Rubisco and C_4 plants

Rubisco

The enzyme ribulose bisphosphate carboxylase/oxygenase (Rubisco) is the most abundant protein on Earth. It is an enzyme that catalyses the carbon fixing step at the beginning of the Calvin cycle.

It is possibly the most important molecule on the planet.

Almost every carbon atom in every organic molecule in every cell of every living organism has been through the active site of this molecule. (Others have been fixed by photosynthetic bacteria).

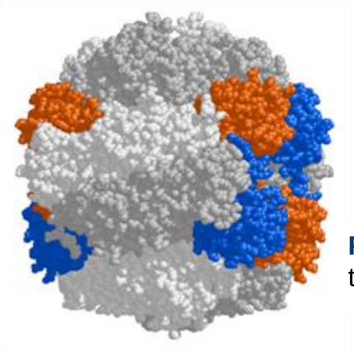

Figure 1 Space-filling view of the structure of Rubisco.

Photorespiration

There is a problem. When ribulose-1,5-biphopshate (RuBP) is carboxylated, it reacts with carbon dioxide and water to give two glycerate-3-phosphate (GP) molecules, which can be utilised in the 'C_3' Calvin cycle. But this reaction is very slow at low carbon dioxide concentrations.

Rubisco also catalyses another reaction – the oxygenation of RuBP. When RuBP reacts with oxygen, it gives a molecule of GP and another of glycollate-2-phosphate.

Glycollate-2-phosphate is converted to GP in reactions which use ATP and release carbon dioxide. As oxygen has been used up and carbon dioxide has been produced, this resembles aerobic respiration, so the process has been called photorespiration (even though ATP is used up, not made).

Photorespiration wastes both carbon and energy, reducing the efficiency of photosynthesis. The C_3 pathway of photosynthesis evolved when oxygen concentrations in the atmosphere were very low, much less than 1%. Carbon dioxide levels were much higher than today. In those conditions photorespiration would hardly occur if at all.

C_4 plants

Some plants are able to combat the limitations of Rubisco and the C_3 pathway. They have another carbon fixing enzyme in addition to Rubisco; this is often phosphoenolpyruvate carboxylase (PEP carboxylase). This catalyses the conversion of 3 carbon phosphoenolpyruvate (PEP) to oxaloacetete, using hydrogencarbonate ions. Hydrogencarbonate is formed when carbon dioxide reacts with water.

As oxaloacetate is a 4 carbon compound, this is known as the C_4 pathway. PEP is able to rapidly fix carbon at very low concentrations of hydrogen carbonate.

Plants using PEP carboxylase have a ring of specialised cells, called bundle sheath cells, around the vascular bundles (veins) in their leaves. PEP carboxylase forms part of a carbon dioxide pumping mechanism. Oxaloacetate can be converted to malate in the leaf mesophyll cells and transferred to the bundle sheath cells. Here 4 carbon malate is converted to 3 carbon pyruvate, yielding carbon dioxide and reducing NADP to NADPH for use in the C_3 carbon fixing cycle. This keeps carbon dioxide levels high, so that Rubisco is used almost entirely as a carboxylase, minimising photorespiration.

In sunny tropical habitats, the rate of photosynthesis is very high and carbon dioxide levels would be kept very low inside leaves. C_4 plants use a variety of pathways to raise carbon dioxide concentration and supply NADPH for more efficient C_3 carbon fixation.

Figure 2 Maize and many tropical grasses are C_4 plants.

CAM plants

CAM is short for Crassulacean Acid Metabolism. It is a type of photosynthesis that was discovered in the *Crassulaceae* family of succulents, which include sedums. So the name refers to acid metabolism in *Crassulaceae*, not the metabolism of Crassulacean acid.

CAM are C_4 plants that fix carbon dioxide during the night. They store it as 4 carbon malate, releasing carbon dioxide during daylight when the light dependent reactions of photosynthesis can take place.

This allows the plants to survive in very hot, dry conditions. They are able to conserve water by shutting their stomata during the hot part of the day, to reduce water loss by transpiration. They only open them at night, when temperatures are low and transpiration rates are at their minimum.

During the night carbon dioxide enters through the open stomata, and is fixed by PEP carboxylase as oxaloacetate. This is converted to malate which accumulates in cell vacuoles, giving a store of fixed carbon.

During the day the stomata close. ATP and NADPH are formed in the light dependent reactions. Malate is removed from the vacuoles and decarboxylated, releasing carbon dioxide to be refixed by Rubisco to enter the Calvin cycle.

Figure 3 CAM plants like pineapples can grow in conditions that would be far too dry for C_3 plants. The latter typically lose 97% of the water that they take in through their roots in transpiration through the stomata.

Finding out

Rubisco catalyses the reaction between ribulose-1,5-bisphosphate and carbon dioxide. This is a carbon-fixation reaction. The product is glycerate 3-phosphate.

What is the structure of ribulose-1,5-bisphosphate?

What is the structure of glycerate 3-phosphate?