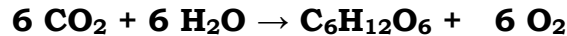


## 1 PHOTOSYNTHESIS

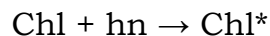
Life on earth ultimately depends on energy derived from the sun. Photosynthesis is the only process of biological importance that can harvest this energy. The term photosynthesis means literally “**synthesis using light**.” photosynthetic organisms use solar energy to synthesize carbon compounds that cannot be formed without the input of energy. More specifically, light energy drives the synthesis of carbohydrates from carbon dioxide and water with the generation of oxygen:



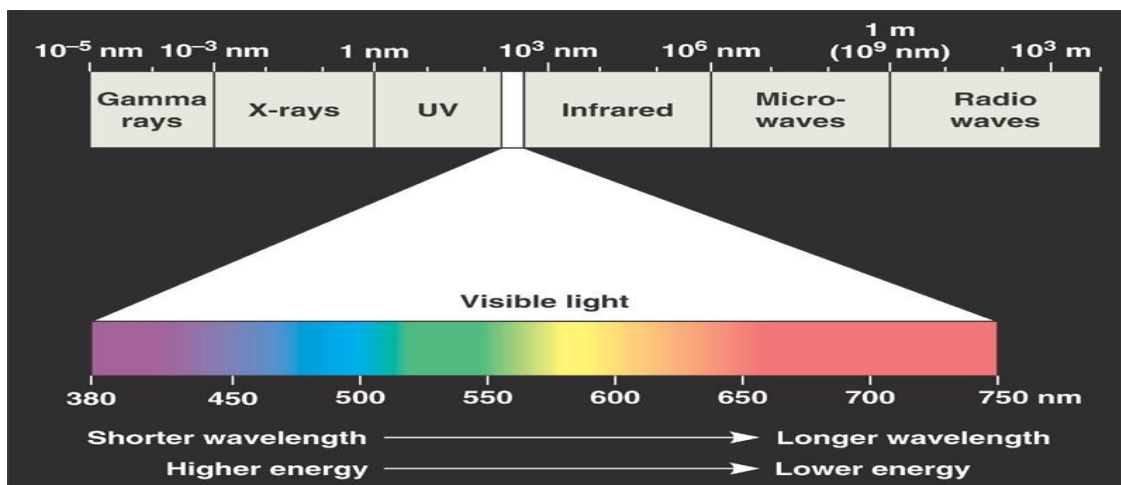
### 1.1 When Molecules Absorb or Emit Light, They Change Their Electronic State

Chlorophyll appears **green** to our eyes because it **absorbs light mainly in the red and blue parts** of the spectrum, so only some of the light enriched in **green** wavelengths (**about 550 nm**) is reflected into our eyes. In autumn, green leaves of certain plants change colors; **brilliant reds, yellows**, oranges, and browns. The pigments that reflect those colors were in the leaf all along. They were masked by the dominant chlorophyll A. In the **fall** the plants **stop making chlorophyll A** and that allows the accessory pigments to appear.

The absorption of light is represented by the following Equation, in which chlorophyll (Chl) in its lowest-energy, or ground, state absorbs a **photon** (represented by **hn**) and makes a transition to a higher-energy, or excited, state:

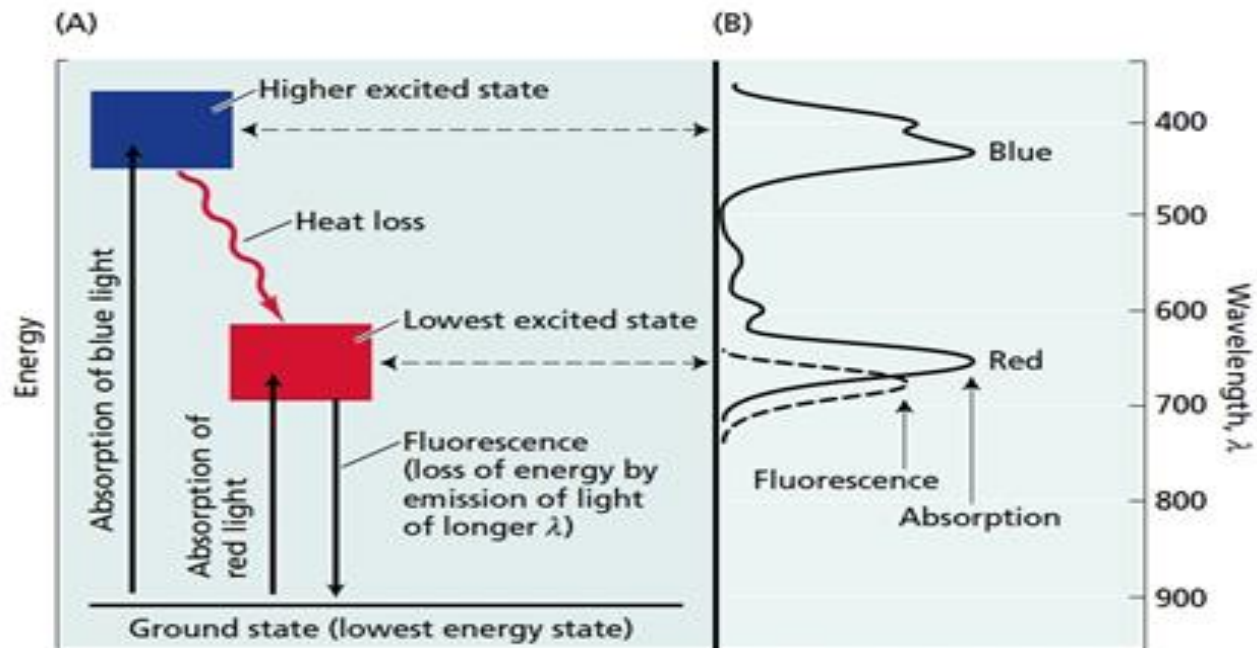


The distribution of electrons in the excited molecule is somewhat different from the distribution in the ground state molecule. Absorption of **blue** light excites the chlorophyll to a **higher** energy state than absorption of **red** light because the energy of photons is **higher** when their wavelength is shorter.



