

B.Sc. II Semester

Paper: BBT 2002

Unit III

Photosynthesis

Source: Plant Physiology by L. Taiz and E. Zeiger

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PHOTOSYNTHESIS: THE

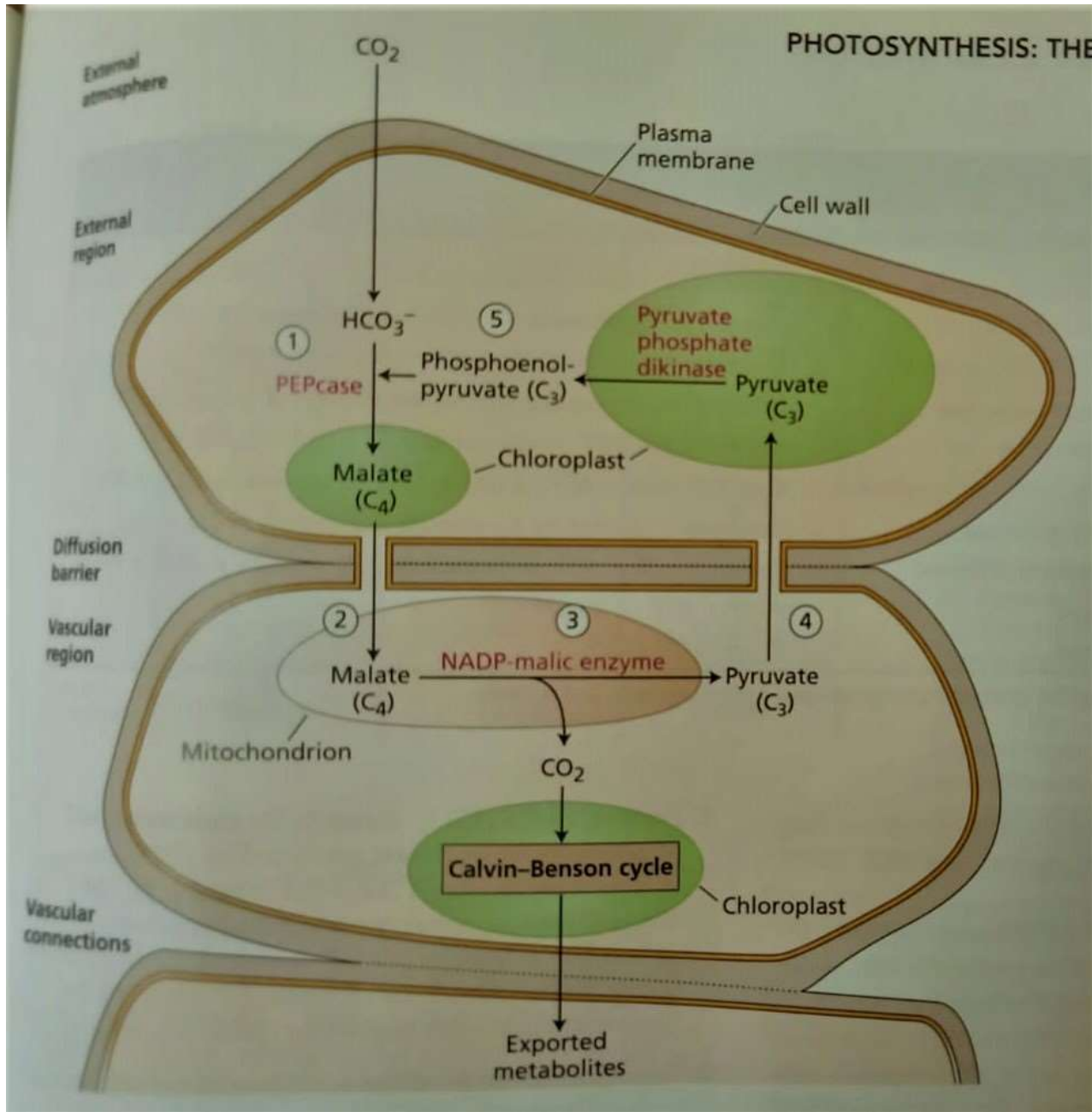
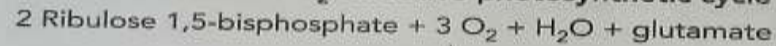


