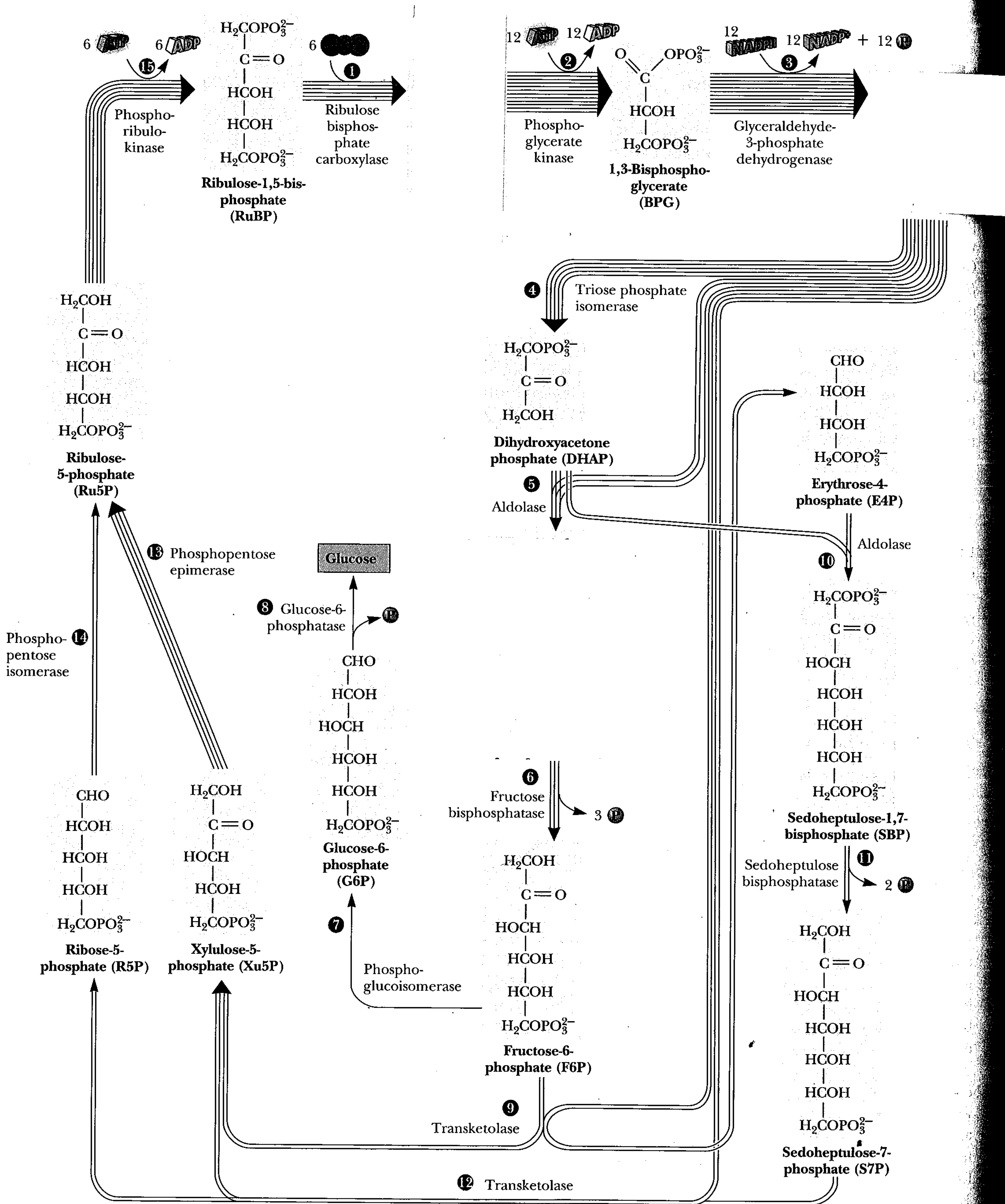

Figure **22.28** The Calvin–Benson cycle of reactions. The number of arrows at each step indicates the number of molecules reacting in a turn of the cycle that produces one molecule of glucose. Reactions are numbered as in Table 22.1.

Table **22.1**
The Calvin Cycle Series of Reactions

Reactions 1 through 15 constitute the cycle that culminates in the formation of one equivalent of glucose. The enzyme catalyzing each step, a concise reaction, and the overall carbon balance is given. Numbers in parentheses denote the numbers of carbon atoms in the substrate and product molecules. Prefix numbers indicate in a stoichiometric fashion how many times each step is carried out in order to provide a balanced net reaction.

