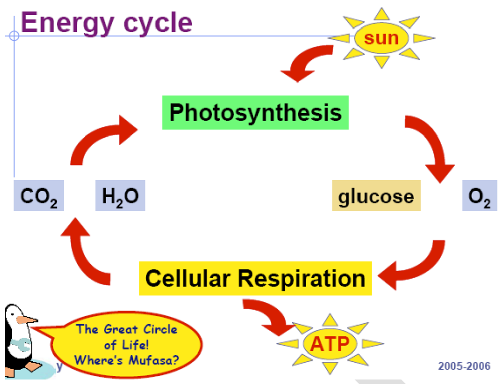
PHOTOSYNTHESIS

Photosynthesis is the most important chemical process on earth. It provides food for all organisms.

PLANTS AND PHOTOSYNTHESIS

The plants are important to life on earth. Throughout the day, plants absorb **light energy** from the sun and use this energy to produce **organic molecules**. While making these molecules, plants also give off the **oxygen** that allows much of earth's life to flourish. The process by which plants do this is known as **photosynthesis**.

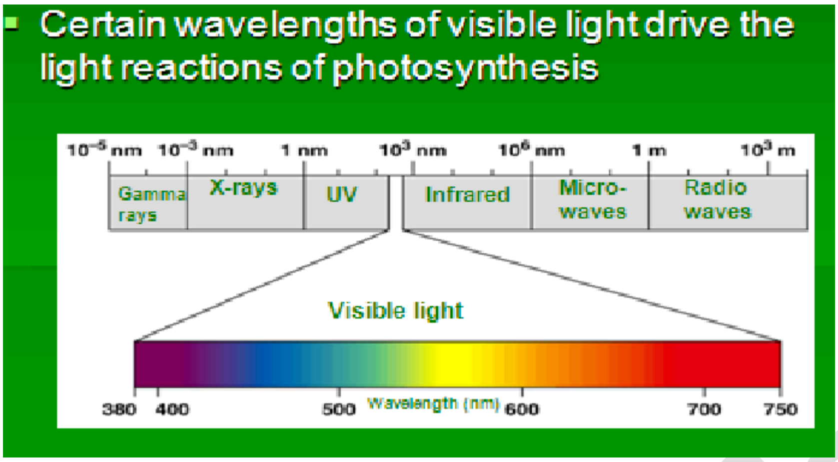
Plants require **three** things to carry out photosynthesis: **light**, which is often provided by the sun, **water** (H_2O) and **carbon dioxide** (CO_2).



In photosynthesis, plants absorb energy from the sun. This energy is in the form of light. Through a series of **chemical reactions**, this light energy is converted into **chemical energy**. This chemical bond energy is most frequently **stored** in the sugar molecule known as **glucose**. Glucose is in turn used later as an energy source for the plant to grow and reproduce. Water and carbon dioxide are required at various stages in photosynthesis. These two compounds provide **electrons, hydrogen ions, and carbon atoms** that the plants need to make glucose.

CHARACTERISTICS OF LIGHT

Light exists as a **wave**. Light waves have peaks and troughs. The distance from one peak to the next is known as the **wavelength**. The total wavelengths that are possible for light (from the shortest to the longest) are known as the **spectrum**.



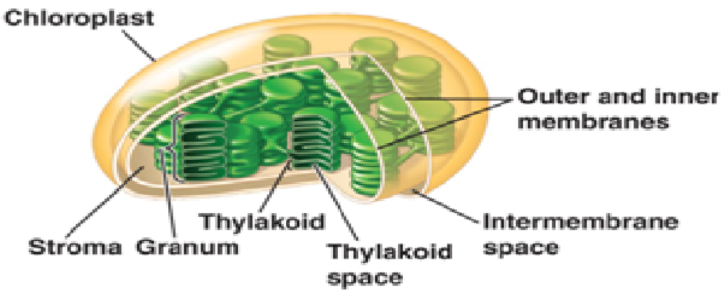
There are many different wavelengths of light that the eye can detect. Together, these wavelengths make up the visible light spectrum. Different wavelengths correspond to **different colors** in the spectrum. For instance **violet** has a very **short** wavelength. This is the smallest wavelength that can be detected by the human eye. **Red**, on the other hand, has a very **long** wavelength. This is the longest wavelength detectable by the human eye. All other colors the human eye can detect have wavelengths that lie between **violet and red**. Sunlight, which appears to be white until passed through a prism, is a **blend** of all wavelengths of light. Not all light is visible to our eyes. **X-rays** are light waves with wavelengths too **short** for the human eye to detect and **radio** waves, although converted to sound waves in stereo equipment, are light waves with wavelengths too **long** for the human eye to detect.

