SPECIAL INTEREST BOX 13.1 Starch and Sucrose Metabolism

Because glyceraldehyde-3-phosphate and dihydroxyacetone phosphate are readily interconverted, these two molecules (referred to the **triose phosphates**) are both considered to be Calvin cycle products. The synthesis of triose phosphate is sometimes referred to as the *C3 pathway*. Plants that produce triose phosphates during photosynthesis are called *C3 plants*. Triose phosphate molecules are used by plant cells in such biosynthetic processes as the formation of polysaccharides, fatty acids, and amino acids. Initially, most triose phosphate is used in the synthesis of starch and sucrose (Figure 13A). The metabolism of each of these molecules is briefly discussed below.

Starch Metabolism

During very active periods of photosynthesis, triose phosphates are converted to starch. Under normal conditions, approximately 30% of the CO_2 fixed by leaves is incorporated into starch, which is stored as water-insoluble granules. During a subsequent dark period, most chloroplast starch is degraded and converted to sucrose. Sucrose is then exported to storage organs and rapidly growing tissues. In these tissues (e.g, tubers and seeds), most sucrose molecules are used to synthesize starch, which is stored primarily within a specialized plastid called an *amyloplast*.

Triose phosphates retained within the chloroplast are converted to fructose-6-phosphate by aldolase and fructose-1,6-bisphosphatase. Glucose-1-phosphate, the starting material for starch synthesis, is produced from fructose-6-phosphate by phosphoglucoisomerase and phosphoglucomutase. The conversion of glucose-1-phosphate to ADP-glucose by ADP-glucose pyrophosphorylase is the rate-limiting step in starch synthesis. ADP-glucose is incorporated into starch by starch synthase. Like glycogen synthase (p. 264), starch synthase adds each monosaccharide unit to a preexisting polysaccharide chain. The $\alpha(1,6)$ branch points of amylopectin are introduced by branching enzyme.

Several enzymes contribute to starch breakdown. Both α- and β-amylases cleave $\alpha(1,4)$ glycosidic bonds. β-Amylase catalyzes the successive removal of maltose units from the nonreducing ends of starch chains. Maltose is degraded to form glucose by α-glucosidase. Glucose-1-phosphate is the product when $\alpha(1,4)$ glycosidic bonds at nonreducing ends are broken by starch phosphorylase. Branch points in starch are removed by debranching enzyme. The products of starch digestion, glucose and glucose-1-phosphate, are then converted to triose phosphate and exported to the cytoplasm. In photosynthesizing cells, most triose phosphate is converted to sucrose.

Sucrose imported from leaves is the substrate for most of the starch synthesis in nonphotosynthesizing cells. Sucrose is converted into fructose and UDP-glucose in a reversible reaction catalyzed by sucrose synthase. Fructose is then converted to glucose-1-phosphate by hexokinase and phosphoglucomutase. UDP-glucose is converted to glucose-1-phosphate by UDP-glucose pyrophosphorylase. The conversion of sucrose to two molecules of glucose-1-phosphate is a cytoplasmic process. After its transport into an amyloplast, glucose-1-phosphate is used in starch synthesis. (Smaller amounts of the glycolytic intermediates glyceraldehyde-3-phosphate and dihydroxyacetone phosphate are also transported into amyloplasts and used in starch synthesis.)

Sucrose Metabolism

Sucrose has several important roles in plants. First, sucrose accounts for a large portion of the CO_2 absorbed during photosynthesis. Second, most of the carbon translocated throughout plants is in the form of sucrose. Finally, sucrose is an important energy storage form in many plants.

Sucrose is synthesized in the cytoplasm. After their transport from chloroplasts, triose phosphates are converted to fructose-1,6-bisphosphate and subsequently to glucose-6-phosphate. The latter molecule is converted to glucose-1-phosphate by phosphoglucomutase. UDP-glucose (formed by glucose-1-phosphate uridyltransferase from glucose-1-phosphate) and fructose-6-phosphate combine to form sucrose-6-phosphate. Sucrose-6-phosphate synthesis is catalyzed by sucrose phosphate synthase. Sucrose phosphatase catalyzes the hydrolysis of sucrose-6-phosphate to form sucrose and P_i. The free energy change of the latter reaction ($\Delta G^{\circ\prime} = -18.4$ kJ/mol) ensures that sucrose production continues in sucrose-storing tissues.

