Making More ATP

- The passage of an electron from water to NADPH in the noncyclic photophosphorylation described previously generates one molecule of NADPH and slightly more than one molecule of ATP. However, building organic molecules takes more energy than that—it takes one-and-a-half ATP molecules per NADPH molecule to fix carbon. To produce the extra ATP, many plant species are capable of short-circuiting photosystem I, switching photosynthesis into a cyclic photophosphorylation mode, so that the light-excited electron leaving photosystem I is used to make ATP instead of NADPH.

- The energetic electron is simply passed back to the b6-f complex rather than passing on to $NADP^+$. The b6-f complex pumps out a proton, adding to the proton gradient driving the chemiosmotic synthesis of ATP.

- The relative proportions of cyclic and noncyclic photophosphorylation in these plants determines the relative amounts of ATP and NADPH available for building organic molecules.
- The electrons that photosynthesis strips from water molecules provide the energy to form ATP and NADPH. The residual oxygen atoms of the water molecules combine to form oxygen gas.

The Calvin Cycle

- Photosynthesis is a way of making organic molecules from carbon dioxide (CO_2). These organic molecules contain many C—H bonds and are highly reduced compared with CO_2. To build organic molecules, cells use raw materials provided by the light reactions:
- **1. Energy.** ATP (provided by cyclic and noncyclic photophosphorylation) drives the endergonic* reactions
- **2. Reducing power.** NADPH (provided by photosystem I) provides a source of hydrogens and the energetic electrons needed to bind them to carbon atoms. Much of the light energy captured in photosynthesis ends up invested in the energy-rich C—H bonds of sugars.

(*in an endergonic reaction, the energy released due to cellular respiration is used forthe reactions within the cell).

Carbon Fixation

- The key step in the Calvin cycle—the event that makes the reduction of CO_2 possible—is the attachment of CO_2 to a very special organic molecule. Photosynthetic cells produce this molecule by reassembling the bonds of two intermediates in glycolysis, fructose 6-phosphate and glyceraldehyde 3-phosphate, to form the energy-rich five-carbon sugar, ribulose 1,5-bisphosphate (RuBP), and a four-carbon sugar. CO_2 binds to RuBP in the key process called **carbon fixation**, forming two three-carbon molecules of phosphoglycerate (PGA)

- The enzyme that carries out this reaction, ribulose bisphosphate carboxylase/oxygenase (usually abbreviated as rubisco) is a very large four-subunit enzyme present in the chloroplast stroma. This enzyme works very slowly, processing only about three molecules of RuBP per second (a typical enzyme processes about 1000 substrate molecules per second). Because it works so slowly, many molecules of rubisco are needed. In a typical leaf, over 50% of all the protein is rubisco. It is thought to be the most abundant protein on earth.

Discovering the Calvin Cycle

- Nearly 100 years ago, Blackman concluded that, because of its temperature dependence, photosynthesis might involve enzyme-catalyzed reactions. These reactions form a cycle of enzyme-catalyzed steps similar to the Krebs cycle.
- This cycle of reactions is called the Calvin cycle, after its discoverer, Melvin Calvin of the University of California, Berkeley. Because the cycle begins when CO_2 binds RuBP to form PGA, and PGA contains three carbon atoms, this process is also called C3 photosynthesis.

The Energy Cycle

- The energy-capturing metabolisms of the chloroplasts and the mitochondria are intimately related. Photosynthesis uses the products of respiration as starting substrates, and respiration uses the products of photosynthesis as its starting substrates. The Calvin cycle even uses part of the ancient glycolytic pathway, run in reverse, to produce glucose. And, the principal proteins involved in electron transport in plants are related to those in mitochondria, and in many cases are actually the same.

- Chloroplasts put ATP and NADPH to work building carbon-based molecules, a process that essentially reverses the breakdown of such molecules that occurs in mitochondria. Taken together, chloroplasts and mitochondria carry out a cycle in which energy enters from the sun and leaves as heat and work.

Reactions of the Calvin Cycle

- In a series of reactions three molecules of CO_2 are fixed by rubisco to produce six molecules of PGA (containing 6 × 3 = 18 carbon atoms in all, three from CO_2 and 15 from RuBP). The 18 carbon atoms then undergo a cycle of reactions that regenerates the three molecules of RuBP used in the initial step (containing 3 × 5 = 15 carbon atoms). This leaves one molecule of glyceraldehyde 3-phosphate (three carbon atoms) as the net gain.

