[Template:Pp-vandalism](/wiki/Template:Pp-vandalism" \o "Template:Pp-vandalism) [thumb|Schematic of photosynthesis in plants. The carbohydrates produced are stored in or used by the plant.](/wiki/File:Photosynthesis.gif) [400 px|thumb|Overall equation for the type of photosynthesis that occurs in plants](/wiki/File:Photosynthesis_equation.svg) [400 px|thumb|right|Composite image showing the global distribution of photosynthesis, including both oceanic](/wiki/File:Seawifs_global_biosphere.jpg) [phytoplankton](/wiki/Phytoplankton) and terrestrial [vegetation](/wiki/Vegetation). Dark red and blue-green indicate regions of high photosynthetic activity in ocean and land respectively.

**Photosynthesis** is a process used by plants and other organisms to convert [light](/wiki/Light) energy, normally from the [Sun](/wiki/Sun), into [chemical energy](/wiki/Chemical_energy) that can be later [released](/wiki/Cellular_respiration) to fuel the organisms' activities ([energy transformation](/wiki/Energy_transformation)). This chemical energy is stored in [carbohydrate molecules](/wiki/Carbohydrates), such as [sugars](/wiki/Sugar), which are synthesized from [carbon dioxide](/wiki/Carbon_dioxide) and [water](/wiki/Water) – hence the name photosynthesis, from the [Greek](/wiki/Greek_language) [φῶς](/wiki/Wiktionary:φῶς), *phōs*, "light", and [σύνθεσις](/wiki/Wiktionary:σύνθεσις), *synthesis*, "putting together".<ref name=OnlineEtDict>[Template:Cite web](/wiki/Template:Cite_web)</ref><ref name=LSJ1>[Template:LSJ](/wiki/Template:LSJ)</ref><ref name=LSJ2>[Template:LSJ](/wiki/Template:LSJ)</ref> In most cases, oxygen is also released as a waste product. Most [plants](/wiki/Plant), most [algae](/wiki/Algae), and [cyanobacteria](/wiki/Cyanobacteria) perform photosynthesis; such organisms are called [photoautotrophs](/wiki/Photoautotroph). Photosynthesis maintains [atmospheric oxygen](/wiki/Atmospheric_oxygen) levels and supplies all of the organic compounds and most of the energy necessary for [life on Earth](/wiki/Life).<ref name=bryantfrigaard>[Template:Cite journal](/wiki/Template:Cite_journal)</ref>

Although photosynthesis is performed differently by different species, the process always begins when energy from light is absorbed by [proteins](/wiki/Protein) called [reaction centres](/wiki/Photosynthetic_reaction_centre) that contain green [chlorophyll](/wiki/Chlorophyll) pigments. In plants, these proteins are held inside [organelles](/wiki/Organelle) called [chloroplasts](/wiki/Chloroplast), which are most abundant in leaf cells, while in bacteria they are embedded in the [plasma membrane](/wiki/Plasma_membrane). In these light-dependent reactions, some energy is used to strip [electrons](/wiki/Electron) from suitable substances, such as water, producing oxygen gas. The hydrogen freed by water splitting is used in the creation of two further compounds: reduced [nicotinamide adenine dinucleotide phosphate](/wiki/Nicotinamide_adenine_dinucleotide_phosphate) (NADPH) and [adenosine triphosphate](/wiki/Adenosine_triphosphate) (ATP), the "energy currency" of cells.

In plants, algae and cyanobacteria, sugars are produced by a subsequent sequence of light-independent reactions called the [Calvin cycle](/wiki/Calvin_cycle), but some bacteria use different mechanisms, such as the [reverse Krebs cycle](/wiki/Reverse_Krebs_cycle). In the Calvin cycle, atmospheric carbon dioxide is [incorporated](/wiki/Carbon_fixation) into already existing organic carbon compounds, such as [ribulose bisphosphate](/wiki/Ribulose_bisphosphate) (RuBP).[[1]](#cite_note-1) Using the ATP and NADPH produced by the light-dependent reactions, the resulting compounds are then [reduced](/wiki/Biological_reductant) and removed to form further carbohydrates, such as [glucose](/wiki/Glucose).

The first photosynthetic organisms probably [evolved](/wiki/Evolution) early in the [evolutionary history of life](/wiki/Evolutionary_history_of_life) and most likely used [reducing agents](/wiki/Reducing_agent) such as [hydrogen](/wiki/Hydrogen) or [hydrogen sulfide](/wiki/Hydrogen_sulfide), rather than water, as sources of electrons.[[2]](#cite_note-2) Cyanobacteria appeared later; the excess oxygen they produced contributed to the [oxygen catastrophe](/wiki/Oxygen_catastrophe),[[3]](#cite_note-3) which rendered the [evolution of complex life](/wiki/Evolution_of_multicellularity) possible. Today, the average rate of energy capture by photosynthesis globally is approximately 130 [terawatts](/wiki/Terawatts),[[4]](#cite_note-4)[[5]](#cite_note-5)[[6]](#cite_note-6) which is about three times the current [power consumption of human civilization](/wiki/World_energy_resources_and_consumption).<ref name=EIA>[Template:Cite web](/wiki/Template:Cite_web)</ref> Photosynthetic organisms also convert around 100–115 thousand million metric tonnes of carbon into [biomass](/wiki/Biomass) per year.[[7]](#cite_note-7)[[8]](#cite_note-8)

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## Overview[[edit](/index.php?title=(none)&action=edit&section=1)]

[thumb|Photosynthesis changes sunlight into chemical energy, splits water to liberate O2, and fixes CO2 into sugar.](/wiki/File:Simple_photosynthesis_overview.svg) Photosynthetic organisms are [photoautotrophs](/wiki/Photoautotroph), which means that they are able to [synthesize](/wiki/Chemical_synthesis) food directly from carbon dioxide and water using energy from light. However, not all organisms that use light as a source of energy carry out photosynthesis, since [*photoheterotrophs*](/wiki/Photoheterotroph) use organic compounds, rather than carbon dioxide, as a source of carbon.<ref name=bryantfrigaard/> In plants, algae and cyanobacteria, photosynthesis releases oxygen. This is called *oxygenic photosynthesis*. Although there are some differences between oxygenic photosynthesis in [plants](/wiki/Plants), [algae](/wiki/Algae), and [cyanobacteria](/wiki/Cyanobacteria), the overall process is quite similar in these organisms. However, there are some types of bacteria that carry out [anoxygenic photosynthesis](/wiki/Anoxygenic_photosynthesis). These consume carbon dioxide but do not release oxygen.

Carbon dioxide is converted into sugars in a process called [carbon fixation](/wiki/Carbon_fixation). Carbon fixation is an [endothermic](/wiki/Endothermic) [redox](/wiki/Redox) reaction, so photosynthesis needs to supply both a source of energy to drive this process, and the electrons needed to convert carbon dioxide into a [carbohydrate](/wiki/Carbohydrate) via a reduction reaction. The addition of electrons to a chemical species is called a [reduction reaction](/wiki/Reduction_(chemistry)). In general outline and in effect, photosynthesis is the opposite of [cellular respiration](/wiki/Cellular_respiration), in which glucose and other compounds are oxidized to produce carbon dioxide and water, and to release chemical energy (an [exothermic](/wiki/Exothermic) reaction) to drive the organism's [metabolism](/wiki/Metabolism). The two processes, of reduction of carbon dioxide to carbohydrate and then the later oxidation of the carbohydrate, take place through a different sequence of chemical reactions and in different cellular compartments.

