

Photorespiration and C4 Plants

All plants carry on photosynthesis by

- adding carbon dioxide (CO2) 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 **C3** pathway.

Photorespiration

As its name suggests, **RUBISCO** catalyzes two different reactions:

- adding CO2 to ribulose bisphosphate the carboxylase activity
- adding O2 to ribulose bisphosphate the **oxygenase** activity.
- Which one predominates depends on the relative concentrations of O2 and CO2 with
- high CO2, low O2 favoring the carboxylase action,
- high O2, low CO2 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 $\sim 30^{\circ}$ C) favor the second reaction.

The details of photorespiration

The uptake of O2 by RUBISCO forms the 3-carbon molecule 3-phosphoglyceric acid — just as in the Calvin cycle the 2-carbon molecule glycolate. The glycolate enters peroxisomes where it uses O2 to form intermediates that enter mitochondria where they are broken down to CO2.

So this process uses O2 and liberates CO2 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 CO2 concentrations continue to rise, perhaps this will enhance the net productivity of the world's crops by reducing losses to photorespiration.

C4 Plants

Over 8000 species of angiosperms, scattered among 18 different families, have developed adaptations which minimize the losses to photorespiration. They all use a **supplementary** method of CO2 uptake which forms a 4-carbon molecule instead of the two 3-carbon molecules of the Calvin cycle. Hence these plants are called C4 plants. (Plants that have only the Calvin cycle are thus C3 plants.)

- Some C4 plants called CAM plants separate their C3 and C4 cycles by time. CAM plants are discussed below.
- Other C4 plants have structural changes in their leaf anatomy so that their C4 and C3 pathways are separated in different parts of the leaf with RUBISCO sequestered where the CO2 level is high; the O2 level low. These adaptations are described now.

The details of the C4 cycle

After entering through stomata, CO2 diffuses into a mesophyll cell.

Being close to the leaf surface, these cells are exposed to high levels of O2, but have no RUBISCO so cannot start photorespiration Instead the CO2 is inserted into a 3-carbon compound (C3) called phosphoenolpyruvic acid (PEP) forming the 4-carbon compound oxaloacetic acid (C4). 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; often have thylakoids with reduced photosystem II complexes (the one that produces O2). Both of these features keep oxygen levels low. Here the 4-carbon compound is broken down into carbon dioxide, which enters the Calvin cycle to form sugars and starch. pyruvic acid (C3), 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 intense sunlight. Some examples: • corn (maize) sugarcane sorghum

crabgrass

C4 cells in C3 plants

The ability to use the C4 pathway has evolved repeatedly in different families of angiosperms. Perhaps the potential is in them all. 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**

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

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

These adaptations also enable their owners to thrive in conditions of

- high davtime temperatures intense sunlight Some examples of CAM plants:
- cacti
- Bryophyllum
- the "ice plant" that grows in sandy parts of the scrub forest biome
- the pineapple and all epiphytic bromeliads

low soil moisture.

sedums