- The net equation of the Calvin cycle is:

$$3\ CO_2 + 9\ ATP + 6\ NADPH + water \rightarrow glyceraldehyde\ 3\text{-}phosphate + 8\ Pi + 9\ ADP + 6\ NADP^+$$

- With three full turns of the cycle, three molecules of carbon dioxide enter, a molecule of glyceraldehyde 3-phosphate (G3P) is produced, and three molecules of RuBP are regenerated. We now know that light is required indirectly for different segments of the CO_2 reduction reactions.
- Five of the Calvin cycle enzymes—including rubisco—are light activated; that is, they become functional or operate more efficiently in the presence of light. Light also promotes transport of three-carbon intermediates across chloroplast membranes that are required for Calvin cycle reactions. And finally, light promotes the influx of Mg^{++} into the chloroplast stroma, which further activates the enzyme rubisco.

- Output of the Calvin Cycle The glyceraldehyde 3-phosphate that is the product of the Calvin cycle is a three-carbon sugar that is a key intermediate in glycolysis.
- Much of it is exported from the chloroplast to the cytoplasm of the cell, where the reversal of several reactions in glycolysis allows it to be converted to fructose 6-phosphate and glucose 1-phosphate, and from that to sucrose, a major transport sugar in plants (sucrose, common table sugar, is a disaccharide made of fructose and glucose).

- In times of intensive photosynthesis, glyceraldehyde 3-phosphate levels in the stroma of the chloroplast rise.
- As a consequence, some glyceraldehyde 3-phosphate in the chloroplast is converted to glucose 1-phosphate, in an analogous set of reactions to those done in the cytoplasm, by reversing several reactions similar to those of glycolysis.
- The glucose 1-phosphate is then combined into an insoluble polymer, forming long chains of starch stored as bulky starch grains in chloroplasts.

Photorespiration

- Evolution does not necessarily result in optimum solutions. Rather, it favours workable solutions that can be derived from others that already exist. Photosynthesis is no exception. Rubisco, the enzyme that catalyses the key carbon-fixing reaction of photosynthesis, provides a decidedly suboptimal solution. This enzyme has a second enzyme activity that interferes with the Calvin cycle, oxidizing ribulose 1,5- bisphosphate. In this process, called photorespiration, O_2 is incorporated into ribulose 1,5-bisphosphate, which undergoes additional reactions that actually release CO_2. Hence, photorespiration releases CO_2—essentially undoing the Calvin cycle which reduces CO_2 to carbohydrate.

The C4 Pathway

- Plants that adapted to these warmer environments have evolved two principal ways that use the C4 pathway to deal with this problem. In one approach, plants conduct C4 photosynthesis in the mesophyll cells and the Calvin cycle in the bundle sheath cells. This creates high local levels of CO_2 to favour the carboxylation reaction of rubisco. These plants are called C4 plants and include corn sugarcane, sorghum, and a number of other grasses.

- In the C4 pathway, the three-carbon metabolite phosphoenolpyruvate is carboxylated to form the four-carbon molecule oxaloacetate, which is the first product of CO_2 fixation. In C4 plants, oxaloacetate is in turn converted into the intermediate malate, which is transported to an adjacent bundle-sheath cell. Inside the bundlesheath cell, malate is decarboxylated to produce pyruvate, releasing CO_2. Because bundle-sheath cells are impermeable to CO_2, the $CO_2$is retained within them in high concentrations. Pyruvate returns to the mesophyll cell, where two of the high-energy bonds in an ATP molecule are split to convert the pyruvate back into phosphoenolpyruvate, thus completing the cycle.

The enzymes that carry out the Calvin cycle in a C4 plant are located within the bundle-sheath cells, where the increased CO_2 concentration decreases photorespiration.

Because each CO_2 molecule is transported into the bundlesheath cells at a cost of two high-energy ATP bonds, and since six carbons must be fixed to form a molecule of glucose, 12 additional molecules of ATP are required to form a molecule of glucose. In C4 photosynthesis, the energetic cost of forming glucose is almost twice that of C3 photosynthesis:

30 molecules of ATP versus 18.

