flower.

Light intensity and temperature

As has been mentioned, the complex mechanism of photosynthesis includes a photochemical, or light-dependent, stage and an enzymatic, or dark, stage that involves chemical reactions. These stages can be distinguished by studying the rates of photosynthesis at various degrees of light saturation (*i.e.*, intensity) and at different temperatures. Over a range of moderate temperatures and at low to medium light intensities (relative to the normal range of the plant species), the rate of photosynthesis increases as the intensity increases and is independent of temperature. As the light intensity increases to higher levels, however, the rate becomes increasingly dependent on temperature and less dependent on intensity; light "saturation" is achieved at a specific light intensity, and the rate then is dependent only on temperature if all other factors are constant. In the light-dependent range before saturation, therefore, the rate of photosynthesis is determined by the rates of photochemical steps. At high light intensities, some of the chemical reactions of the dark stage become rate-limiting. At light saturation, rate increases with temperature until a point is reached beyond which no further rate increase can occur. In many land plants, moreover, a process called photorespiration occurs at high light intensities and temperatures. Photorespiration competes with photosynthesis and limits further increases in the rate of photosynthesis, especially if the supply of water is limited.

Carbon dioxide

Included among the rate-limiting steps of the dark stage of photosynthesis are the chemical reactions by which organic compounds are formed using carbon dioxide as a carbon source.
The rates of these reactions can be increased somewhat by increasing the carbon dioxide concentration.
During the past century, the level of carbon dioxide in the atmosphere has been rising due to the extensive combustion of fossil fuels.
The atmospheric level of carbon dioxide climbed from about 0.028 percent in 1860 to 0.0315 percent by 1958 (when improved measurements began), and to 0.034 percent by 1981.
This increase in carbon dioxide directly increases plant photosynthesis, but the size of the increase depends on the species and physiological condition of the plant.
Furthermore, if increasing levels of atmospheric carbon dioxide result in climatic changes, including increased global temperatures as some meteorologists predict, these changes will affect photosynthesis rates.

Water

For land plants, water availability can function as a limiting factor in photosynthesis and plant growth. Besides the requirement for water in the photosynthetic reaction itself, water is transpired from the leaves; that is, water evaporates from the leaves to the atmosphere via the stomates. These stomates are small openings through the leaf epidermis, or outer skin; they permit the entry of carbon dioxide but also allow the exit of water vapour. The stomates open and close according to the physiological needs of the leaf. In hot and arid climates the stomates may close to conserve water, but this closure limits the entry of carbon dioxide and hence the rate of photosynthesis, while the wasteful process of photorespiration may increase. If the level of carbon dioxide in the atmosphere increases, more carbon dioxide could enter through a smaller opening of the stomates, so that more photosynthesis could occur with a given supply of water.

Minerals

Several minerals are required for healthy plant growth and for maximum rates of photosynthesis. Nitrate or ammonia, sulfate, phosphate, iron, magnesium, and potassium are required in substantial amounts for the synthesis of amino acids, proteins, coenzymes, deoxyribonucleic acid (DNA) and ribonucleic acid (RNA), chlorophyll and other pigments, and other essential plant constituents. Smaller amounts of such elements as manganese, copper, and chlorine are required in photosynthesis. Some other trace elements are needed for various nonphotosynthetic functions in plants.

Internal factors

Each plant species adapts to a range of environmental factors. Within this normal range of conditions, complex regulatory mechanisms in the plant's cells adjust the activities of enzymes (*i.e.,* organic catalysts). These adjustments maintain a balance in the overall photosynthetic process and control it in accordance with the needs of the whole plant. With a given plant species, for example, doubling the carbon dioxide level might cause a temporary increase of nearly twofold in the rate of photosynthesis; a few hours later, however, the rate might fall to the original level because photosynthesis had made more sucrose than the rest of the plant could use. By contrast, another plant species provided with such carbon dioxide enrichment might be able to use more sucrose and would continue to photosynthesize and to grow faster throughout most of its life cycle.

<u>Energy efficiency of photosynthesis</u>

The energy efficiency of photosynthesis is the ratio of the energy stored to the energy of light absorbed. The chemical energy stored is the difference between that contained in gaseous oxygen and organic compound products and the energy of water, carbon dioxide, and other reactants. The amount of energy stored can only be estimated because many products are formed, and these vary with the plant species and environmental conditions. If the equation for glucose formation given earlier is used to approximate the actual storage process, the production of one mole (*i.e.*, 6.02×10^{23} molecules; abbreviated N) of oxygen and one-sixth mole of glucose results in the storage of about 117 kilocalories (kcal) of chemical energy. This amount must then be compared to the energy of light absorbed to produce one mole of oxygen in order to calculate the efficiency of photosynthesis.

Light can be described as a wave of particles known as photons; these are units of energy, or light quanta.
The quantity N photons is called an einstein.
The energy of light varies inversely with the length of the photon waves; that is, the shorter the wavelength, the greater the energy content.
The energy (e) of a photon is given by the equation $e = hc/\lambda$, where c is the velocity of light, h is Planck's constant, and λ is the light wavelength.

The energy (E) of an einstein is $E = Ne = Nhc/\lambda = 28{,}600/\lambda$, when E is in kilocalories and λ is given in nanometres (nm; 1 nm = 10^{-9} metres).
An einstein of red light with a wavelength of 680 nm has an energy of about 42 kcal.
Blue light has a shorter wavelength and therefore more energy than red light.
Regardless of whether the light is blue or red, however, the same number of einsteins are required for photosynthesis per mole of oxygen formed.
The part of the solar spectrum used by plants has an estimated mean wavelength of 570 nanometres; therefore, the energy of light used during photosynthesis is approximately 28,600/570, or 50 kilocalories per einstein.

In order to compute the amount of light energy involved in photosynthesis, one other value is needed: the number of einsteins absorbed per mole of oxygen evolved.
This is called the quantum requirement. The minimum quantum requirement for photosynthesis under optimal conditions is about nine.
Thus the energy used is 9×50, or 450 kilocalories per mole of oxygen evolved.
Therefore, the estimated maximum energy efficiency of photosynthesis is the energy stored per mole of oxygen evolved—117 kilocalories—divided by 450; that is, 117/450, or 26 percent.

The actual percentage of solar energy stored by plants is much less than the maximum energy efficiency of photosynthesis.
An agricultural crop in which the biomass (total dry weight) stores as much as 1 percent of total solar energy received on an annual area-wide basis is exceptional, although a few cases of higher yields (perhaps as much as 3.5 percent in sugarcane) are reported.
There are several reasons for this difference between the predicted maximum efficiency of photosynthesis and the actual energy stored in biomass.

First, more than half of the incident sunlight is composed of wavelengths too long to be absorbed, while some of the remainder is reflected or lost to the leaves.
Consequently, plants can at best absorb only about 34 percent of the incident sunlight.

Second, plants must carry out a variety of physiological processes in such nonphotosynthetic tissues as roots and stems; these processes, as well as cellular respiration in all parts of the plant, use up stored energy.

Third, rates of photosynthesis in bright sunlight sometimes exceed the needs of the plants, resulting in the formation of excess sugars and starch.
When this happens, the regulatory mechanisms of the plant slow down the process of photosynthesis, allowing more absorbed sunlight to go unused.

Fourth, in many plants, energy is wasted by the process of photorespiration.

Finally, the growing season may last only a few months of the year; sunlight received during other seasons is not used.
Furthermore, it should be noted that if only agricultural products (*e.g.*, seeds, fruits, and tubers, rather than total biomass) are considered as the end product of the energy conversion process of photosynthesis, the efficiency falls even further.