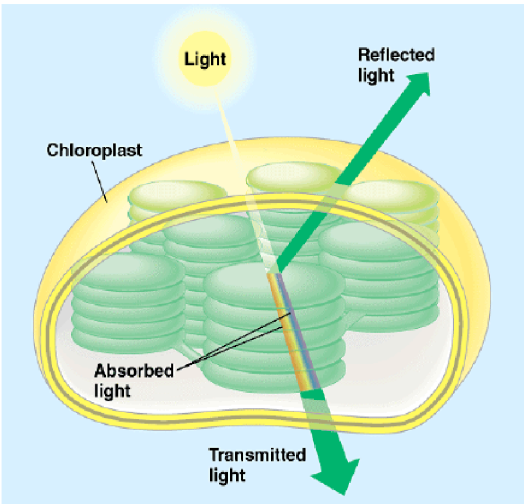
Although light can exist and travel as a wave, it can also exist as a **particle**. These particles of light energy are known as **photons.**

CHLOROPLASTS AND PIGMENTS

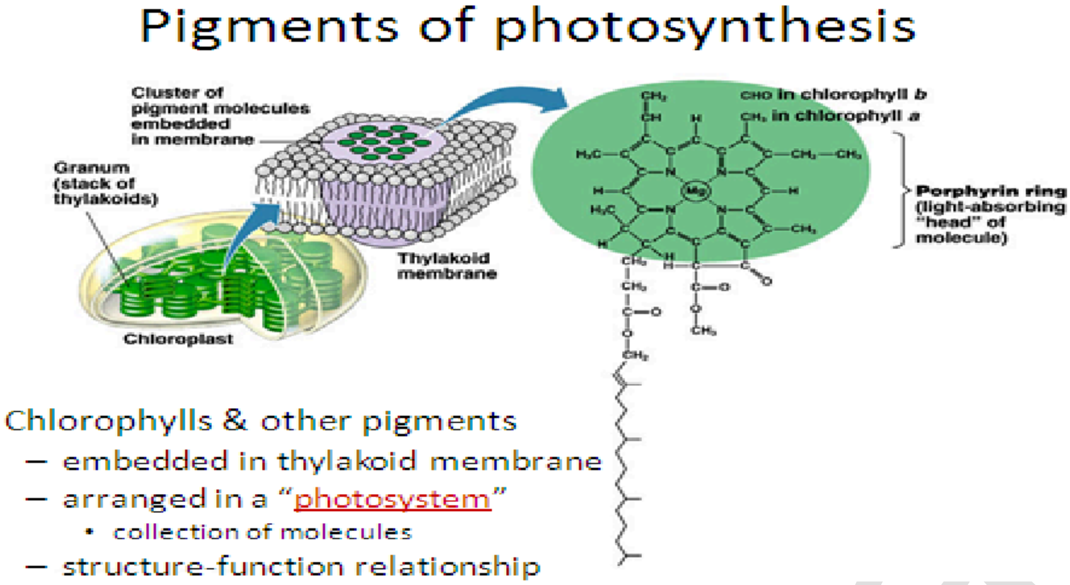
To **absorb** light, plants use highly specialized structures or organelles known as **chloroplasts**. These organelles are dispersed throughout much of the plant surface and are the organelles in which photosynthesis takes place.

A **double membrane** surrounds chloroplasts. Inside of chloroplasts are disc-like structures called **thylakoids**. These thylakoids are stacked one on top of the other. A stack of thylakoids is called a granum and several stacks of thylakoids are called granna. Within the chloroplast and surrounding the granna is a thick solution called the **stroma.**