In the higher **excited state**, chlorophyll is extremely **unstable**, very rapidly gives up some of its energy to the surroundings as heat, and enters the lowest excited state, where it can be stable for a maximum of several nanoseconds (**10<sup>-9</sup> s**). In the lowest excited state, the excited chlorophyll has **four alternative** pathways for **disposing** of its available energy.

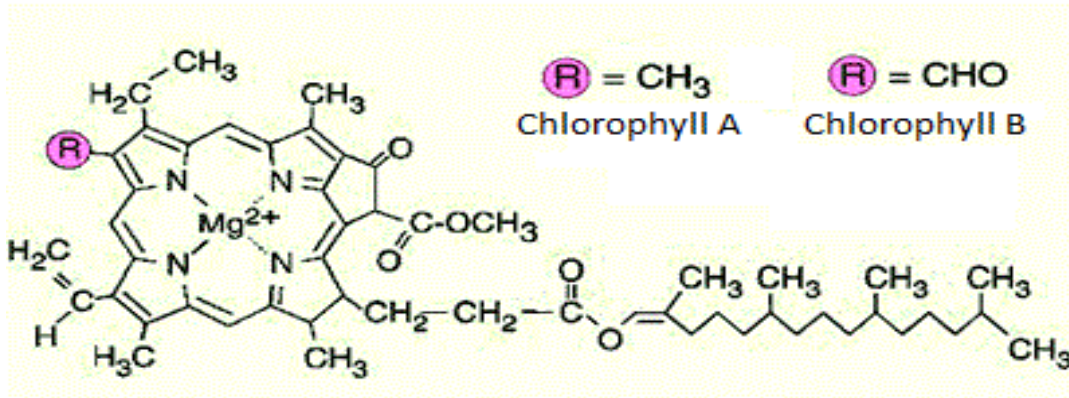
1. Excited chlorophyll can **re-emit a photon** as **light** but at a longer wavelength and thereby return to its ground state, a process known as **fluorescence**.
2. The excited chlorophyll can **return** to its ground state by directly converting its excitation energy into **heat**, with **no emission** of a photon.
3. **Chlorophyll** may participate in **energy transfer**, during which excited chlorophyll transfers its energy to another molecule.
4. A fourth process is **photochemistry**, in which the **energy of the excited** state causes **chemical reactions** to occur.



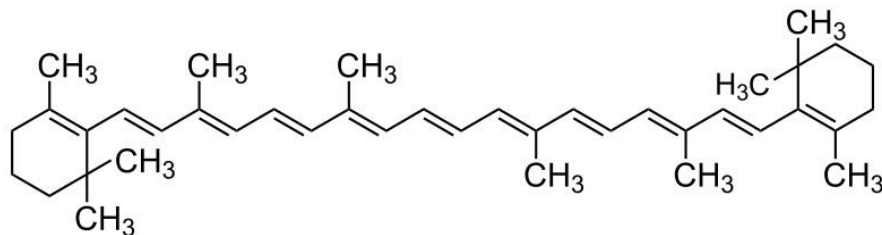
## 1.2 Photosynthetic Pigments Absorb the Light that Powers Photosynthesis

The energy of sunlight is first absorbed by the pigments of the plant. All pigments active in photosynthesis are found in the chloroplast.

**Chlorophylls a and b** are **abundant in green plants**, and **c and d** are found in some **protists** and **cyanobacteria**. All chlorophylls have a complex **ring structure** that is chemically related to the **porphyrin**-like groups found in **haemoglobin** and **cytochromes**. In addition, a **long hydrocarbon tail** is almost always attached to the ring structure. The ring structure contains some **loosely bound electrons** and is the part of the molecule involved in **electron transitions and redox reactions**.

