Photosynthesis

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Photosynthesis is the process by which higher plants, algae, and a broad class of bacteria transform light energy and store it in the form of energy-rich organic molecules. In plants and algae, as well as some species of bacteria, photosynthesis removes carbon dioxide from the atmosphere and produces molecular oxygen. In addition there are evolutionarily more primitive bacteria that use light energy to create energy-rich molecules, but do not split water to produce oxygen.

Introductory article

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Introduction

Photosynthetic organisms use light energy to produce energy-rich organic molecules. Because these molecules provide the energy and building blocks for nonphotosynthetic as well as photosynthetic organisms, virtually all life on Earth depends on photosynthesis. In plants and algae, as well as a broad class of photosynthetic bacteria, photosynthesis removes carbon dioxide from the atmosphere and produces molecular oxygen. Evolutionarily more primitive photosynthetic bacteria use light energy to create energy-rich molecules, but do not split water to produce oxygen. This article focuses on photosynthesis in higher plants. The goal is to describe the conceptual framework that underlies our current understanding of the photosynthetic process. Despite the diversity that exists among photosynthetic organisms, the key molecular processes share common features.

In higher plants photosynthesis occurs within subcellular organelles known as chloroplasts (**Figure 1**), which are most abundant in leaves, where they typically number between 50 and 200 per cell. Higher plant chloroplasts are bound by two distinct membranes, the outer envelope membrane, which is permeable to many of the soluble molecules in the cytoplasm of the cell, and the inner envelope membrane, which controls the molecular traffic between the chloroplast and the cytoplasm. Transporter proteins bound to the inner envelope mediate the flow of photosynthate from the chloroplast to the cytoplasm where sucrose biosynthesis takes place. Within the chloroplast are the thylakoid membranes, which contain the chlorophyll and photosynthetic machinery for the light-driven production of ATP and NADPH. Thylakoid membranes form flat vesicles, which separate an inner aqueous space (the lumen) from the outer aqueous space of the chloroplast (the stroma). The separation of these two aqueous phases by the thylakoid vesicle is essential for the photosynthetic transformation of light energy into chemical energy. In many chloroplasts the stroma-exposed surfaces of the thylakoid membranes are pressed tightly against one another, forming structures known as grana stacks. The stromal aqueous phase of the chloroplast contains the enzymes responsible for photosynthetic carbon reduction in which carbon dioxide is used to produce carbohydrates. In addition to producing carbohydrates, the chloroplast is the site for the biosynthesis of other compounds (e.g. lipids) that are essential for plant growth.

An endosymbiotic origin of higher plant chloroplasts accounts for the exceptionally close functional and structural parallels between the photosynthetic apparatus of subcellular chloroplasts and free-living bacteria. The evolutionary progenitor of higher plant chloroplasts was an oxygen-evolving photosynthetic prokaryote similar to Cyanobacteria currently in existence. There are living examples in which the invading endosymbiont retains a vestigial cyanobacterial cell wall. These recent invaders differ sufficiently from fully 'evolved' chloroplasts that they are termed cyanelles rather than chloroplasts. It is believed that the ancestry of the chloroplast in higher plants can be traced back to an organism closely related to *Prochloron didemni*, an apparently obligate ectosymbiont living in association with a marine sea squirt (*Didemnum*).

Photosynthetic Energy Conversion – Thylakoid Membranes Use Light Energy to Produce ATP and NADPH

An antenna system containing chlorophyll and carotenoid pigments captures light energy and delivers it to reaction centres

The action spectrum of higher plant photosynthesis, that is the colours of light that can energize photosynthesis, include wavelengths from about 350 nm (violet) to 700 nm (red). About 60% of the sunlight incident on the Earth's surface falls within this photosynthetically active range. Two classes of coloured compounds, chlorophylls and carotenoids, are responsible for the absorption of light that

