LIGHT AND PHOTOSYNTHESIS
PART 2 - PHOTOSYNTHESIS

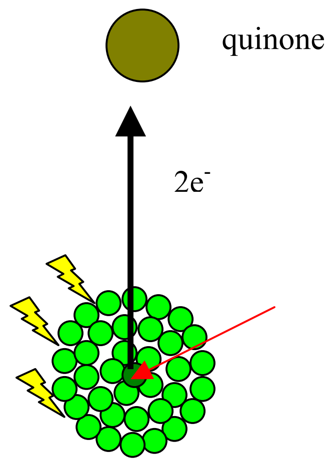
Now that you have been exposed to the principles of light and that you know how chlorophyll traps that light, it's time to discuss the actual process of photosynthesis. First, you need to know scientists don't know everything about photosynthesis. What scientists do know is amazing. For our purposes, we will only brush the topic. However, you will probably feel you have been overexposed to the process after finishing this lecture. Just keep your eye on the concept this is *the* most important biochemical process on earth and everyone needs to understand a little about it.

Autotrophic *vs* Heterotrophic
Scientists often categorize organisms into their forms of energy sources. Organisms that convert carbon dioxide (an inorganic compound) into organic compounds (such as glucose) utilizing some energy source (in our case, the sun) are called autotrophic. Organisms that depend on other organisms for their source of organic compounds (such as food) are called heterotrophic. Plants and some bacteria are autotrophic through the process of photosynthesis.

Photosynthesis
There are two basic sets of reactions in photosynthesis: light dependent and light independent. Like their name indicates, light dependent reactions require sunlight to take place. The light independent reactions may take place in daylight or in darkness.

The light dependent reactions have two subsets of reactions: Photosystem I and Photosystem II. The light independent reactions have one of three possible tracks: Calvin-Benson Cycle, C-4 pathway, or the Crassulacean Acid Metabolism pathway (CAM photosynthesis).

Light Dependent Reactions
Photosystem II
The light dependent reactions begin with Photosystem II (not Photosystem I). Photosystem II is actually a cluster of chlorophyll molecules. These molecules of chlorophyll trap sunlight in the 680 nanometer range of the visible spectrum. The cluster of molecules is sometimes referred to as the P680 site or receptor site. As these molecules trap sunlight, the energy is transferred to a special chlorophyll molecule called the acceptor molecule within the site. The massive input of energy from the other chlorophyll molecules causes two electrons to not only be bounced to a higher energy level, but to be totally bounced out of the orbit of the molecule. These two electrons are then trapped by another molecule within the Photosystem called Quinone.



