photosynthesis

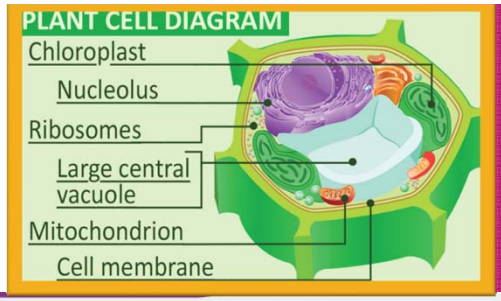
chloroplast, a specialized organelle

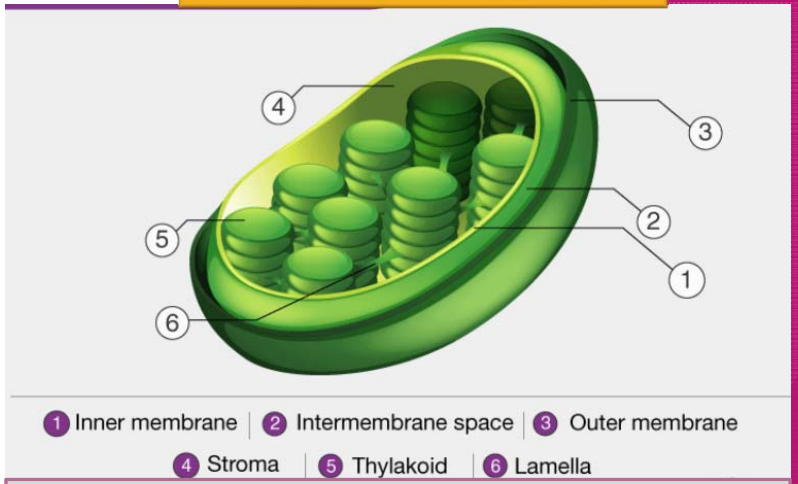
In eukaryotes, photosynthesis occur in a specialized plastid, the **chloroplast**.

All the reactions required for photosynthesis take place in this organelle.

The complex structure of the chloroplast reflects its diverse biochemical functions.

Chloroplasts are surrounded by a double-membrane system consisting of an **outer and inner envelope** and also contain a complex internal membrane system.





گرانوم ها (grana pl. granum sing): مجموعه های متشکل از کیسه های پهن و مسطح یا تیلاکوئیدها، در داخل کلروپلاست که دارای رنگیزه و انزیم های واکنش های مرحله نوری فتوسنتز هستند.

لاملا: غشای گرانوم ها

تیلاکوئید: کیسه های پهن و مسطح تشکیل دهنده گرانوم ها

استروما: بخشی از کلروپلاست که در بین گرانوم ها قرار گرفته است.

Photosynthesis consists of light reactions and carbon reactions

photosynthetic process involves two phases:

- the light reactions, which produce O_2, ATP, and NADPH;
- and carbon reactions (the carbon reduction cycle, also called the **Calvin-Benson cycle**, (after its co-discoverers, Melvin Calvin and Andrew Benson), which reduce CO_2 to carbohydrate and consume the ATP and NADPH produced in the light reactions.
- The two phases of photosynthesis occur simultaneously, but they reside in different regions of the chloroplast (Fig).

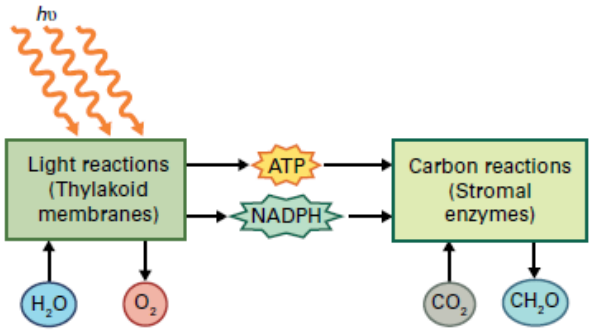
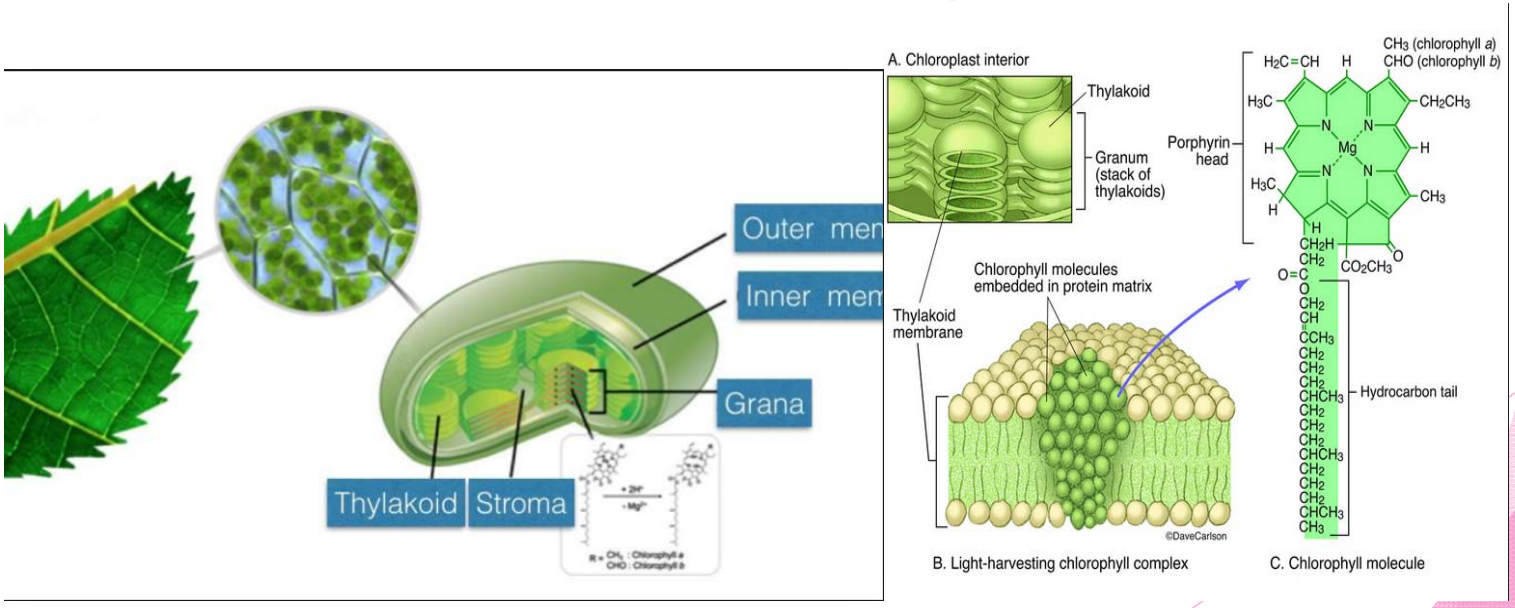