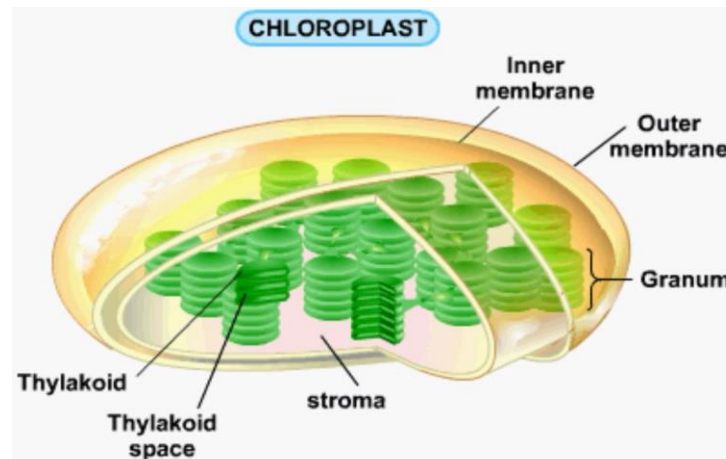


The different types of **carotenoids** found in photosynthetic organisms are all **linear molecules** with **multiple conjugated double bonds**. Absorption bands in the **400 to 500 nm** region give carotenoids their characteristic **orange color**. The color of carrots, for example, is due to the carotenoid  **$\beta$ -carotene**. Carotenoids are integral constituents of the **thylakoid** membrane and are usually associated intimately with both antenna and reaction center pigment proteins. The **light** absorbed by the **carotenoids** is **transferred** to **chlorophyll** for photosynthesis; because of this role they are called **accessory** pigments. **Help capture light**, but they also have an important role in **getting rid of excess light energy**. When a leaf is exposed to **full sun**, it receives a **huge amount of energy**; if that energy is not handled properly, it can damage the photosynthetic machinery. Carotenoids in chloroplasts help **absorb the excess energy and dissipate it as heat**.



### 1.3 Organization of the photosynthetic apparatus

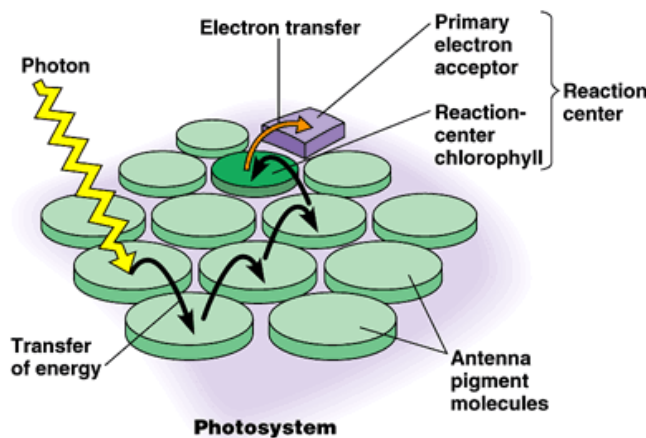
Photosynthesis occurs in **green parts** of the plant, mostly the **leaves**, sometimes the **green stems** and **floral buds**. The leaves contain specialized cells called **mesophyll cells** which contain the chloroplast the pigment containing organelle. These are the actual sites for photosynthesis. The most striking aspect of the structure of the chloroplast is the extensive system of **internal membranes** known as **thylakoids**. All the chlorophyll is contained within this membrane system, which is the site of the light reactions of photosynthesis. Two membranes contain and protect the inner parts of the chloroplast. They are appropriately named the **outer** and **inner membranes**. The inner membrane surrounds the **stroma** and the **grana** (stacks of **thylakoids**). One **thylakoid stack** is called a **granum**. The stacks of thylakoid sacs are connected by **stroma lamellae**. The chloroplast also contains its own DNA, RNA, and ribosomes.



#### 1.4 The light reaction and Photosystem:

The light reaction is the conversion of light energy into chemical energy in the thylakoid membrane using **photosystems**.

Each photosystem composed of The **COMBINATION** of the **antenna** molecules, **reaction center**, and **primary electron acceptor**.

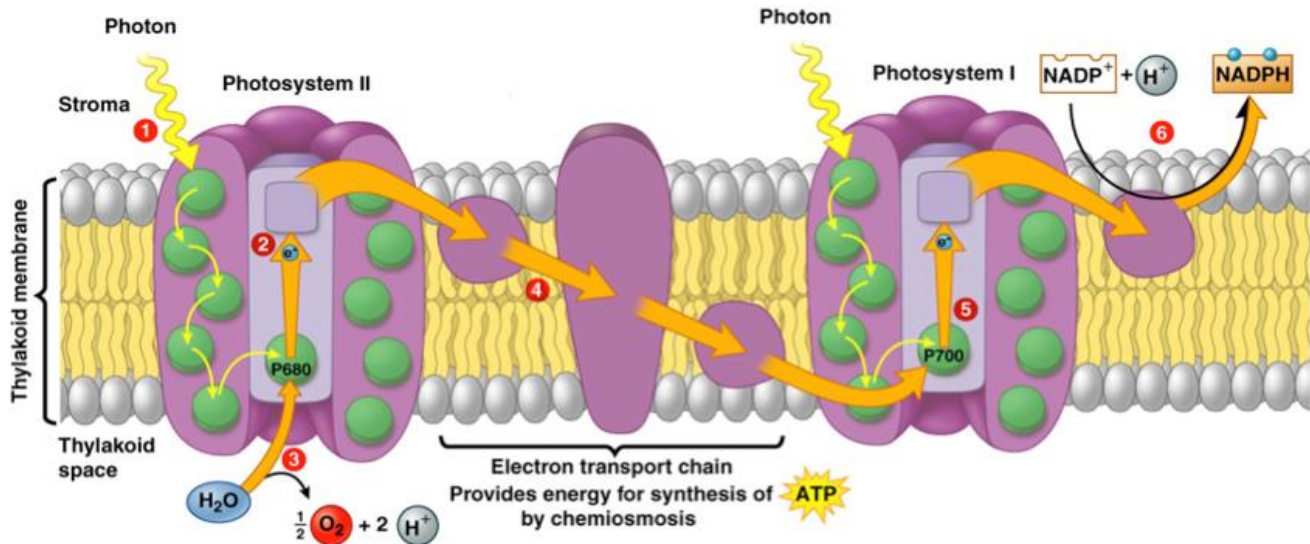


The pigment molecules (chlorophylls **a** and **b**, and the **carotenoids**) in a leaf are **CLUSTERED TOGETHER** in assemblies of **200-300 molecules** to form **antenna** to capture light energy. When one of these pigments absorbs a photon of light, an **excited electron** is generated that is passed from **pigment molecule** to pigment molecule until it reaches a special chlorophyll a molecule (the **reaction center**) in the antenna assembly. The reaction center is associated with another molecule called the **primary electron acceptor** that will act as the **FIRST electron-carrier** in an electron-transport chain. There are actually **TWO** kinds of photosystems in the thylakoid membrane:

1. **Photosystem II**: has a reaction center called P680 (chlorophyll **a** molecule that preferentially absorbs light of 680 nm wavelength).

**2. Photosystem I:** has a reaction center called P700 (chlorophyll **a** molecule that preferentially absorbs light of 700 nm wavelength).

These two photosystems are LINKED TOGETHER in the light reactions.



### The function of the light reactions:

1. To produce **ATP** and **NADPH** that will be used in the Calvin Cycle (“dark reactions”) to drive synthesis of glucose.
2. **Water** is **split** to yield both electrons and hydrogen atoms (H) that will be carried by the “electron shuttle” NADPH. Oxygen (O<sub>2</sub>) is produced as water is split.

### What is oxidation-reduction reaction?

1. **Oxidation:** When an atom or molecule **loses an electron**, it is known as **oxidation**. We say the substance has been **oxidized**.
2. **Reduction:** If an atom or molecule **gains an electron**, it is called **reduction**. We say the substance has been **reduced**.

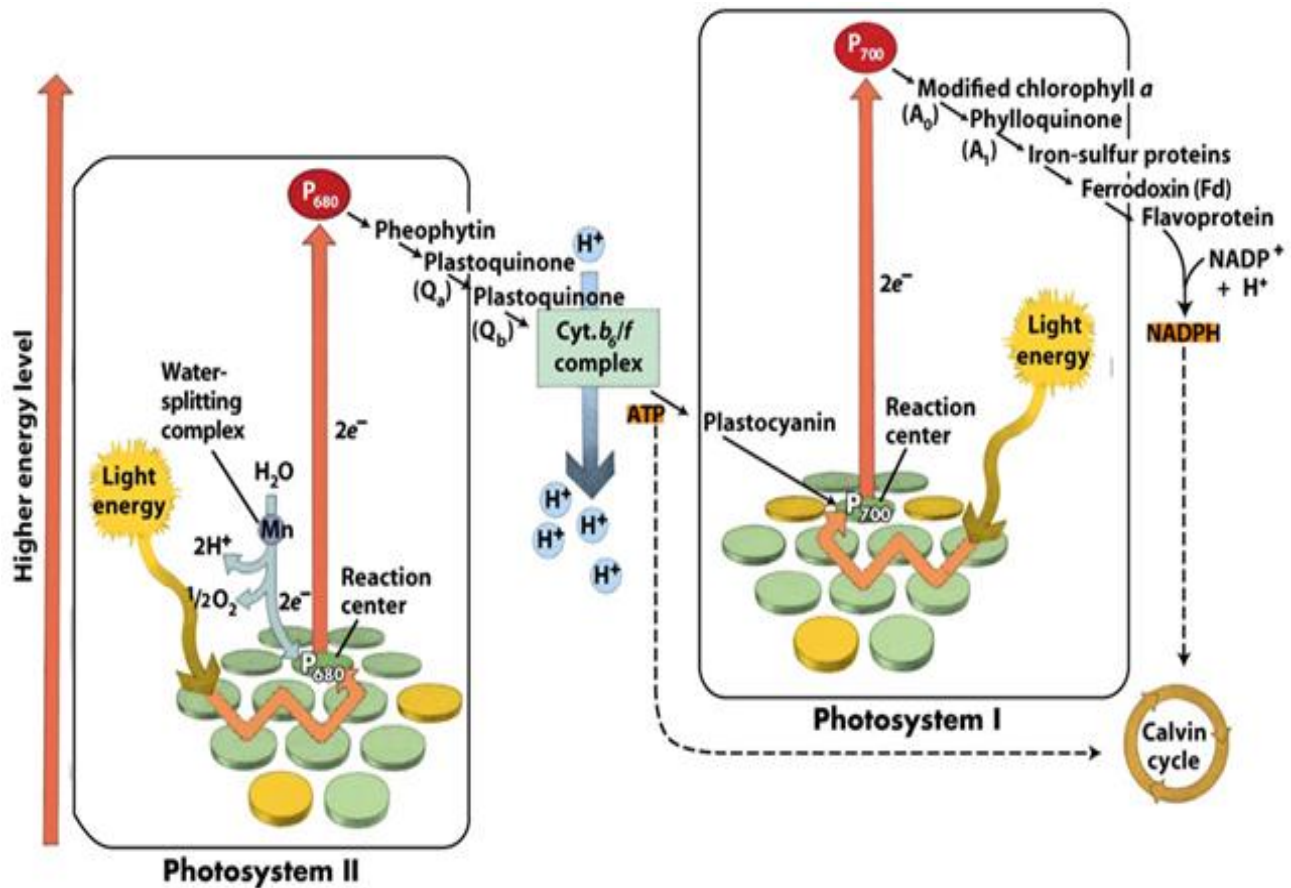
Hydrogen atoms often tag along with electrons as they are passed. So often a reduced substance will not only gain an electron but a hydrogen atom as well.