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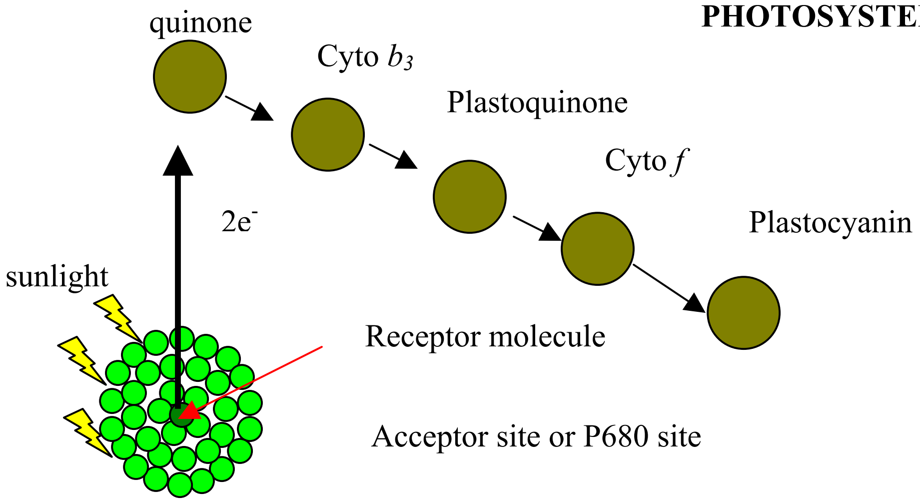
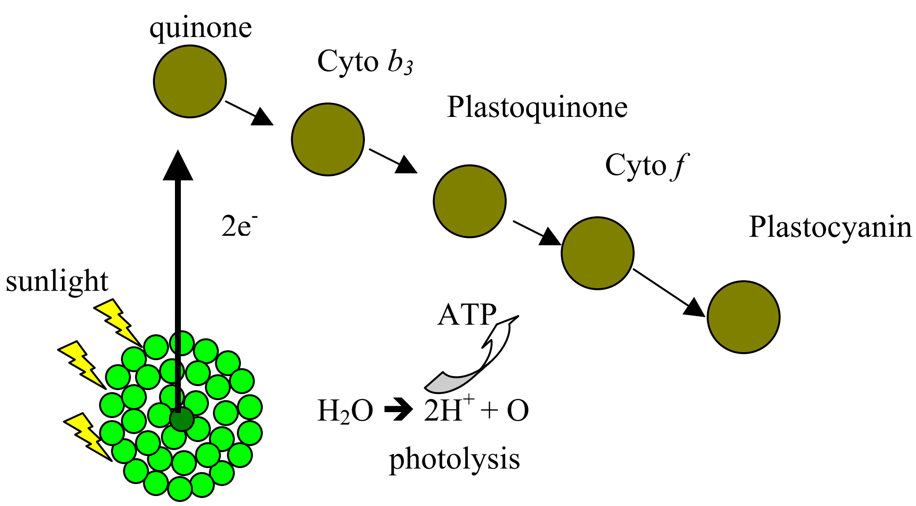
Quinone becomes reduced (gains two electrons) and the acceptor molecule becomes oxidized (loses two electrons). Remember oxidation-reduction reactions go hand in hand. As one material is oxidized, another must be reduced, in turn. Quinone passes these highly energized electrons to cytochrome b_3, one of the many cytochrome pigments associated with photosynthesis and respiration. Cytochrome b_3 becomes reduced and Quinone is oxidized. Cytochrome b_3 passes the electrons to Plastoquinone which becomes reduced as Cytochrome b_3 becomes oxidized. Plastoquinone passes the electrons to Cytochrome *f* which becomes reduced. Cytochrome *f* finally passes the electrons to Plastocyanin which becomes reduced.

PHOTOSYSTEM II

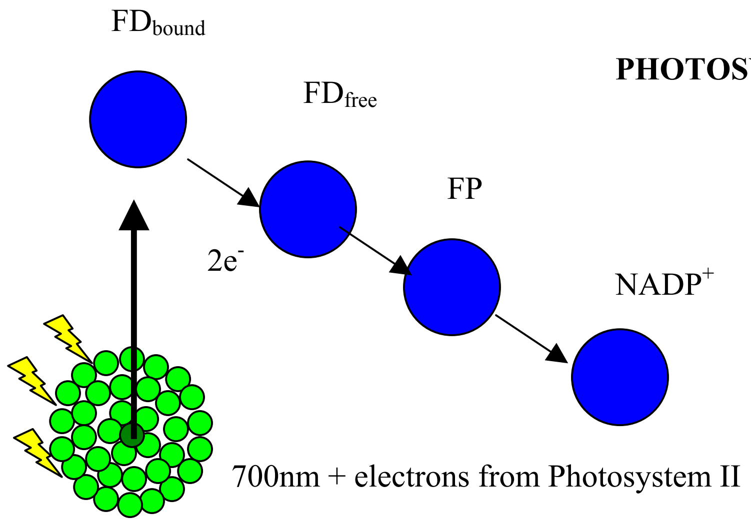


Photolysis
While these electrons are being passed from molecule to molecule, back at the aggregation site, water is split into hydrogen atoms and the oxide ion. This splitting of water with light is called photolysis. The hydrogen ions are used to eventually form ATP.



