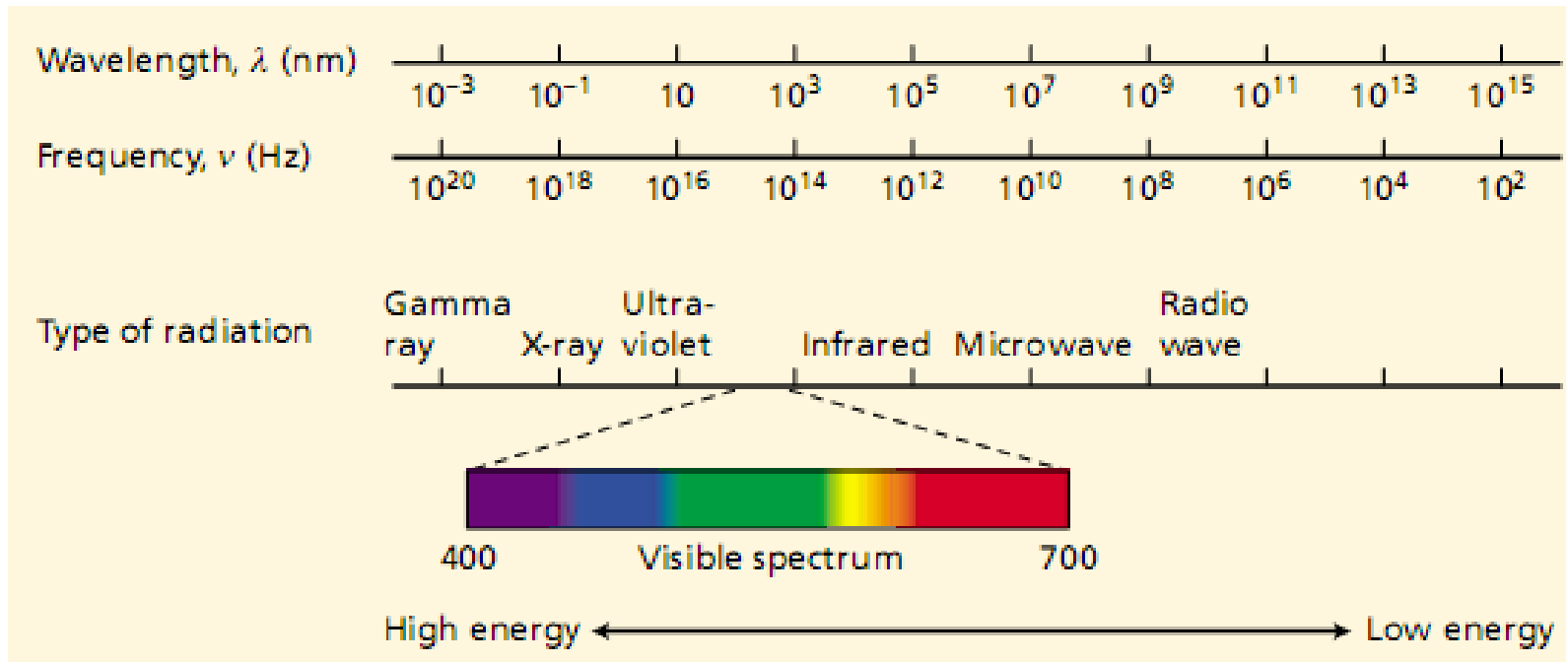
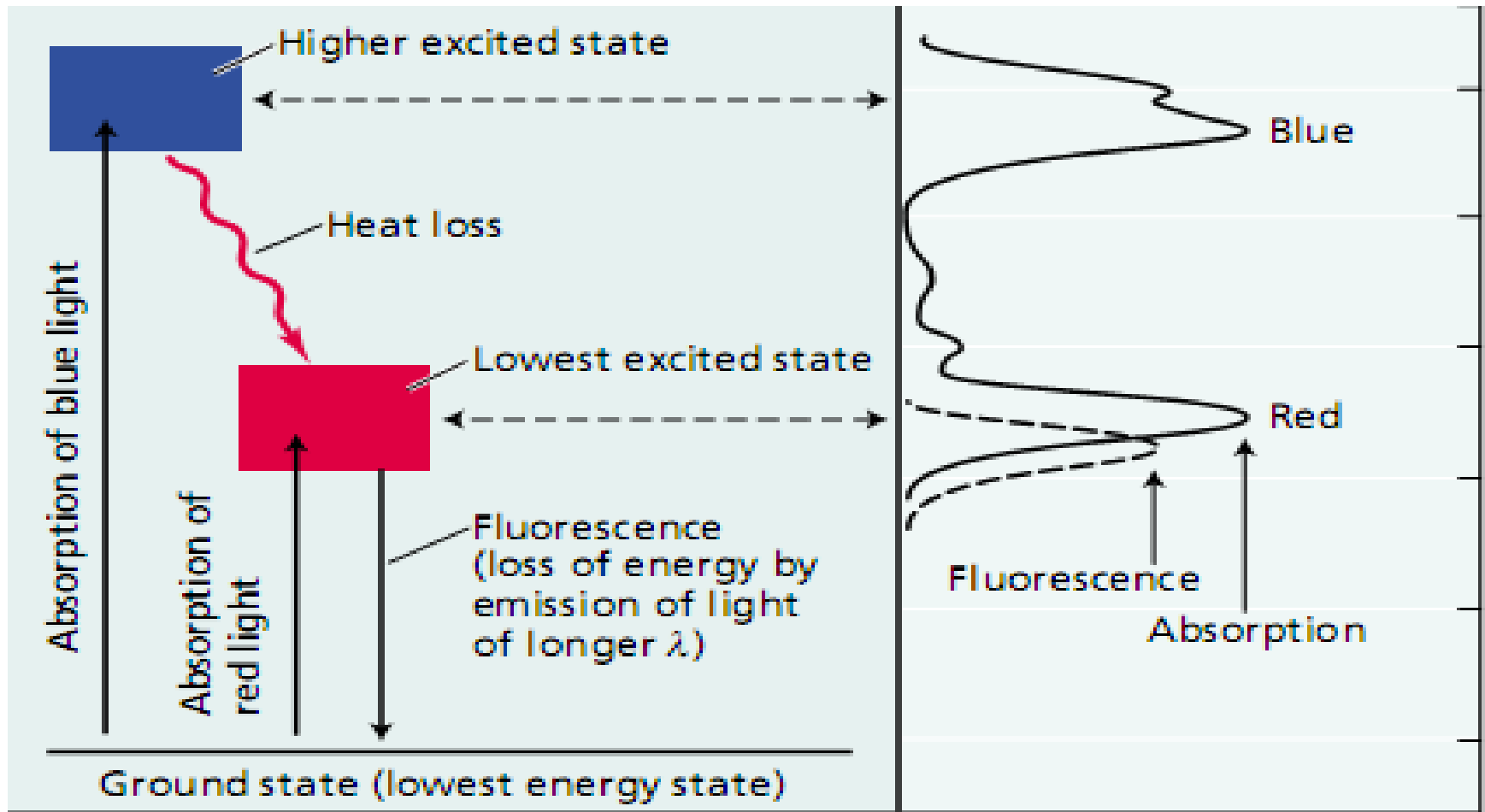


Electromagnetic spectrum



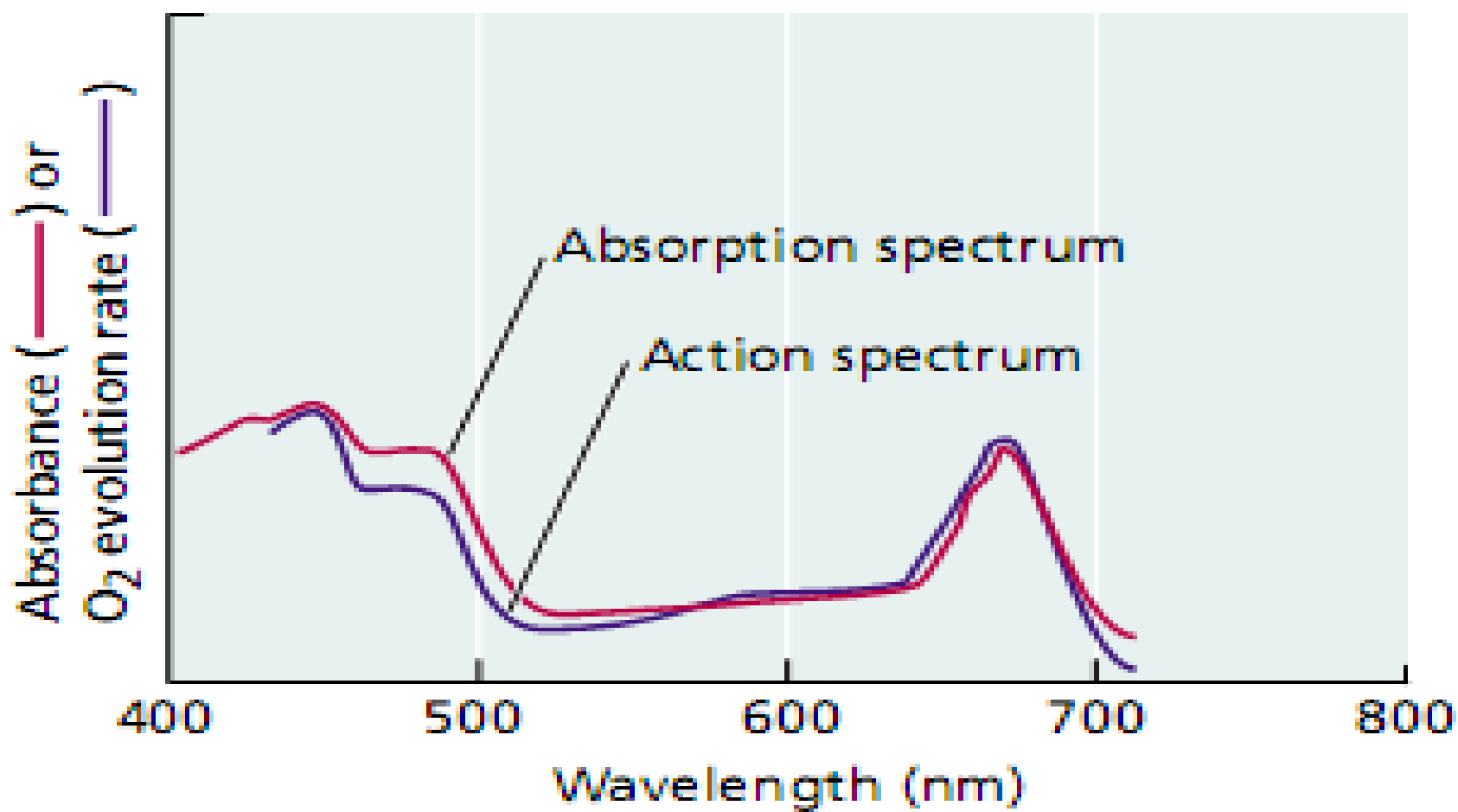
Light absorption and emission by chlorophyll



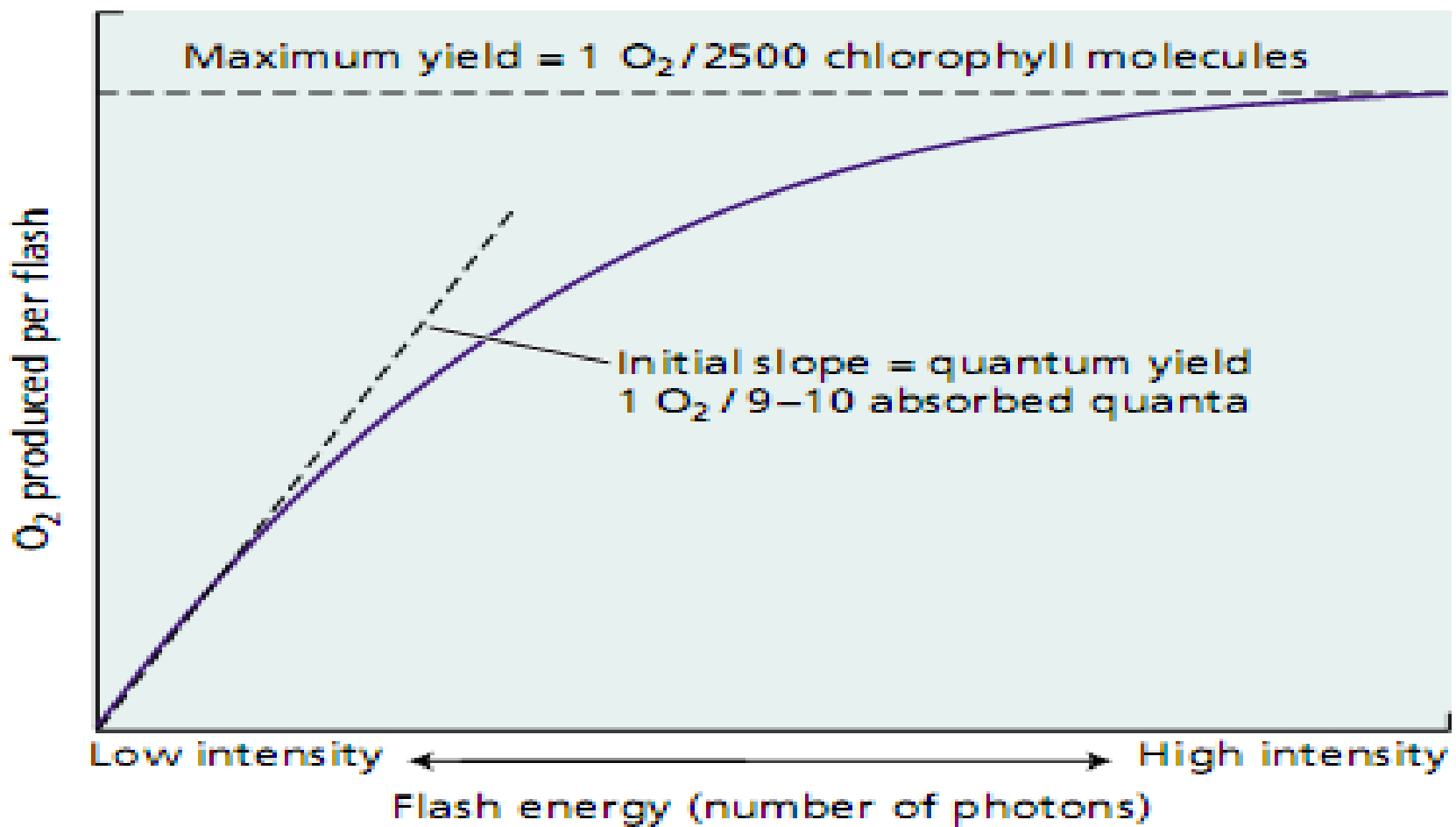
In the lowest excited state, the excited chlorophyll has four alternative pathways for disposing of its available energy.

1. Excited chlorophyll can re-emit a photon and thereby return to its ground state—a process known as fluorescence. When it does so, the wavelength of fluorescence is slightly longer (and of lower energy) than the wavelength of absorption because a portion of the excitation energy is converted into heat before the fluorescent photon is emitted. Chlorophylls fluoresce in the red region of the spectrum.
2. The excited chlorophyll can return to its ground state by directly converting its excitation energy into heat, with no emission of a photon.