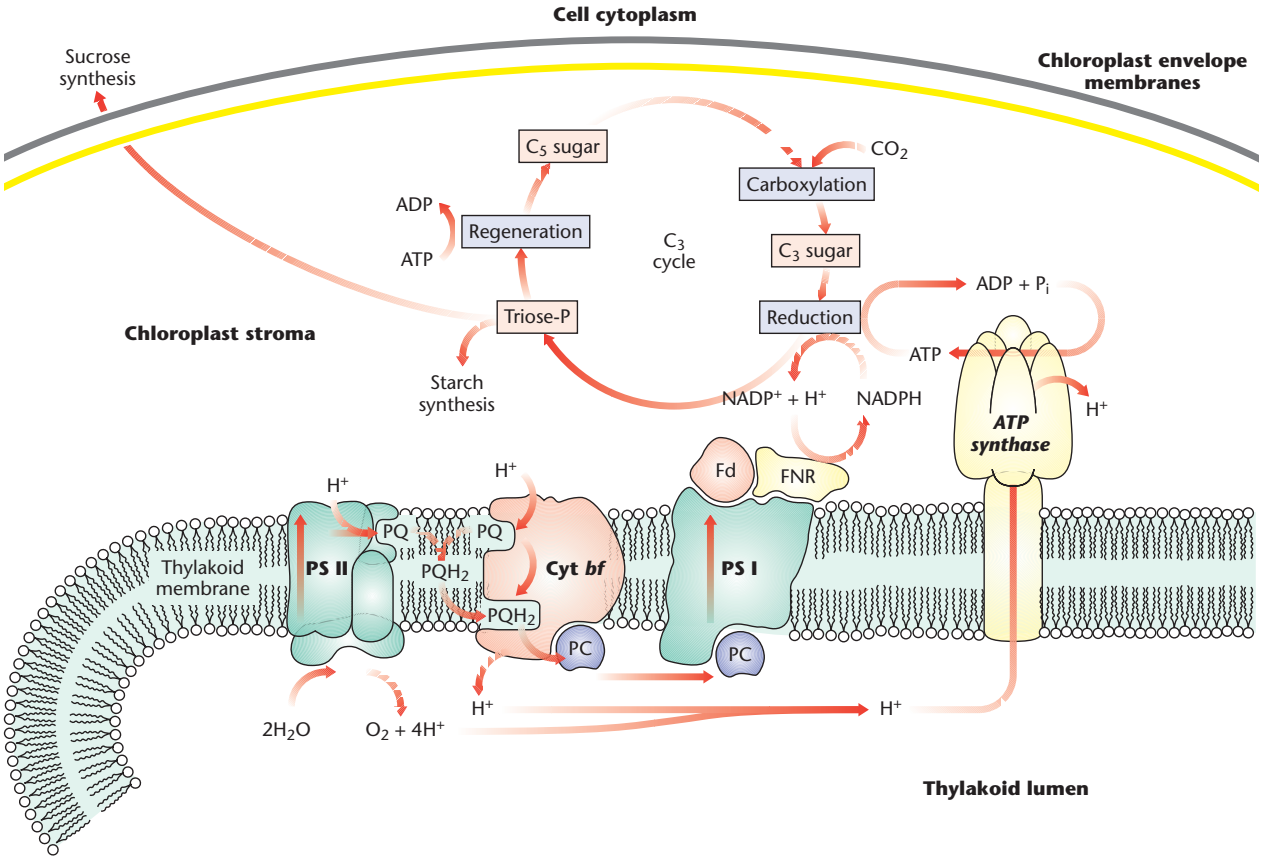

Figure 1 Schematic drawing showing part of a chloroplast. The thylakoid membrane contains the major protein complexes of the photosynthetic machinery responsible for light absorption and electron and proton transfer. The reactions of the thylakoid membrane drive the C_3 photosynthetic carbon reduction cycle that takes place in the chloroplast stroma. Illustrated is the concept of light-driven linear electron flow coupled to the accumulation of protons in the thylakoid lumen, which is in turn used to drive ATP formation by the ATP synthase. In addition to the energy stored in ATP formation, energy derived from absorbed light is stored by the reactions of the thylakoid membrane in the formation of NADPH. Photosynthetic carbon reduction is shown as a three-stage cycle. (1) Carboxylation: a molecule of carbon dioxide is covalently linked to a carbon skeleton. (2) Reduction: energy in the form of NADPH and ATP is used to form simple carbohydrate. (3) Regeneration: energy in the form of ATP is used to regenerate the carbon skeleton for carboxylation. Key: PS II, photosystem II; PS I, photosystem I; PQ and PQH_2, plastoquinone and reduced plastoquinone; cyt, cytochrome; FeS, Rieske iron–sulfur protein; PC, plastocyanin; Fd, ferredoxin; FNR, ferredoxin-NADP reductase.

