Lehninger

SIXTH EDITION

Principles of Biochemistry

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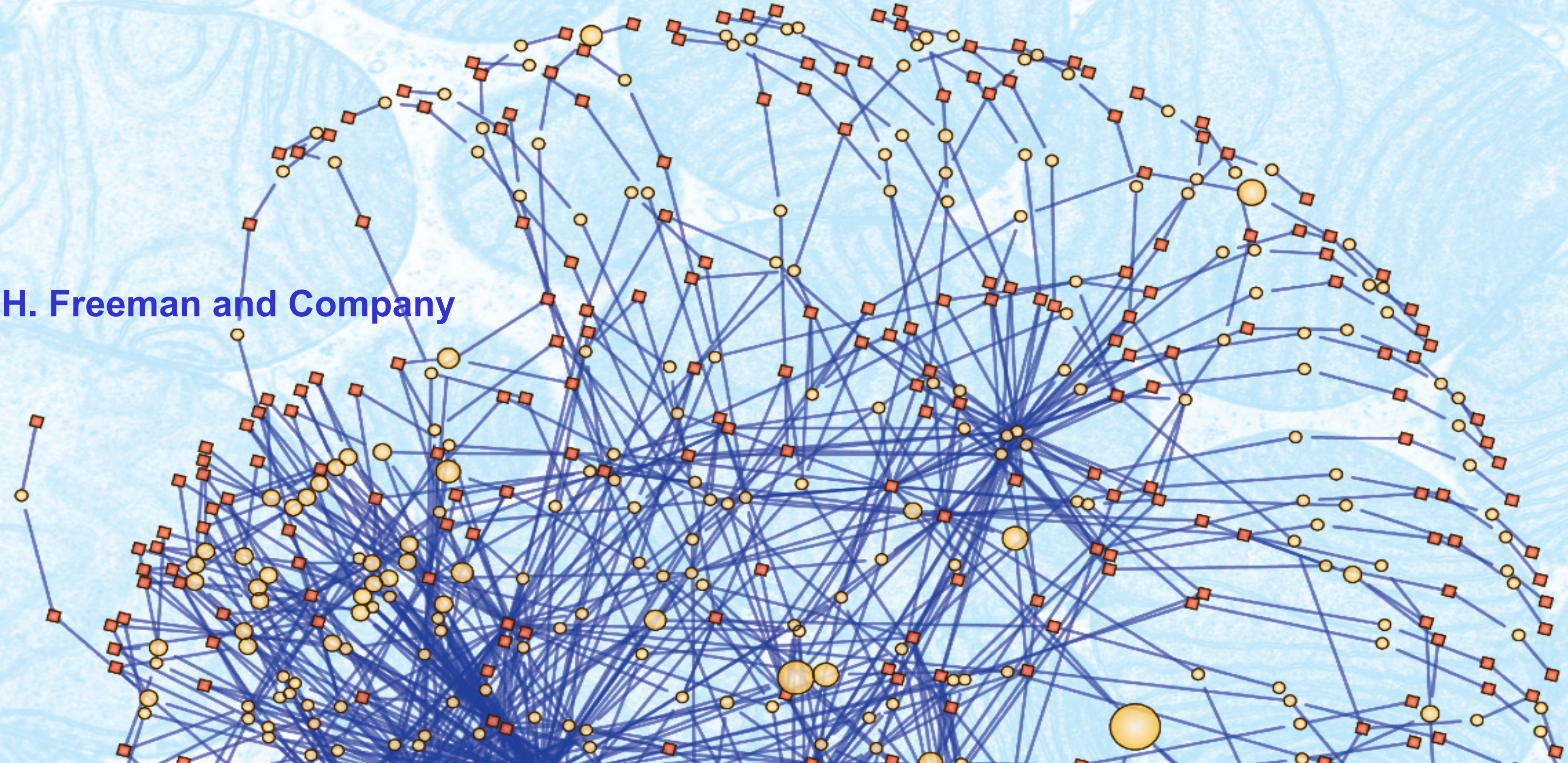
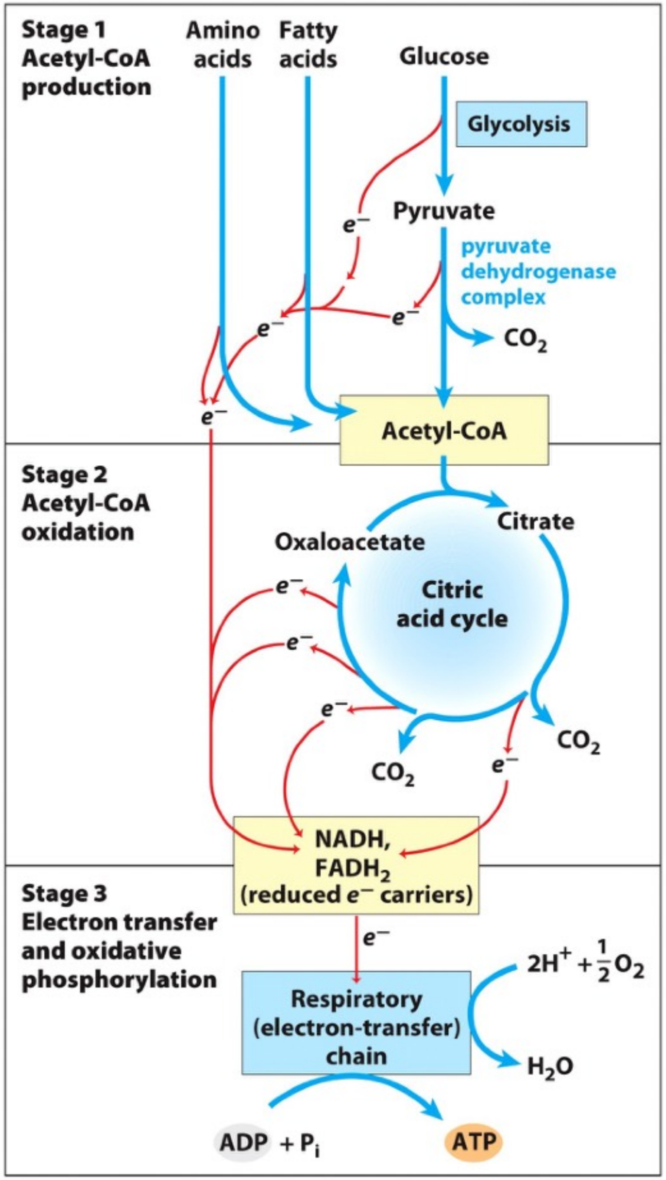
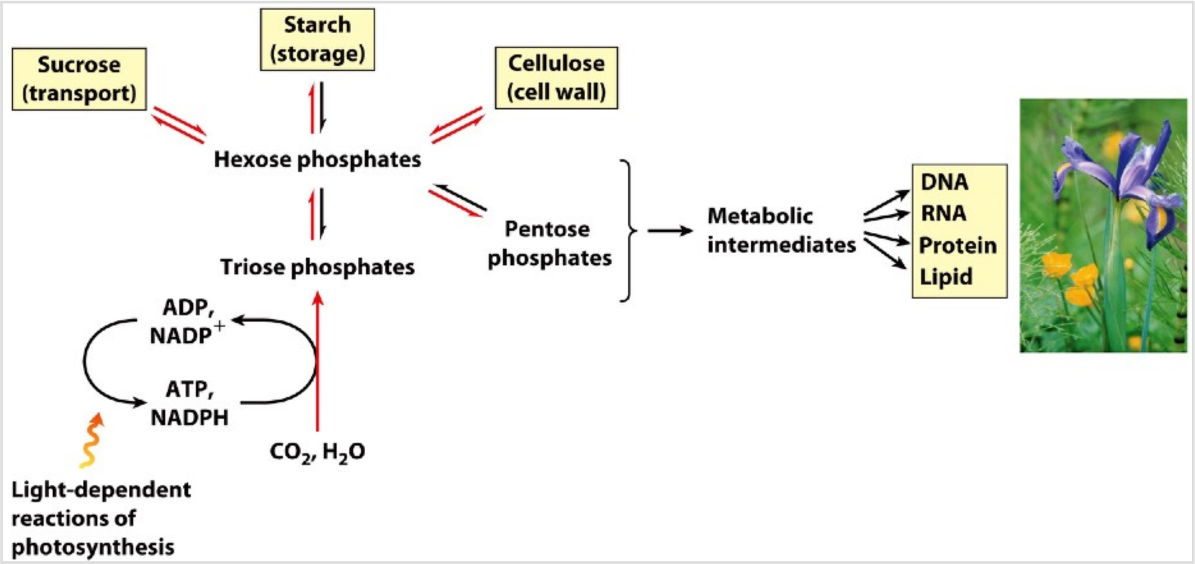
20| Carbohydrate Biosynthesis in Plants and Bacteria



Catabolism vs. Anabolism

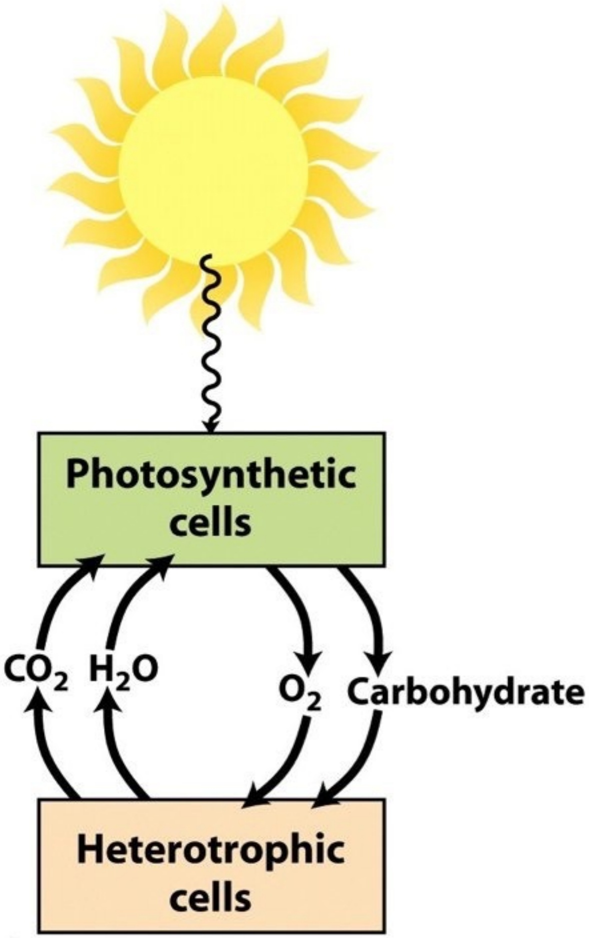


- The previous chapters were mainly concerned with ***catabolism***: how to extract energy from biomolecules.
- This and the following chapters are concerned with ***anabolism***: how to build biomolecules.



Plants Are Extremely Versatile

- Autotrophs, able to convert inorganic carbon (CO_2) into organic compounds.
- Biosynthesis of carbohydrates occurs in chloroplast. Movement of intermediates between cellular compartments is important.
- Have metabolic flexibility to adapt to changing conditions.
- Have thick cell walls made of carbohydrate polymers (polysaccharides), which must be assembled outside plasma membrane.



Week 14 Carbohydrate Biosynthesis

20.1 Photosynthetic Carbohydrate Synthesis

20.2 Photorespiration

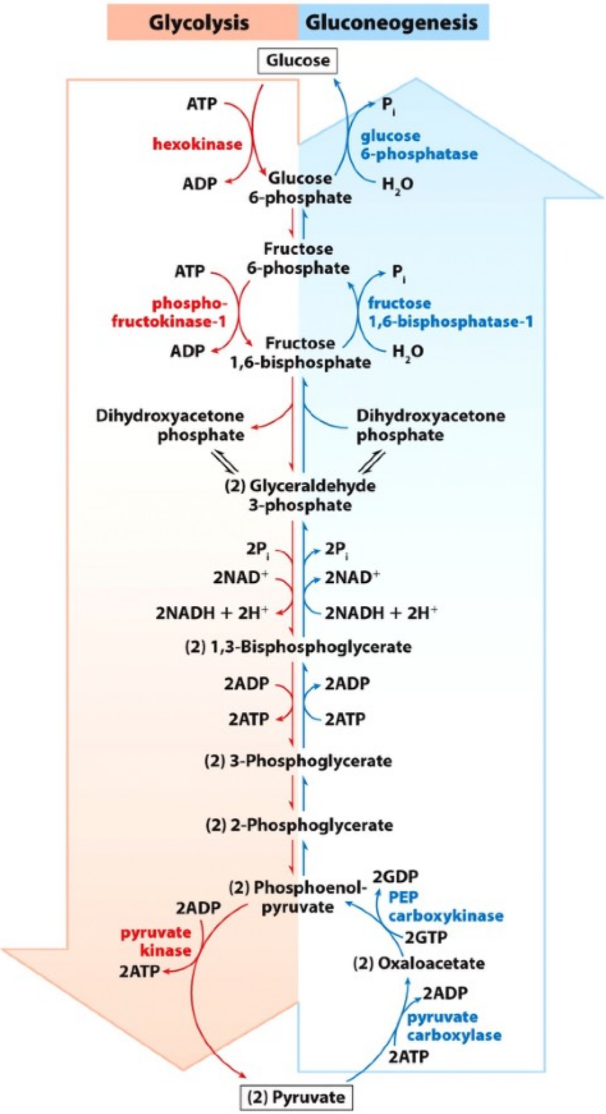
20.3 Biosynthesis of Starch and Sucrose

20.4 Synthesis of Cell Wall Polysaccharides

20.5 Integration of Carbohydrate Metabolism

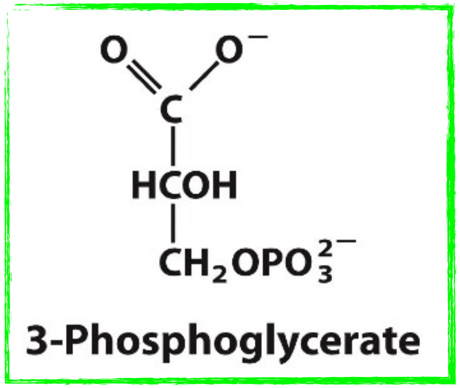
Gluconeogenesis in Animals

- Similar to 10 glycolytic reactions in the opposite direction with 3 exceptions.
  - Pyruvate -> phosphoenolpyruvate.
  - Fructose 1,6-bisphosphate -> fructose 6-phosphate.
  - Glucose 6-phosphate -> glucose.
- Start with 3-carbon precursor molecules.
- 4 ATPs, 2 GTPs, and 2 NADHs are consumed per glucose produced.
  - Only 2 ATPs and 2 NADHs are produced in conversion of 1 glucose to 2 pyruvates.

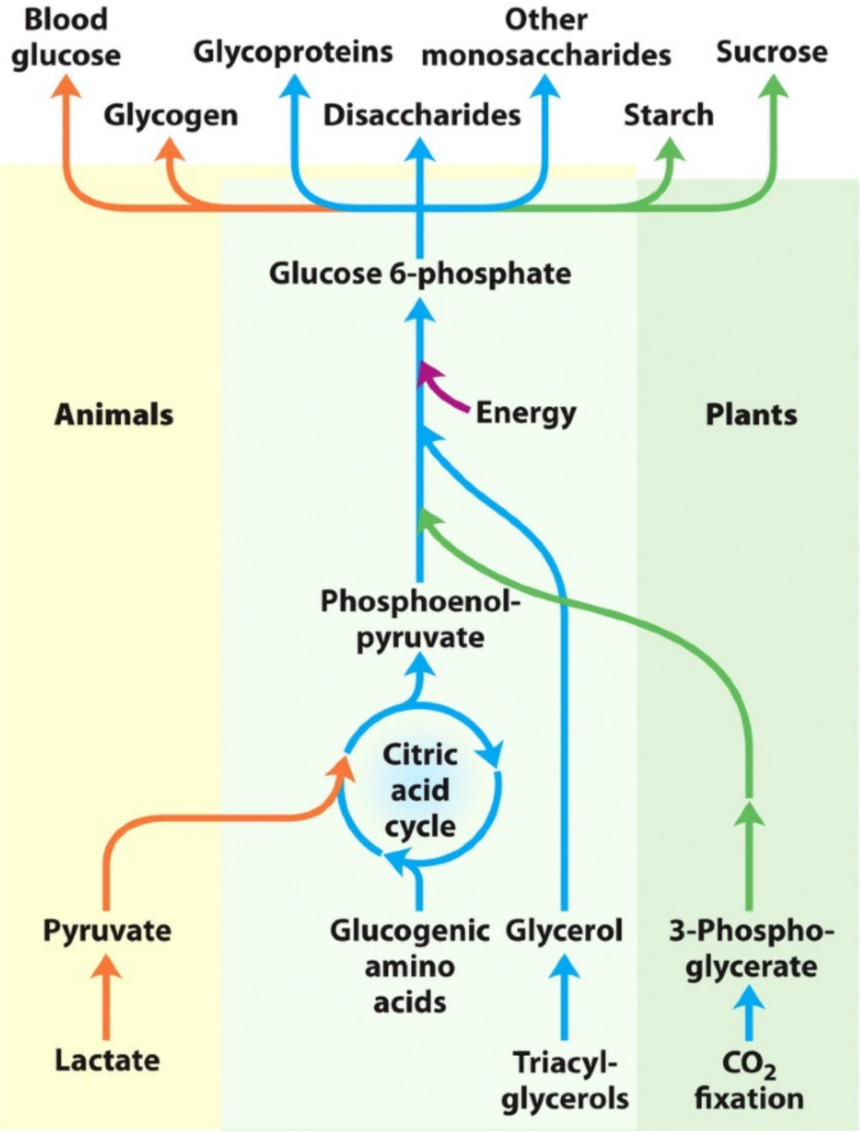


CO_2 Assimilation by Plants

- Animal cells use 3-C compounds (pyruvate, lactate) for synthesis.
- Plant cells use CO_2 to make 3-C compound (3-phosphoglycerate) for further synthesis.
  - ATP and NADPH are required.
  - Conversion of CO_2 to simple organic compound is called **CO_2 assimilation**.

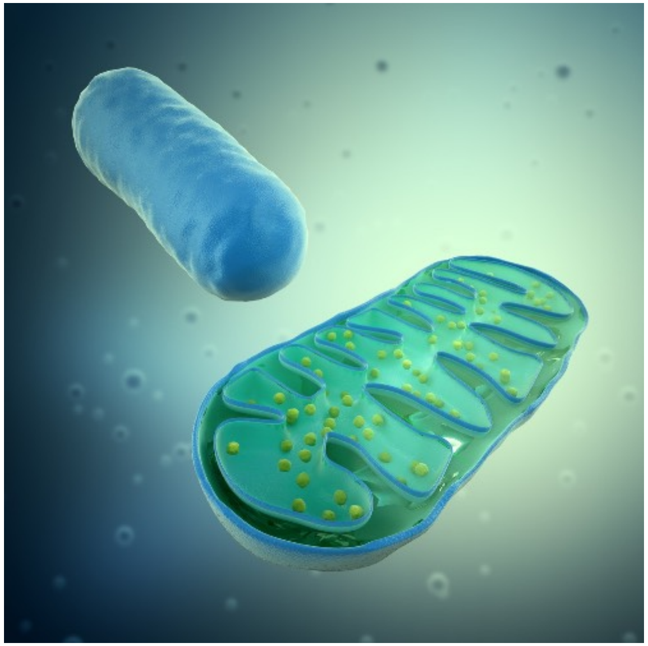


3-Phosphoglycerate



CO_2 Assimilation Occurs in Chloroplast

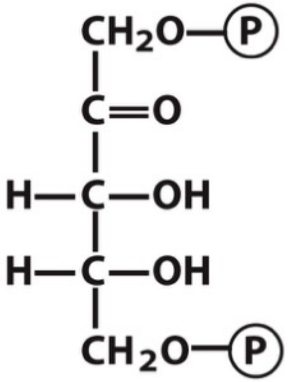
- A chloroplast is similar to a mitochondrion in a number of ways.
  - Enclosed by a double membrane.
    - Inner membrane is impermeable to ions and polar molecules.
    - Traffic across membrane is mediated by specific transporters.
  - Has own small circular genome.
    - Encode some proteins and RNAs.
    - Most proteins are encoded by nuclear genes.



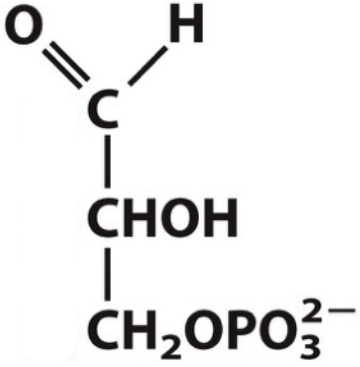
CO_2 Assimilation in Chloroplast

- Occurs in the stroma of chloroplasts via a cyclic process known as the **Calvin cycle**.
- Key intermediate ribulose 1,5-bisphosphate is constantly regenerated.
- Net result: 3 molecules of CO_2 are reduced to form 1 molecule of triose phosphate.