Photosystem I

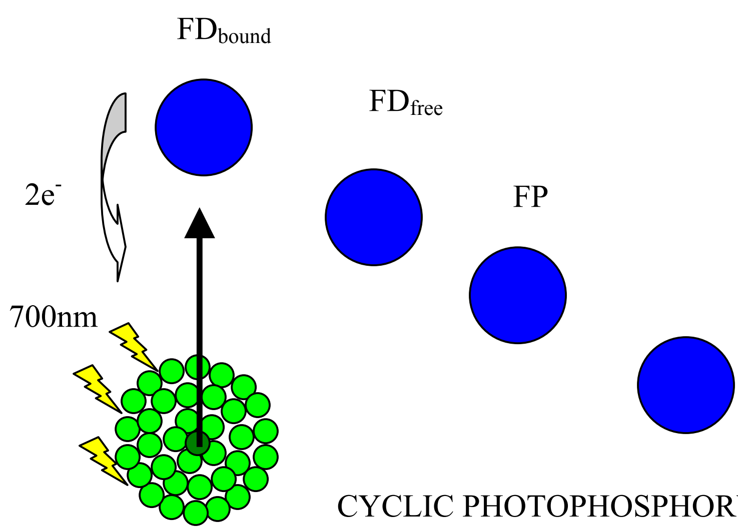
Photosystem I is another aggregation of chlorophyll molecules. These trap light in the 700 nanometer range. The acceptor molecule of the P700 site accepts the electrons from Plastocyanin of Photosystem II. Sunlight energizes the P700 site and that energy is channeled into the acceptor molecule. The two electrons (from Photosystem II) are then shot out of their orbit to a molecule of Ferrodoxin bound which becomes reduced. Ferrodoxin bound passes the electrons to Ferrodoxin free, (again one material is oxidized, another reduced) and Ferrodoxin free passes them to Flavoprotein. Flavoprotein passes the electrons to Nicotinamide Adenine Dinucleotide Phosphate (NADP) which is reduced.



PHOTOSYSTEM I

Path of Electrons

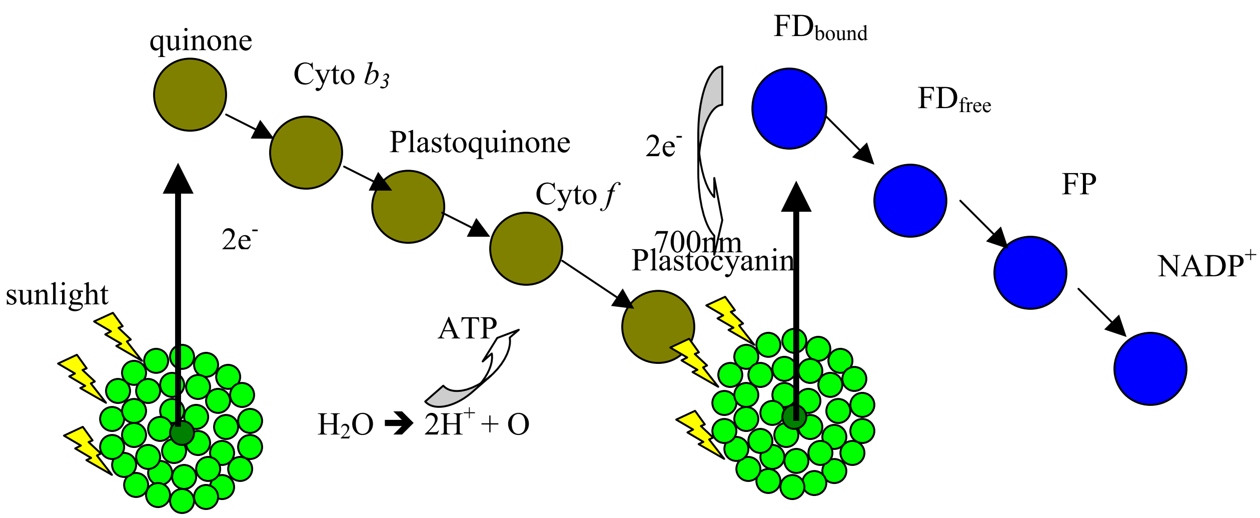
The electrons can, indeed, pass down the electron chain from Ferrodoxin bound to NADP. However, the electrons can just as easily lose their energy and fall back to the acceptor molecule. That energy that is lost may be converted to ATP. This process of elevating electrons and their falling back to their original position may occur over and over – thus a cycle.