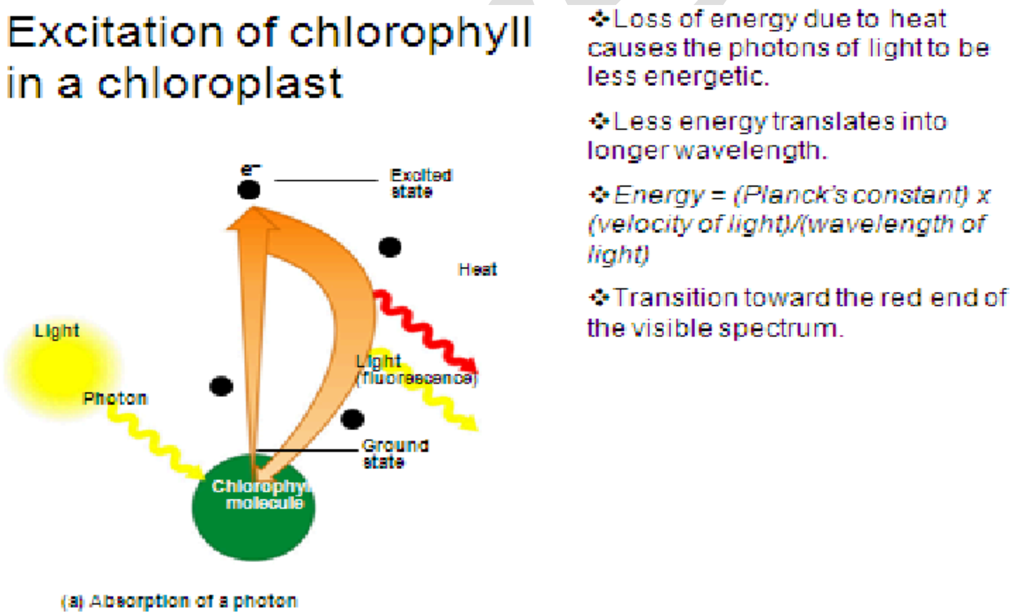


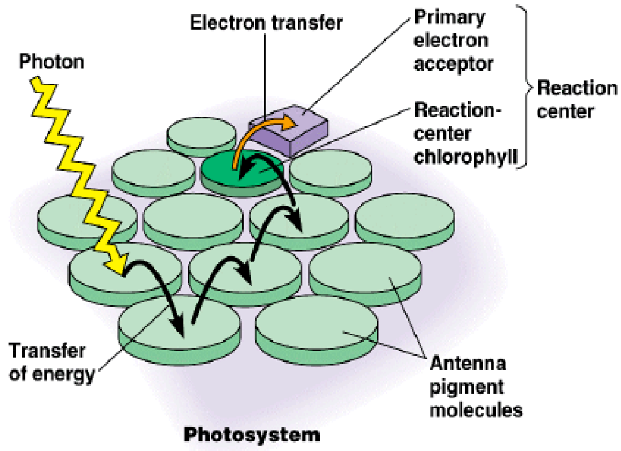


Lying within the thylakoid membrane are **pigments**. Pigments are molecules that absorb specific wavelengths of light. Wavelengths that pigments are not able to absorb are reflected instead. **Chlorophyll *a*** is a pigment commonly found in plants. It can absorb violet, blue, and red wavelengths of light, but cannot absorb green wavelengths. What happens to the wavelengths of green light? They are reflected. This reflected green light is picked up by your eye when you look at, for example, grass. This is why grass looks green in color.



Other pigments that are common in leaves are **chlorophyll *b***, which absorbs light at wavelengths similar to chlorophyll *a*, and **carotenoids**. Although chlorophyll *b* and the carotenoids are able to absorb light, they must work in conjunction with chlorophyll *a*. For the plant to use any light absorbed by these two pigments, the light energy must first be passed along to chlorophyll *a*. For this reason, chlorophyll *a* is considered to be the **main** photosynthetic pigment.





Once the chlorophyll *a* molecules absorb photons, the molecules became **excited**. In this excited state, chlorophyll *a* molecules are able to release **electrons**. These electrons are passed along the chlorophyll *a* molecules within the antenna assembly until they reach a special chlorophyll molecule known as the **reaction center**. As electrons bombard the reaction center, it in turn passes electrons to an **acceptor molecule**. The name biologists have given to an antenna assembly, reaction center, and acceptor molecule is a **Photosystem.**

There are **two** Photosystems involved in photosynthesis. These have been named **Photosystem I and Photosystem II**. Both of these thylakoid-bound photosystems work in conjunction during the first series of reactions in photosynthesis. This series of reactions is known as the **light reactions**.

THE LIGHT REACTIONS

The **overall** chemical reaction involved is:

$$\mathbf{6CO_2 + 6H_2O + energy \longrightarrow 1\ C_6H_{12}O_6 + 6O_2}$$

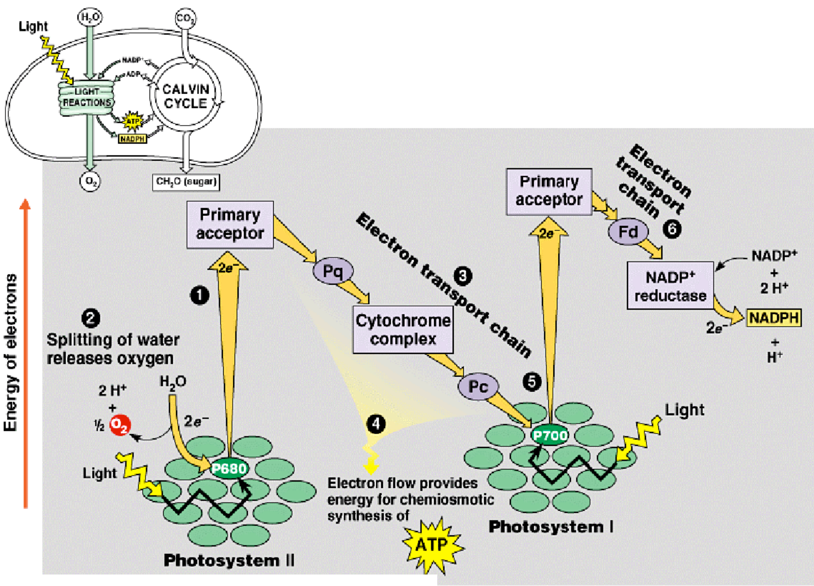
During photosynthesis, plants combine 6 molecules of carbon dioxide, 6 molecules of water, and energy from the sun to produce one molecule of glucose ($C_6H_{12}O_6$) and 6 molecules of oxygen. This occurs in a series of reactions taking place in different locations within the chloroplast.

The first stage of photosynthesis is a series of reactions, known as **the light reactions**, that takes its name from the fact that **light is required**. The **products** of the light reactions are **ATP, NADPH, and oxygen**. ATP and NADPH are special **energy-storing molecules.** The energy stored in these molecules is later used to make glucose, which is the molecule plants use for long-term energy storage.