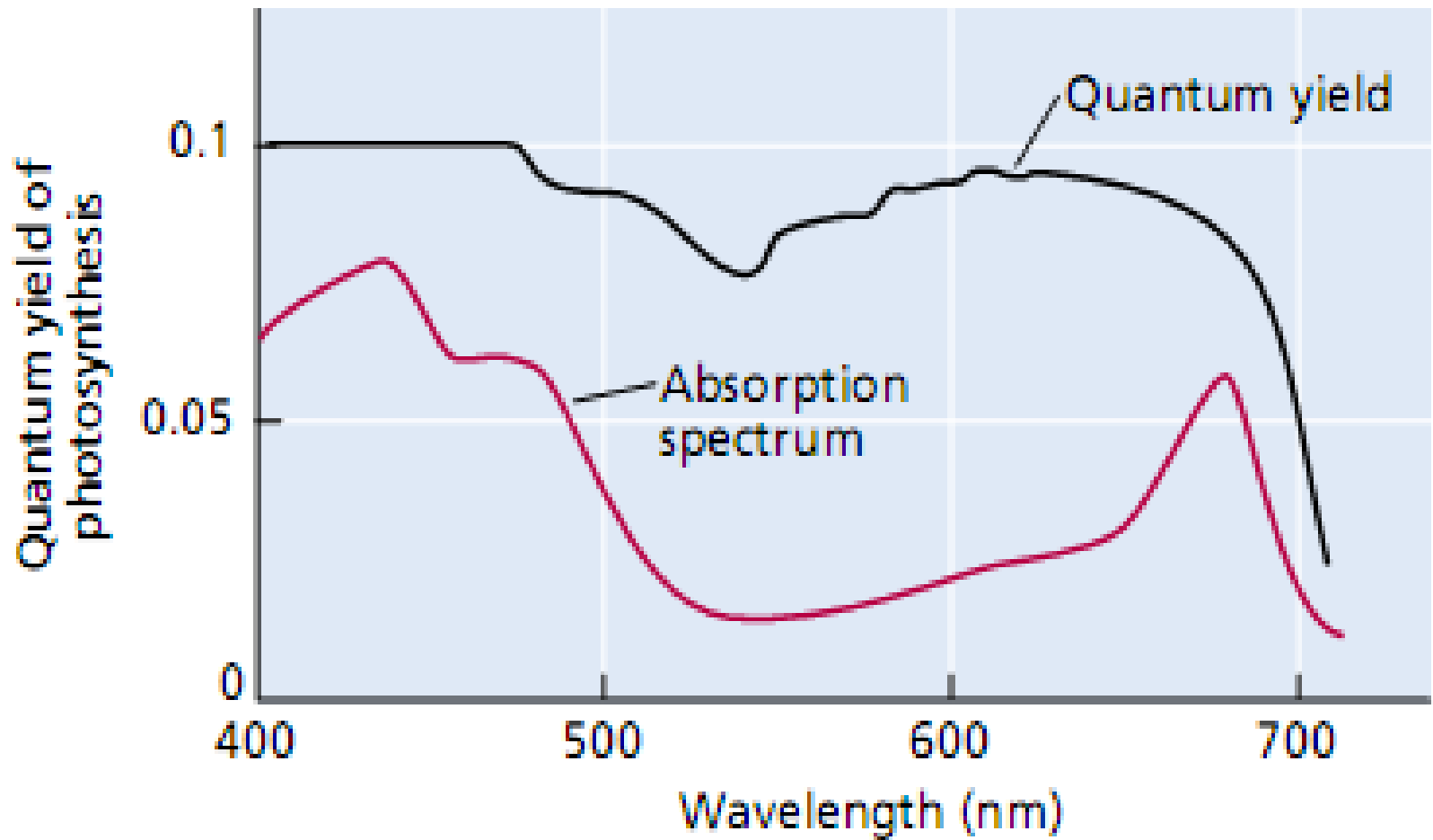
3. Chlorophyll may participate in energy transfer, during which an excited chlorophyll transfers its energy to another molecule.
4. A fourth process is photochemistry, in which the energy of the excited state causes chemical reactions to occur. The photochemical reactions of photosynthesis are among the fastest known chemical reactions. This extreme speed is necessary for photochemistry to compete with the three other possible reactions of the excited state just described.



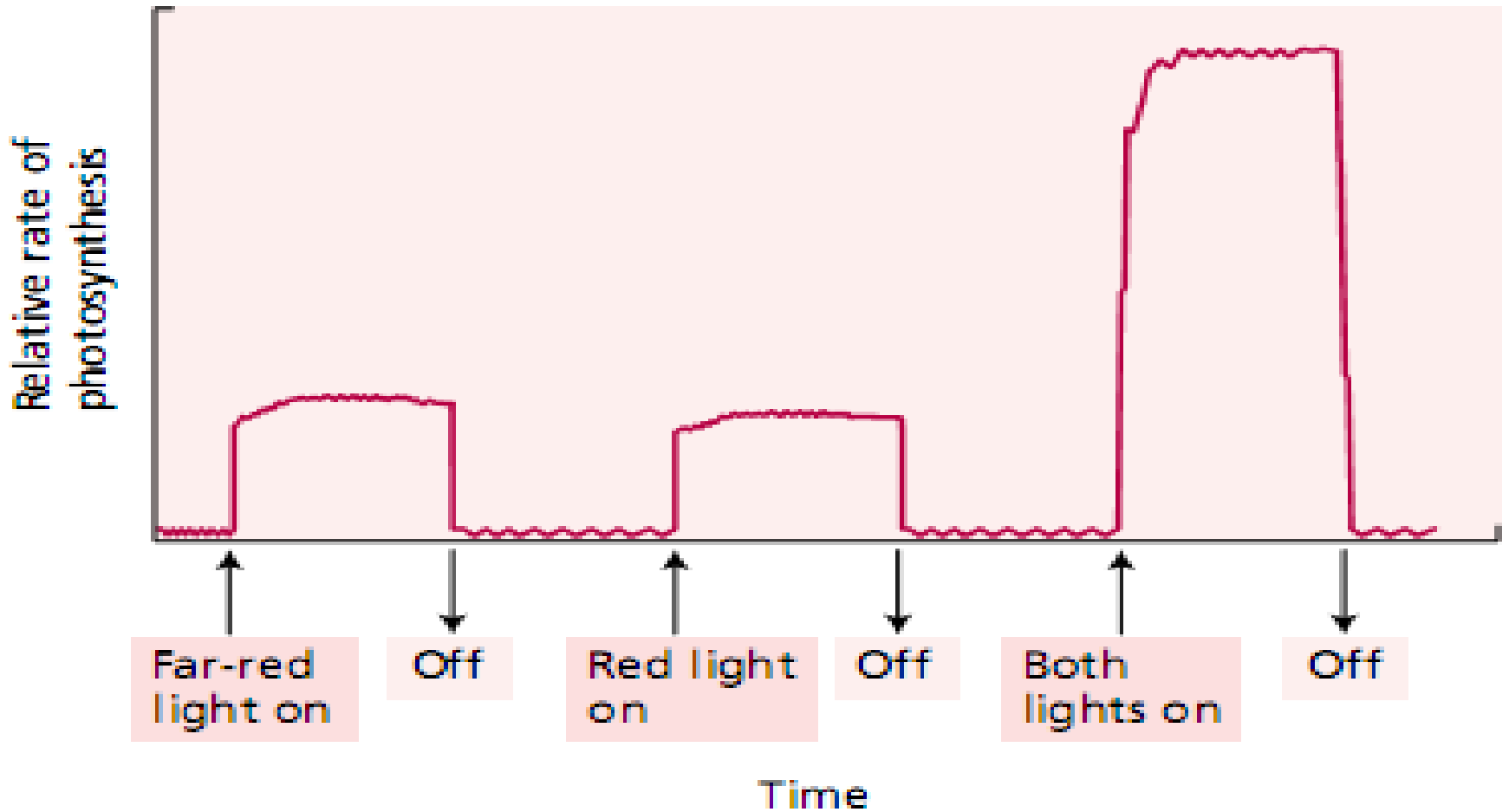
$$\Phi = \frac{\text{Number of photochemical products}}{\text{Total number of quanta absorbed}}$$