The general [equation](/wiki/Chemical_equation) for photosynthesis as first proposed by [Cornelius van Niel](/wiki/C._B._van_Niel) is therefore:[[9]](#cite_note-9):CO2 + 2H2A + [photons](/wiki/Photons) → [​[CH2O](/wiki/Carbohydrate)​] + 2A + H2O

carbon dioxide + electron donor + light energy → carbohydrate + oxidized electron donor + water

Since water is used as the electron donor in oxygenic photosynthesis, the equation for this process is:

CO2 + 2H2O + photons → [CH2O] + O2 + H2O

carbon dioxide + water + light energy → carbohydrate + oxygen + water

This equation emphasizes that water is both a reactant in the [light-dependent reaction](/wiki/#Light-dependent_reactions) and a product of the [light-independent reaction](/wiki/#Light-independent_reactions), but canceling *n* water molecules from each side gives the net equation:

CO2 + H2O + photons → [CH2O] + O2

carbon dioxide + water + light energy → carbohydrate + oxygen

Other processes substitute other compounds (such as [arsenite](/wiki/Arsenite)) for water in the electron-supply role; for example some microbes use sunlight to oxidize arsenite to [arsenate](/wiki/Arsenate):[[10]](#cite_note-10) The equation for this reaction is:

CO2 + (AsO33−) + photons → (AsO43−) + CO[[11]](#cite_note-11): carbon dioxide + arsenite + light energy → arsenate + carbon monoxide (used to build other compounds in subsequent reactions)

Photosynthesis occurs in two stages. In the first stage, *light-dependent reactions* or *light reactions* capture the energy of light and use it to make the energy-storage molecules [ATP](/wiki/Adenosine_triphosphate) and [NADPH](/wiki/NADPH). During the second stage, the *light-independent reactions* use these products to capture and reduce carbon dioxide.

Most organisms that utilize photosynthesis to produce oxygen use [visible light](/wiki/Visible_spectrum) to do so, although at least three use shortwave [infrared](/wiki/Infrared) or, more specifically, far-red radiation.[[12]](#cite_note-12) [Archaeobacteria](/wiki/Archaeobacteria) use a simpler method using a pigment similar to the pigments used for vision. The [archaearhodopsin](/wiki/Archaearhodopsin) changes its configuration in response to sunlight, acting as a proton pump. This produces a proton gradient more directly which is then converted to chemical energy. The process does not involve carbon dioxide fixation and does not release oxygen. It seems to have evolved separately.[[13]](#cite_note-13)[[14]](#cite_note-14)

## Photosynthetic membranes and organelles[[edit](/index.php?title=(none)&action=edit&section=2)]

[[File:Chloroplast.svg|thumb|275px|right|**Chloroplast ultrastructure**:  
1. outer membrane  
2. intermembrane space

3. inner membrane (1+2+3: envelope)

4. stroma (aqueous fluid)

5. thylakoid lumen (inside of thylakoid)

6. thylakoid membrane

7. granum (stack of thylakoids)

8. thylakoid (lamella)

9. starch

10. ribosome

11. plastidial DNA

12. plastoglobule (drop of lipids)

]] [Template:Main](/wiki/Template:Main) In photosynthetic bacteria, the proteins that gather light for photosynthesis are embedded in [cell membranes](/wiki/Cell_membrane). In its simplest form, this involves the membrane surrounding the cell itself.[[15]](#cite_note-15) However, the membrane may be tightly folded into cylindrical sheets called [thylakoids](/wiki/Thylakoid),<ref name=Mullineaux1999/> or bunched up into round [vesicles](/wiki/Vesicle_(biology)) called *intracytoplasmic membranes*.[[16]](#cite_note-16) These structures can fill most of the interior of a cell, giving the membrane a very large surface area and therefore increasing the amount of light that the bacteria can absorb.<ref name=Mullineaux1999>[Template:Cite journal](/wiki/Template:Cite_journal)</ref>

In plants and algae, photosynthesis takes place in [organelles](/wiki/Organelle) called [chloroplasts](/wiki/Chloroplast). A typical [plant cell](/wiki/Plant_cell) contains about 10 to 100 chloroplasts. The chloroplast is enclosed by a membrane. This membrane is composed of a phospholipid inner membrane, a phospholipid outer membrane, and an intermembrane space between them. Enclosed by the membrane is an aqueous fluid called the stroma. Embedded within the stroma are stacks of thylakoids (grana), which are the site of photosynthesis. The thylakoids appear as flattened disks. The thylakoid itself is enclosed by the thylakoid membrane, and within the enclosed volume is a lumen or thylakoid space. Embedded in the thylakoid membrane are integral and [peripheral membrane protein](/wiki/Peripheral_membrane_protein) complexes of the photosynthetic system, including the pigments that absorb light energy.

Plants absorb light primarily using the [pigment](/wiki/Pigment) [chlorophyll](/wiki/Chlorophyll). The green part of the light spectrum is not absorbed but is reflected which is the reason that most plants have a green color. Besides chlorophyll, plants also use pigments such as [carotenes](/wiki/Carotene) and [xanthophylls](/wiki/Xanthophyll).[[17]](#cite_note-17) Algae also use chlorophyll, but various other pigments are present, such as [phycocyanin](/wiki/Phycocyanin), [carotenes](/wiki/Carotene), and [xanthophylls](/wiki/Xanthophyll) in [green algae](/wiki/Green_algae), [phycoerythrin](/wiki/Phycoerythrin) in [red algae](/wiki/Red_algae) (rhodophytes) and [fucoxanthin](/wiki/Fucoxanthin) in [brown algae](/wiki/Brown_algae) and [diatoms](/wiki/Diatoms) resulting in a wide variety of colors.

These pigments are embedded in plants and algae in complexes called antenna proteins. In such proteins, the pigments are arranged to work together. Such a combination of proteins is also called a [light-harvesting complex](/wiki/Light-harvesting_complex).

Although all cells in the green parts of a plant have chloroplasts, the majority of those are found in specially adapted structures called [leaves](/wiki/Leaf). Certain species adapted to conditions of strong sunlight and [aridity](/wiki/Arid), such as many [Euphorbia](/wiki/Euphorbia) and [cactus](/wiki/Cactus) species, have their main photosynthetic organs in their stems. The cells in the interior tissues of a leaf, called the [mesophyll](/wiki/Mesophyll_tissue), can contain between 450,000 and 800,000 chloroplasts for every square millimeter of leaf. The surface of the leaf is coated with a water-resistant [waxy](/wiki/Wax) [cuticle](/wiki/Plant_cuticle) that protects the leaf from excessive [evaporation](/wiki/Evaporation) of water and decreases the absorption of [ultraviolet](/wiki/Ultraviolet) or [blue](/wiki/Blue) [light](/wiki/Light) to reduce [heating](/wiki/Heat). The transparent [epidermis](/wiki/Leaf#Epidermis) layer allows light to pass through to the [palisade](/wiki/Mesophyll_tissue) mesophyll cells where most of the photosynthesis takes place.

