The Calvin cycle

How the products of the light reactions, ATP and NADPH, are used to fix carbon into sugars in the second stage of photosynthesis.

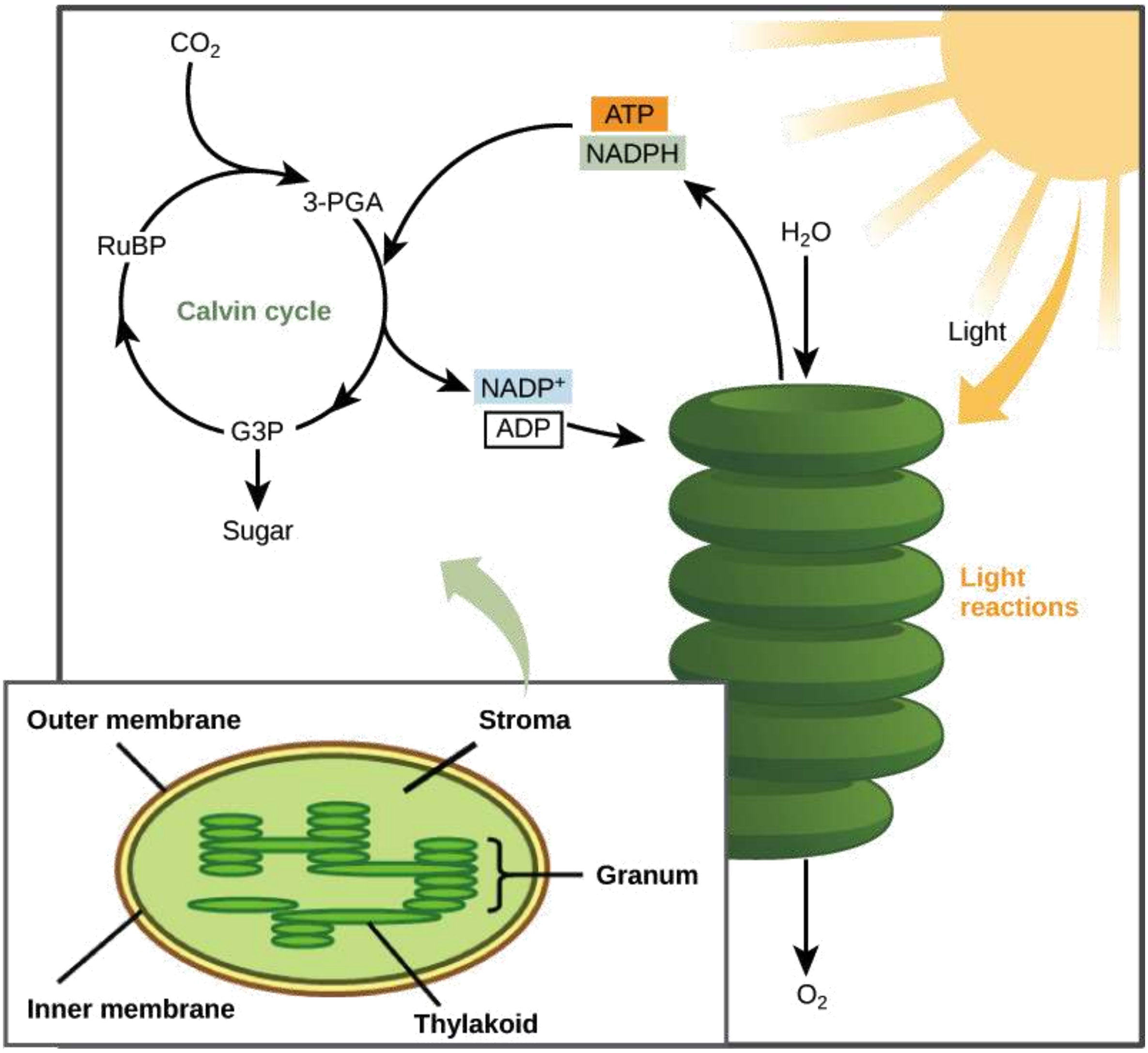
Introduction

You, like all organisms on Earth, are a carbon-based life form. In other words, the complex molecules of your amazing body are built on carbon backbones. You might already know that you’re carbon-based, but have you ever wondered where all of that carbon comes from?
As it turns out, the atoms of carbon in your body were once part of carbon dioxide (CO_2) molecules in the air. Carbon atoms end up in you, and in other life forms, thanks to the second stage of photosynthesis, known as the **Calvin cycle** (or the **light-independent reactions**).

Overview of the Calvin cycle

In plants, carbon dioxide (CO_2) enters the interior of a leaf via pores called stomata and diffuses into the stroma of the chloroplast—the site of the **Calvin