Laboratory of Growth Regulators

Miroslav Strnad

Photosynthesis-secondary reactions [chapter 08]

- Univerzita Palackého & Ústav experimentální botaniky AV CR

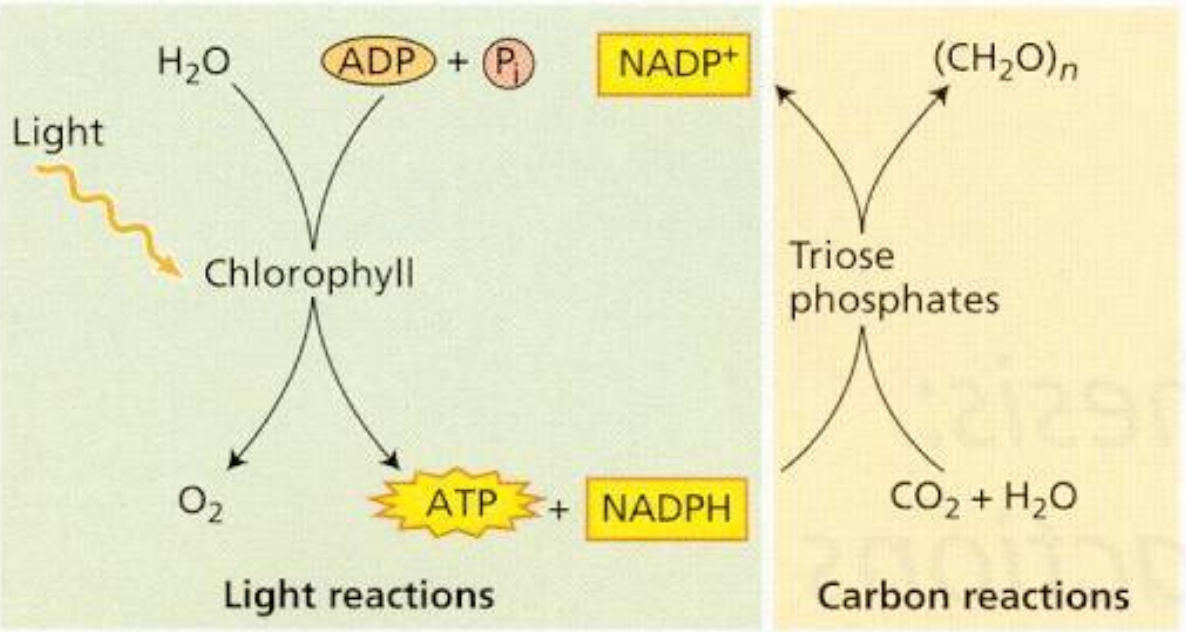


FIGURE 8.1 The light and carbon reactions of photosynthesis. Light is required for the generation of ATP and NADPH. The ATP and NADPH are consumed by the carbon reactions, which reduce CO_2 to carbohydrate (triose phosphates).

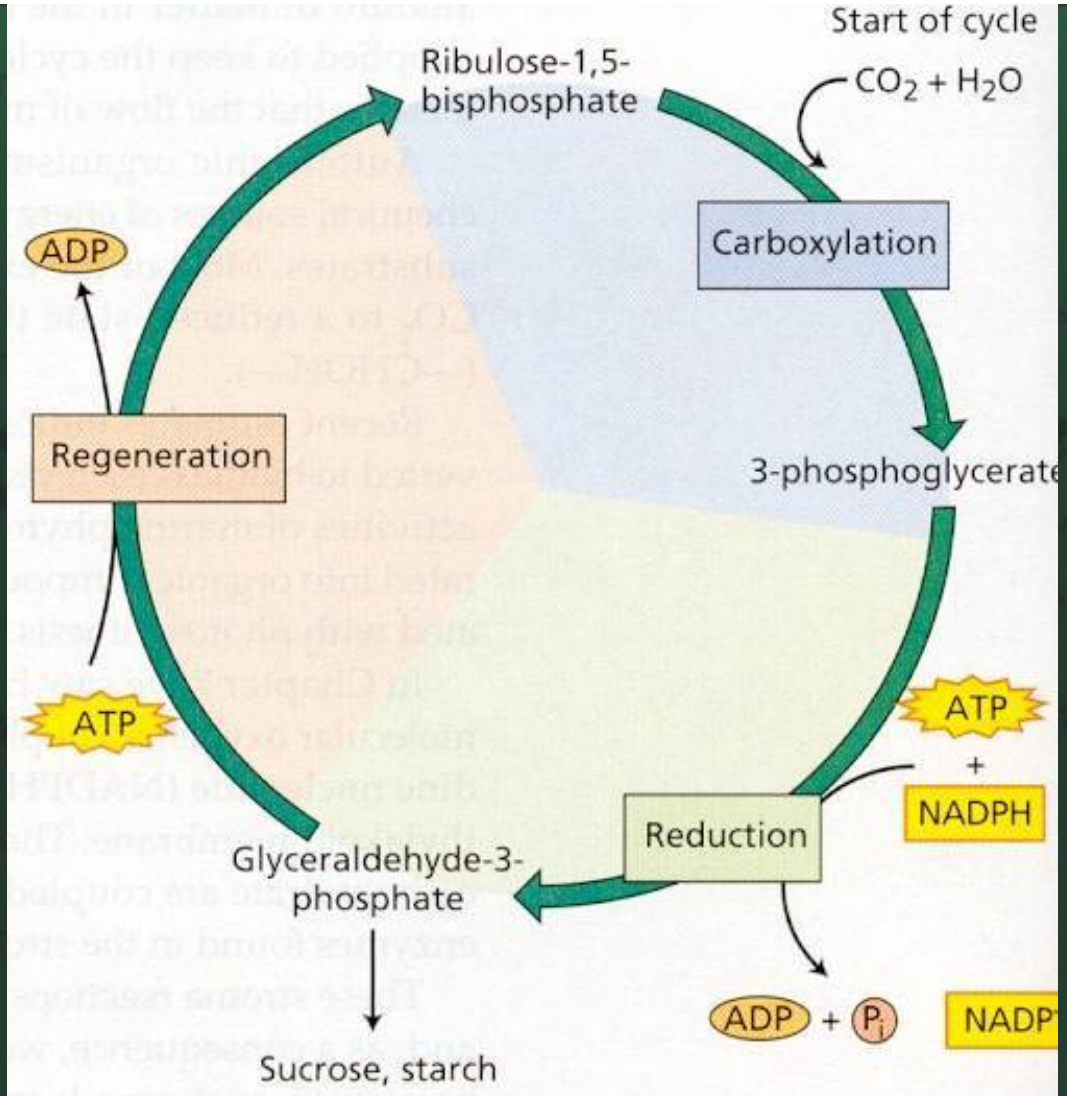


FIGURE 8.2 The Calvin cycle proceeds in three stages: (1) carboxylation, during which CO_2 is covalently linked to a carbon skeleton; (2) reduction, during which carbohydrate is formed at the expense of the photochemically derived ATP and reducing equivalents in the form of NADPH; and (3) regeneration, during which the CO_2 acceptor ribulose-1,5-bisphosphate re-forms.

