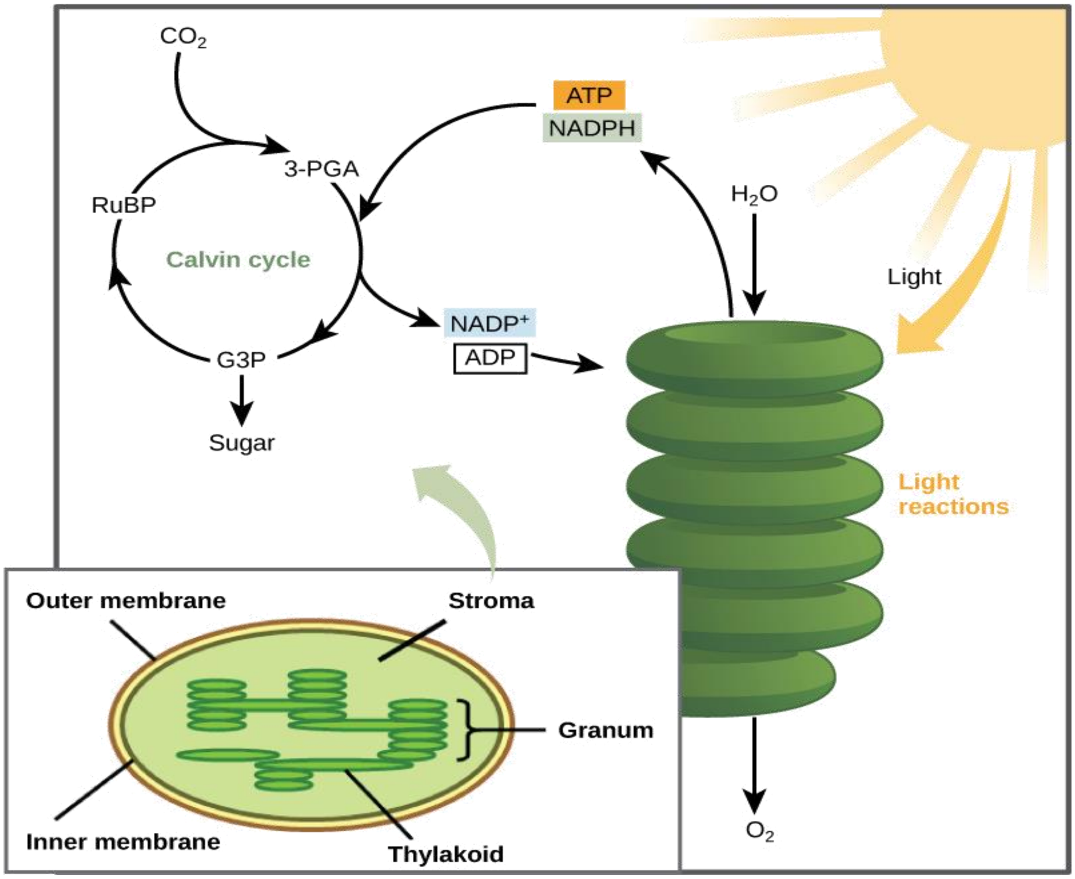
Photosynthesis: Dark reactions

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_2 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).



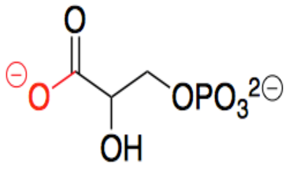
Reactions of the Calvin cycle

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

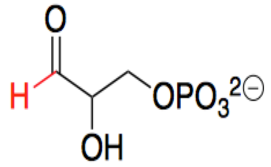
1. **Carbon fixation:** A CO_2 molecule combines with a **five-carbon** acceptor molecule, ribulose-1, 5-bisphosphate (**RuBP**). This step makes a **six-carbon** compound that splits into two molecules of a **three-carbon** compound, 3-phosphoglyceric acid (**3-PGA**). This reaction is catalyzed by the **enzyme 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**).