Nevertheless, C4 photosynthesis is **advantageous in a hot climate**: photorespiration would otherwise remove more than half of the carbon fixed.

The Crassulacean Acid Pathway

A second strategy to decrease photorespiration in hot regions has been adopted by many succulent (water-storing) plants such as cacti, pineapples, and some members of about two dozen other plant groups. This mode of initial carbon fixation is called crassulacean acid metabolism (CAM), after the plant family Crassulaceae (e.g. the stonecrops (*Sedum* sp.)), in which it was first discovered. In these plants, the stomata (singular, stoma), specialized openings in the leaves of all plants through which CO_2 enters and water vapor is lost, open during the night and close during the day. This pattern of stomatal opening and closing is the reverse of that in most plants. CAM plants open stomata at night and initially fix CO_2 into organic compounds using the C4 pathway.

- These organic compounds accumulate throughout the night and are decarboxylated during the day to yield high levels of CO_2.
- In the day, these high levels of CO_2 drive the Calvin cycle and minimize photorespiration. Like C4 plants, CAM plants use both C4 and C3 pathways.
- They differ from C4 plants in that they use the C4 pathway at night and the C3 pathway during the day within the same cells. In C4 plants, the two pathways take place in different cells.
- Photorespiration results in decreased yields of photosynthesis. C4 and CAM plants circumvent this problem through modifications of leaf architecture and photosynthetic chemistry that locally increase CO_2 concentrations.
- C4 plants isolate CO_2 production spatially, CAM plants temporally.

Factors affecting photosynthesis

If factors affecting photosynthesis are optimum, then photosynthesis is rapid and therefore the plant grows faster. The most important factors among others are:

- CO_2 concentration of the air
- Light intensity
- Temperature
- Mineral elements
- Water
- O_2 concentration
- Chlorophyll amount

- CO_2 concentration: CO_2 ratio in the air is approximately 0.03%. If this amount is increased 10 times, photosynthesis also increased proportionally. However, if this ratio is also increased, photosynthesis can not increase anymore. In greenhouses CO_2 ratio is increased and thus plants perform photosynthesis more.

Even if there is plenty of light, a plant cannot perform photosynthesis if there is insufficient carbon dioxide.

- Light intensity: Without enough light, a plant cannot perform photosynthesis very quickly, even if there is plenty of water and carbon dioxide. Increasing the light intensity will boost the speed of photosynthesis. However in too intense light photosynthesis will not increase any longer. In addition, if sufficient CO_2 is not present, then photosynthesis rate will not increase.

Temperature: If it gets too cold, the rate of photosynthesis will decrease. And also, plants cannot perform photosynthesis if it gets too hot. The effect of temperature varies accroding to the climate. In general, photosynthesis stops in plants growing in the tropics or subtropics aslightly above the freezng point of water. However it continues in plants growing in temperate regions till the freezing point of water. The optimal temperature for photosynthesis in most plants is between +20 and +30°C.

- Mineral elements: Minerals such as Mg, Fe, Mn, K andN has to be present at a sufficient level for photosynthesis.

- Water: Without water, photosynthesis can not be performed. Plants need water both to survive and also as a hydrogen source. A plant uses 1% of water that it gets for photosynthesis.

- O_2 concentration: The atmosphere has 21% oxygen. Above this percentage photosynthesis halts and below it increases.

- Chlorophyll amount: Increase in chlorophyll amount affects photosynthesis positively.

COMPARISON OF PHOTOSYNTHESIS WITH CELLULAR RESPIRATION

	CELLULAR RESPIRATION	PHOTOSYNTHESIS
a) Used substance:	Glucose, lipids, proteins, O_2	CO_2, H_2O
b) Final product:	CO_2, H_2O, Energy	Glucose, H_2O, O_2
c) Chemical change:	Breakdown of organic molecules	Production of organic molecules
d) Occurs when?	Continuously	During daylight
e) Where:	In all living cells	In cells that contain chlorophyll
f) General formula:	A) Cellular respiration: $C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + 38\ ATP$ (via enzyme)	Solar energy B) Photosynthesis: $6CO_2 + 12H_2O \rightarrow C_6H_{12}O_6 + 6H_2O + 6O_2$ (via solar energy)