CYCLIC PHOTOPHOSPHORYLATION

Cyclic Photophosphorylation

The process of forming ATP by the above process in Photosystem I is called cyclic photophosphorylation. "Photo" because it occurs in the presence of light. "Phosphorylation" because adding a phosphate group to a compound is called phosphorylation.



What's Been Done

In reality, only two things have been accomplished in Photosystems II and I. ATP has been produced (photolysis in Photosystem II and cyclic photophosphorylation in Photosystem I). Also, NADP has been reduced.

Refer to the summary equation of photosynthesis.

$$6CO_2 + 12\ H_2O \xrightarrow[\text{chlorophyll}]{\text{sunlight}} \underset{\text{glucose}}{C_6H_{12}O_6} + 6\ O_2 + 6\ H_2O$$

The only issues addressed in the above reaction by Photosystem II and Photosystem I are shown in red. Water was split during photolysis and oxygen generated in photolysis. No carbon dioxide was used and no glucose was made. This occurs during the light independent reactions of photosynthesis.

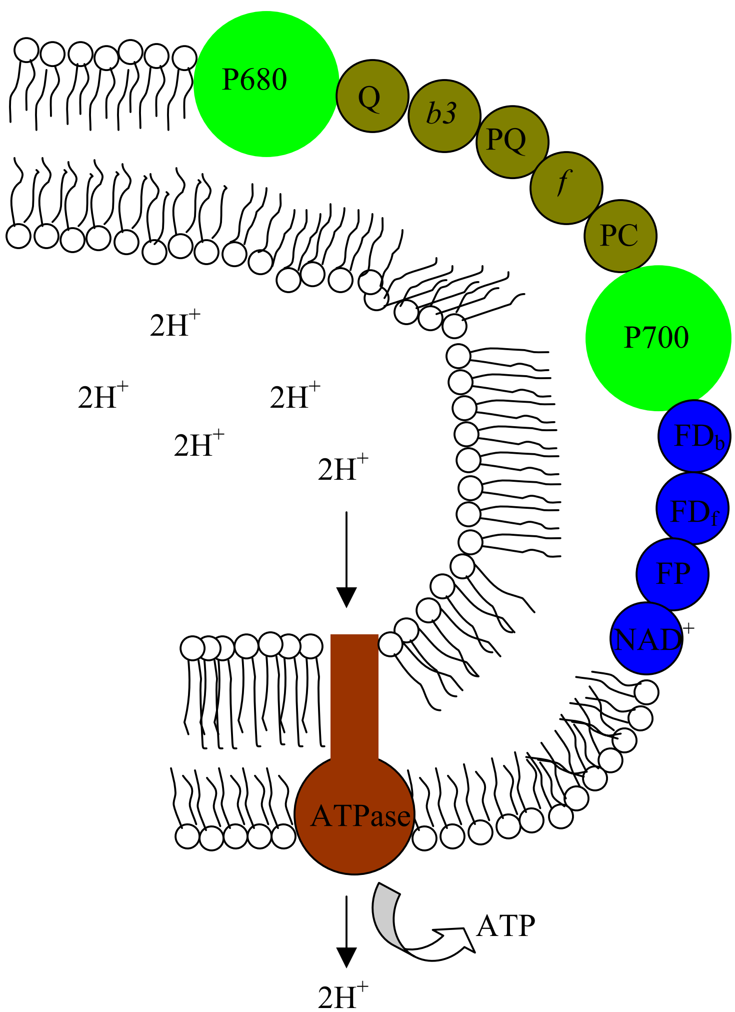
Why Cover Photosystem II First?