The first step in the light reactions is the absorption of a **photon** by Photosystem II. When a pigment in this photosystem is struck by light of the correct wavelength, it absorbs the photon and becomes excited. In this excited state, the pigment gives up an electron that moves along a series of **chlorophyll *a*** molecules until reaching the reaction center. The reaction center in turn becomes excited and releases its own electrons to the acceptor molecule. Once reaching the acceptor molecule, the electrons leave Photosystem II. Where do these electrons go?

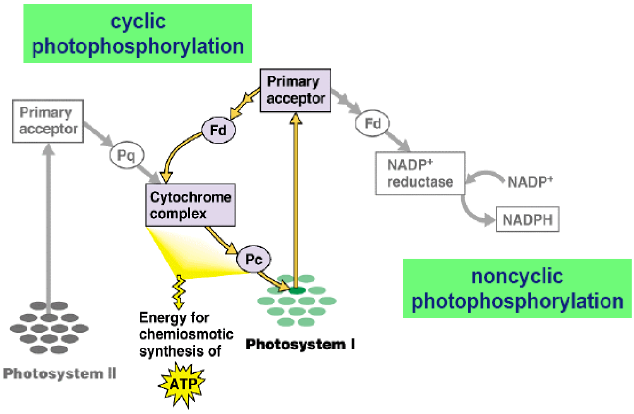
Photosystem II needs to replace all of the electrons leaving, or it would very quickly run out of electrons. This is where **water** enters the picture. For each pair of electrons Photosystem II loses, a water molecule is **split**. In the process, **two electrons** are stripped from water and move to the reaction center. These electrons from water replace the pair of electrons the photosystem lost. After water is split into hydrogen and oxygen, two oxygen atoms combine to form $\mathbf{O_2}$ (it is in this form that oxygen is used by animals). The oxygen is then released into the atmosphere. The plant uses the hydrogen ions in a later stage of photosynthesis.

From the acceptor molecule, electrons enter an **electron transport chain**. This electron transport chain, or **ETC** for short, is located on the **thylakoid membrane** and **connects** Photosystem II to Photosystem I. As the electrons slide along the ETC from Photosystem II **to** Photosystem I, they **lose** energy. The energy given up by the electrons is stored in **ATP** molecules.



Photosystem I and Cyclic versus Non-Cyclic Electron Flow

Photosystem I, like Photosystem II, is able to absorb light. When sunlight is available, excited electrons are constantly passed from *chlorophyll a* molecules, to the reaction center, and ultimately to the acceptor molecule for Photosystem I. The electrons leaving Photosystem I are replenished by the steady stream of electrons coming into the system from Photosystem II. From the acceptor molecule, electrons leaving Photosystem I can follow one of two paths. These paths are known as cyclic electron flow and non-cyclic electron flow.



In cyclic electron flow, electrons begin at the acceptor molecule and are passed to an electron transport chain. This ETC, like the one connecting the two photosystems, is a series of receptor molecules able to pass along electrons. Unlike the ETC you learned of earlier however, the one involved in cyclic electron flow leads directly back to Photosystem I. These electrons begin at the acceptor molecule for Photosystem I and wind up **back** at Photosystem I again. As the electrons slide along this chain of receptor molecules in cyclic electron flow, they lose energy. This energy is in turn stored in ATP molecules. Energy from the electrons involved in cyclic electron flow is used to produce ATP.

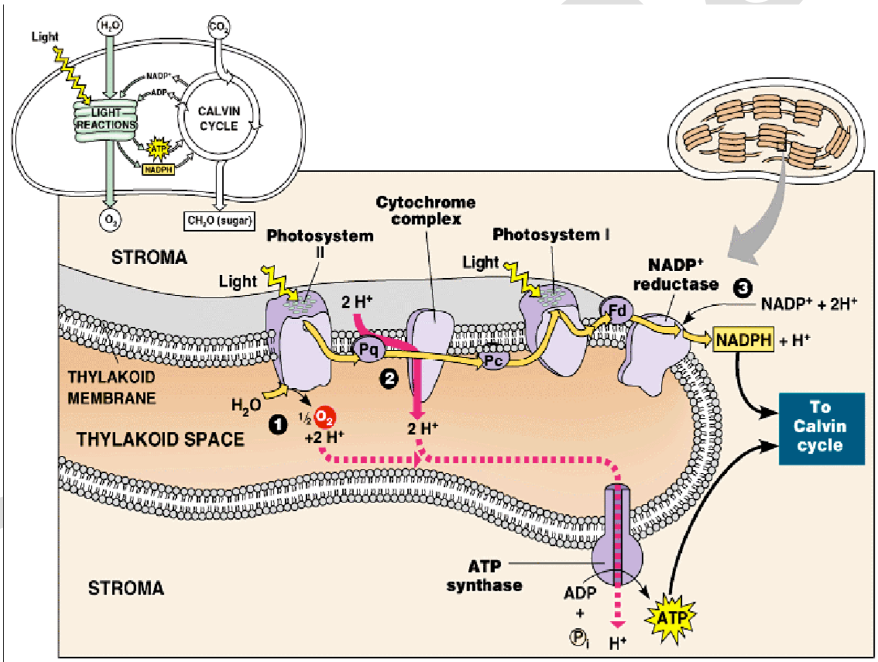
In non-cyclic electron flow, electrons begin at the acceptor molecule and are once again passed to an electron transport chain. This series of receptor molecules, however, leads directly to an **enzyme** known as **$NADP^+$ reductase**. Once at this enzyme, the electrons are passed to a molecule of $NADP^+$, (nicotinamide adenine dinucleotide phosphate). This $NADP^+$ molecule then quickly picks up a hydrogen ion (a proton, or H^+) and becomes **NADPH**. NADPH is able to **store** electrons at a high state of energy for later use. Electrons involved in non-cyclic electron flow are used in the generation of NADPH.