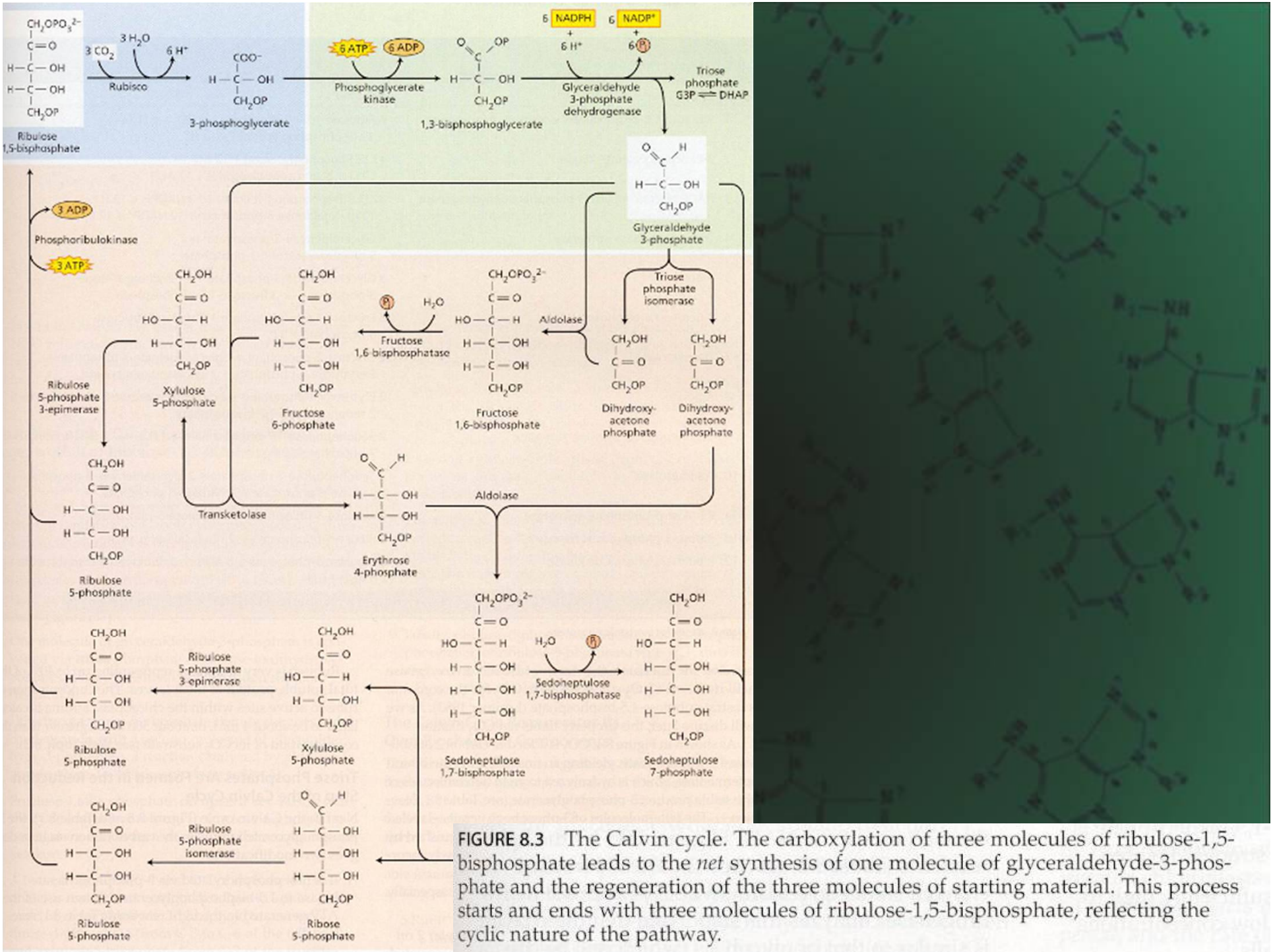


FIGURE 8.3 The Calvin cycle. The carboxylation of three molecules of ribulose-1,5-bisphosphate leads to the *net* synthesis of one molecule of glyceraldehyde-3-phosphate and the regeneration of the three molecules of starting material. This process starts and ends with three molecules of ribulose-1,5-bisphosphate, reflecting the cyclic nature of the pathway.

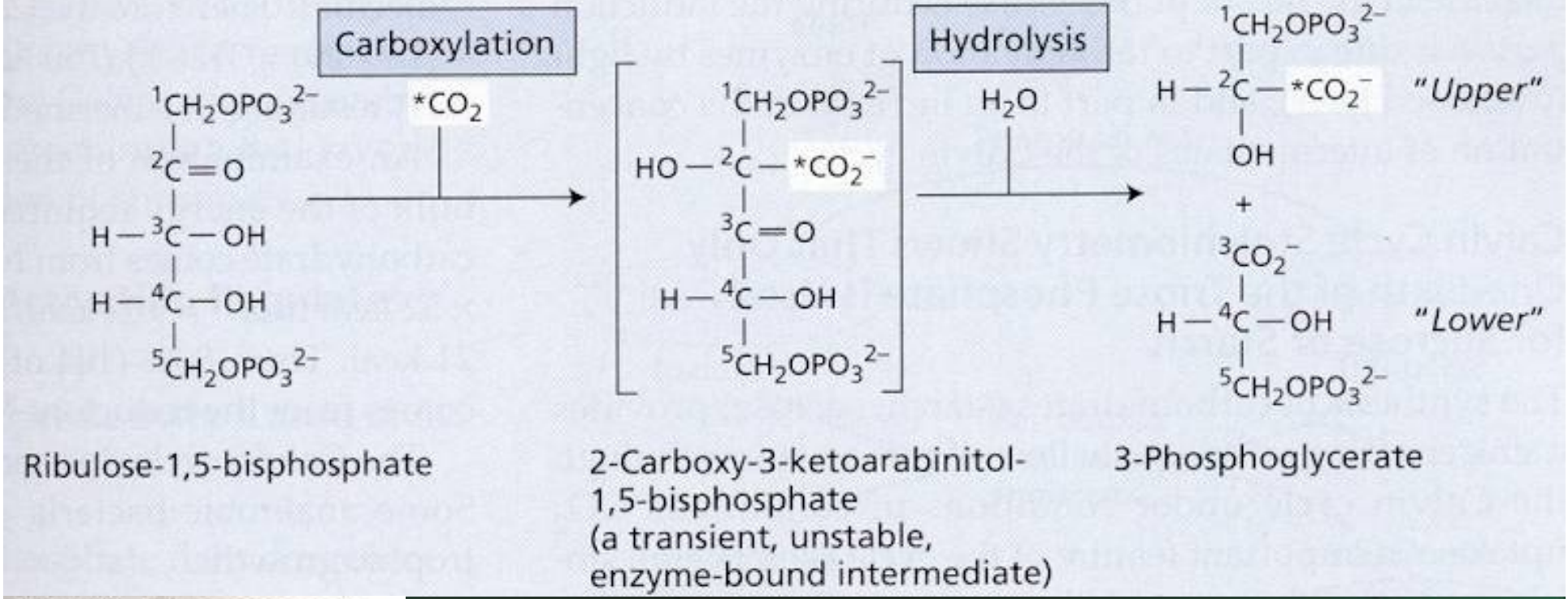


FIGURE 8.4 The carboxylation of ribulose-1,5-bisphosphate by rubisco.

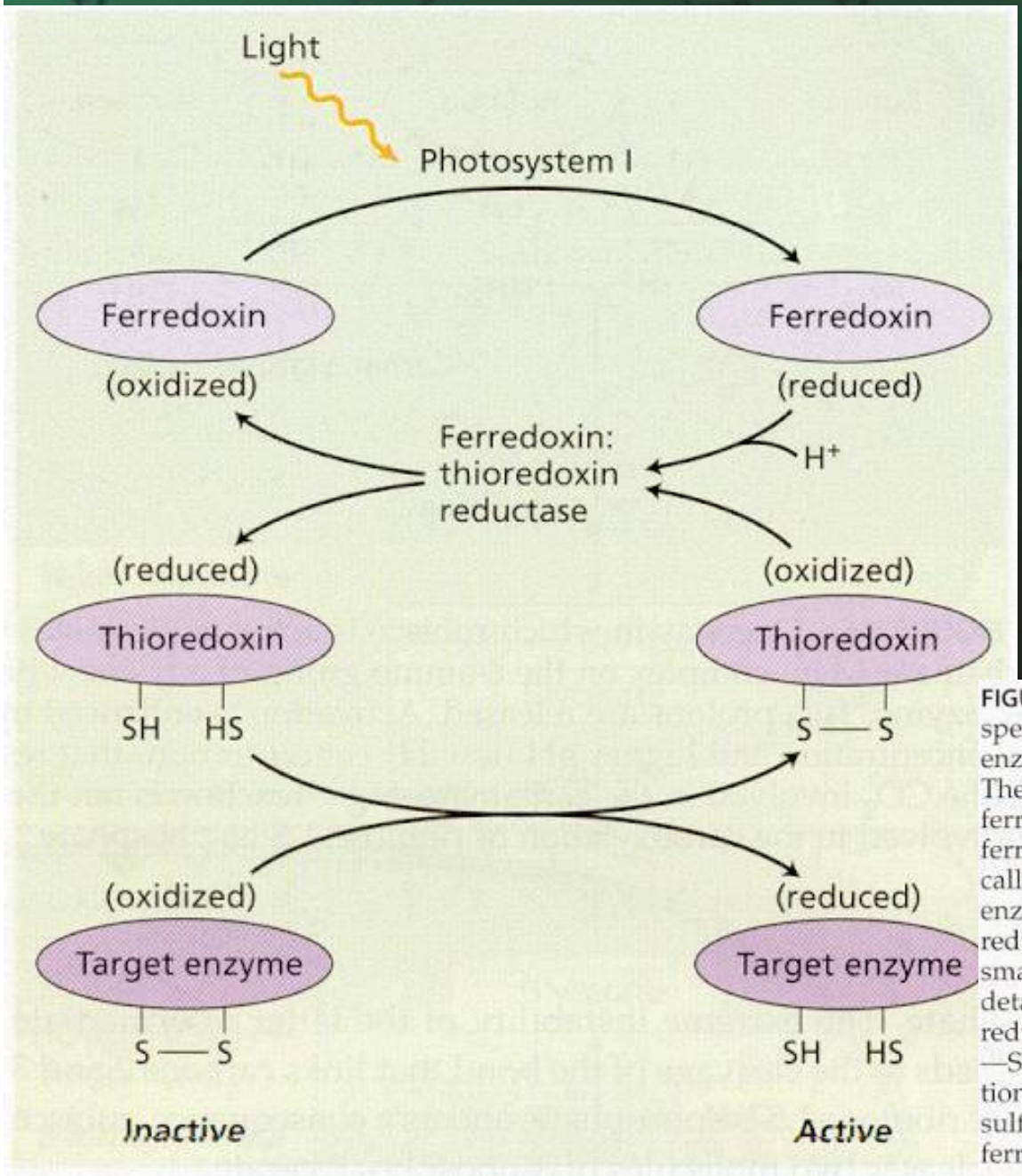


FIGURE 8.5 The ferredoxin–thioredoxin system reduces specific enzymes in the light. Upon reduction, biosynthetic enzymes are converted from an inactive to an active state. The activation process starts in the light by a reduction of ferredoxin by photosystem I (see Chapter 7). The reduced ferredoxin plus two protons are used to reduce a catalytically active disulfide (—S—S—) group of the iron–sulfur enzyme ferredoxin:thioredoxin reductase, which in turn reduces the highly specific disulfide (—S—S—) bond of the small regulatory protein thioredoxin (see Web Topic 8.4 for details). The reduced form (—SH HS—) of thioredoxin then reduces the critical disulfide bond (converts —S—S— to —SH HS—) of a target enzyme and thereby leads to activation of that enzyme. The light signal is thus converted to a sulfhydryl, or —SH, signal via ferredoxin and the enzyme ferredoxin:thioredoxin reductase.