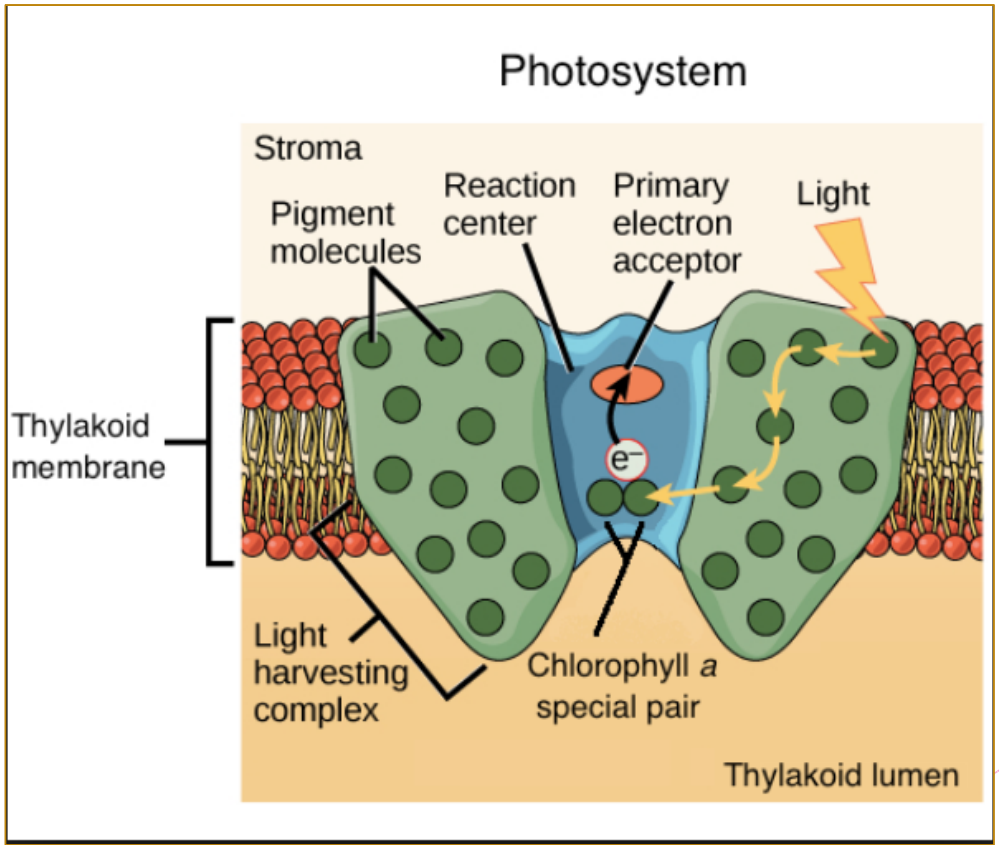
FIGURE 12.2 *The light and carbon (formerly "dark") reactions of photosynthesis occur in separate chloroplast compartments. Light is required for the synthesis of ATP and NADPH substrates in a series of reactions that occur in thylakoid membranes of the chloroplast. These products of the light reactions are then used by a series of stromal enzymes that fix CO_2 into carbohydrates during the carbon reactions.*

All photosynthetic organisms contain chlorophyll or a related pigment

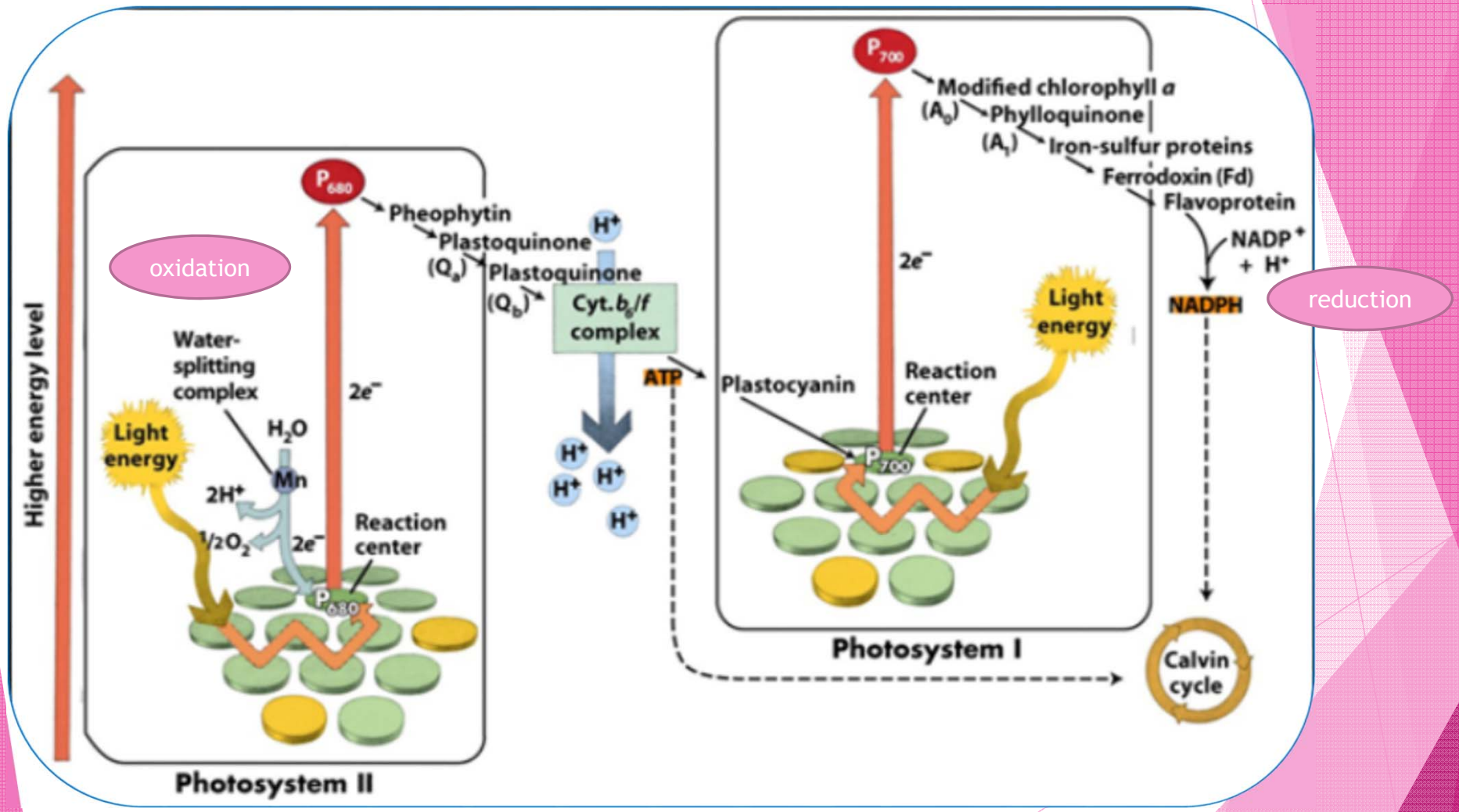
- All photoautotrophic organisms contain some form of the light-absorbing pigment **chlorophyll**.
- Plants, algae, and cyanobacteria synthesize chlorophyll.



- The special chlorophyll in the reaction center can be excited directly by absorption of a photon, or it can be excited upon receipt of excitation energy from the antenna. Thus, the antenna, which consists of many pigment molecules, increases the absorption cross-section of the reaction center. (P: 300)



Oxygenic photosynthetic organisms contain two photochemical reaction centers, **PSI** and **PSII**