### 1.5 Electron transport chain in light reaction

After receiving light **PSII** absorbs light energy and passes it on to its **reaction center**, **P680**. When **P680 absorbs light**, it is **excited** and its electrons are transferred to an electron acceptor molecule (**Primary electron acceptor** i.e. **pheophytin**) and itself comes to the ground state. However, by losing an electron **P680** is **oxidized** and in turn it splits water molecule to release O<sub>2</sub>. This **light dependent splitting of water** is called **photolysis**. Thus, the oxidized P680 regains its lost electrons from water molecules. The electrons are finally

passed onto the reaction center **P700** or **PSI**. During this process, energy is released and stored in the form of ATP.

Similarly, **PSI** also gets **excited** when it absorbs light and **P700** (Reaction center of PSI) gets oxidized as it transfers its electrons to another primary acceptor molecule. While the oxidized **P700** draws its electrons from **PSII**, the reduced primary acceptors molecule of PSI transfers its electrons via other electron carrier to **NADP** (Nicotinamide Adenine Dinucleotide Phosphate) to produce **NADPH<sub>2</sub>** a strong reducing agent. Thus, we see that there is a continuous flow of electrons from the H<sub>2</sub>O molecules to PSII to PSI, and finally to the NADP molecule which is reduced to NADPH<sub>2</sub>. NADPH<sub>2</sub> is then utilized in reduction of CO<sub>2</sub> to carbohydrates in dark reaction (Calvin cycle).



## 1.6 Dark reactions

In plants, **carbon dioxide** enters the leaf via pores called **stomata** and diffuses into the stroma of the chloroplast—the site of the **Calvin cycle** reactions, where **sugar** is synthesized. These reactions are also called the **light-independent** reactions because they are not directly driven by light.

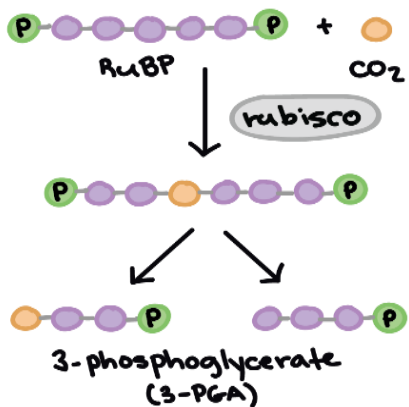
In the Calvin cycle, carbon atoms from CO<sub>2</sub> are **fixed** (incorporated into organic molecules) and used to build **three-carbon sugars**. This process is fueled by, and dependent

on, **ATP** and **NADPH** from the **light reactions**. Unlike the light reactions, which take place in the thylakoid membrane, the reactions of the Calvin cycle take place in the **stroma** (the inner space of chloroplasts).

### 1.7 Reactions of the Calvin cycle

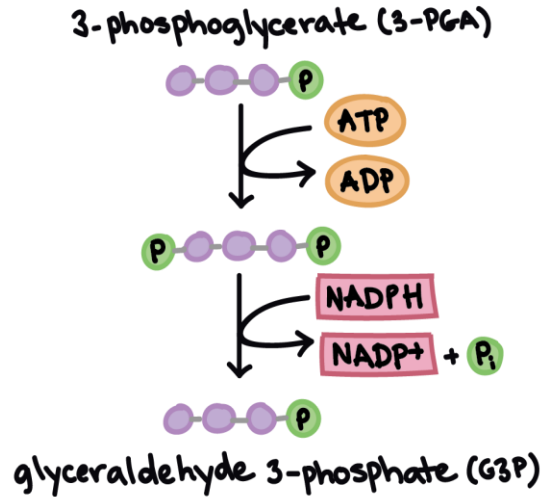
The Calvin cycle reactions can be divided into three main stages: carbon fixation, reduction, and regeneration of the starting molecule.

1. **Carbon fixation.** A  $\text{CO}_2$  molecule combines with a **five-carbon** acceptor molecule, ribulose-1, 5-bisphosphate (**RuBP**). This step makes a **six-carbon** compound that splits into two molecules of a **three-carbon** compound, 3-phosphoglyceric acid (**3-PGA**). This reaction is catalyzed by the **enzyme** RuBP-carboxylase or xygenase, or **rubisco**.



2. **Reduction.** In the second stage, **ATP** and **NADPH** are used to convert the **3-PGA** molecules into molecules of a **three-carbon sugar**, glyceraldehyde-3-phosphate (**G3P**). This stage gets its name because **NADPH** donates **electrons** to, or **reduces**, a three-carbon intermediate to make **G3P**.