In conclusion, one may **summaries light reactions** as follow: Light strikes and is absorbed by Photosystem II. This excites electrons which are passed to the reaction center and then to the acceptor molecule. Water is split to replace these electrons lost by Photosystem II and oxygen is given off. The electrons pass along an ETC to Photosystem I. As they move along this ETC, ATP is produced. Photosystem I can also absorb light, and send excited electrons to its acceptor molecule. Electrons leaving Photosystem I are replaced by the electrons arriving from Photosystem II. Electrons exiting Photosystem I can travel along two distinct paths. Cyclic electron flow returns electrons back to Photosystem I and results in the production of ATP. Non-cyclic electron flow delivers electrons to the enzyme $NADP^+$ reductase that in turn delivers them to NADPH molecules. NADPH stores high-energy electrons for later use. The big picture then: electrons flow in a constant stream from water molecules to NADPH molecules, generating ATP as they go.

ATP GENERATION AND PROTON GRADIENT

ATP (a high energy molecule) is produced at **two points** during the light reactions: while electrons are moving along the **ETC** connecting Photosystem II to Photosystem I, and during **cyclic** electron flow.

While electrons are moving along these two paths, some of their energy is used to move hydrogen ions across the thylakoid membrane. These hydrogen ions (protons) are pumped from the stroma into the thylakoid compartment. This results in a **proton gradient**, with more protons on the inside of the thylakoid compartment than on the outside. Protons want to move back into the stroma, but can only pass through the thylakoid membrane in specific locations. The protons must pass through a very specialized enzyme known as **ATP synthase**.



ATP synthase is a tunnel shaped enzyme that spans the thylakoid membrane. In a very orderly manner, protons exit the thylakoid compartment through the passage provided by this enzyme. ATP synthase **converts** ADP (a low energy molecule) into ATP (a molecule containing one very high energy bond). On the stroma side of the membrane, this enzyme adds an **inorganic phosphate** group to ADP molecules. With the addition of this phosphate group, ADP becomes ATP. The energy needed to accomplish this is provided by the passage of protons through ATP synthase. It is **important** to note one thing: electrons sliding along the ETC are **not** transferred to ATP. Electrons are only transferred to **NADP$^+$** molecules. Electrons moving along the ETC and involved in cyclic electron flow provide the energy to **pump** protons across the thylakoid membrane.

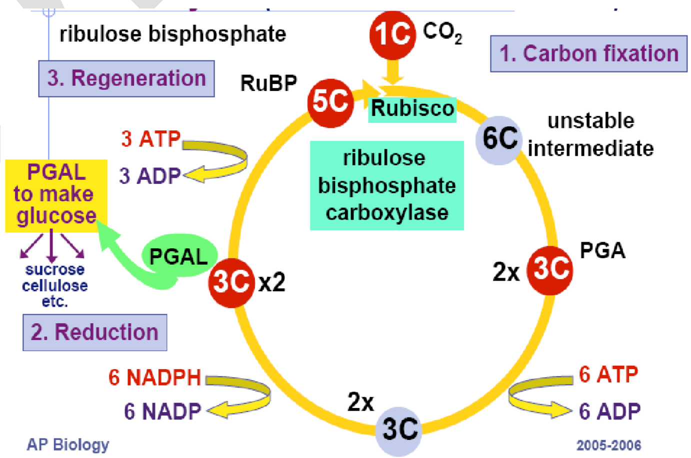
In summary, **electrons** passing from Photosystem II to Photosystem I, and electrons involved in cyclic electron flow, provide **energy** to pump protons from the stroma into the thylakoid compartment. This establishes a **proton gradient**, with a higher concentration of protons inside of the thylakoid than is found outside of the thylakoid. These protons want to move back into the stroma, but to do so must pass through the enzyme ATP synthase. As they pass through this enzyme, their energy is used to add an inorganic phosphate group to an ADP molecule. With the addition of the phosphate group, ADP becomes ATP. The **bond** linking this extra phosphate group is **very high in energy**, and this energy is used at later stages in photosynthesis.

THE DARK REACTIONS

Now that you know how light energy is used to generate ATP and NADPH, and how water is split to provide electrons and produce oxygen, it is time to look at the second stage of photosynthesis. This stage of photosynthesis is named the chemical not **dark reactions** because **no light** is required for them to proceed.