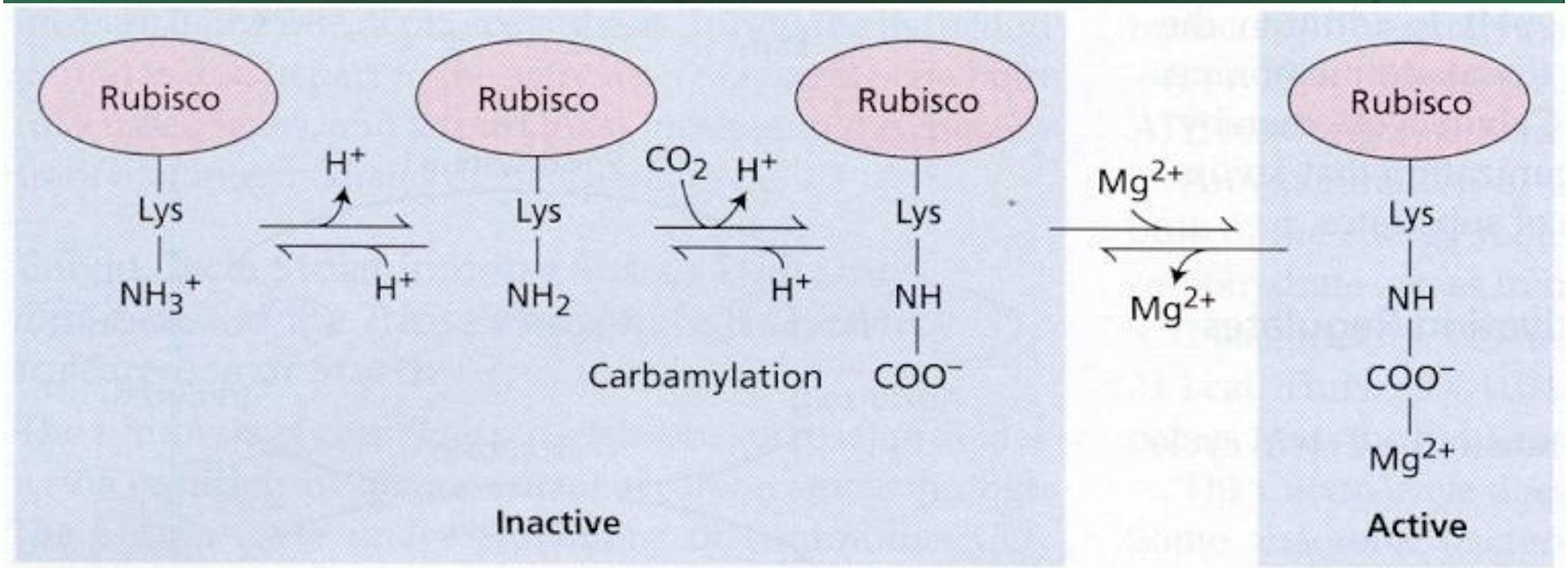


FIGURE 8.6 One way in which rubisco is activated involves the formation of a carbamate–Mg^{2+} complex on the ε-amino group of a lysine within the active site of the enzyme. Two protons are released. Activation is enhanced by the increase in Mg^{2+} concentration and higher pH (low H^+ concentration) that result from illumination. The CO_2 involved in the carbamate–Mg^{2+} reaction is not the same as the CO_2 involved in the carboxylation of ribulose-1,5-bisphosphate.

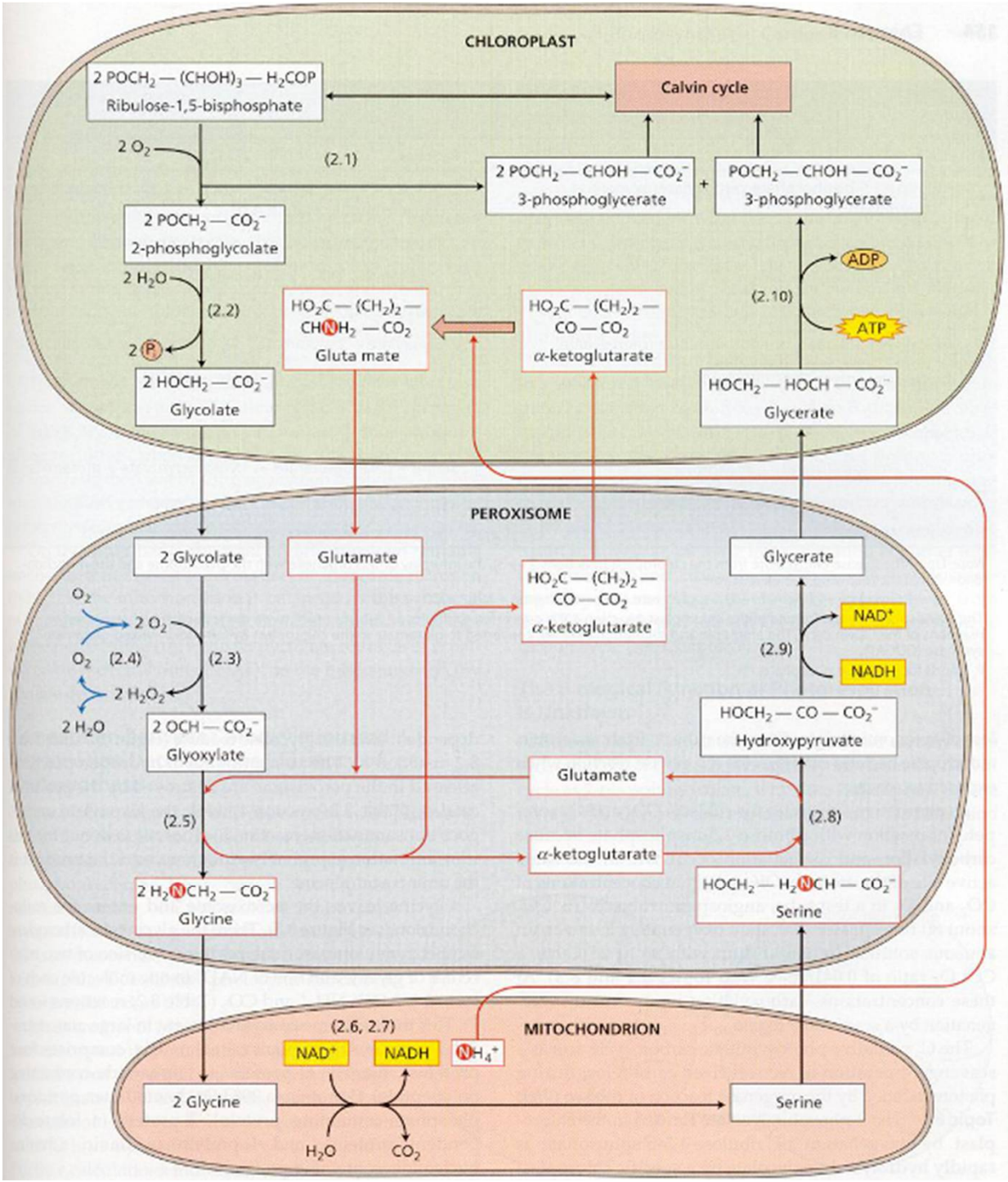
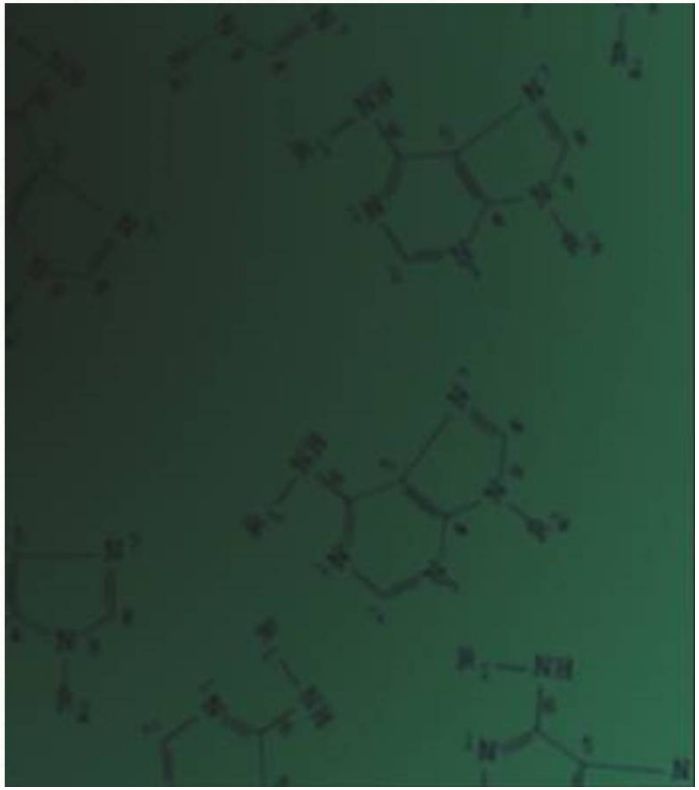


FIGURE 8.7 The main reactions of the photorespiratory cycle. Operation of the C_2 oxidative photosynthetic cycle involves the cooperative interaction among three organelles: chloroplasts, mitochondria, and peroxisomes. Two molecules of glycolate (four carbons) transported from the chloroplast into the peroxisome are converted to glycine, which in turn is exported to the mitochondrion and transformed to serine (three carbons) with the concurrent release of carbon dioxide (one carbon). Serine is transported to the peroxisome and transformed to glycerate. The latter flows to the chloroplast where it is phosphorylated to 3-phosphoglycerate and incorporated into the Calvin cycle. Inorganic nitrogen (ammonia) released by the mitochondrion is captured by the chloroplast for the incorporation into amino acids by using appropiate skeletons (α-ketoglutarate). The heavy arrow in red marks the assimilation of ammonia into glutamate catalyzed by glutamine synthetase. In addition, the uptake of oxygen in the peroxisome supports a short oxygen cycle coupled to oxidative reactions. The flow of carbon, nitrogen and oxygen are indicated in black, red and blue, respectively. See Table 8.2 for a description of each numbered reaction.



