Figure 8.1 Light and carbon reactions of photosynthesis in chloroplasts of land plants

- Light-driven reactions
  - $\text{H}_2\text{O}$
  - $\text{O}_2$
  - $\text{PSII + PSI}$
  - Chlorophyll

- Carbon reactions (stroma)
  - $\text{CO}_2 + \text{H}_2\text{O}$
  - $(\text{CH}_2\text{O})_n$
  - NADP$^+$
  - ADP + $P_i$
  - NADPH
  - ATP

- Chloroplast

**Fundamentals of Plant Physiology 1e, Figure 8.1**
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Figure 8.2 The Calvin–Benson cycle proceeds in three phases

- **Carbon input**
  - CO₂ + H₂O

- **Carboxylation**
  - Ribulose 1,5-bisphosphate

- **Regeneration**
  - Triose phosphates (Glyceraldehyde 3-phosphate + dihydroxyacetone phosphate)

- **Reduction**
  - 3-Phosphoglycerate

- **Starch (chloroplasts)**
- **Sucrose (cytosol)**
- **Sucrose (phloem)**

- **Carbon output**
  - Growth, storage polysaccharides
Figure 8.3 Calvin–Benson cycle

The carboxylation phase

The reduction phase

The regeneration phase

$P = \text{PO}_3^{2-}$

$\text{P} = \text{Inorganic phosphate}$
Figure 8.3 Calvin–Benson cycle (Part 1)

The carboxylation phase

P = PO$_3^{2-}$

$P_i$ = Inorganic phosphate
Figure 8.3  Calvin–Benson cycle (Part 2)

The reduction phase

\[ \text{P} = \text{PO}_3^{2-} \]
\[ \text{P}_i = \text{Inorganic phosphate} \]
Figure 8.3  Calvin–Benson cycle (Part 3)

3 ATP

The regeneration phase

P = PO$_3^{2-}$

$P_i$ = Inorganic phosphate
### Table 8.1 Reactions of the Calvin–Benson cycle

<table>
<thead>
<tr>
<th>Enzyme</th>
<th>Reaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco)</td>
<td>Ribulose 1,5-bisphosphate + CO₂ + H₂O → 2 3-phosphoglycerate</td>
</tr>
<tr>
<td>2. 3-Phosphoglycerate kinase</td>
<td>3-Phosphoglycerate + ATP → 1,3-bisphosphoglycerate + ADP</td>
</tr>
<tr>
<td>3. NADP-glyceraldehyde-3-phosphate dehydrogenase</td>
<td>1,3-Bisphosphoglycerate + NADPH + H⁺ → glyceraldehyde 3-phosphate + NADP⁺ + Pᵢ</td>
</tr>
<tr>
<td>4. Triose phosphate isomerase</td>
<td>Glyceraldehyde 3-phosphate → dihydroxyacetone phosphate</td>
</tr>
<tr>
<td>5. Aldolase</td>
<td>Glyceraldehyde 3-phosphate + dihydroxyacetone phosphate → fructose 1,6-bisphosphate</td>
</tr>
<tr>
<td>6. Fructose 1,6-bisphosphatase</td>
<td>Fructose 1,6-bisphosphate + H₂O → fructose 6-phosphate + Pᵢ</td>
</tr>
<tr>
<td>7. Transketolase</td>
<td>Fructose 6-phosphate + glyceraldehyde 3-phosphate → erythrose 4-phosphate + xylulose 5-phosphate</td>
</tr>
<tr>
<td>8. Aldolase</td>
<td>Erythrose 4-phosphate + dihydroxyacetone phosphate → sedoheptulose 1,7-bisphosphate</td>
</tr>
<tr>
<td>9. Sedoheptulose 1,7-bisphosphatase</td>
<td>Sedoheptulose 1,7-bisphosphate + H₂O → sedoheptulose 7-phosphate + Pᵢ</td>
</tr>
<tr>
<td>10. Transketolase</td>
<td>Sedoheptulose 7-phosphate + glyceraldehyde 3-phosphate → ribose 5-phosphate + xylulose 5-phosphate</td>
</tr>
<tr>
<td>11a. Ribulose 5-phosphate epimerase</td>
<td>Xylulose 5-phosphate → ribulose 5-phosphate</td>
</tr>
<tr>
<td>11b. Ribose 5-phosphate isomerase</td>
<td>Ribose 5-phosphate → ribulose 5-phosphate</td>
</tr>
<tr>
<td>12. Phosphoribulokinase (ribulose 5-phosphate kinase)</td>
<td>Ribulose 5-phosphate + ATP → ribulose 1,5-bisphosphate + ADP + H⁺</td>
</tr>
</tbody>
</table>