energizes photosynthesis in higher plants. These antenna pigments operate exclusively within the thylakoid membrane, where they are bound to specialized proteins. Chlorophyll is the dominant pigment and occurs in two forms, chlorophyll *a* and chlorophyll *b*. Light absorption by chlorophyll depends on a metal atom, magnesium, which is bound within a complex ring structure known as porphyrin. Chlorophyll strongly absorbs red and blue light, while scattering most of the incident green light (which is why many plants appear green). Carotenoids, which are present in much lower amounts in the thylakoid membrane than chlorophyll, are linear polyenes. In addition to serving as accessory pigments, carotenoids help protect the photosynthetic apparatus from photo-oxidative damage caused by excess light energy.

To convert the transient energy of a photon into chemical energy, the photosynthetic apparatus performs a series of energy-transforming reactions. The process is initiated by absorption of a photon by a chlorophyll or carotenoid molecule that converts light energy to an excited electronic state known as an exciton. The antenna system for each reaction centre contains 250–300 antenna molecules that are anchored to light-harvesting proteins within the photosynthetic membrane. The fate of the exciton is determined by the structure of the light-harvesting protein, which serves as a scaffolding for the precise arrangement of each antenna molecule. Because of the proximity of other antenna molecules with the same or similar energy states, the exciton is rapidly transferred over the antenna system. During this process most of the excitons are 'trapped' by a reaction centre, while others are

converted into heat or back into light. Under optimum conditions over 90% of the absorbed quanta are transferred from the antenna system to a reaction centre, where the excited state energy drives the next step in photosynthesis – primary charge separation.

Reaction centres use the energy from light to separate positive and negative charge

The thylakoid membranes of chloroplasts perform the remarkable feat of converting a transient form of energy, light, into stable chemical energy of NADPH and ATP. As discussed above, the first step is the conversion of light energy into excited state energy in the antenna system, which is delivered to a reaction centre. In plants (and all other oxygen evolving organisms) there are two types of reaction centres, photosystem II and photosystem I. These two reaction centres are the site of the primary photochemical reaction of photosynthesis, which is charge separation. In photosystem II the excited state energy is trapped by a pair of chlorophyll molecules, known as P680, which is located at the core of the reaction centre (**Figure 2**). The primary photochemical reaction is the transfer of an electron from the excited state of P680 to an electron acceptor, pheophytin, creating $P680^+$ and $pheophytin^-$. The transfer of an electron from one molecular species to another is called an oxidation–reduction reaction, or redox reaction, and the energy available with which to do biological work is referred to as redox energy. The redox energy in the reaction centres drives all subsequent electron transfer reactions in the thylakoid membrane. In photosystem II the energy is used to remove electrons from water (oxidation) and to add electrons, as well as protons, to plastoquinone (reduction).

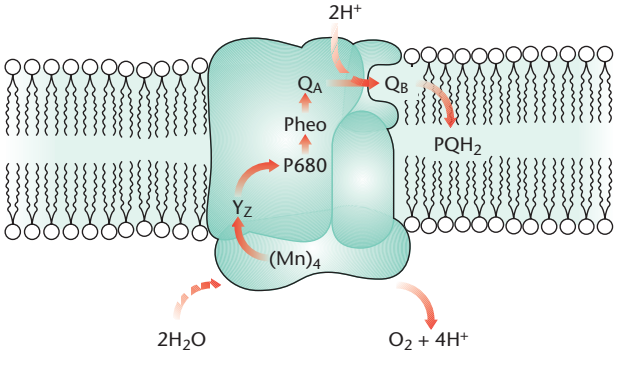

Figure 2 Schematic drawing of the photosystem II reaction centre in the thylakoid membrane. Photosystem II uses light energy to remove electrons from water, resulting in the release of oxygen and protons. The electrons from water are transferred via redox cofactors in the protein complex to form reduced plastoquinone. Key: $(Mn)_4$, manganese cluster involved in removing electrons from water; P680, reaction centre chlorophyll of photosystem II; Pheo, pheophytin; Q_A and Q_B, plastoquinones that bind and unbind from photosystem II; Y_Z, a tyrosine residue in photosystem II that serves as an electron carrier.