FIGURE 8.8 Operation of the C_2 oxidative photosynthetic cycle involves cooperation among three organelles: chloroplasts, peroxisomes, and mitochondria. In chloroplasts, the oxygenase activity of rubisco yields two molecules of 2-phosphoglycolate, which phosphoglycolate phosphatase converts into two molecules of glycolate and two molecules of inorganic phosphate. Two molecules of glycolate (four carbons) and one molecule of glutamate flow from chloroplasts to peroxisomes. In peroxisomes, the glycolate is oxidized by O_2 to glyoxylate in a reaction catalyzed by glycolate oxidase. Glyoxylate:glutamate aminotransferase catalyzes the conversion of glyoxylate and glutamate into glycine and 2-oxoglutarate. Glycine flows from peroxisomes to mitochondria, where two molecules of glycine (four carbons) yield a molecule of serine (three carbons) with the concurrent release of CO_2 (one carbon) and NH_4^+ by the successive action of the glycine decarboxylase complex and serine hydroxymethyl transferase. Serine is then transported back to the peroxisome and transformed into glycerate (three carbons) by the successive action of serine aminotransferase and hydroxypyruvate reductase. Glycerate and 2-oxoglutarate (from peroxisomes) and NH_4^+ (from mitochondria) return to chloroplasts in a process that recovers part of the carbon (three carbons) and all the nitrogen lost in photorespiration. Glycerate is phosphorylated to 3-phosphoglycerate and incorporated back into the Calvin-Benson cycle. In the chloroplast stroma, glutamine synthetase and ferredoxin-dependent glutamate synthase (GOGAT)—using the inorganic nitrogen (NH_4^+) and 2-oxoglutarate—recover the nitrogen initially lost in the exported glutamate. See Table 8.2 for a description of each numbered reaction.

Reactions of the C₂ oxidative photosynthetic cycle

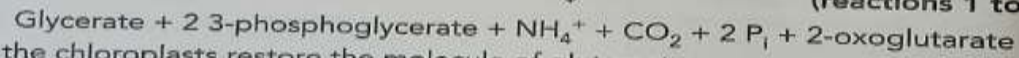
Reaction ^a	Enzyme
1. 2 Ribulose 1,5-bisphosphate + 2 O ₂ → 2 2-phosphoglycolate + 2 3-phosphoglycerate	Rubisco
2. 2 2-Phosphoglycolate + 2 H ₂ O → 2 glycolate + 2 P _i	Phosphoglycolate phosphatase
3. 2 Glycolate + 2 O ₂ → 2 glyoxylate + 2 H ₂ O ₂	Glycolate oxidase
4. 2 H ₂ O ₂ → 2 H ₂ O + O ₂	Catalase
5. 2 Glyoxylate + 2 glutamate → 2 glycine + 2-oxoglutarate	Glyoxylate:glutamate aminotransferase
6. Glycine + NAD ⁺ + [GDC] → CO ₂ + NH ₄ ⁺ + NADH + methylene-[GDC]	Glycine decarboxylase complex (GDC)
7. Methylene-[GDC] + glycine + H ₂ O → serine + [GDC]	Serine hydroxymethyl transferase
8. Serine + 2-oxoglutarate → hydroxypyruvate + glutamate	Serine aminotransferase
9. Hydroxypyruvate + NADH + H ⁺ → glycerate + NAD ⁺	Hydroxypyruvate reductase
10. Glycerate + ATP → 3-phosphoglycerate + ADP	Glycerate kinase
11. Glutamate + NH ₄ ⁺ + ATP → glutamine + ADP + P _i	Glutamine synthetase
12. 2-Oxoglutarate + glutamine + 2 Fd _{red} + 2 H ⁺ → 2 glutamate + 2 Fd _{oxid}	Ferredoxin-dependent glutamate synthase (GOGAT)

Net reaction of the C₂ oxidative photosynthetic cycle

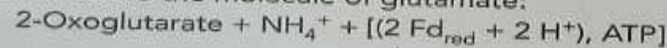


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(reactions 1 to 9)

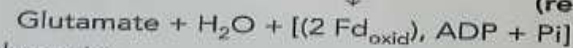


Two reactions in the chloroplasts restore the molecule of glutamate:

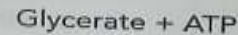


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(reactions 11 and 12)

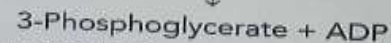


and the molecule of 3-phosphoglycerate:



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(reaction 10)



Hence, the consumption of 3 molecules of atmospheric oxygen in the C₂ oxidative photosynthetic cycle (two in the oxygenase activity of Rubisco and one in peroxisomal oxidations) elicits

- the release of one molecule of CO₂ and
- the consumption of two molecules of ATP and two molecules of reducing equivalents (2 Fd_{red} + 2 H⁺)

for

- incorporating a 3-carbon skeleton back into the Calvin-Benson Cycle, and
- restoring glutamate from NH₄⁺ and α-ketoglutarate.