*Note: Pᵢ stands for inorganic phosphate.*

**Fundamentals of Plant Physiology 1st Edition, Table 8.1**
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Figure 8.4  Carboxylation and oxygenation of ribulose 1,5-bisphosphate catalyzed by Rubisco
Figure 8.5 Ferredoxin–thioredoxin system
Figure 8.6 Operation of the C₂ oxidative photosynthetic carbon cycle
Table 8.2  Reactions of the C\textsubscript{2} oxidative photosynthetic carbon cycle

<table>
<thead>
<tr>
<th>Enzyme*</th>
<th>Reaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Rubisco</td>
<td>2 Ribulose 1,5-bisphosphate + 2 \text{O}_2 \rightarrow 2 \text{2-phosphoglycerate} + 2 \text{3-phosphoglycerate}</td>
</tr>
<tr>
<td>2. Phosphoglycotope phosphatase</td>
<td>2 \text{2-Phosphoglycerate} + 2 \text{H}_2\text{O} \rightarrow 2 \text{glycolate} + 2 \text{P}_i</td>
</tr>
<tr>
<td>3. Glycolate oxidase</td>
<td>2 \text{Glycolate} + 2 \text{O}_2 \rightarrow 2 \text{glyoxylate} + 2 \text{H}_2\text{O}_2</td>
</tr>
<tr>
<td>4. Catalase</td>
<td>2 \text{H}_2\text{O}_2 \rightarrow 2 \text{H}_2\text{O} + \text{O}_2</td>
</tr>
<tr>
<td>5. Glutamate:glyoxylate aminotransferase</td>
<td>2 \text{Glyoxylate} + 2 \text{glutamate} \rightarrow 2 \text{glycine} + 2 \text{2-oxoglutarate}</td>
</tr>
<tr>
<td>6. Glycine decarboxylase complex (GDC)</td>
<td>\text{Glycine} + \text{NAD}^+ + \text{[GDC]} \rightarrow \text{CO}_2 + \text{NH}_4^+ + \text{NADH} + \text{[GDC-THF-CH}_2_2\text{]}</td>
</tr>
<tr>
<td>7. Serine hydroxymethyltransferase</td>
<td>\text{[GDC-THF-CH}_2_2\text{]} + \text{glycine} + \text{H}_2\text{O} \rightarrow \text{serine} + \text{[GDC]}</td>
</tr>
<tr>
<td>8. Serine:2-oxoglutarate aminotransferase</td>
<td>\text{Serine} + 2-\text{oxoglutarate} \rightarrow \text{hydroxypropionate} + \text{glutamate}</td>
</tr>
<tr>
<td>9. Hydroxypropionate reductase</td>
<td>\text{Hydroxypropionate} + \text{NADH} + \text{H}^+ \rightarrow \text{glyceraldehyde} + \text{NAD}^+</td>
</tr>
<tr>
<td>10. Glycerate kinase</td>
<td>\text{Glycerate} + \text{ATP} \rightarrow \text{3-phosphoglycerate} + \text{ADP}</td>
</tr>
<tr>
<td>11. Glutamine synthetase</td>
<td>\text{Glutamine} + \text{NH}_4^+ + \text{ATP} \rightarrow \text{glutamine} + \text{ADP} + \text{P}_i</td>
</tr>
<tr>
<td>12. Ferredoxin-dependent glutamate synthetase (GOGAT)</td>
<td>2-\text{Oxoglutarate} + \text{glutamine} + 2 \text{F}<em>{\text{red}} + 2 \text{H}^+ \rightarrow 2 \text{glutamate} + 2 \text{F}</em>{\text{oxid}}</td>
</tr>
</tbody>
</table>

**Net reaction of the C\textsubscript{2} oxidative photosynthetic carbon cycle**

\[
2 \text{Ribulose 1,5-bisphosphate} + 3 \text{O}_2 + \text{H}_2\text{O} + \text{glutamate} \rightarrow \text{Glycerate} + 2 \text{3-phosphoglycerate} + \text{NH}_4^+ + \text{CO}_2 + 2 \text{P}_i + 2 \text{oxoglutarate} \quad \text{(reactions 1 to 9)}
\]