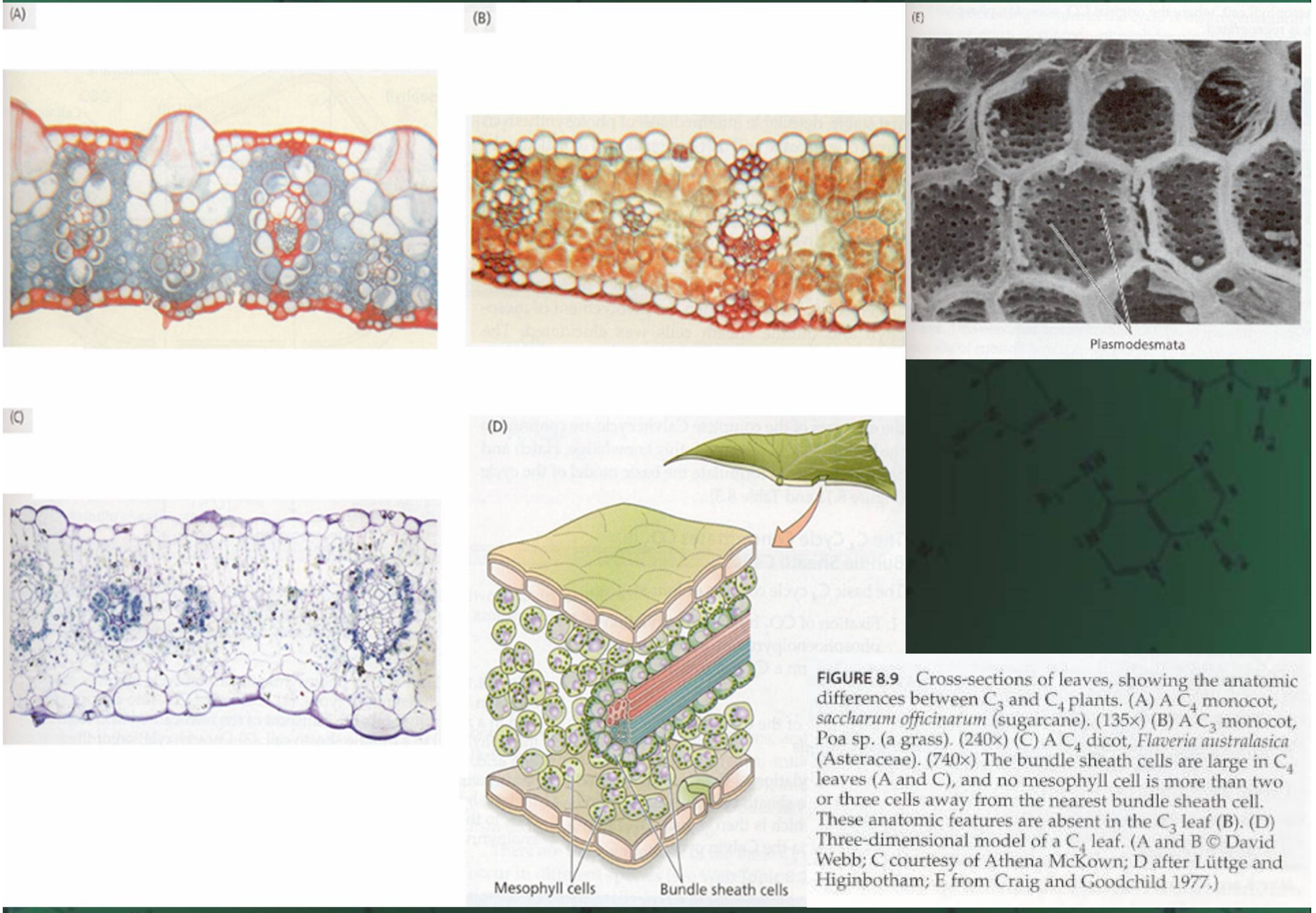


FIGURE 8.9 Cross-sections of leaves, showing the anatomic differences between C_3 and C_4 plants. (A) A C_4 monocot, *saccharum officinarum* (sugarcane). (135×) (B) A C_3 monocot, Poa sp. (a grass). (240×) (C) A C_4 dicot, *Flaveria australasica* (Asteraceae). (740×) The bundle sheath cells are large in C_4 leaves (A and C), and no mesophyll cell is more than two or three cells away from the nearest bundle sheath cell. These anatomic features are absent in the C_3 leaf (B). (D) Three-dimensional model of a C_4 leaf. (A and B © David Webb; C courtesy of Athena McKown; D after Lüttge and Higinbotham; E from Craig and Goodchild 1977.)

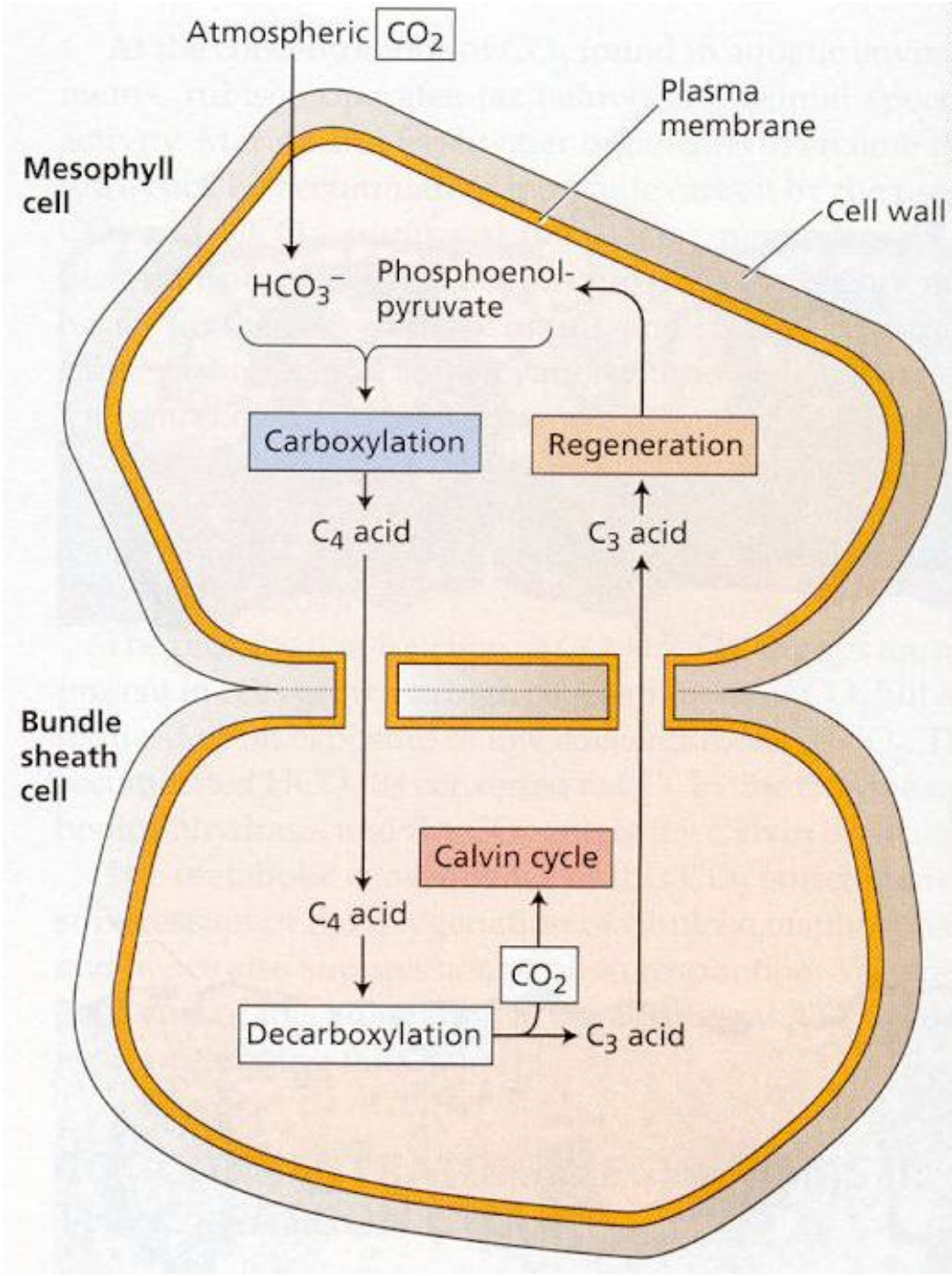
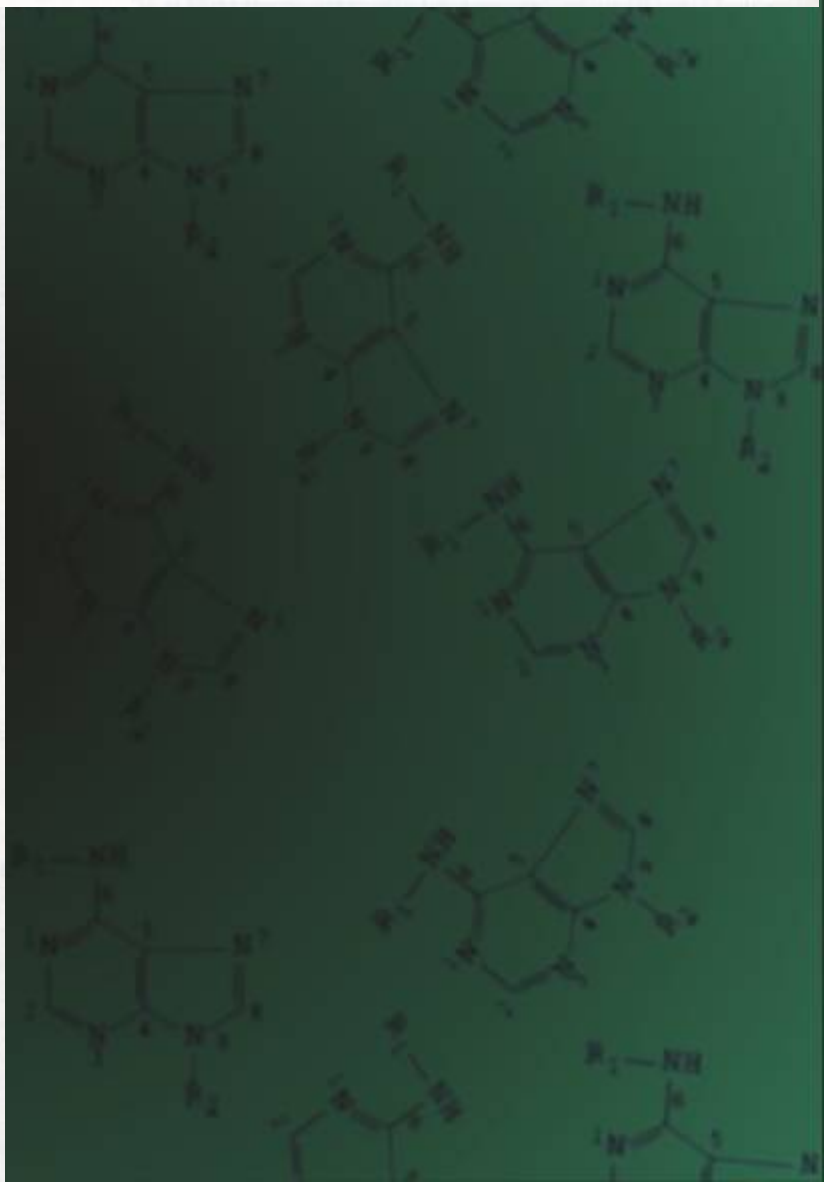