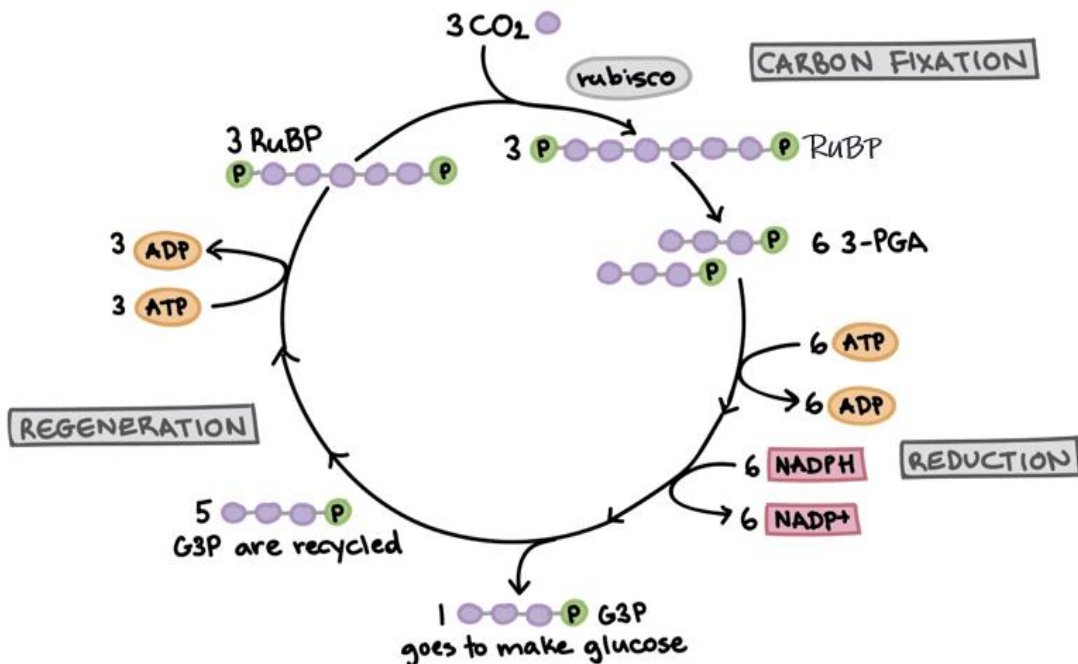
A molecule of **3-PGA** first **receives** a second **phosphate** group from **ATP** (generating ADP). Then, the **doubly phosphorylated molecule receives** electrons from **NADPH** and is reduced to form glyceraldehyde-3-phosphate. This reaction generates **NADP<sup>+</sup>** and also releases an **inorganic phosphate**.



3. **Regeneration:** Some G3P molecules go to make **glucose**, while **others** must be recycled to regenerate the **RuBP** acceptor. **Regeneration requires ATP** and involves a complex network of reactions

In order for **one G3P** to **exit** the cycle (and **go towards glucose synthesis**), **three** CO<sub>2</sub> molecules must enter the cycle, providing **three** new atoms of fixed carbon. When three CO<sub>2</sub> molecules enter the cycle, six **G3P** molecules are made. **One exits** the cycle and is used to make **glucose**, while the other **five** must be **recycled** to **regenerate** three molecules of the **RuBP acceptor**.

**Two** of the glyceraldehyde 3-phosphate (**G3P**) molecules then are combined to form a **glucose** molecule. Thus, six molecules of carbon dioxide and light energy are needed to make one molecule of glucose for photosynthesis.

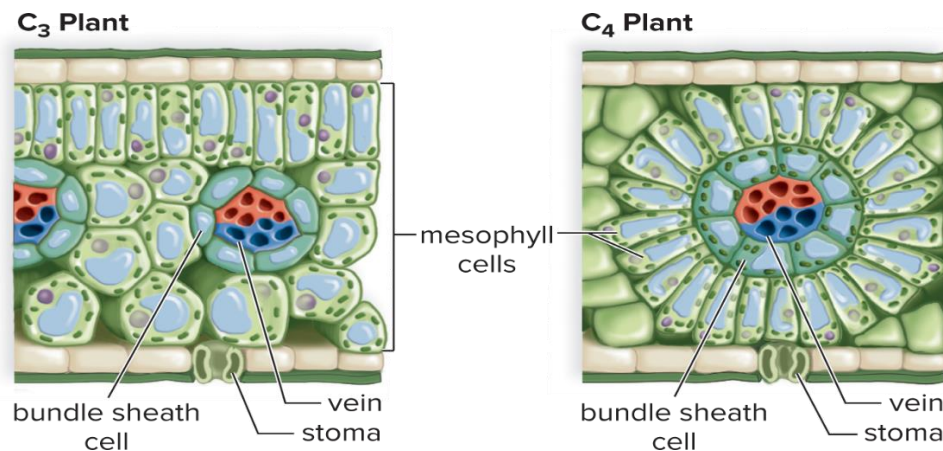




## 1.8 plants classification according to their carbon fixation pathways:

### C<sub>3</sub> plants

In a typical C<sub>3</sub> leaf, the majority of chloroplasts are distributed throughout the palisade mesophyll (below the epidermis) and the spongy mesophyll. These cells are somewhat randomly arranged between large gas-spaces that connect to the stomatal pores. A "normal" plant—one that doesn't have photosynthetic adaptations. The first step of the Calvin cycle is the **fixation** of carbon dioxide by **rubisco**, and plants that **use only** this "standard" mechanism of carbon fixation are called C<sub>3</sub> plants, for the three-carbon compound (**3-PGA**) the reaction produces. About 85% of the plant species on the planet are C<sub>3</sub> plants, including rice, wheat, soybeans and all trees.