cycle** reactions, where sugar is synthesized. These reactions are also called the **light-independent** reactions because they are not directly driven by light.

In the Calvin cycle, carbon atoms from CO_2 are **fixed** (incorporated into organic molecules) and used to build three-carbon sugars. This process is fuelled by, and dependent on, ATP and NADPH from the light reactions. Unlike the light reactions, which take place in the thylakoid membrane, the reactions of the Calvin cycle take place in the stroma (the inner space of chloroplasts).



This illustration shows that ATP and NADPH produced in the light reactions are used in the Calvin cycle to make sugar.

Reactions of the Calvin cycle

The Calvin cycle reactions can be divided into three main stages: carbon fixation, reduction, and regeneration of the starting molecule.
Here is a general diagram of the cycle:

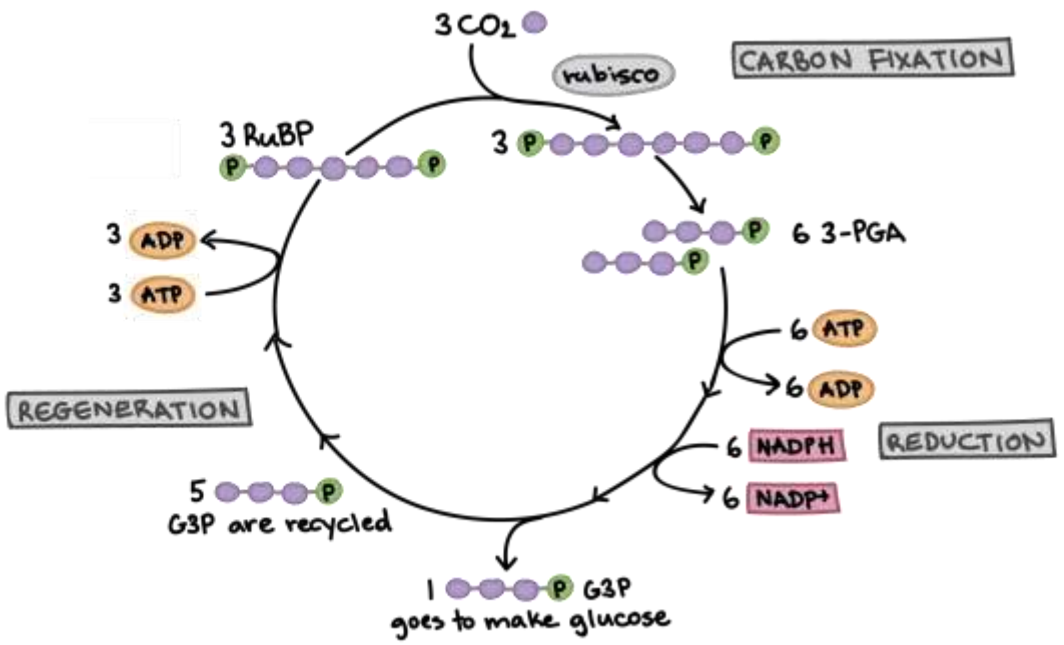
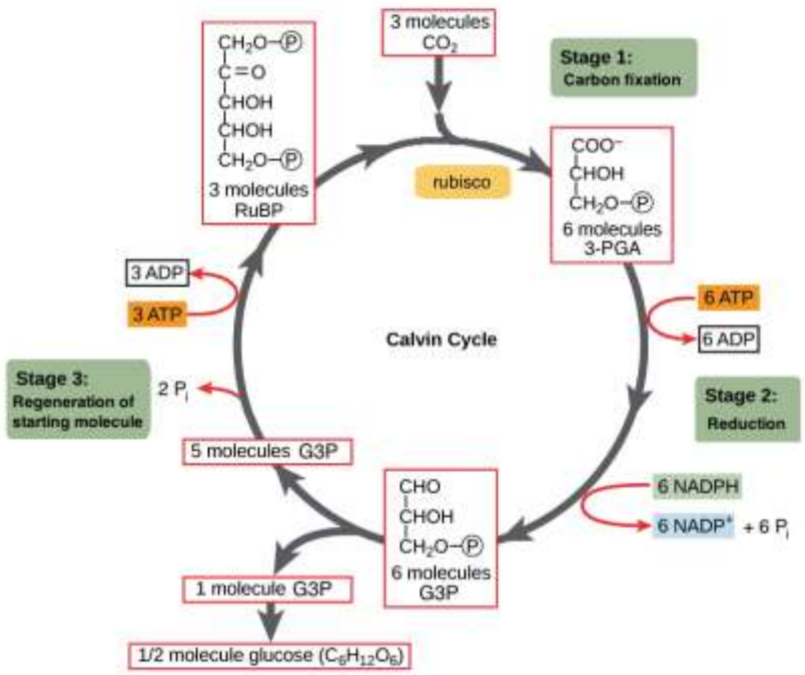