## Light-dependent reactions[[edit](/index.php?title=(none)&action=edit&section=3)]

[thumb|450px|right|Light-dependent reactions of photosynthesis at the thylakoid membrane](/wiki/File:Thylakoid_membrane_3.svg) [Template:Main](/wiki/Template:Main) In the [light-dependent reactions](/wiki/Light-dependent_reactions), one molecule of the [pigment](/wiki/Pigment) [chlorophyll](/wiki/Chlorophyll) absorbs one [photon](/wiki/Photon) and loses one [electron](/wiki/Electron). This electron is passed to a modified form of chlorophyll called [pheophytin](/wiki/Pheophytin), which passes the electron to a [quinone](/wiki/Quinone) molecule, starting the flow of electrons down an [electron transport chain](/wiki/Electron_transport_chain) that leads to the ultimate reduction of [NADP](/wiki/Nicotinamide_adenine_dinucleotide_phosphate) to [NADPH](/wiki/Nicotinamide_adenine_dinucleotide_phosphate). In addition, this creates a [proton gradient](/wiki/Electrochemical_gradient) (energy gradient) across the [chloroplast membrane](/wiki/Chloroplast_membrane), which is used by [ATP synthase](/wiki/ATP_synthase) in the synthesis of [ATP](/wiki/Adenosine_triphosphate). The chlorophyll molecule ultimately regains the electron it lost when a water molecule is split in a process called [photolysis](/wiki/Photodissociation), which releases a [dioxygen](/wiki/Dioxygen) (O2) molecule as a waste product.

The overall equation for the light-dependent reactions under the conditions of non-cyclic electron flow in green plants is:[[18]](#cite_note-18)

2 H2O + 2 NADP+ + 3 ADP + 3 Pi + light → 2 NADPH + 2 H+ + 3 ATP + O2

Not all [wavelengths](/wiki/Wavelength) of light can support photosynthesis. The photosynthetic action spectrum depends on the type of [accessory pigments](/wiki/Accessory_pigment) present. For example, in green plants, the [action spectrum](/wiki/Action_spectrum) resembles the [absorption spectrum](/wiki/Absorption_spectrum) for [chlorophylls](/wiki/Chlorophyll) and [carotenoids](/wiki/Carotenoid) with peaks for violet-blue and red light. In red algae, the action spectrum is blue-green light, which allows these algae to use the blue end of the spectrum to grow in the deeper waters that filter out the longer wavelengths (red light) used by above ground green plants. The non-absorbed part of the [light spectrum](/wiki/Electromagnetic_spectrum) is what gives photosynthetic organisms their color (e.g., green plants, red algae, purple bacteria) and is the least effective for photosynthesis in the respective organisms.

### Z scheme[[edit](/index.php?title=(none)&action=edit&section=4)]

[thumb|675px|center|The "Z scheme"](/wiki/File:Z-scheme.png) In plants, [light-dependent reactions](/wiki/Light-dependent_reaction) occur in the [thylakoid membranes](/wiki/Thylakoid_membrane) of the [chloroplasts](/wiki/Chloroplast) where they drive the synthesis of ATP and NADPH. The light-dependent reactions are of two forms: cyclic and non-cyclic.

In the non-cyclic reaction, the [photons](/wiki/Photon) are captured in the light-harvesting [antenna complexes](/wiki/Antenna_complex) of [photosystem II](/wiki/Photosystem) by [chlorophyll](/wiki/Chlorophyll) and other [accessory pigments](/wiki/Accessory_pigments) (see diagram at right). The absorption of a photon by the antenna complex frees an electron by a process called [photoinduced charge separation](/wiki/Photoinduced_charge_separation). The antenna system is at the core of the chlorophyll molecule of the photosystem II reaction center. That freed electron is transferred to the primary electron-acceptor molecule, pheophytin. As the electrons are shuttled through an [electron transport chain](/wiki/Electron_transfer_chain) (the so-called ***Z-scheme*** shown in the diagram), it initially functions to generate a [chemiosmotic potential](/wiki/Chemiosmotic_potential) by pumping proton cations (H+) across the membrane and into the thylakoid space. An [ATP synthase](/wiki/ATP_synthase) enzyme uses that chemiosmotic potential to make ATP during photophosphorylation, whereas [NADPH](/wiki/NADPH) is a product of the terminal [redox](/wiki/Redox) reaction in the *Z-scheme*. The electron enters a chlorophyll molecule in [Photosystem I](/wiki/Photosystem_I). There it is further excited by the light absorbed by that [photosystem](/wiki/Photosystem). The electron is then passed along a chain of [electron acceptors](/wiki/Electron_acceptor) to which it transfers some of its energy. The energy delivered to the electron acceptors is used to move hydrogen ions across the thylakoid membrane into the lumen. The electron is eventually used to reduce the co-enzyme NADP with a H+ to NADPH (which has functions in the light-independent reaction); at that point, the path of that electron ends.

The cyclic reaction is similar to that of the non-cyclic, but differs in that it generates only ATP, and no reduced NADP (NADPH) is created. The cyclic reaction takes place only at photosystem I. Once the electron is displaced from the photosystem, the electron is passed down the electron acceptor molecules and returns to photosystem I, from where it was emitted, hence the name *cyclic reaction*.

### Water photolysis[[edit](/index.php?title=(none)&action=edit&section=5)]

[Template:Main](/wiki/Template:Main) The NADPH is the main [reducing agent](/wiki/Reducing_agent) produced by chloroplasts, which then goes on to provide a source of energetic electrons in other cellular reactions. Its production leaves chlorophyll in photosystem I with a deficit of electrons (chlorophyll has been oxidized), which must be balanced by some other reducing agent that will supply the missing electron. The excited electrons lost from chlorophyll from [photosystem I](/wiki/Photosystem_I) are supplied from the electron transport chain by [plastocyanin](/wiki/Plastocyanin). However, since [photosystem II](/wiki/Photosystem_II) is the first step of the *Z-scheme*, an external source of electrons is required to reduce its oxidized **chlorophyll *a*** molecules. The source of electrons in green-plant and cyanobacterial photosynthesis is water. Two water molecules are oxidized by four successive charge-separation reactions by photosystem II to yield a molecule of diatomic [oxygen](/wiki/Oxygen) and four [hydrogen](/wiki/Hydrogen) ions; the electrons yielded are transferred to a redox-active [tyrosine](/wiki/Tyrosine) residue that then reduces the oxidized chlorophyll *a* (called P680) that serves as the primary light-driven electron donor in the photosystem II reaction center. That photo receptor is in effect reset and is then able to repeat the absorption of another photon and the release of another photo-dissociated electron. The oxidation of water is [catalyzed](/wiki/Catalysis) in photosystem II by a redox-active structure that contains four [manganese](/wiki/Manganese) ions and a calcium ion; this [oxygen-evolving complex](/wiki/Oxygen-evolving_complex) binds two water molecules and contains the four oxidizing equivalents that are used to drive the water-oxidizing reaction. Photosystem II is the only known biological [enzyme](/wiki/Enzyme) that carries out this oxidation of water. The hydrogen ions released contribute to the transmembrane chemiosmotic potential that leads to ATP synthesis. Oxygen is a waste product of light-dependent reactions, but the majority of organisms on Earth use oxygen for [cellular respiration](/wiki/Cellular_respiration), including photosynthetic organisms.[[19]](#cite_note-19)[[20]](#cite_note-20)