   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+** and also releases an **inorganic phosphate**.
   This step is called "**reduction**" because **NADPH** donates **electrons** to the **3-phosphoglyceric acid (3PGA)** molecules to create glyceraldehyde-3 phosphate (**G3P**).



3-phosphoglycerate

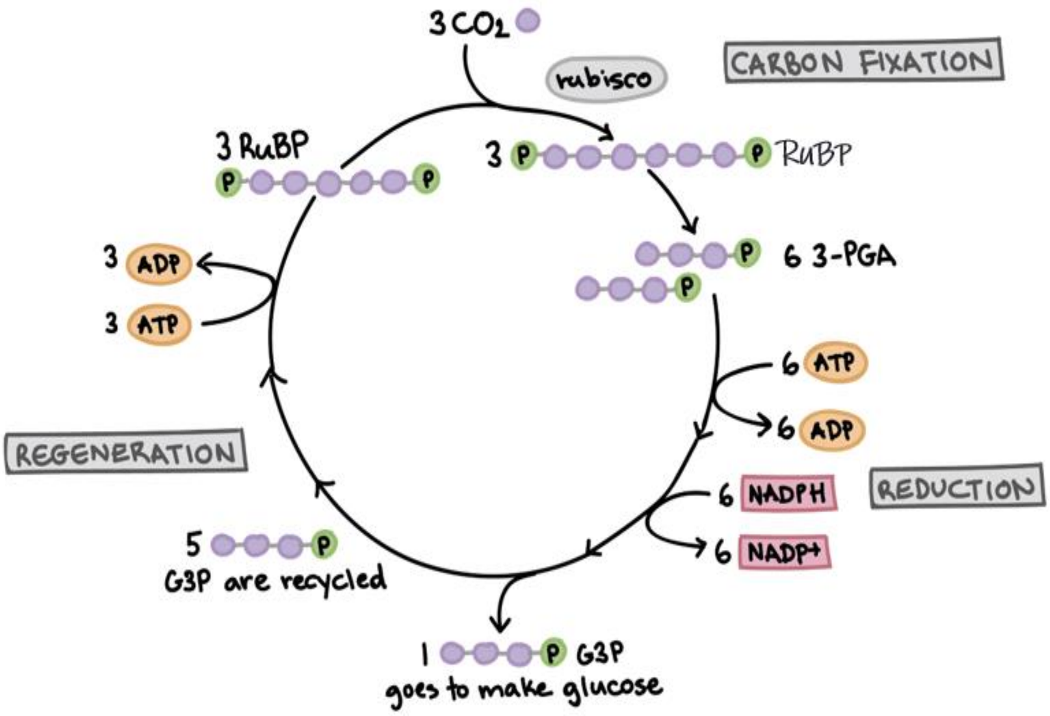


glyceraldehyde-3-phosphate

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_2 molecules must enter the cycle, providing **three** new atoms of fixed carbon. When three CO_2 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.



Types of plants due to the dark reaction stage:

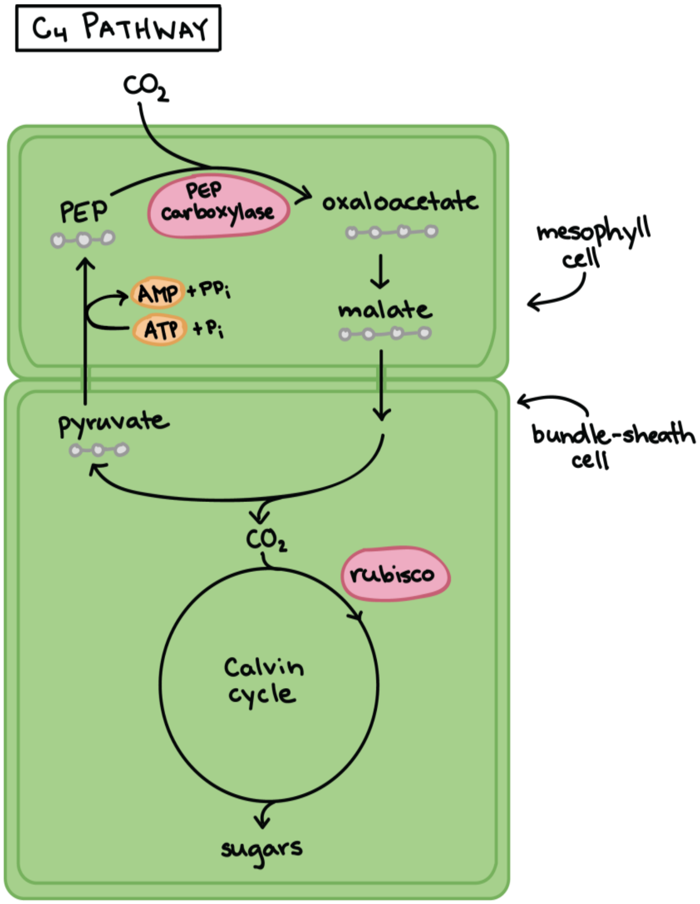
C3plants

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** the above "standard" mechanism of carbon fixation are called **C3 plants**, for the three-carbon compound (**3-PGA**) the reaction produces. About **85%** of the plant species on the planet are C3 plants, including rice, wheat, soybeans and all trees.

C4 Plants

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

First, atmospheric **CO_2** is fixed in the **mesophyll cells** to form a simple, **4-carbon** organic acid (**oxaloacetate**). This step is carried out by **PEP carboxylase enzyme**. 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_2. The CO_2 then fixed by **rubisco** and made into sugars via the Calvin cycle, **exactly as in C3 photosynthesis.**

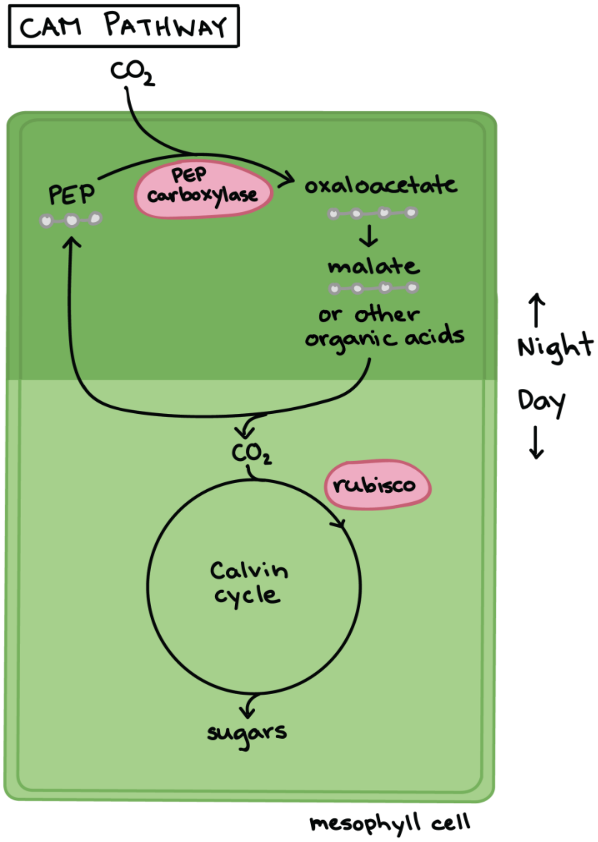


CAM plants

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_2 to diffuse into the leaves**. This CO_2 is fixed into **oxaloacetate** by **PEP carboxylase** (the same step used by C4 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 do photosynthesis. That's because the organic acids are transported out of the vacuole and broken down to release CO2, which enters the Calvin cycle. This controlled release maintains a high concentration of CO2 around rubisco.