Diagram of the Calvin cycle, illustrating how the fixation of three carbon dioxide molecules allows one net G3P molecule to be produced (that is, allows one G3P molecule to leave the cycle).
3 CO_2 molecules combine with three molecules of the five-carbon acceptor molecule (RuBP), yielding three molecules of an unstable six-carbon compound that splits to form six molecules of a three-carbon compound (3-PGA). This reaction is catalysed by the enzyme rubisco.
In the second stage, six ATP and six NADPH are used to convert the six 3-PGA molecules into six molecules of a three-carbon sugar (G3P). This reaction is considered a reduction because NADPH must donate its electrons to a three-carbon intermediate to make G3P.

3. **Regeneration.** One G3P molecule leaves the cycle and will go towards making glucose, while five G3Ps must be recycled to regenerate the RuBP acceptor. Regeneration involves a complex series of reactions and requires ATP.



1) Fixation. For every three turns of the Calvin cycle, three atoms of carbon are fixed from three molecules of carbon dioxide. In the carbon fixation stage, carbon dioxide is attached to RuBP by

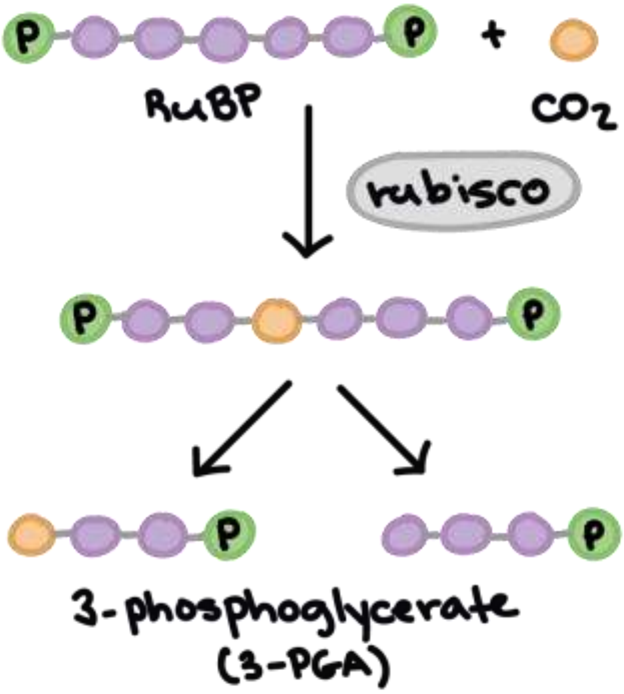
the enzyme rubisco. The resulting 6-carbon product quickly splits into two molecules of a three-carbon compound (3-phosphoglycerate). When three carbon dioxide molecules enter the cycle, six molecules of 3-phosphoglycerate are produced.

