C3, C4, and CAM plants

How the C4 and CAM pathways help minimize photorespiration.

Key points:

- **Photorespiration** is a wasteful pathway that occurs when the Calvin cycle enzyme rubisco acts on oxygen rather than carbon dioxide.
- The majority of plants are C3 **plants**, which have no special features to combat photorespiration.
- C4 **plants** minimize photorespiration by separating initial CO_2 fixation and the Calvin cycle in space, performing these steps in different cell types.
- **Crassulacean acid metabolism** (**CAM**) plants minimize photorespiration and save water by separating these steps in time, between night and day.

Introduction

High crop yields are pretty important—for keeping people fed, and also for keeping economies running. If you heard there was a single factor that reduced the yield of wheat by 20 percent and the yield of soybeans by 36 percent in the United States, for instance, you might be curious to know what it was.

As it turns out, the factor behind those (real-life) numbers is photorespiration. This wasteful metabolic pathway begins when rubisco, the carbon-fixing enzyme of the Calvin cycle, grabs O_2 rather than CO_2. It uses up fixed carbon, wastes energy, and tends to happens when plants close their stomata (leaf pores) to reduce water loss. High temperatures make it even worse.

Some plants, unlike wheat and soybean, can escape the worst effects of photorespiration. The C4 and CAM pathways are two adaptations—beneficial features arising by natural selection—that allow certain species to minimize photorespiration. These pathways work by ensuring that Rubisco always encounters high concentrations of CO_2, making it unlikely to bind to O_2.

In the rest of this article, we'll take a closer look at the C4 and CAM pathways and see how they reduce photorespiration.

C3 plants

A "normal" plant—one that doesn't have photosynthetic adaptations to reduce photorespiration—is called a C3 plant. 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 C3 plants, for the three-carbon compound (3-PGA) the reaction produces. About 85 percent of the plant species on the planet are C3 plants, including rice, wheat, soybeans and all trees.

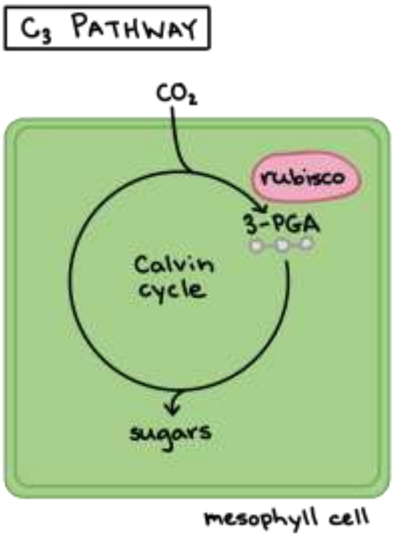
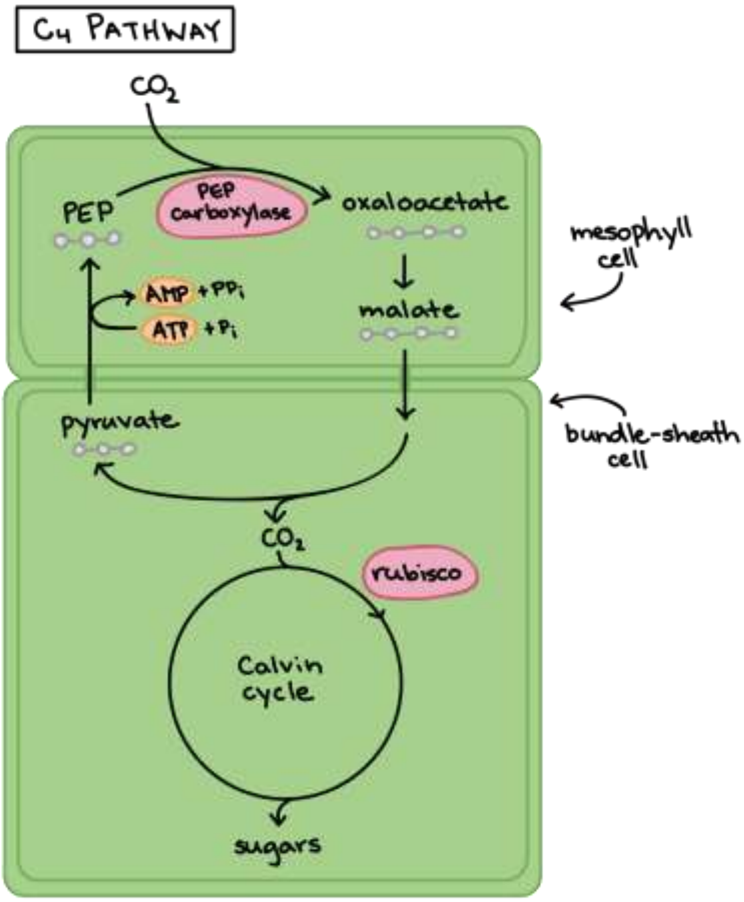


Image of the C3 pathway. Carbon dioxide enters a mesophyll cell and is fixed immediately by rubisco, leading to the formation of 3-PGA molecules, which contain three carbons.

C_4 subscript plants

In C_4 plants, the light-dependent reactions and the Calvin cycle are physically separated, with the light-dependent reactions occurring in the mesophyll cells (spongy tissue in the middle of the leaf) and the Calvin cycle occurring in special cells around the leaf veins. These cells are called **bundle-sheath** cells.

To see how this division helps, let's look at an example of C_4 photosynthesis in action. 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 a non-rubisco enzyme, PEP carboxylase that has no tendency to bind O_2. 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 is then fixed by rubisco and made into sugars via the Calvin cycle, exactly as in C_3 photosynthesis.