## Light-independent reactions[[edit](/index.php?title=(none)&action=edit&section=6)]

### Calvin cycle[[edit](/index.php?title=(none)&action=edit&section=7)]

[Template:Main](/wiki/Template:Main) In the [light-independent](/wiki/Light-independent_reactions) (or "dark") reactions, the [enzyme](/wiki/Enzyme) [RuBisCO](/wiki/RuBisCO) captures [CO2](/wiki/Carbon_dioxide) from the [atmosphere](/wiki/Earth's_atmosphere) and, in a process called the [Calvin-Benson cycle](/wiki/Calvin-Benson_cycle), it uses the newly formed NADPH and releases three-carbon sugars, which are later combined to form sucrose and starch. The overall equation for the light-independent reactions in green plants is[[18]](#cite_note-18)[Template:Rp](/wiki/Template:Rp)

3 CO2 + 9 ATP + 6 NADPH + 6 H+ → C3H6O3-phosphate + 9 ADP + 8 Pi + 6 NADP+ + 3 H2O

[thumb|right|400px|Overview of the Calvin cycle and carbon fixation](/wiki/File:Calvin-cycle4.svg) Carbon fixation produces the intermediate three-carbon sugar product, which is then converted to the final carbohydrate products. The simple carbon sugars produced by photosynthesis are then used in the forming of other organic compounds, such as the building material [cellulose](/wiki/Cellulose), the precursors for [lipid](/wiki/Lipid) and [amino acid](/wiki/Amino_acid) biosynthesis, or as a fuel in [cellular respiration](/wiki/Cellular_respiration). The latter occurs not only in plants but also in [animals](/wiki/Animal) when the energy from plants is passed through a [food chain](/wiki/Food_chain).

The fixation or reduction of carbon dioxide is a process in which [carbon dioxide](/wiki/Carbon_dioxide) combines with a five-carbon sugar, [ribulose 1,5-bisphosphate](/wiki/Ribulose_1,5-bisphosphate), to yield two molecules of a three-carbon compound, [glycerate 3-phosphate](/wiki/Glycerate_3-phosphate), also known as 3-phosphoglycerate. Glycerate 3-phosphate, in the presence of [ATP](/wiki/Adenosine_triphosphate) and [NADPH](/wiki/NADPH) produced during the light-dependent stages, is reduced to [glyceraldehyde 3-phosphate](/wiki/Glyceraldehyde_3-phosphate). This product is also referred to as 3-phosphoglyceraldehyde ([PGAL](/wiki/PGAL)) or, more generically, as [triose](/wiki/Triose) phosphate. Most (5 out of 6 molecules) of the glyceraldehyde 3-phosphate produced is used to regenerate ribulose 1,5-bisphosphate so the process can continue. The triose phosphates not thus "recycled" often condense to form [hexose](/wiki/Hexose) phosphates, which ultimately yield [sucrose](/wiki/Sucrose), [starch](/wiki/Starch) and [cellulose](/wiki/Cellulose). The sugars produced during carbon [metabolism](/wiki/Metabolism) yield carbon skeletons that can be used for other metabolic reactions like the production of [amino acids](/wiki/Amino_acids) and [lipids](/wiki/Lipids).

### Carbon concentrating mechanisms[[edit](/index.php?title=(none)&action=edit&section=8)]

#### On land[[edit](/index.php?title=(none)&action=edit&section=9)]

[thumb|right|400px|Overview of](/wiki/File:HatchSlackpathway2.svg) [C4 carbon fixation](/wiki/C4_carbon_fixation) In hot and dry conditions, plants close their [stomata](/wiki/Stomata) to prevent water loss. Under these conditions, [Template:Co2](/wiki/Template:Co2) will decrease and oxygen gas, produced by the light reactions of photosynthesis, will increase, causing an increase of [photorespiration](/wiki/Photorespiration) by the [oxygenase](/wiki/Oxygenase) activity of [ribulose-1,5-bisphosphate carboxylase/oxygenase](/wiki/Rubisco) and decrease in carbon fixation. Some plants have [evolved](/wiki/Evolution) mechanisms to increase the [Template:Co2](/wiki/Template:Co2) concentration in the leaves under these conditions.[[21]](#cite_note-21) [Template:Main](/wiki/Template:Main)

Plants that use the [C4](/wiki/C4_carbon_fixation) carbon fixation process chemically fix carbon dioxide in the cells of the mesophyll by adding it to the three-carbon molecule [phosphoenolpyruvate (PEP)](/wiki/Phosphoenolpyruvate), a reaction catalyzed by an enzyme called [PEP carboxylase](/wiki/Phosphoenolpyruvate_carboxylase), creating the four-carbon organic acid [oxaloacetic acid](/wiki/Oxaloacetic_acid). Oxaloacetic acid or [malate](/wiki/Malate) synthesized by this process is then translocated to specialized [bundle sheath](/wiki/Bundle_sheath) cells where the enzyme [RuBisCO](/wiki/RuBisCO) and other Calvin cycle enzymes are located, and where [Template:Co2](/wiki/Template:Co2) released by [decarboxylation](/wiki/Decarboxylation) of the four-carbon acids is then fixed by RuBisCO activity to the three-carbon [3-phosphoglyceric acids](/wiki/3-phosphoglyceric_acid). The physical separation of RuBisCO from the oxygen-generating light reactions reduces photorespiration and increases [Template:Co2](/wiki/Template:Co2) fixation and, thus, the [photosynthetic capacity](/wiki/Photosynthetic_capacity) of the leaf.[[22]](#cite_note-22) [Template:C4](/wiki/Template:C4) plants can produce more sugar than [Template:C3](/wiki/Template:C3) plants in conditions of high light and temperature. Many important crop plants are [Template:C4](/wiki/Template:C4) plants, including maize, sorghum, sugarcane, and millet. Plants that do not use PEP-carboxylase in carbon fixation are called [C3 plants](/wiki/C3_carbon_fixation) because the primary carboxylation reaction, catalyzed by RuBisCO, produces the three-carbon 3-phosphoglyceric acids directly in the Calvin-Benson cycle. Over 90% of plants use [Template:C3](/wiki/Template:C3) carbon fixation, compared to 3% that use [Template:C4](/wiki/Template:C4) carbon fixation;[[23]](#cite_note-23) however, the evolution of [Template:C4](/wiki/Template:C4) in over 60 plant lineages makes it a striking example of [convergent evolution](/wiki/Convergent_evolution).[[21]](#cite_note-21) [Template:Main](/wiki/Template:Main)