It was a little strange to cover Photosystem II first. The reason is Photosystem I was the first Photosystem to evolve. Primitive plants have only Photosystem I. Higher plants on the evolutionary scale evolved Photosystem II to boost the production in Photosystem I.

Hydrogen to ATP

How does the chloroplast make ATP from hydrogen ions? The process is called the chemiosmotic theory. Remember that chlorophyll is found in the thylakoids of the chloroplasts. The thylakoids, like most membranes in cells, are composed of a phospholipids bilayer, just like the cell membrane with proteins scattered in and about. The materials scattered in and about not only include proteins, but may also include Photosystem I and Photosystem II receptor sites with other pigments and molecules, as previously discussed.

A part of the thylakoids bilayer of lipids includes the P680 site of chlorophyll molecules. Next to that is the molecule Quinone, followed by cytochrome b_3, Plastoquinone, cytochrome *f*, and Plastocyanin. Next to this line of molecules is the P700 site of chlorophyll molecules followed by Ferrodoxin bound, ferrodoxin free, flavoprotein, and NADP. All of this is repeated over and over in the lipid bilayer of the thylakoids. In addition, there is another molecule (a protein called ATP synthetase) found as a channel between the lipid bilayer.



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In Photosystem II, as water is split to form hydrogen ions, the hydrogen ions build up in the lumen of the thylakoids. Soon there is a concentration gradient between hydrogen ions *inside* the thylakoids and the outside of the thylakoids. Osmosis occurs with the hydrogen ions passing through the molecule of ATP synthetase on their way to the outside of the thylakoids. This pumping mechanism, coupled with ATP synthetase, forms the ATP. Therefore, the pumping of hydrogen ions across a thylakoids membrane forms ATP and is the process is called the chemiosmotic theory.

Light Independent Reactions
To finish off the equation of photosynthesis – the production of glucose – we must study the light independent reactions. There are three possible paths for plants, depending upon the species of plants:

1. Calvin-Benson Cycle – temperate plants
2. C-4 Pathway – tropical plants
3. CAM Photosynthesis (Crassulacean Acid Metabolism) – desert plants

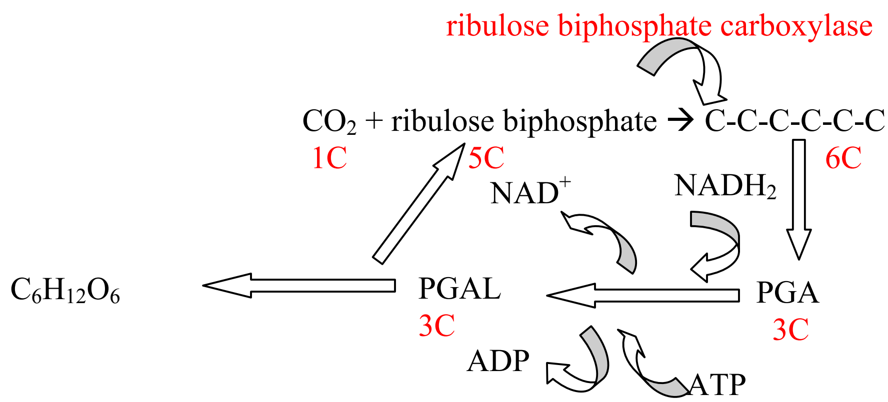
Calvin-Benson Cycle
The Calvin-Benson Cycle begins when carbon dioxide (a single carbon compound) combines with a five carbon compound called ribulose biphosphate carboyxlase (sometimes written as diphosphate). This results in the formation of a six carbon intermediate. An intermediate is simply a short-lived compound. This reaction is catalyzed by an enzyme called ribulose biphosphate carboyxlase. (Most enzymes end in "ase".)