2) Reduction. In the reduction stage, each 3-phosphoglycerate first gains a phosphate group from an ATP molecule (which is converted to ADP). The phosphorylated molecule is then reduced by NADPH (which is converted to $NADP^+$ and H^+) in a reaction that releases a phosphate group. The net result of this process is conversion of a 3-phosphoglycerate molecule into a molecule of the three-carbon sugar glyceraldehyde 3-phosphate (G3P). In three turns of the cycle, six molecules of G3P are produced, six ATP are converted to ADP and Pi, and six NADPH are converted to $NADP^+$ and H^+.

3) Regeneration. For every three turns, one molecule of G3P exits the cycle and goes towards making glucose. (Two G3Ps can combine to make one glucose, so one G3P can be thought of as "half" a glucose molecule.) The other five G3P molecules are recycled to regenerate three molecules of RuBP, the starting compound of the cycle. In the regeneration stage, the five G3Ps are reorganized into three five-carbon compounds through a complex series of reactions. Each five-carbon compound ultimately gains a phosphate from ATP (which is converted to ADP) to regenerate the starting molecule, RuBP. For three turns of the cycle, three RuBPs are produced and three ATPs are converted to ADP.

1. **Carbon fixation.** A $CO2$ molecule combines with a five-carbon acceptor molecule, ribulose-1,5-bisphosphate (**RuBP**). This step makes a six-carbon compound that splits into two molecules of a three-carbon compound, 3-phosphoglyceric acid (3-PGA). This reaction is catalyzed by the enzyme RuBP carboxylase/oxygenase, or **rubisco**.

   The first stage of the Calvin cycle incorporates carbon from CO_2 into an organic molecule, a process called **carbon fixation**. In plants, atmospheric CO_2 enters the mesophyll layer of leaves by passing through pores on the leaf surface called stomata. It can then diffuse into mesophyll cells, and into the stroma of chloroplasts, where the Calvin cycle takes place.



Simplified diagram (showing carbon atoms but not full molecular structures) illustrating the reaction catalysed by rubisco. Rubisco attaches a carbon dioxide molecule to an RuBP molecule, and the six-carbon intermediate thus produced breaks down into two 3-phosphoglycerate (3-PGA) molecules.

In the first step of the cycle, an enzyme nicknamed **rubisco** (RuBP carboxylase-oxygenase) catalyses attachment of CO_2 to a five-carbon sugar called **ribulose bisphosphate (RuBP**). The resulting 6-carbon molecule is unstable, however, and quickly splits into two molecules of a three-carbon compound called 3-phosphoglycerate (3-PGA). Thus, for each CO_2 that enters the cycle, two 3-PGA molecules are produced.