During the chemical reactions, energy rich ATP and NADPH molecules produced earlier are used to help convert carbon dioxide **(CO_2)** into organic molecules needed by the plant, such as **glucose**. This involves a very complex **series of reactions** known as the **Calvin cycle**.

Glucose is a sugar molecule containing 6 carbon atoms. CO_2, the compound used to form glucose, contains only one carbon atom. Therefore, **six** molecules of carbon dioxide must come into the Calvin cycle to make a **single** glucose molecule. For this reason, we'll follow the path of 6 CO_2 molecules at once.

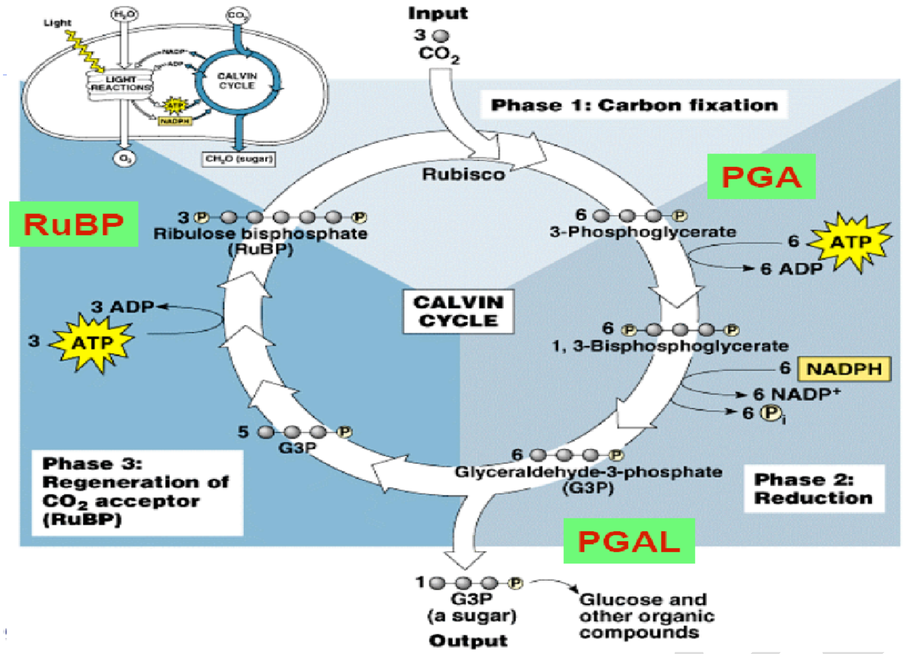


Carbon dioxide from the atmosphere enters plant cells and then diffuses into the **stroma** of chloroplasts. There, it is brought into the Calvin cycle. The first step in this cycle is the **combination** of **6** CO_2 molecules with **6** molecules of a compound known as **ribulose bisphosphate**, (or **RuBP**). These new formed compounds are **unstable**, and quickly break in half, forming **12** molecules of a stable, **3** carbon-containing compounds.

These 12 molecules now undergo a series of reactions fueled by the ATP and NADPH produced earlier. At the end of these reactions, **12** molecules of a compound known as **phosphoglyceraldehyde** (or **PGAL**) are formed. PGAL is a very important compound in the Calvin cycle. This is the compound used to make glucose. Two molecules of PGAL are combined to make one molecule of glucose (which contains **6** carbon atoms). Glucose contains six carbone atomes. Do you remember how many CO_2 molecules entered the cycle at the start? Six CO_2 molecules entered the Calvin Cycle. These 6 CO_2 molecules contributed a total of six carbon atoms to the Calvin Cycle. The 6 carbon dioxide molecules that entered the cycle provided the carbon atoms that eventually become glucose.

The plant has now converted 6 molecules of CO_2 into one molecule of glucose. The plant used two molecules of PGAL in doing so, and we are still left with 10 additional molecules of PGAL.

The plant has just made one molecule of glucose without using a single carbon atom of its own (remember, these carbon atoms come from CO_2, which is readily available in the atmosphere). The plant therefore has exactly the same number of carbon atoms it had to begin with, but these are in the form of PGAL and the cycle started out with the compound RuBP. Using the ATP and NADPH made earlier, the plant converts these **10** molecules of **PGAL** into **6** molecules of **RuBP**. These 6 RuBP molecules are then able to react with 6 molecules of CO_2 and start the cycle once more. In this way, plants are able to continuously recycle and combine their own carbon-containing molecules with CO_2 to make glucose. **Rubisco** Enzyme which fixes carbon from atmosphere (ribulose bisphosphate carboxylase) is the most important and abundant enzyme in the world.



Plants that exhibit the type of photosynthetic carbon reduction that we described above are termed **C_3** plants. In other words, the first product of carbon dioxide fixation is a 3-carbon compound (PGA).

C_3, C_4, AND CAM PLANTS

One of the functions of stomata is gas exchange which includes: CO_2 in for Calvin cycle and O_2 out from light reactions. The other function is controlling water loss from leaves on hot or dry days, therefore stomata close to conserve water by the act of guard cells. (When cells gain H_2O = stomata open, lose H_2O = stomata close).