[Xerophytes](/wiki/Xerophytes), such as [cacti](/wiki/Cacti) and most [succulents](/wiki/Succulents), also use PEP carboxylase to capture carbon dioxide in a process called [Crassulacean acid metabolism](/wiki/CAM_photosynthesis) (CAM). In contrast to [Template:C4](/wiki/Template:C4) metabolism, which *physically* separates the [Template:Co2](/wiki/Template:Co2) fixation to PEP from the Calvin cycle, CAM *temporally* separates these two processes. CAM plants have a different leaf anatomy from [Template:C3](/wiki/Template:C3) plants, and fix the [Template:Co2](/wiki/Template:Co2) at night, when their stomata are open. CAM plants store the [Template:Co2](/wiki/Template:Co2) mostly in the form of [malic acid](/wiki/Malic_acid) via carboxylation of [phosphoenolpyruvate](/wiki/Phosphoenolpyruvate) to oxaloacetate, which is then reduced to malate. Decarboxylation of malate during the day releases [Template:Co2](/wiki/Template:Co2) inside the leaves, thus allowing carbon fixation to 3-phosphoglycerate by RuBisCO. Sixteen thousand species of plants use CAM.[[24]](#cite_note-24)

#### In water[[edit](/index.php?title=(none)&action=edit&section=10)]

[Cyanobacteria](/wiki/Cyanobacteria) possess [carboxysomes](/wiki/Carboxysome), which increase the concentration of [Template:Co2](/wiki/Template:Co2) around RuBisCO to increase the rate of photosynthesis. An enzyme, [carbonic anhydrase](/wiki/Carbonic_anhydrase), located within the carboxysome releases CO2 from the dissolved hydrocarbonate ions (HCO3−). Before the CO2 diffuses out it is quickly sponged up by RuBisCO, which is concentrated within the carboxysomes. HCO3− ions are made from CO2 outside the cell by another carbonic anhydrase and are actively pumped into the cell by a membrane protein. They cannot cross the membrane as they are charged, and within the cytosol they turn back into CO2 very slowly without the help of carbonic anhydrase. This causes the HCO3− ions to accumulate within the cell from where they diffuse into the carboxysomes.[[25]](#cite_note-25) [Pyrenoids](/wiki/Pyrenoid) in [algae](/wiki/Algae) and [hornworts](/wiki/Hornwort) also act to concentrate [Template:Co2](/wiki/Template:Co2) around rubisco.[[26]](#cite_note-26)

## Order and kinetics[[edit](/index.php?title=(none)&action=edit&section=11)]

The overall process of photosynthesis takes place in four stages:[[8]](#cite_note-8){| class="wikitable" |- ! Stage !! Description !! Time scale |- | 1 || Energy transfer in antenna chlorophyll (thylakoid membranes) || [femtosecond](/wiki/Femtosecond) to [picosecond](/wiki/Picosecond) |- | 2 || Transfer of electrons in photochemical reactions (thylakoid membranes) || [picosecond](/wiki/Picosecond) to [nanosecond](/wiki/Nanosecond) |- | 3 || Electron transport chain and ATP synthesis (thylakoid membranes) || [microsecond](/wiki/Microsecond) to [millisecond](/wiki/Millisecond) |- | 4 || Carbon fixation and export of stable products || [millisecond](/wiki/Millisecond) to [second](/wiki/Second) |}

## Efficiency[[edit](/index.php?title=(none)&action=edit&section=12)]

[thumb|right|Probability distribution resulting from one-dimensional discrete time random walks. The quantum walk created using the Hadamard coin is plotted (blue) vs a classical walk (red) after 50 time steps.](/wiki/File:One_dimensional_quantum_random_walk.png) [Template:Main](/wiki/Template:Main) [Plants](/wiki/Plant) usually convert light into [chemical energy](/wiki/Chemical_energy) with a [photosynthetic efficiency](/wiki/Photosynthetic_efficiency) of 3–6%.[[27]](#cite_note-27)Absorbed light that is unconverted is dissipated primarily as heat, with a small fraction (1–2%)[[28]](#cite_note-28) re-emitted as [chlorophyll fluorescence](/wiki/Chlorophyll_fluorescence) at longer (redder) wavelengths.

Actual plants' photosynthetic efficiency varies with the frequency of the light being converted, light intensity, temperature and proportion of carbon dioxide in the atmosphere, and can vary from 0.1% to 8%.[[29]](#cite_note-29) By comparison, [solar panels](/wiki/Photovoltaic_module) convert light into [electric energy](/wiki/Electric_energy) at an efficiency of approximately 6–20% for mass-produced panels, and above 40% in laboratory devices.

Photosynthesis measurement systems are not designed to directly measure the amount of light absorbed by the leaf. But analysis of chlorophyll-fluorescence, P700- and P515-absorbance and gas exchange measurements reveal detailed information about e.g. the photosystems, quantum efficiency and the CO2 assimilation rates. With some instruments even wavelength-dependency of the photosynthetic efficiency can be analyzed.[[30]](#cite_note-30) A phenomenon known as [quantum walk](/wiki/Quantum_walk) increases the efficiency of the energy transport of light significantly. In the photosynthetic cell of an algae, bacterium, or plant, there are light-sensitive molecules called [chromophores](/wiki/Chromophore) arranged in an antenna-shaped structure named a photocomplex. When a photon is absorbed by a chromophore, it is converted into a [quasiparticle](/wiki/Quasiparticle) referred to as an [exciton](/wiki/Exciton), which jumps from chromophore to chromophore towards the reaction center of the photocomplex, a collection of molecules that traps its energy in a chemical form that makes it accessible for the cell's metabolism. The exciton's wave properties enable it to cover a wider area and try out several possible paths simultaneously, allowing it to instantaneously "choose" the most efficient route, where it will have the highest probability of arriving at its destination in the minimum possible time. Because that quantum walking takes place at temperatures far higher than quantum phenomena usually occur, it is only possible over very short distances, due to obstacles in the form of destructive interference that come into play. These obstacles cause the particle to lose its wave properties for an instant before it regains them once again after it is freed from its locked position through a classic "hop". The movement of the electron towards the photo center is therefore covered in a series of conventional hops and quantum walks.[[31]](#cite_note-31)[[32]](#cite_note-32)[[33]](#cite_note-33)

## Evolution[[edit](/index.php?title=(none)&action=edit&section=13)]

[Template:Life timeline](/wiki/Template:Life_timeline) [Template:Main](/wiki/Template:Main) Early photosynthetic systems, such as those in [green](/wiki/Green_sulfur_bacteria) and [purple sulfur](/wiki/Purple_sulfur_bacteria) and [green](/wiki/Chloroflexi_(phylum)) and [purple nonsulfur bacteria](/wiki/Purple_bacteria), are thought to have been anoxygenic, and used various other molecules as [electron donors](/wiki/Electron_donor) rather than water. Green and purple sulfur bacteria are thought to have used [hydrogen](/wiki/Hydrogen) and [sulfur](/wiki/Sulfur) as electron donors. Green nonsulfur bacteria used various [amino](/wiki/Amino_acid) and other [organic acids](/wiki/Organic_acid) as an electron donor. Purple nonsulfur bacteria used a variety of nonspecific organic molecules. The use of these molecules is consistent with the geological evidence that Earth's early atmosphere was highly [reducing](/wiki/Reducing_environment) at [that time](/wiki/History_of_Earth#Hadean_and_Archaean).[Template:Citation needed](/wiki/Template:Citation_needed)

Fossils of what are thought to be [filamentous](/wiki/Protein_filament) photosynthetic organisms have been dated at 3.4 billion years old.[[34]](#cite_note-34)[[35]](#cite_note-35) The main source of [oxygen](/wiki/Oxygen) in the [Earth's atmosphere](/wiki/Earth's_atmosphere) derives from [oxygenic photosynthesis](/wiki/Oxygen_evolution), and its first appearance is sometimes referred to as the [oxygen catastrophe](/wiki/Oxygen_catastrophe). Geological evidence suggests that oxygenic photosynthesis, such as that in [cyanobacteria](/wiki/Cyanobacteria), became important during the [Paleoproterozoic](/wiki/Paleoproterozoic) era around 2 billion years ago. Modern photosynthesis in plants and most photosynthetic prokaryotes is oxygenic. Oxygenic photosynthesis uses water as an electron donor, which is [oxidized](/wiki/Redox) to molecular oxygen ([Template:Chem](/wiki/Template:Chem)) in the [photosynthetic reaction center](/wiki/Photosynthetic_reaction_center).