FIGURE 8.10 The basic C_4 photosynthetic carbon cycle involves four stages in two different cell types: (1) Fixation of CO_2 into a four-carbon acid in a mesophyll cell; (2) Transport of the four-carbon acid from the mesophyll cell to a bundle sheath cell; (3) Decarboxylation of the four-carbon acid, and the generation of a high CO_2 concentration in the bundle sheath cell. The CO_2 released is fixed by rubisco and converted to carbohydrate by the Calvin cycle.(4) Transport of the residual three-carbon acid back to the mesophyll cell, where the original CO_2 acceptor, phosphoenolpyruvate, is regenerated.



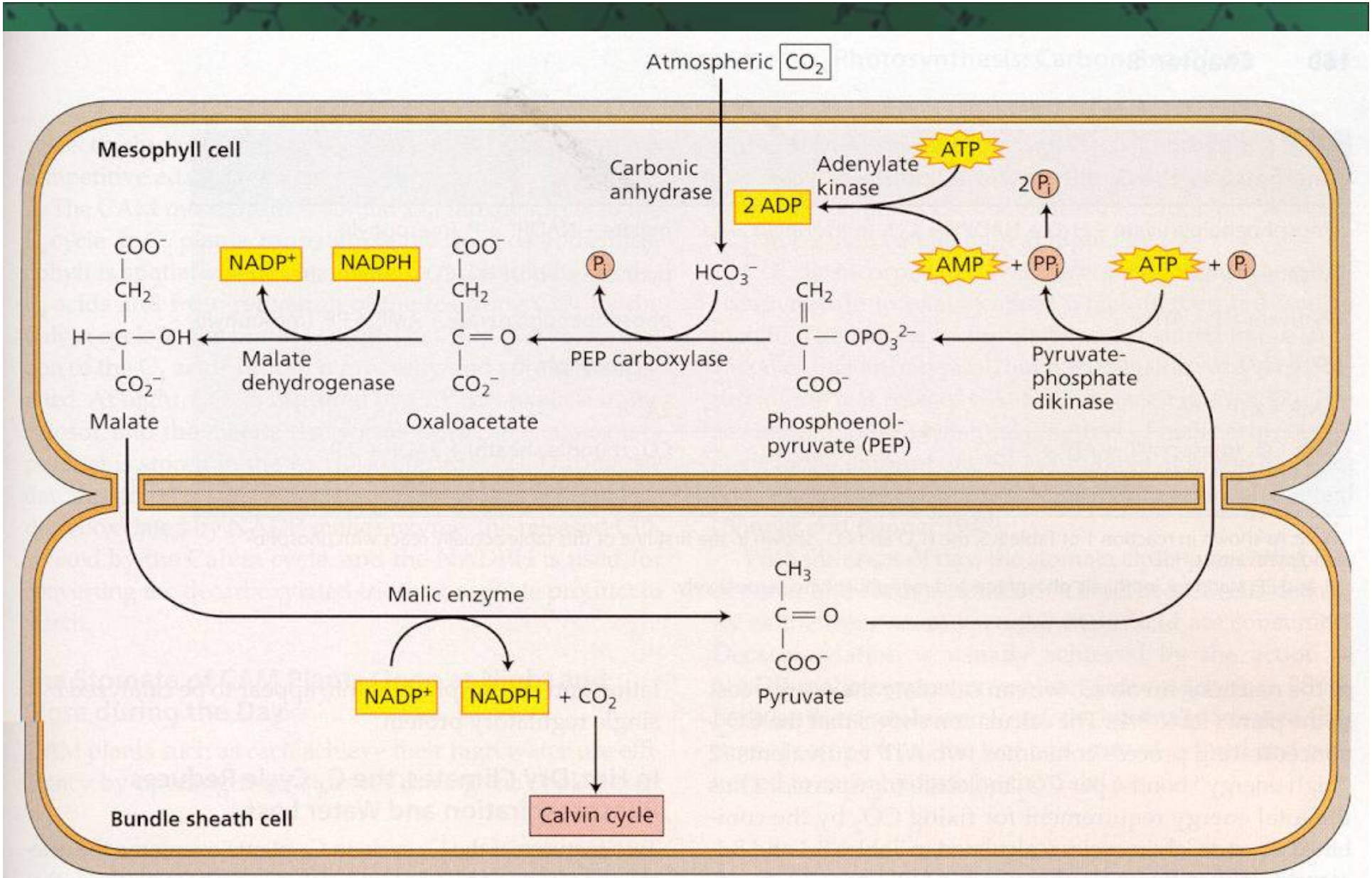


FIGURE 8.11 The C_4 photosynthetic pathway. The hydrolysis of two ATP drives the cycle in the direction of the arrows, thus pumping CO_2 from the atmosphere to the Calvin cycle of the chloroplasts from bundle sheath cells.

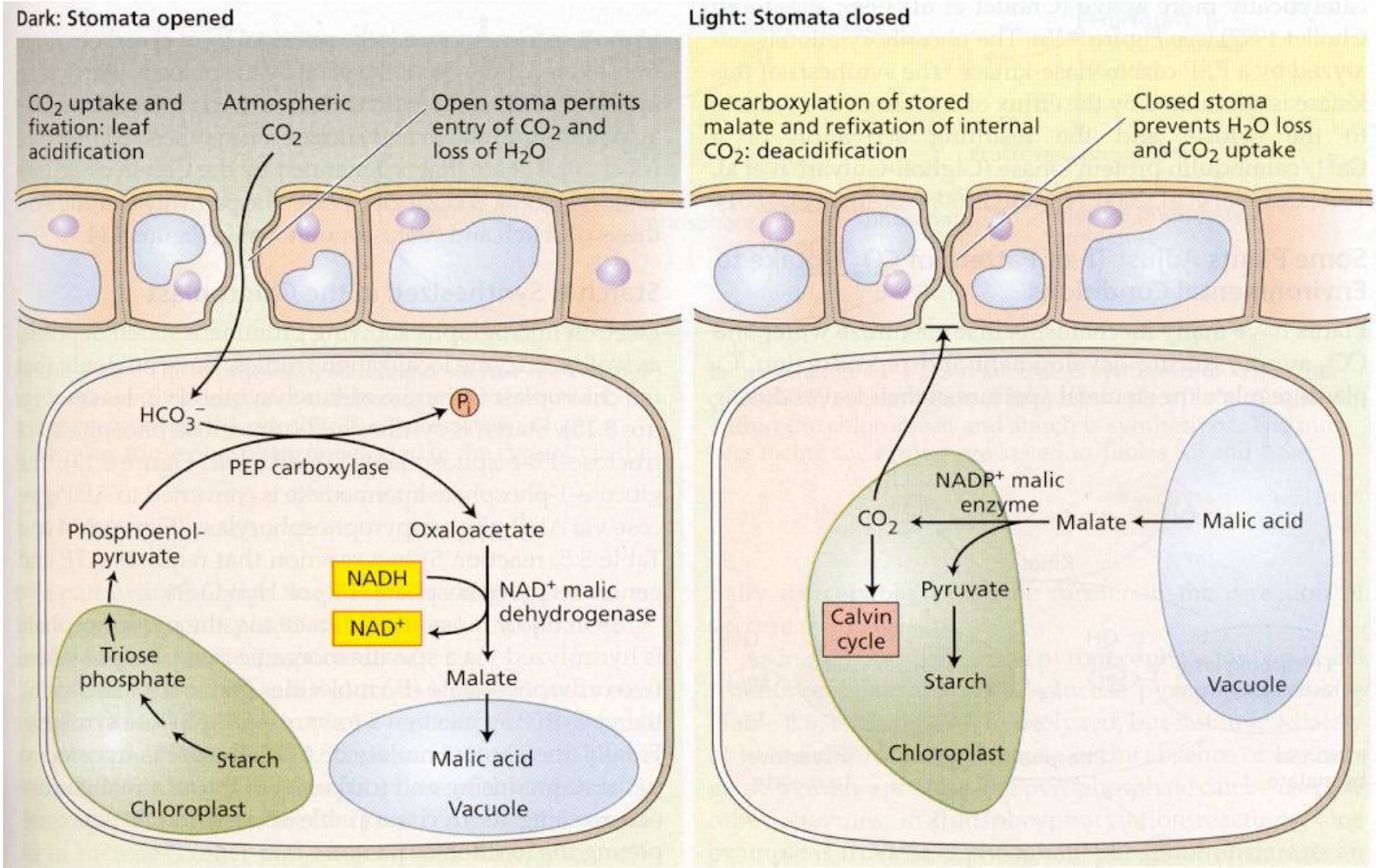


FIGURE 8.12 Crassulacean acid metabolism (CAM). Temporal separation of CO_2 uptake from photosynthetic reactions: CO_2 uptake and fixation take place at night, and decarboxylation and refixation of the internally released CO_2 occur during the day. The adaptive advantage of CAM is the reduction of water loss by transpiration, achieved by the stomatal opening during the night.