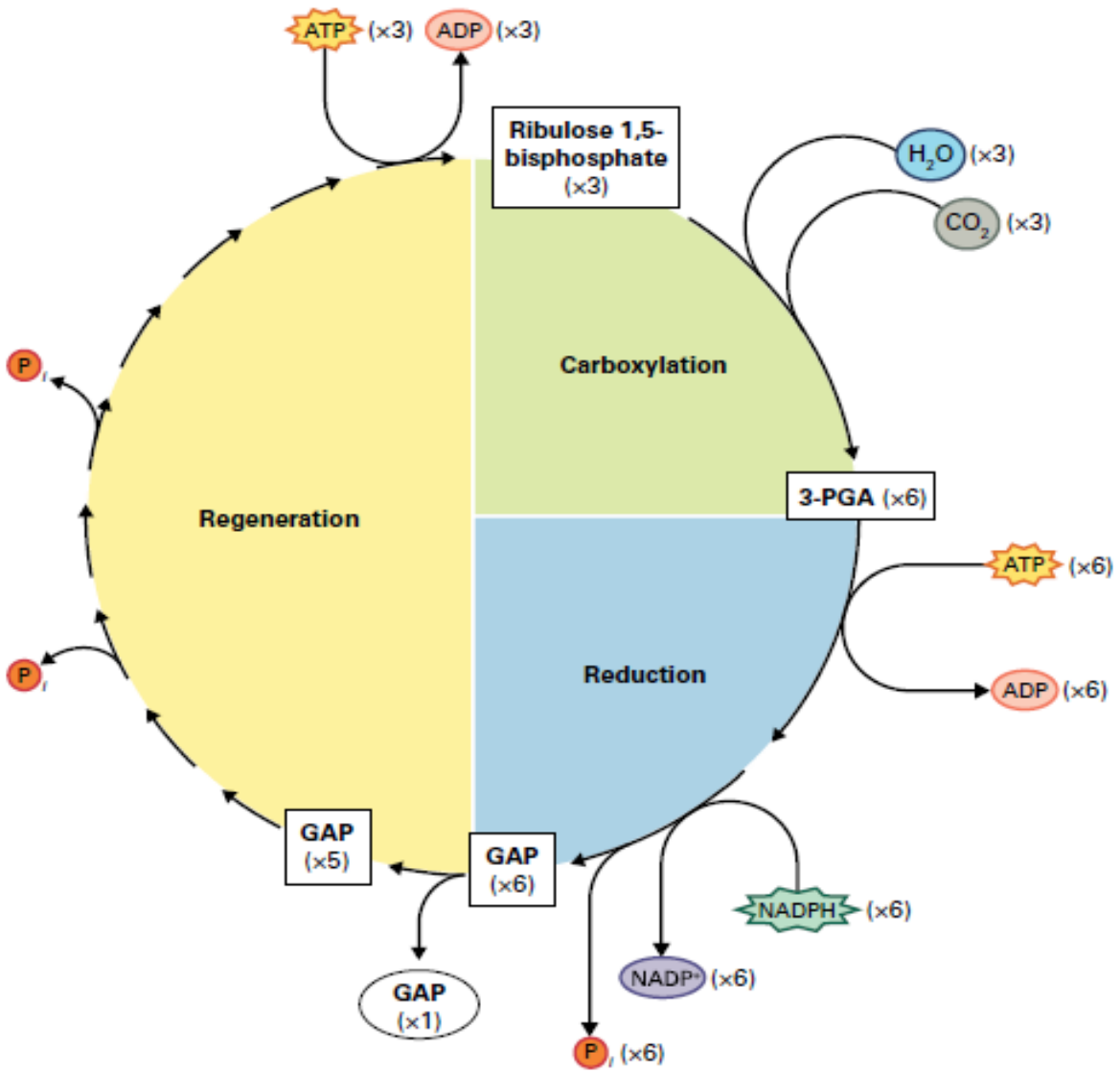
The Calvin–Benson cycle proceeds through 13 biochemical reactions

- The Calvin–Benson cycle proceeds through 13 biochemical reactions that can be analyzed separately in three highly coordinated phases:

carboxylation, reduction, and regeneration

- Carboxylation of the CO2-acceptor molecule: ribulose 1,5-bisphosphate (RuBP; five-carbon acceptor molecule) reacts with one molecule each of CO2 and water to yield two molecules of 3-phosphoglycerate (3-PGA) in the first enzymatic step of the cycle.
- Reduction of 3-PGA: Photochemically generated ATP and NADPH are used in two enzymatic reactions for the reduction of 3-PGA to glyceraldehyde 3-phosphate (GAP).
- Regeneration of RuBP: The regeneration of the CO2 acceptor RuBP closes the cycle through ten enzyme-catalyzed reactions, one requiring ATP.

FIGURE 12.34 *Three phases of the Calvin–Benson cycle: carboxylation, reduction, and regeneration. Overall, the fixation of three molecules of CO_2 into one molecule of triose phosphate requires six molecules of NADPH and nine of ATP (3 CO_2: 6 NADPH : 9 ATP ≡ CO_2 : 2 NADPH : 3 ATP). The net glyceraldehyde 3-phosphate (GAP) formed is utilized either for immediate metabolic needs or converted to a storage form of carbohydrate—starch in the chloroplast or sucrose in the cytosol. 3-PGA, 3-phosphoglycerate.*



Rubisco

- Rubisco, the predominant protein in plant leaves, catalyzes the initial reaction of the Calvin–Benson cycle, the carboxylation of RuBP. In addition, Rubisco catalyzes a competing oxygenation reaction (**photorespiration**), which reduces the efficiency of photosynthetic carbon fixation.
- In addition to its role as a carboxylase, Rubisco has an oxygenase activity that uses O2 as a substrate instead of CO2 to produce 3-PGA and the two-carbon molecule, 2-phosphoglycolate.
- The two substrates, CO2 and O2, compete for the same active site on the enzyme, and the activity of the enzyme toward these substrates is dictated by the relative amounts of O2 and CO2 in the environment. In air, the carboxylation reaction proceeds approximately three times faster than the oxygenation reaction; the oxygenase activity, however, proceeds at a rate that can have profound effects on the overall efficiency of CO2 fixation in C3 plants: in some cases, an estimated 50% of CO2 fixed via photosynthesis is lost through this process of photorespiration.

photorespiration

The oxygenation of RuBP (ribulose bisphosphate) in the presence of O_2 is first reaction of photorespiration that leads to the formation of one molecule of phosphoglycolate, a two-carbon compound and one molecule of PGA. P.361

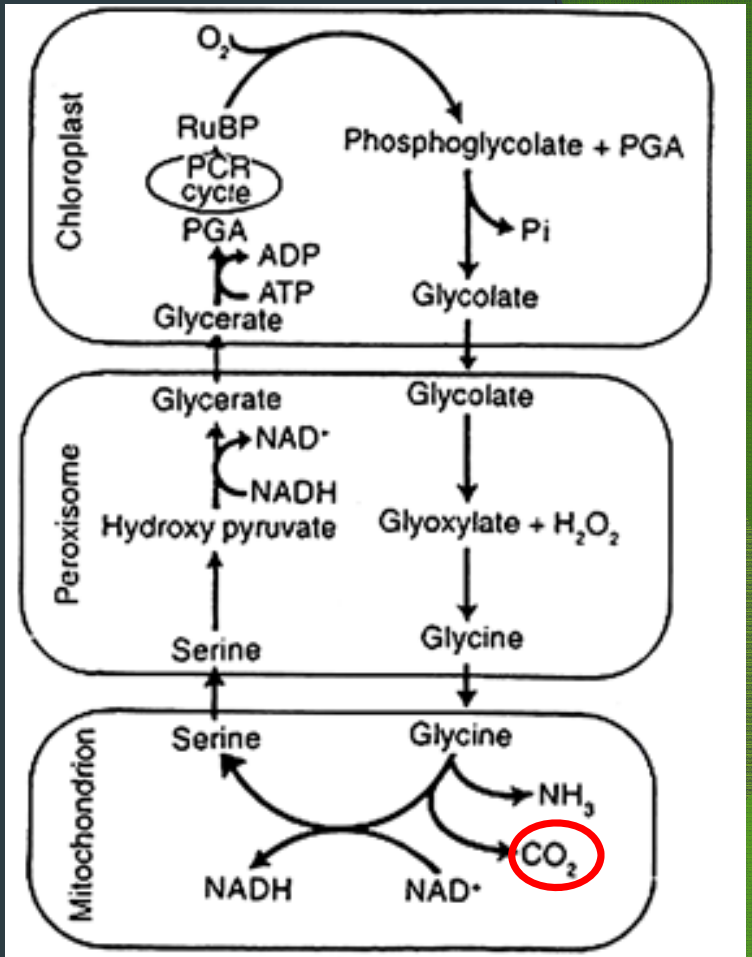


Fig. 5.10. Photorespiration.