The photosystem II complex (i.e. the reaction centre and the light-harvesting proteins) is made of several different redox components and more than 20 different polypeptides that are a mixture of chloroplast and nuclear gene products. These intricately assembled polypeptides bind and precisely orient about 300 chlorophyll molecules, about 50 carotenoid molecules, two molecules of plastoquinone (Q_A, Q_B), one iron atom, two pheophytin molecules, one or two cytochrome b_{559} molecules, four atoms of manganese, and an undetermined number of chloride and calcium ions (**Figure 2**). Photosystem II reaction centres work independently and must coordinate the oxidation of two water molecules, a four-electron process, and the reduction of plastoquinone, a two-electron process. The oxidation of water depends on a cluster of four manganese atoms and requires four sequential photochemical reactions. The result is the release of protons into the thylakoid lumen, the release of molecular oxygen, and the transfer of four electrons across the thylakoid membrane. Each electron passes rapidly ($\approx 10^{-10}$ s) from pheophytin to a permanently bound quinone, Q_A. The electron is then transferred to a second plastoquinone, Q_B. After plastoquinone at the Q_B site is fully reduced, which requires two electrons and two protons, it unbinds from the site and diffuses into the lipid matrix of the thylakoid membrane. The net result of these electron transfer reactions within photosystem II is the utilization of light energy to separate electrical charge and the chemical activity of protons on opposite sides of the thylakoid membrane, and to produce reduced plastoquinone, a reductant far more energy-rich than water, which was the original source of the electrons.

Although photosystem I and photosystem II differ in structure and catalytic activity, their key energetic transformations are similar. The primary reaction in photosystem I is the separation of positive and negative charge, which drives the oxidation of plastocyanin, a soluble copper-containing protein located in the thylakoid lumen, and the reduction of ferredoxin, a soluble iron-containing protein located in the chloroplast stroma. As with photosystem II, the reactions of photosystem I produce an electric potential across the thylakoid membrane and generate a strong reductant. Photosystem I differs from photosystem II in that its oxidized primary donor, $P700^+$, is a weaker oxidant than $P680^+$, and photosystem I does not deposit protons into the thylakoid lumen.

Electron carriers in the thylakoid membrane produce NADPH and create a pH difference plus an electric potential across the thylakoid membrane

The light-driven electron and proton transfer reactions of the two photosystems are interconnected through the

activity of the cytochrome *bf* complex, which catalyses the energetically downhill reaction of oxidizing plastoquinol and reducing plastocyanin. Plastoquinone serves as a mobile hydrogen carrier, transporting hydrogen from photosystem II to the cytochrome *bf* complex, while plastocyanin serves as a mobile electron carrier, transporting electrons from the cytochrome *bf* complex to photosystem I. The cytochrome *bf* complex is constructed of four major polypeptides that bind two *b*-type cytochrome haems (cytochrome b_6), a *c*-type cytochrome haem (cytochrome *f*), and an Fe_2S_2 centre (Rieske iron–sulfur cluster). In addition to linking the activity of photosystem II and I, the cytochrome *bf* complex plays a central role in energy transformation and storage by converting redox free energy available in reduced plastoquinone (PQH_2) into a transmembrane pH difference and an electric potential difference. To accomplish this, the cytochrome *bf* complex oxidizes PQH_2 at a site near the lumenal side of the membrane, resulting in the release of protons into the lumen. Because plastoquinone is reduced by photosystem II near the stromal side of the membrane, the protons for its reduction are taken up from the stroma (**Figure 1**). In addition to oxidizing plastoquinone, the cytochrome *bf* complex also reduces plastoquinone at a second site that is near the stromal side of the membrane. The net result of these reactions is the transfer of protons from the stroma to the lumen, creating a transmembrane pH difference, and the transfer of unpaired charge across the membrane, creating an electric potential difference. The energy stored across the thylakoid membrane is known as a proton electrochemical potential, and represents an essential form of energy in the photosynthetic process that links two otherwise independent processes, electron transport and ATP synthesis.