Naming Enyzmes
Enzymes are often named for what they do. In the case with ribulose biphosphate carboyxlase, the enzyme takes ribulose biphosphate and adds carbon dioxide to it. Remember that adding a phosphate is called phosphorylation. Adding a carbon dioxide is called carboxylation, thus the name ribulose biphosphate carboyxl*ase*.

ribulose biphosphate carboxylase

CO_2 + ribulose biphosphate → C-C-C-C-C-C

The six carbon intermediate breaks apart to form phosphogylceric acid (PGA). PGA, a 3 carbon compound, combines with $NADP_{reduced}$ and ATP to form phosphoglyceraldehyde (PGAL) another 3 carbon compound. Some of the PGAL goes to form glucose (6 carbons) and some other goes to form additional ribulose biphosphate (5 carbons). The ribulose biphosphate combines with another carbon dioxide and the cycle starts again.



You Do the Math
At first, from the above description of events, it seems a 3 carbon compound (PGAL) is forming a 6 carbon compound (glucose) and a five carbon compound (ribulose biphosphate). Nice trick if you can do it. Of course, you cannot. However, remember the summary equation for photosynthesis called for 6 carbon dioxides. That would combine with 6 ribulose biphosphates (and 6 enzymes) to for 6 six carbon intermediates (36 carbons). That would split to form 12 PGA's and that forms 12 PGAL's (36 carbons). Six of those carbons form glucose and the other 30 form 6 ribulose biphosphates.

Calvin-Benson and C-4 Pathway
The Calvin-Benson cycle occurs in temperate plants. These are plants found in the temperate zones of the world. Most of the continental United States falls within a temperate zone where the winters are cold, but not too cold and the summers are hot, but not too hot – thus temperate. South Florida exhibits subtropical climate and Alaska exhibits some arctic climates. C-4 plants are found primarily in the tropics. The plants include palms, sugar cane (a grass), most grasses, bananas, and others. What's the difference? It mostly has to do with leaf anatomy.

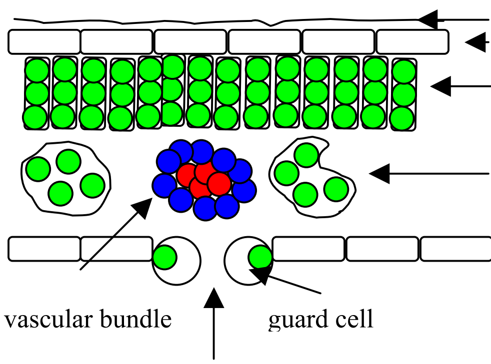
Corn Is A Tropical Plant
Strangely, corn is a tropical plant. At first, you think, corn is grown in Iowa and Iowa is anything but tropical. You're right on that account, but the ancestor to corn is a plant called *Teosinte*, found in Central America and Mexico, thus tropical.

Structure of A Leaf

A leaf is composed of three basic parts. The part most people recognize is called the blade or lamina. What attaches the leaf to the stem is called a petiole. At the base of the petiole may be a couple of leaf-like structures called stipules. If a leaf has all three parts, it is said to be complete. Some leaves are incomplete – they are missing one or more parts. For example, some leaves do not have stipules. Other leaves may not have petioles – the blade is attached directly to the stem as in grass. This condition is referred to as a sessile leaf. Still other leaves may not have blades. The cactus "spines" are actually the petiole and midvein of a leaf without the blade.

Leaf Anatomy of Calvin-Benson Leaf

Think of a leaf and cut that leaf in cross section. Look down into the leaf and imagine what you would see.



*See insert on the right on stomata and their mechanisms.

There is an upper and lower epidermis. The upper epidermis is often covered in a waxy cuticle. Just beneath the upper epidermis is a group of columnar cells called the palisade layer which is has abundant chloroplasts in the cell. Underneath the palisade layer is a middle layer (mesophyll) that also contains chloroplasts. The lower epidermis has a variation from the upper epidermis. There are openings on the undersurface called stomata. The stomata are formed by guard cells. The guard cells also contain chloroplasts, although epidermal cells do not. The vascular bundle is composed primarily of two types of tissue: xylem and phloem. Xylem (in red) is tissue that is specialized for the conduction of water (typically upward from the roots) and phloem (in blue) is specialized tissue for the conduction of food (typically downward from the leaves to the rest of the plant).