Melvin Calvin, 1911–1997

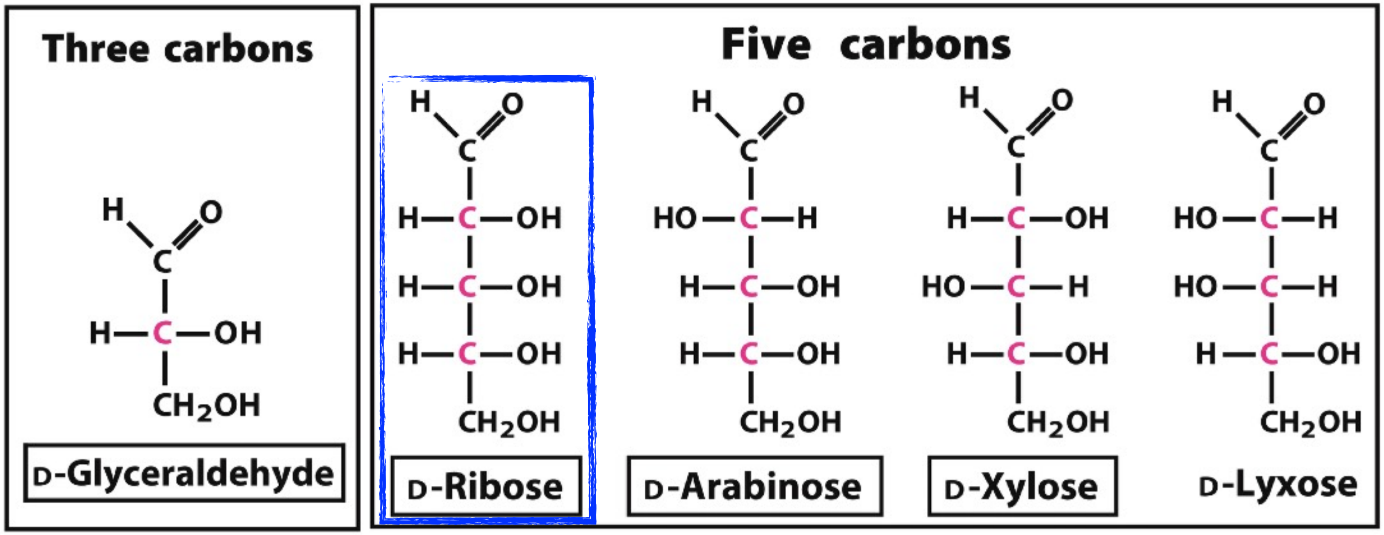


Ribulose 1,5-bisphosphate

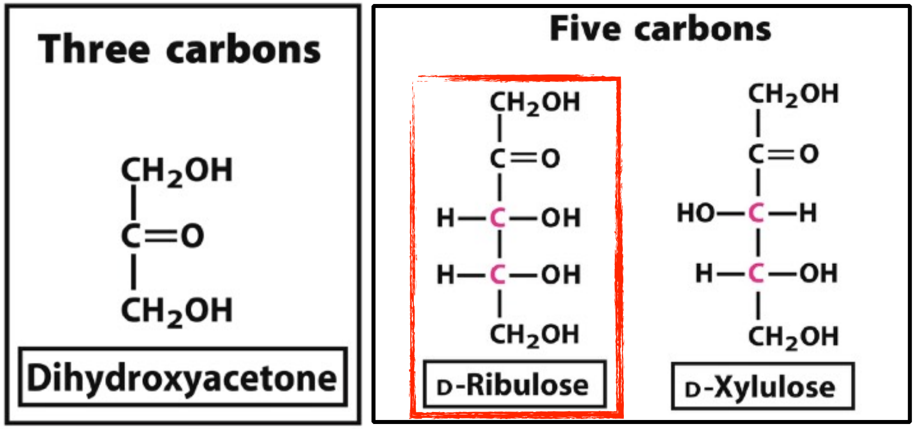


Glyceraldehyde 3-phosphate

Review of Carbohydrates



Aldose

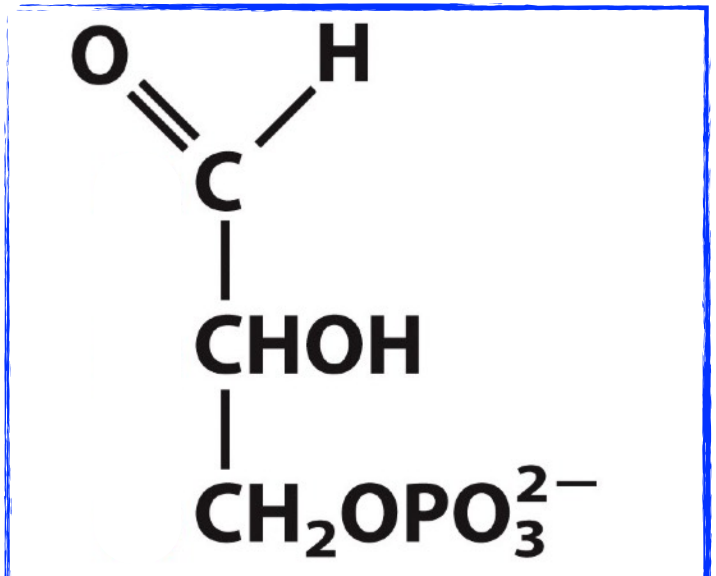


Ketose

- 5-C ketoses are designated by inserting “ul” to name of a corresponding aldose.
  - Rib<u>ul</u>ose from ribose.
  - Xyl<u>ul</u>ose from xylose.

Overview of the Calvin Cycle

1. 3 CO_2 + **3** ribulose 1,5-bisphosphate -> **6** 3-phosphoglycerate.
2. **6** 3-phosphoglycerate -> **6** glyceraldehyde 3-phosphate.
   - Glyceraldehyde 3-phosphate <-> dihydroxyacetone phosphate.
3. **5** glyceraldehyde 3-phosphate -> **3** ribulose 1,5-bisphosphate.
   - **1** Glyceraldehyde 3-phosphate used to make glucose (sucrose and starch).



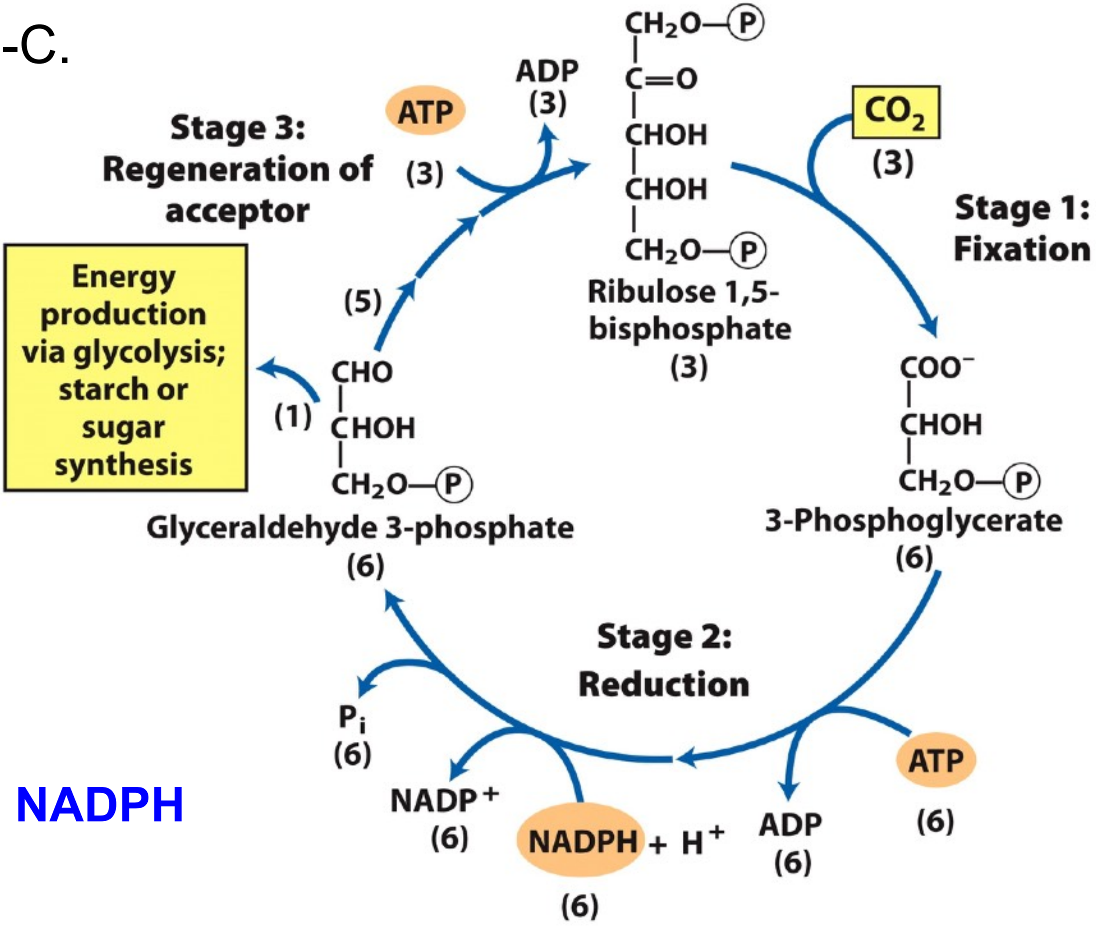
Glyceraldehyde 3-phosphate

Overall reaction of carbon atoms:

3 CO_2 -> glyceraldehyde 3-phosphate.

Three Stages of the Calvin Cycle

1. CO_2 fixation.
   - (3) 1-C + (3) 5-C -> (6) 3-C.
2. Reduction.
   - (6) 3-C-> (6) 3-C.
   - Carboxyl -> Aldehyde.
   - Requires (6) ATP.
   - Requires (6) NADPH.
3. Regeneration.
   - (5) 3-C -> (3) 5-C.
   - Requires (3) ATP.

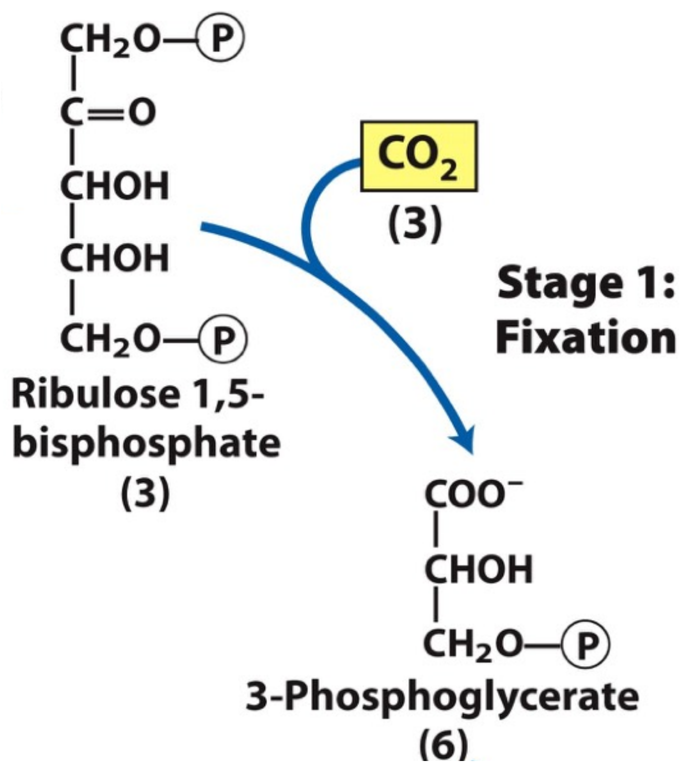


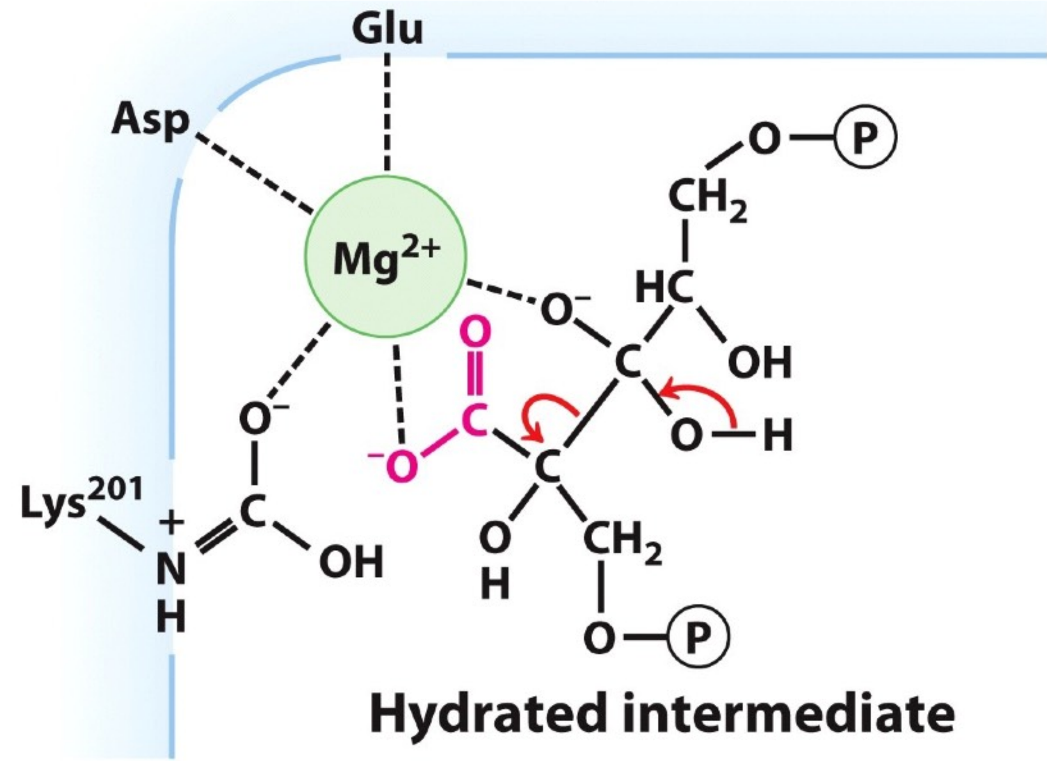
Overall reaction:

$$3\ CO_2 + 9\ ATP + 6\ NADPH$$
$$\downarrow$$
$$\text{glyceraldehyde 3-phosphate} + 9\ ADP + 8\ P_i + 6\ NADP^+$$

First Stage Catalyzed by Rubisco

- Rubisco = <u>R</u>ib<u>u</u>lose 1,5-<u>bis</u>phosphate <u>c</u>arboxylase/<u>o</u>xygenase.
- Large Mg^{2+} enzyme.
- **Ribulose 1,5-bisphosphate + CO_2 -> two 3-phosphoglycerate.**

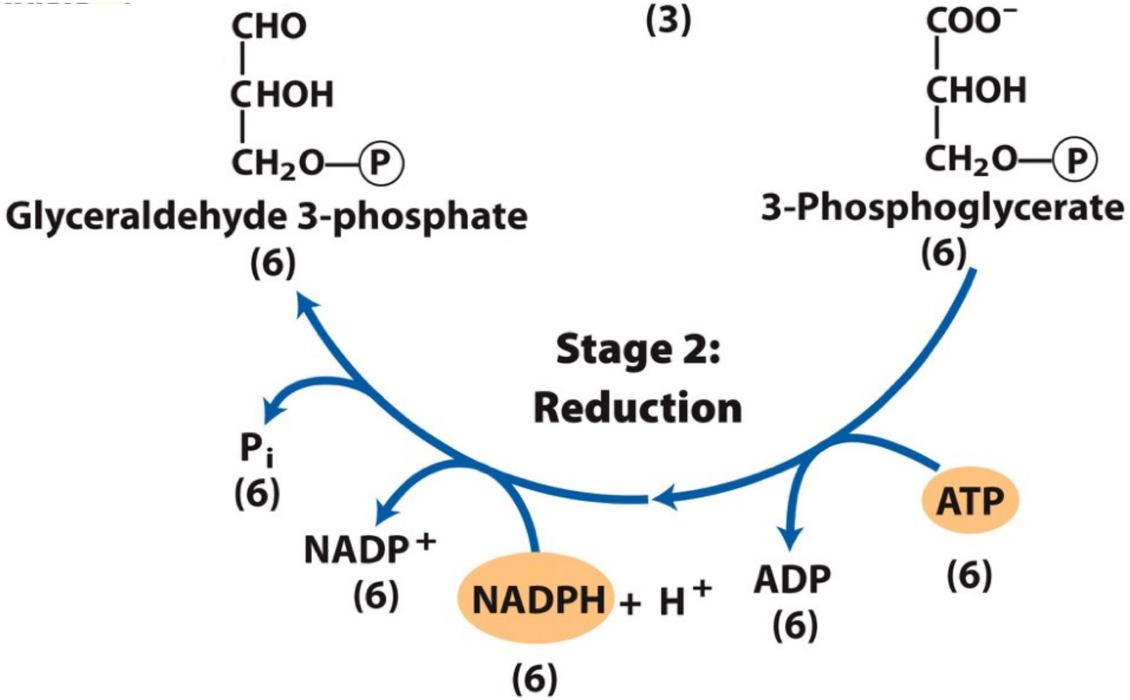




Hydrated intermediate

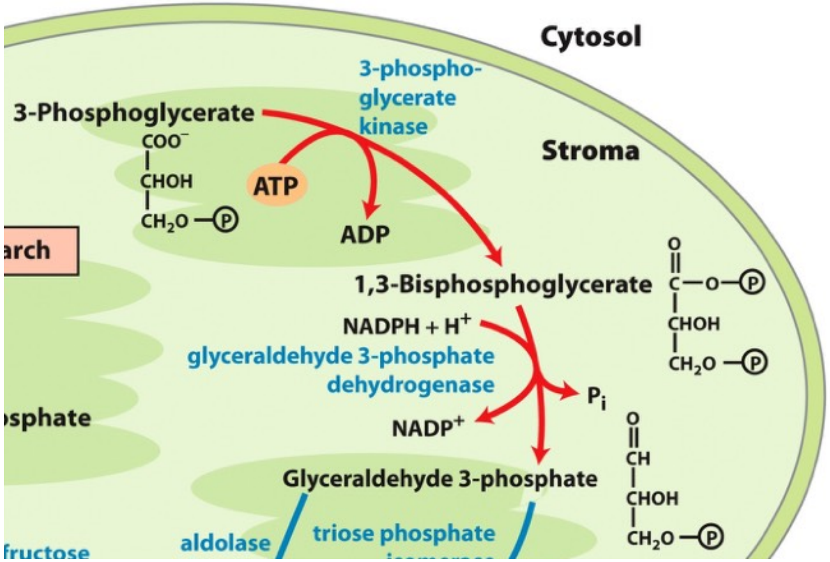
Second Stage: Carboxyl to Aldehyde

- Overall reaction.
  - 3-phosphoglycerate + ATP + NADPH -> glyceraldehyde 3-phosphate + ADP + $NADP^+$.
- Has two steps. Requires ATP and NADPH.
  - Phosphorylation and reduction.
- Essentially reversal of corresponding steps in glycolysis.
  - Use NADPH instead of NADH as cofactor.



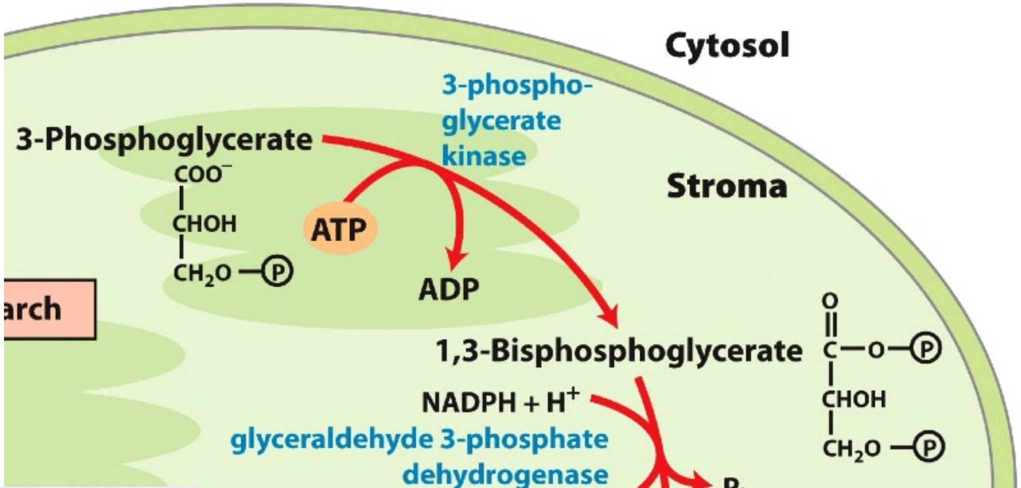
Two Reactions in Second Stage

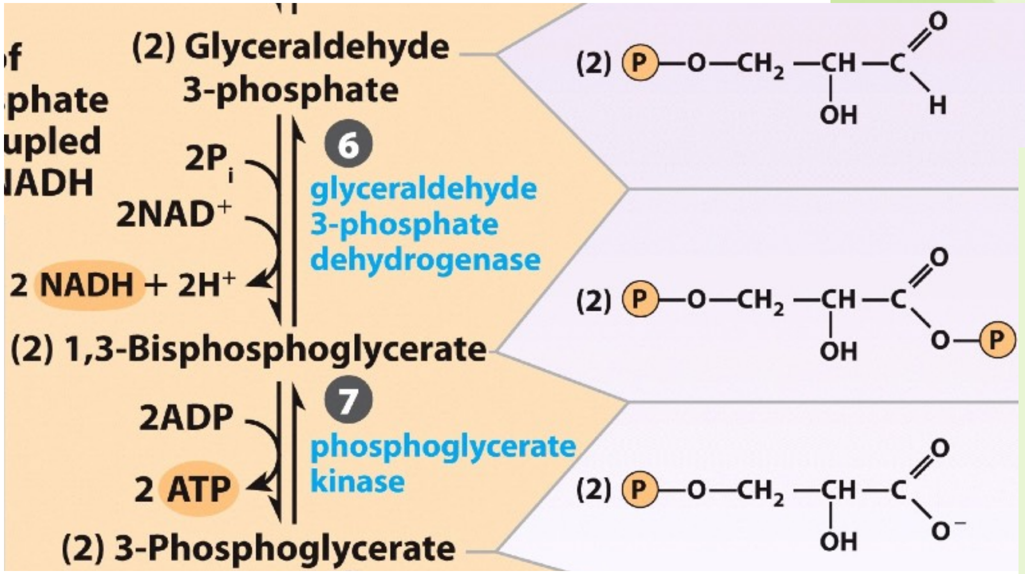
- First step is a phosphorylation reaction.
  - Catalyzed by 3-phosphoglycerate kinase.
  - ATP donates phosphoryl group.
  - Produces 1,3-bisphosphoglycerate.
- Second step is a reduction reaction.
  - Catalyzed by glyceraldehyde 3-phosphate dehydrogenase.
  - NADPH is oxidized and P_i is released.
  - Produces glyceraldehyde 3-phosphate.



Reversal of Glycolytic Reactions

- **Glycolysis.**
  - Step 6 is catalyzed by dehydrogenase and yields NADH.
  - Step 7 is catalyzed by kinase and yields ATP.