C4 plants utilize two distinct metabolic compartments for fixing CO2

- Not all organisms that contain the Calvin–Benson cycle produce 3-PGA as the first stable photosynthetic intermediate.

- several plant species form large amounts of four-carbon organic acids as the first products of CO2 fixation. On this basis, plants are classified as C3 or **C4 plants** based on the primary product of carbon fixation in photosynthesis: three-carbon (3-PGA) and four-carbon (oxaloacetic acid, OAA) compounds are the primary products of carbon fixation in C3 and C4 plants, respectively.

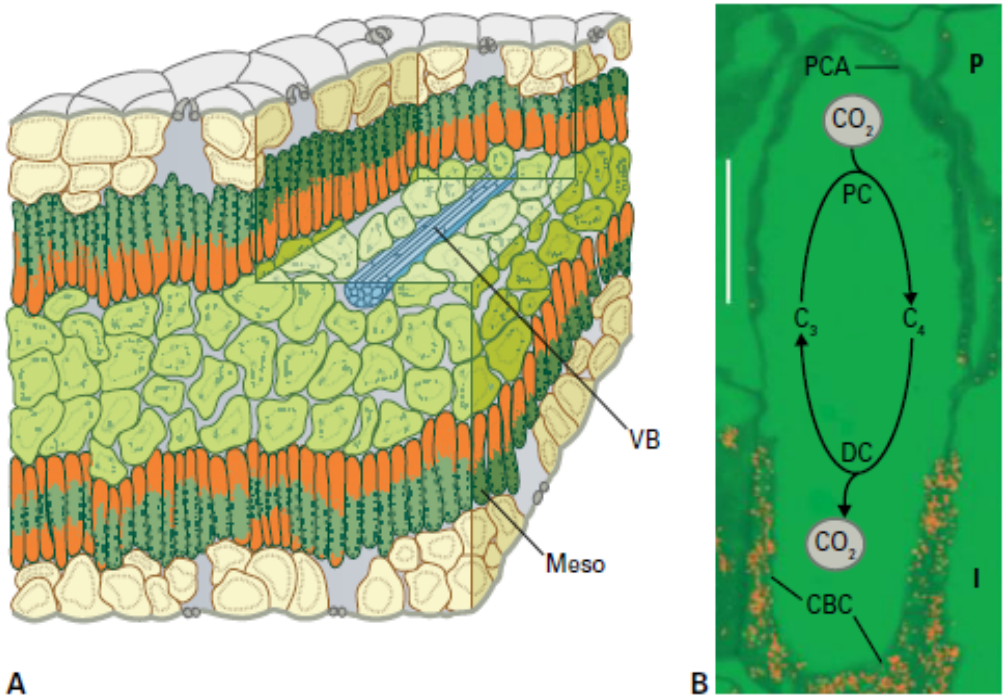


FIGURE 12.44 *Leaf anatomy of single-cell C4 plants. (A) Three-dimensional drawing of the leaf anatomy of* Borszczowia aralocaspica, *a single-cell C_4 plant. Meso, mesophyll; VB, vascular bundles. Note the lack of differentiation in the cells. (B) Immunolocalization of Rubisco at the internal region (I) of a photosynthetic cell from* Borszczowia aralocaspica. *Red chloroplasts containing the Calvin–Benson cycle (CBC) are functionally equivalent to C_4 bundle sheath chloroplasts. Chloroplasts containing PPDK, which are functionally equivalent to C_4 mesophyll chloroplasts, are situated at the peripheral region (P) where they contribute to the photosynthetic carbon assimilation (PCA). PC and DC refer to the initial carboxylation catalyzed by PEPCase and the decarboxylation of C_4 acids, respectively.*

The C4 pathway increases the concentration of CO2 in internal compartments close to vascular tissues

- The C4 pathway of CO2 fixation requires a complex interaction between two different compartments and involves the following steps:

1 Primary carboxylation: fixation of HCO_3^- by PEPCase in the outer compartment (for example, mesophyll cells) to yield OAA.

2 Transformation of OAA into another four-carbon acid (malate or aspartate) and transport of the four-carbon acids from the outer to the internal compartment (e.g., bundle sheath cells)

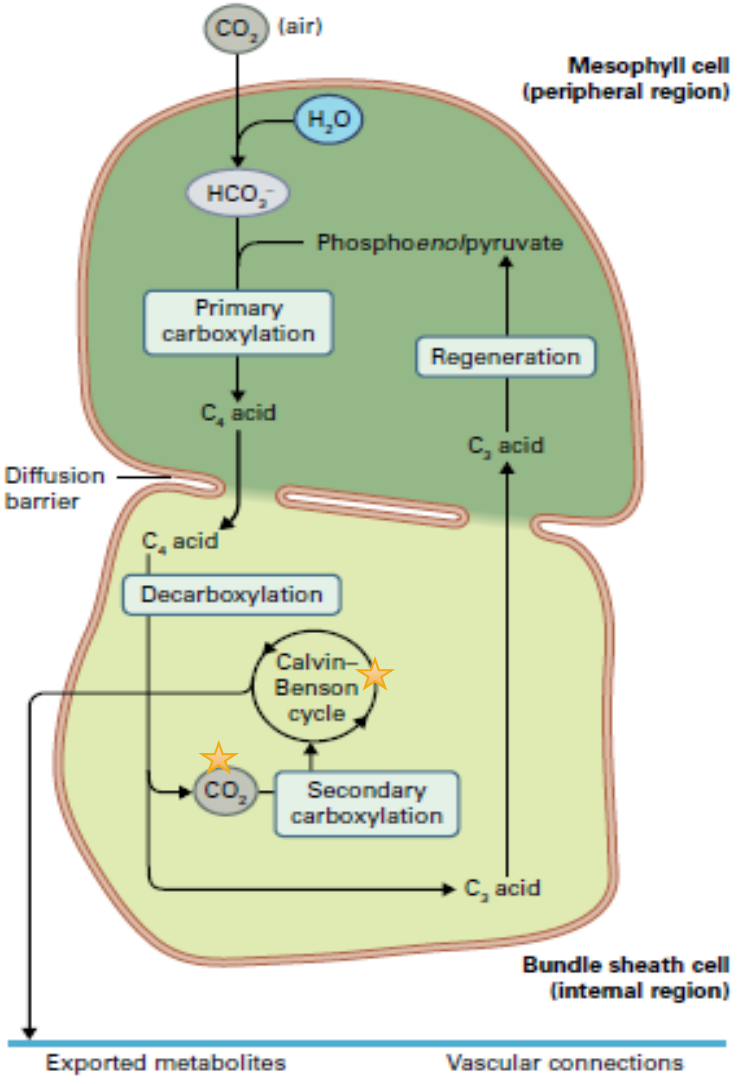
3 Decarboxylation: release of CO_2 from the four-carbon acid.

4 Secondary carboxylation: subsequent refixation of the CO_2 by Rubisco and the Calvin–Benson cycle.

5 Transfer of the three-carbon intermediates (pyruvate or alanine) resulting from decarboxylation of the four-carbon acids back to the outer compartment.