### C<sub>4</sub> Plants

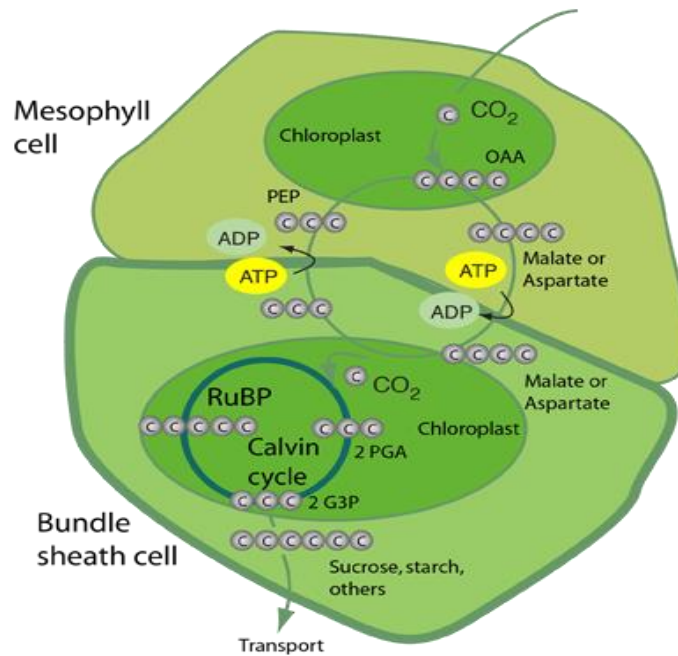
The C<sub>4</sub> syndrome occurs in many plant families. The syndrome is most common in **arid environments**. **C<sub>4</sub> plants** are distributed throughout the world and C<sub>4</sub> crops such as **maize** have been successfully introduced into **temperate climates**. C<sub>4</sub> plants are found in a number of families, but by no means all the members of those families are C<sub>4</sub> species.

In the leaf of a C<sub>4</sub> plant, the **vascular bundles** are surrounded by a ring of **bundle-sheath cells** (special cells around the leaf veins) containing **chloroplasts**. These are surrounded by loosely **packed mesophyll cells** and air-spaces. This is known as '**Krantz' anatomy**. The **bundle-sheath and mesophyll cells** are interconnected by many **plasmodesmata** and no bundle sheath cell is separated by more than a few cells from a mesophyll cell.

The light-dependent reactions and the Calvin cycle are **physically separated**. The **light-dependent reactions** occurring in the **mesophyll cells** and the **Calvin cycle** occurring in **bundle-sheath** cells.

First, atmospheric CO<sub>2</sub> is fixed in the mesophyll cells to form a simple, **4-carbon** organic acid (**oxaloacetate**). This step is carried out by a non-rubisco enzyme, **PEP carboxylase (phosphor enol pyruvate carboxylase)** as happen in C<sub>3</sub> plants. **Oxaloacetate** is then converted to a similar molecule, **malate** that can be transported in to the bundle-

sheath cells. Inside the **bundle sheath**, **malate breaks down**, releasing a molecule of CO<sub>2</sub>. The **CO<sub>2</sub>** then **fixed by rubisco** and made into **sugars** via the Calvin cycle, exactly as in C<sub>3</sub> photosynthesis.

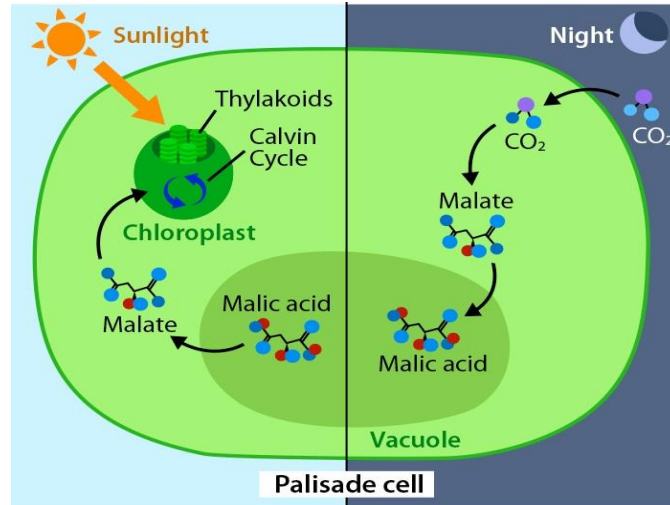


### CAM plants

CAM plants are similarly distributed in many families, mostly succulents (are thickened, fleshy, and swollen, usually to retain water in arid climates) and are distributed in arid zones throughout the world. Some families contain C<sub>3</sub>, CAM and C<sub>4</sub> species. Although there appears to be an advantage to C<sub>4</sub> and CAM, **many arid zone plants are C<sub>3</sub> and use other adaptations to survive.**

CAM plants are generally **adapted** to survive **drought**. Unlike C<sub>4</sub> plants, they lack the physical compartmentation of photosynthesis into two cell types, but instead **fix CO<sub>2</sub>** in the **night** as **C<sub>4</sub> acids** that are **stored in a vacuole** which occupies much of their photosynthetic cells' volume. The stomata of CAM plants are **closed during the most desiccating periods of the day** and are **open at night**. Some plants that are adapted to dry environments, such as cacti and pineapples, use the crassulacean acid metabolism (**CAM**) pathway. This name comes from the family of plants, the **Crassulaceae**, in which scientists first discovered the pathway.