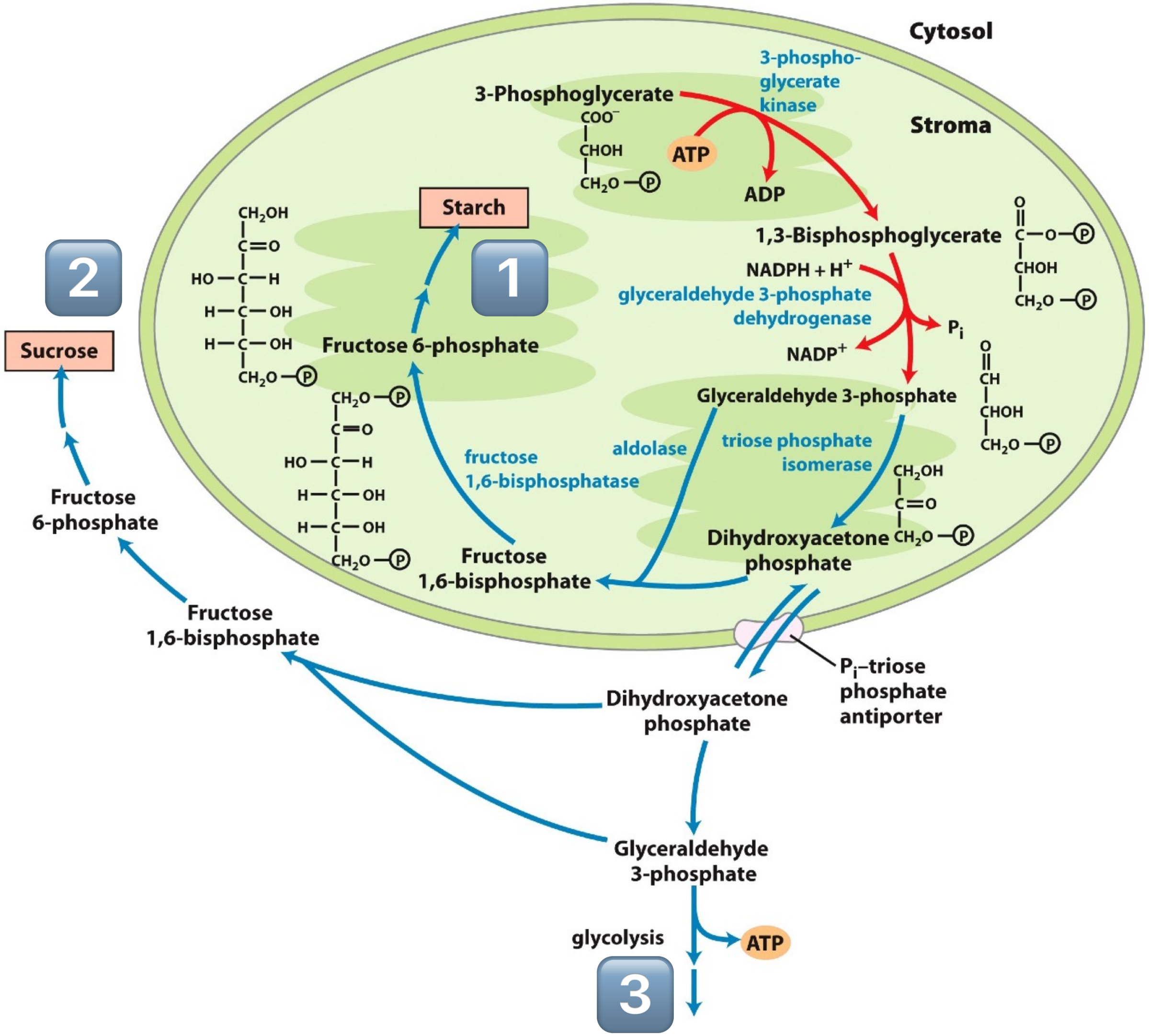
- **2nd stage of CO_2 assimilation.**
  - Step 1 is catalyzed by kinase and consumes ATP.
  - Step 2 is catalyzed by dehydrogenase and consumes NADPH.

Driven forward by high concentration of NADPH and ATP in stroma.

Fates of Glyceraldehyde 3-Phosphate

- **Five** of the **six** are **recycled** to ribulose 1,5-bisphosphate (Stage 3).
- Remaining **one** is the net product.

1. Can be **converted to starch** in the chloroplast.
2. Can be **converted to sucrose** in the cytosol for export.
3. Can provide energy via glycolysis.



Third Stage: Regeneration

①3C + 3C -> 6C.
- Condensation.

②6C -> 6C.
- Dephosphorylation.

③6C + 3C -> 4C + 5C.
- Transfer.

④3C + 4C -> 7C.
- Condensation.

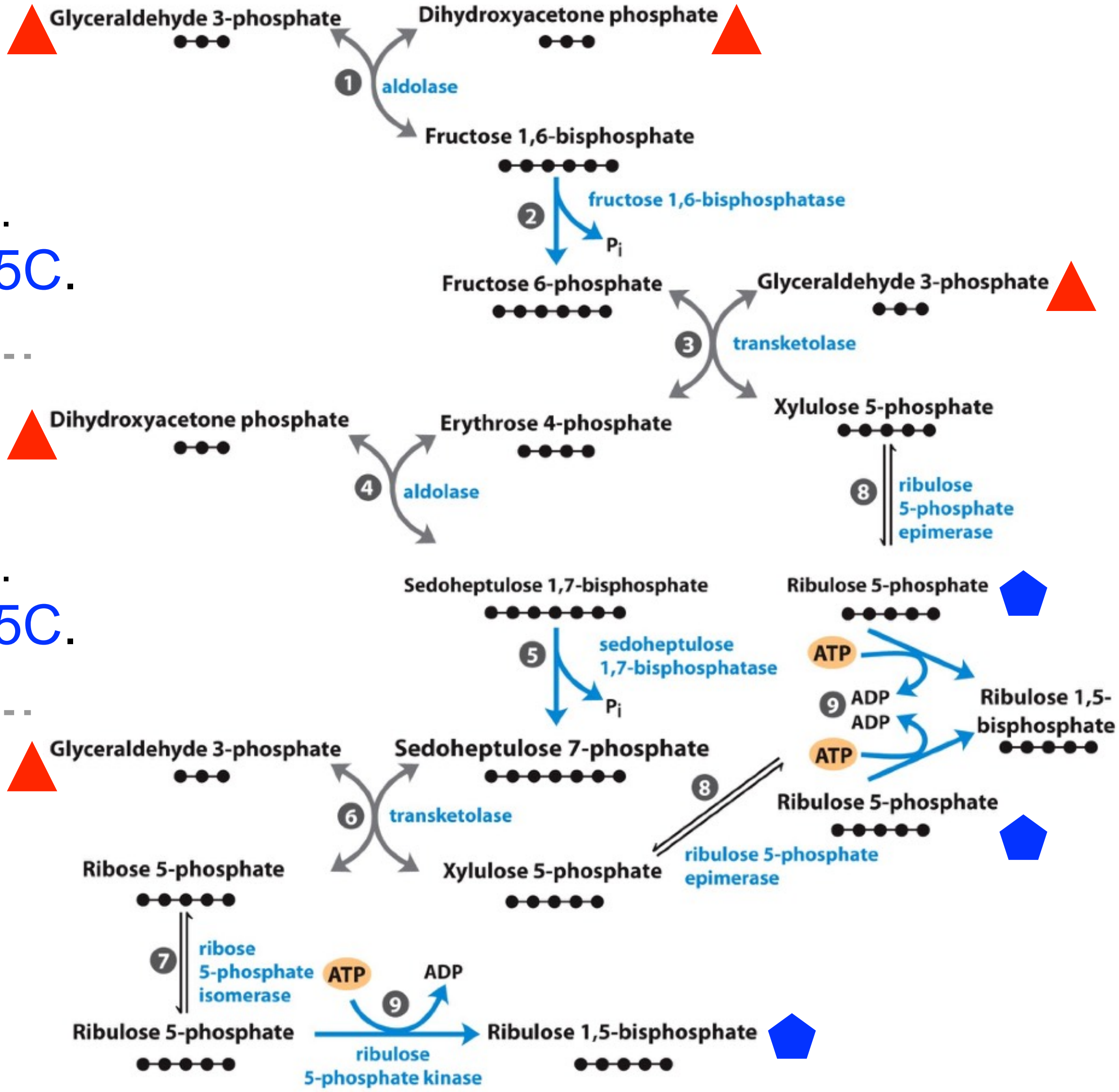
⑤7C -> 7C.
- Dephosphorylation.

⑥7C + 3C -> 5C + 5C.
- Transfer.

⑦5C -> 5C.
- Isomerization.

⑧5C -> 5C.
- Isomerization.

⑨5C -> 5C.
- Phosphorylation.

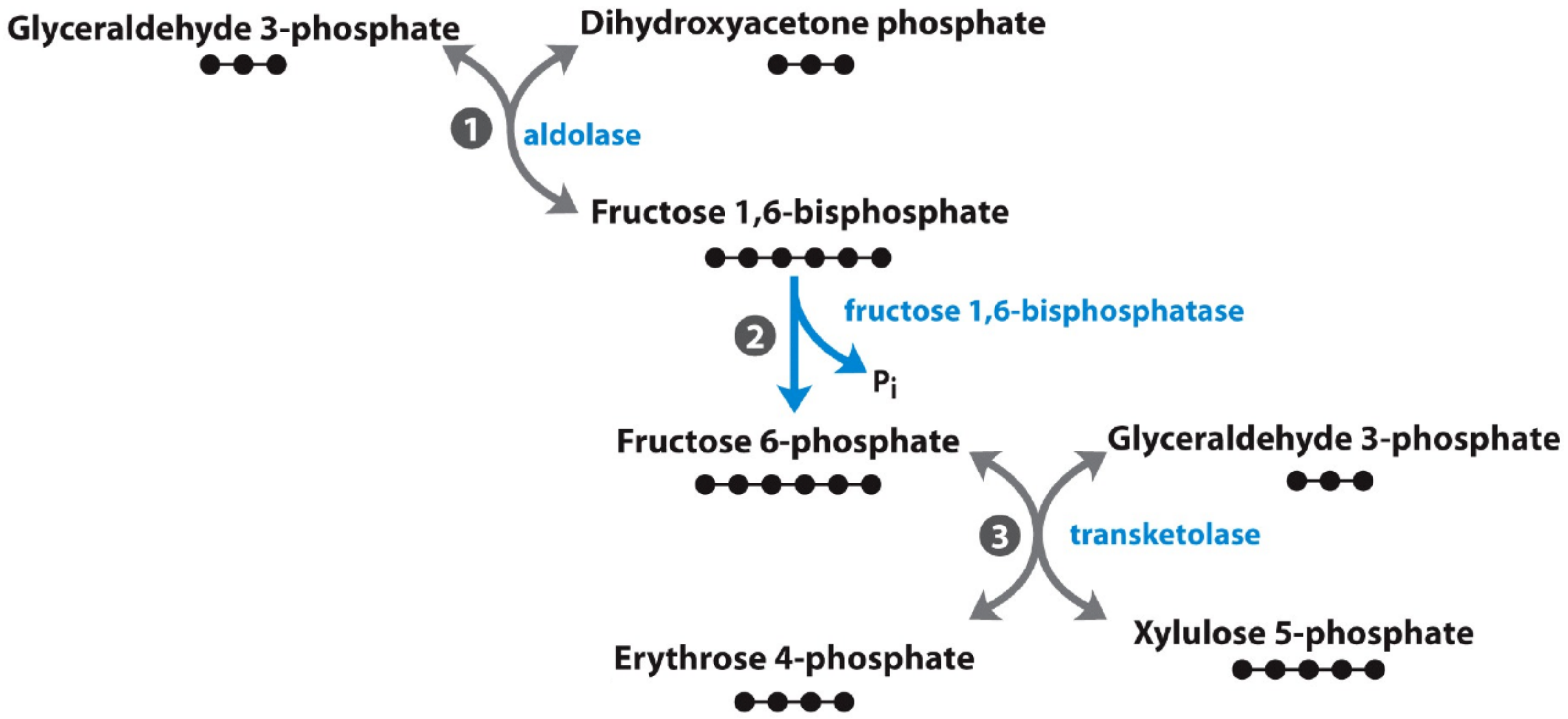


First Three Reactions in Third Stage

①3C + 3C -> 6C.
- Reversal of step 4 in glycolysis. Step 7 in gluconeogenesis.

②6C -> 6C.
- Dephosphorylation. Removal of the 1st phosphate group. Step 8 in gluconeogenesis.

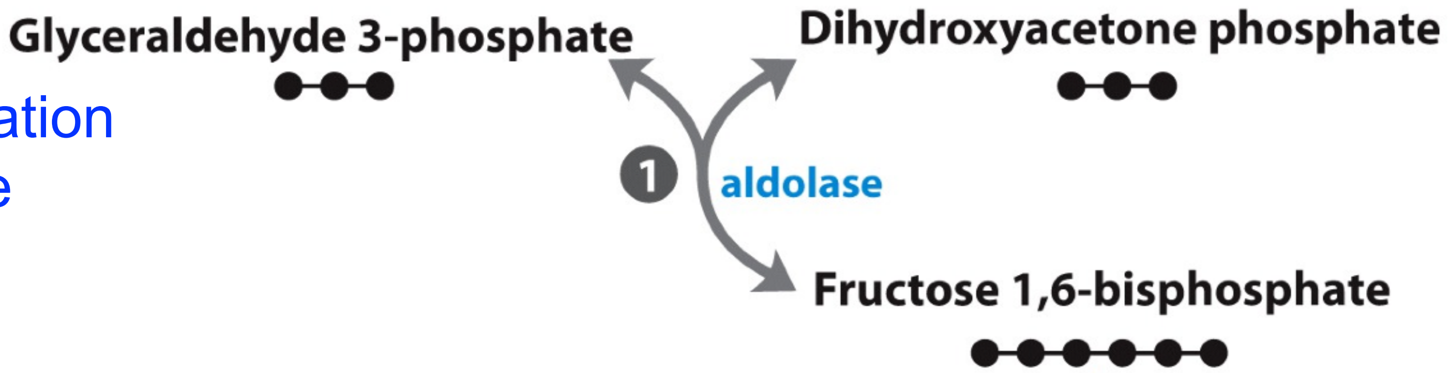
③6C + 3C -> 4C + 5C.
- Transfer of a two-carbon unit.



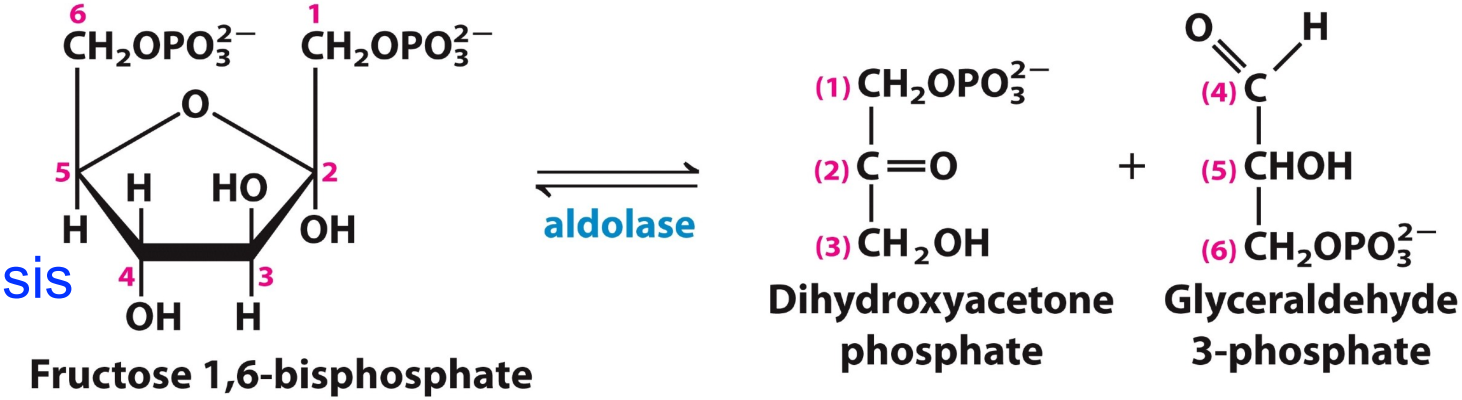
First Reaction in Third Stage

- 3C + 3C -> 6C.
  - Reversal of step 4 in glycolysis (catalyzed by aldolase).
  - Glyceraldehyde = aldotriose; Dihydroxyacetone = ketotriose.
    - Two reactants can be interconverted (step 5 in glycolysis).
    - Interconversion catalyzed by triose phosphate isomerase.

CO_2 assimilation
3rd stage
1st step



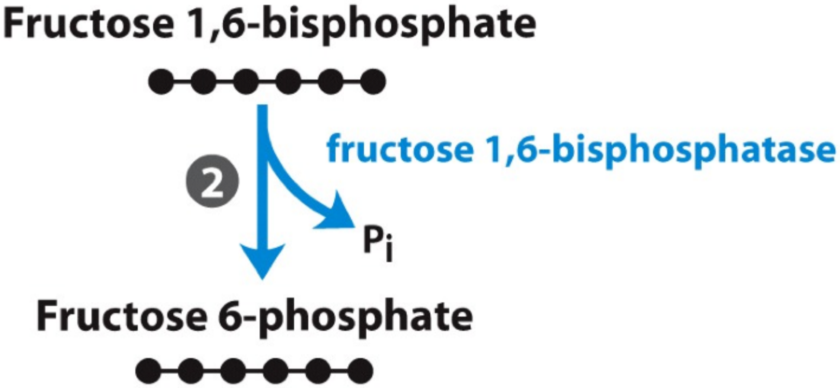
Glycolysis
4th step
Gluconeogenesis
7th step



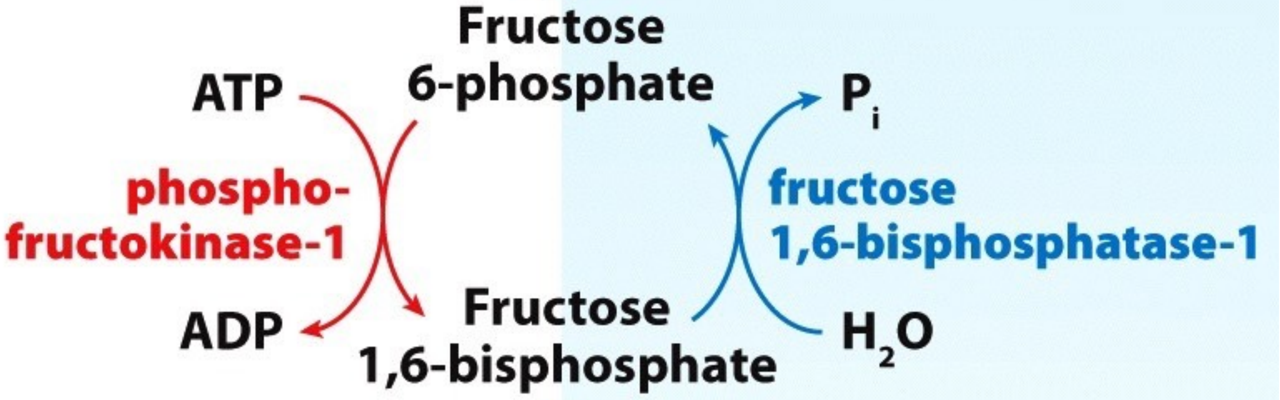
Second Reaction in Third Stage

- 6C -> 6C.
  - Identical to step 8 in gluconeogenesis (catalyzed by phosphatase).
  - Release of inorganic phosphate.

CO$_2$ assimilation
3rd stage
2nd step



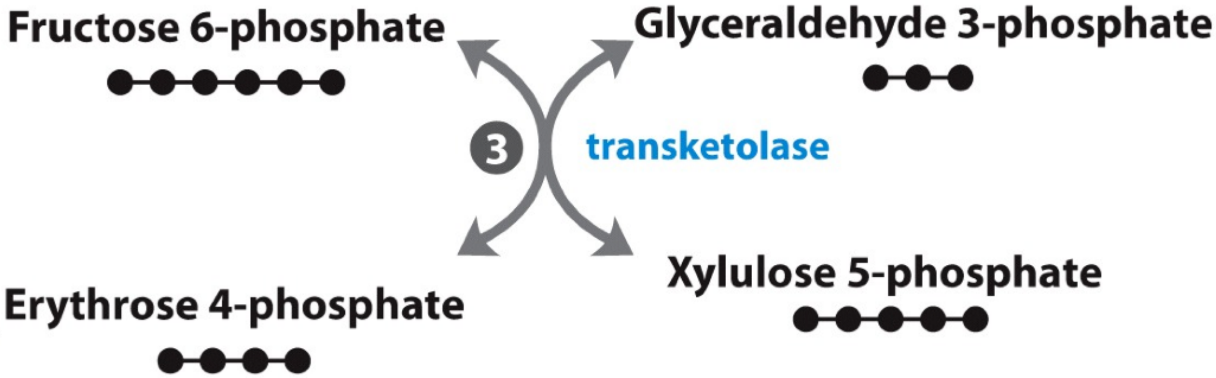
Gluconeogenesis
8th step



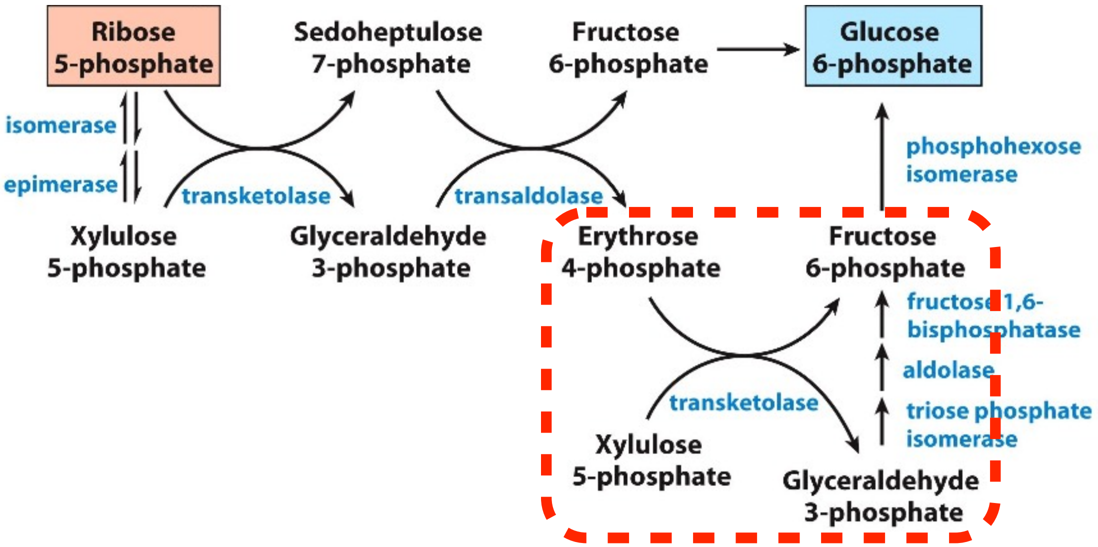
Third Reaction in Third Stage

- 6C + 3C -> 4C + 5C.
  - Reversal of a reaction in pentose phosphate pathway (catalyzed by transketolase).
  - Transfer of a two-carbon unit.