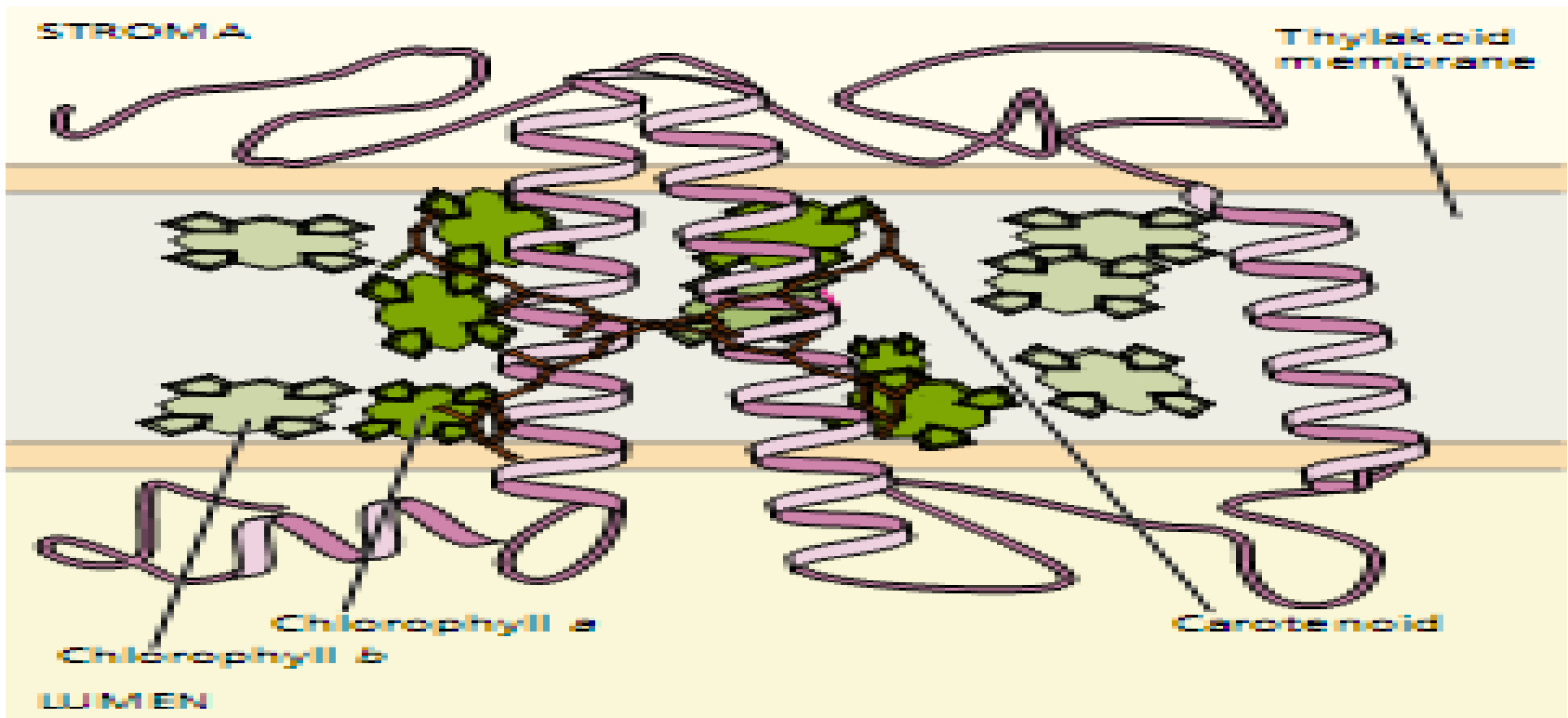
Red drop effect



Enhancement effect

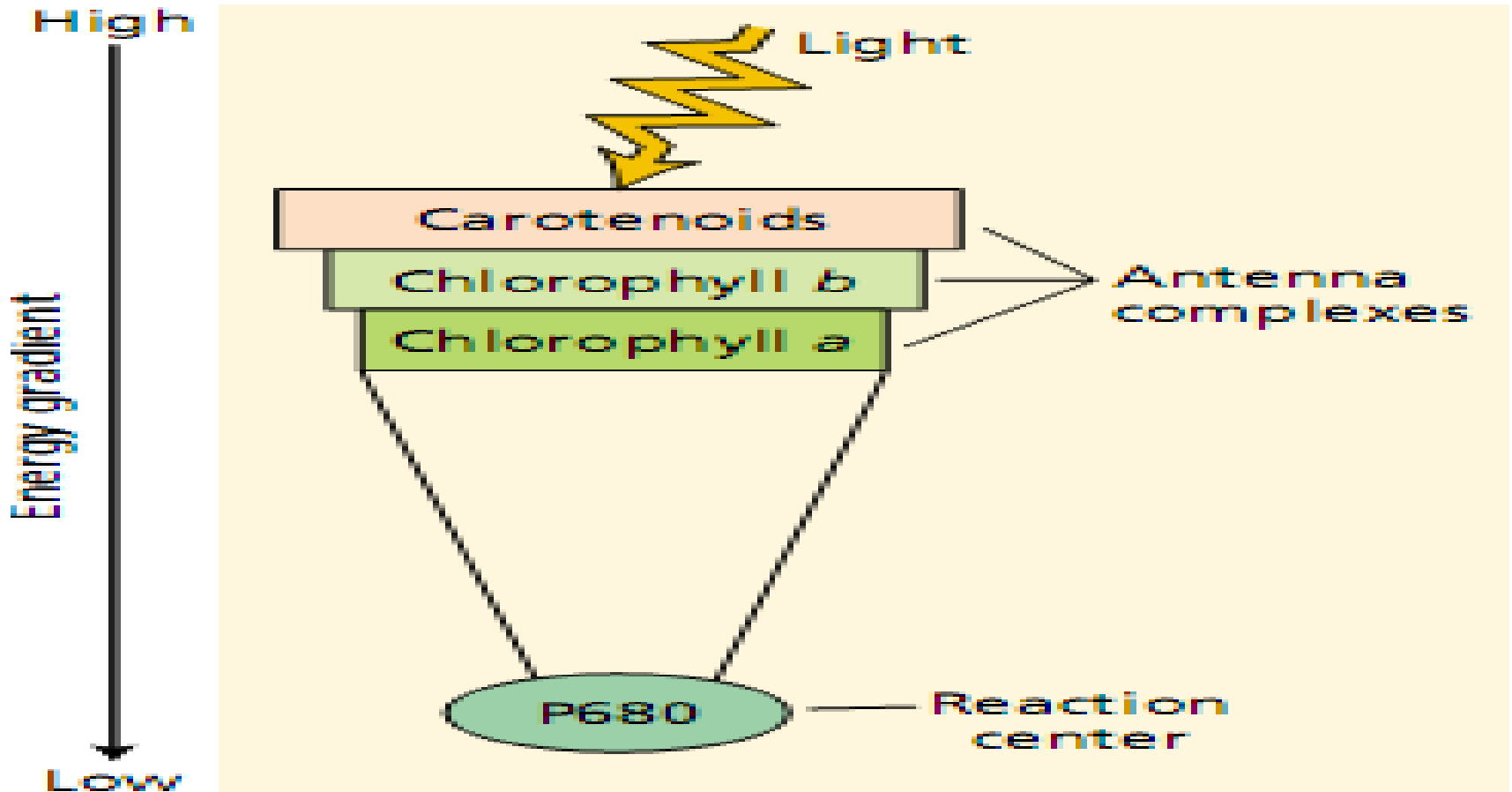


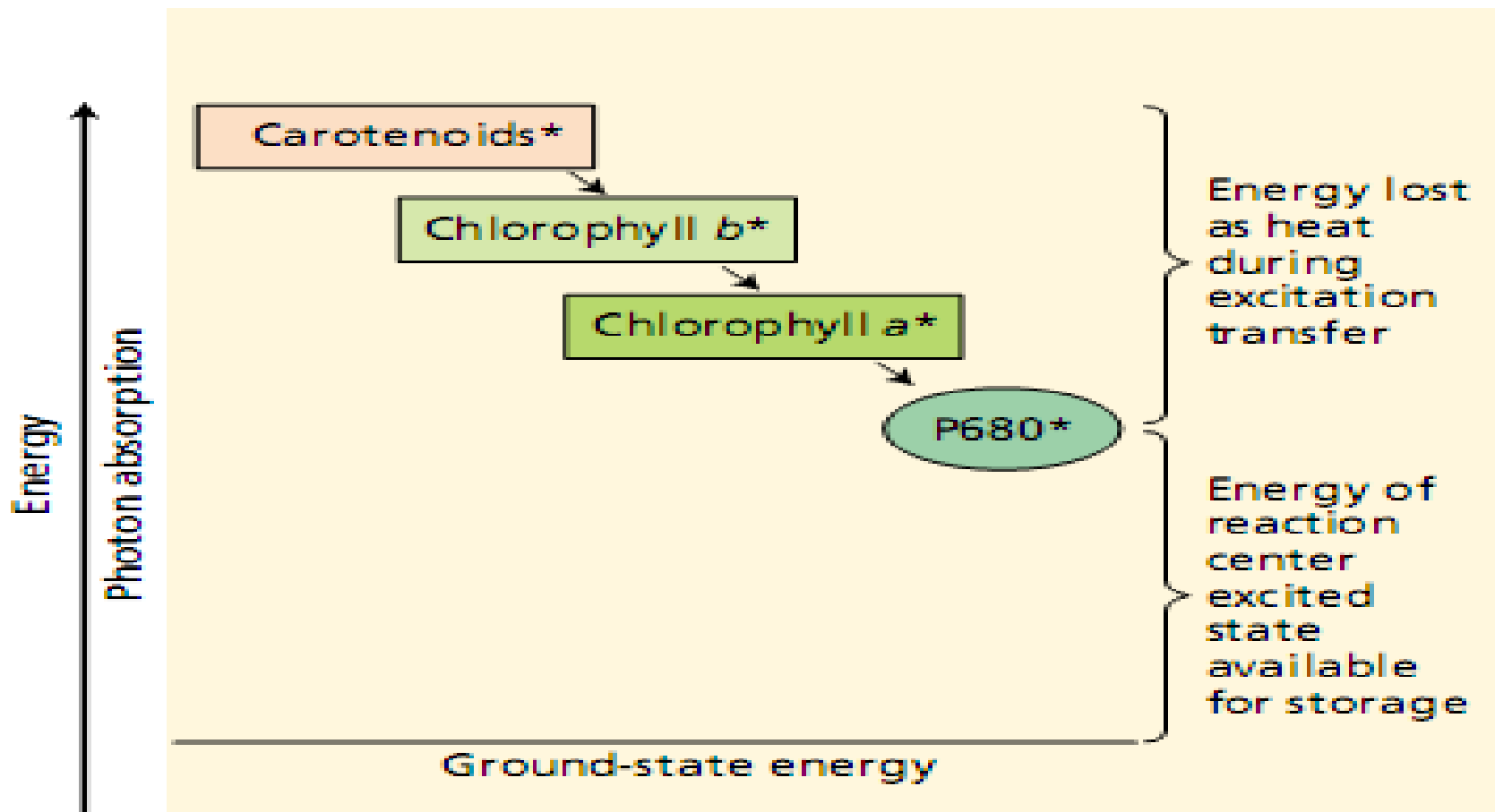
2D view of the LHCII antenna complex from higher plants, determined by a combination of EM and electron crystallography. The antenna complex is a transmembrane pigment protein, with 3 helical regions that cross the nonpolar part of the membrane. Approximately 15 chlorophyll *a* and *b* molecules are associated with the complex, as well as several carotenoids. Two of the carotenoids form an X in the middle of the complex. In the membrane, the complex is trimeric and aggregates around the periphery of the PSII



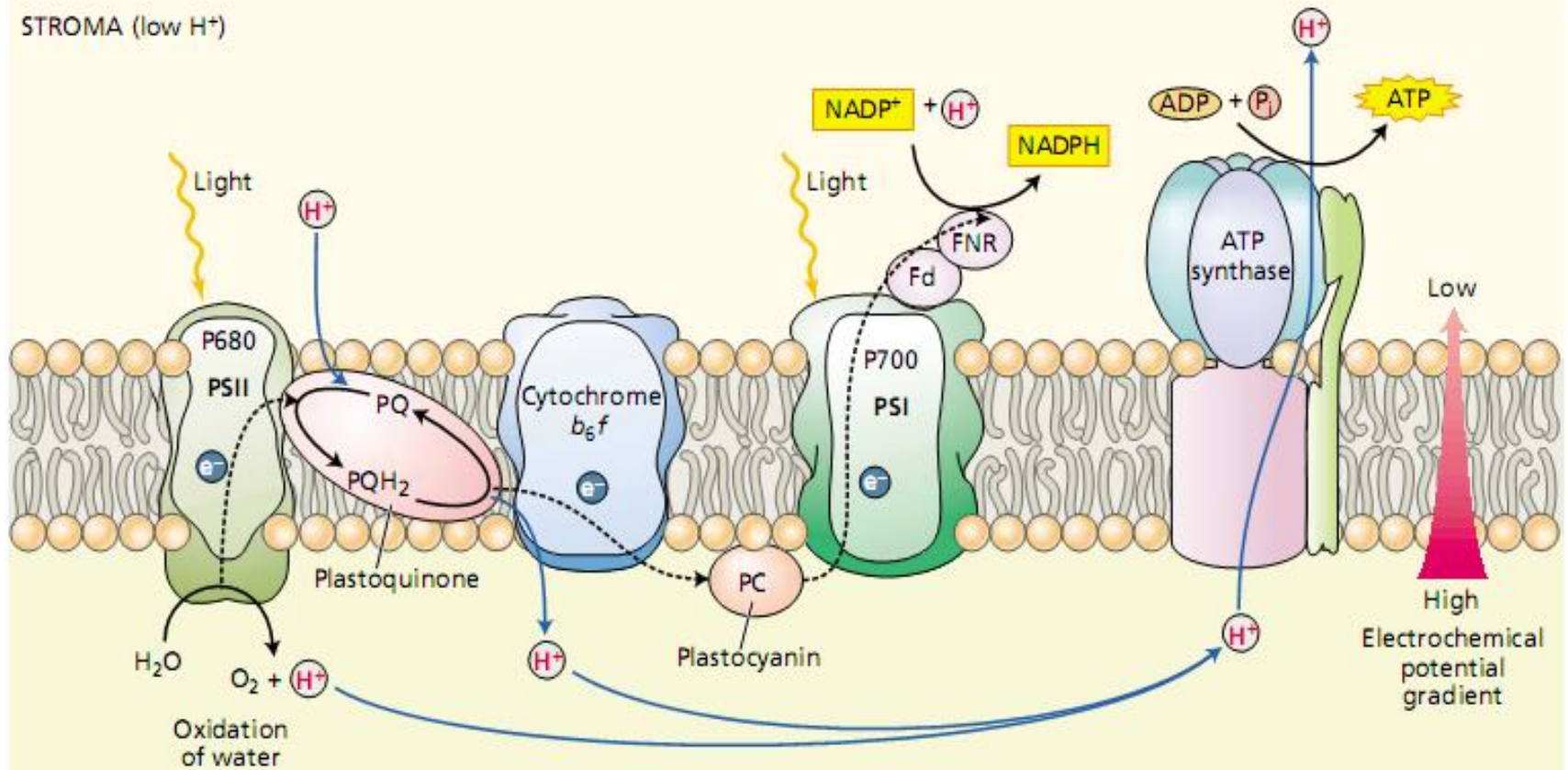
- In all eukaryotic photosynthetic organisms that contain both chlorophyll *a* and chlorophyll *b*, the most abundant antenna proteins are members of a large family of structurally related proteins.
- Some of these proteins are associated primarily with photosystem II and are called light-harvesting complex II (LHCII) proteins;
- others are associated with photosystem I and are called *LHCI* proteins.
- These antenna complexes are also known as chlorophyll *a/b* antenna proteins
- The structure of one of the LHCII proteins has been determined by a combination of electron microscopy and electron crystallography. The protein contains three α -helical regions and binds about 15 chlorophyll *a* and *b* molecules, as well as a few carotenoids. Only some of these pigments are visible in the resolved structure.
- The structure of the LHCI proteins has not yet been determined but is probably similar to that of the LHCII proteins. All of these proteins have significant sequence similarity and are almost certainly descendants of a common ancestral protein

Funneling of the excitation from the antenna system towards the reaction centre





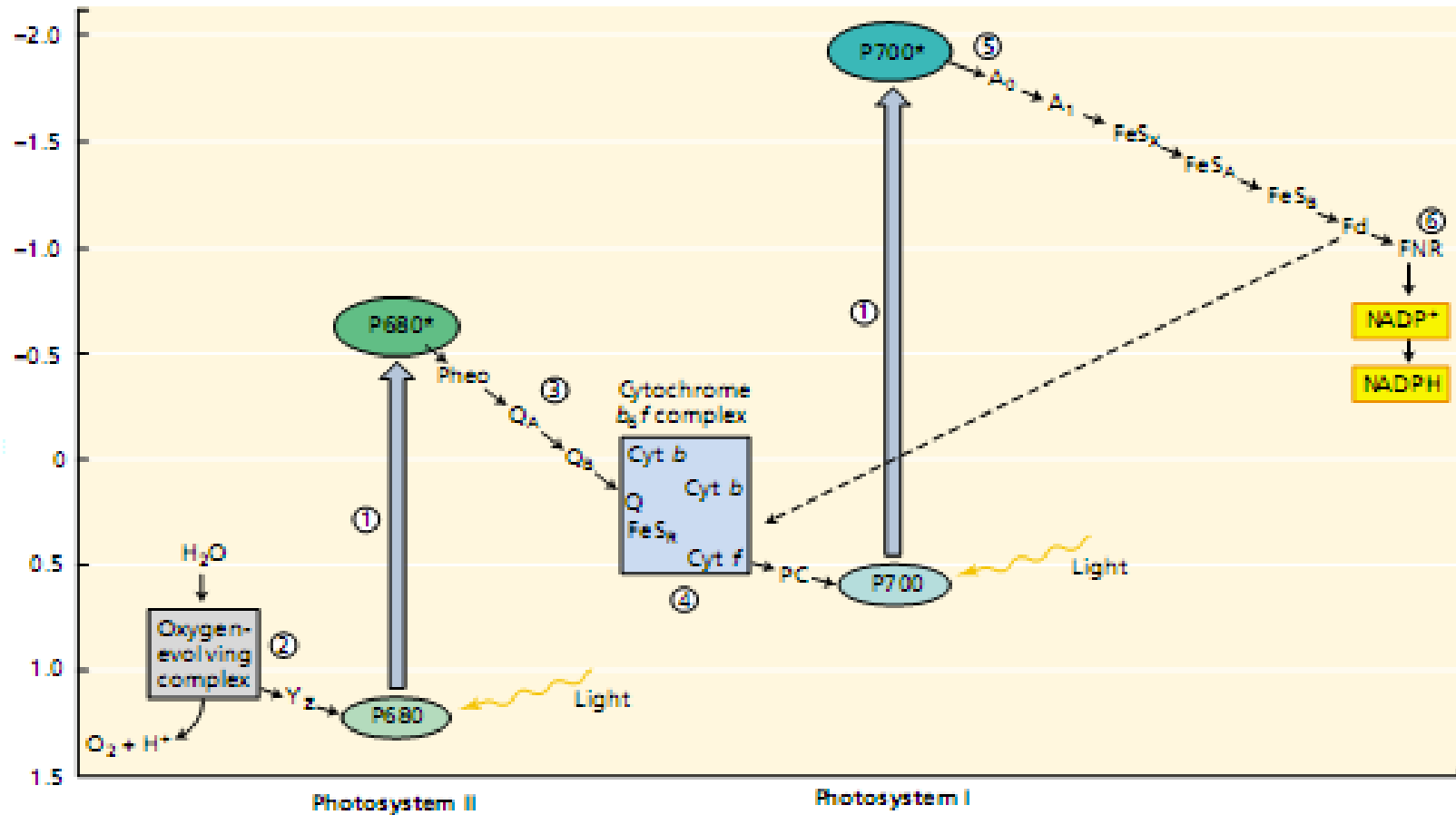
STROMA (low H^+)



LUMEN (high H^+)

- Photosystem II oxidizes water to O_2 in the thylakoid lumen and in the process releases protons into the lumen.
- Cytochrome b_6f receives electrons from PSII and delivers them to PSI. It also transports additional protons into the lumen from the stroma.
- Photosystem I reduces $NADP^+$ to NADPH in the stroma by the action of ferredoxin (Fd) and the flavo-protein ferredoxin–NADP reductase (FNR).
- ATP synthase produces ATP as protons diffuse back through it from the lumen into the stroma.

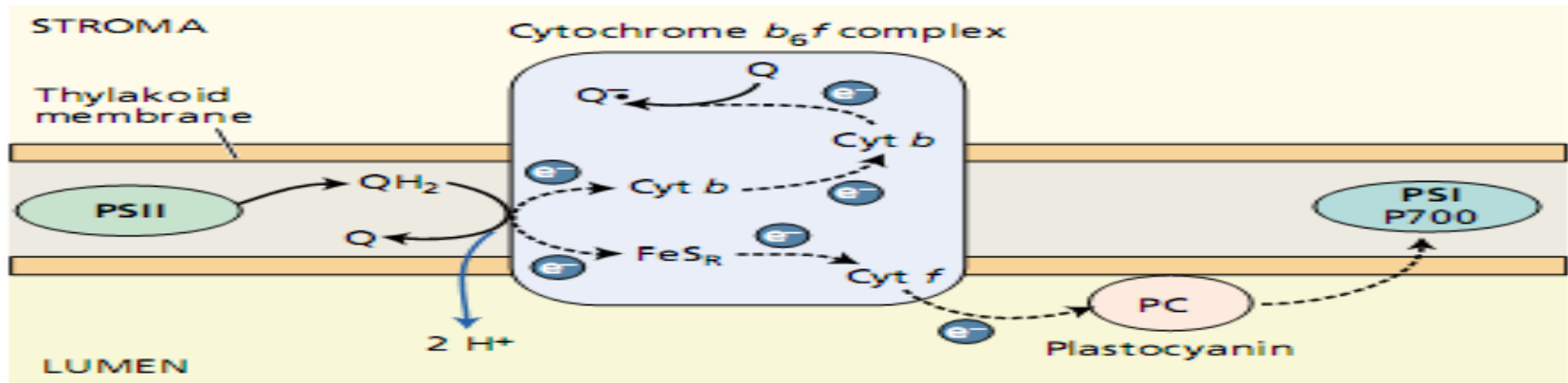
Detailed Z scheme for oxygen evolving photosynthetic organisms



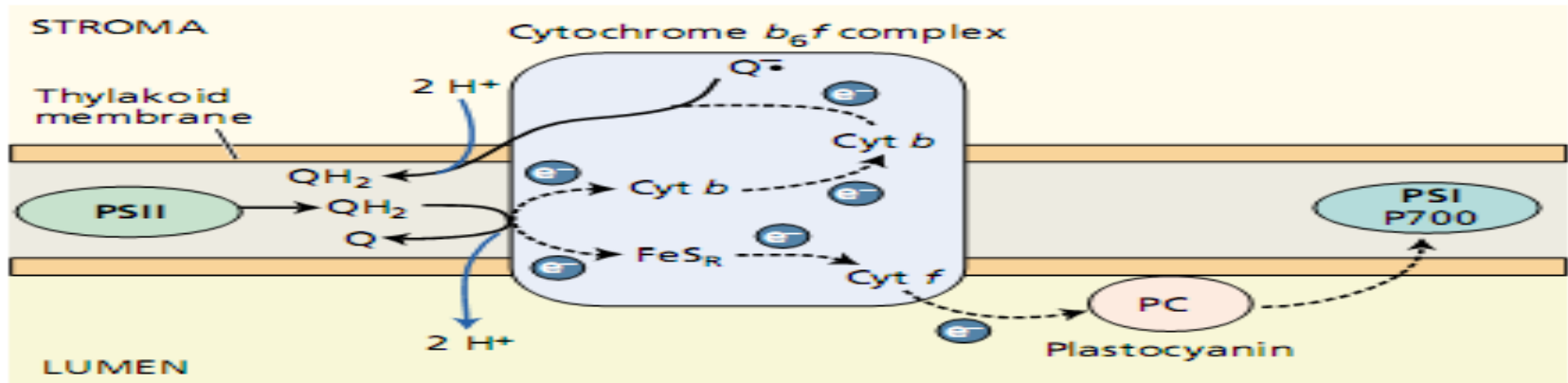
- The excited PSII reaction center chlorophyll, P680*, transfers an electron to pheophytin (Pheo).
- On the oxidizing side of PSII (to the left of the arrow joining P680 with P680*), P680 oxidized by light is re-reduced by Yz that has received electrons from oxidation of water.
- On the reducing side of PSII (to the right of the arrow joining P680 with P680*), pheophytin transfers electrons to the acceptors QA and QB, which are plastoquinones.
- The cytochrome *bf* complex transfers electrons to plastocyanin (PC), a soluble protein, which in turn reduces P700 (oxidized P700).
- The acceptor of electrons from P700* (A0) is thought to be a chlorophyll, and the next acceptor (A1) is a quinone.
- A series of membrane-bound iron–sulfur proteins (FeSX, FeSA, and FeSB) transfers electrons to soluble ferredoxin (Fd).
- The soluble flavoprotein ferredoxin–NADP reductase (FNR) reduces NADP+ to NADPH, which is used in the Calvin cycle to reduce CO2
- There is cyclic electron flow around PSI, generating ATP