Two reactions in the chloroplasts restore the molecule of glutamate:

\[
\text{2-Oxoglutarate} + \text{NH}_4^+ + [(2 \text{F}_{\text{red}} + 2 \text{H}^+), \text{ATP}] \rightarrow \text{Glutamate} + \text{H}_2\text{O} + [(2 \text{F}_{\text{oxid}}), \text{ADP} + \text{P}_i] \quad \text{(reactions 11 and 12)}
\]

and the molecule of 3-phosphoglycerate:

\[
\text{Glycerate} + \text{ATP} \rightarrow \text{3-Phosphoglycerate} + \text{ADP} \quad \text{(reaction 10)}
\]

Hence, the consumption of three molecules of atmospheric oxygen in the C\textsubscript{2} oxidative photosynthetic carbon cycle (two in the oxygenase activity of Rubisco and one in peroxisomal oxidations) elicits
- the release of one molecule of CO\textsubscript{2}, and
- the consumption of two molecules of ATP and two molecules of reducing equivalents (2 \text{F}_{\text{red}} + 2 \text{H}^+) for
  - incorporating a three-carbon skeleton back into the Calvin–Benson Cycle, and
  - restoring glutamate from \text{NH}_4^+ and 2-oxoglutarate.

*Locations: Chloroplasts; peroxisomes; mitochondria. Fd: ferredoxin; THF, tetrahydrofolate.

**FUNDAMENTALS OF PLANT PHYSIOLOGY** 1e, Table 8.2
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<table>
<thead>
<tr>
<th>Enzyme</th>
<th>Reaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Rubisco</td>
<td>2 Ribulose 1,5-bisphosphate + 2 O₂ → 2 2-phosphoglycolate + 2 3-phosphoglycerate</td>
</tr>
<tr>
<td>2. Phosphoglycolate phosphatase</td>
<td>2 2-Phosphoglycolate + 2 H₂O → 2 glycolate + 2 P_i</td>
</tr>
<tr>
<td>3. Glycolate oxidase</td>
<td>2 Glycolate + 2 O₂ → 2 glyoxylate + 2 H₂O</td>
</tr>
<tr>
<td>4. Catalase</td>
<td>2 H₂O₂ → 2 H₂O + O₂</td>
</tr>
<tr>
<td>5. Glutamate:glyoxylate aminotransferase</td>
<td>2 Glyoxylate + 2 glutamate → 2 glycine + 2 2-oxoglutarate</td>
</tr>
<tr>
<td>7. Serine hydroxymethyltransferase</td>
<td>[GDC-THF-CH₂] + glycine + H₂O → serine + [GDC]</td>
</tr>
<tr>
<td>8. Serine:2-oxoglutarate aminotransferase</td>
<td>Serine + 2-oxoglutarate → hydroxypyruvate + glutamate</td>
</tr>
<tr>
<td>9. Hydroxypyruvate reductase</td>
<td>Hydroxypyruvate + NADH + H⁺ → glycerate + NAD⁺</td>
</tr>
<tr>
<td>10. Glycerate kinase</td>
<td>Glycerate + ATP → 3-phosphoglycerate + ADP</td>
</tr>
<tr>
<td>11. Glutamine synthetase</td>
<td>Glutamate + NH₄⁺ + ATP → glutamine + ADP + P_i</td>
</tr>
<tr>
<td>12. Ferredoxin-dependent glutamate synthase (GOGAT)</td>
<td>2-Oxoglutarate + glutamine + 2 Fd_{red} + 2 H⁺ → 2 glutamate + 2 Fd_{oxid}</td>
</tr>
</tbody>
</table>

*Locations: Chloroplasts; peroxisomes; mitochondria. Fd: ferredoxin; THF, tetrahydrofolate.*
TABLE 8.2 Reactions of the $C_2$ oxidative photosynthetic carbon cycle

