1,5-bisphosphate (**Figure 8.4**). The addition of CO_2 to the unstable rubisco-bound enediol intermediate drives the second partial reaction to the irreversible formation of 2-carboxy-3-ketoarabinitol 1,5-bisphosphate. The hydration of 2-carboxy-3-ketoarabinitol 1,5-bisphosphate yields two molecules of 3-phosphoglycerate.

In the reduction phase of the Calvin–Benson cycle, two successive reactions reduce the carbon of the 3-phosphoglycerate produced by the carboxylation phase (see Figure 8.3 and Table 8.1, reactions 2 and 3):

1. First, ATP formed by the light reactions phosphorylates 3-phosphoglycerate at the carboxyl group, yielding a mixed anhydride, 1,3-bisphosphoglycerate, in a reaction catalyzed by 3-phosphoglycerate kinase.
2. Next, NADPH, also generated by the light reactions, reduces 1,3-bisphosphoglycerate to glyceraldehyde 3-phosphate, in a reaction catalyzed by the chloroplast enzyme NADP–glyceraldehyde-3-phosphate dehydrogenase.

The operation of three carboxylation and reduction phases yields six molecules of glyceraldehyde 3-phosphate (6 molecules × 3 carbons/molecule = 18 carbons total) when three molecules of ribulose 1,5-bisphosphate (3 molecules × 5 carbons/molecule = 15 carbons total) react with three molecules of CO_2 (3 carbons total) and the six molecules of 3-phosphoglycerate are reduced (see Figure 8.3).

The regeneration of ribulose 1,5-bisphosphate ensures the continuous assimilation of CO_2

In the regeneration phase, the Calvin–Benson cycle facilitates the continuous uptake of atmospheric CO_2 by restoring the CO_2 acceptor ribulose 1,5-bisphosphate. To this end, three molecules of ribulose 1,5-bisphosphate (3 mol-

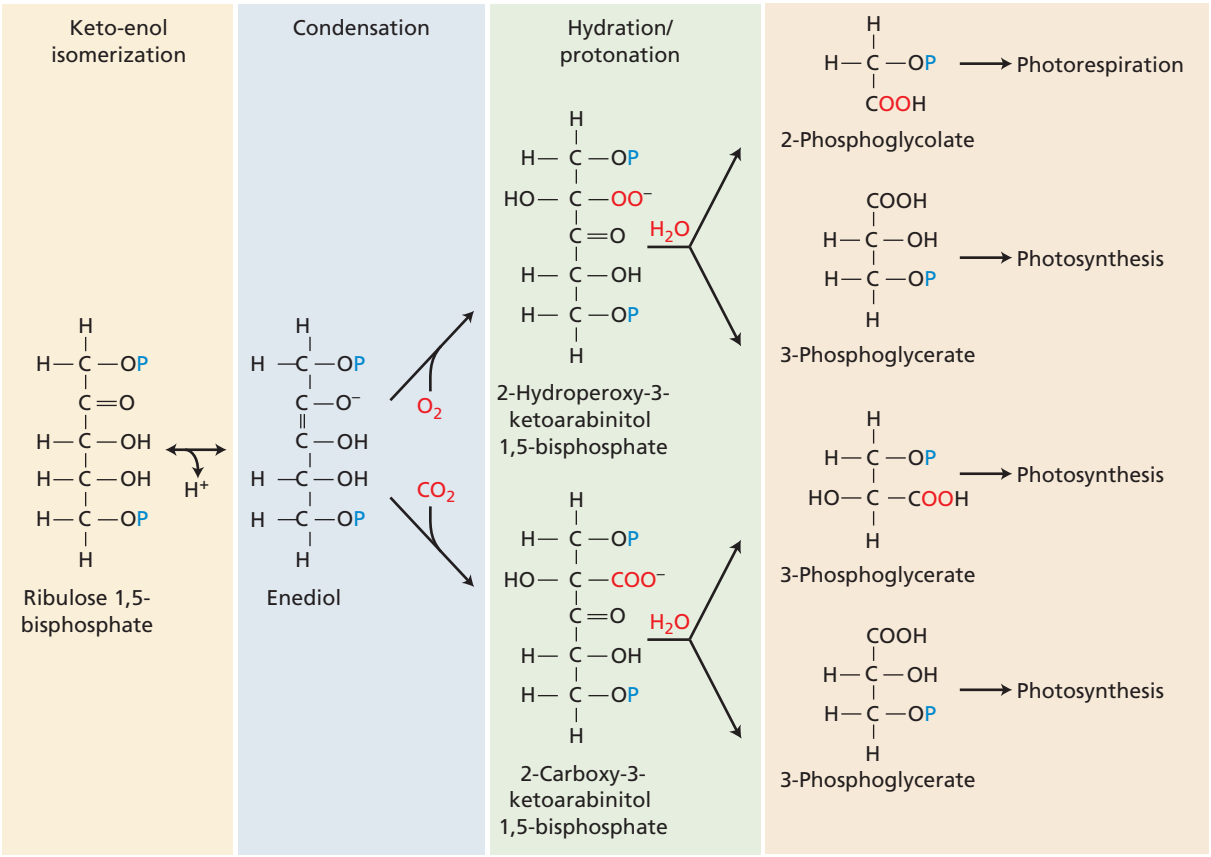

Figure 8.4 Carboxylation and oxygenation of ribulose 1,5-bisphosphate catalyzed by rubisco. The binding of ribulose 1,5-bisphosphate to rubisco facilitates the formation of an enzyme-bound enediol intermediate that can be attacked by CO_2 or O_2 at carbon 2. With CO_2, the product is a six-carbon intermediate (2-carboxy-3-ketoarabinitol 1,5-bisphosphate); with O_2, the product is a five-carbon reactive intermediate (2-hydroperoxy-3-ketoarabinitol 1,5-bisphosphate). The hydration of these intermediates at carbon 3 triggers the cleavage of the carbon–carbon bond between carbons 2 and 3, yielding two molecules of 3-phosphoglycerate (carboxylase activity) or one molecule of 2-phosphoglycolate and one molecule of 3-phosphoglyerate (oxygenase activity). The important physiological effect of the oxygenase activity is described in the section *The C_2 Oxidative Photosynthetic Carbon Cycle*.