### Symbiosis and the origin of chloroplasts[[edit](/index.php?title=(none)&action=edit&section=14)]

[thumb|150px|left|Plant cells with visible chloroplasts (from a moss,](/wiki/File:Plagiomnium_affine_laminazellen.jpeg) [*Plagiomnium affine*](/wiki/Plagiomnium_affine)) Several groups of animals have formed [symbiotic](/wiki/Symbiosis) relationships with photosynthetic algae. These are most common in [corals](/wiki/Coral), [sponges](/wiki/Sponge) and [sea anemones](/wiki/Sea_anemone). It is presumed that this is due to the particularly simple [body plans](/wiki/Body_plan) and large surface areas of these animals compared to their volumes.[[36]](#cite_note-36) In addition, a few marine [mollusks](/wiki/Mollusca) [*Elysia viridis*](/wiki/Elysia_viridis) and [*Elysia chlorotica*](/wiki/Elysia_chlorotica) also maintain a symbiotic relationship with chloroplasts they capture from the algae in their diet and then store in their bodies. This allows the mollusks to survive solely by photosynthesis for several months at a time.[[37]](#cite_note-37)[[38]](#cite_note-38) Some of the genes from the plant [cell nucleus](/wiki/Cell_nucleus) have even been transferred to the slugs, so that the chloroplasts can be supplied with proteins that they need to survive.[[39]](#cite_note-39) An even closer form of symbiosis may explain the origin of chloroplasts. Chloroplasts have many similarities with [photosynthetic bacteria](/wiki/Cyanobacteria), including a circular [chromosome](/wiki/Chromosome), prokaryotic-type [ribosome](/wiki/Ribosome), and similar proteins in the photosynthetic reaction center.[[40]](#cite_note-40)[[41]](#cite_note-41) The [endosymbiotic theory](/wiki/Endosymbiotic_theory) suggests that photosynthetic bacteria were acquired (by [endocytosis](/wiki/Endocytosis)) by early [eukaryotic](/wiki/Eukaryote) cells to form the first [plant](/wiki/Plant) cells. Therefore, chloroplasts may be photosynthetic bacteria that adapted to life inside plant cells. Like [mitochondria](/wiki/Mitochondrion), chloroplasts possess their own DNA, separate from the [nuclear DNA](/wiki/Nuclear_DNA) of their plant host cells and the genes in this chloroplast DNA resemble those found in [cyanobacteria](/wiki/Cyanobacteria).[[42]](#cite_note-42) DNA in chloroplasts codes for [redox](/wiki/Redox) proteins such as those found in the photosynthetic reaction centers. The [CoRR Hypothesis](/wiki/CoRR_Hypothesis) proposes that this **Co**-location is required for **R**edox **R**egulation.[Template:Clarify](/wiki/Template:Clarify)

### Cyanobacteria and the evolution of photosynthesis[[edit](/index.php?title=(none)&action=edit&section=15)]

The biochemical capacity to use water as the source for electrons in photosynthesis evolved once, in a [common ancestor](/wiki/Common_descent) of extant [cyanobacteria](/wiki/Cyanobacteria). The geological record indicates that this transforming event took place early in Earth's history, at least 2450–2320 million years ago (Ma), and, it is speculated, much earlier.[[43]](#cite_note-43)[[44]](#cite_note-44) Because the Earth's atmosphere contained almost no oxygen during the estimated development of photosynthesis, it is believed that the first photosynthetic cyanobacteria did not generate oxygen.[[45]](#cite_note-45) Available evidence from geobiological studies of [Archean](/wiki/Archean) (>2500 Ma) [sedimentary rocks](/wiki/Sedimentary_rock) indicates that life existed 3500 Ma, but the question of when oxygenic photosynthesis evolved is still unanswered. A clear paleontological window on cyanobacterial [evolution](/wiki/Evolution) opened about 2000 Ma, revealing an already-diverse biota of blue-green algae. [Cyanobacteria](/wiki/Cyanobacteria) remained the principal [primary producers](/wiki/Primary_producers) of oxygen throughout the [Proterozoic Eon](/wiki/Proterozoic_Eon) (2500–543 Ma), in part because the redox structure of the oceans favored photoautotrophs capable of [nitrogen fixation](/wiki/Nitrogen_fixation).[Template:Citation needed](/wiki/Template:Citation_needed) [Green algae](/wiki/Green_algae) joined blue-green algae as the major primary producers of oxygen on [continental shelves](/wiki/Continental_shelf) near the end of the [Proterozoic](/wiki/Proterozoic), but it was only with the [Mesozoic](/wiki/Mesozoic) (251–65 Ma) radiations of dinoflagellates, coccolithophorids, and diatoms did the [primary production](/wiki/Primary_production) of oxygen in marine shelf waters take modern form. Cyanobacteria remain critical to [marine ecosystems](/wiki/Marine_ecosystem) as primary producers of oxygen in oceanic gyres, as agents of biological nitrogen fixation, and, in modified form, as the [plastids](/wiki/Plastid) of marine algae.<ref name=Herrero>[Template:Cite book](/wiki/Template:Cite_book)</ref>

The [Oriental hornet](/wiki/Oriental_hornet) (*Vespa orientalis*) converts sunlight into electric power using a pigment called [xanthopterin](/wiki/Xanthopterin). This is the first evidence of a member of the animal kingdom engaging in photosynthesis.[[46]](#cite_note-46)

## Discovery[[edit](/index.php?title=(none)&action=edit&section=16)]

Although some of the steps in photosynthesis are still not completely understood, the overall photosynthetic equation has been known since the 19th century.

[Jan van Helmont](/wiki/Jan_Baptist_van_Helmont) began the research of the process in the mid-17th century when he carefully measured the [mass](/wiki/Mass) of the soil used by a plant and the mass of the plant as it grew. After noticing that the soil mass changed very little, he hypothesized that the mass of the growing plant must come from the water, the only substance he added to the potted plant. His hypothesis was partially accurate — much of the gained mass also comes from carbon dioxide as well as water. However, this was a signaling point to the idea that the bulk of a plant's [biomass](/wiki/Biomass_(ecology)) comes from the inputs of photosynthesis, not the soil itself.