1. Ribulose bisphosphate carboxylase: 6 CO_2 + 6 H_2O + 6 RuBP ⟶ 12 3-PG	6(1) + 6(5) ⟶ 12(3)
2. 3-Phosphoglycerate kinase: 12 3-PG + 12 ATP ⟶ 12 1,3-BPG + 12 ADP	12(3) ⟶ 12(3)
3. $NADP^+$-glyceraldehyde-3-P dehydrogenase: 12 1,3-BPG + 12 NADPH ⟶ 12 $NADP^+$ + 12 G3P + 12 P_i	12(3) ⟶ 12(3)
4. Triose-P isomerase: 5 G3P ⟶ 5 DHAP	5(3) ⟶ 5(3)
5. Aldolase: 3 G3P + 3 DHAP ⟶ 3 FBP	3(3) + 3(3) ⟶ 3(6)
6. Fructose bisphosphatase: 3 FBP + 3 H_2O ⟶ 3 F6P + 3 P_i	3(6) ⟶ 3(6)
7. Phosphoglucoisomerase: 1 F6P ⟶ 1 G6P	1(6) ⟶ 1(6)
8. Glucose phosphatase: 1 G6P + 1 H_2O ⟶ 1 GLUCOSE + 1 P_i	1(6) ⟶ 1(6)
The remainder of the pathway involves regenerating six RuBP acceptors (= 30C) from the leftover two F6P (12C), four G3P (12C), and two DHAP (6C).	
9. Transketolase: 2 F6P + 2 G3P ⟶ 2 Xu5P + 2 E4P	2(6) + 2(3) ⟶ 2(5) + 2(4)
10. Aldolase: 2 E4P + 2 DHAP ⟶ 2 sedoheptulose-1,7-bisphosphate (SBP)	2(4) + 2(3) ⟶ 2(7)
11. Sedoheptulose bisphosphatase: 2 SBP + 2 H_2O ⟶ 2 S7P + 2 P_i	2(7) ⟶ 2(7)
12. Transketolase: 2 S7P + 2 G3P ⟶ 2 Xu5P + 2 R5P	2(7) + 2(3) ⟶ 4(5)
13. Phosphopentose epimerase: 4 Xu5P ⟶ 4 Ru5P	4(5) ⟶ 4(5)
14. Phosphopentose isomerase: 2 R5P ⟶ 2 Ru5P	2(5) ⟶ 2(5)
15. Phosphoribulose kinase: 6 Ru5P + 6 ATP ⟶ 6 RuBP + 6 ADP	6(5) ⟶ 6(5)
Net: 6 CO_2 + 18 ATP + 12 NADPH + 12 H^+ + 12 H_2O ⟶ glucose + 18 ADP + 18 P_i + 12 $NADP^+$	6(1) ⟶ 1(6)

genase, which contrasts with its glycolytic counterpart in its specificity for NADP over NAD and in the direction in which the reaction normally proceeds.

Balancing the Calvin Cycle Reactions To Account for Net Hexose Synthesis

When carbon rearrangements are balanced to account for net hexose synthesis, five of the glyceraldehyde-3-phosphate molecules are converted to dihydroxyacetone phosphate (DHAP). Three of these DHAPs then condense with three glyceraldehyde-3-P via the aldolase reaction to yield hexose in the form of fructose bisphosphate. (Recall that the $\Delta G^{\circ\prime}$ for the aldolase reaction in the glycolytic direction is +23.9 kJ/mol. Thus, the aldolase reaction running "in reverse" in the Calvin cycle would be thermodynamically favored under standard-state conditions.) Taking one FBP to glucose, the desired product of this scheme, leaves 30 carbons, distributed as two fructose-6-phosphates, four glyceraldehyde-3-phosphates, and 2 DHAP. These 30 Cs are reorganized into 6 RuBP by reactions 9 through 15. Step 9 and steps 12 through 14 involve pentose phosphate pathway enzymes. Reaction 11 is mediated by **sedoheptulose-1,7-bisphosphatase.** This phosphatase is unique to plants; it serves to generate the sedoheptulose-7-P form of the seven-carbon sugar that acts as the transketolase substrate. Likewise, **phosphoribulose kinase** carries out the unique plant function of providing RuBP from Ru-5-P (reaction 15). The net conversion accounts for the fixation of six equivalents of carbon dioxide into one hexose at the expense of 18 ATP and 12 NADPH.