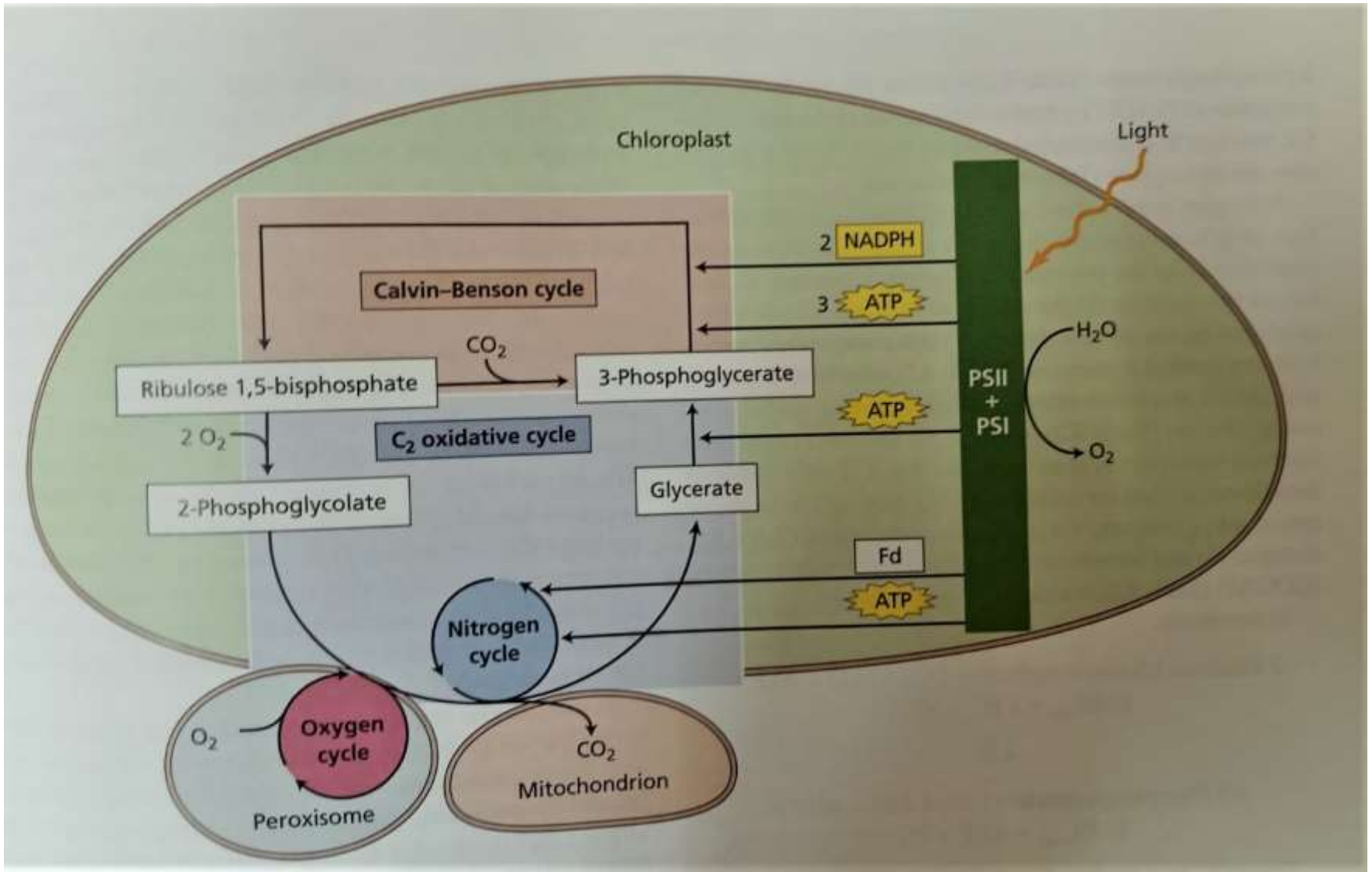
C₂ Oxidative photosynthetic cycle Reactions

TABLE 8.4

Reactions of the C₂ oxidative photosynthetic carbon cycle

Reaction	Enzyme
1. PEPCase	Phosphoenolpyruvate + HCO ₃ ⁻ → oxaloacetate + P _i
2. NADP-malate dehydrogenase	Oxaloacetate + NADPH + H ⁺ → malate + NADP ⁺
3. Aspartate aminotransferase	Oxaloacetate + glutamate ↔ aspartate + 2-oxoglutarate
4. NAD(P)-malic enzyme	Malate + NAD(P) ⁺ → pyruvate + CO ₂ + NAD(P)H + H ⁺
5. Phosphoenolpyruvate carboxykinase	Oxaloacetate + ATP → phosphoenolpyruvate + CO ₂ + ADP
6. Alanine aminotransferase	Pyruvate + glutamate ↔ alanine + 2-oxoglutarate
7. Pyruvate-phosphate dikinase	Pyruvate + P _i + ATP → phosphoenolpyruvate + AMP + PP _i
8. Adenylate kinase	AMP + ATP → 2 ADP
9. Pyrophosphatase	PP _i + H ₂ O → 2 P _i

Note: P_i and PP_i stand for inorganic phosphate and pyrophosphate, respectively.