Adaptation to live on land, requires closed stomata which lead to (O_2 builds up (from light reactions) and CO_2 is depleted (in Calvin cycle). The above situation causes problems in Calvin Cycle (Inefficiency of Rubisco: CO_2 vs. O_2).

Rubisco in Calvin cycle is the carbon fixation enzyme (photosynthesis) normally bonds C to RuBP, reduction of RuBP and sugars are building. On The other hand, when O_2 concentration is high (photorespiration) Rubisco bonds O to RuBP(O_2 is alternative substrate), oxidation of RuBP and breakdown sugars.

Impact of Photorespiration

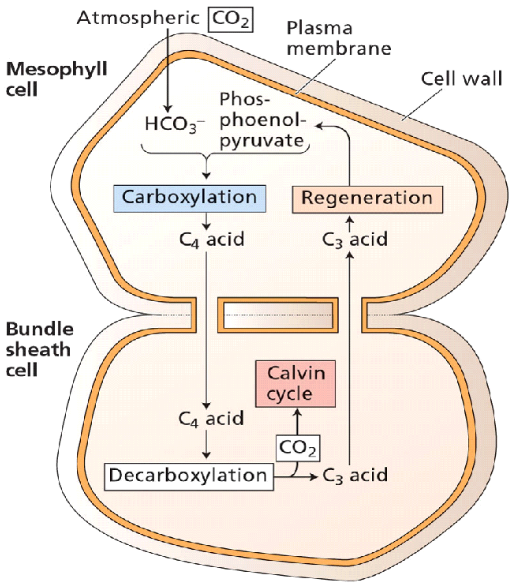
Oxidation of RuBP causes short circuit of Calvin cycle, loss of carbons to CO_2 (can lose 50% of carbons fixed by Calvin cycle), decreases photosynthetic output by siphoning off carbons (no ATP (energy) produced and no $C_6H_{12}O_6$ (food) produced). If photorespiration could be reduced; plant would become 50% more efficient. This can be achieved by separate carbon fixation from Calvin cycle.

◆ C_4 plants physically separate carbon fixation from Calvin cycle. C_4 plants have different leaf structure. They are adapted to hot, dry climates and have to close stomata a lot. Sugar cane, corn, and other grasses are examples. PEP carboxylase enzyme has higher affinity for CO_2 than O_2 (better than Rubisco), fixes CO_2 in 4C compounds, and regenerates CO_2 in inner cells for Rubisco.

phosphoenolpyruvate (3C) + CO_2 → oxaloacetate (4C)

On other words, light reactions, carbon fixation and Calvin cycle are separated reactions in different cells. Outer cells are responsible for light reaction & carbon fixation; pump CO_2 to inner cells (keeps O_2 away from Rubisco). Inner cells are responsible for Calvin cycle and delivering glucose to veins.

Basic C4 photosynthetic carbon cycle



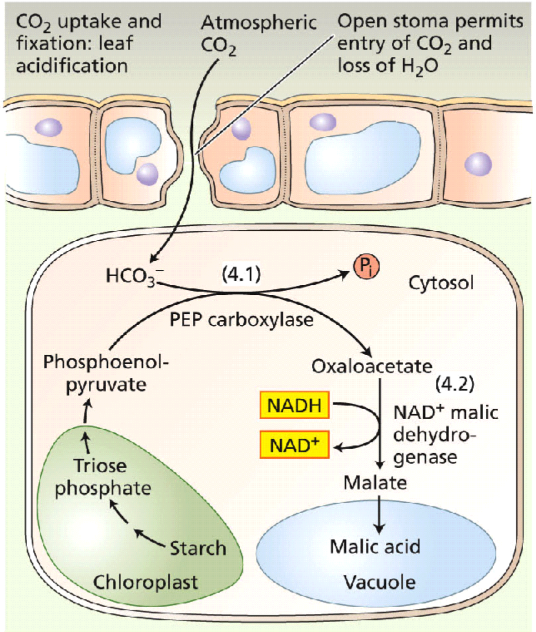
4 Stages

1) Carboxylation: formation of C4 acid in mesophyll cell
2) Transport of C4 acid into bundle sheath cell
3) Decarboxylation of C4 acid → generation of high [CO_2]; Fixation of released CO_2 in Calvin cycle
4) Transport of C3 acid and regeneration of PEP acceptor

Spring 08

◆ CAM plants (Crassulacean Acid Metabolism) separate carbon fixation from Calvin cycle by time of day (different adaptation to hot, dry climates). Succulents, some cacti, pineapple are examples. They close stomata during day and open stomata during night. It is considered a better way to capture CO_2. At night fix carbon in “storage” compounds such as organic acids: malic acid, isocitric acid .In day, close stomata and release CO_2 from “storage” compounds to Calvin cycle. They increase concentration of CO_2 in cells.