6 Conversion of the three-carbon intermediates to PEP to reinitiate the fixation of HCO_3^-.

FIGURE 12.45 *General aspects of the C_4 pathway. Atmospheric CO_2 enters the peripheral region and is converted to HCO_3^- for reaction with PEP, yielding OAA (primary carboxylation). OAA is transformed to a second C_4 acid (malate or aspartate) that flows across a diffusion barrier to the internal region. There, the C_4 acid is decarboxylated, yielding CO_2 and a C_3 acid (pyruvate or PEP) (decarboxylation). The released CO_2 is fixed by Rubisco in the Calvin–Benson cycle (secondary carboxylation) and converted to carbohydrate for export to other parts of the plant. The remaining C_3 acid is transported back to the external region to regenerate PEP (regeneration).*



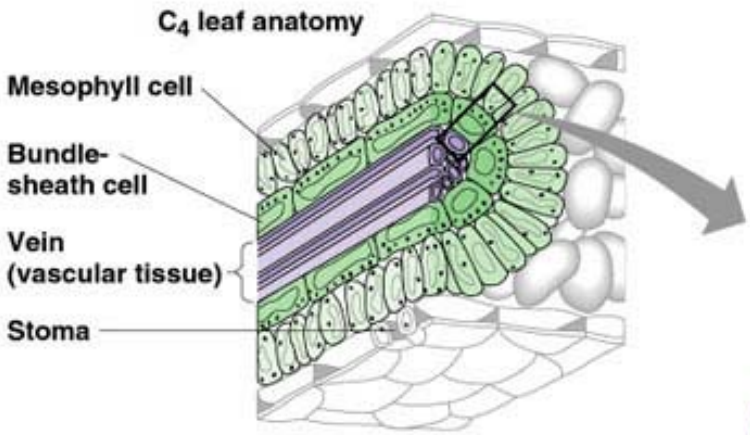
- In the context of the two-cell C4 pathway, all carbon fixation begins in the cytosol of mesophyll cells, where carbonic anhydrase catalyzes the conversion of atmospheric CO2 into HCO3–for subsequent carboxylation.

- OAA is generated from HCO_3^- and PEP in the cytosol of the outer compartment (i.e., mesophyll cells), catalyzed by PEPCase. Whereas

- enzymes unique to the Calvin–Benson cycle are located only in chloroplasts of the internal compartment (i.e., bundle sheath cells).

- In accordance with distinct functions, electron micrographs of bundle sheath and mesophyll chloroplasts (Fig. 12.43) show structural differences:

- chloroplasts of (internal) bundle sheath cells lack stacked membranes and exhibit little PSII activity, whereas chloroplasts of (peripheral) mesophyll cells have retained stacked membranes as well as PSII and PSI activities (Fig. 12.43B).

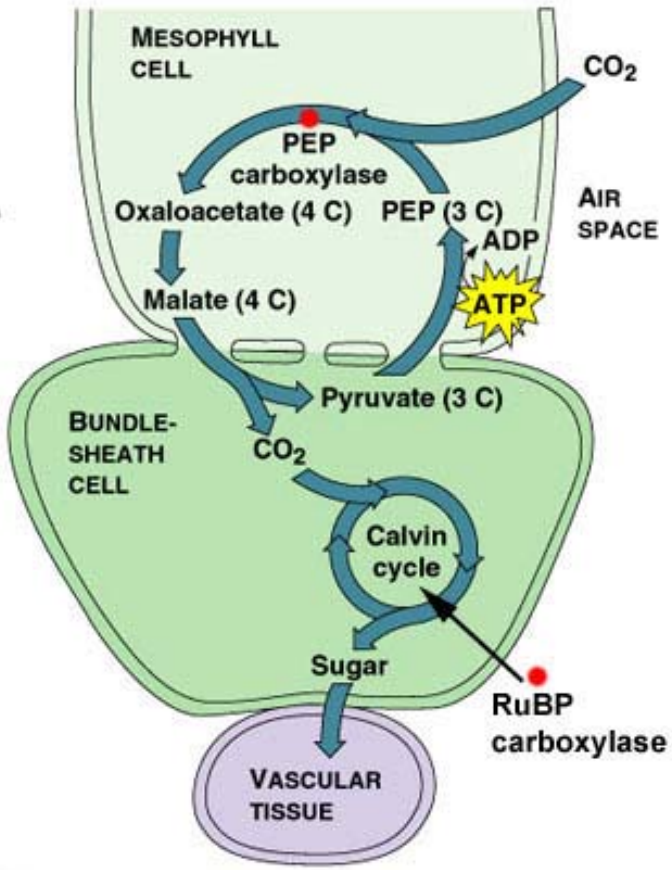


Differences compared to C3 (Calvin) plants

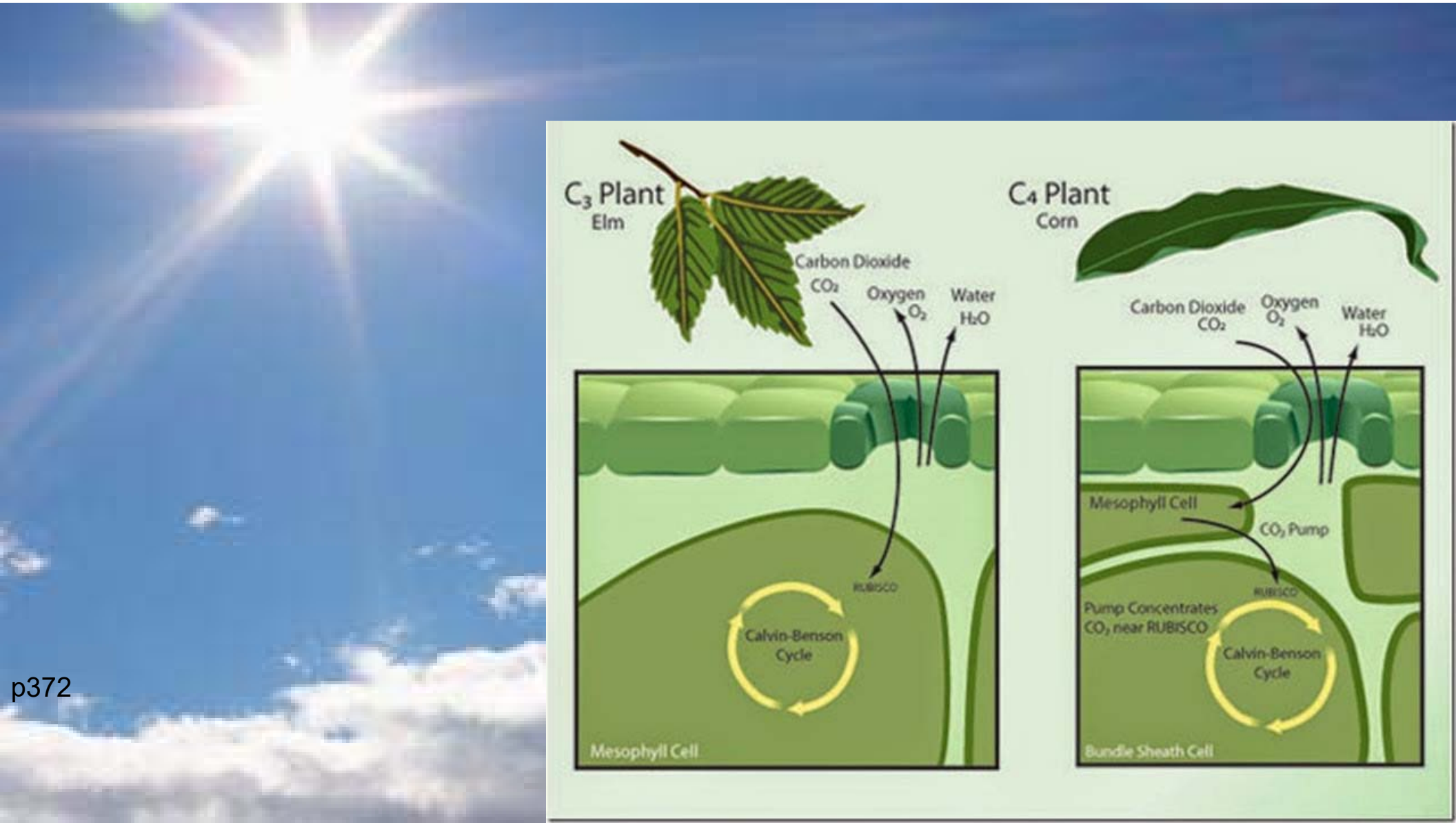
2 cell types: mesophyll & bundle sheath
spatial separation acid & sugar synthesis