The actual molecular structures are show below:

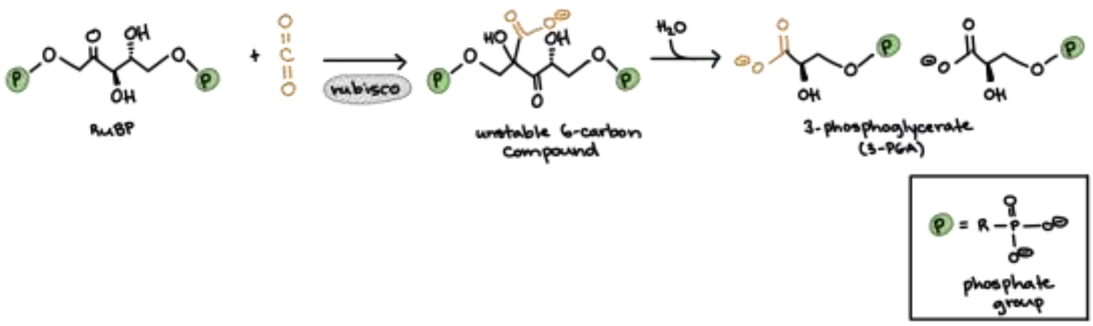
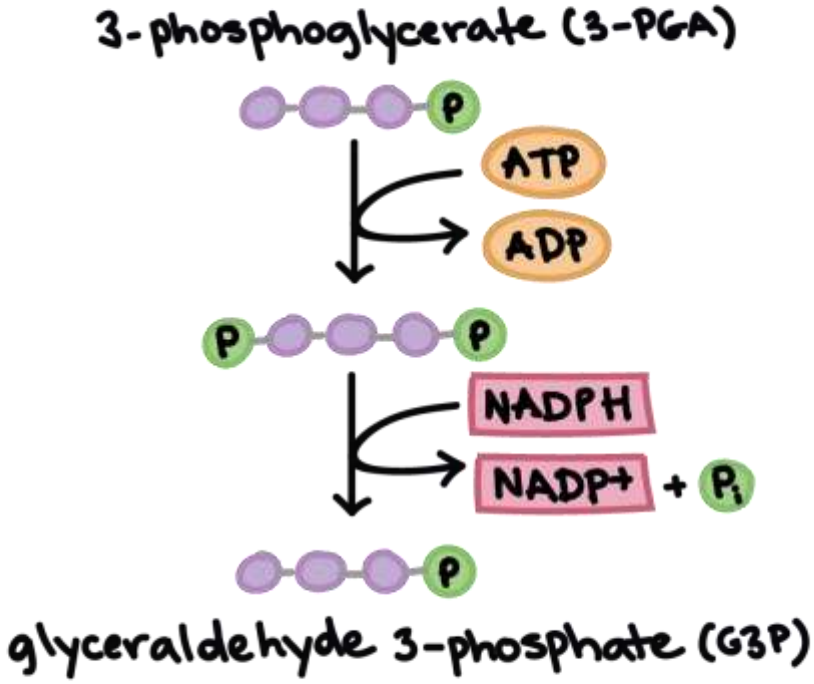


Diagram showing the molecular structures of RuBP and carbon dioxide, the unstable six-carbon intermediate formed when they combine, and the two 3-PGA molecules produced by the intermediate's breakdown.

2. **Reduction.** In the second stage, ATP and NADPH are used to convert the 3-PGA molecules into molecules of a three-carbon sugar, glyceraldehyde-3-phosphate (**G3P**). This stage gets its name because NADPH donates electrons to, or **reduces**, a three-carbon intermediate to make G3P.