[Joseph Priestley](/wiki/Joseph_Priestley), a chemist and minister, discovered that, when he isolated a volume of air under an inverted jar, and burned a candle in it, the candle would burn out very quickly, much before it ran out of wax. He further discovered that a mouse could similarly "injure" air. He then showed that the air that had been "injured" by the candle and the mouse could be restored by a plant.

In 1778, [Jan Ingenhousz](/wiki/Jan_Ingenhousz), repeated Priestley's experiments. He discovered that it was the influence of sunlight on the plant that could cause it to revive a mouse in a matter of hours.

In 1796, [Jean Senebier](/wiki/Jean_Senebier), a Swiss pastor, botanist, and naturalist, demonstrated that green plants consume carbon dioxide and release oxygen under the influence of light. Soon afterward, [Nicolas-Théodore de Saussure](/wiki/Nicolas-Théodore_de_Saussure) showed that the increase in mass of the plant as it grows could not be due only to uptake of CO2 but also to the incorporation of water. Thus, the basic reaction by which photosynthesis is used to produce food (such as glucose) was outlined.

[Cornelis Van Niel](/wiki/Cornelis_Van_Niel) made key discoveries explaining the chemistry of photosynthesis. By studying [purple sulfur bacteria](/wiki/Purple_sulfur_bacteria) and green bacteria he was the first to demonstrate that photosynthesis is a light-dependent [redox](/wiki/Redox) reaction, in which hydrogen reduces carbon dioxide.

Robert Emerson discovered two light reactions by testing plant productivity using different wavelengths of light. With the red alone, the light reactions were suppressed. When blue and red were combined, the output was much more substantial. Thus, there were two photosystems, one absorbing up to 600 nm wavelengths, the other up to 700 nm. The former is known as PSII, the latter is PSI. PSI contains only chlorophyll "a", PSII contains primarily chlorophyll "a" with most of the available chlorophyll "b", among other pigment. These include phycobilins, which are the red and blue pigments of red and blue algae respectively, and fucoxanthol for brown algae and diatoms. The process is most productive when the absorption of quanta are equal in both the PSII and PSI, assuring that input energy from the antenna complex is divided between the PSI and PSII system, which in turn powers the photochemistry.[[8]](#cite_note-8)[thumb|170px|Melvin Calvin works in his photosynthesis laboratory.](/wiki/File:Melvin_Calvin.jpg)

[Robert Hill](/wiki/Robin_Hill_(biochemist)) thought that a complex of reactions consisting of an intermediate to cytochrome b6 (now a plastoquinone), another is from cytochrome f to a step in the carbohydrate-generating mechanisms. These are linked by plastoquinone, which does require energy to reduce cytochrome f for it is a sufficient reductant. Further experiments to prove that the oxygen developed during the photosynthesis of green plants came from water, were performed by Hill in 1937 and 1939. He showed that isolated [chloroplasts](/wiki/Chloroplast) give off oxygen in the presence of unnatural reducing agents like [iron](/wiki/Iron) [oxalate](/wiki/Oxalate), [ferricyanide](/wiki/Ferricyanide) or [benzoquinone](/wiki/Benzoquinone) after exposure to light. The Hill reaction[[47]](#cite_note-47) is as follows:

2 H2O + 2 A + (light, chloroplasts) → 2 AH2 + O2

where A is the electron acceptor. Therefore, in light, the electron acceptor is reduced and oxygen is evolved.

[Samuel Ruben](/wiki/Sam_Ruben) and [Martin Kamen](/wiki/Martin_Kamen) used [radioactive isotopes](/wiki/Radionuclide) to determine that the oxygen liberated in photosynthesis came from the water.

[Melvin Calvin](/wiki/Melvin_Calvin) and [Andrew Benson](/wiki/Andrew_Benson), along with [James Bassham](/wiki/James_Bassham), elucidated the path of carbon assimilation (the photosynthetic carbon reduction cycle) in plants. The carbon reduction cycle is known as the [Calvin cycle](/wiki/Calvin_cycle), which ignores the contribution of Bassham and Benson. Many scientists refer to the cycle as the Calvin-Benson Cycle, Benson-Calvin, and some even call it the Calvin-Benson-Bassham (or CBB) Cycle.

[Nobel Prize](/wiki/Nobel_Prize)-winning scientist [Rudolph A. Marcus](/wiki/Rudolph_A._Marcus) was able to discover the function and significance of the electron transport chain.

[Otto Heinrich Warburg](/wiki/Otto_Heinrich_Warburg) and [Dean Burk](/wiki/Dean_Burk) discovered the I-quantum photosynthesis reaction that splits the CO2, activated by the respiration.[[48]](#cite_note-48) [Louis N.M. Duysens](/wiki/Louis_N.M._Duysens) and [Jan Amesz](/wiki/Jan_Amesz) discovered that chlorophyll a will absorb one light, oxidize cytochrome f, chlorophyll a (and other pigments) will absorb another light, but will reduce this same oxidized cytochrome, stating the two light reactions are in series.

### Development of the concept[[edit](/index.php?title=(none)&action=edit&section=17)]

In 1893, [Charles Reid Barnes](/wiki/Charles_Reid_Barnes) proposed two terms, *photosyntax* and *photosynthesis*, for the biological process of *synthesis of complex carbon compounds out of carbonic acid, in the presence of chlorophyll, under the influence of light*. Over time, the term *photosynthesis* came into common usage as the term of choice. Later discovery of anoxygenic photosynthetic bacteria and photophosphorylation necessitated redefinition of the term.[[49]](#cite_note-49)

## Factors[[edit](/index.php?title=(none)&action=edit&section=18)]

[thumb|The](/wiki/File:Leaf_1_web.jpg) [leaf](/wiki/Leaf) is the primary site of photosynthesis in plants. There are three main factors affecting photosynthesis and several corollary factors. The three main are:

* Light [irradiance](/wiki/Irradiance) and [wavelength](/wiki/Wavelength)
* [Carbon dioxide](/wiki/Carbon_dioxide) [concentration](/wiki/Concentration)
* [Temperature](/wiki/Temperature).

### Light intensity (irradiance), wavelength and temperature[[edit](/index.php?title=(none)&action=edit&section=19)]

[Template:See also](/wiki/Template:See_also) [thumb|](/wiki/File:Chlorophyll_ab_spectra-en.svg)[Absorbance](/wiki/Absorbance) spectra of free chlorophyll *a* (green) and *b* (red) in a solvent. The **action spectra** of chlorophyll molecules are slightly modified *in vivo* depending on specific pigment-protein interactions. The process of photosynthesis provides the main input of free energy into the biosphere, and is one of four main ways in which radiation is important for plant life.[[50]](#cite_note-50) The radiation climate within plant communities is extremely variable, with both time and space.

In the early 20th century, [Frederick Blackman](/wiki/Frederick_Blackman) and [Gabrielle Matthaei](/wiki/Gabrielle_Matthaei) investigated the effects of light intensity ([irradiance](/wiki/Irradiance)) and temperature on the rate of carbon assimilation.

* At constant temperature, the rate of carbon assimilation varies with irradiance, increasing as the irradiance increases, but reaching a plateau at higher irradiance.
* At low irradiance, increasing the temperature has little influence on the rate of carbon assimilation. At constant high irradiance, the rate of carbon assimilation increases as the temperature is increased.

