

3.3

Light-independent reactions

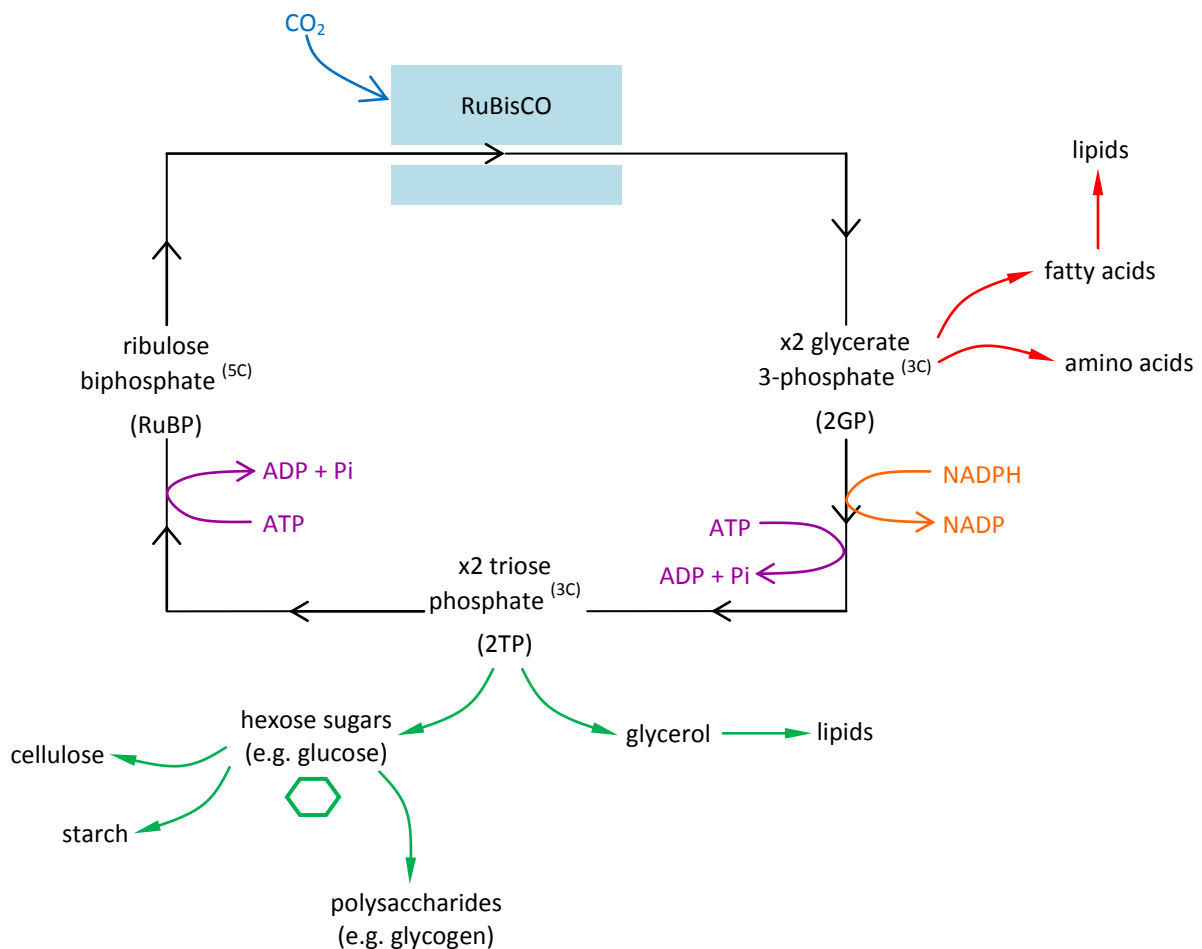
Stage two of photosynthesis: the Calvin cycle

The **light-independent** stage of photosynthesis is the second and final set of reactions. It is named so because the reactions involved do *not* need light to occur, and so technically can take place without light. However, the products (ATP and reduced NADP) of the light-dependent reactions are required, and so in practice, these reactions will not continue for very long without light, as the light-dependent stage will stop producing ATP and NADPH.