ATP synthase uses the energy stored in the proton electrochemical potential across the thylakoid membrane to produce ATP

The energy stored in the proton electrochemical potential is used for the energy-requiring reaction of ADP phosphorylation by a reversible ATP synthase located in the thylakoid membrane (**Figure 1**). The catalytic mechanism of this multisubunit enzyme complex is only partially understood, despite more than two decades of research. Five polypeptide subunits make up the hydrophilic domain of the ATP synthase that protrudes into the stroma and contains the catalytic sites that are involved in ADP binding and phosphorylation. This enzyme complex also contains an integral membrane portion, consisting of four different polypeptides, which is involved in conducting protons across the thylakoid membrane to drive the catalytic reactions of the hydrophilic domain. There is evidence that proton flow drives the rotation of a portion of the hydrophilic domain of the ATP synthase, temporarily converting the energy into a conformational change in the enzyme that is then used to form ATP.

The daily cycle of light and dark that plants live in requires that the catalytic activity of the chloroplast ATP synthase be regulated. Otherwise, the energetically downhill hydrolysis of ATP would drain the chloroplast of energy in the dark. On the other hand, the regulatory control of ATP synthase must respond dynamically in the light if energy is to be stored efficiently during the day. Experiments show that several factors (e.g. the size of the pH difference across the thylakoid membrane, the oxidation state of a regulatory disulfide group on one of the ATP synthase polypeptide subunits, and nucleotide binding) act together to allow the catalytic inactivation of the ATP synthase at night and dynamic modulation of activity during the day.

Photosynthetic Carbon Metabolism – Enzymes in the Chloroplast Stroma Use Energy Stored in NADPH and ATP to Produce Carbohydrates

The C_3 photosynthetic carbon reduction cycle fixes carbon dioxide and produces sugar

Although the energy stored in ATP and NADPH is chemically stable, plants do not accumulate high levels of these compounds. The ATP and NADPH are rapidly cycled in the biosynthesis of carbohydrates from atmospheric carbon dioxide and water. This intricate biosynthetic pathway, known as the C_3 photosynthetic carbon reduction cycle (C_3 cycle), takes place in the stroma of the chloroplast and involves more than a dozen different enzymes (**Figure 1**). The products of the C_3 cycle are triose phosphates (phosphorylated three-carbon sugars), which are used as building blocks for more complex carbohydrates. The net reaction of the C_3 cycle can be written as in eqn [I].

$$3CO_2 + 9ATP + 6NADPH \rightarrow \text{Triose-P} + 9ADP + 8P_i + 6NADP^+ \quad [I]$$

Overall, the synthesis of one six-carbon sugar requires 12 molecules of NADPH and 18 molecules of ATP. The C_3 cycle is energetically very efficient. Nearly 90% of the energy originally available in the ATP and NADPH is available in the final carbohydrate products. The six-carbon sugars are used to produce carbohydrates for transport to other parts of the plant (e.g. sucrose) and for storage (e.g. starch). Through oxidation reactions the energy stored in photosynthetically produced carbohydrates can be used to drive energy-requiring reactions elsewhere in the plant.

The first step in the C_3 cycle is a carboxylation reaction in which atmospheric carbon dioxide is attached to a five-carbon acceptor molecule, ribulose 1,5-bisphosphate (RuBP) (**Figure 1**). The resulting six-carbon intermediate is not stable and immediately breaks down (by hydrolysis) into two three-carbon compounds (3-phosphoglycerate, PGA), which accounts for the C_3 designation of the cycle. The covalent attachment of carbon dioxide to RuBP is catalysed by Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase). Rubisco is an exceptionally abundant enzyme in leaves, often accounting for 40% or more of the soluble leaf protein; this makes it the most abundant enzyme in the biota.