CO_2 assimilation
3rd stage
3rd step

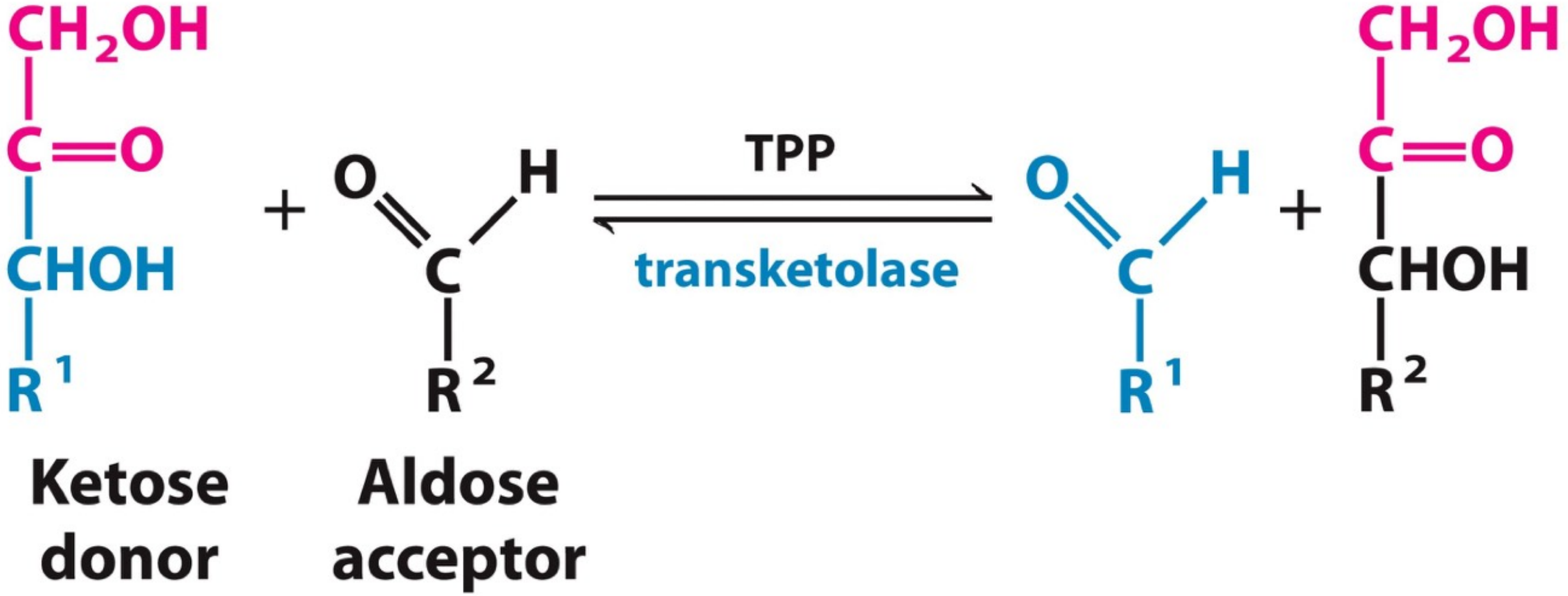


Pentose phosphate pathway



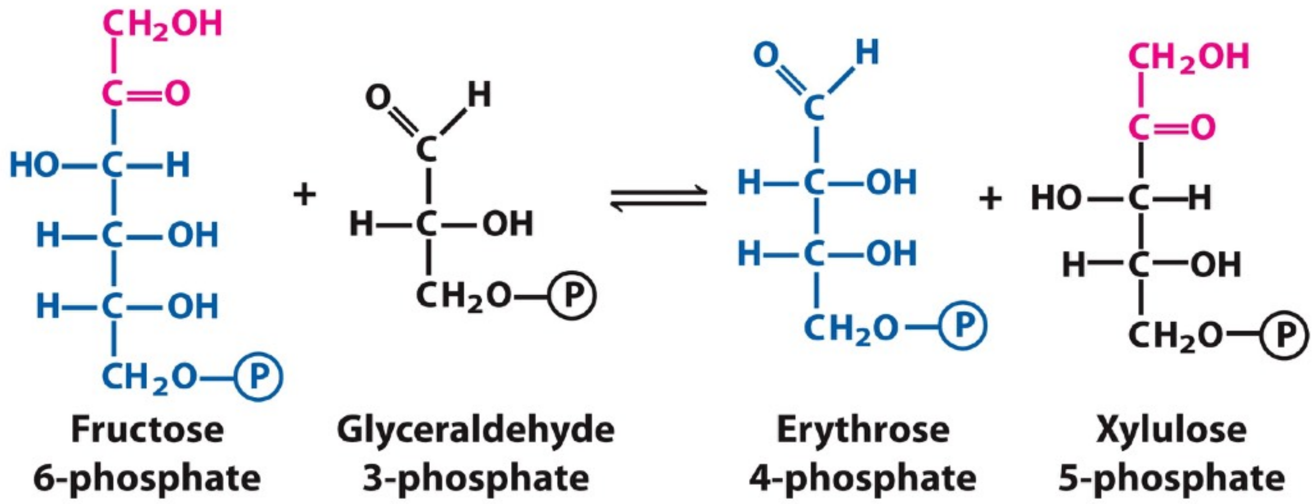
Transketolase Transfers 2-Carbon Unit

- Transfer of a 2-carbon **ketol** group from a ketose to an aldose.
  - Ketose is donor, and aldose is acceptor.
  - Ketose is converted to aldose, and aldose is converted ketose.
  - Two examples.
    - 6-carbon ketose + 3-carbon aldose <-> 4-carbon aldose + 5-carbon ketose.
    - 7-carbon ketose + 3-carbon aldose <-> 5-carbon aldose + 5-carbon ketose.

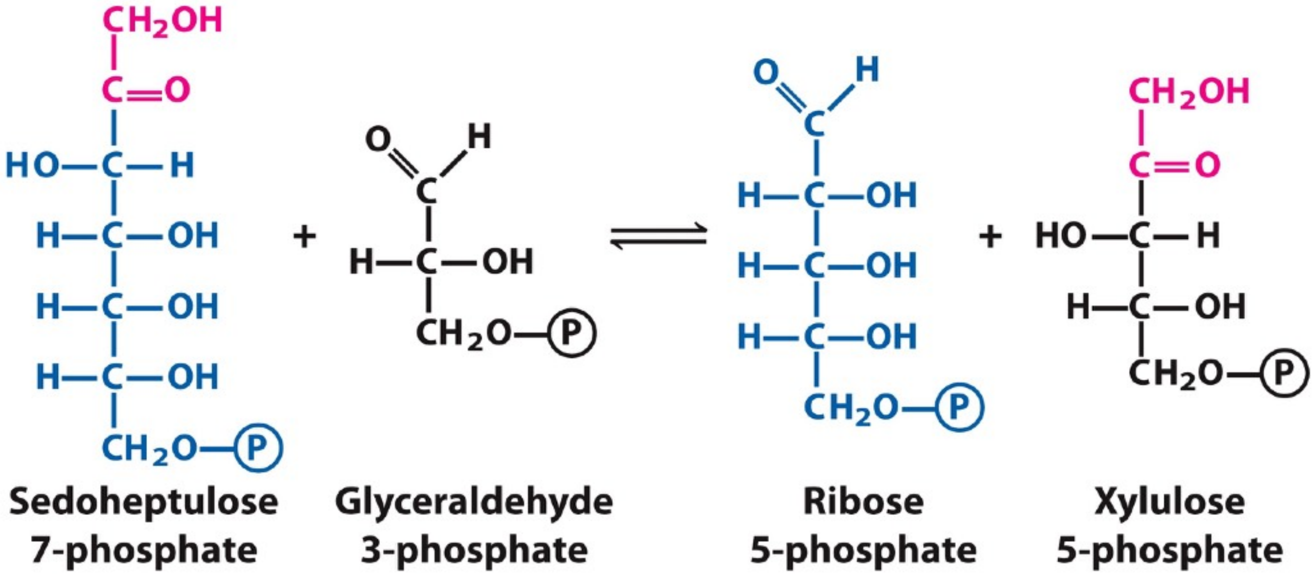


Two Reactions Catalyzed by Transketolase

CO_2 assimilation
3rd stage
Step 3

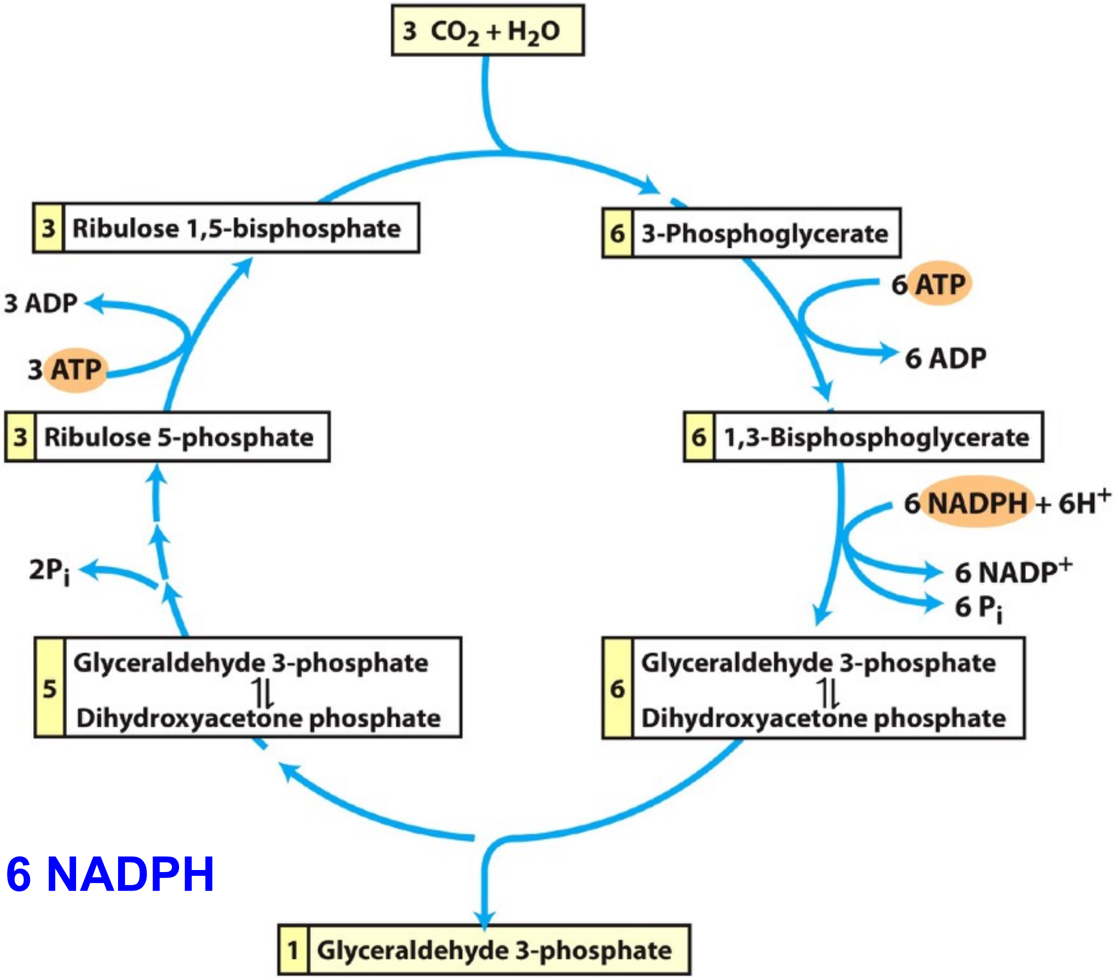


CO_2 assimilation
3rd stage
Step 6



Stoichiometry and Energy Cost of CO_2 Assimilation

- Fixation of three CO_2 molecules yields one glyceraldehyde 3-phosphate.
- Nine ATP molecules and six NADPH molecules are consumed.

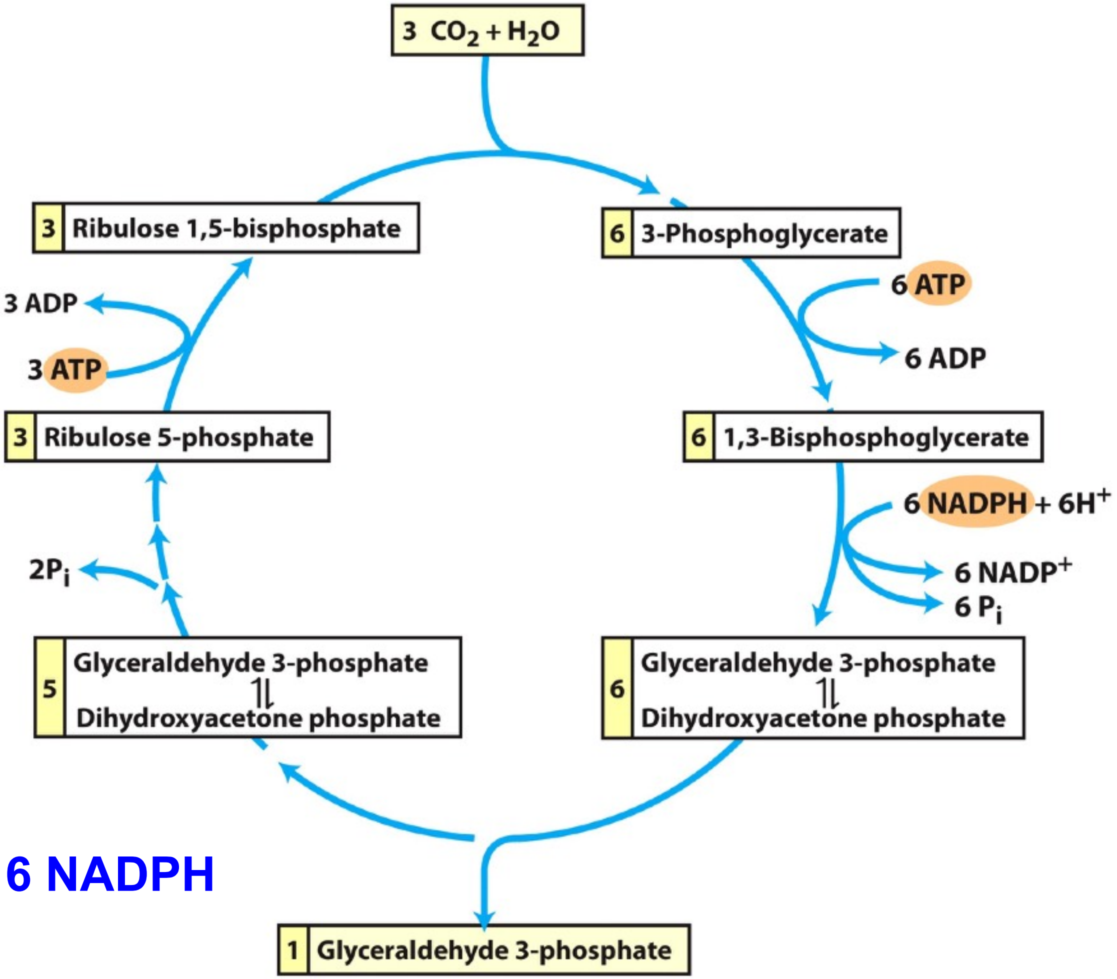


Overall reaction:

$$3\ CO_2 + 9\ ATP + 6\ NADPH \longrightarrow \text{glyceraldehyde 3-phosphate} + 9\ ADP + 8\ P_i + 6\ NADP^+$$

Fate of P_i from ATP Hydrolysis in Stage 2

- Nine ATP molecules are consumed but only eight P_i are released.
- The 9th P_i is incorporated into glyceraldehyde 3-phosphate.

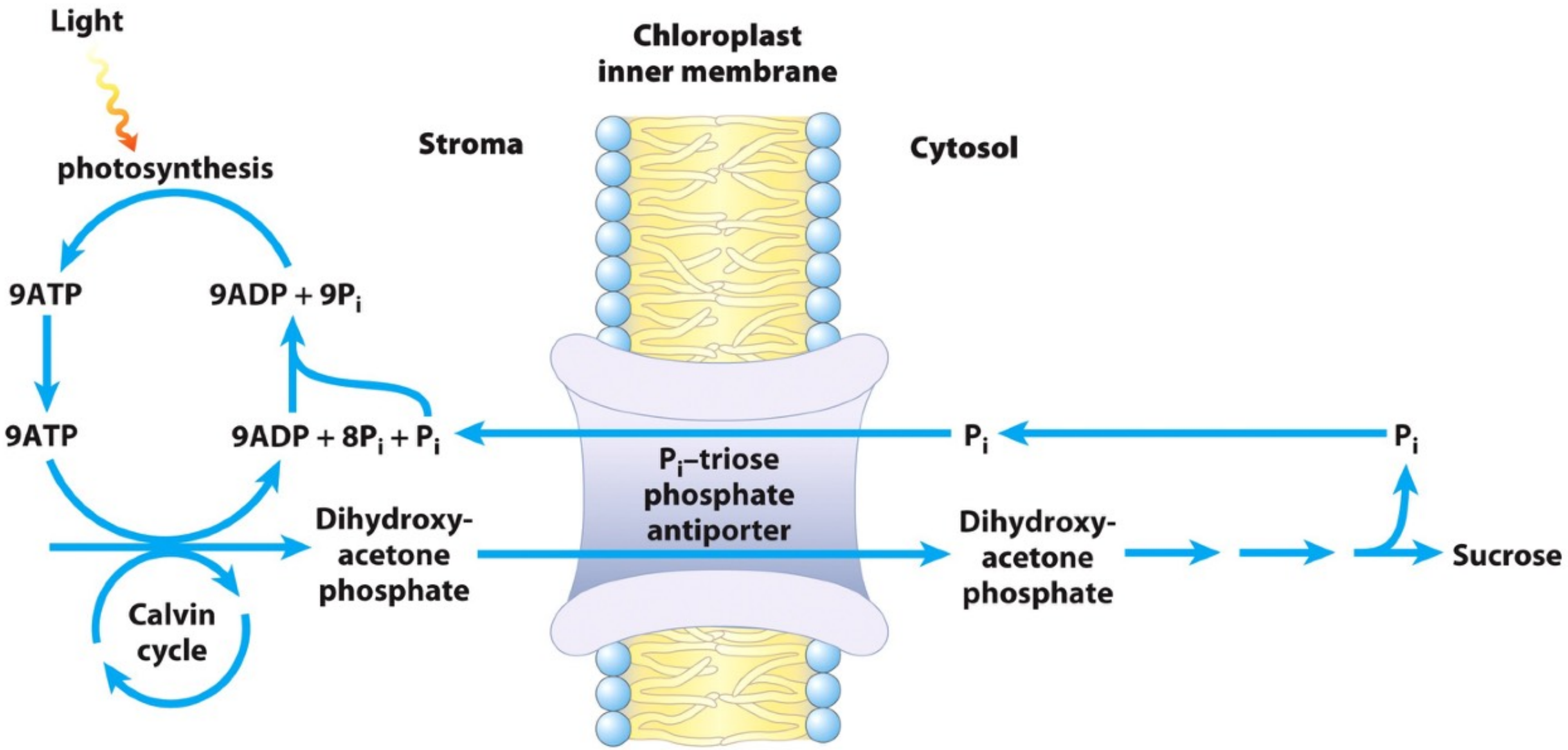


Overall reaction:

$$3\ CO_2 + 9\ ATP + 6\ NADPH \longrightarrow \text{glyceraldehyde 3-phosphate} + 9\ ADP + 8\ P_i + 6\ NADP^+$$

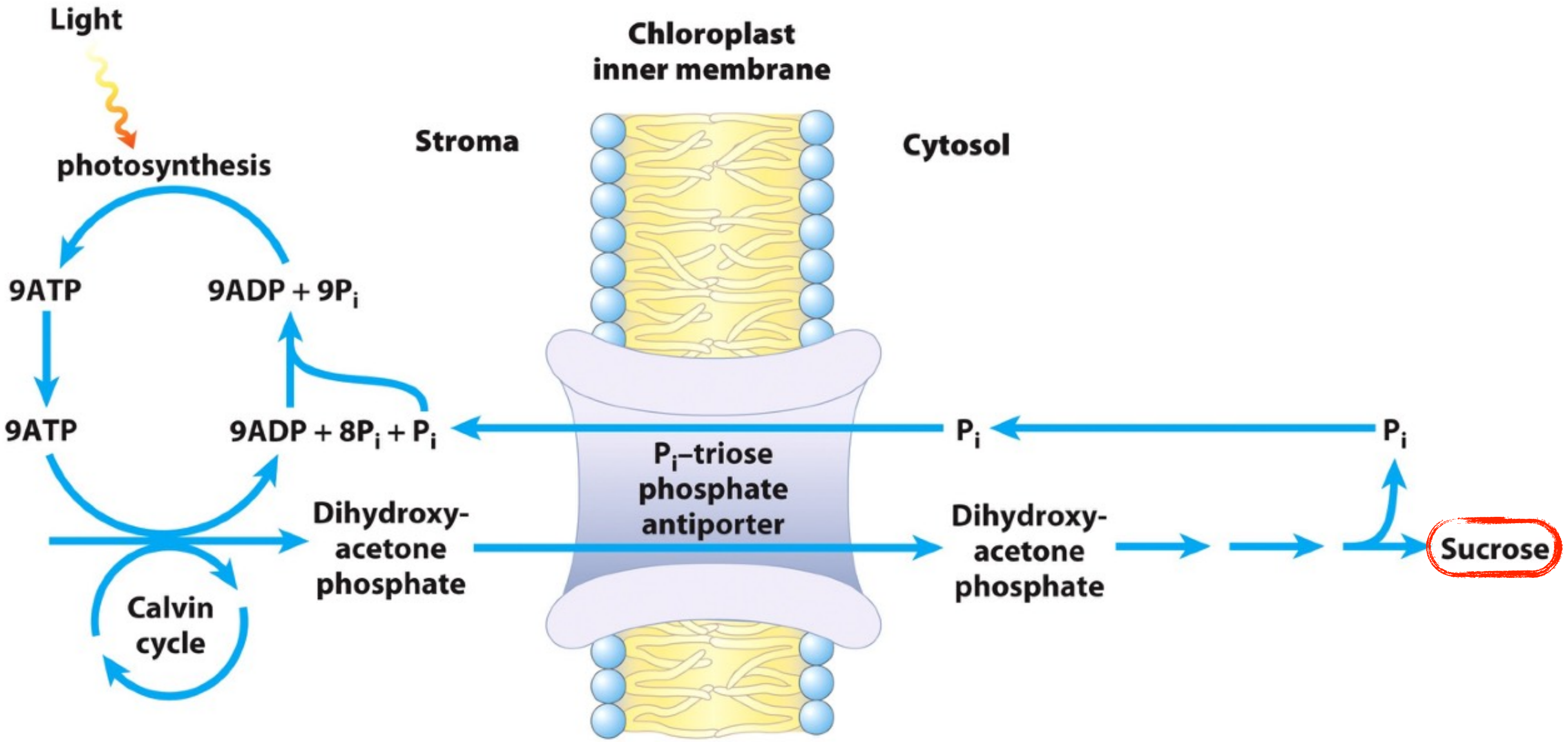
P_i-Triose Phosphate Antiporter

- The 9th P_i is incorporated into glyceraldehyde 3-phosphate.
  - Requires P_i to be transported from cytosol into stroma.
  - 9 ADP and 9 P_i are combined to regenerate 9 ATP in photosynthesis.
  - Antiporter transports two molecules in opposite directions.