<table>
<thead>
<tr>
<th>Net reaction of the $C_2$ oxidative photosynthetic carbon cycle</th>
</tr>
</thead>
<tbody>
<tr>
<td>2 Ribulose 1,5-bisphosphate + 3 $O_2$ + $H_2$O + glutamate</td>
</tr>
<tr>
<td>$\downarrow$</td>
</tr>
<tr>
<td>Glycerate + 2 3-phosphoglycerate + $NH_4^+$ + $CO_2$ + 2 $P_i$ + 2-oxoglutarate</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>Two reactions in the chloroplasts restore the molecule of glutamate:</td>
</tr>
<tr>
<td>2-Oxoglutarate + $NH_4^+$ + [(2 $Fd_{\text{red}}$ + 2 $H^+$), ATP]</td>
</tr>
<tr>
<td>$\downarrow$</td>
</tr>
<tr>
<td>Glutamate + $H_2$O + [(2 $Fd_{\text{oxid}}$), ADP + $P_i$]</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>and the molecule of 3-phosphoglycerate:</td>
</tr>
<tr>
<td>Glycerate + ATP</td>
</tr>
<tr>
<td>$\downarrow$</td>
</tr>
<tr>
<td>3-Phosphoglycerate + ADP</td>
</tr>
<tr>
<td></td>
</tr>
</tbody>
</table>

Hence, the consumption of three molecules of atmospheric oxygen in the $C_2$ oxidative photosynthetic carbon cycle (two in the oxygenase activity of Rubisco and one in peroxisomal oxidations) elicits
- the release of one molecule of $CO_2$ and
- the consumption of two molecules of ATP and two molecules of reducing equivalents (2 $Fd_{\text{red}}$ + 2 $H^+$) for
  - incorporating a three-carbon skeleton back into the Calvin–Benson Cycle, and
  - restoring glutamate from $NH_4^+$ and 2-oxoglutarate.
Figure 8.7 Dependence of the C$_2$ oxidative photosynthetic carbon cycle on chloroplast metabolism
Figure 8.8 The $C_4$ photosynthetic carbon cycle involves five successive stages in two distinct cell types.
### Table 8.3 Reactions of C₄ and CAM photosynthesis

<table>
<thead>
<tr>
<th>Enzyme</th>
<th>Compartment</th>
<th>Reaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. PEPCase</td>
<td>Cytosol</td>
<td>Phosphoenol/pyruvate + HCO₃⁻ → oxaloacetate + P_i</td>
</tr>
<tr>
<td>2. NADP–malate dehydrogenase</td>
<td>Chloroplast</td>
<td>Oxaloacetate + NADPH + H⁺ → malate + NADP⁺</td>
</tr>
<tr>
<td>3. Aspartate aminotransferase</td>
<td>Cytosol/mitochondrion</td>
<td>Oxaloacetate + glutamate → aspartate + 2-oxoglutarate</td>
</tr>
<tr>
<td><strong>Decarboxylating enzymes</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4a. NAD–malic enzyme</td>
<td>Chloroplast</td>
<td>Malate + NADP⁺ → pyruvate + CO₂ + NADPH + H⁺</td>
</tr>
<tr>
<td>4b. NAD–malic enzyme</td>
<td>Mitochondrion</td>
<td>Malate + NAD⁺ → pyruvate + CO₂ + NADH + H⁺</td>
</tr>
<tr>
<td>5. Phosphoenol/pyruvate carboxykinase</td>
<td>Cytosol</td>
<td>Oxaloacetate + ATP → phosphoenol/pyruvate + CO₂ + ADP</td>
</tr>
<tr>
<td>6. Alanine aminotransferase</td>
<td>Cytosol</td>
<td>Pyruvate + glutamate → alanine + 2-oxoglutarate</td>
</tr>
<tr>
<td>7. Pyruvate–phosphate dikinase</td>
<td>Chloroplast</td>
<td>Pyruvate + P_i + ATP → phosphoenol/pyruvate + AMP + PP_i</td>
</tr>
<tr>
<td>8. Adenylate kinase</td>
<td>Chloroplast</td>
<td>AMP + ATP → 2 ADP</td>
</tr>
<tr>
<td>9. Pyrophosphatase</td>
<td>Chloroplast</td>
<td>PP_i + H₂O → 2 P_i</td>
</tr>
</tbody>
</table>

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

*FUNDAMENTALS OF PLANT PHYSIOLOGY 1e, Table 8.3*  
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Figure 8.9  C₄ photosynthetic pathway in leaves of different plants

(A) Kranz anatomy

Mesophyll cell
Diffusion barrier (plasma membranes and walls)
Bundle sheath cell
Vascular tissues

Kranz anatomy
Atmospheric CO₂
Carbon assimilation (e.g., sucrose)
Sucrose

Single-cell C₄ cycle
Atmospheric CO₂
Diffusion gradients
Growth in unicellular organisms (e.g., diatoms)
Transport to vascular tissues in pluricellular organisms (e.g., land plants)