These two experiments illustrate several important points: First, it is known that, in general, [photochemical](/wiki/Photochemical) reactions are not affected by [temperature](/wiki/Temperature). However, these experiments clearly show that temperature affects the rate of carbon assimilation, so there must be two sets of reactions in the full process of carbon assimilation. These are, of course, the [light-dependent 'photochemical'](/wiki/Light-dependent_reaction) temperature-independent stage, and the [light-independent, temperature-dependent](/wiki/Light-independent_reaction) stage. Second, Blackman's experiments illustrate the concept of [limiting factors](/wiki/Limiting_factor). Another limiting factor is the wavelength of light. Cyanobacteria, which reside several meters underwater, cannot receive the correct wavelengths required to cause photoinduced charge separation in conventional photosynthetic pigments. To combat this problem, a series of proteins with different pigments surround the reaction center. This unit is called a [phycobilisome](/wiki/Phycobilisome).[Template:Clarify](/wiki/Template:Clarify)

### Carbon dioxide levels and photorespiration[[edit](/index.php?title=(none)&action=edit&section=20)]

[thumb|350px|Photorespiration](/wiki/File:Photorespiration.svg) As carbon dioxide concentrations rise, the rate at which sugars are made by the [light-independent reactions](/wiki/Light-independent_reaction) increases until limited by other factors. [RuBisCO](/wiki/RuBisCO), the enzyme that captures carbon dioxide in the light-independent reactions, has a binding affinity for both carbon dioxide and oxygen. When the concentration of carbon dioxide is high, RuBisCO will [fix carbon dioxide](/wiki/Carbon_fixation). However, if the carbon dioxide concentration is low, RuBisCO will bind oxygen instead of carbon dioxide. This process, called [photorespiration](/wiki/Photorespiration), uses energy, but does not produce sugars.

RuBisCO oxygenase activity is disadvantageous to plants for several reasons:

1. One product of oxygenase activity is phosphoglycolate (2 carbon) instead of [3-phosphoglycerate](/wiki/3-phosphoglycerate) (3 carbon). Phosphoglycolate cannot be metabolized by the Calvin-Benson cycle and represents carbon lost from the cycle. A high oxygenase activity, therefore, drains the sugars that are required to recycle ribulose 5-bisphosphate and for the continuation of the [Calvin-Benson cycle](/wiki/Calvin-Benson_cycle).
2. Phosphoglycolate is quickly metabolized to glycolate that is toxic to a plant at a high concentration; it inhibits photosynthesis.
3. Salvaging glycolate is an energetically expensive process that uses the glycolate pathway, and only 75% of the carbon is returned to the Calvin-Benson cycle as 3-phosphoglycerate. The reactions also produce [ammonia](/wiki/Ammonia) (NH3), which is able to [diffuse](/wiki/Molecular_diffusion) out of the plant, leading to a loss of nitrogen.

A highly simplified summary is:

2 glycolate + ATP → 3-phosphoglycerate + carbon dioxide + ADP + NH3

The salvaging pathway for the products of RuBisCO oxygenase activity is more commonly known as [photorespiration](/wiki/Photorespiration), since it is characterized by light-dependent oxygen consumption and the release of carbon dioxide.

## See also[[edit](/index.php?title=(none)&action=edit&section=21)]

[Template:Portal](/wiki/Template:Portal) [Template:Div col](/wiki/Template:Div_col)

* [Jan Anderson (scientist)](/wiki/Jan_Anderson_(scientist))
* [Artificial photosynthesis](/wiki/Artificial_photosynthesis)
* [Calvin-Benson cycle](/wiki/Calvin-Benson_cycle)
* [Carbon fixation](/wiki/Carbon_fixation)
* [Cellular respiration](/wiki/Cellular_respiration)
* [Chemosynthesis](/wiki/Chemosynthesis)
* [Integrated fluorometer](/wiki/Integrated_fluorometer)
* [Light-dependent reaction](/wiki/Light-dependent_reaction)
* [Organic reaction](/wiki/Organic_reaction)
* [Photobiology](/wiki/Photobiology)
* [Photoinhibition](/wiki/Photoinhibition)
* [Photosynthetic reaction center](/wiki/Photosynthetic_reaction_center)
* [Photosynthetically active radiation](/wiki/Photosynthetically_active_radiation)
* [Photosystem](/wiki/Photosystem)
* [Photosystem I](/wiki/Photosystem_I)
* [Photosystem II](/wiki/Photosystem_II)
* [Quantum biology](/wiki/Quantum_biology)
* [Red edge](/wiki/Red_edge)
* [Vitamin D](/wiki/Vitamin_D)
* [Hill reaction](/wiki/Hill_reaction)

[Template:Div col end](/wiki/Template:Div_col_end)

## References[[edit](/index.php?title=(none)&action=edit&section=22)]

[Template:Reflist](/wiki/Template:Reflist)

## Further reading[[edit](/index.php?title=(none)&action=edit&section=23)]

### Books[[edit](/index.php?title=(none)&action=edit&section=24)]

[Template:Refbegin](/wiki/Template:Refbegin)

* [Template:Cite book](/wiki/Template:Cite_book)
* [Template:Cite book](/wiki/Template:Cite_book)
* [Template:Cite book](/wiki/Template:Cite_book)
* [Template:Cite book](/wiki/Template:Cite_book)

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### Papers[[edit](/index.php?title=(none)&action=edit&section=25)]

[Template:Refbegin](/wiki/Template:Refbegin)

* [Template:Cite journal](/wiki/Template:Cite_journal)
* [Template:Cite journal](/wiki/Template:Cite_journal)

[Template:Refend](/wiki/Template:Refend)

## External links[[edit](/index.php?title=(none)&action=edit&section=26)]

[Template:Commons category](/wiki/Template:Commons_category)

* [A collection of photosynthesis pages for all levels from a renowned expert (Govindjee)](http://www.life.uiuc.edu/govindjee/linksPSed.htm)
* [In depth, advanced treatment of photosynthesis, also from Govindjee](http://www.life.uiuc.edu/govindjee/paper/gov.html)
* [Science Aid: Photosynthesis](http://scienceaid.co.uk/biology/biochemistry/photosynthesis.html) Article appropriate for high school science
* [Metabolism, Cellular Respiration and Photosynthesis – The Virtual Library of Biochemistry and Cell Biology](http://www.biochemweb.org/metabolism.shtml)
* [Overall examination of Photosynthesis at an intermediate level](http://www.chemsoc.org/networks/learnnet/cfb/Photosynthesis.htm)
* [Overall Energetics of Photosynthesis](http://www.life.uiuc.edu/govindjee/photosynBook.html)
* [Photosynthesis Discovery Milestones](http://www.juliantrubin.com/bigten/photosynthesisexperiments.html) – experiments and background
* [The source of oxygen produced by photosynthesis](http://bcs.whfreeman.com/thelifewire/content/chp08/0802001.html) Interactive animation, a textbook tutorial
* [Template:Cite web](/wiki/Template:Cite_web)
* [Photosynthesis – Light Dependent & Light Independent Stages](http://www.biology-innovation.co.uk/pages/plant-biology-ecology/photosynthesis/)
* [Khan Academy, video introduction](http://www.khanacademy.org/video/photosynthesis?playlist=Biology)

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