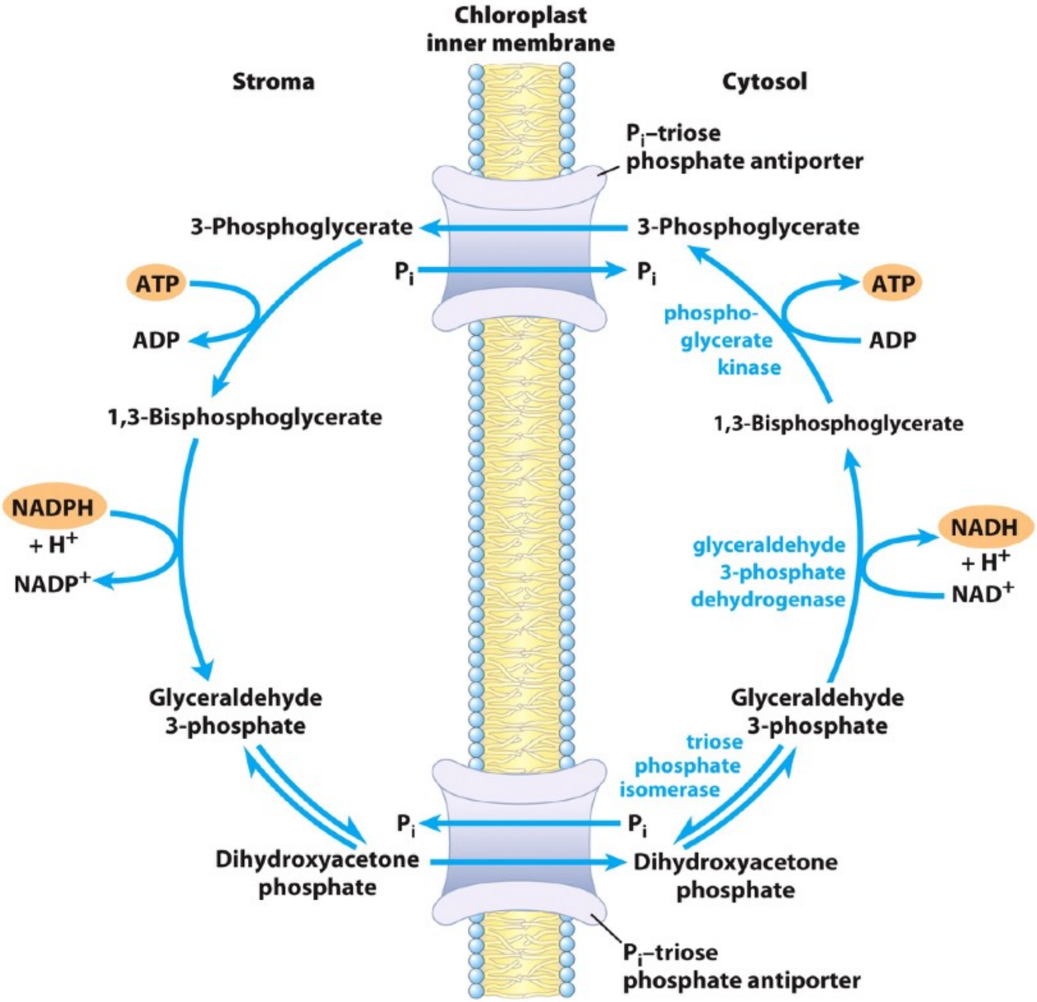
Antiporter Needed for Sucrose Synthesis

- Unlike starch, which is made in stroma, sucrose is made in cytosol.
  - Used for transport to distant plant tissues.
- Inner membrane is impermeable to phosphorylated compounds.
- Antiporter exchanges DHAP for P_i, sending the triose phosphates to cytosol for sucrose synthesis.



Antiporter Transports ATP and NADPH

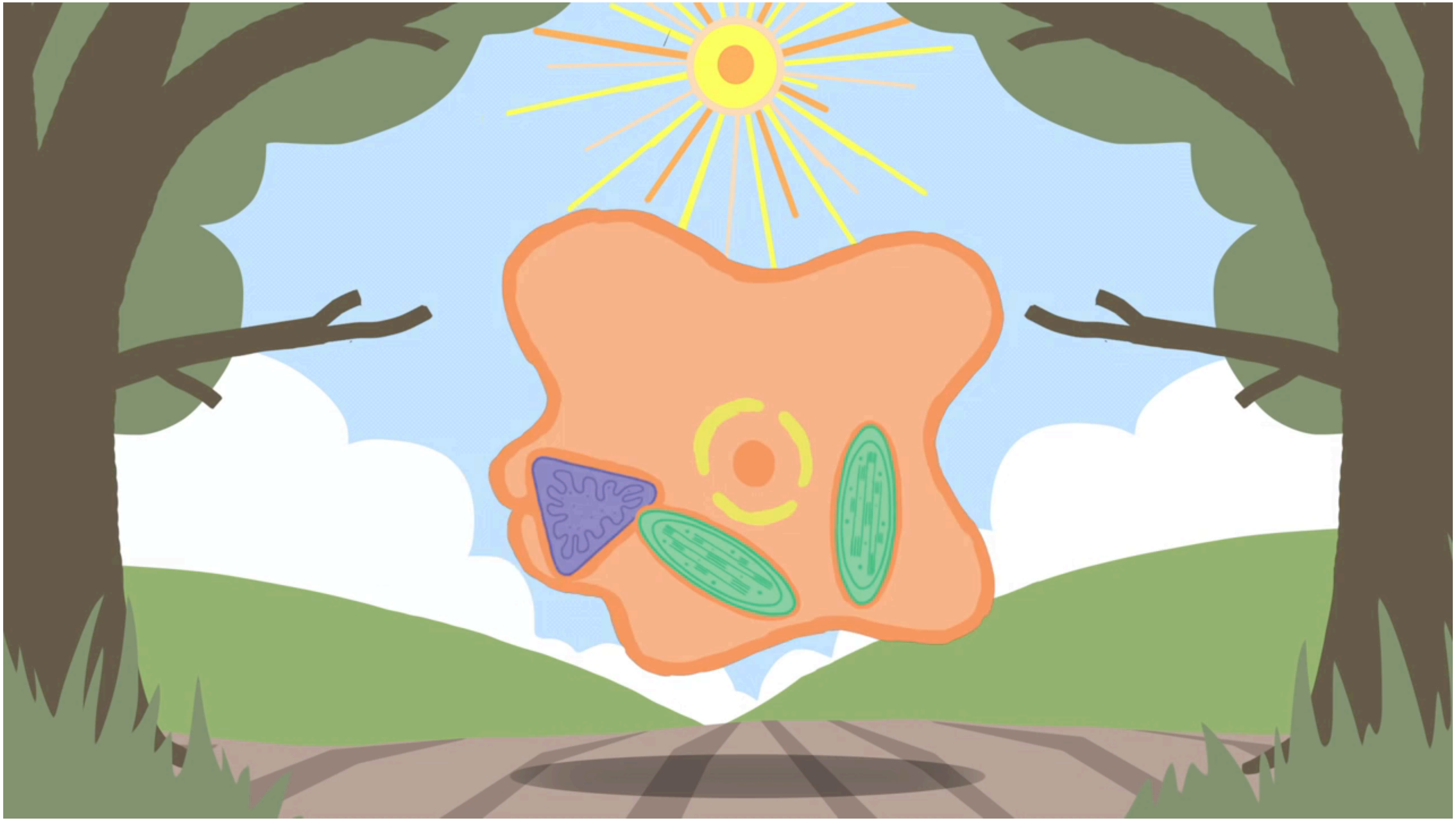
- Dihydroxyacetone phosphate (DHAP) leaves stroma and enters cytosol.
- DHAP is converted to 3-phosphoglycerate, and ATP and NADH are produced in this process (steps 6 and 7 in glycolysis).
- 3-phosphoglycerate leaves cytosol and enters stroma, and is converted to triose phosphate (stage 2).



Summary 20.1 Photosynthetic Synthesis

- In CO_2 assimilation (Calvin cycle), ATP and NADPH are used to reduce CO_2 to triose phosphate.
    1. CO_2 fixation, catalyzed by rubisco.
    2. Reduction of 3-P-glycerate to glyceraldehyde-3-P.
    3. Regeneration of ribulose-1,5-bis-P from triose-P.
- Rubisco condenses CO_2 with ribulose 1,5-bis-P to form two 3-P-glycerate. Each 3-P-glycerate reduced requires one ATP and one NADPH. Carbon skeletons of triose-P are re-arranged to yield pentose-P, which is isomerized and phosphorylated to regenerate ribulose 1,5-bis-P.
- Cost is 9 ATP and 6 NADPH for each triose-P. Antiporter exchanges P_i for triose-P, and move ATP and reducing equivalents.

Endosymbiosis



Week 14 Carbohydrate Biosynthesis

20.1 Photosynthetic Carbohydrate Synthesis

20.2 Photorespiration

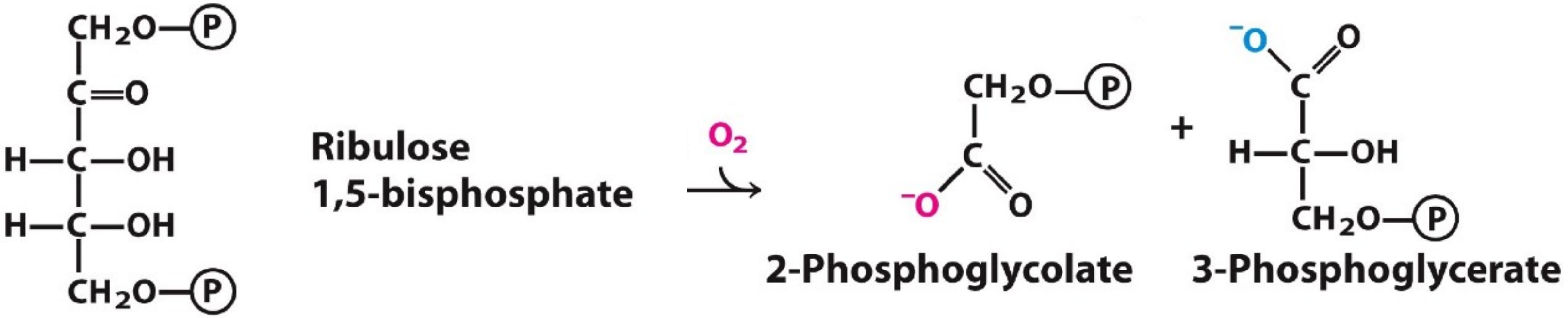
20.3 Biosynthesis of Starch and Sucrose

20.4 Synthesis of Cell Wall Polysaccharides

20.5 Integration of Carbohydrate Metabolism

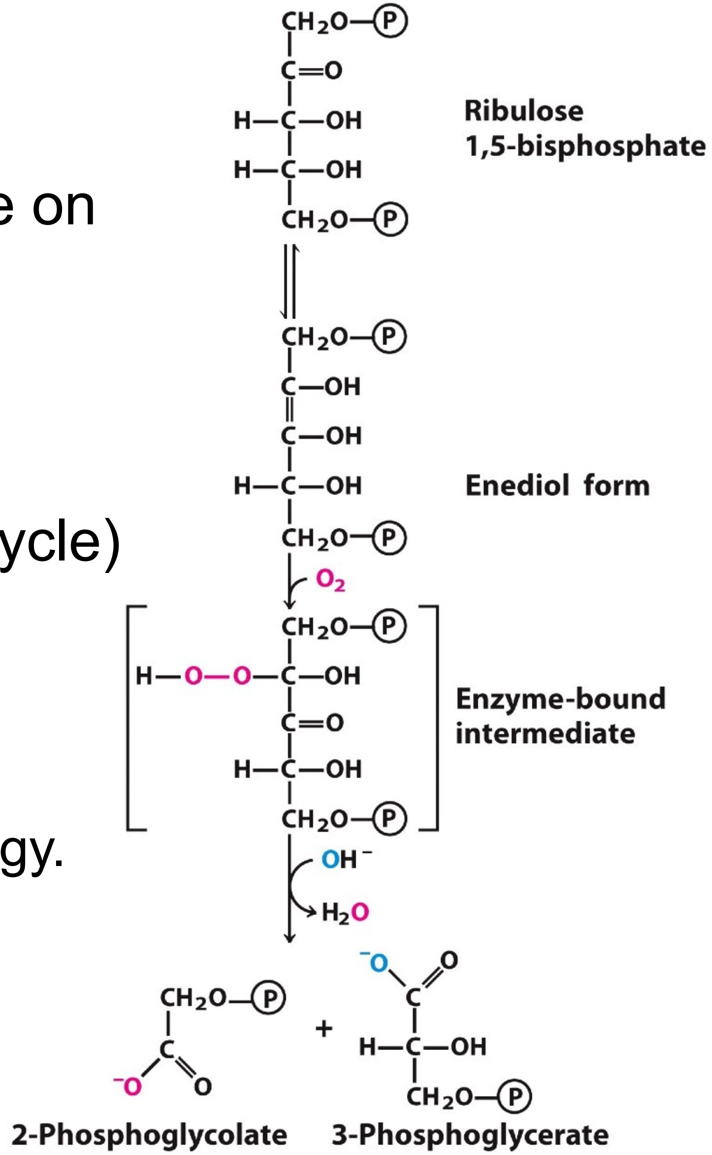
Photorespiration

- Plants oxidize water to O_2 and reduce CO_2 to carbohydrates.
  - Net result of photosynthesis: $CO_2 + H_2O \rightarrow O_2 + (CH_2O)$.
- Plants also carry out the reverse reactions in mitochondria.
  - O_2 is reduced to water (electron transfer in respiratory chain).
  - Substrates are oxidized to CO_2 (citric acid cycle).
- In addition, a wasteful side reaction catalyzed by **rubisco** occurs in mitochondria that consumes O_2 and yields CO_2.
  - **Lack of specificity of enzyme rubisco.**
  - Driven by light and coupled with a costly salvage pathway.
  - **Does not yield energy (unlike mitochondrial respiration).**



Oxygenase Activity of Rubisco

- Oxygenase oxidizes a substrate by transferring oxygen from O_2 to it.
- O_2 competes with CO_2 for the active site on rubisco enzyme.
  - O_2 binds once in every 3 or 4 turnovers.
- Carbonyl carbon adds to O_2 to form 3-phosphoglycerate (same as in Calvin Cycle) and 2-phosphoglycolate (2-PG).
  - **Results in no net fixation of carbon.**
  - 2-PG is metabolically useless.
  - Salvaging its carbon atoms requires energy.



Salvage of Phosphoglycolate

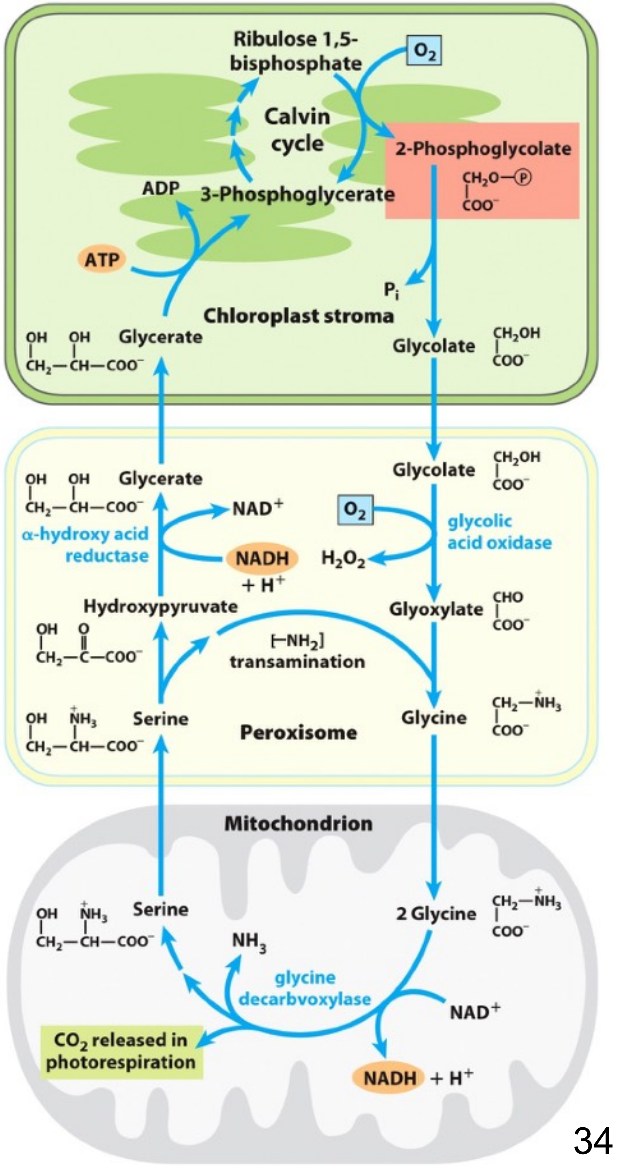
- Glycolate pathway: process for recovery of two-carbon fragment from photorespiration in three subcellular organelles.
  - Chloroplast.
  - Peroxisome.
  - Mitochondrion.
- O_2 is consumed and CO_2 is produced.
- Energy is consumed, NOT produced.

Net reaction of carbon atoms

2 phosphoglycolate

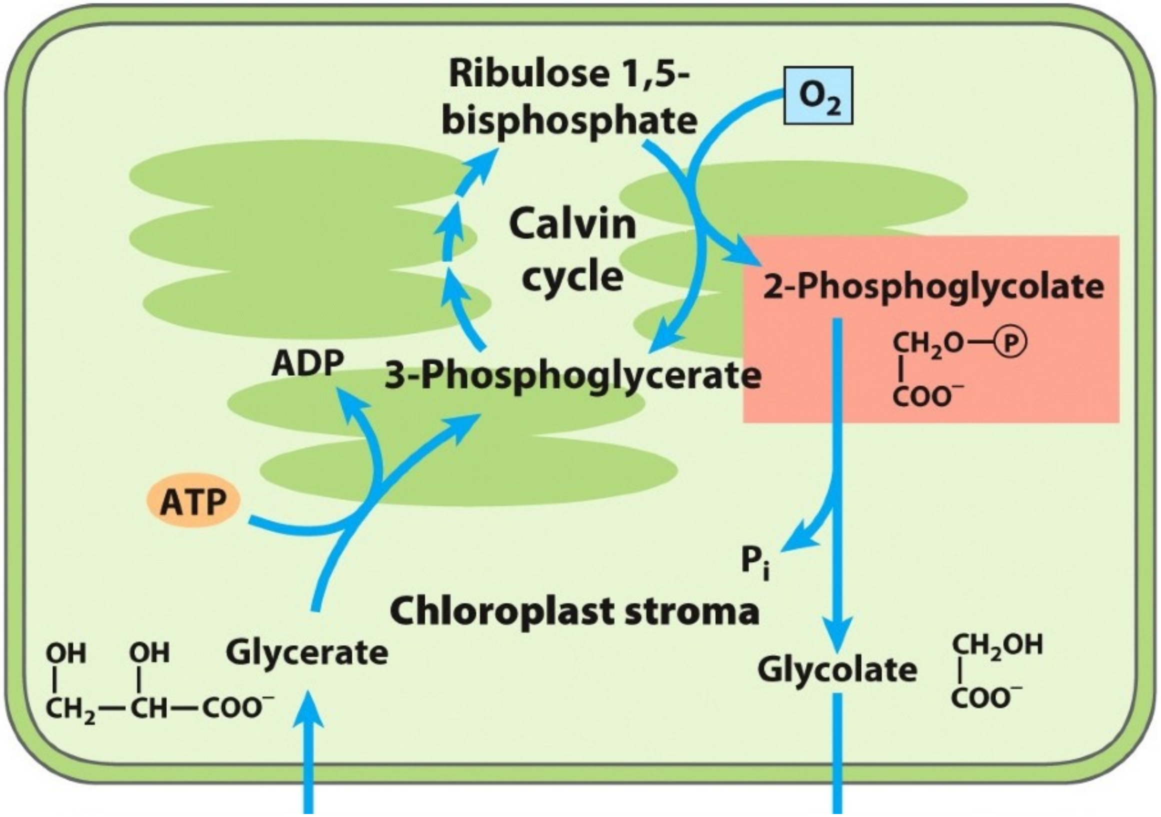
↓

3-phosphoglycerate + CO_2.



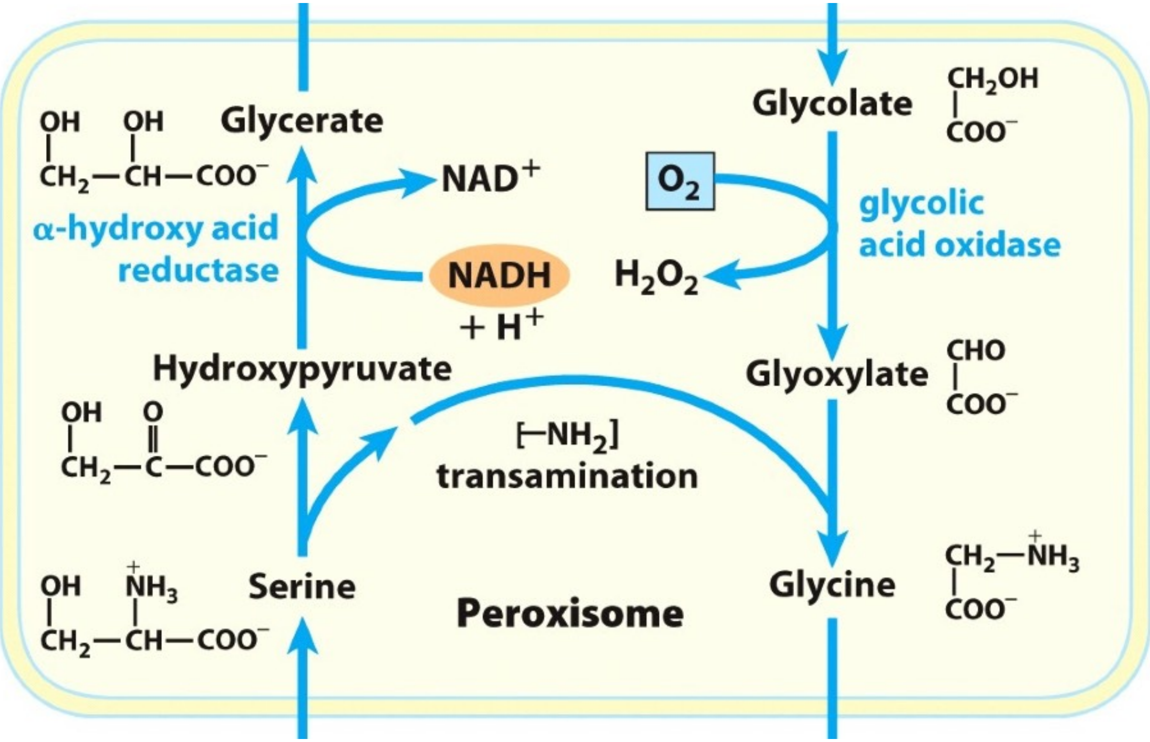
Salvage of Phosphoglycolate 1

- In chloroplast.
- 2-phosphoglycolate -> P_i + glycolate (exported to peroxisome).
  - Dephosphorylation catalyzed by phosphatase.