The light-independent reactions occur in the **stroma** of the chloroplast (fluid matrix surrounding the grana). It is also called the **Calvin cycle**, named after Melvin Calvin et al. (1946-53). Whilst the products of the light-dependent stage (ATP and NADPH) are needed for this stage, carbon dioxide is also required. This comes from the atmosphere. Carbon dioxide diffuses through the stomata of leaves, and enters leaf cells and then the chloroplasts.

The Calvin cycle

The Calvin cycle cannot take place without carbon dioxide. When it enters a leaf, *diffusing* through stomata (almost exclusively on the underside of the leaf), it diffuses through tiny air spaces in the **spongy mesophyll** layer, until it reaches the **palisade** mesophyll layer. It then diffuses through a thin cellulose cell wall, the plasma membrane, the cytoplasm and through the chloroplast envelope (double membrane), into the stroma.



- 1 The carbon dioxide combines with a molecule called **ribulose biphosphate (RuBP)**, a five-carbon compound and a carbon dioxide acceptor. This reaction is catalysed by **RuBisCO** (ribulose biphosphate carboxylase-oxygenase), an enzyme which adds a carboxyl group to the RuBP molecule
- 2 This combination forms an unstable six-carbon compound, before splitting into the products of the reaction, which are two molecules of **glycerate 3-phosphate (GP)**, a three-carbon compound, and at this stage the carbon dioxide is fixed

- 3 The GP molecules are **reduced** (using two hydrogen atoms donated by reduced NADP from the light-dependent stage) and then **phosphorylated** (using an inorganic phosphate group from one molecule of ATP, also from the light-dependent stage) to form another three-carbon compound called **triose phosphate** (either **TP** or **GALP**)
- 4 Five out of every six molecules of TP/GALP are recycled via phosphorylation (using another ATP molecule from the light-dependent stage of photosynthesis) into three more molecules of RuBP (five-carbon compound), the remaining molecule of TP produced (per molecule of RuBP) can be used to form other biological molecules (see below)

Formation of products

Fairly obviously, the Calvin cycle would be of no use if all of these products went around producing no other products. Fortunately, some molecules which are found in these reactions can be used to synthesise other molecules which are of use to organisms:

- one of every six molecules of TP/GALP produced are *not* recycled as RuBP, but are actually used to make other biological molecules such as saccharides – two molecules of TP can combine to form a hexose sugar, e.g. **glucose** and such structures can polymerise to form starches, sugars and cellulose
- molecules of GP can be used to form amino acids and fatty acids
- TP can also be used to form glycerol, which can combine with the fatty acids made by GP to form various **lipids**

RuBisCO

The enzyme RuBisCO (short for *ribulose biphosphate carboxylase-oxygenase*) is the most abundant enzyme on earth, as it makes approximately 50% of leaf protein. It is of utmost importance to life. Although you can see that the Calvin cycle uses RuBisCO to combine a molecule of RuBP and carbon dioxide, as the name of RuBisCO suggests, oxygen can also fit into the enzyme complex. This results in a reaction called **photorespiration**.

Photorespiration is a process whereby oxygen combines with RuBP in the place of carbon dioxide. This lowers the efficiency of photosynthesis in plants, as this undoes a lot of the work of the process so far and also leads to the formation of the toxic hydrogen peroxide.

When photorespiration begins to occur, i.e. when there is a high concentration of oxygen in the atmosphere in relation to the concentration of carbon dioxide, the reactions catalysed by RuBisCO produce two products: **phosphoglycerate** (PGA) and **phosphoglycolate** (PPG). PGA re-enters the Calvin cycle, being converted back into RuBP, and so is not too problematic, but this does slow down rate of photosynthesis somewhat. PPG, however, is much more difficult to get rid of, as it has to leave the chloroplast and enter mitochondria (among other organelles), undergoing a long series of reactions before the end products can re-enter the Calvin cycle. This obviously lowers photosynthetic efficiency.

So why does RuBisCO have oxygenase functions? Due to the controversial functions of photorespiration, there is no exact answer at the moment, although many scientists have speculated. Certain theories have suggested that, since the combination of RuBP and oxygen leads to the formation of hydrogen peroxide (H₂O₂), it is to aid homeostatic mechanisms as this substance makes a key contribution to cellular redox homeostasis. It has also been suggested that RuBisCO allows oxygen to combine with RuBP to stop free ATP and NADP from mixing with oxygen and forming **radicals** (compounds with unpaired electrons and incomplete outer energy levels) which can damage the cell's metabolic function.