(C) Single-cell C₄ cycle

Cytosol (diffusion barrier)
Cytosol (internal region)
Cytosol (external region)

(A) Kranz anatomy

Vascular bundle
Mesophyll cell
Bundle sheath cell

Figure 8.9  C₄ photosynthetic pathway in leaves of different plants (Part 1)
Figure 8.9  C₄ photosynthetic pathway in leaves of different plants (Part 2)

(B) Kranz anatomy

Atmospheric CO₂

Mesophyll cell

Diffusion barrier (plasma membranes and walls)

Bundle sheath cell

Vascular tissues

Carbon assimilation (e.g., sucrose)

CO₂

Sucrose

Single-cell C₄ cycle

Atmospheric CO₂

External side

Diffusion gradients

Growth in unicellular organisms (e.g., diatoms)

Carbon assimilation

Transport to vascular tissues in pluricellular organisms (e.g., land plants)
Figure 8.9  C₄ photosynthetic pathway in leaves of different plants (Part 3)

(C) Single-cell C₄ cycle

CO₂

Cytosol (internal region)

C₄

C₃

Cytosol (external region)

Cytosol (diffusion barrier)

C₃

C₄

[CO₂]

20 µm

2 µm


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Figure 8.10 Crassulacean acid metabolism (CAM) in *Kalanchoe*

**Dark: Stomata opened**
- Atmospheric CO₂
- Open stoma permits the uptake of CO₂ and the loss of H₂O (transpiration).

**Light: Stomata closed**
- Atmospheric CO₂
- Closed stoma prevents the loss of prefixed CO₂ and H₂O (transpiration).

**Diagram Description**
- **Cytosol**
  - Phosphoenolpyruvate
  - Oxaloacetate
  - Triose phosphates
  - Starch
- **Mitochondrion**
  - Respiratory CO₂
  - HCO₃⁻
- **PEPCase**
- **Chloroplast**
  - Malic acid
  - Starch
  - Malate
- **Vacuole**
  - Malate
  - NADH
  - NAD⁺
- **Calvin–Benson cycle**
  - Triose phosphate
  - NAD(P)H
  - NAD(P)⁺-malate dehydrogenase
- **Pyruvate**

*FUNDAMENTALS OF PLANT PHYSIOLOGY* 1e, Figure 8.10
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Figure 8.10 Crassulacean acid metabolism (CAM) in *Kalanchoe* (Part 1)

Dark: Stomata opened

Atmospheric CO₂

Open stoma permits the uptake of CO₂ and the loss of H₂O (transpiration).

Respiratory CO₂

Mitochondrion

Cytosol

HCO₃⁻

(3.1)

PEPCase

Phosphoenolpyruvate

Oxaloacetate

NAD(P)H

NAD(P)⁺

NAD(P)–malate dehydrogenase

Triose phosphates

Starch

Chloroplast

Malate

Malic acid

Vacuole

FUNDAMENTALS OF PLANT PHYSIOLOGY 1e, Figure 8.10 (Part 1)
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Figure 8.10 Crassulacean acid metabolism (CAM) in *Kalanchoe* (Part 2)

Light: Stomata closed

- Atmospheric CO₂
- Closed stoma prevents the loss of prefixed CO₂ and H₂O (transpiration).

**Diagram:***
- Triose phosphate
- Calvin-Benson cycle
- Starch
- Chloroplast
- Pyruvate
- NAD–malic enzyme
- NADH
- NAD⁺
- Vacuole
- Malic acid
- Malate
- Cytosol
- Mitochondrion

*FUNDAMENTALS OF PLANT PHYSIOLOGY 1e, Figure 8.10 (Part 2)*
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Figure 8.11  Carbon mobilization in land plants

**DAY**
- CO₂ enters the chloroplast through the Calvin-Benson cycle.
- Starch is synthesized from ADP-glucose.
- Fructose is produced from ADP-glucose.
- Triose phosphates are converted to sucrose.
- Sucrose moves through the phloem to vascular tissues.

**NIGHT**
- Maltose and glucose are transported into the cytosol from the chloroplast.
- Maltose-glucose translocators facilitate the movement of sugars into the cytosol.
- Fructose is transported to the chloroplast.
- Starch is converted to maltose-glucose.
- Sucrose is transported to the cytosol for storage in grains, tubers, or growth in roots and stems.

Leaf cells

Vascular tissues

Carbohydrate storage (e.g., starch, fructans)

Growth

Roots, stems

Grains, tubers