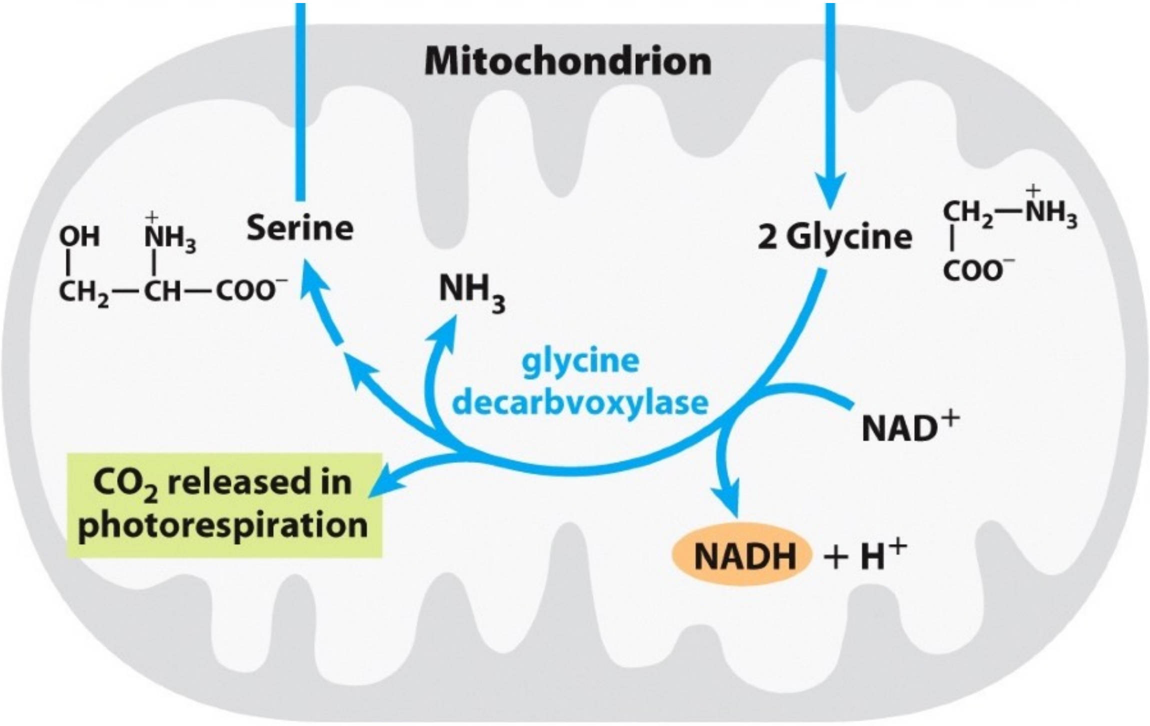
Salvage of Phosphoglycolate 2

- In peroxisome.
- Glycolate + O_2 -> glyoxylate + H_2O_2.
  - Conversion of alcohol to aldehyde catalyzed by oxidase.
- Glyoxylate -> glycine (exported to mitochondrion).
  - Replacement of carbonyl oxygen by amino group catalyzed by aminotransferase.



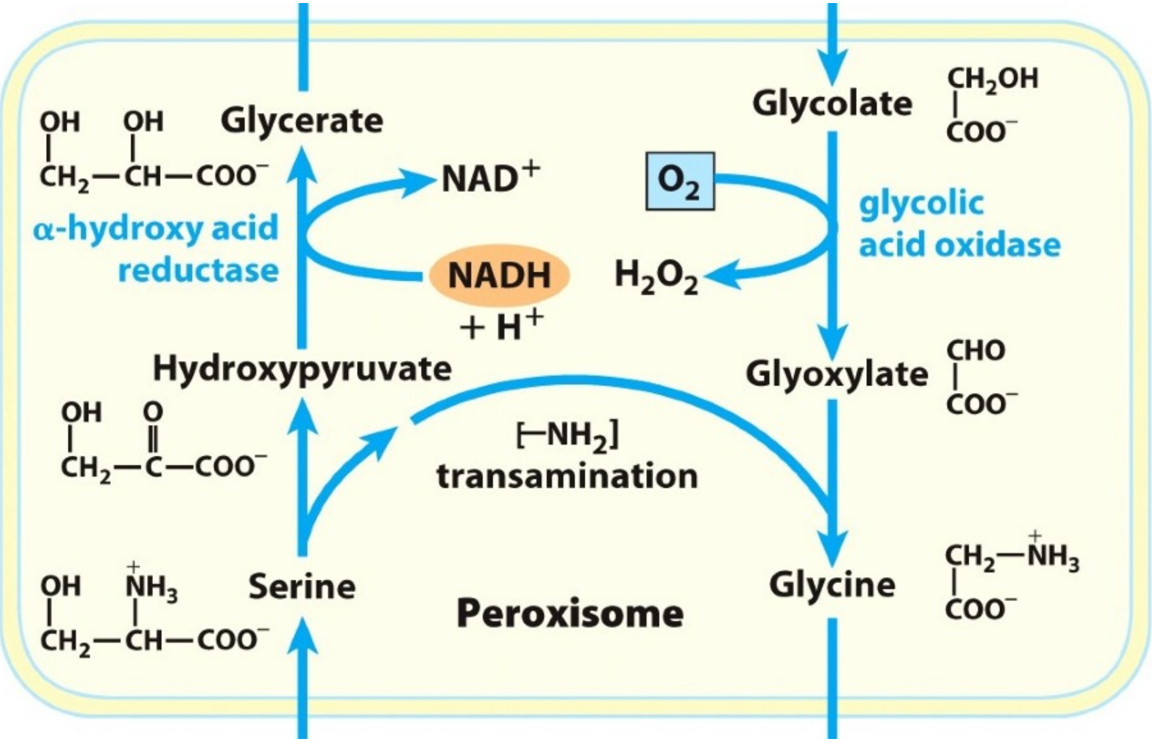
Salvage of Phosphoglycolate 3

- In mitochondrion.
- 2 glycine -> serine (exported to peroxisome) + ammonia + CO_2.
  - Oxidative decarboxylation catalyzed by decarboxylase. CO_2 is released.
  - NAD^+ is reduced to produce NADH as glycine is oxidized.



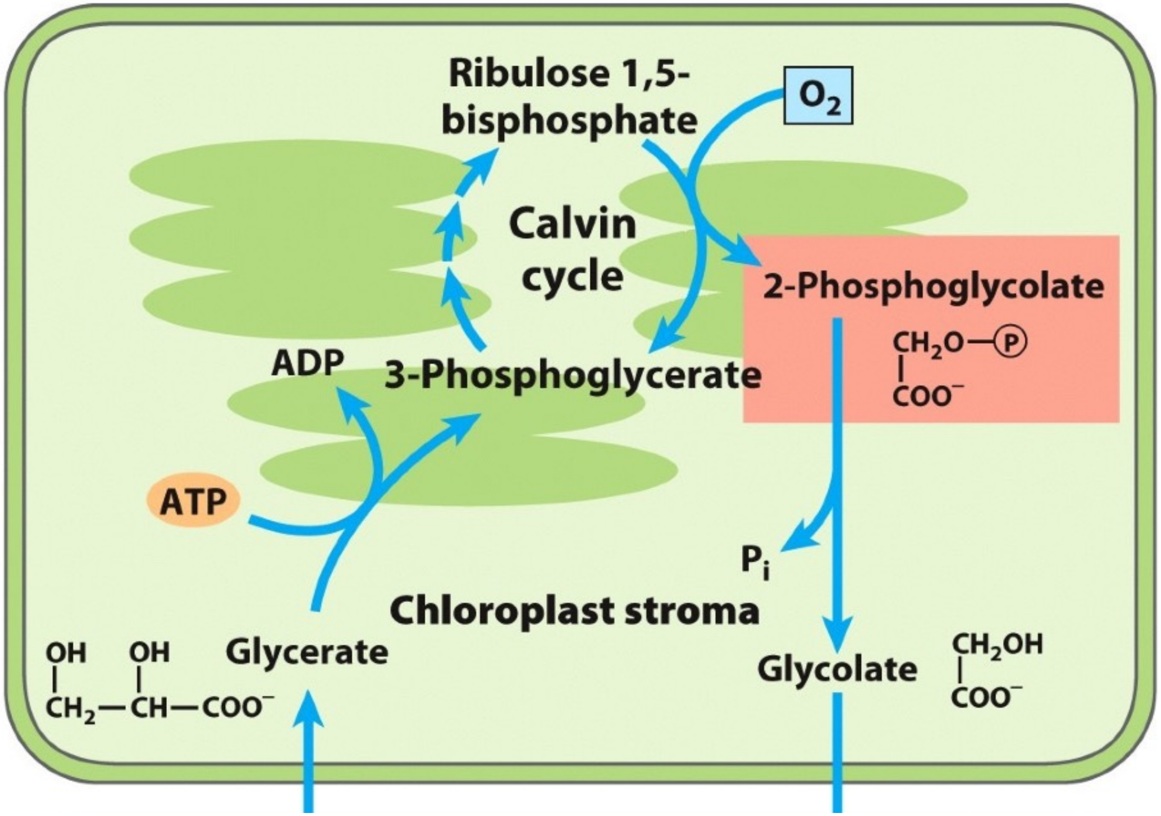
Salvage of Phosphoglycolate 4

- In peroxisome.
- Serine -> hydroxypyruvate.
  - Replacement of amino group by carbonyl oxygen catalyzed by aminotransferase.
- Hydroxypyruvate -> glycerate (exported to chloroplast).
  - Reduction of ketone to alcohol catalyzed by reductase. NADH is oxidized.



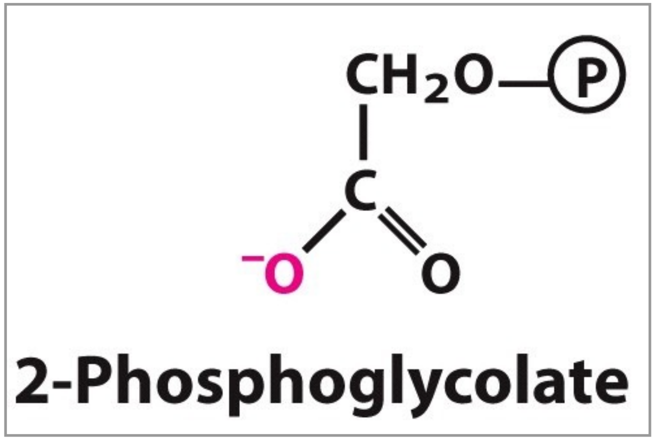
Salvage of Phosphoglycolate 5

- In chloroplast.
- Glycerate -> 3-phosphoglycerate (enters Calvin cycle).
  - Phosphorylation catalyzed by kinase. ATP is consumed.

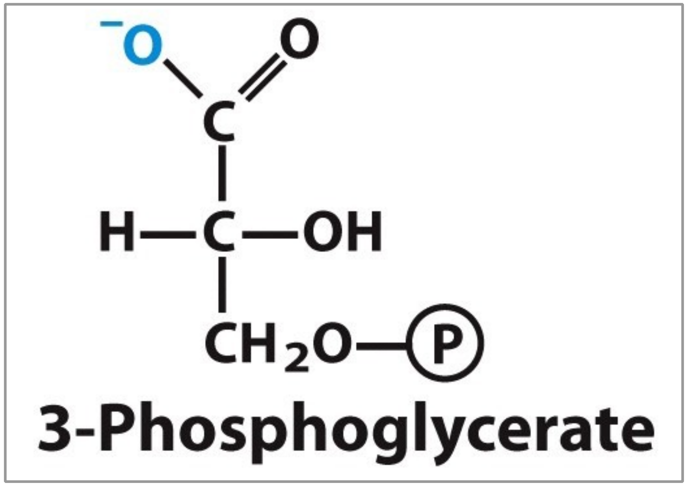


Photorespiration

- Combined activity of rubisco oxygenase and glycolate salvage pathway.
  - **Consumes O_2 and produces CO_2.**
- Photorespiration is also called C_2 cycle.
  - Unlike mitochondrial respiration.
  - **NOT conserve energy. No carbon fixation.**
- Net reaction of glycolate pathway.
  - (2) 2-PG + (2) O_2 + ATP -> 3-PG + CO_2 + (2) H_2O_2 + ADP + (2) P_i.



2-Phosphoglycolate



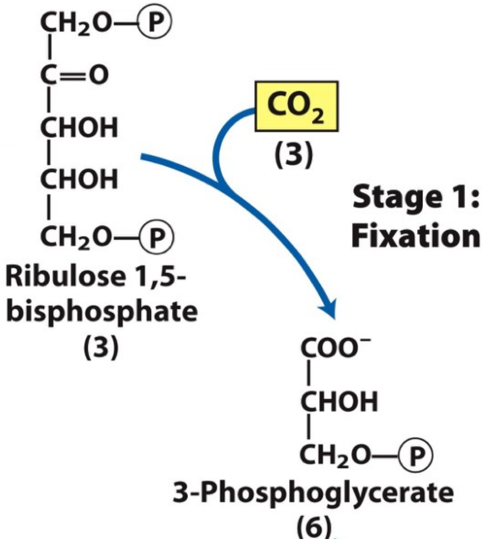
3-Phosphoglycerate

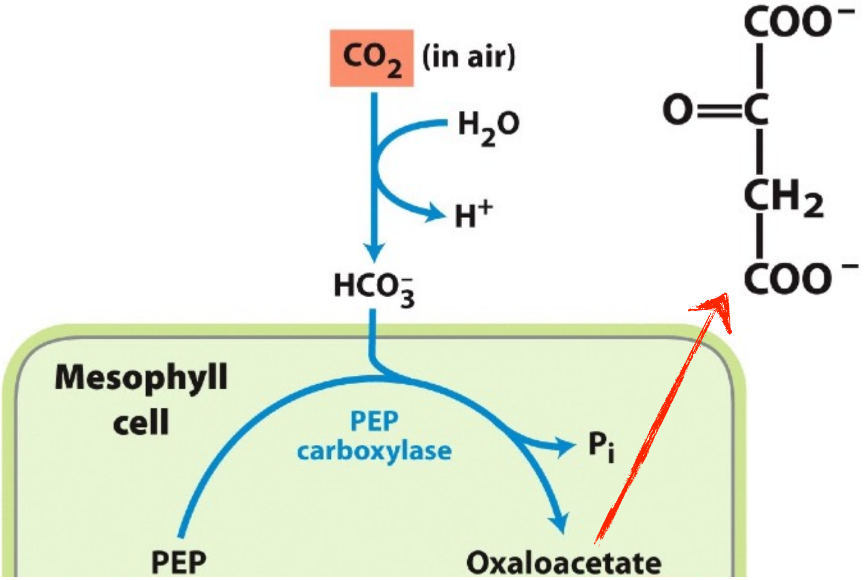
Photorespiration: Waste of Energy

- Function of rubisco is likely evolved before production of O_2.
  - No selective pressure to discriminate between CO_2 and O_2.
- Rubisco binds CO_2 more tightly, but O_2 content is much higher than CO_2. There is a significant O_2 “fixation” (waste of energy).
  - K_m for CO_2 is 9 μM. K_m for O_2 is 350 μM.
  - Modern atmosphere contains 20% O_2 and only 0.04% CO_2.
  - Solution concentration of CO_2 and O_2 is 11 μM and 250 μM.
- Several factors make things even worse.
  - Temperature.
    - Ratio of O_2 to CO_2 in solution increases at higher temperature.
    - Affinity of rubisco for CO_2 decreases at higher temperature.
  - As CO_2 is consumed in Calvin cycle, ratio of O_2 to CO_2 increases.

C_4 vs. C_3 Plants

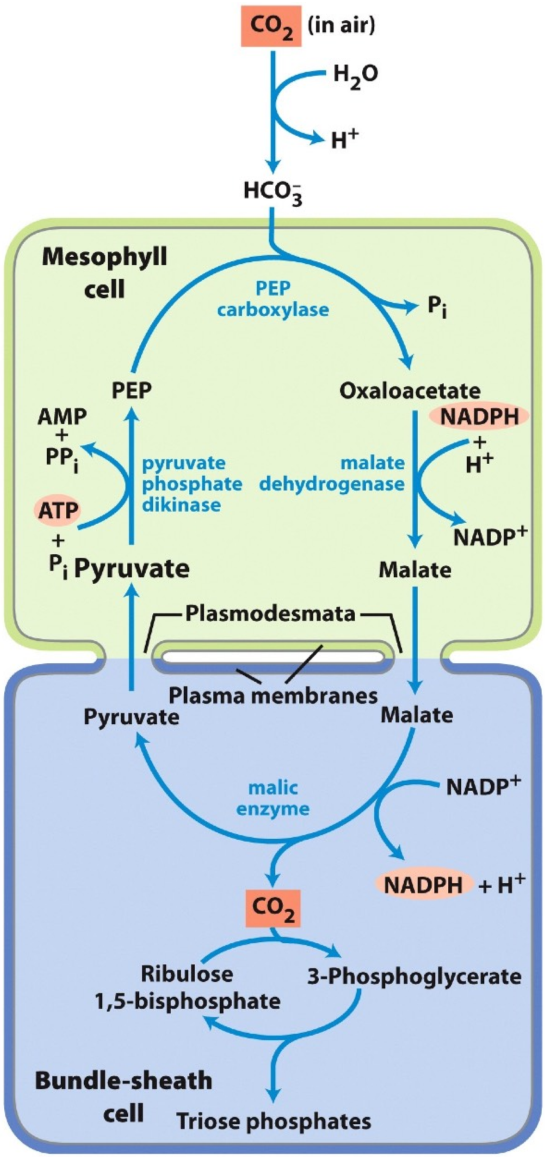
- Most crop plants are C_3.
  - First step in Calvin Cycle is CO_2 fixation into **3-C** product, 3-phosphoglycerate.
    - Wheat, barley, and potatoes.
- C_4 plants have earlier steps before rubisco.
  - Tend to grow in hotter, sunnier climates.
  - Bypass C-3 fixation step by fixing CO_2 into a **4-C** compound (**oxaloacetate**).
  - High rates of growth and photosynthesis. Low rates of photorespiration and water loss.
    - Sugarcane, maize, and sorghum.





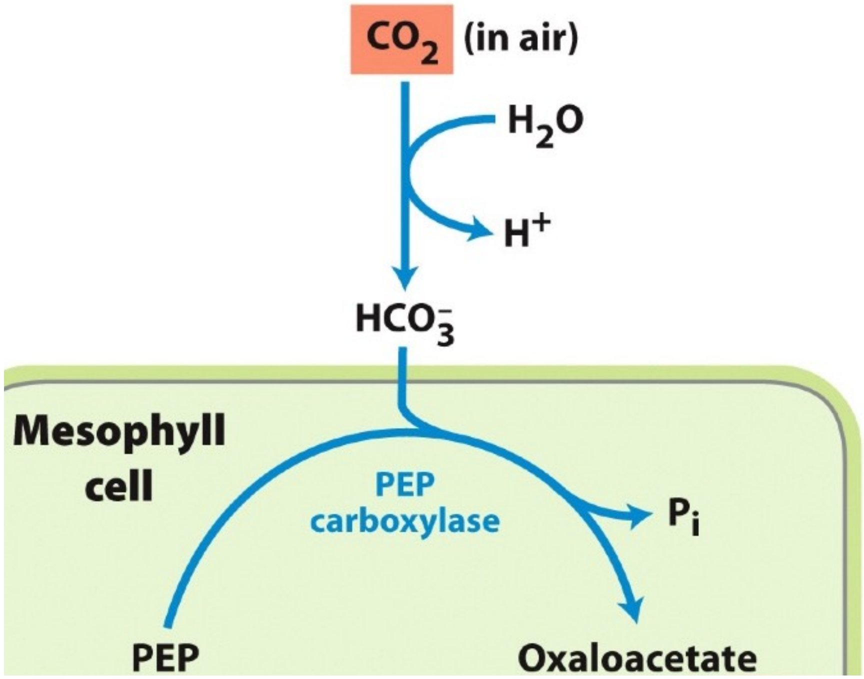
CO_2 Fixation Separated from Rubisco

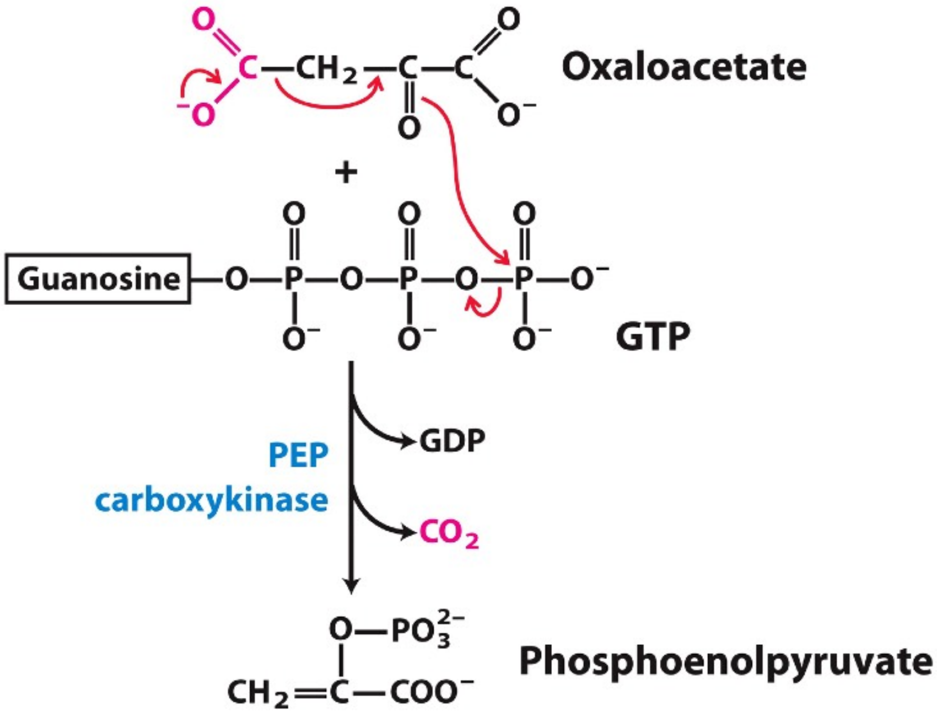
- In C_4 plants, conversion of CO_2 to triose involves **two cell types**.
  - Mesophyll cells.
    - CO_2 + PEP -> oxaloacetate -> malate.
    - Pyruvate -> PEP.
  - Bundle-sheath cells.
    - Malate -> CO_2 + pyruvate.
- Energy costs.
  - Mesophyll cells.
    - 1 NADPH consumed.
    - 2 ATPs consumed.
  - Bundle-sheath cells.
    - 1 NADPH produced.