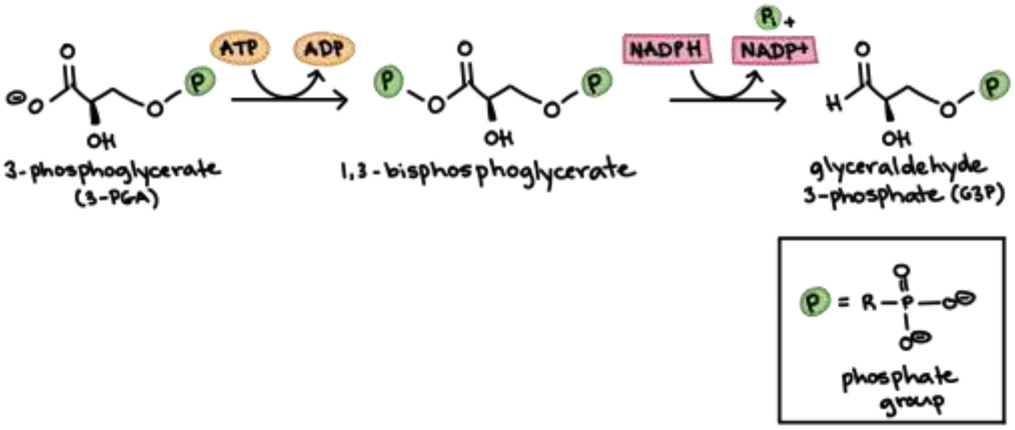
   The reduction stage of the Calvin cycle, which requires ATP and NADPH, converts 3-PGA (from the fixation stage) into a three-carbon sugar. This process occurs in two major steps:



Simplified diagram of the reduction stage of the Calvin cycle, showing carbon atoms but not full molecular structures. A molecule of 3-PGA first receives a second phosphate group from ATP (generating ADP). Then, the doubly phosphorylated molecule receives electrons from NADPH and is reduced to form glyceraldehyde-3-phosphate. This reaction generates $NADP^+$ and also releases an inorganic phosphate.

- First, each molecule of 3-PGA receives a phosphate group from ATP, turning into a doubly phosphorylated molecule called 1,3-bisphosphoglycerate (and leaving behind ADP as a by-product).
- Second, the 1,3-bisphosphoglycerate molecules are reduced (gain electrons). Each molecule receives two electrons from NADPH and loses one of its phosphate groups, turning into a three-carbon sugar called **glyceraldehyde 3-phosphate (G3P)**. This step produces $NADP^+$ and phosphate (P_i) as by-products.

The actual chemical structures and reactions are:



Reactions of the reduction stage of the Calvin cycle, showing the molecular structures of the molecules involved.

The ATP and NADPH used in these steps are both products of the light-dependent reactions (the first stage of photosynthesis). That is, the chemical energy of ATP and the reducing power of NADPH, both of which are generated using light energy, keep the Calvin cycle running. Reciprocally, the Calvin cycle regenerates ADP and $NADP^+$, providing the substrates needed by the light-dependent reactions.

3. **Regeneration.** Some G3P molecules go to make glucose, while others must be recycled to regenerate the RuBP acceptor. Regeneration requires ATP and involves a complex network of reactions, which my college bio professor liked to call the "carbohydrate scramble."

In order for one G3P to exit the cycle (and go towards glucose synthesis), three CO_2 molecules must enter the cycle, providing three new atoms of fixed carbon. When three CO_2 molecules enter the cycle, six G3P molecules are made. One exits the cycle and is used to make glucose, while the other five must be recycled to regenerate three molecules of the RuBP acceptor.

Summary of Calvin cycle reactants and products

Three turns of the Calvin cycle are needed to make one G3P molecule that can exit the cycle and go towards making glucose. Let's summarize the quantities of key molecules that enter and exit the Calvin cycle as one net G3P is made. In three turns of the Calvin cycle:

- **Carbon.** 3 CO_2 combine with 3 RuBP acceptors, making 6 molecules of glyceraldehyde-3-phosphate (G3P).
  - 1 G3P molecule exits the cycle and goes towards making glucose.
  - 5 G3P molecules are recycled, regenerating 3 RuBP acceptor molecules.
- **ATP.** 9 ATP are converted to 9 ADP (6 during the fixation step, 3 during the regeneration step).
- **NADPH**. 6 NADPH are converted to 6 $NADP^+$ (during the fixation step).

A G3P molecule contains three fixed carbon atoms, so it takes two G3Ps to build a six-carbon glucose molecule. It would take six turns of the cycle, or 6 CO_2, 18 ATP, and 12 NADPH, to produce one molecule of glucose.