2 fixation enzymes: 1) RuBP carboxylase
2) PEP carboxylase

CO_2 is reduced twice



The C_4 pathway


C3 Plant
Elm
Carbon Dioxide
CO2
Oxygen
O2
Water
H2O
RUBISCO
Calvin-Benson Cycle
Mesophyll Cell
C4 Plant
Corn
Carbon Dioxide
CO2
Oxygen
O2
Water
H2O
Mesophyll Cell
CO2 Pump
RUBISCO
Pump Concentrates CO2 near RUBISCO
Calvin-Benson Cycle
Bundle Sheath Cell

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CAM photosynthesis involves the temporal separation of CO2 capture and carbon fixation

- Another modification of the C3 pathway occurs in plants utilizing Crassulacean acid metabolism (CAM).
- Named after the Crassulaceae family of succulent plants, this pathway has evolved mechanisms for maximizing carbon uptake under environmental conditions that limit productivity, such as high temperature or shortage of water.
- Thus, CAM photosynthesis is commonly associated with plants that inhabit arid environments (e.g., succulents, including cacti and some commercially significant plants, such as pineapple and agave).
- To enhance water conservation, these plants have evolved anatomical and morphological structures, such as thick cuticles, that prevent water loss.
- They have also evolved mechanisms for ensuring a high concentration of CO2 at the active site of Rubisco to minimize photorespiration.

- The biochemical pathway of CO2 fixation in terrestrial CAM plants is similar to the C4 pathway, but instead of a spatial separation of the two carboxylations necessary for CO2 fixation, terrestrial CAM plants use a temporal separation of the initial fixation reaction from the assimilation by Rubisco (Fig.).

- At night, when it is cold and leaf stomata are open, CO2 is fixed initially into OAA and then malate via PEPCase and NADP-malate dehydrogenase. The malic acid is stored in vacuoles, where it can reach high concentrations.

- During the day, stomata close to prevent the loss of water, and malic acid is transported out of the vacuole. At this stage, NADP-ME catalyzes the decarboxylation of malate, yielding CO2 and pyruvate, and the released CO2 is fixed by Rubisco via the Calvin–Benson cycle, while pyruvate is used to form starch. The starch confined to photosynthesizing tissues of terrestrial CAM plants, named **transitory starch**, is broken down at night via glycolysis and serves as a source of PEP for the fixation of CO2 via PEPCase.

- In this circadian rhythm, the opening/closing of stomata, variations of organic acids and storage carbohydrates, and the activities of carboxylation and decarboxylation enzymes modulate the proportion of CO2 taken up via PEPCase at night and Rubisco during the day.

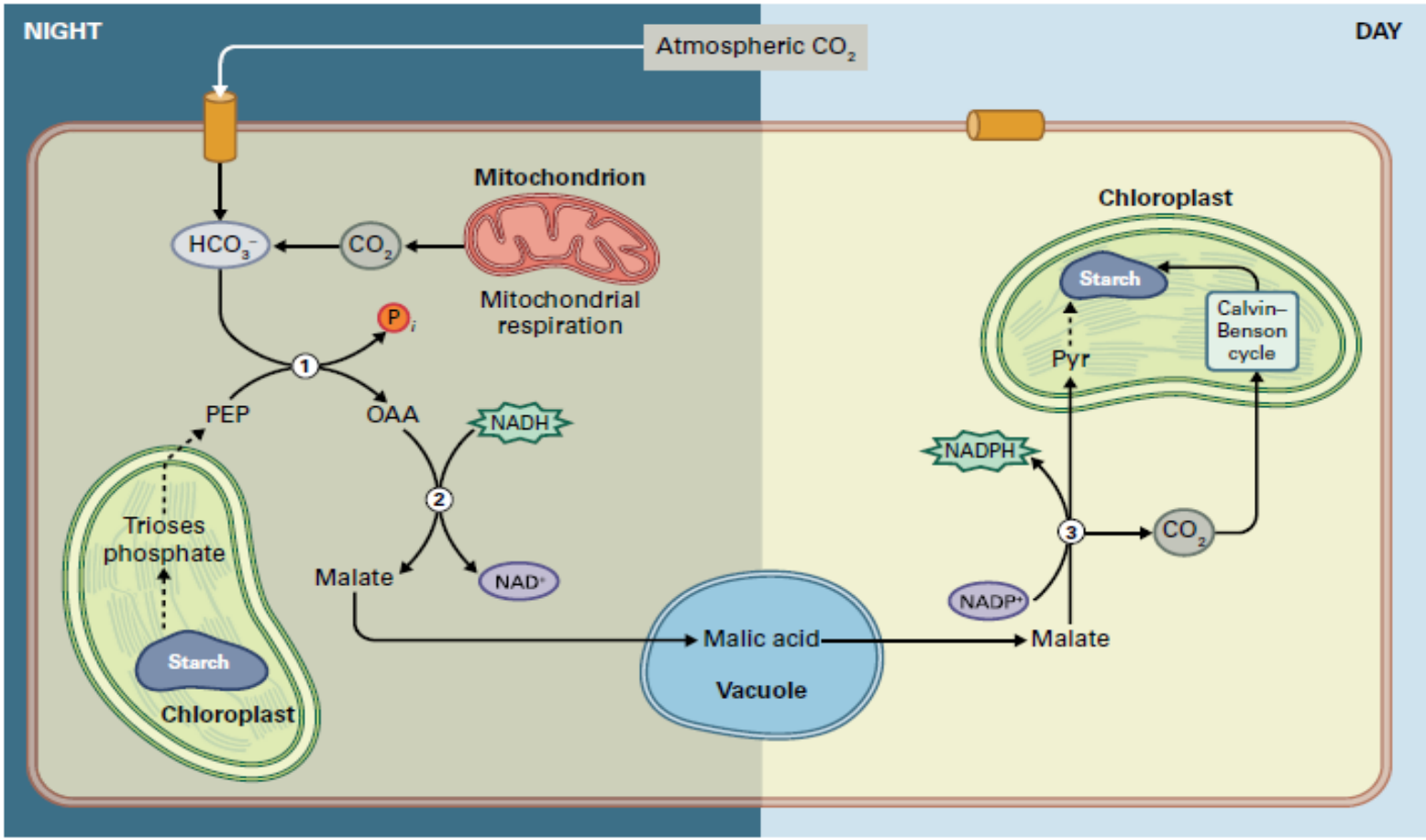
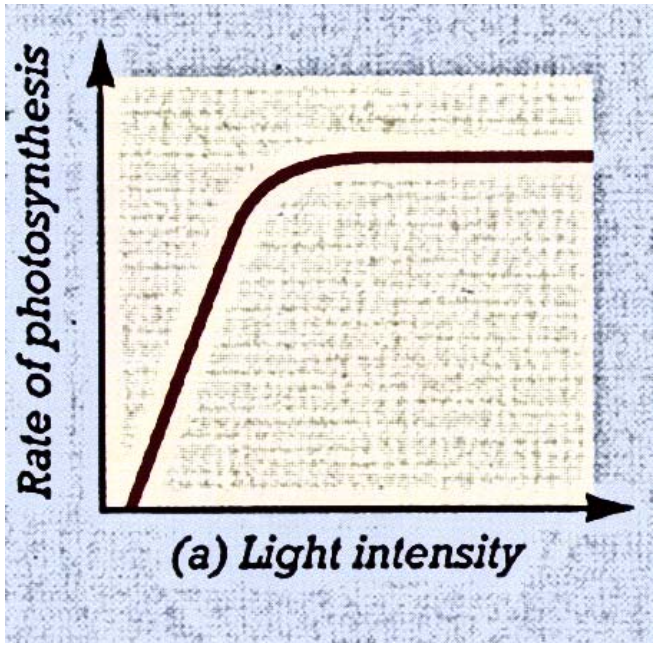