The next stage of the C_3 cycle requires an input of energy for the reduction of carbon to form carbohydrate. The energy comes from ATP, which is utilized to phosphorylate PGA, the three-carbon product of the carboxylation reaction. A triose phosphate (glyceraldehyde 3-phosphate) is then formed using the reducing power stored in NADPH. Triose phosphate is the principal branch point within the C_3 cycle (see **Figure 1**). A portion of triose phosphate is transported out of the chloroplast and used in the synthesis of sucrose, while triose phosphate within the chloroplast is used for starch synthesis. In addition, triose phosphate must be reinvested into the C_3 cycle to regenerate RuBP for the carboxylation step, which completes the photosynthetic carbon reduction cycle. In fact, the majority of the enzymes in the C_3 cycle are used in regenerating RuBP from glyceraldehyde 3-phosphate. The regeneration process requires energy in the form of ATP and proceeds through ten intermediate compounds.

A fascinating puzzle in photosynthesis is the coordination of the energy-capturing reactions of the thylakoid membrane with the energy-utilizing reactions of the C_3 cycle. This synchronization is accomplished through a variety of interrelated processes. For example, the catalytic activity of Rubisco is dependent on another stromal protein, Rubisco activase. Although the detailed mechanism of activase interaction with Rubisco remains to be worked out, it is known that Rubisco activase depends both on the level of stromal ATP that is generated by the machinery of the thylakoid membrane as well as the redox poise of the stroma. In addition to control by activase, Rubisco activity is modulated by the pH and Mg^{2+} concentration of the stroma that change in response to light-driven proton transport. Light is a factor in controlling the activities of several other enzymes in the C_3 cycle through reversible redox reactions. In the light, disulfide groups on certain C_3 enzymes are reduced by thioredoxin, a soluble stromal protein. Because the redox state of thioredoxin is controlled by light-driven electron transport through photosystem I, the catalytic activation of these C_3 cycle enzymes is regulated by and coordinated with the activity of the thylakoid membrane.

The C_2 photorespiration cycle retrieves reduced carbon after Rubisco fixes oxygen rather than carbon dioxide

The fossil record indicates that photosynthetic organisms have been producing oxygen for over 3 billion years, although stable molecular oxygen did not appear in the Earth's atmosphere until about 2 billion years ago; this means that the evolution of photosynthesis occurred in an oxygen-free atmosphere. This fact probably explains a curious feature about Rubisco that is the origin of a major inefficiency in higher plant photosynthesis. In addition to the carboxylation of RuBP by carbon dioxide, Rubisco will also catalyse its oxidation by atmospheric oxygen to yield one molecule of PGA and a molecule of a two-carbon compound, phosphoglycolate. This oxygenation reaction creates a significant inefficiency in the photosynthetic process because the two-carbon compound cannot enter the C_3 cycle. In a typical C_3 crop (e.g. soya bean), the rate of Rubisco-catalysed oxygenation is about 20% of the rate of carbon dioxide fixation. The inability of Rubisco to differentiate between molecular oxygen and carbon dioxide appears to be an unavoidable consequence of having evolved in an oxygen-free atmosphere.

To compensate for the oxygenation of RuBP by Rubisco, a metabolic pathway evolved to recover the two-carbon carbon skeletons that are diverted from the C_3 cycle by the oxygenation reaction. However, this scavenging operation, known as the C_2 photorespiratory carbon oxidation cycle, is energetically expensive and involves two additional organelles, mitochondria and peroxisomes. In the C_2 cycle, two molecules of phosphoglycolate are converted into one molecule of 3-phosphoglycerate at the expense of one ATP molecule. The C_2 cycle succeeds in returning 75% of photorespiratory carbon to the C_3 cycle, with the remainder released as carbon dioxide.