Mechanism of electron and proton transfer in the cytochrome b_6f complex

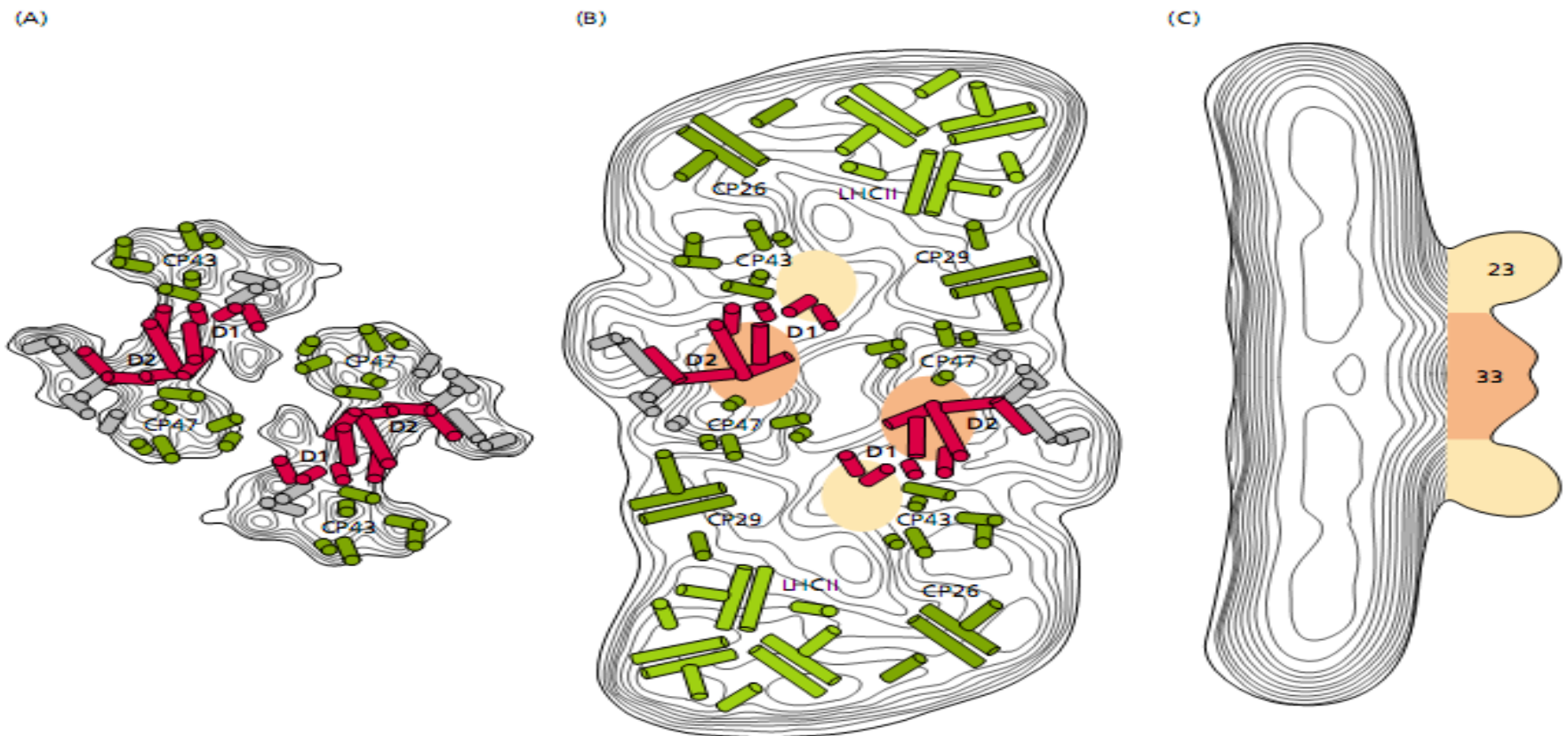
(A) First QH_2 oxidized



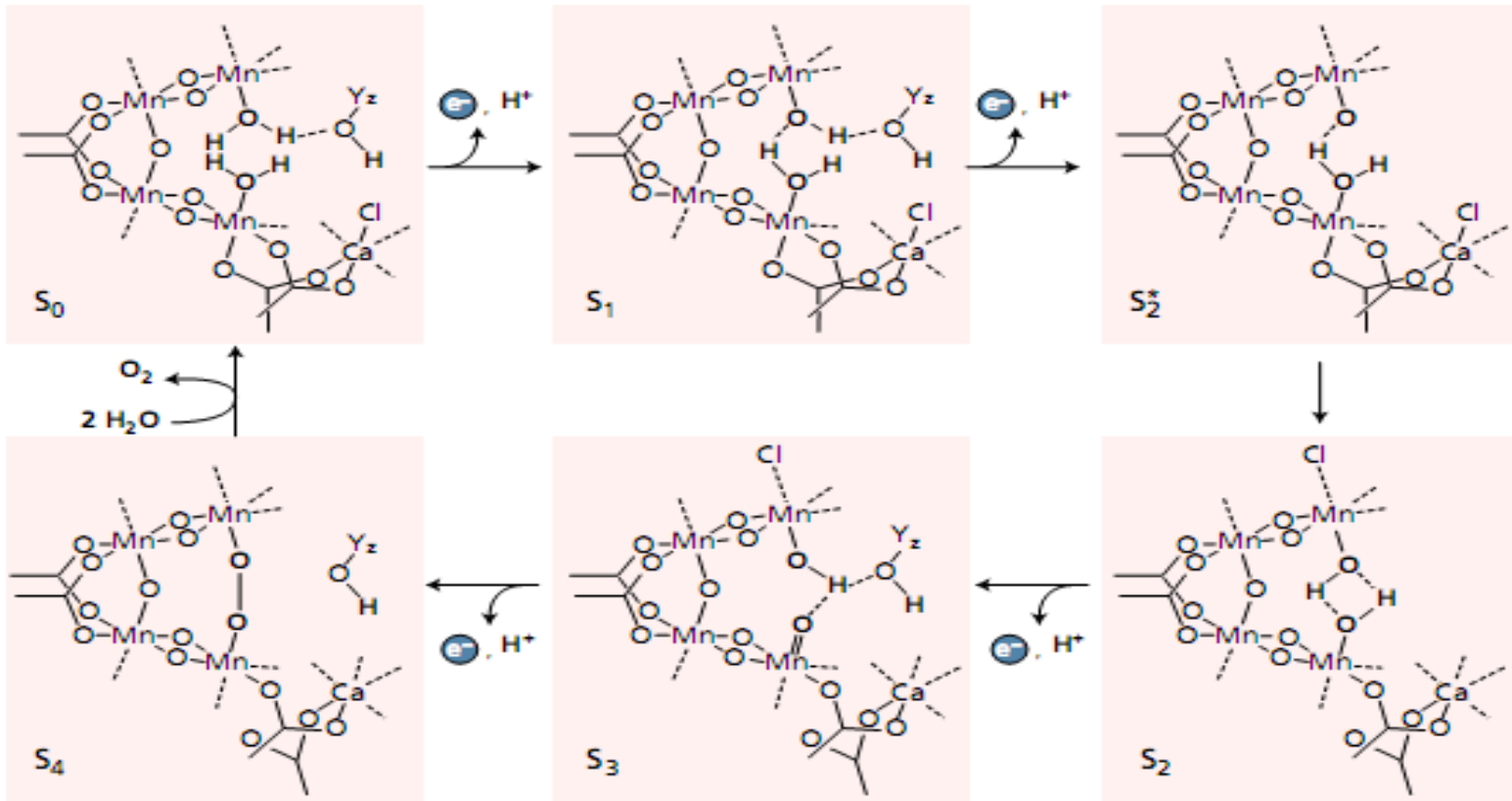
(B) Second QH_2 oxidized



Structure of dimeric multisubunit protein supercomplex of photosystem II from higher plants, as determined by electron microscopy. The figure shows two complete reaction centers, each of which is a dimeric complex. (A) Helical arrangement of the D1 and D2 (red) and CP43 and CP47 (green) core subunits. (B) View from the luminal side of the supercomplex, including additional antenna complexes, LHClI, CP26 and CP29, and extrinsic oxygen-evolving complex, shown as orange and yellow circles. Unassigned helices are shown in gray. (C) Side view of the complex illustrating the arrangement of the extrinsic proteins of the OEC-evolving

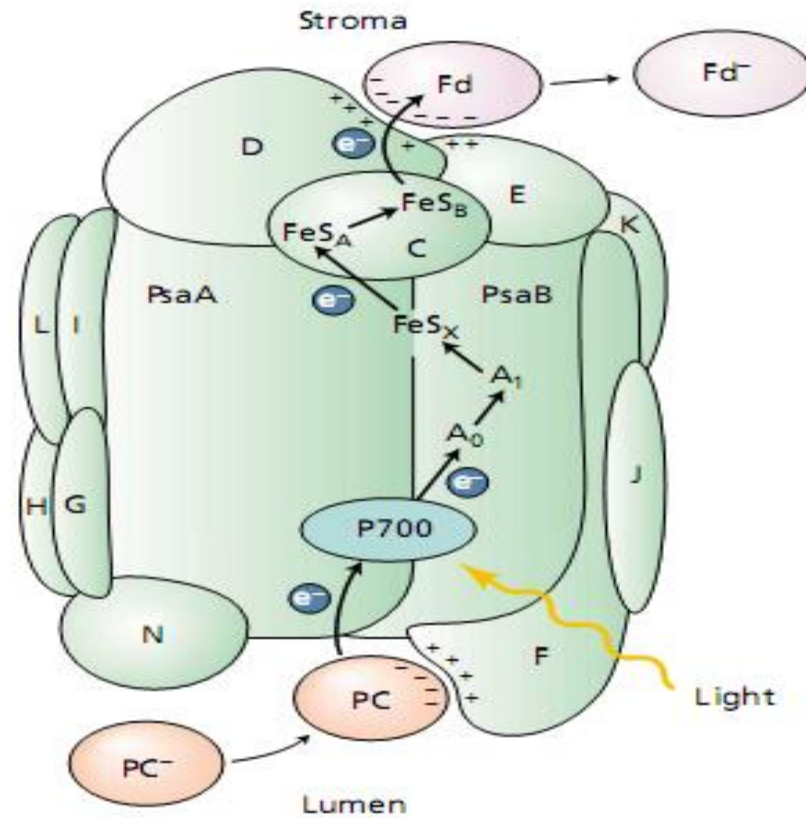


Model of the S state cycle of oxygen evolution in PSII.

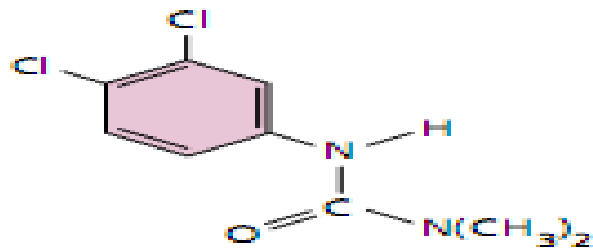


Structure of PSI

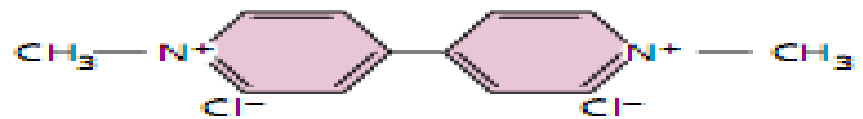
(A)



(A)

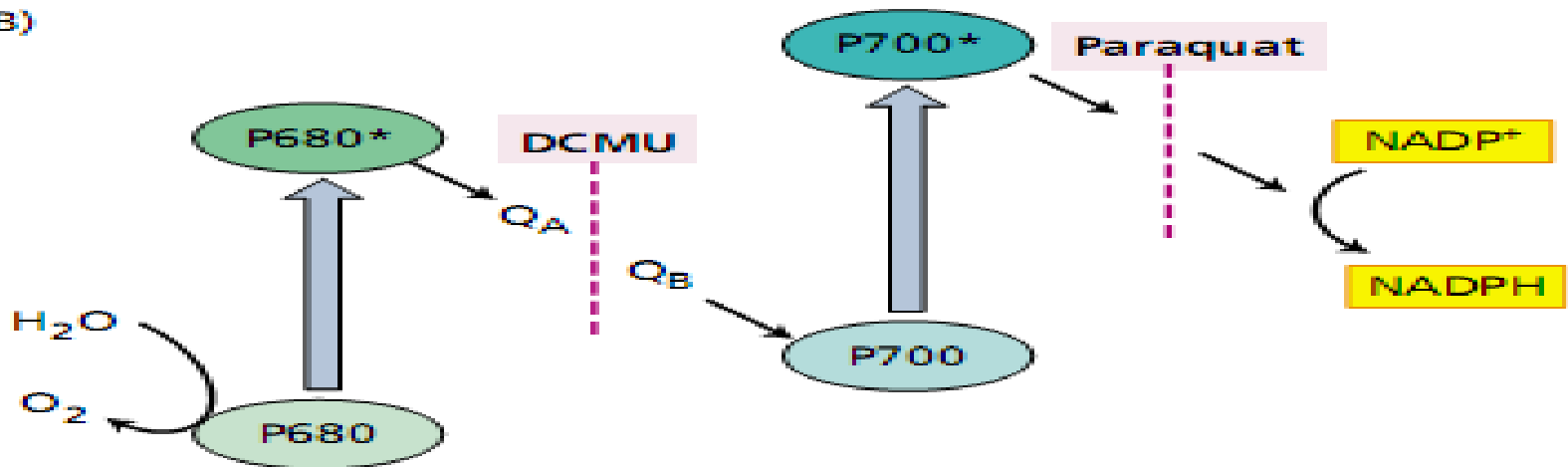


DCMU (diuron)
(dichlorophenyl-dimethylurea)