FIGURE 12.49 *Crassulacean acid metabolism (CAM). At night, both atmospheric and respiratory CO_2 provide HCO_3^- for carboxylation of PEP catalyzed by PEPCase (reaction 1). NAD-malate dehydrogenase catalyzes the reduction of the C_4 organic acid—oxaloacetic (OAA)—to malate (reaction 2). Malate is stored in the vacuole overnight. During the day, the stored malate is decarboxylated by NAD(P)-ME yielding NAD(P)H, pyruvate, and CO_2 (reaction 3). In the chloroplast, pyruvate and CO_2 are used for synthesis of carbohydrates via gluconeogenesis and the Calvin–Benson cycle, respectively.*

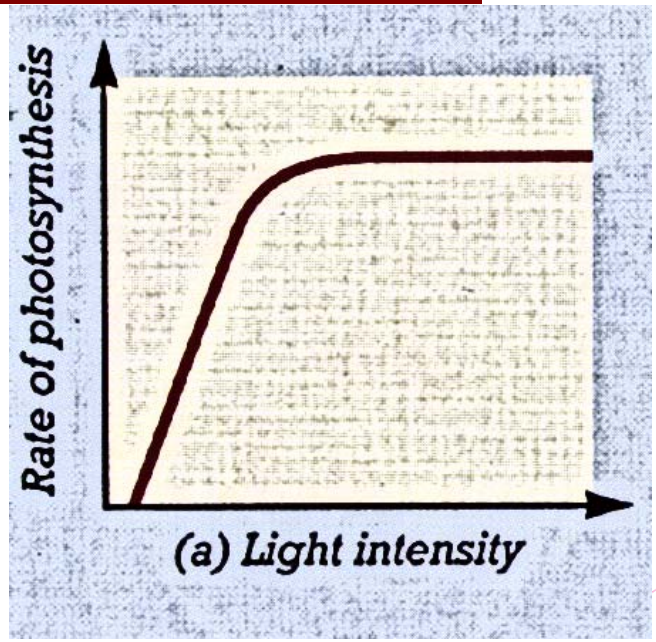
- This plateau represents the **maximum rate of photosynthesis** ---as seen in the diagram.

- Higher light intensity initially causes more electrons in the chlorophyll molecules to become excited *(gain energy).*



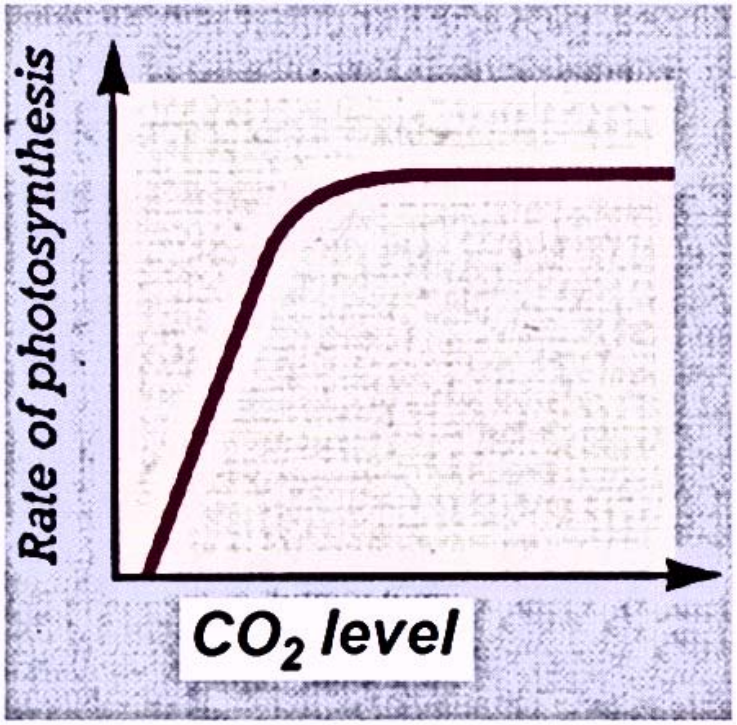
- **As more and more electrons are excited, the light reactions occur more rapidly.**

- **At a certain light intensity, however, all the available electrons are excited and a further increase in light intensity will not increase the rate of photosynthesis.**



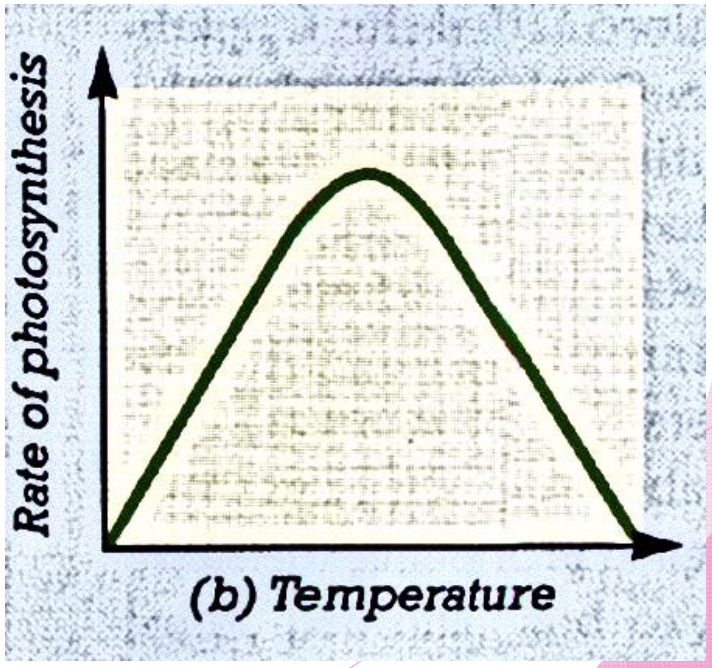
2) Carbon dioxide

Like increasing light intensity, increasing levels of carbon dioxide around the plant stimulates photosynthesis until it reaches a plateau. This graph would resemble that of light intensity.



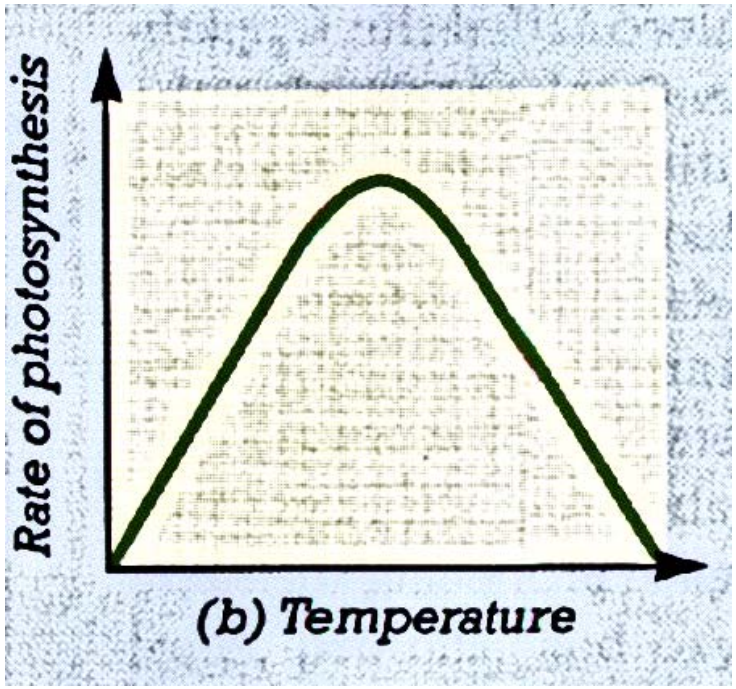
3) Temperature

a) Raising the temperature accelerates various chemical reactions of photosynthesis. As a result, the rate of photosynthesis increases, over a certain range.