C_4 and CAM photosynthetic metabolism defeats photorespiration but at a considerable energetic cost

The C_2 cycle discussed above makes the best of the wasteful reaction created by the oxygenase activity of Rubisco. An alternative 'strategy' taken by evolution is to prevent or greatly reduce Rubisco's oxygenase activity by exploiting the competition between carbon dioxide and oxygen as alternative substrates. Plants such as maize, sorghum and sugar cane suppress, or even eliminate, the oxygenation reaction of Rubisco by concentrating carbon dioxide in specialized leaf cells that contain Rubisco. These species are known as C_4 plants because the initial carboxylation reaction produces a C_4 acid. They have a unique leaf anatomy with two distinct photosynthetic cell types in which chloroplast-containing mesophyll cells surround chloroplast-containing bundle sheath cells, which in turn

encircle the vascular bundles of leaf. The cytoplasm of mesophyll cells and bundle sheath cells is interconnected by membrane-surrounded channels.

The basic pathway of C_4 photosynthesis and the interplay of the two photosynthetic cell types are shown in **Figure 3**. A key feature of C_4 photosynthesis is that the initial fixation of atmospheric carbon dioxide takes place in mesophyll cell and involves the carboxylation of phosphoenolpyruvate (PEP) by PEP carboxylase to form oxaloacetate. Unlike Rubisco, oxygen is not a competitive substrate for PEP carboxylase. Oxaloacetate is converted to a four-carbon acid, either aspartate or malate, transported to the bundle sheath cell and decarboxylated to release carbon dioxide. The decarboxylation of the four-carbon acids results in a significant elevation of the carbon dioxide concentration in the bundle sheath cell chloroplast where Rubisco and the other enzymes of the C_3 cycle are localized. The elevated concentration of carbon dioxide effectively competes with oxygen, virtually eliminating the first step in photorespiration, phosphoglycolate formation. The C_4 cycle is completed by the transport of a C_3 acid back to the mesophyll cell where regeneration of the original carbon dioxide acceptor, PEP, takes place.

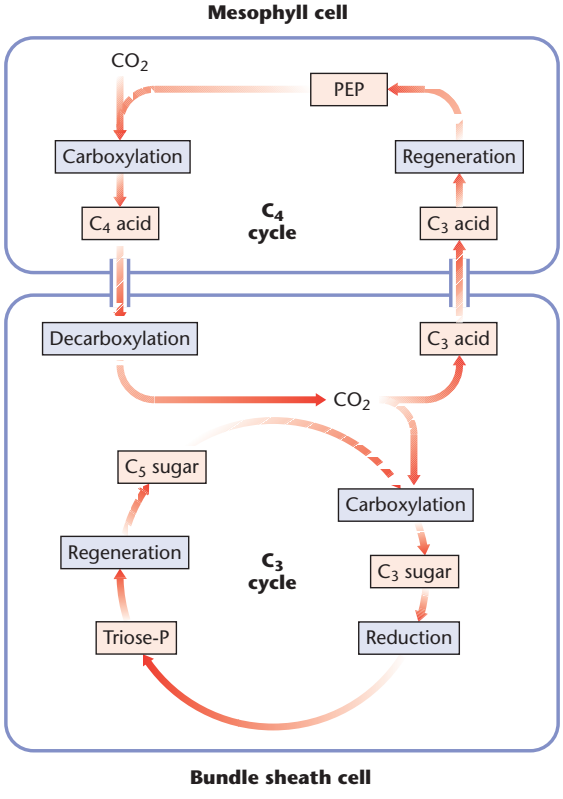

Figure 3 The C_4 photosynthetic carbon metabolism pathway suppresses photorespiration by concentrating carbon dioxide at the site of carboxylation by Rubisco. The C_4 pathway involves two different cell types, mesophyll cells and bundle sheath cells. Shown in the C_4 cycle are: carboxylation of carbon dioxide into a four-carbon acid in mesophyll cells; transport of the four-carbon acid into bundle sheath cells; decarboxylation of the four-carbon acid producing a high concentration of carbon dioxide within bundle sheath cells where the C_3 cycle produces carbohydrate; transport of the resulting three-carbon acid back to the mesophyll cell; and the regeneration of the carbon dioxide acceptor, PEP.