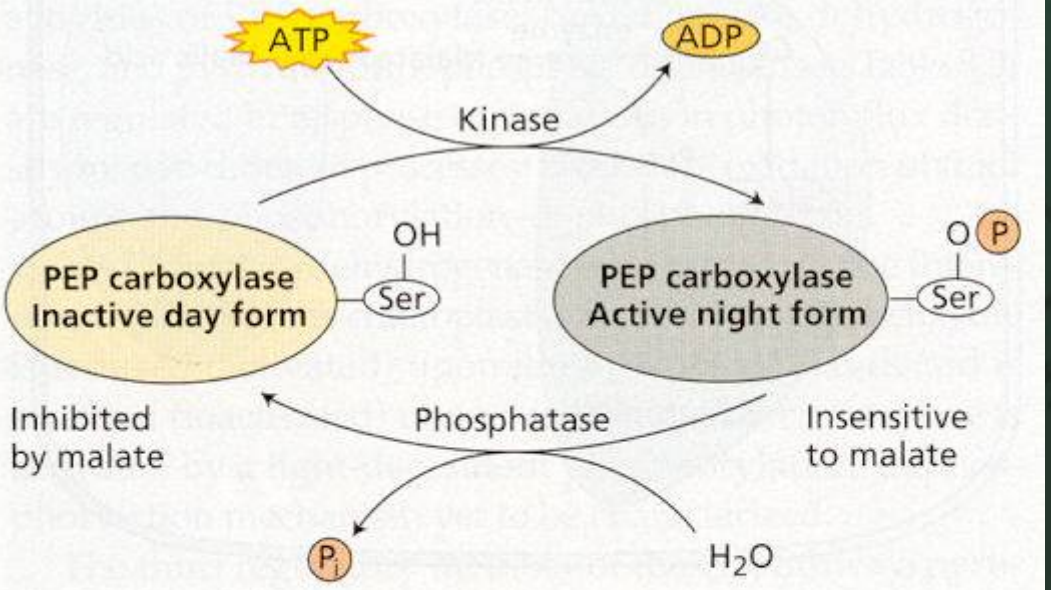


FIGURE 8.13 Diurnal regulation of CAM phosphoenolpyruvate (PEP) carboxylase. Phosphorylation of the serine residue (Ser-OP) yields a form of the enzyme which is active during the night and relatively insensitive to malate. During the day, dephosphorylation of the serine (Ser-OH) gives a form of the enzyme which is inhibited by malate.

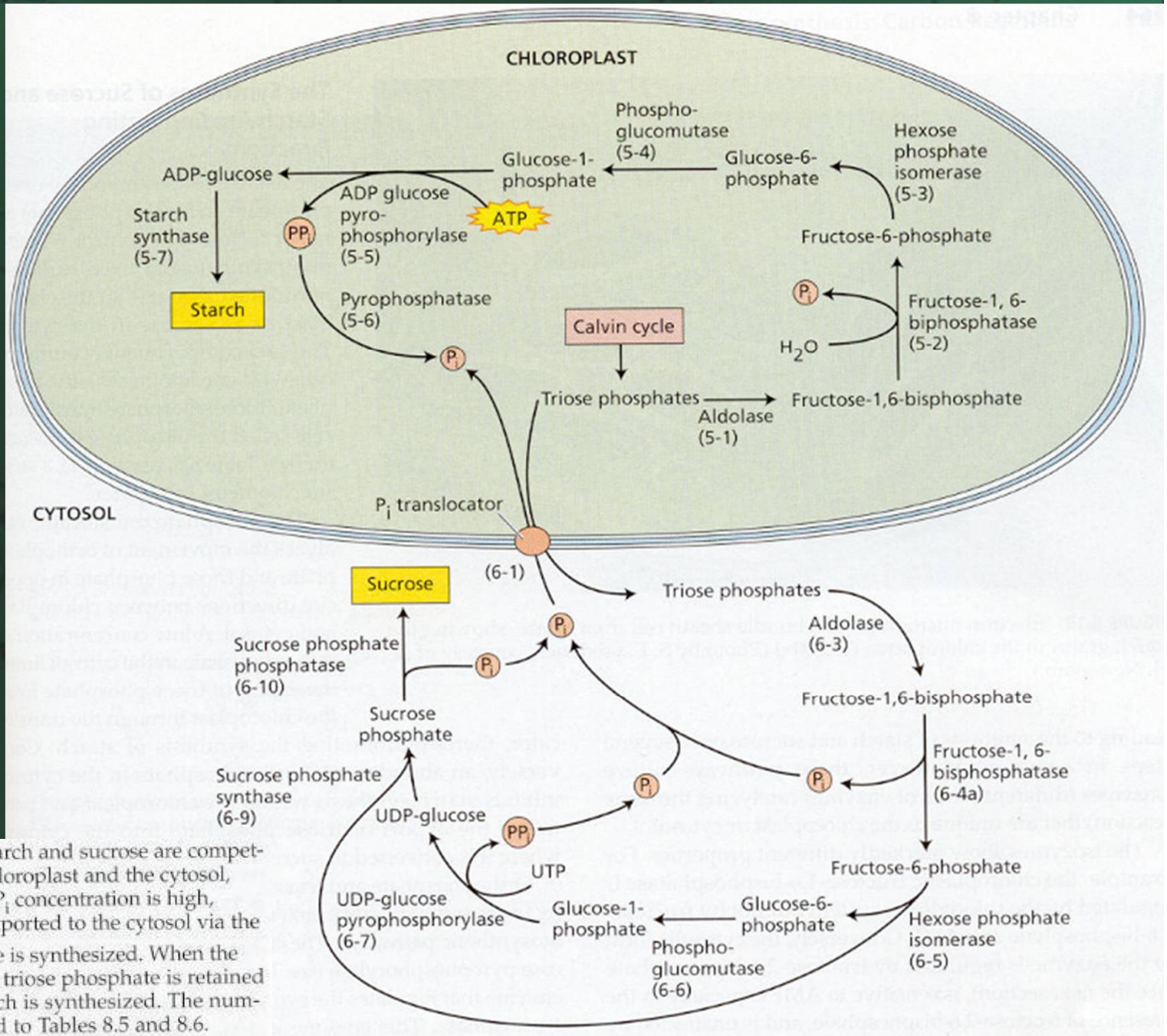
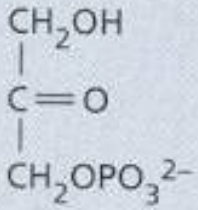
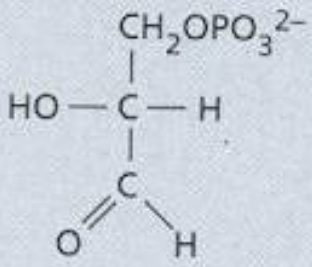


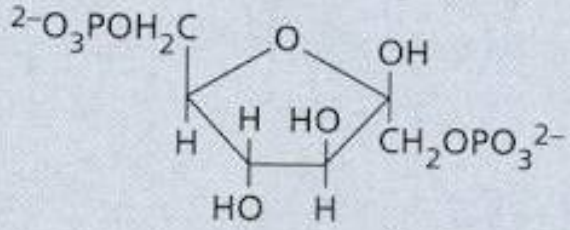
FIGURE 8.14 The syntheses of starch and sucrose are competing processes that occur in the chloroplast and the cytosol, respectively. When the cytosolic P_i concentration is high, chloroplast triose phosphate is exported to the cytosol via the P_i in exchange for P_i, and sucrose is synthesized. When the cytosolic P_i concentration is low, triose phosphate is retained within the chloroplast, and starch is synthesized. The numbers facing the arrows are keyed to Tables 8.5 and 8.6.