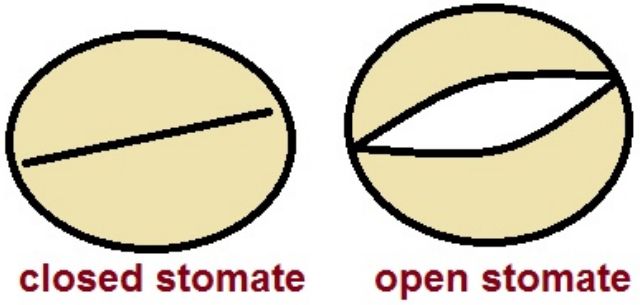


- b) The rate of photosynthesis generally **peaks at a certain temperature**, as seen in the graph.

c) **Above this temperature, the rate decreases.**



d) As the temperature increases, the **stomates begin to close**, to limit water loss. This will have the effect of **stopping the carbon dioxide from entering** the leaf. This will also decrease the rate of photosynthesis. (Also: Enzymes do not function well at too high a temperature.)



4) Water

- A lack of water will also slow the rate of photosynthesis. Stomata can close from water loss.
- Plants such as the cactus have adaptations to prevent water loss in dry, desert climates.

Comparison between C3, C4, and CAM

	C3	C4	CAM
product	G3P Day &night	Malate Day &night	Malate Night only
Anatomy	No bundle sheet cell	Bundle sheet cell	No bundle sheet cell
No of stomata	2000-31000	10000-16000	100-800
Photorespiration	Up to 40%	Not detectable	Not detectable
Species	Wheat, rice, potato	Sugar cane	Pineapple, vanilla, cacti

TABLE 10.1

Comparison of Photosynthesis in C_3, C_4, and CAM Plants

	C_3 PLANTS	C_4 PLANTS	CAM PLANTS
Calvin cycle used?	Yes	Yes	Yes
Primary CO_2 acceptor	RuBP	PEP	PEP
CO_2-fixing enzyme	Rubisco	PEP carboxylase	PEP carboxylase
First product of CO_2 fixation	3PG (3-carbon)	Oxaloacetate (4-carbon)	Oxaloacetate (4-carbon)
Affinity of carboxylase for CO_2	Moderate	High	High
Photosynthetic cells of leaf	Mesophyll	Mesophyll and bundle sheath	Mesophyll with large vacuoles
Photorespiration	Extensive	Minimal	Minimal

CARACTERISTICA	MECANISMO DE FIJACIÓN DE CO2		
	C3	C4	CAM
Requerimiento teórico de energía (CO2:ATP:NADPH)	1 : 3 : 2	1 : 5 : 2	1 : 6,5 : 2
Enzima Carboxilante	RuDP carboxilasa	PEP carboxilasa y RuDp carboxilasa	PEP carboxilasa y RuDp carboxilasa
Tasa máxima de fotosíntesis neta (mg de CO2 / dm2 hoja/ hora)	15 - 35	40 - 80	1 - 18
Fotorespiración	Presente	Difícil de detectar	Difícil de detectar
Sensibilidad de la fotosíntesis a cambios de [O2]	si	no	-
Temperatura Optima para: a.- Fijación de CO2 b.- Crecimiento	 15 a 25 ° C 20 a 35 ° C	 30 a 47 ° C 30 a 35 ° C	 ≈ 35 ° C ≈ 35 ° C
Saturación a la luz	En ¼ a ½ de la plana exposición	Si se satura es a plana exposición	
Relación de transpiración (g de agua/ g de MS)	450 - 950	250 - 350	50 - 55
Producción de materia seca (Ton/ha/ año)	22 ± 3,3	38, 6 ± 16,9	Variable

Summary

- Photosynthesis produces organic compounds from inorganic carbon by using the energy of sunlight.
- These redox processes are carried out in plants, algae, and various bacteria.
- In all cases, the photosynthetic reactions may be divided into two phases: the light reactions and the carbon reactions.
- In eukaryotic organisms, photosynthesis takes place in the chloroplast.
- The two phases of photosynthesis occur simultaneously but take place in different regions of the chloroplast
- The light reactions being localized to the thylakoid membranes and the carbon reactions to the stroma

Summary

- The light reactions of photosynthesis involve the photosynthetic pigments, the photosynthetic electron transport chain, and the ATP synthesis machinery
- Light is absorbed by pigments localized in pigment–protein complexes (photosystems) within the thylakoid membrane.
- This light energy can be transferred from antenna pigments to special pigment–protein complexes, known as reaction centers, where the light energy is converted into chemical products (photochemistry)
- Oxygenic photosynthetic organisms contain two reaction centers and two photosystems, PSII and PSI.
- In plants the two photosystems are spatially separated: PSII is localized in appressed thylakoids, and PSI is localized in stroma-exposed thylakoids.

Summary

- During noncyclic electron transfer, the two photosystems cooperate in the transfer of electrons from water to $NADP^+$ via a series of redox reactions
- In addition to O_2, reduced ferredoxin, and NADPH, the noncyclic electron transfer reactions are coupled to the formation of ATP
- In addition to the noncyclic mechanism for ATP synthesis, chloroplasts synthesize ATP via two cyclic pathways that involve only PSI.
- The reduction of CO_2 to carbohydrates requires the reduced ferredoxin, NADPH, and ATP that are synthesized by the photosynthetic light reactions.
- All plants employ the C3 photosynthetic pathway (Calvin–Benson cycle) to fix CO2, using the enzyme Rubisco to convert CO2 and RuBP into the C3 product, 3-PGA.

Summary

- Calvin–Benson cycle occurs in three phases—carboxylation, reduction, and regeneration—and requires three ATP and two NADPH molecules per molecule of CO_2 fixed.
- Reactions of the Calvin–Benson cycle reactions are catalyzed by soluble enzymes localized in the chloroplast stroma.
- Regulation of the cycle is linked to multiple light-dependent mechanisms, including the active removal of Rubisco inhibitors, changes in pH and Mg_{2+}, and disulfide redox transitions catalyzed by the ferredoxin–thioredoxin system.
- Variants of C_3 photosynthesis exist in many plants.

Summary

- In one variation, the C_4 pathway, plants fix CO_2 into a C_4 acid in mesophyll cells, and transport this fixed CO_2 to anatomically distinct bundle sheath cells, where the CO_2 is released, refixed, and assimilated by Rubisco and other enzymes of the Calvin–Benson cycle.
- This sequence of reactions enhances the productivity of C_4 plants by (i) providing a higher concentration of CO_2 for Rubisco in the bundle sheath cell, and (ii) decreasing the oxygenase activity of Rubisco—a reaction that competes with the fixation of CO_2 in C_3 chloroplasts.
- In another variant, CAM metabolism, CO_2 is fixed at night into malate, which is decarboxylated during the day to provide CO_2 for Rubisco.
- CAM photosynthesis aids in the retention of water and enables plant to grow in arid environments.
- Several photosynthetic enzymes in C_4 and CAM plants are regulated to ensure efficient interaction of the CO_2- concentrating mechanisms with the Calvin–Benson cycle.