Crassulacean Acid Metabolism

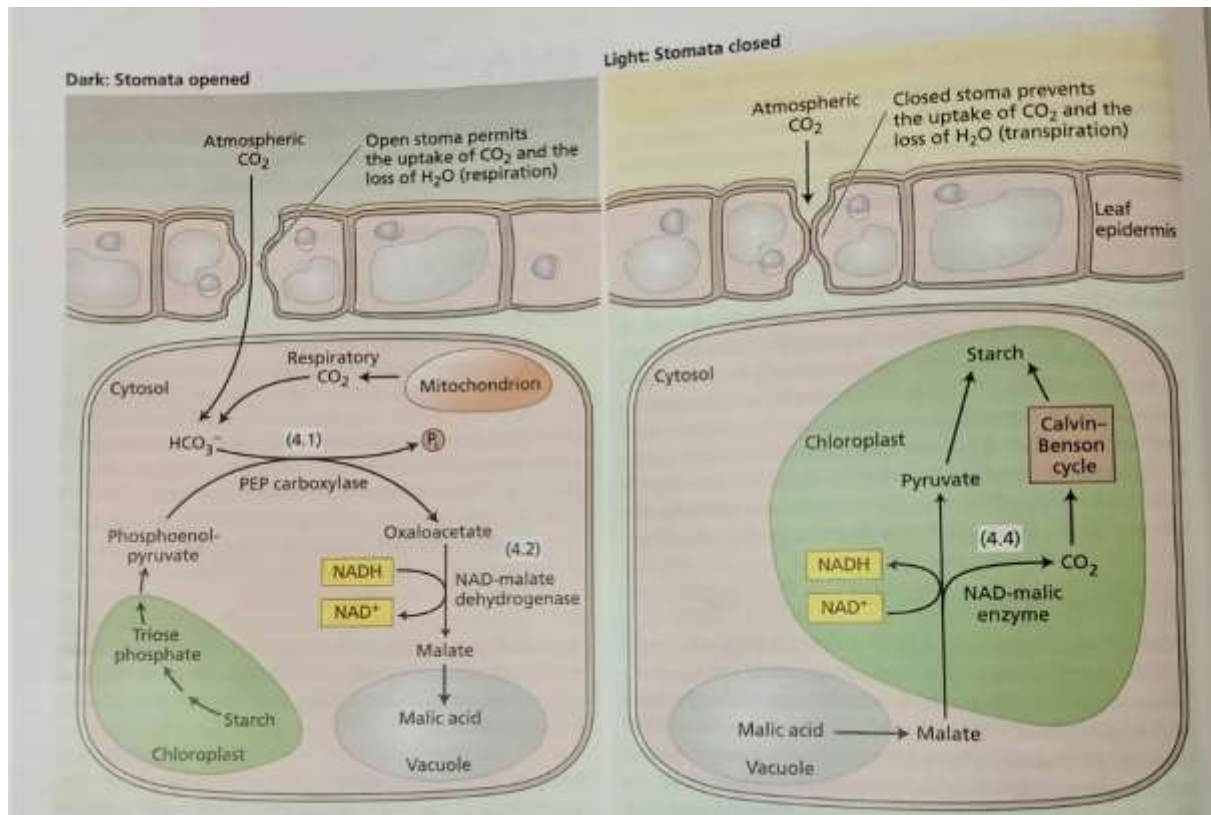


FIGURE 8.13 Crassulacean acid metabolism (CAM). In CAM metabolism, CO₂ uptake is separated temporally from fixation via the Calvin-Benson cycle. The uptake of atmospheric CO₂ takes place at night when stomata are open. At this stage, gaseous CO₂ in the cytosol, coming from both the external atmosphere and mitochondrial respiration, increases levels of HCO₃⁻ [CO₂ + H₂O ↔ HCO₃⁻ + H⁺]. Then cytosolic PEPCase catalyzes a reaction between HCO₃⁻ and phosphoenolpyruvate provided by the nocturnal breakdown of chloroplast starch. The resulting four-carbon acid, oxaloacetate, is reduced to

malate which, in turn, proceeds to the acid milieu of the vacuole. During the day, the malic acid that was stored in the vacuole at night flows back to the cytosol. Malate decarboxylase (NAD-malic enzyme) acts on malate to release CO₂, which is refixed into carbon skeletons by the Calvin-Benson cycle. In essence, the diurnal accumulation of starch in the chloroplast constitutes the net gain of the nocturnal uptake of inorganic carbon. The adaptive advantage of stomatal closure during the day is that it prevents not only water loss by transpiration, but also the exchange of internal CO₂ with the external atmosphere.

Thanks