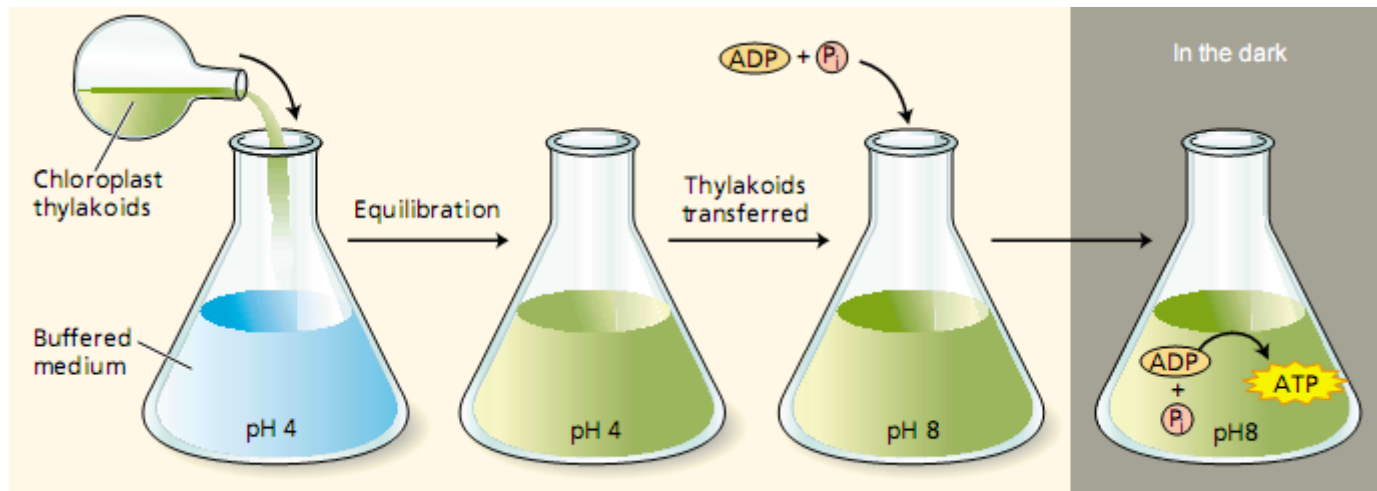


Paraquat
(methyl viologen)

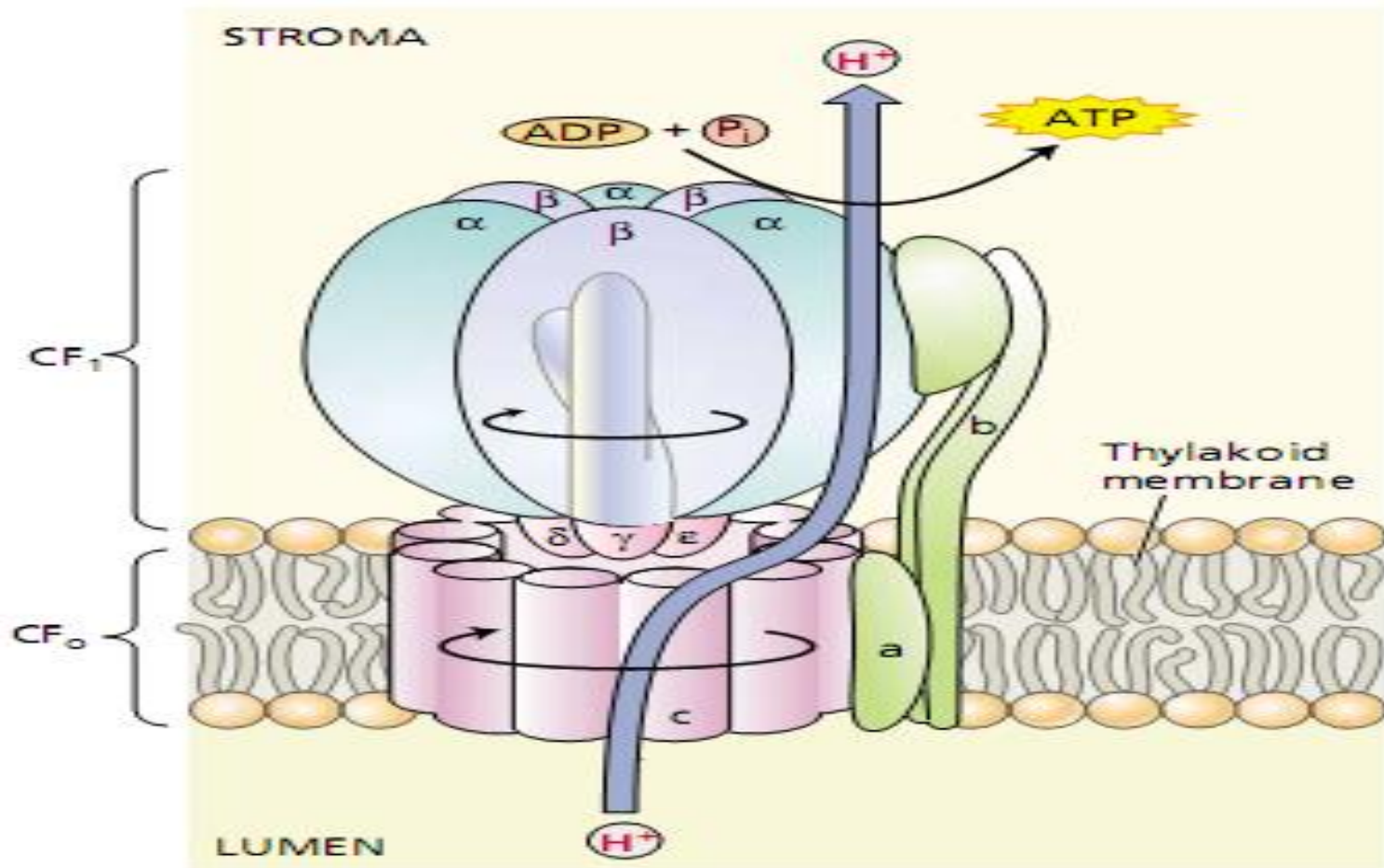
(B)