DARK: Stomata opened



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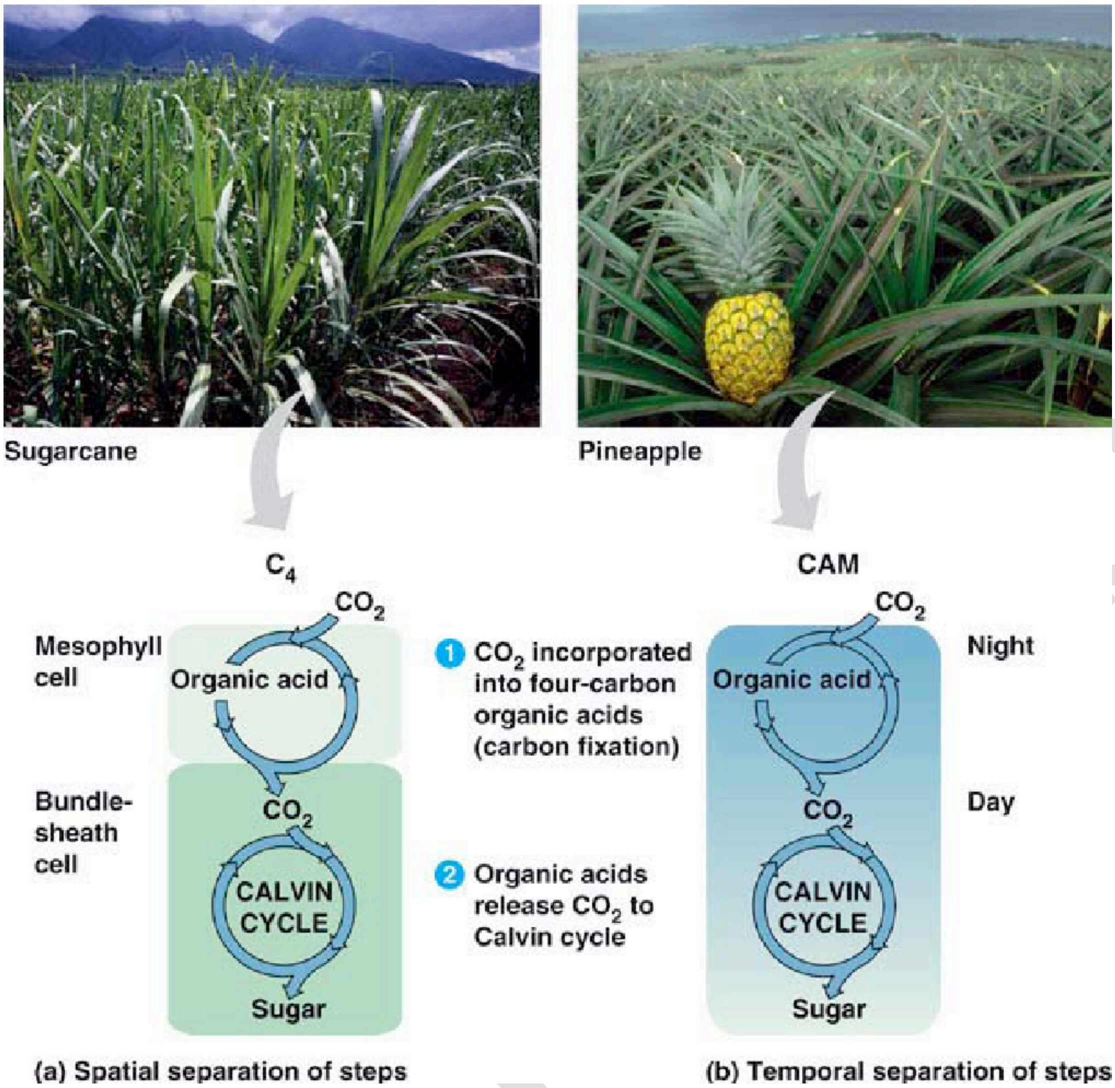

Comparison of C3, C4 and CAM Photosynthesis

Feature	C3	C4	CAM
Leaf anatomy	no distinct bundle sheath	Kranz anatomy	Usually no palisade cells, large vacuoles
Initial carboxylating enzyme	rubisco	PEPcase	PEPcase
Product of CO_2 fixation	PGA (C3)	OAA (C4)	OAA (C4)
Chloroplasts	one type	dimorphic	one type

Theoretical energy requirements (CO_2: ATP: NADPH)	1: 3: 2	1: 5 : 2	1: 3: 2
Transpiration ratio (g H_2O/g dry wt)	450-950	250-350	18-125
Photosynthesis rate (mg CO_2 fixed dm^{-2} h^{-1})	15 - 30	40 - 80	(low)
chl a/b ratio	2.8	3.9	2.5 - 3.0
Requirement for sodium as a micronutrient?	No	Yes	No
Carbon dioxide compensation point (ppm)	50 - 150 (Hi)	0-10 (low)	0-5 (in dark)
Response to light	Light saturation easily achieved	No light saturation	-
Temperature optimum for photosynthesis	15-25	30-47	35

Factors Affecting Rate of Photosynthesis

1. Temperature: increases rate up to a certain point
2. Light Intensity: increases rate up to a certain point
3. CO2 level: Increases rate up to a certain point
4. Water: decrease water, decrease photosynthesis
5. Minerals; Ex. Magnesium, Nitrogen