Although the C_4 photosynthetic pathway effectively suppresses photorespiration, it is important to recognize that there are substantial energetic costs (from ATP) tied up in achieving elevated carbon dioxide levels within bundle sheath cells. It is estimated that only about 5% of all terrestrial higher plant species are C_4, indicating that the pathway, with its higher energetic costs, has an advantage in relatively few habitats. However, the much higher representation of C_4 species in hot/dry climates is well documented and probably reflects the higher water use efficiency that is associated with C_4 metabolism, as well as the increasing affinity of Rubisco for oxygen with increasing temperature.

Another mechanism found in plants to overcome photorespiration is known as crassulacean acid metabolism (CAM). Like the C_4 photosynthetic pathway, CAM plants concentrate carbon dioxide at the site of carboxylation by Rubisco, but they differ in morphology and metabolic pathways. It is important to keep in mind that although different mechanisms have evolved to remove carbon dioxide from the atmosphere, all plants depend on Rubisco and the C_3 cycle for the synthesis of carbohydrates.

It is worth noting that as the atmospheric carbon dioxide levels increase over the next century, we may expect a global suppression of photorespiration, which may lead to increased biomass accumulation and agricultural production. Indeed, production increases have already been reported that have been attributed to increases in atmospheric carbon dioxide. Nevertheless, increasing atmospheric carbon dioxide portends global changes in temperature and rainfall that may negate the gains of lower photorespiration.

Regulation – Special Mechanisms Protect the Photosynthetic Machinery from Damage by Excess Light but at a Cost to Photosynthetic Efficiency

Higher plant photosynthesis has the capacity to be extremely efficient. At low levels of irradiance with photorespiration suppressed by low atmospheric oxygen, well-watered C_3 plants require only about 10 quanta of light to reduce carbon dioxide to carbohydrate. However, in the real world environmental conditions conspire to reduce both the rate and efficiency of photosynthetic carbon dioxide reduction. For example, in many plants water availability is one of the most important factors

limiting photosynthesis under natural conditions. Because water is lost from leaves through the same pores (known as stomata) that carbon dioxide enters, the plant must balance carbon dioxide uptake against water loss. Under conditions of limited water availability, the stomata restrict water loss, which exerts a strong control on the net rate of photosynthesis by limiting the availability of carbon dioxide within the leaf. Under these conditions the amount of light absorbed by the antenna system can far exceed the photosynthetic capacity of the plant, which can lead to photodamage of the photosynthetic machinery.

In response plants have evolved elaborate mechanisms to avoid injury under stress conditions. For example, some plant species have the ability to reorient leaves (and even chloroplasts within the cell) to minimize light interception. However, other important protective mechanisms operate within the chloroplast itself. Although the underlying mechanism remains under investigation, it is clear that dynamic regulation of energy transfer pathways within the antenna pigment beds of chloroplasts play a very significant role in protecting the photosynthetic machinery. While excitation transfer within the antenna pigment bed can occur with nearly 100% efficiency, it is not unusual at midday for half of the absorbed quanta to be directed from the antenna array into heat, thus providing protection of the photosynthetic apparatus. However, the efficiency of photosynthetic light energy conversion can be reduced by more than 50% by the photoprotective process.

Even with a large proportion of the absorbed light energy directed into heat, other mechanisms are needed to deal with overexcitation when the entry of carbon dioxide into the leaf is restricted by partially closed stomata. For example, molecular oxygen can intercept electrons from ferredoxin, thus preventing overreduction of $NADP^+$. Because the reduction of oxygen frequently results in the generation of potentially harmful oxygen radicals, plants produce an elaborate ensemble of radical-scavenging enzymes and compounds to deal with this secondary threat. There is evidence that separate electron transport cycles around photosystem I and photosystem II may provide a further outlet for overexcitation and serve to prevent radical formation. However, even with all these measures in place, light-induced damage to the photosynthetic apparatus is common, particularly to components in photosystem II, and robust repair processes exist to rapidly correct the dysfunction. Thus, while evolution has crafted a photosynthetic mechanism capable of exceptional efficiency, it has also found it necessary to add dynamic regulatory mechanisms poised to trade photosynthetic efficiency for protection from photodamage.

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