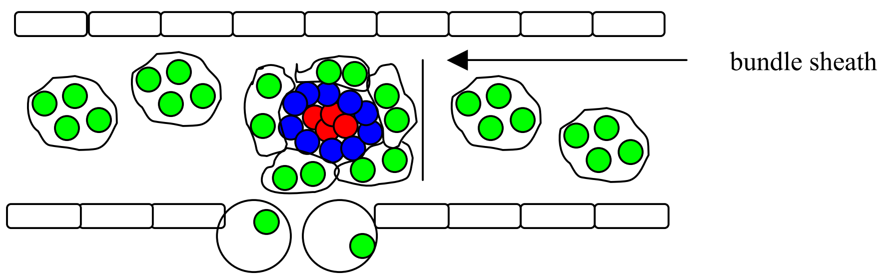
Stomata

The word "stoma" meaning opening. The plural is stomata. Higher plants typically have stomata on the lower surfaces of their leaves (although you may also find them on upper surfaces, unless it is an aquatic plant with floating leaves). These openings allow the passage of three gases in and out of the leaf: carbon dioxide, oxygen, and water vapor.

The openings are formed by cells called guard cells. Guard cells have a large, single chloroplast in each cell. Based on the condition of the environment around the guard cell, the guard cells either swell or shrink based on hypertonic or hypotonic environments.

The question is: do guard cells open or close in a hypertonic environment? The answer is they close. The guard cells open (and form the stoma) when they are exposed to hypotonic environments. Think of two long, slender balloons full of air. Place the balloons between two solid surfaces so they line up like two hotdogs (parallel) and their ends are blocked by something. Think of those balloons if you continue to add air. Since the ends are blocked, the balloons have to expand and the only way they can do it is to bow outward from the middle, thus creating a gap between the balloons. That's the same way stomata work.