TABLE 8.5
Reactions of starch synthesis from triose phosphate in chloroplasts

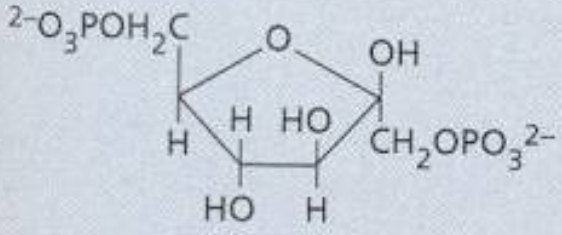
1. *Fructose-1,6,bisphosphate aldolase*
   Dihydroxyacetone-3-phosphate + glyceraldehyde-3-phosphate→ fructose-1,6-bisphosphate

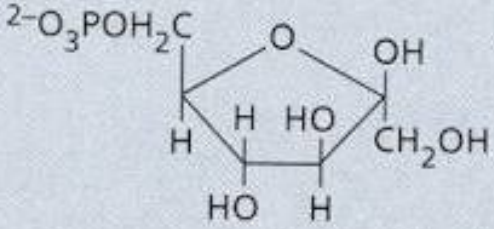




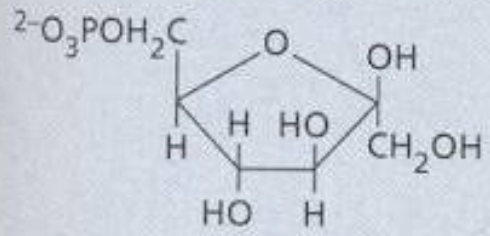


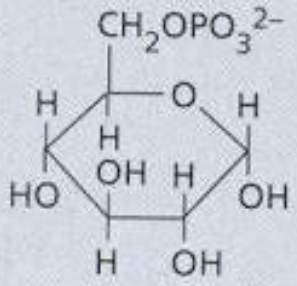
2. *Fructose-1,6-bisphosphatase*
   Fructose-1,6-bisphosphate + H_2O → fructose-6-phosphate + P_i



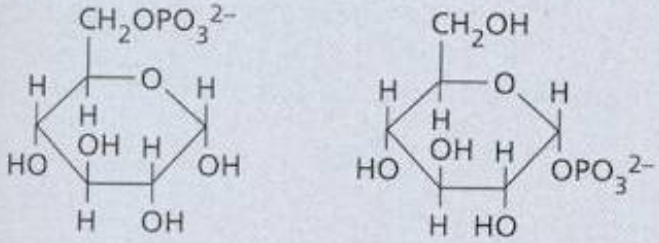


3. *Hexose phosphate isomerase*
   Fructose-6-phosphate → glucose-6-phosphate

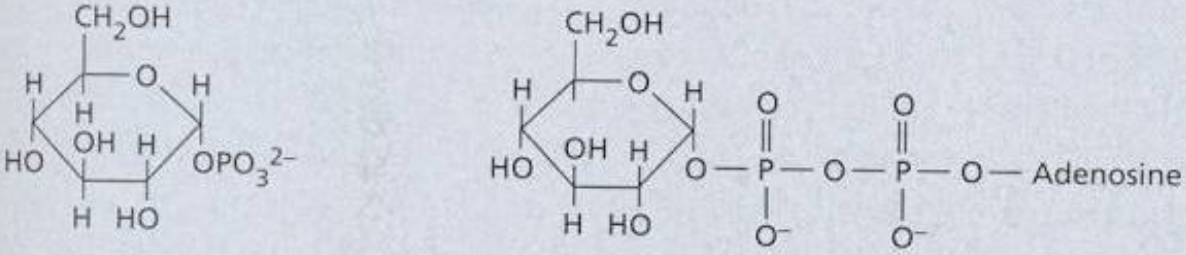




4. *Phosphoglucomutase*
Glucose-6-phosphate → glucose-1-phosphate



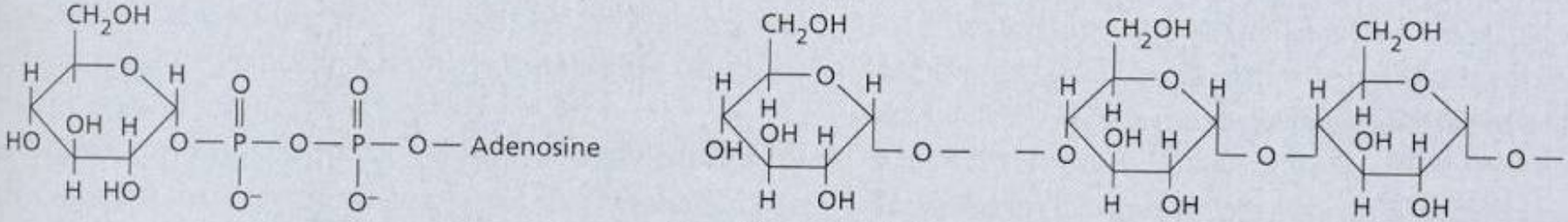
5. *ADP-glucose pyrophosphorylase*
Glucose-1-phosphate + ATP → ADP-glucose + PP_i



6. *Pyrophosphatase*

$PP_i + H_2O \rightarrow 2\ P_i + 2H^+$

7. *Starch synthase*
ADP-glucose + $(1,4\text{-}\alpha\text{-D-glucosyl})_n \rightarrow$ ADP + $(1,4\text{-}\alpha\text{-D-glucosyl})_{n+1}$



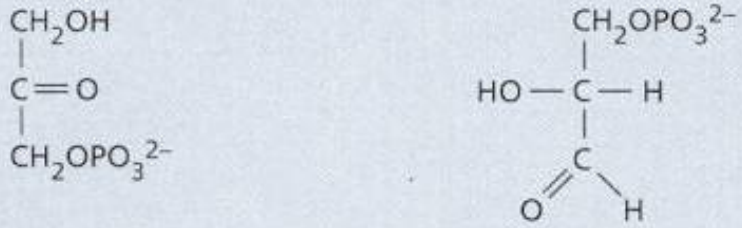
Nonreducing end of a starch chain with *n* residues

Elongated starch with *n* + 1 residues

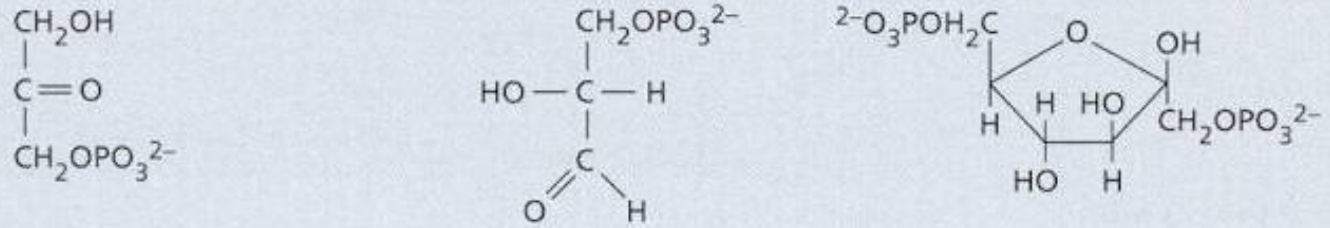
TABLE 8.6
Reactions of sucrose synthesis from triose phosphate in the cytosol

1. *Phosphate/triose phosphate translocator*
   Triose phosphate (chloroplast) + P_i (cytosol) → triose phosphate (cytosol) + P_i (chloroplast)

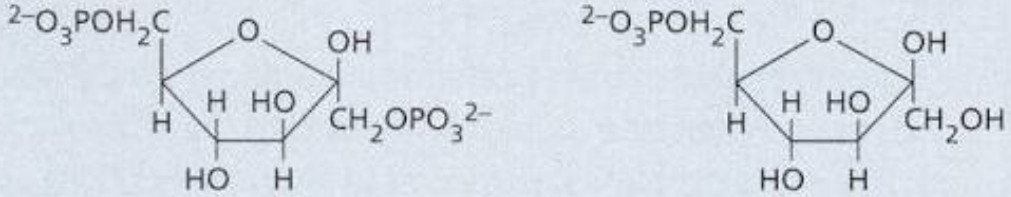
2. *Triose phosphate isomerase*
   Dihydroxyacetone-3-phosphate → glyceraldehyde-3-phosphate



3. *Fructose-1,6-bisphosphate aldolase*
   Dihydroxyacetone-3-phosphate + glyceraldehyde-3-phosphate → fructose-1,6-bisphosphate

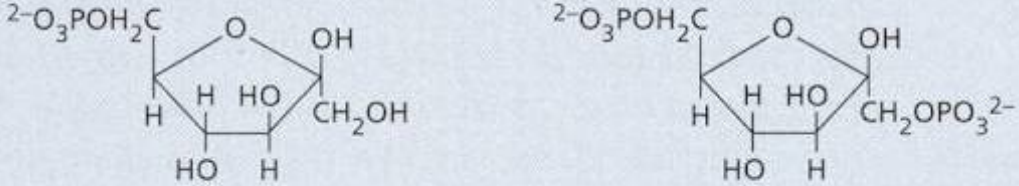


4a. *Fructose-1,6-phosphatase*
   Fructose-1,6-bisphosphate + H_2O → fructose-6-phosphate + P_i