Reaction 1. PEP -> Oxaloacetate.

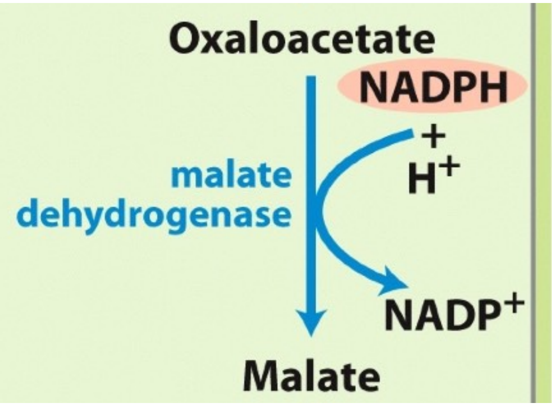
- Phosphoenolpyruvate + HCO_3^- -> oxaloacetate + P_i.
  - Occurs in mesophyll cells.
  - Catalyzed by phosphoenolpyruvate carboxylase.
  - Compare with oxaloacetate -> PEP reaction in gluconeogenesis.

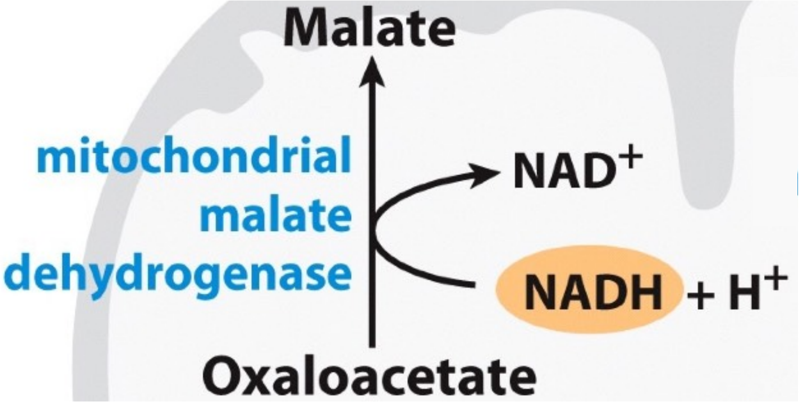


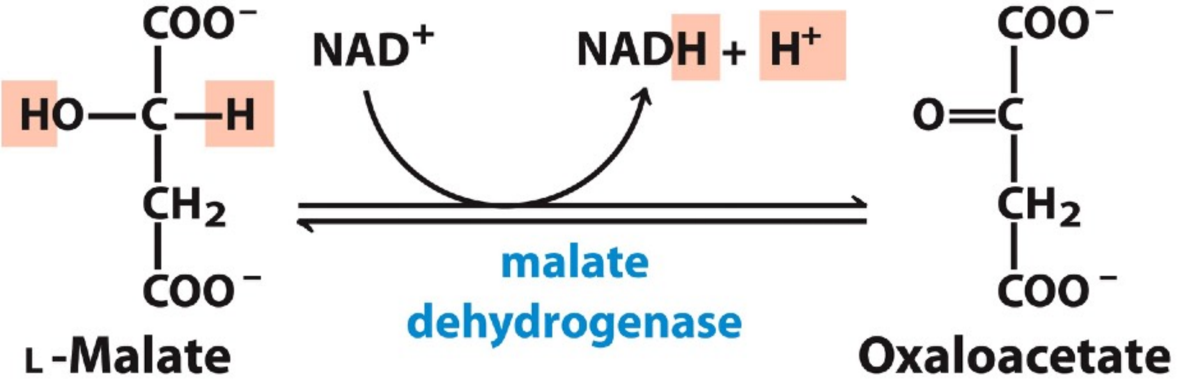


Reaction 2. Oxaloacetate -> Malate.

- Oxaloacetate + NADPH -> malate + $NADP^+$.
  - Occurs in mesophyll cells. Malate then passes into bundle-sheath cells.
  - Catalyzed by malate dehydrogenase (reversible reaction).
  - Compare with similar reactions in gluconeogenesis and in CAC.

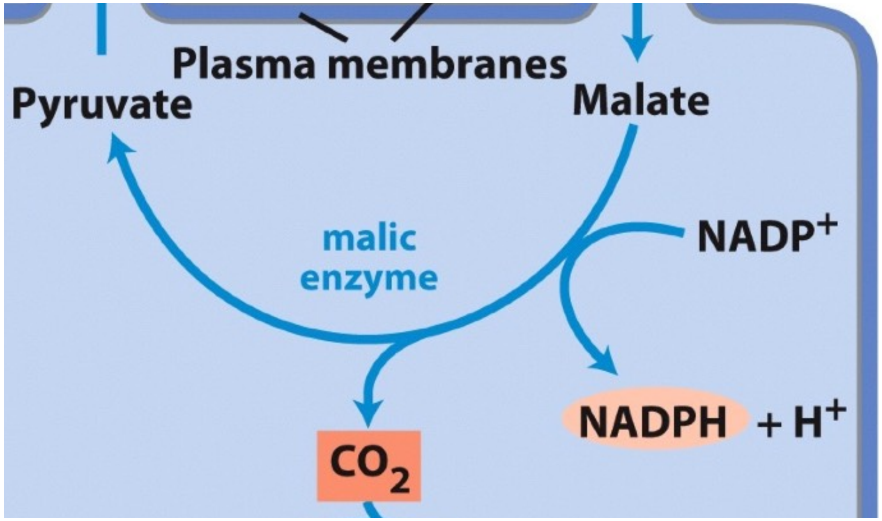






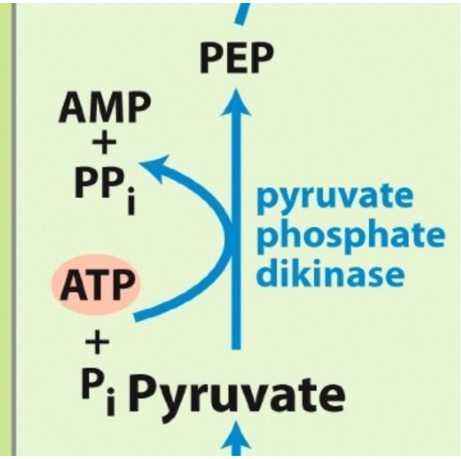
Reaction 3. Malate -> Pyruvate + CO_2.

- Malate + $NADP^+$ -> pyruvate + CO_2 + NADPH.
  - Occurs in bundle-sheath cells. Pyruvate is then transferred back to mesophyll cells.
  - Catalyzed by malic enzyme.
  - Malate is oxidized and decarboxylated.
    - CO_2 is released.
    - CO_2 is fixed again by rubisco to form 3-phosphoglycerate.



Reaction 4. Pyruvate -> PEP.

- Pyruvate + ATP -> phosphoenolpyruvate + AMP.
  - Occurs in mesophyll cells. Completes one cycle.
  - Catalyzed by pyruvate phosphate dikinase.
    - Pyruvate is phosphorylated to phosphoenolpyruvate.
    - Phosphate is phosphorylated to pyrophosphate, which is then hydrolyzed.
    - Two high-energy phosphate groups of ATP are used.
  - Compare with pyruvate -> PEP reaction in gluconeogenesis.

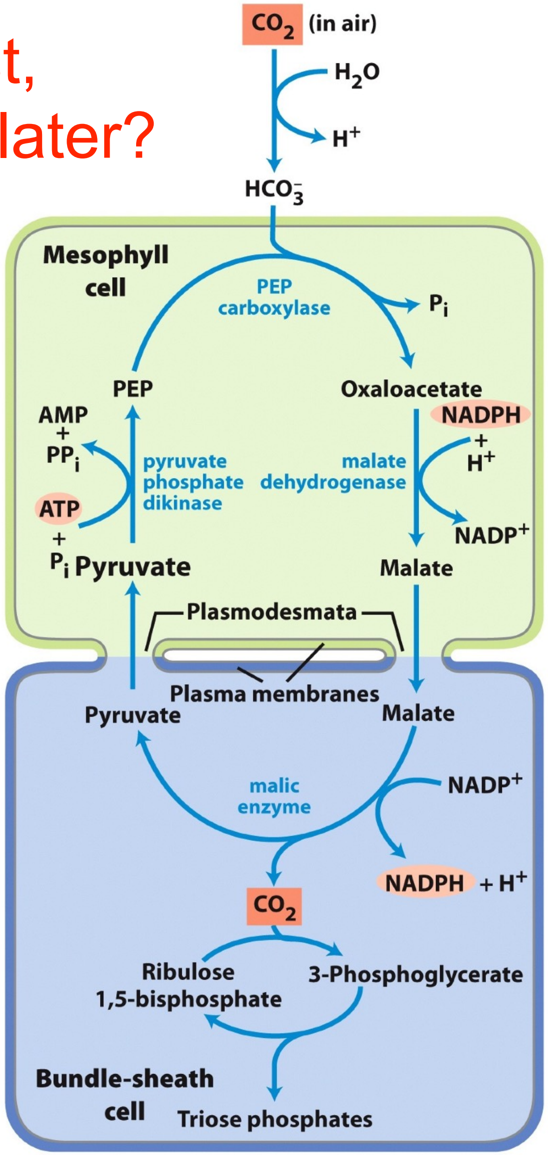


$$\text{Pyruvate} + \text{ATP} + \text{GTP} \xrightarrow{\text{2 steps}} \text{PEP} + \text{ADP} + \text{GDP}$$

Why This Two-Step Process?

Why fixing CO_2 using PEP carboxylase first, then releasing CO_2 for fixation by Rubisco later?

- PEP carboxylase has a high affinity for HCO_3^-, and can fix CO_2 more efficiently than rubisco.
  - Unlike rubisco, not use O_2 as substrate.
    - No competition between CO_2 and O_2.
  - Release of CO_2 creates a high local concentration of CO_2 in bundle-sheath cells.
    - $[CO_2] >> [O_2]$.
    - Rubisco's oxygenase activity suppressed.



Energy Cost of C_4 Pathway

- Two additional ATP molecules are consumed for each CO_2 that is captured in C_4 pathway and released later to enter C_3 pathway.
  - In C_3 pathway of CO_2 assimilation, 9 ATPs are consumed per triose.
    - 3 ATP molecules are consumed for each CO_2 captured.
- C_4 plants need **five** ATP molecules to assimilate one molecule of CO_2 and C_3 plants need only **three**.
- C_4 plants outgrow most C_3 plants in summer.
  - As temperature increases, photorespiration wastes more energy in C_3 plants.
  - C_4 plants have minimal photorespiration.
  - Elimination of photorespiration > energetic cost of C_4 pathway.

Summary 20.2 Photorespiration

- Photorespiration occurs when rubisco uses O_2 rather than CO_2 as substrate. 2-phosphoglycolate formed is disposed of in an oxygen-dependent pathway (C_2 cycle or glycolate salvage pathway).
  - 2-phosphoglycolate is converted to glycolate, to glyoxylate, to glycine, to serine, to hydroxypyruvate, to glycerate, and finally to 3-phosphoglycerate.
  - Involves enzymes in chloroplast, in peroxisome, and in mitochondrion.
- In C_4 plants, CO_2 assimilation pathway minimizes photorespiration.
  - CO_2 is first fixed into a 4-C compound in mesophyll cells.
  - CO_2 is then released to create a high local concentration.

Oxygen Catastrophe

Week 14 Carbohydrate Biosynthesis

20.1 Photosynthetic Carbohydrate Synthesis

20.2 Photorespiration

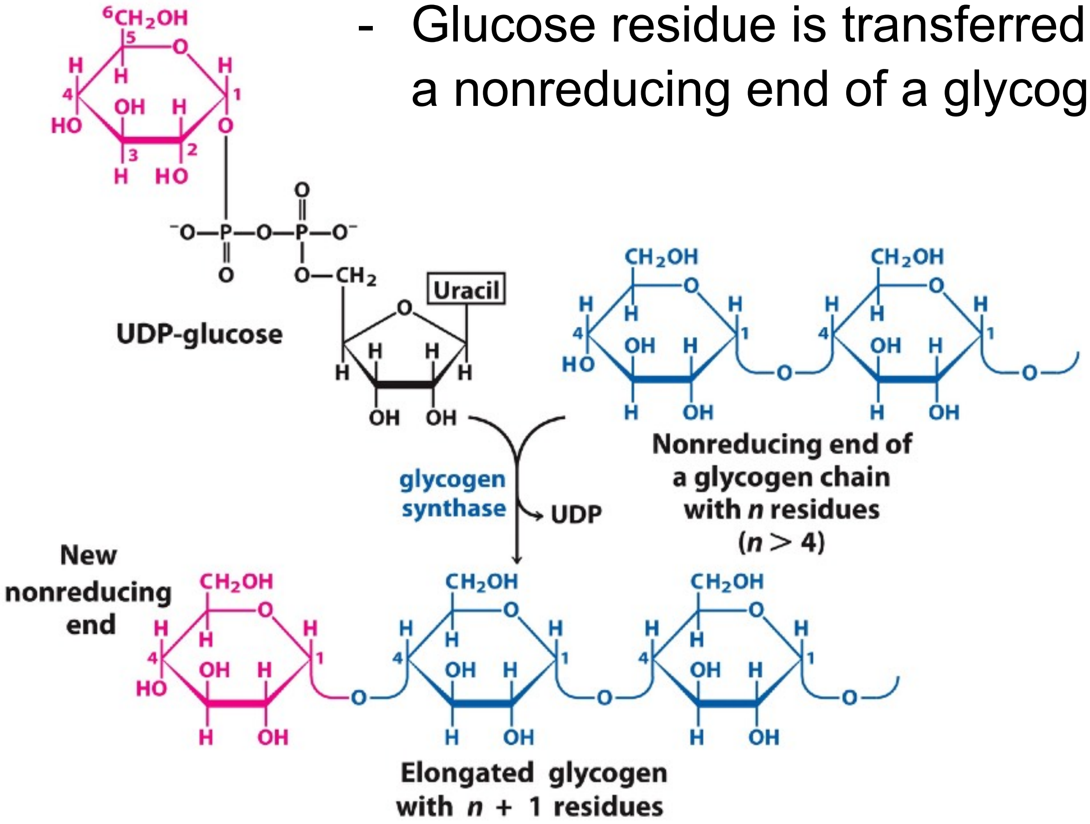
20.3 Biosynthesis of Starch and Sucrose

20.4 Synthesis of Cell Wall Polysaccharides

20.5 Integration of Carbohydrate Metabolism

ADP-Glucose for Starch Synthesis

- Starch is synthesized in chloroplast for storage via a two-step reaction.
  - Glucose is first activated to form **ADP-glucose**.
  - Glucose residue is transferred to preexisting starch molecules.
- Similar to glycogen synthesis in animals.
  - Glucose residue is transferred from activated **UDP-glucose** to a nonreducing end of a glycogen molecule.

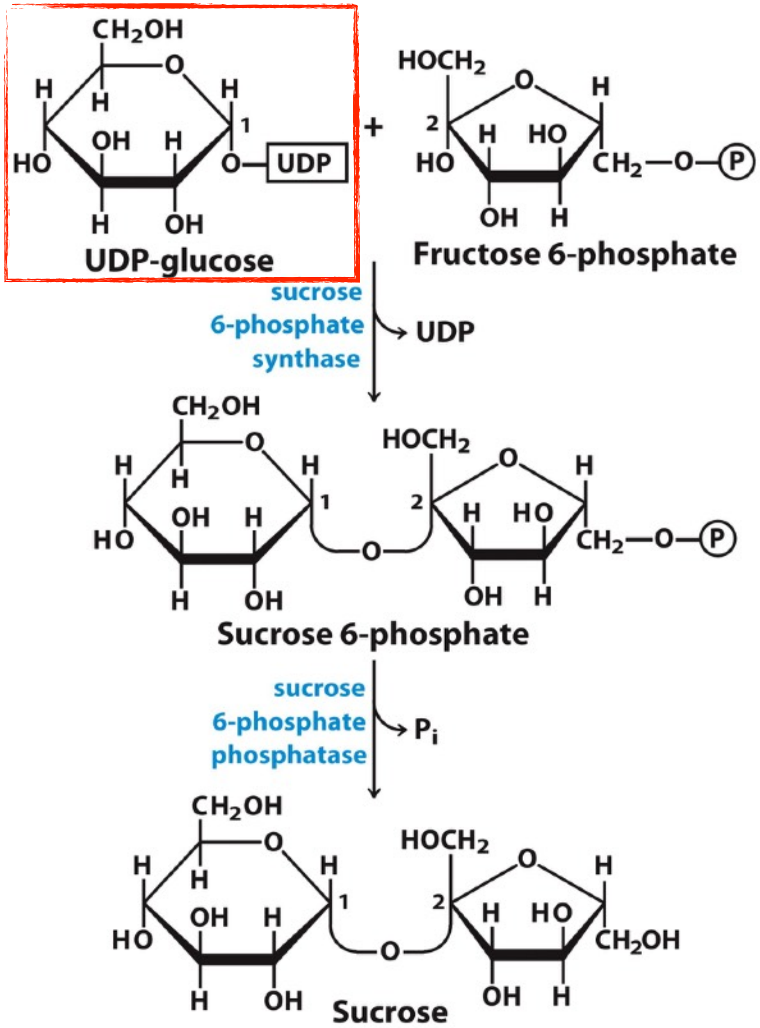


Overall reaction:

$$\text{Starch}_n + \text{ATP} + \text{glucose 1-phosphate} \xrightarrow{\text{starch synthase}} \text{Starch}_{n+1} + \text{ADP} + 2\,P_i$$

UDP-Glucose for Sucrose Synthesis

- Sucrose is synthesized in cytosol and transported to other parts.
  - Starts with triose phosphate.
    - DHAP and G3P exported from chloroplast.
  - Condensation to form F1,6BP.
    - Catalyzed by aldolase.
  - Dephosphorylation to form F6P.
    - Catalyzed by fructose 1,6-bisphosphatase.
  - Formation of sucrose 6-phosphate.
    - Catalyzed by S6P synthase.
    - Precursors: **F6P** and **UDP-glucose**.
  - Dephosphorylation.
    - Catalyzed by S6P phosphatase.



Week 14 Carbohydrate Biosynthesis

20.1 Photosynthetic Carbohydrate Synthesis

20.2 Photorespiration

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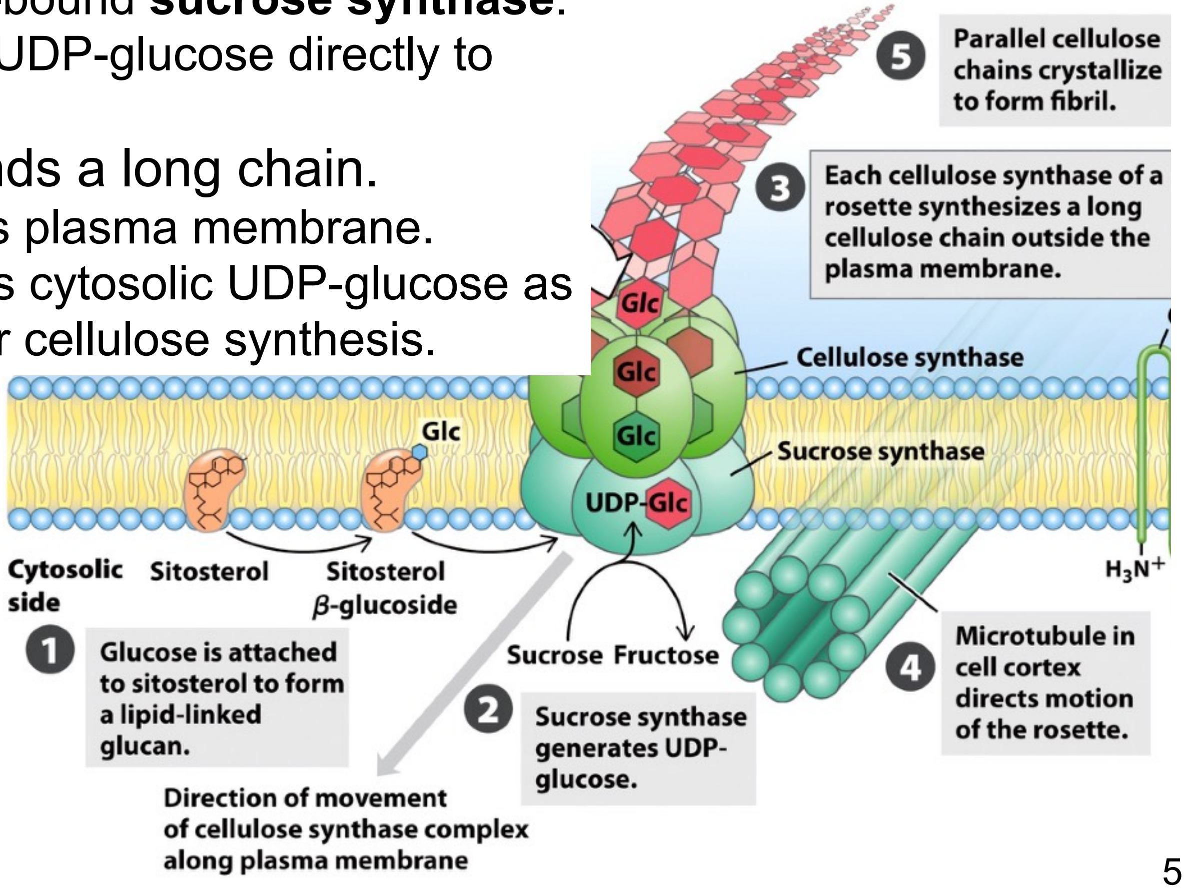
20.5 Integration of Carbohydrate Metabolism

Cellulose Synthesized on Membrane

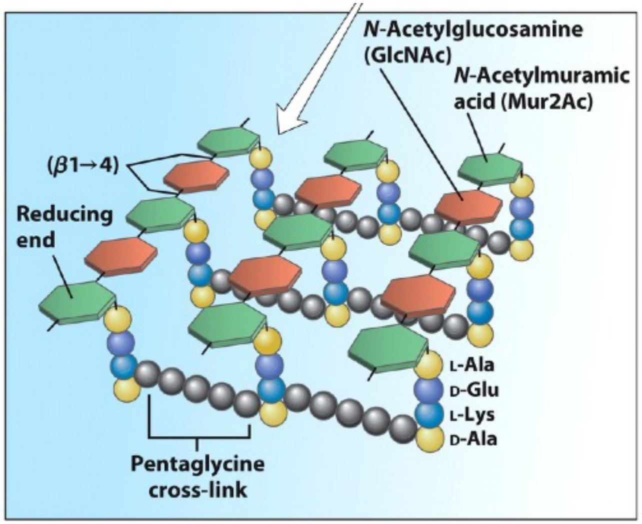
1. Glucose is transferred to a membrane lipid.
    - Forms a short oligosaccharide chain.
    - Catalyzed by **cellulose synthase**.
2. UDP-glucose is generated from sucrose.
    - Sucrose + UDP -> UDP-glucose + fructose.
    - Catalyzed by membrane-bound **sucrose synthase**.
    - Sucrose synthase feeds UDP-glucose directly to cellulose synthase.
3. Cellulose synthase extends a long chain.
    - Cellulose synthase spans plasma membrane.
    - **Cellulose synthase** uses cytosolic UDP-glucose as precursor for extracellular cellulose synthesis.