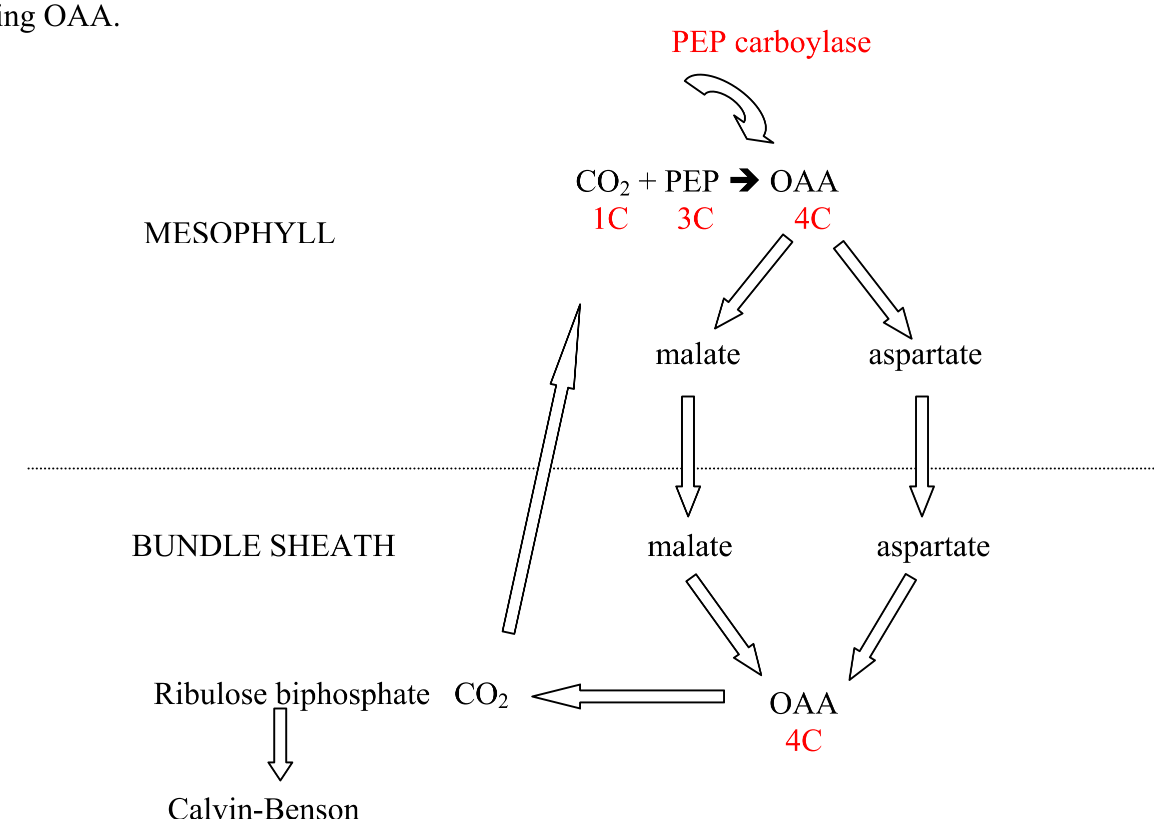
Leaf Anatomy of C-4 Leaf



There are two major differences between a Calvin-Benson leaf and a C-4 leaf. The first should be obvious in that there is no palisade layer in a C-4 leaf. In addition, the C-4 leaf has another set of cells surrounding the vascular bundle called the bundle sheath.

C-4 Pathway

In the C-4 pathway, carbon dioxide combines with a three carbon compound called phosphoenolpyruvate (PEP). This forms a 4-carbon compound called oxaloacetate (OAA). The reaction to form OAA from PEP and carbon dioxide is catalyzed by phosphoenolpyruvate carboyxlase (PEP carboyxlase). OAA breaks apart to form two compounds: malate and aspartate. These two compound diffuse from the mesophyll cells to the bundle sheath. In the bundle sheath, they recombine to form OAA. OAA, in the bundle sheath, then splits to form PEP and carbon dioxide. The carbon dioxide then feeds into the Calvin-Benson cycle in the bundle sheath to make glucose. The PEP diffuses from the bundle sheath back to the mesophyll to begin again the process of forming OAA.



At first, it seems mother nature has gone a little crazy. Why go through the C-4 pathway in the mesophyll if all you are going to do is go through Calvin-Benson in the bundle sheath? Mother nature doesn't do anything capriciously.

Oxygen Inhibition of Ribulose Biphosphate Carboxylase

Review the material on the Calvin-Benson. Ribulose biphosphate carboyxlase, the enzyme important in Calvin-Benson, is inhibited by high levels of oxygen. In the tropics, you find plenty of water, plenty of carbon dioxide, and plenty of sunlight for the light dependent part of photosynthesis – which makes oxygen. This oxygen would shut down the light independent reaction of Calvin Benson and the plant would starve as it produced oxygen. Instead, in the tropics, plants run the C-4 pathway in the mesophyll. PEP carboyxlase is not inhibited by high levels of oxygen, so it runs quite nicely in the tropics. The products of C-4 are then sent to the bundle sheath which has much less surface area than the rest of the leaf. Oxygen inhibition is not a problem there since oxygen, even though abundant, cannot get access to the ribulose biphosphate carboyxlase in the bundle sheath. In essence, the C-4 pathway is a means of getting around oxygen inhibition.

Crassulacean Acid Metabolism (CAM Photosynthesis)

CAM photosynthesis occurs in a group of plants collectively known as succulents. Succulents are plants with fleshy stems and/or leaves, such as cacti, *Aloe vera*, and stonecrops. These are plants of dry climates or deserts. Their chief problem is water loss by transpiration through the stomata on the leaves. As a consequence, desert plants do not open their stomata during the day – the time of greatest potential water loss. Instead, they open them only at night with threat of evaporation and transpiration is less and they then run a modified Calvin-Benson cycle to produce glucose.