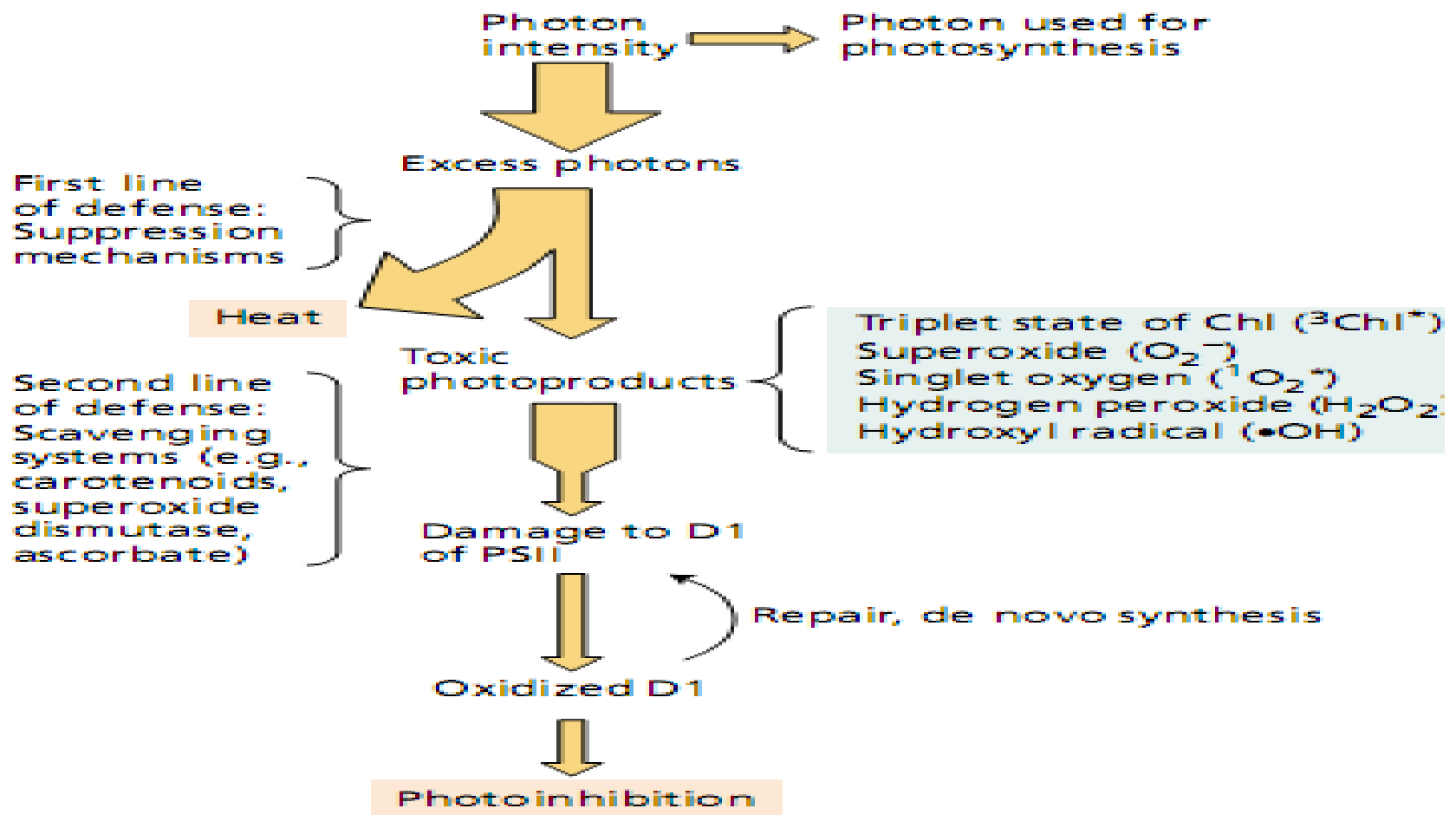


Experiment of Jagendorf and coworkers

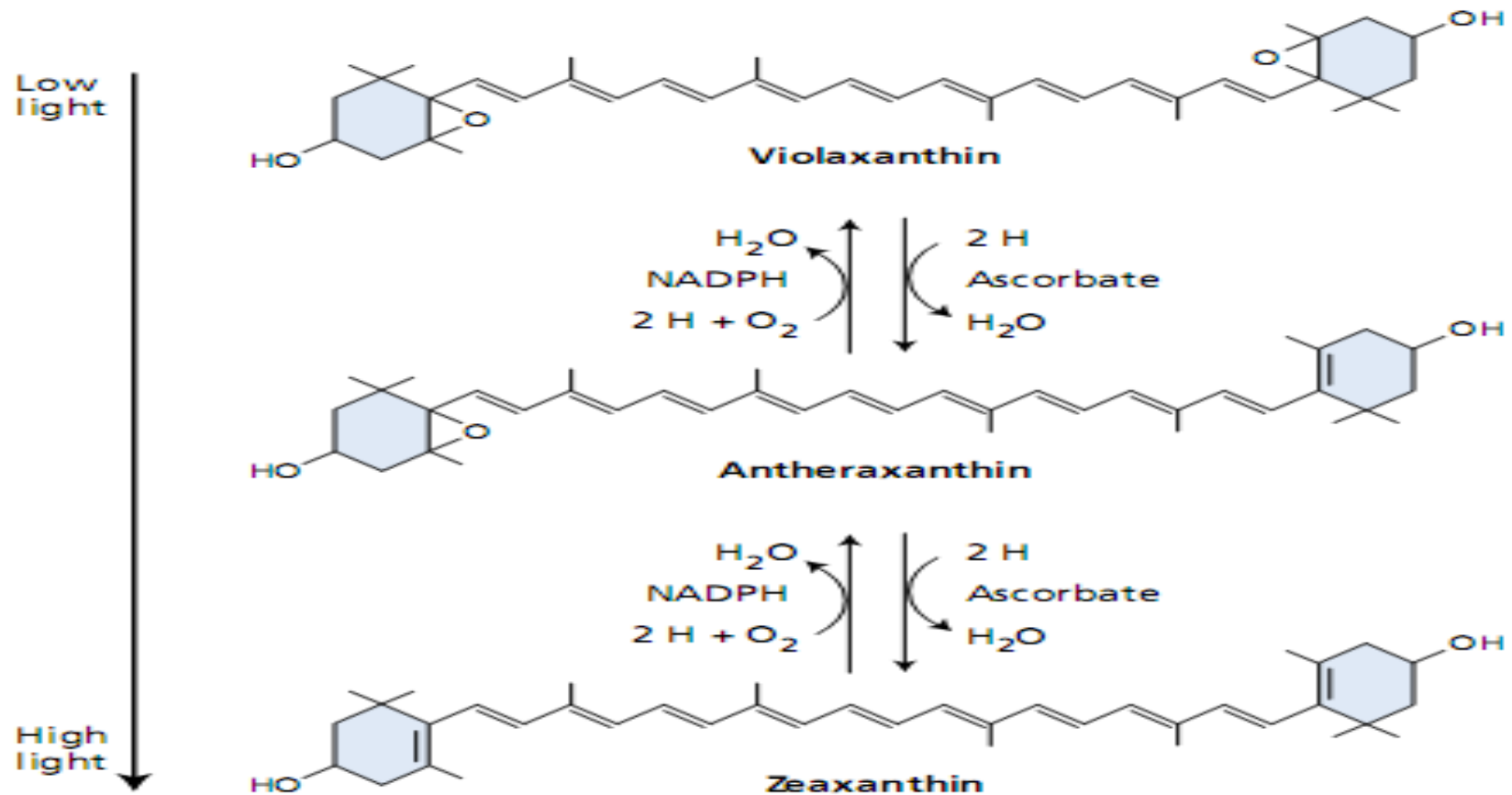


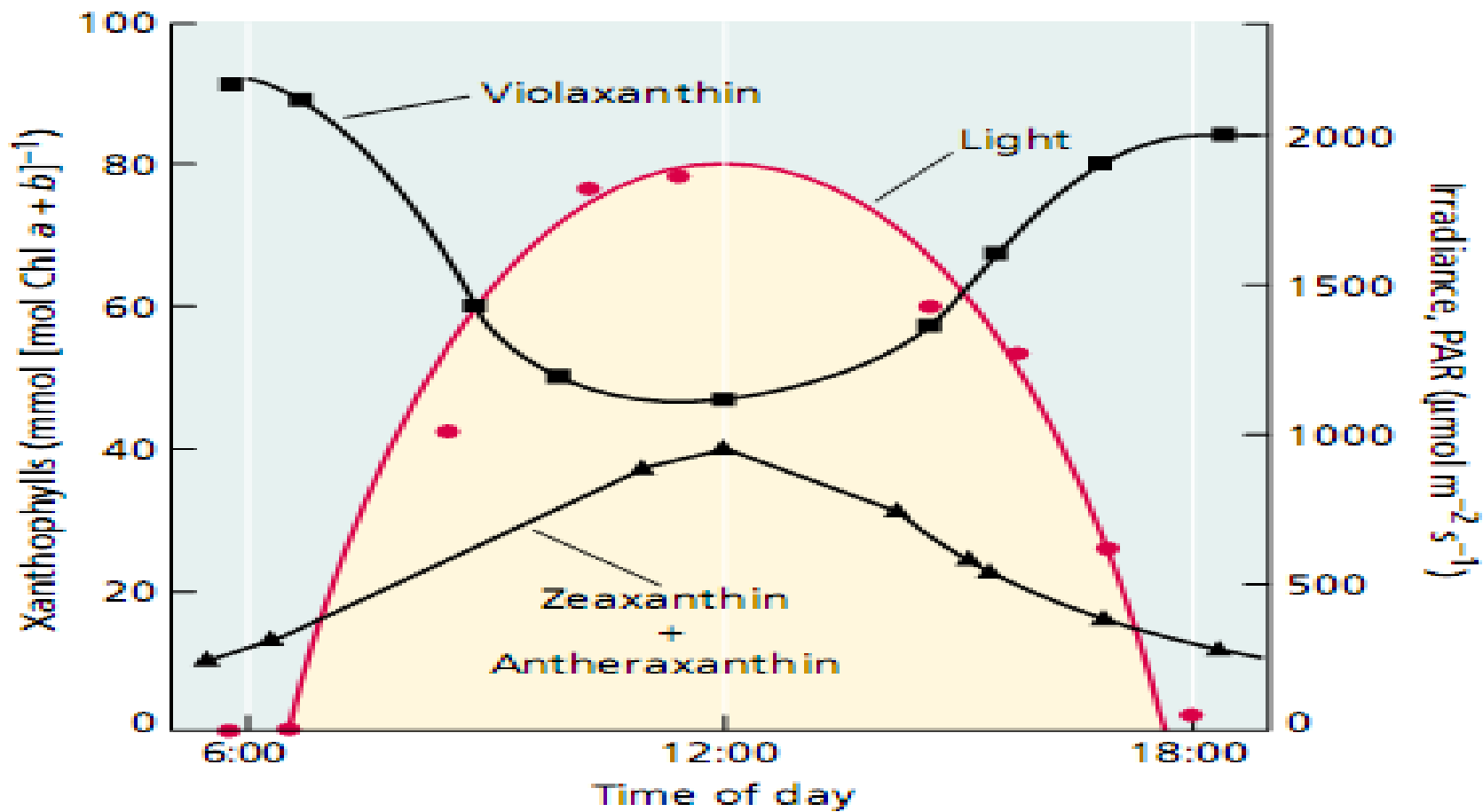
Structure of ATP synthase

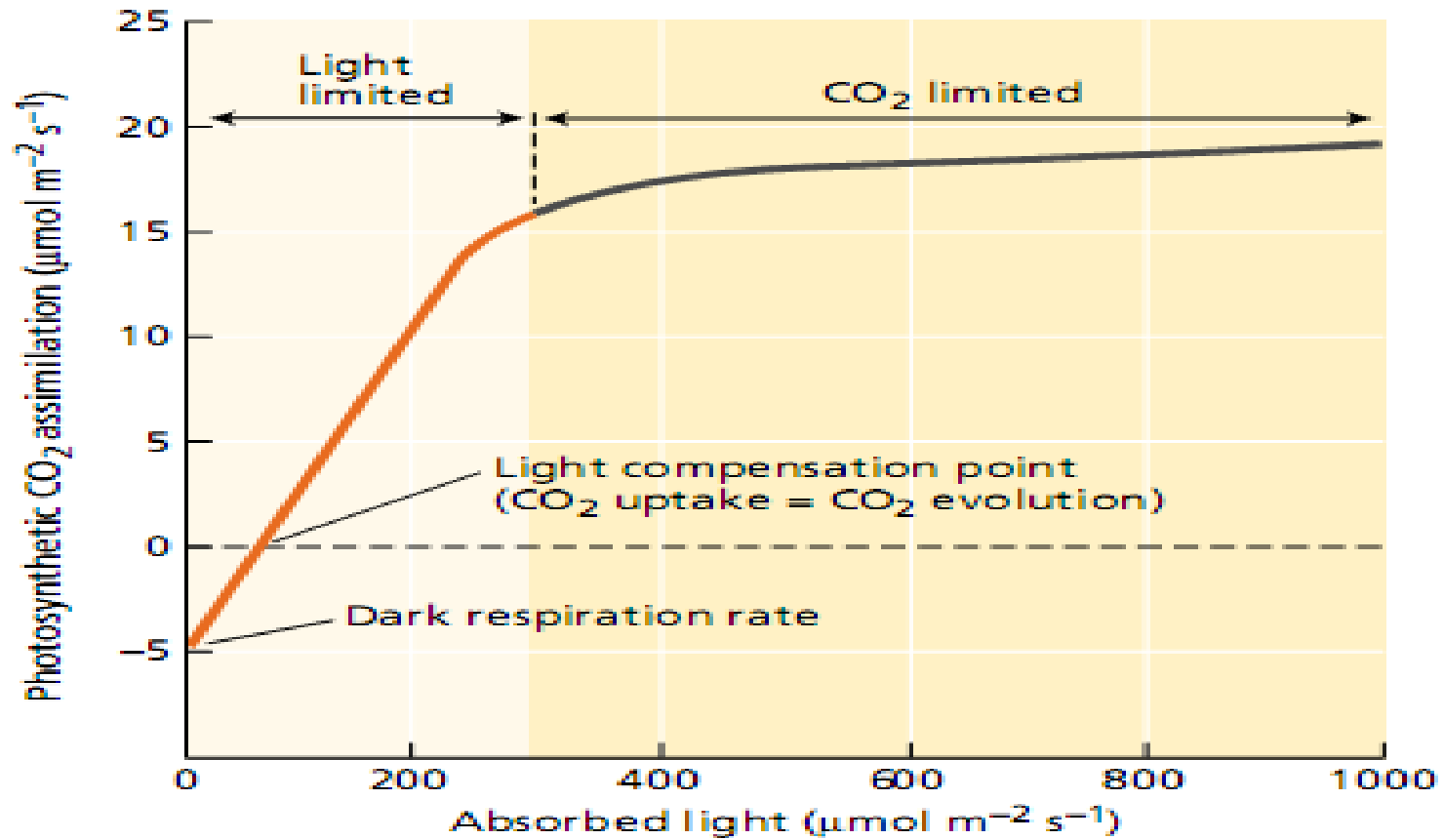


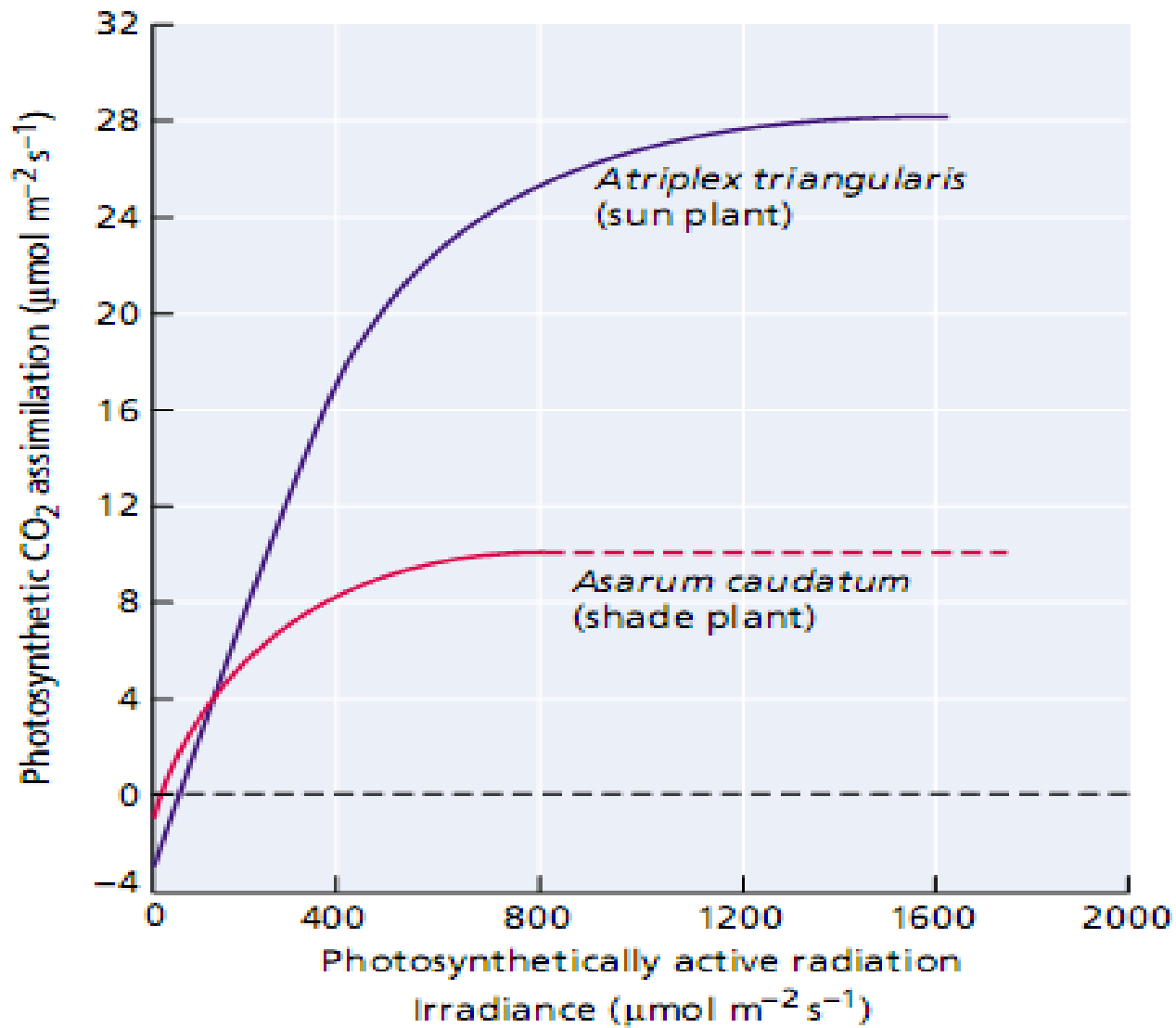


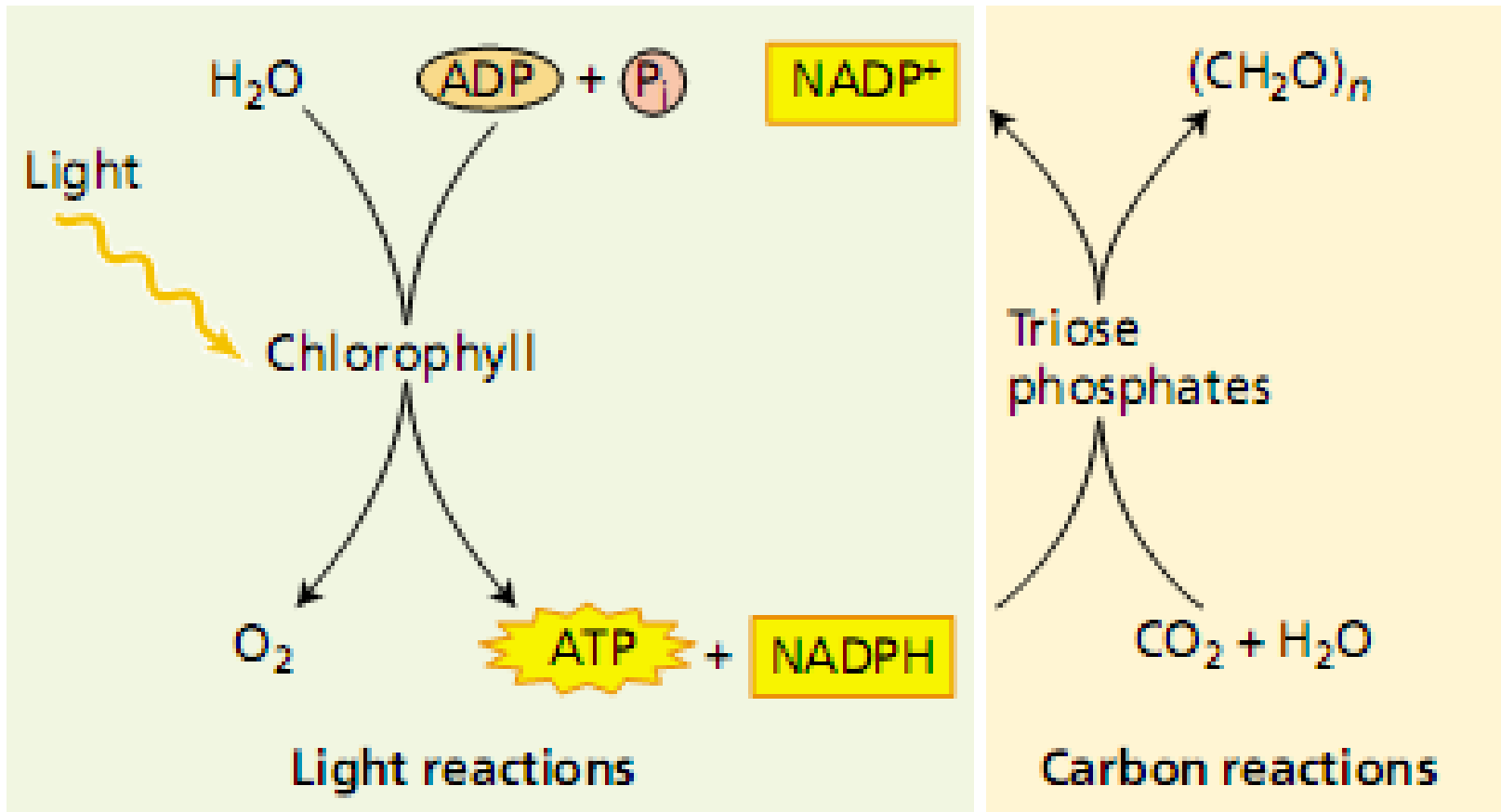
In high light, violaxanthin is converted into zeaxanthin, via the intermediate antheraxanthin, by the enzyme violaxanthin de-epoxidase. When light intensity decreases, the process is reversed. Binding of protons and zeaxanthin to light-harvesting antenna proteins is thought to cause conformational changes that lead to quenching and heat dissipation (Demmig-