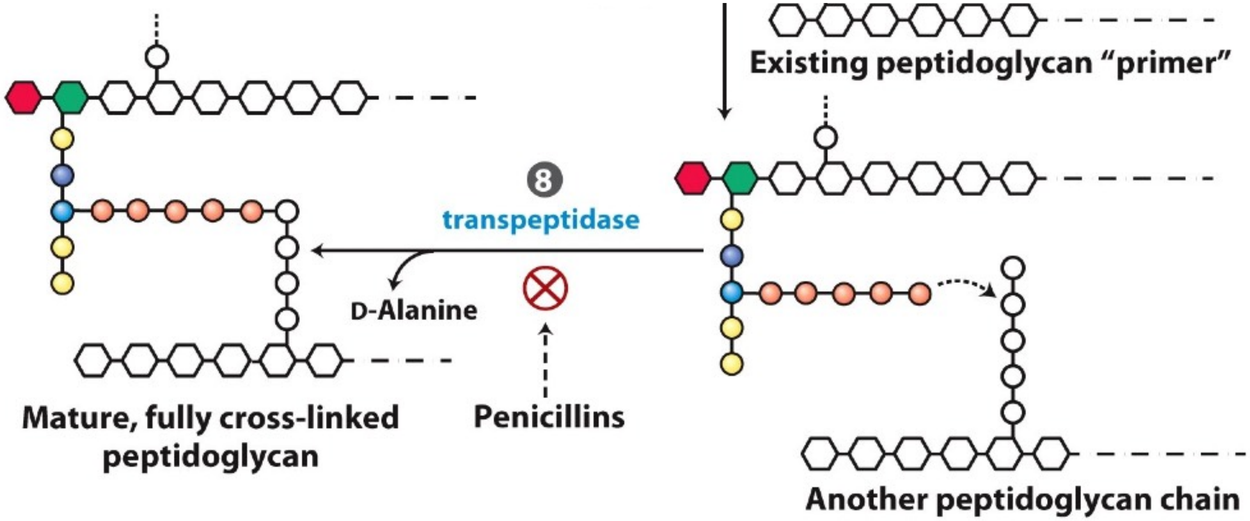
Cellulose synthesized by supramolecular structures in plasma membrane



Synthesis of Peptidoglycan

- Peptidoglycan is a heteropolysaccharide cross-linked by short peptides.
- Alternating GlcNAc and Mur2Ac.
  - GlcNAc = N-acetylglucosamine.
  - Mur2Ac = N-acetylmuramic acid.
  - Linked by (β1->4) glycosidic bond.
- Last step is a transpeptidation reaction.
  - Catalyzed by **transpeptidase** (crosslink formation)
  - **Penicillins** kill bacteria by inhibiting this enzyme.





Week 14 Carbohydrate Biosynthesis

20.1 Photosynthetic Carbohydrate Synthesis

20.2 Photorespiration

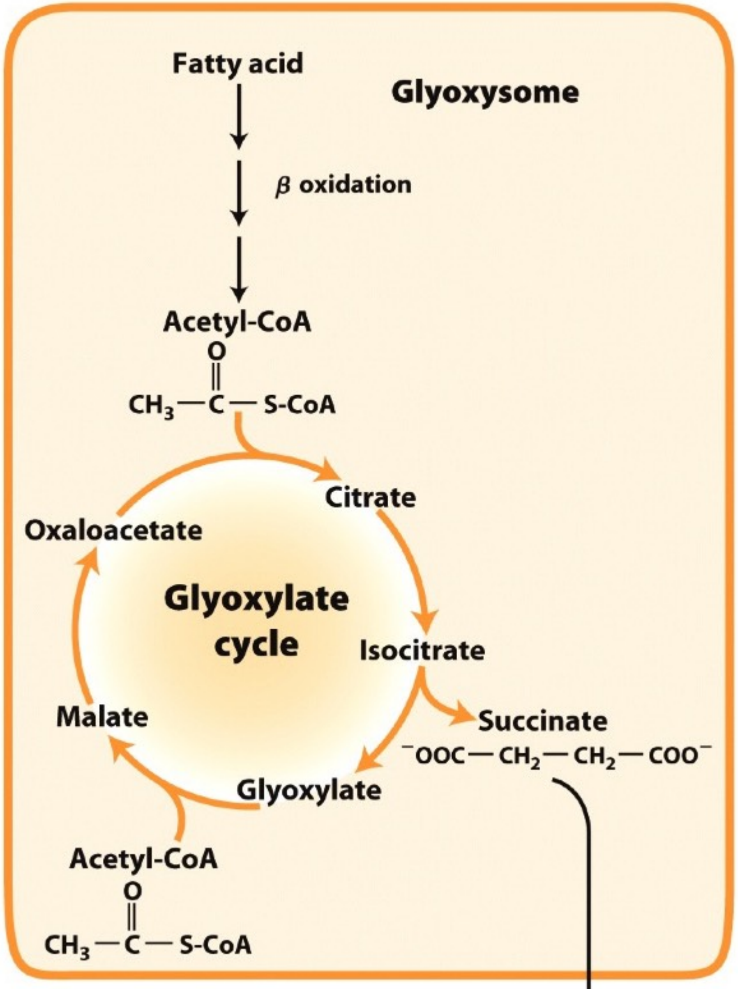
20.3 Biosynthesis of Starch and Sucrose

20.4 Synthesis of Cell Wall Polysaccharides

20.5 Integration of Carbohydrate Metabolism

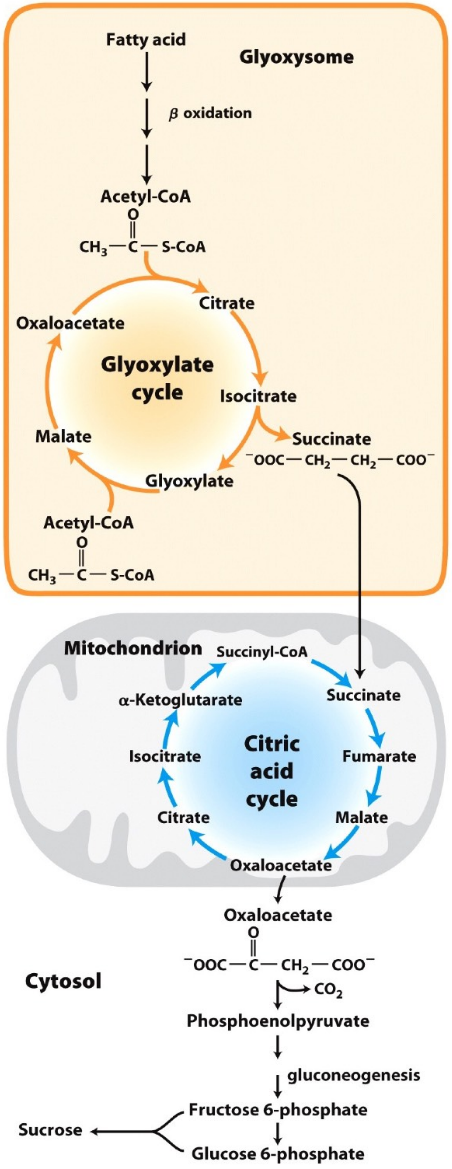
Carbohydrate Metabolism in Plant Cell

- Carbohydrate metabolism in a typical animal cell.
  - Glycolysis (glucose -> pyruvate).
  - Citric acid cycle (acetyl-CoA -> CO_2).
  - Oxidative phosphorylation (NADH -> ATP).
  - Gluconeogenesis (pyruvate -> glucose).
  - Pentose phosphate pathway (hexose -> pentose).
  - Synthesis and degradation of polysaccharide (glycogen <-> glucose).
- Plant cells share all the above with animal cells, and can do even more.
  - Calvin cycle (CO_2 -> triose and hexose).
  - Glyoxylate cycle (acetyl-CoA -> succinate).



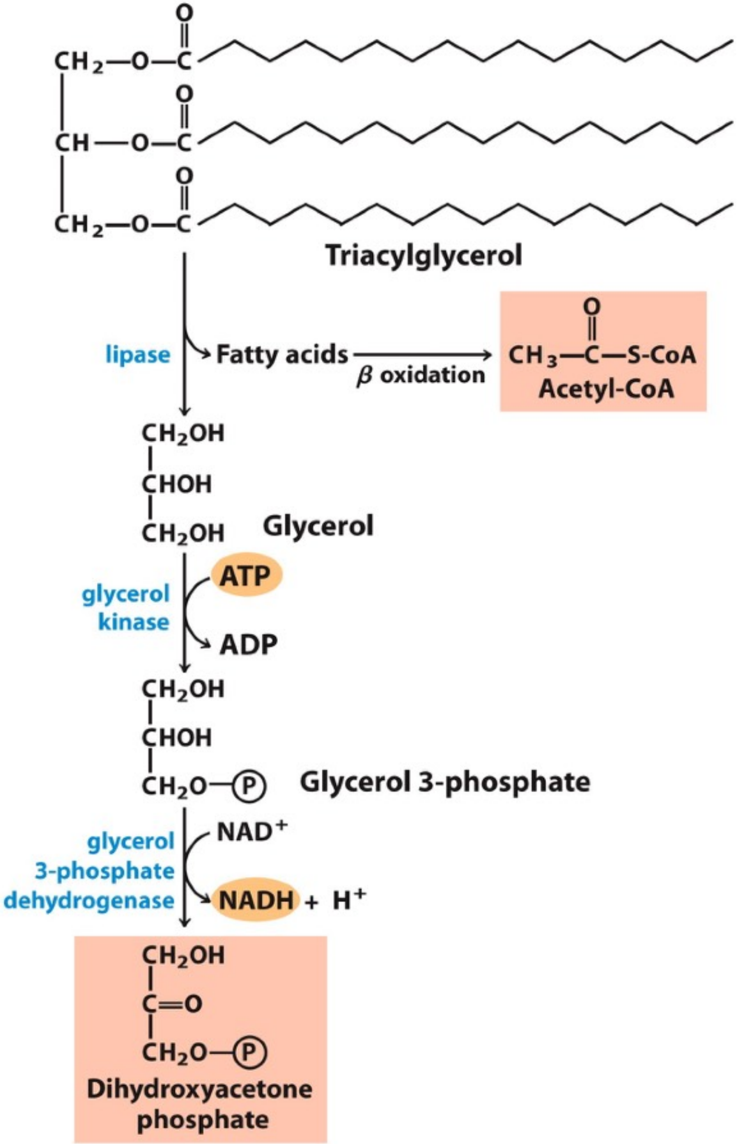
Fatty Acid -> Glucose

- Fatty acids can be converted to sucrose in germinating seeds.
  - Four biochemical processes.
    - β-oxidation (fatty acid -> acetyl-CoA).
    - Glyoxylate cycle (acetyl-CoA -> succinate).
    - Citric acid cycle (succinate -> oxaloacetate).
    - Gluconeogenesis (oxaloacetate -> sucrose).
  - Three subcellular compartments.
    - Glyoxysome (fatty acid -> succinate).
    - Mitochondrion (succinate -> oxaloacetate).
    - Cytosol (oxaloacetate -> sucrose).
  - Only 75% carbon atoms converted.
    - 25% is lost as CO_2 in oxaloacetate -> PEP.

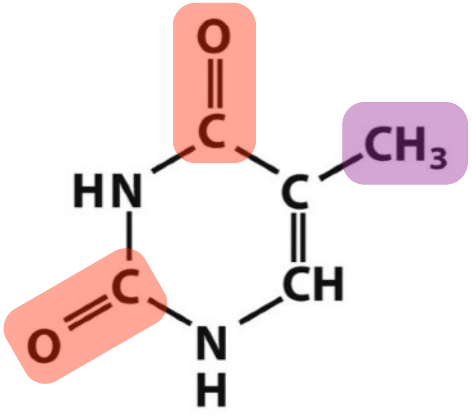


Glycerol -> Glucose

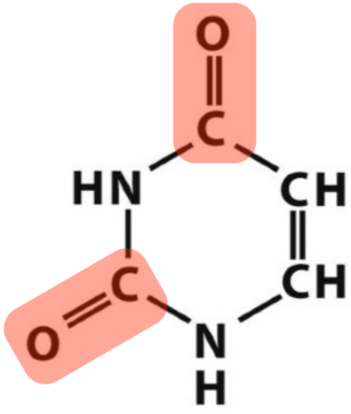
- Glycerol can also be converted to sucrose in germinating seeds.
  1. Glycerol is phosphorylated.
     - Catalyzed by glycerol kinase.
     - Consumes ATP.
     - Produces glycerol 3-phosphate.
  2. Glycerol 3-phosphate is oxidized.
     - Catalyzed by G3P dehydrogenase.
     - Reduces NAD+ to NADH.
     - Produces DHAP.
  3. DHAP enters gluconeogenesis.



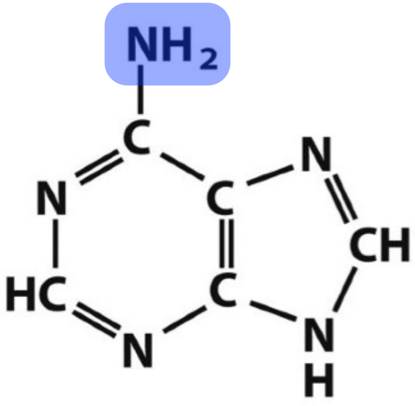
Structures of This Week: T and U



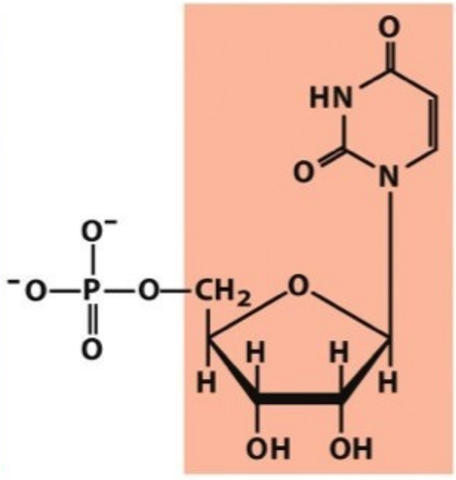
Thymine



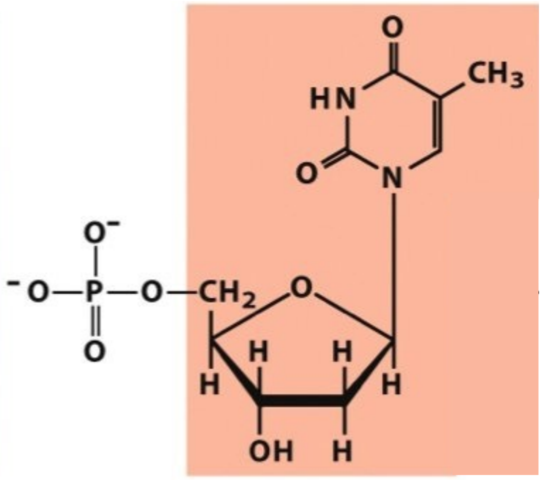
Uracil



Adenine

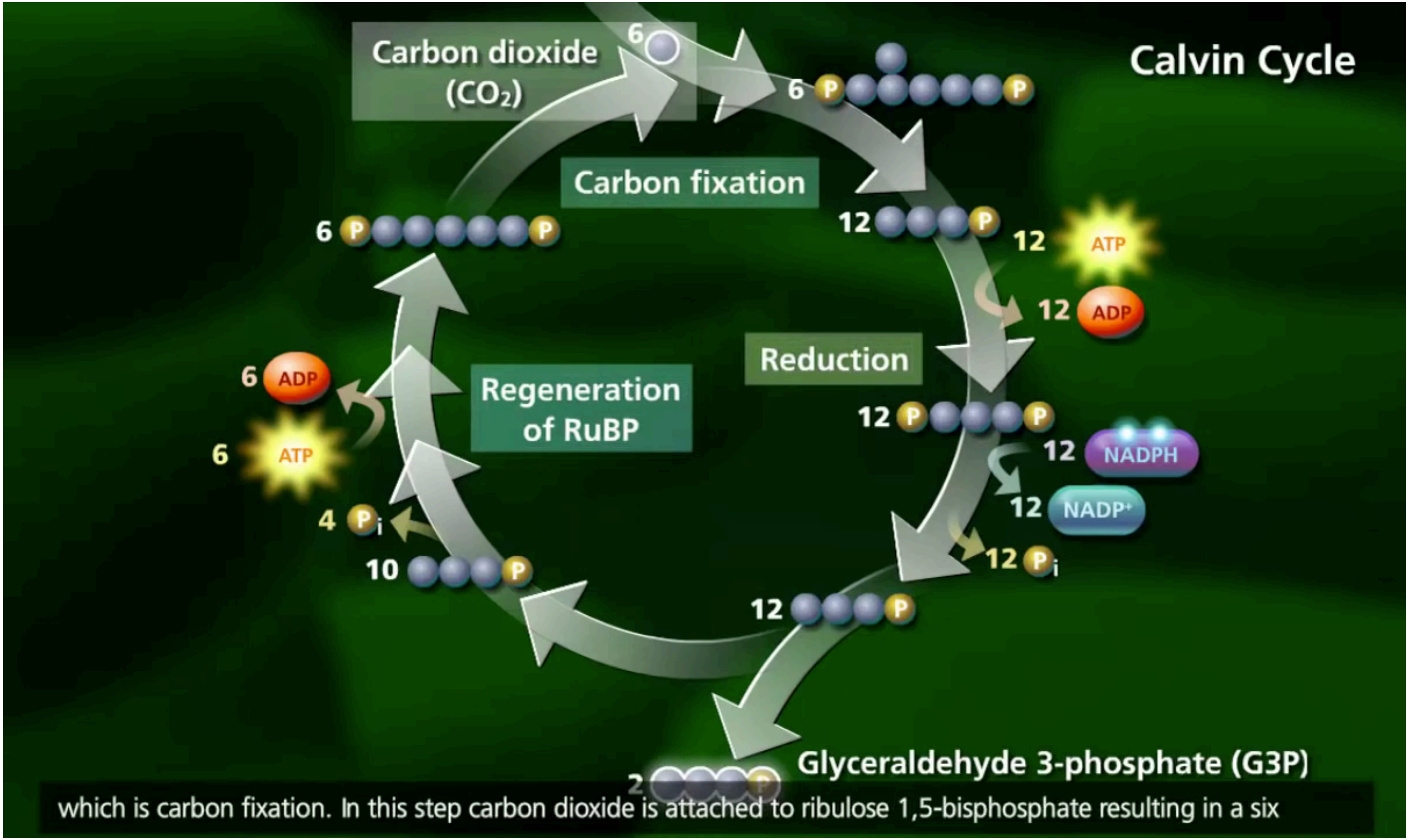


Uridine 5’-monophosphate



Deoxythymidine 5’-monophosphate

Photosynthesis



which is carbon fixation. In this step carbon dioxide is attached to ribulose 1,5-bisphosphate resulting in a six

Example Question

Which of these enzymes is *not* part of the Calvin cycle?

A) Aldolase
B) Glyceraldehyde 3-phosphate dehydrogenase
[✓ C) Phosphofructokinase-1]
D) Ribulose-5-phosphate kinase
E) Transketolase

Example Question

When transketolase acts on fructose 6-phosphate and glyceraldehyde 3-phosphate, the products are:

A) 3-phosphoglycerate and glyceraldehyde 3-phosphate.
B) 3-phosphoglycerate and two molecules of glyceraldehyde 3-phosphate.
C) dihydroxyacetone phosphate and glucose 6-phosphate.
[✓ D) xylulose 5-phosphate and erythrose 4-phosphate.]
E) xylulose 5-phosphate and ribose 5-phosphate.

Example Question

Which of these compounds is *not* directly involved in the Calvin cycle?

A) Erythrose 4-phosphate
B) Glyceraldehyde 3-phosphate
[✓ C) Mannose 6-phosphate]
D) Ribulose 5-phosphate
E) Sedoheptulose 7-phosphate

Example Question

The glycine decarboxylase complex is localized mainly in the:

A) chloroplast.
B) endoplasmic reticulum.
[✓ C) mitochondrion.]
D) cell membrane.
E) peroxisome.

Example Question

The synthesis of starch in plants uses ________ as the substrate.
The synthesis of sucrose in plants uses _______ as the substrate.
The synthesis of glycogen in animal cells uses _ as the substrate.

A) ADP-fructose; glucose and fructose; UDP-glucose
[✓ B) ADP-glucose; UDP-glucose and fructose 6-phosphate; UDP-glucose]
C) fructose 1-phosphate; UDP-fructose and glucose 6-phosphate; glucose 1-phosphate
D) glucose 1-phosphate; UDP-glucose and fructose; glucose 6-phosphate
E) UDP-glucose; UDP-glucose and UDP-fructose; ADP-glucose

Example Question

Which of the following compounds is a component of peptidoglycan of bacterial cell?

A) galactose.
B) glucose.
C) glucuronic acid.
[✓ *D)* N-acetylglucosamine.]
E) penicillin.

Example Question

Name one similarity and one difference between the glycogen and cellulose (structure or biosynthesis).

Example Question

Describe how plants can, unlike animals, convert acetyl-CoA derived from fatty acids into glucose or sucrose.