16.2E: Photorespiration and C4 Plants

All plants carry on photosynthesis by adding carbon dioxide (CO$_2$) to a phosphorylated 5-carbon sugar called ribulose bisphosphate. This reaction is catalyzed by the enzyme ribulose bisphosphate carboxylase oxygenase (RUBISCO). The resulting 6-carbon compound breaks down into two molecules of 3-phosphoglyceric acid (PGA). These 3-carbon molecules serve as the starting material for the synthesis of glucose and other food molecules. The process is called the Calvin cycle and the pathway is called the C$_3$ pathway.

Photorespiration

As its name suggests, RUBISCO catalyzes two different reactions:

- adding CO$_2$ to ribulose bisphosphate — the carboxylase activity
- adding O$_2$ to ribulose bisphosphate — the oxygenase activity

Which one predominates depends on the relative concentrations of O$_2$ and CO$_2$ with

- high CO$_2$, low O$_2$ favoring the carboxylase action
- high O$_2$, low CO$_2$ favoring the oxygenase action

The light reactions of photosynthesis liberate oxygen and more oxygen dissolves in the cytosol of the cell at higher temperatures. Therefore, high light intensities and high temperatures (above ~ 30°C) favor the second reaction.

The uptake of O$_2$ by RUBISCO forms the 3-carbon molecule 3-phosphoglyceric acid, just as in the Calvin cycle, and the 2-carbon molecule glycolate. The glycolate enters peroxisomes where it uses O$_2$ to form intermediates that enter mitochondria where they are broken down to CO$_2$. So this process uses O$_2$ and liberates CO$_2$ as cellular respiration.
does which is why it is called **photorespiration**. It undoes the good anabolic work of photosynthesis, reducing the net productivity of the plant. For this reason, much effort so far largely unsuccessful has gone into attempts to alter crop plants so that they carry on less photorespiration. The problem may solve itself. If atmospheric CO$_2$ concentrations continue to rise, perhaps this will enhance the net productivity of the world's crops by reducing losses to photorespiration.

### C$_4$ Plants

Over 8,000 species of **angiosperms** have developed adaptations which minimize the losses to photorespiration. They all use a supplementary method of CO$_2$ uptake which forms a 4-carbon molecule instead of the two 3-carbon molecules of the Calvin cycle. Hence these plants are called **C$_4$** plants. (Plants that have only the Calvin cycle are thus **C$_3$** plants).

Some C$_4$ plants - called CAM plants - separate their C$_3$ and C$_4$ cycles by **time**, while other C$_4$ plants have structural changes in their leaf anatomy so that their C$_4$ and C$_3$ pathways are separated in different parts of the leaf with RUBISCO sequestered where the CO$_2$ level is high; the O$_2$ level low.

After entering through stomata, CO$_2$ diffuses into a **mesophyll cell**. Being close to the leaf surface, these cells are exposed to high levels of O$_2$, but they have no RUBISCO so cannot start photorespiration (nor the dark reactions of the **Calvin cycle**).

![C4 Anatomy](https://bio.libretexts.org/Bookshelves/Introductory_and_General_Biology/Book%3A_Biology_(Kimball)/16%3A_The_Anatomy_of_Plants/16.2.5.1_C4_Anatomy)

Instead the CO$_2$ is inserted into a **3-carbon** compound (C$_3$) called **phosphoenolpyruvic acid (PEP)** forming the **4-carbon** compound **oxaloacetic acid (C$_4$)**. Oxaloacetic acid is converted into malic acid or aspartic acid (both have 4 carbons), which is transported (by **plasmodesmata**) into a **bundle sheath cell**. Bundle sheath cells are deep in the leaf so atmospheric oxygen cannot diffuse easily to them and often have thylakoids with reduced photosystem II complexes (the one that produces O$_2$). Both of these features keep oxygen levels low in Bundle sheath cells, which is where the 4-carbon compound is broken down into **carbon dioxide**, which enters the Calvin cycle to form sugars and starch, and **pyruvic acid (C$_3$)**, which is transported back to a mesophyll cell where it is converted back into PEP.
These C₄ plants are well adapted to (and likely to be found in) habitats with high daytime temperatures and intense sunlight. Some examples crabgrass, corn (maize), sugarcane, and sorghum. Although only ~3% of the angiosperms, C₄ plants are responsible for ~25% of all the photosynthesis on land.

4 cells in C₃ plants

The ability to use the C₄ pathway has evolved repeatedly in different families of angiosperms - a remarkable example of convergent evolution. Perhaps the potential is in all angiosperms.

A report in the 24 January 2002 issue of Nature (by Julian M. Hibbard and W. Paul Quick) describes the discovery that tobacco, a C₃ plant, has cells capable of fixing carbon dioxide by the C₄ path. These cells are clustered around the veins (containing xylem and phloem) of the stems and also in the petioles of the leaves. In this location, they are far removed from the stomata that could provide atmospheric CO₂. Instead, they get their CO₂ and/or the 4-carbon malic acid in the sap that has been brought up in the xylem from the roots.

If this turns out to be true of many C₃ plants, it would explain why it has been so easy for C₄ plants to evolve from C₃ ancestors.

CAM Plants

CAM plants are also C₄ plants (CAM stands for crassulacean acid metabolism because it was first studied in members of the plant family Crassulaceae.). However, instead of segregating the C₄ and C₃ pathways in different parts of the leaf, CAM plants separate them in time instead (Table 1).

<table>
<thead>
<tr>
<th>Night</th>
<th>Morning</th>
</tr>
</thead>
<tbody>
<tr>
<td>• CAM plants take in CO₂ through their open stomata (they tend to have reduced numbers of them).</td>
<td>• The stomata close (thus conserving moisture as well as reducing the inward diffusion of oxygen).</td>
</tr>
<tr>
<td>• The CO₂ joins with PEP to form the 4-carbon oxaloacetic acid.</td>
<td>• The accumulated malic acid leaves the vacuole and is broken down to release CO₂.</td>
</tr>
<tr>
<td>• This is converted to 4-carbon malic acid that accumulates during the night in the central vacuole of the cells.</td>
<td>• The CO₂ is taken up into the Calvin (C₃) cycle.</td>
</tr>
</tbody>
</table>

These adaptations also enable their owners to thrive in conditions of high daytime temperatures, intense sunlight, and low soil moisture. Some examples of CAM plants include cacti, Bryophyllum, the pineapple and all epiphytic bromeliads, sedums, and the "ice plant" that grows in sandy parts of the scrub forest biome.
C4 Diatoms

On 26 October 2000, *Nature* reported the discovery of both the C3 and C4 pathways in a marine diatom. In this unicellular organism, the two paths are kept separate by having the C4 path in the cytosol, and the C3 path confined to the chloroplast. The presence of a C4 pathway probably reflects the frequent low concentrations of CO2 in ocean waters.

Contributors and Attributions

- John W. Kimball. This content is distributed under a Creative Commons Attribution 3.0 Unported (CC BY 3.0) license and made possible by funding from The Saylor Foundation.