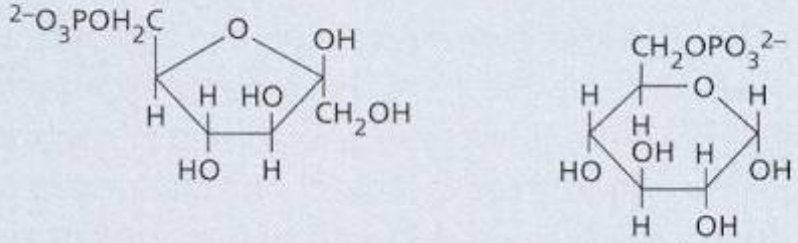
4b. *PP_i-linked phosphofructokinase*

Fructose-6-phosphate + PP_i → fructose-1,6-bisphosphate + P_i



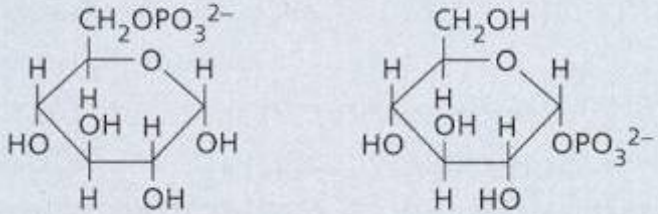
5. *Hexose phosphate isomerase*

Fructose-6-phosphate → glucose-6-phosphate



6. *Phosphoglucomutase*

Glucose-6-phosphate → glucose-1-phosphate



7. *UDP-glucose pyrophosphorylase*

Glucose-1-phosphate + UTP → UDP-glucose + PP_i

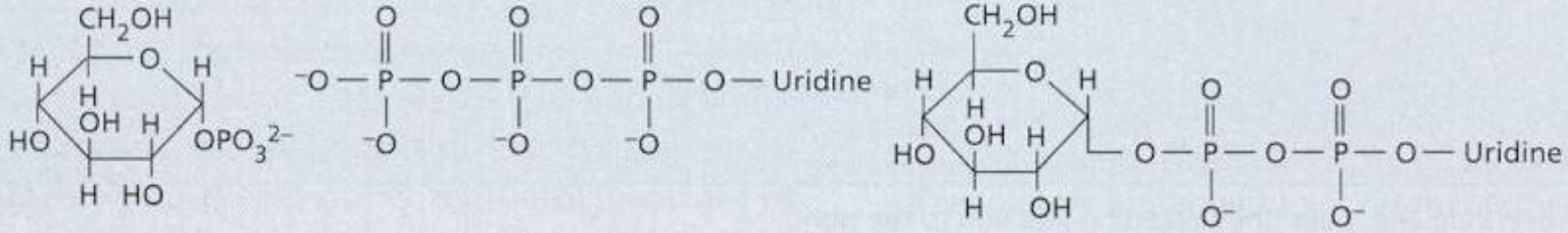
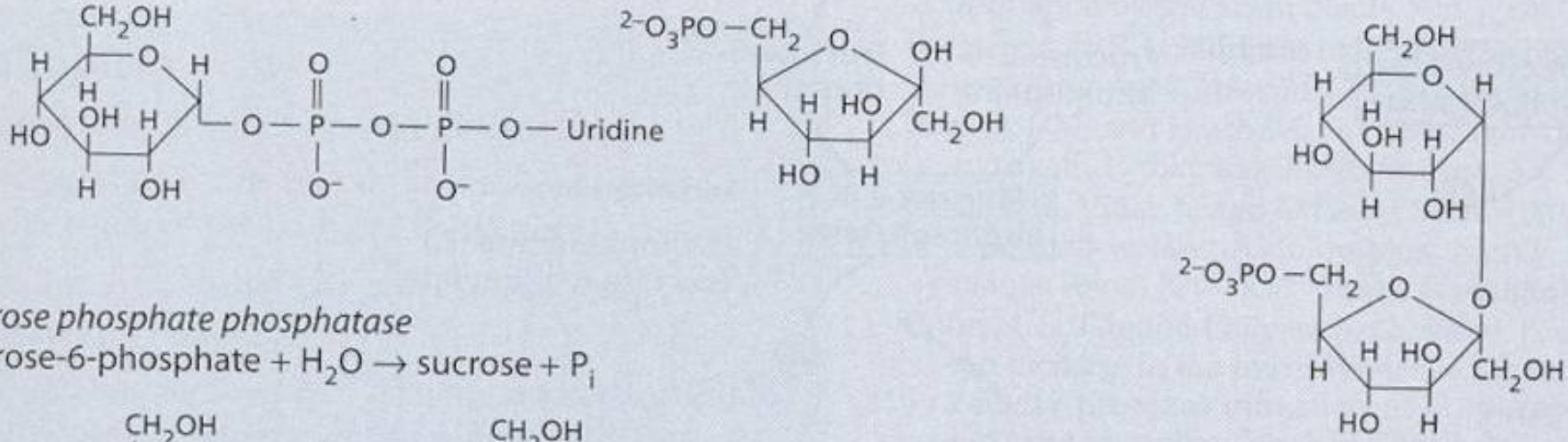


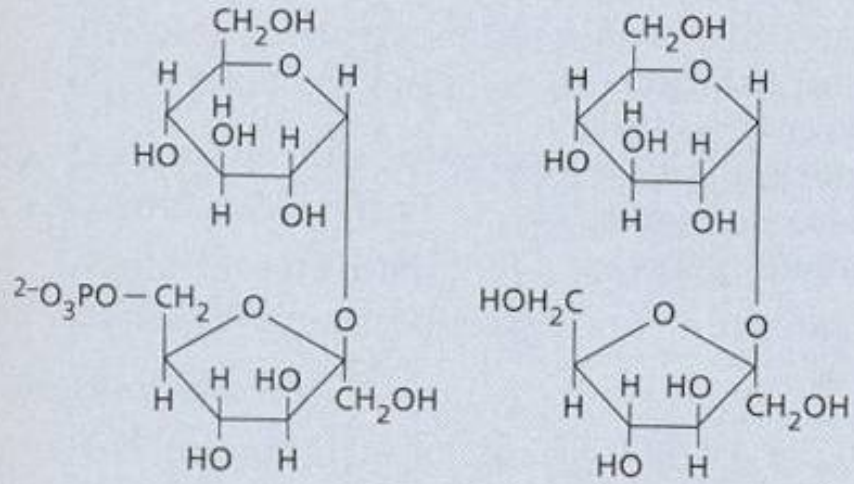
TABLE 8.6 (continued)
Reactions of sucrose synthesis from triose phosphate in the cytosol

8. *Pyrophosphatase*
   $PP_i + H_2O \rightarrow 2\ P_i + 2\ H^+$

9. *Sucrose phosphate synthase*
   UDP-glucose + fructose-6-phosphate → UDP + sucrose-6-phosphate



10. *Sucrose phosphate phosphatase*
    Sucrose-6-phosphate + H_2O → sucrose + P_i



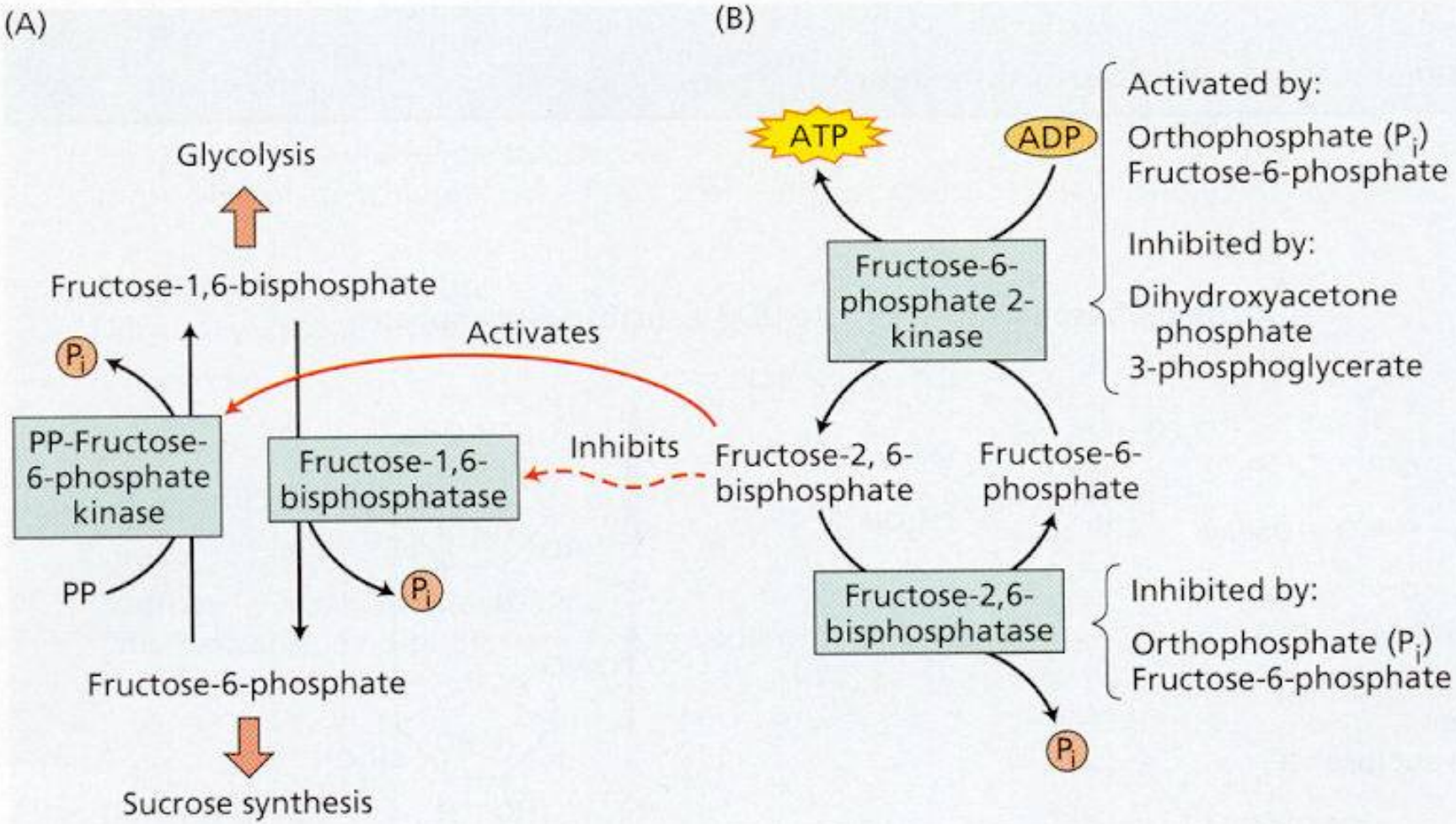


FIGURE 8.16 Regulation of the cytosolic interconversion of fructose-6-phosphate and fructose-1,6-bisphosphate. (A) The key metabolites in the allocation between glycolysis and sucrose synthesis. The regulatory metabolite fructose 2,6-bisphosphate regulates the interconversion by inhibiting the phosphatase and activating the kinase, as shown. (B) The synthesis of fructose-2,6-bisphosphate itself is under strict regulation by the activators and inhibitors shown in the figure.