In the C4 pathway, initial carbon fixation takes place in mesophyll cells and the Calvin cycle takes place in bundle-sheath cells. PEP carboxylase attaches an incoming carbon dioxide molecule to the three-carbon molecule PEP, producing oxaloacetate (a four-carbon molecule). The oxaloacetate is converted to malate, which travels out of the mesophyll cell and into a neighbouring bundle-sheath. Inside the bundle sheath cell, malate is broken down to release CO_2, which then enters the Calvin cycle. Pyruvate is also produced in this step and moves back into the mesophyll cell, where it is converted into PEP (a reaction that converts ATP and Pi into AMP and PPi).

This process isn't without its energetic price: ATP must be expended to return the three-carbon “ferry” molecule from the bundle sheath cell and get it ready to pick up another molecule of atmospheric CO_2. However, because the mesophyll cells constantly pump CO_2 into neighbouring bundle-sheath cells in the form of malate, there’s always a high concentration of CO_2 relative to O_2 right around rubisco. This strategy minimizes photorespiration.

The C4 pathway is used in about 3 percent of all vascular plants; some examples are crabgrass, sugarcane and corn. C4 plants are common in habitats that are hot, but are less abundant in areas that are cooler. In hot conditions, the benefits of reduced photorespiration likely exceed the ATP cost of moving CO_2 from the mesophyll cell to the bundle-sheath cell.

CAM plants

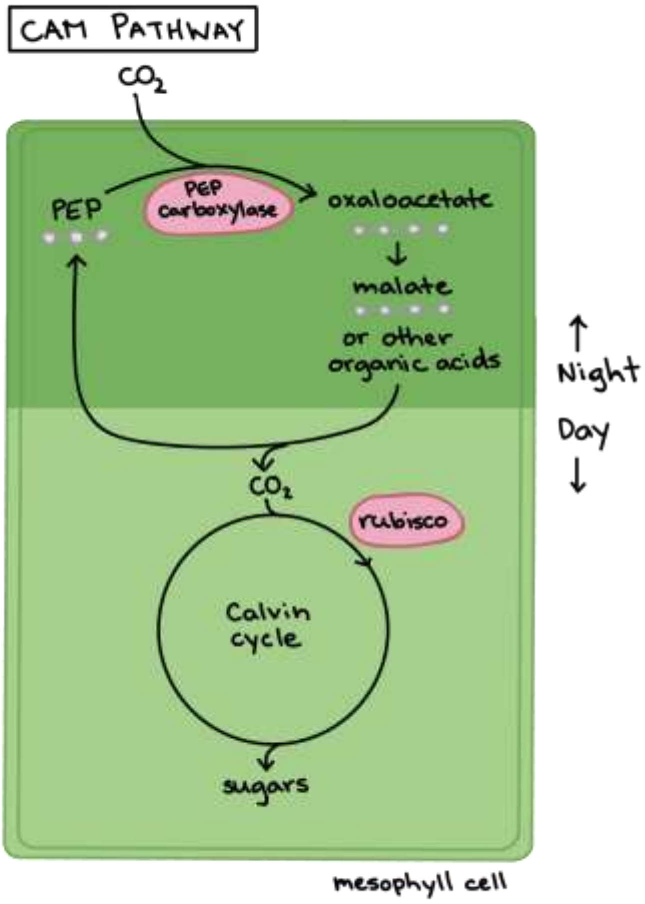
Some plants that are adapted to dry environments, such as cacti and pineapples, use the **crassulacean acid metabolism** (**CAM**) pathway to minimize photorespiration. This name comes from the family of plants, the Crassulaceae, in which scientists first discovered the pathway.

Image of a succulent.

Image credit: "Crassulaceae," by Guyon Morée (CC BY 2.0).

Instead of separating the light-dependent reactions and the use of CO_2 in the Calvin cycle in space, CAM plants separate these processes in time. 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 photosynthesis. That's because the organic acids are transported out of the vacuole and broken down to release CO_2, which enters the Calvin cycle. This controlled release maintains a high concentration of CO_2 around rubisco.



CAM plants temporally separate carbon fixation and the Calvin cycle. Carbon dioxide diffuses into leaves during the night (when stomata are open) and is fixed into oxaloacetate by PEP carboxylase, which attaches the carbon dioxide to the three-carbon molecule PEP. The oxaloacetate is converted to another organic acid, such as malate. The organic acid is stored until the next day and is then broken down, releasing carbon dioxide that can be fixed by rubisco and enter the Calvin cycle to make sugars.

The CAM pathway requires ATP at multiple steps (not shown above), so like C_4 photosynthesis, it is not an energetic "freebie." However, plant species that use CAM photosynthesis not only avoid photorespiration, but are also very water-efficient. Their stomata only open at night, when humidity tends to be higher and temperatures are cooler, both factors that reduce water loss from leaves. CAM plants are typically dominant in very hot, dry areas, like deserts.

Comparisons of, C_4 and CAM plants

C_3, C_4 and CAM plants all use the Calvin cycle to make sugars from CO_2. These pathways for fixing CO_2 have different advantages and disadvantages and make plants suited for different habitats. The C_3 mechanism works well in cool environments, while C_4 and CAM plants are adapted to hot, dry areas.

Both the C_4 and CAM pathways have evolved independently over two dozen times, which suggests they may give plant species in hot climates a significant evolutionary advantage.

Type	Separation of initial CO_2 fixation and Calvin cycle	Stomata open	Best adapted to
$C3$	No separation	Day	Cool, wet environments
$C4$	Between mesophyll and bundle-sheath cells (in space)	Day	Hot, sunny environments
CAM	Between night and day (in time)	Night	Very hot, dry environments