The Pathways of Photosynthesis (continued)

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4. The Calvin cycle uses ATP and NADPH to convert CO$_2$ to sugar: a closer look

- The Calvin cycle regenerates its starting material after molecules enter and leave the cycle.
- CO$_2$ enters the cycle and leaves as sugar.
- The cycle spends the energy of ATP and the reducing power of electrons carried by NADPHH to make the sugar.
- The actual sugar product of the Calvin cycle is not glucose, but a three-carbon sugar, glyceraldehyde-3-phosphate (G3P).
• Each turn of the Calvin cycle fixes one carbon.

• For the net synthesis of one G3P molecule, the cycle must take place three times, fixing three molecules of CO₂.

• To make one glucose molecules would require six cycles and the fixation of six CO₂ molecules.
• The Calvin cycle has three phases.
• In the carbon fixation phase, each CO$_2$ molecule is attached to a five-carbon sugar, ribulose bisphosphate (RuBP).
  • This is catalyzed by RuBP carboxylase or **rubisco**.
  • The six-carbon intermediate splits in half to form two molecules of 3-phosphoglycerate per CO$_2$. 
Fig. 10.17.1

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• During reduction, each 3-phosphoglycerate receives another phosphate group from ATP to form 1,3 bisphosphoglycerate.

• A pair of electrons from NADPH reduces each 1,3 bisphosphoglycerate to G3P.
  • The electrons reduce a carboxyl group to a carbonyl group.
Fig. 10.17.2
• If our goal was to produce one G3P net, we would start with 3 CO₂ (3C) and three RuBP (15C).

• After fixation and reduction we would have six molecules of G3P (18C).
  • One of these six G3P (3C) is a net gain of carbohydrate.
    • This molecule can exit the cycle to be used by the plant cell.
  • The other five (15C) must remain in the cycle to regenerate three RuBP.
• In the last phase, regeneration of the CO$_2$ acceptor (RuBP), these five G3P molecules are rearranged to form 3 RuBP molecules.

• To do this, the cycle must spend three more molecules of ATP (one per RuBP) to complete the cycle and prepare for the next.
Fig. 10.17.3

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• For the net synthesis of one G3P molecule, the Calvin recycle consumes nine ATP and six NAPDH.
  • It “costs” three ATP and two NADPH per CO$_2$.
• The G3P from the Calvin cycle is the starting material for metabolic pathways that synthesize other organic compounds, including glucose and other carbohydrates.
5. Alternative mechanisms of carbon fixation have evolved in hot, arid climates

• One of the major problems facing terrestrial plants is dehydration.

• At times, solutions to this problem conflict with other metabolic processes, especially photosynthesis.

• The stomata are not only the major route for gas exchange (CO$_2$ in and O$_2$ out), but also for the evaporative loss of water.

• On hot, dry days plants close the stomata to conserve water, but this causes problems for photosynthesis.
• In most plants (C₃ plants) initial fixation of CO₂ occurs via rubisco and results in a three-carbon compound, 3-phosphoglycerate.
  • These plants include rice, wheat, and soybeans.

• When their stomata are closed on a hot, dry day, CO₂ levels drop as CO₂ is consumed in the Calvin cycle.

• At the same time, O₂ levels rise as the light reaction converts light to chemical energy.

• While rubisco normally accepts CO₂, when the O₂/CO₂ ratio increases (on a hot, dry day with closed stomata), rubisco can add O₂ to RuBP.
• When rubisco adds $O_2$ to RuBP, RuBP splits into a three-carbon piece and a two-carbon piece in a process called **photorespiration**.

• The two-carbon fragment is exported from the chloroplast and degraded to $CO_2$ by mitochondria and peroxisomes.

• Unlike normal respiration, this process produces no ATP, nor additional organic molecules.

• Photorespiration **decreases** photosynthetic output by siphoning organic material from the Calvin cycle.
• A hypothesis for the existence of photorespiraton (a
inexact requirement for CO$_2$ versus O$_2$ by rubisco) is
that it is evolutionary baggage.