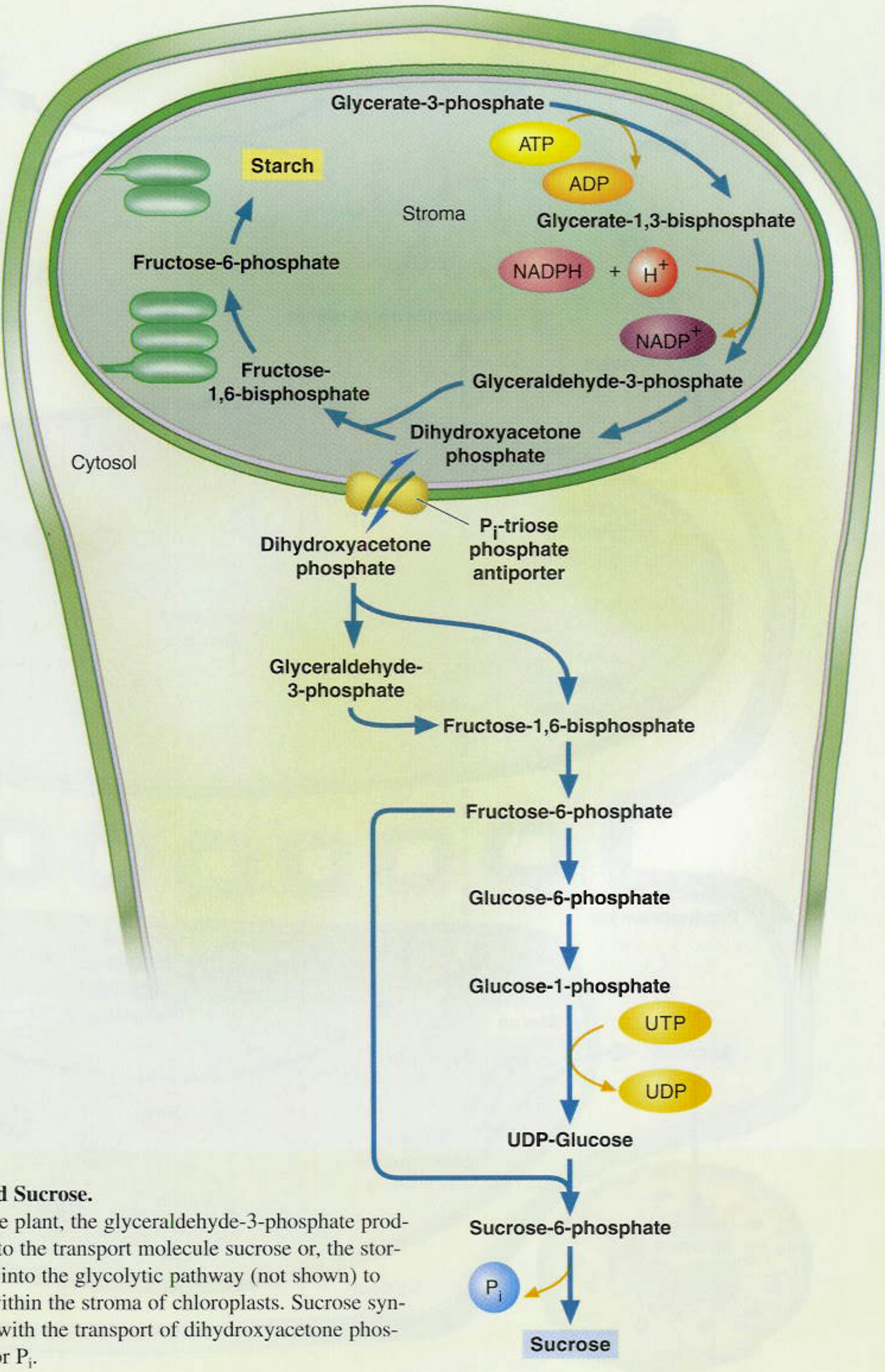

FIGURE 13A Synthesis of Starch and Sucrose.
Depending on the physiological state of the plant, the glyceraldehyde-3-phosphate product of photosynthesis may be converted into the transport molecule sucrose or, the storage molecule starch, or it may be diverted into the glycolytic pathway (not shown) to generate energy. Starch synthesis occurs within the stroma of chloroplasts. Sucrose synthesis, which occurs in cytoplasm, begins with the transport of dihydroxyacetone phosphate out of the chloroplast in exchange for P_i.