TRANSPORTATION OF PHOTOSYNTHATES IN THE PHLOEM

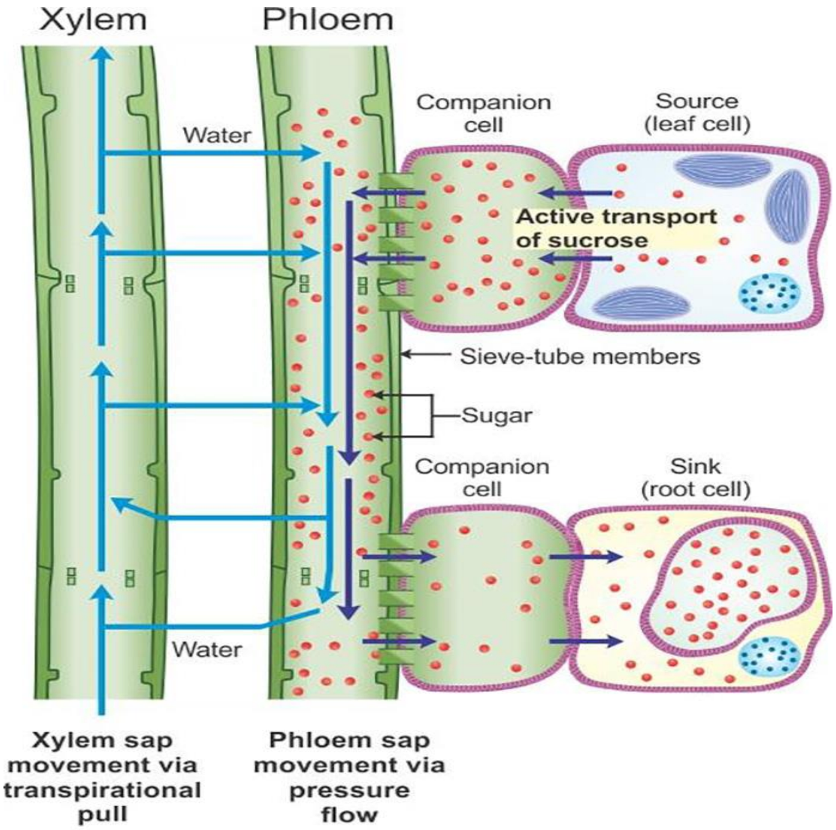
Plants **need an energy source to grow**. In seeds and bulbs, **food is stored** in polymers (such as **starch**) that are **converted** by metabolic processes into **sucrose** for newly developing plants. Once **green shoots** and leaves are growing, plants are able to produce their own food by **photosynthesizing**. The **products of photosynthesis** are called **Photosynthates**, which are usually in the form of **simple sugars** such as **sucrose**.

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**. For example, the highest leaves will send Photosynthates upward to the growing shoot tip, whereas lower leaves will direct Photosynthates downward to the roots. 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. Photosynthates are directed primarily to the roots early on, to shoots and leaves during vegetative growth, and to seeds and fruits during reproductive development. They are also directed to tubers for storage.

Translocation: Transport from Source to Sink (Mass flow hypothesis):

Mesophyll cells are connected by cytoplasmic channels called **plasmodesmata**. Photosynthates move through these channels to reach **phloem sievetube** elements (STEs). From the mesophyll cells, the photosynthates are loaded into the phloem STEs. The sucrose is **actively transported against its concentration gradient** (a process requiring ATP) into the phloem cells using the **electrochemical potential** of the proton gradient. This is coupled to the uptake of sucrose with a carrier protein called the **Sucrose-H$^+$ symporter**. Phloem STEs have reduced cytoplasmic contents, and are connected by a sieve plate with pores that allow for pressure-driven bulk flow, or translocation, of phloem sap. **Companion cells** are associated with STEs. They **assist with metabolic activities** and **produce energy** for the STEs



Mass Flow Hypothesis