• When rubisco first evolved, the atmosphere had far
less O$_2$ and more CO$_2$ than it does today.
  • The inability of the active site of rubisco to exclude O$_2$
    would have made little difference.

• Today it does make a difference.
  • Photorespiration can drain away as much as 50% of the
carbon fixed by the Calvin cycle on a hot, dry day.

• Certain plant species have evolved alternate modes
of carbon fixation to minimize photorespiration.
• The C₄ plants fix CO₂ first in a four-carbon compound.
  • Several thousand plants, including sugarcane and corn, use this pathway.

• In C₄ plants, mesophyll cells incorporate CO₂ into organic molecules.
  • The key enzyme, phosphoenolpyruvate carboxylase, adds CO₂ to phosphoenolpyruvate (PEP) to form oxaloacetetate.
  • PEP carboxylase has a very high affinity for CO₂ and can fix CO₂ efficiently when rubisco cannot - on hot, dry days with the stomata closed.
• The mesophyll cells pump these four-carbon compounds into bundle-sheath cells.
  • The bundle sheath cells strip a carbon, as CO$_2$, from the four-carbon compound and return the three-carbon remainder to the mesophyll cells.
  • The bundle sheath cells then uses rubisco to start the Calvin cycle with an abundant supply of CO$_2$. 
Fig. 10.18

C₄ leaf anatomy

Mesophyll cell

Bundle-sheath cell

Vein (vascular tissue)

Stoma

Mesophyll cell

CO₂

PEP carboxylase

Oxaloacetate (4 C)

PEP (3 C)

ADP

Malate (4 C)

Pyruvate (3 C)

CO₂

CALVIN CYCLE

Sugar

The C₄ pathway

Vascular tissue

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• In effect, the mesophyll cells pump CO\textsubscript{2} into the bundle sheath cells, keeping CO\textsubscript{2} levels high enough for rubisco to accept CO\textsubscript{2} and not O\textsubscript{2}.

• C\textsubscript{4} photosynthesis minimizes photorespiration and enhances sugar production.

• C\textsubscript{4} plants thrive in hot regions with intense sunlight.
A second strategy to minimize photorespiration is found in succulent plants, cacti, pineapples, and several other plant families.

- These plants, known as CAM plants for crassulacean acid metabolism (CAM), open stomata during the night and close them during the day.
  - Temperatures are typically lower at night and humidity is higher.
  - During the night, these plants fix CO$_2$ into a variety of organic acids in mesophyll cells.
  - During the day, the light reactions supply ATP and NADPH to the Calvin cycle and CO$_2$ is released from the organic acids.
• Both $C_4$ and CAM plants add $CO_2$ into organic intermediates before it enters the Calvin cycle.

  • In $C_4$ plants, carbon fixation and the Calvin cycle are spatially separated.

  • In CAM plants, carbon fixation and the Calvin cycle are temporally separated.

• Both eventually use the Calvin cycle to incorporate light energy into the production of sugar.
Fig. 10.19  
(a) Spatial separation of steps  
(b) Temporal separation of steps
6. Photosynthesis is the biosphere’s metabolic foundation: a review

- In photosynthesis, the energy that enters the chloroplasts as sunlight becomes stored as chemical energy in organic compounds.
• Sugar made in the chloroplasts supplies the entire plant with chemical energy and carbon skeletons to synthesize all the major organic molecules of cells.

• About 50% of the organic material is consumed as fuel for cellular respiration in plant mitochondria.

• Carbohydrate in the form of the disaccharide sucrose travels via the veins to nonphotosynthetic cells.

• There, it provides fuel for respiration and the raw materials for anabolic pathways including synthesis of proteins and lipids and building the extracellular polysaccharide cellulose.
• Plants also store excess sugar by synthesizing starch.
  • Some is stored as starch in chloroplasts or in storage cells in roots, tubers, seeds, and fruits.

• Heterotrophs, including humans, may completely or partially consume plants for fuel and raw materials.

• On a global scale, photosynthesis is the most important process to the welfare of life on Earth.
  • Each year photosynthesis synthesizes 160 billion metric tons of carbohydrate per year.