At **night**, CAM plants **open** their **stomata**, allowing CO<sub>2</sub> to diffuse into the leaves. This CO<sub>2</sub> is fixed into oxaloacetate by **PEP carboxylase** (the same step used by C<sub>4</sub> plants), then converted to **malate** or another type of **organic acid**. The organic acid is **stored** inside **vacuoles** until the next day. In the daylight, the CAM plants do not open their stomata, but they can still photosynthesis. That's because the organic acids are transported out of the vacuole and broken down to release CO<sub>2</sub>, which enters the Calvin cycle. This controlled release maintains a high concentration of CO<sub>2</sub> around rubisco.



## TRANSPORTATION OF PHOTOSYNTHATES IN THE PHLOEM

The **products of photosynthesis** are called **Photosynthates**, which are usually in the form of **simple sugars** such as **sucrose**. Plants convert the sugars made during photosynthesis into sucrose by combining **glucose** with another sugar called **fructose**. Sucrose is translocated rather than glucose because **sucrose** is a **nonreducing** sugar. This means that sucrose does **not react with oxygen** during aerobic respiration while being transported.

Sugars produced in sources, such as **leaves**, need to be delivered to growing parts of the plant **via the phloem** in a process called **translocation**. The points of sugar **delivery**, such as **roots**, young **shoots**, and developing **seeds**, are called **sinks**. Seeds, tubers, and bulbs can be either a source or a sink, depending on the plant's stage of development and the season.

The products from the source are usually **translocated to the nearest sink** through the **phloem**.

1. The highest leaves will send Photosynthates upward to the growing shoot tip,
2. The lower leaves will direct Photosynthates downward to the roots.
3. Intermediate leaves will send products in both directions, unlike the flow in the **xylem**, which is always **unidirectional** (soil to leaf to atmosphere).

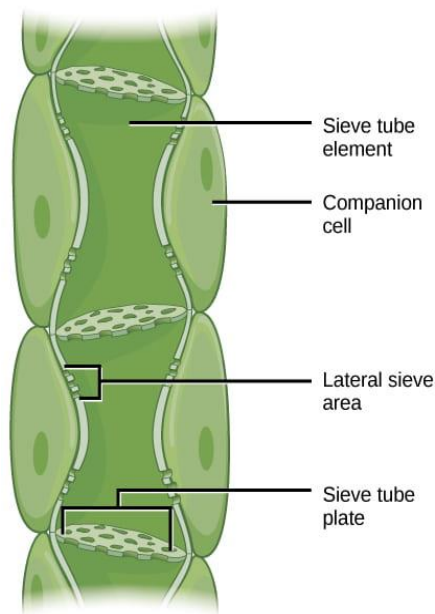
The pattern of Photosynthates flow changes as the plant grows and develops:

1. Photosynthates are directed primarily to the **roots** early on, to **shoots** and **leaves during vegetative growth**,
2. To **seeds** and **fruits** during **reproductive** development. They are also directed to tubers for storage.

### Translocation: Transport from Source to Sink

Photosynthates such as sucrose are *actively transported* (requires ATP) from source cells into companion cells, which are associated with the sieve-tube elements in the vascular bundles. This active transport of sugar into the companion cells allows the companion cells to accumulate a higher concentration of sugar than is present in the photosynthesizing leaves. To make this process work, the companion cells use an **ATP-powered proton pump** to create an electrochemical gradient outside of the cell; then a **proton-sucrose cotransporter** couples the movement of a proton *down* its concentration gradient with sucrose *against* its concentration gradient and into the companion cells.

Once inside the companion cells, the sugar **diffuses** down its concentration gradient from the companion cell and into the phloem sieve-tube elements through the plasmodesmata that link the companion cell to the sieve tube elements. The phloem sieve-tube elements have reduced cytoplasmic contents and are connected by pores that allow for pressure-driven bulk flow, or translocation, of phloem sap.



the presence of high concentrations of sugar in the sieve tube elements drastically increases  $\Psi_s$ ; as a result, water then moves by osmosis from xylem into the phloem cells. This movement of water into the sieve tube cells then causes  $\Psi_p$  to increase, which increases both the turgor pressure in the phloem and the total water potential in the phloem at the source. This increase in water potential then drives the bulk flow of phloem from source to sink.

Unloading at the sink end of the phloem tube can occur either by diffusion, if the concentration of sucrose is lower at the sink than in the phloem, or by active transport, if the concentration of sucrose is higher at the sink than in the phloem:

- If the sink is an area of active growth, such as a new leaf or a reproductive structure, then the sucrose concentration in the sink cells is usually lower than in the phloem sieve-tube elements because the sink sucrose is rapidly metabolized for growth.

- If the sink is an area of storage where sugar is converted to starch, such as a root or bulb, then the sugar concentration in the sink is usually lower than in the phloem sieve-tube elements because the sink sucrose is rapidly converted to starch for storage.
- If the sink is an area of storage where the sugar is stored as sucrose, such as a sugar beet or sugar cane, then the sink may have a higher concentration of sugar than the phloem sieve-tube cells. In this situation, active transport by a proton-sucrose cotransporter (which relies on an ATP-powered proton pump) is typically used to transport sugar from the companion cells into storage vacuoles in the storage cells.

Once sugar is unloaded at the sink cells, the  $\Psi_s$  increases, causing water to diffuse by osmosis from the phloem back into the xylem. This movement of water out of the phloem causes  $\Psi_p$  to decrease, reducing the turgor pressure in the phloem at the sink and maintaining the direction of bulk flow from source to sink.