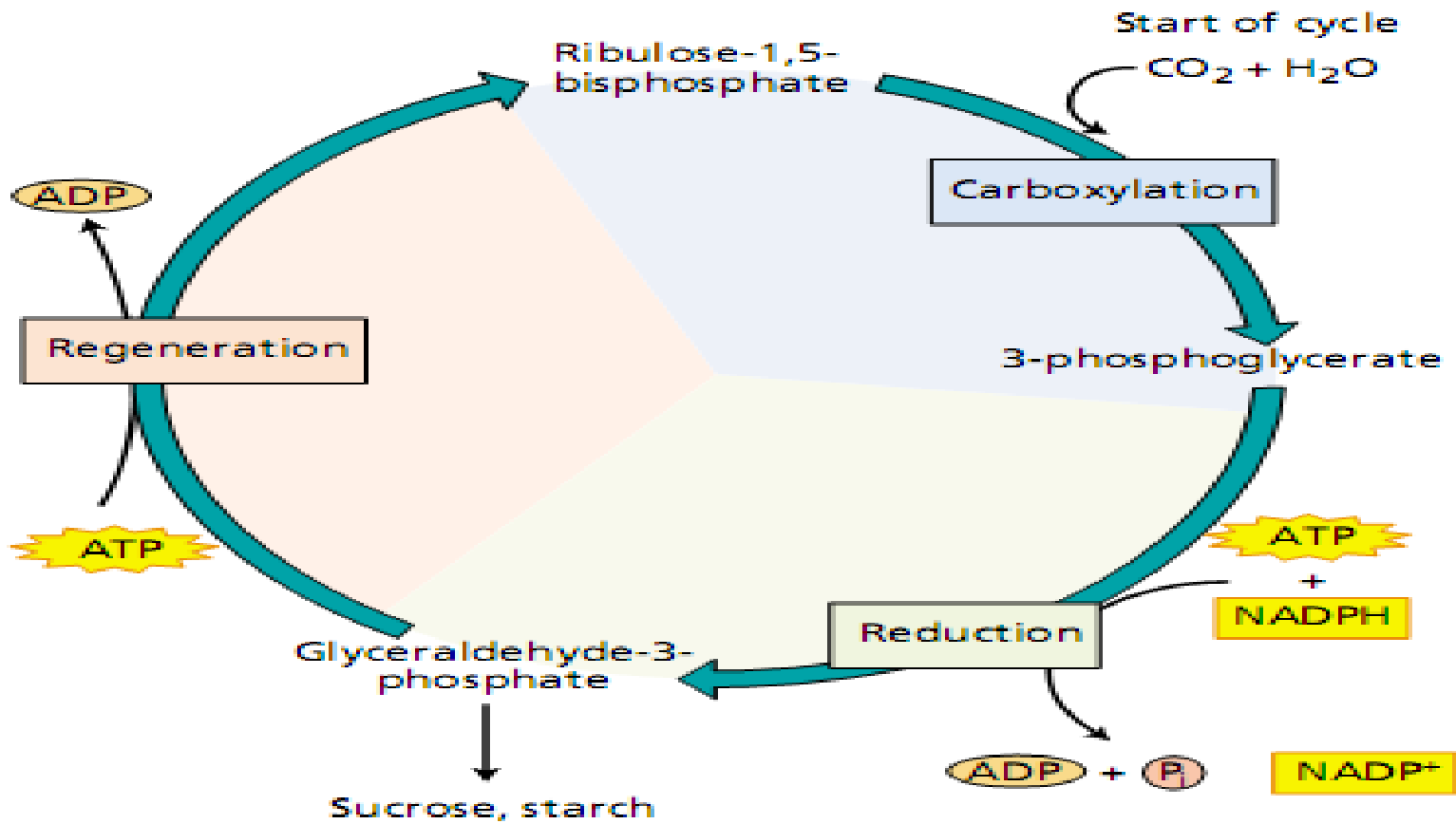


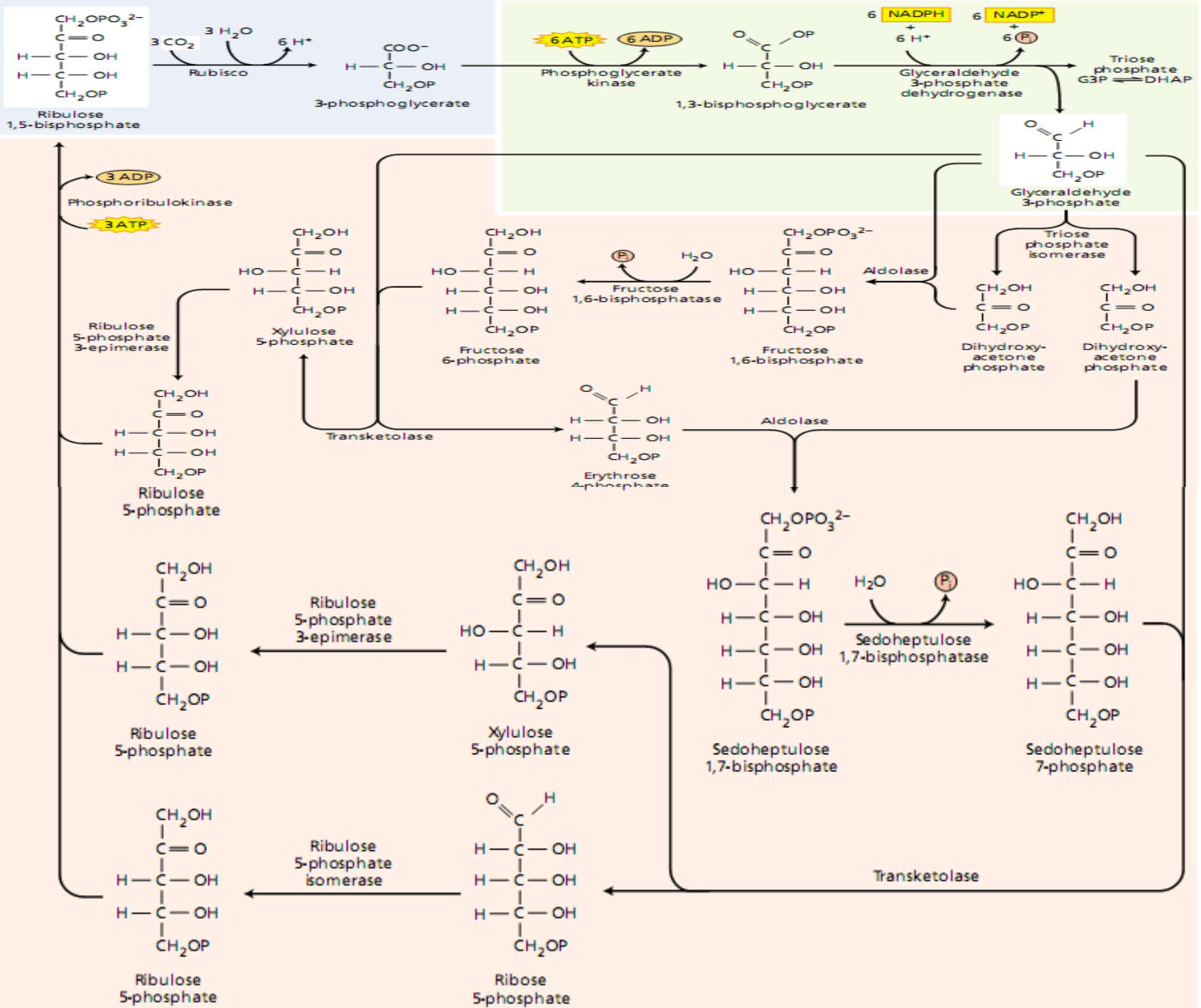






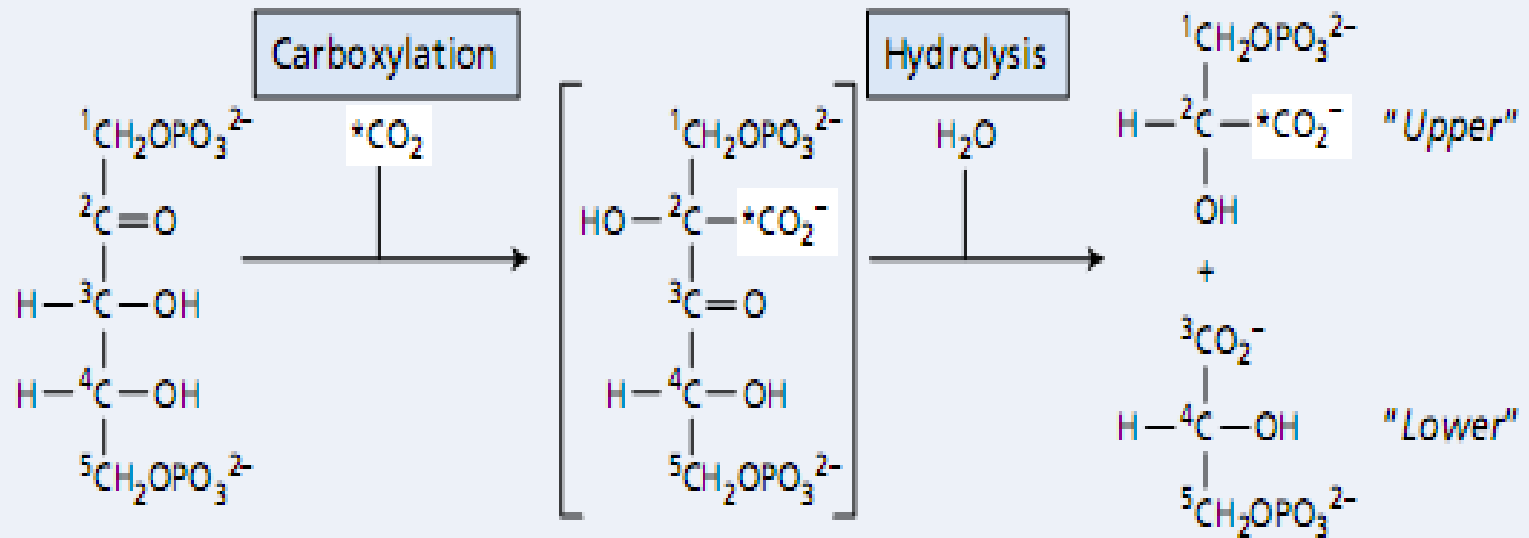






Two properties of the carboxylase reaction are especially important:

1. The negative change in free energy (see Chapter 2 on the web site for a discussion of free energy) associated with the carboxylation of ribulose-1,5-bisphosphate is large; thus the forward reaction is strongly favored.
2. The affinity of rubisco for CO_2 is sufficiently high to ensure rapid carboxylation at the low concentrations of CO_2 found in photosynthetic cells.



Ribulose-1,5-bisphosphate

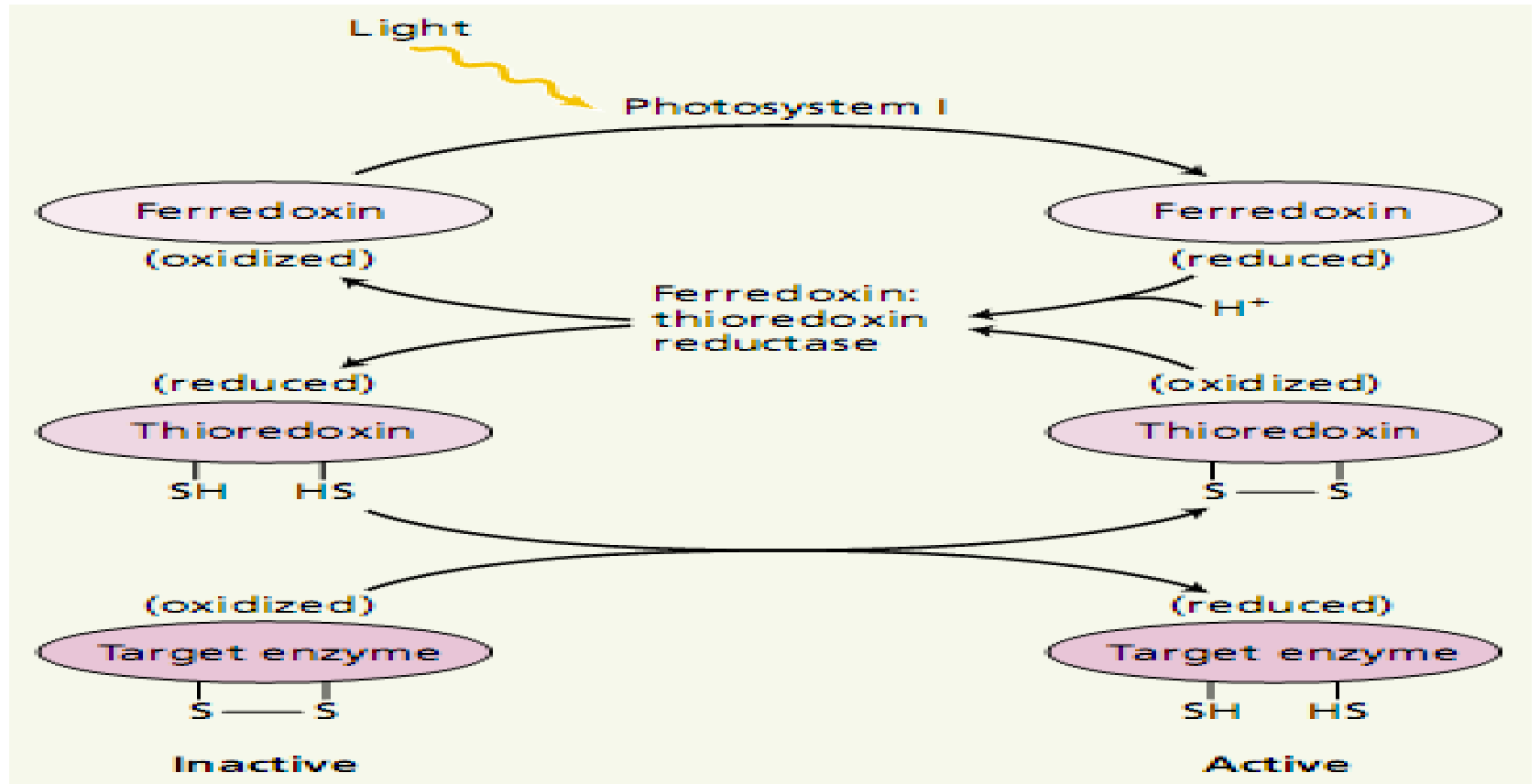
2-Carboxy-3-ketoarabinitol-1,5-bisphosphate
(a transient, unstable, enzyme-bound intermediate)

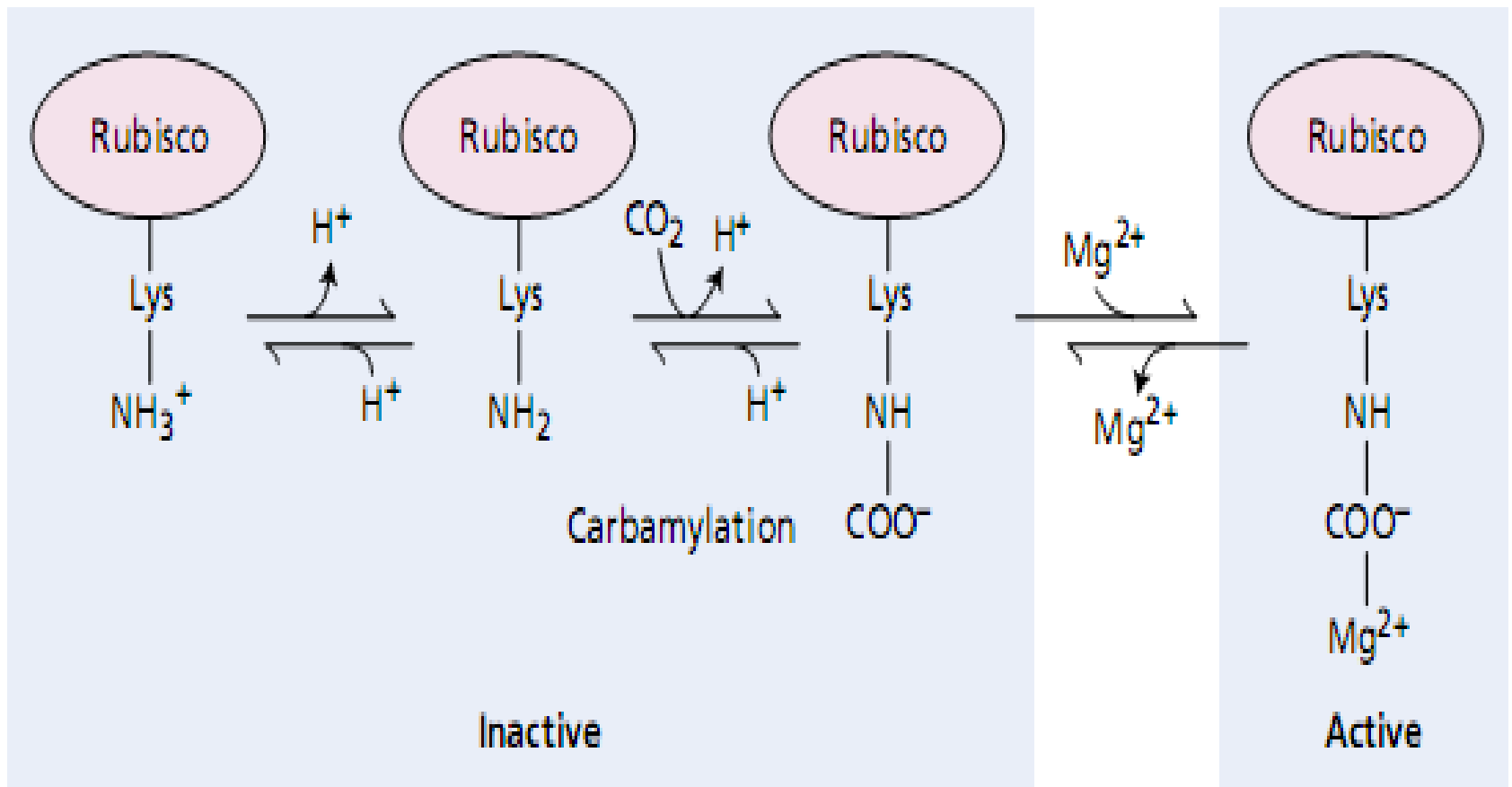
3-Phosphoglycerate

Light-Dependent Enzyme Activation Regulates the Calvin Cycle

Five light-regulated enzymes operate in the Calvin cycle:

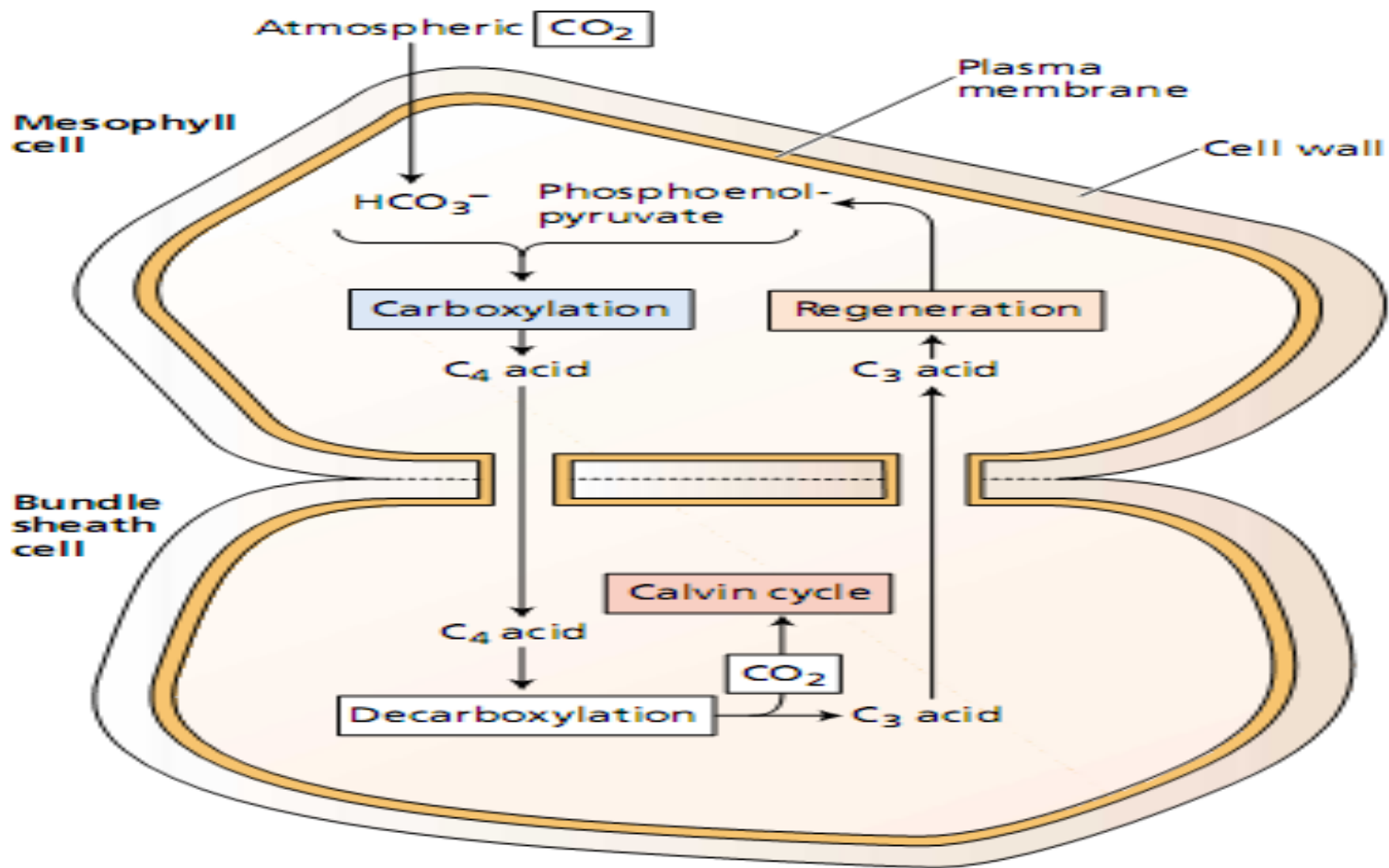
1. Rubisco
2. NADP:glyceraldehyde-3-phosphate dehydrogenase
3. Fructose-1,6-bisphosphatase
4. Sedoheptulose-1,7-bisphosphatase
5. Ribulose-5-phosphate kinase

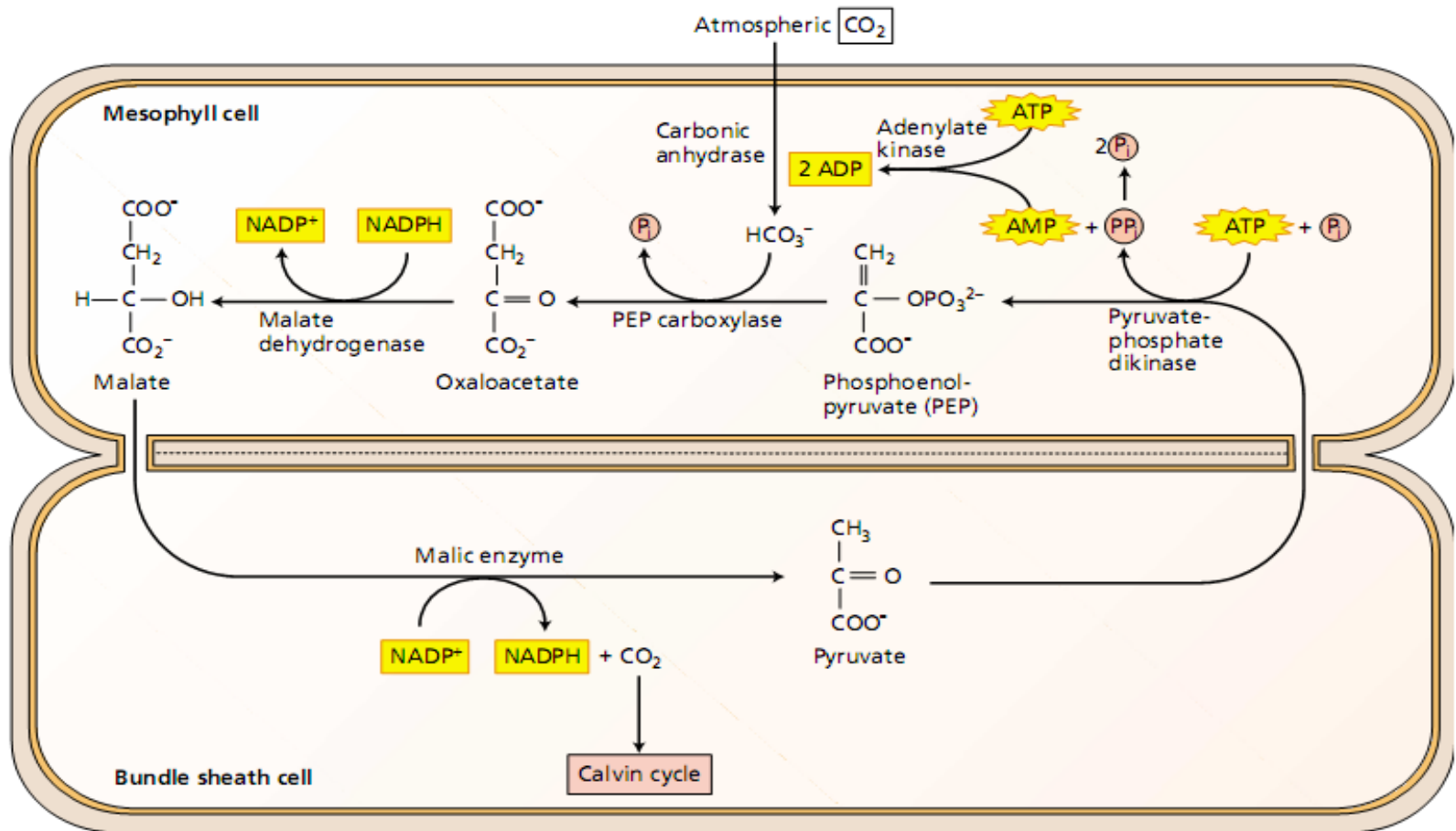




CO₂ Concentrating mechanisms

1. C₄ photosynthetic carbon fixation (C₄)
2. Crassulacean acid metabolism (CAM)
3. CO₂ pumps at the plasma membrane





The basic C_4 cycle consists of four stages:

1. Fixation of CO_2 by the carboxylation of phosphoenolpyruvate in the mesophyll cells to form a C_4 acid (malate and/or aspartate)
2. Transport of the C_4 acids to the bundle sheath cells
3. Decarboxylation of the C_4 acids within the bundle sheath cells and generation of CO_2 , which is then reduced to carbohydrate via the Calvin cycle
4. Transport of the C_3 acid (pyruvate or alanine) that is formed by the decarboxylation step back to the mesophyll cell and regeneration of the CO_2 acceptor phosphoenolpyruvate

Energetics of the C₄ photosynthetic carbon cycle

Phosphoenolpyruvate + H₂O + NADPH + CO₂ (mesophyll) → malate + NADP⁺ + P_i (mesophyll)

Malate + NADP⁺ → pyruvate + NADPH + CO₂ (bundle sheath)

Pyruvate + P_i + ATP → phosphoenolpyruvate + AMP + PP_i (mesophyll)

PP_i + H₂O → 2 P_i (mesophyll)

AMP + ATP → 2ADP

Net: CO₂ (mesophyll) + ATP + 2 H₂O → CO₂ (bundle sheath) + 2ADP + 2 P_i

Cost of concentrating CO₂ within the bundle sheath cell = 2 ATP per CO₂

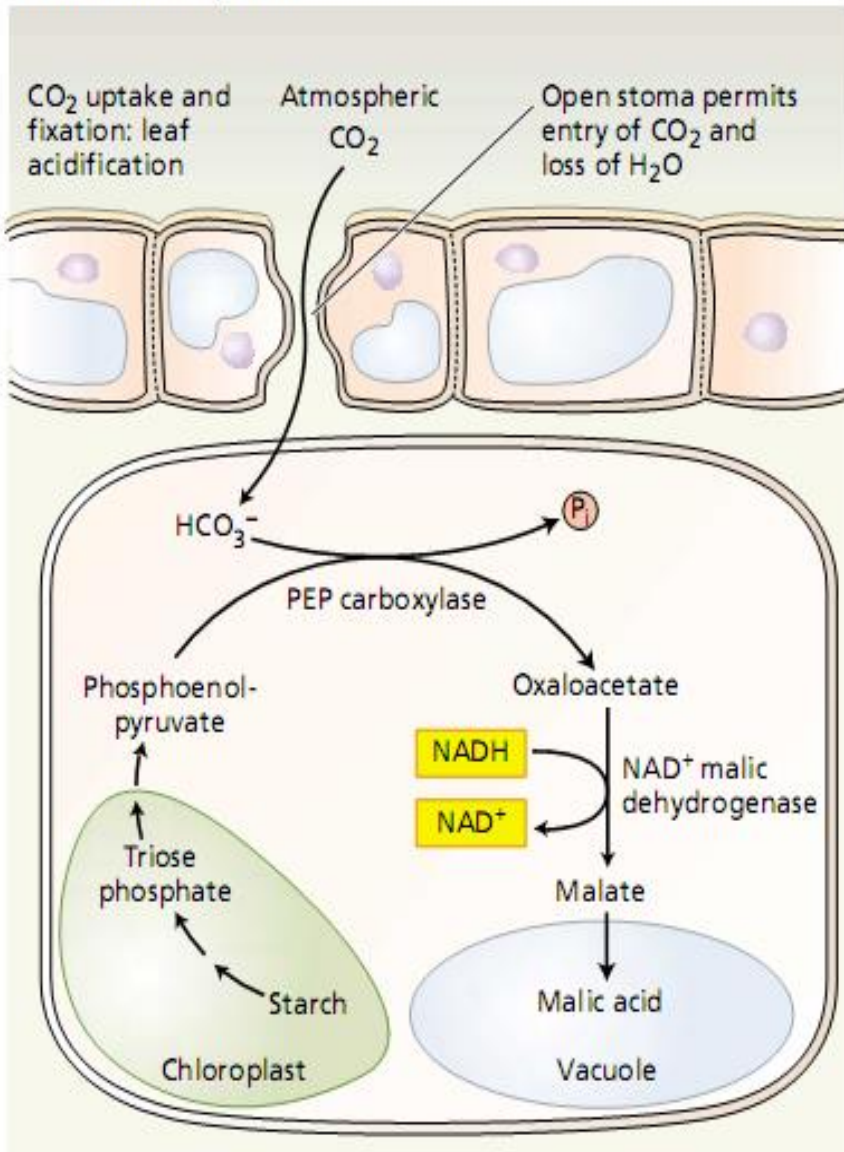
Light Regulates the Activity of Key C₄ Enzymes

NADP:malate dehydrogenase is regulated via the thioredoxin system of the chloroplast (see Figure 8.5). The enzyme is reduced (activated) upon illumination of leaves and is oxidized (inactivated) upon darkening. PEP carboxylase is activated by a light-dependent phosphorylation–dephosphorylation mechanism yet to be characterized.

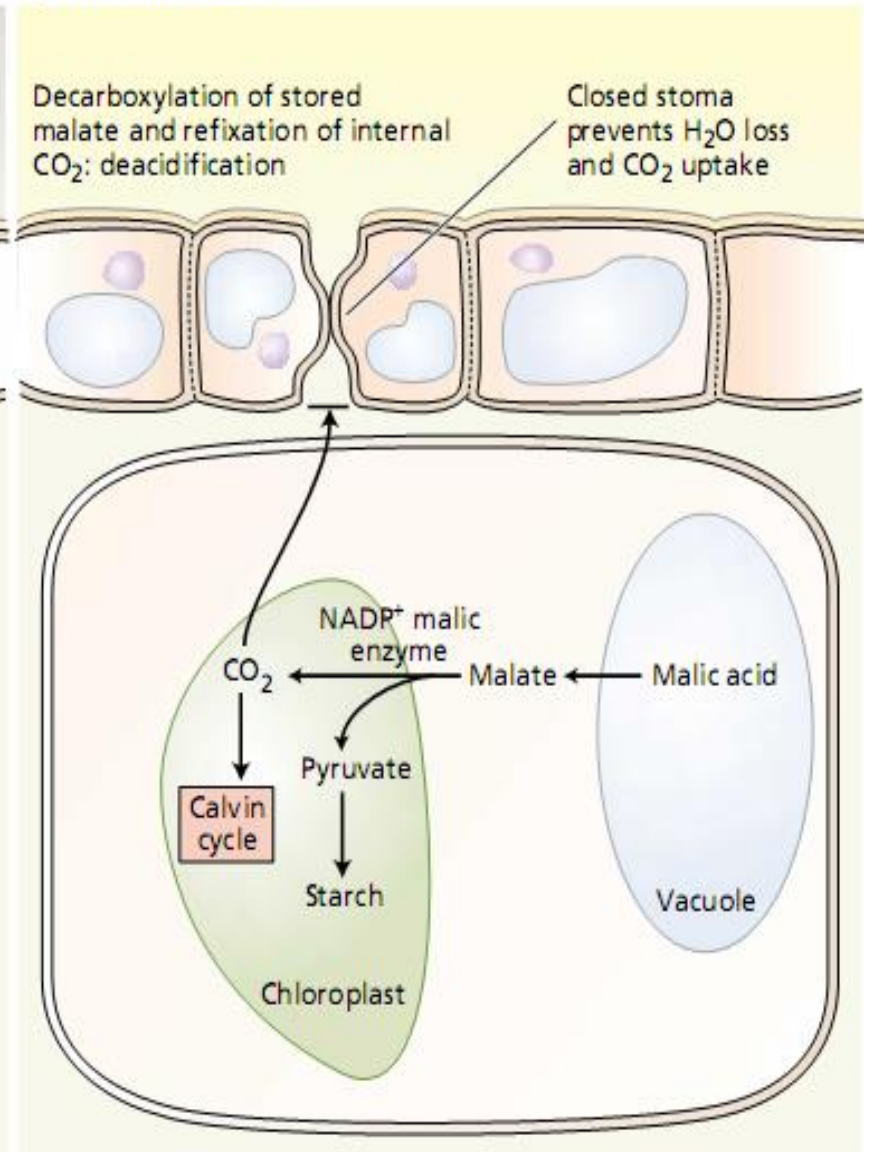
The third regulatory member of the C₄ pathway, pyruvate–orthophosphate dikinase, is rapidly inactivated by an unusual ADP-dependent phosphorylation of the enzyme when the photon flux density drops (Burnell and Hatch 1985). Activation is accomplished by phosphorolytic cleavage of this phosphate group. Both reactions, phosphory-

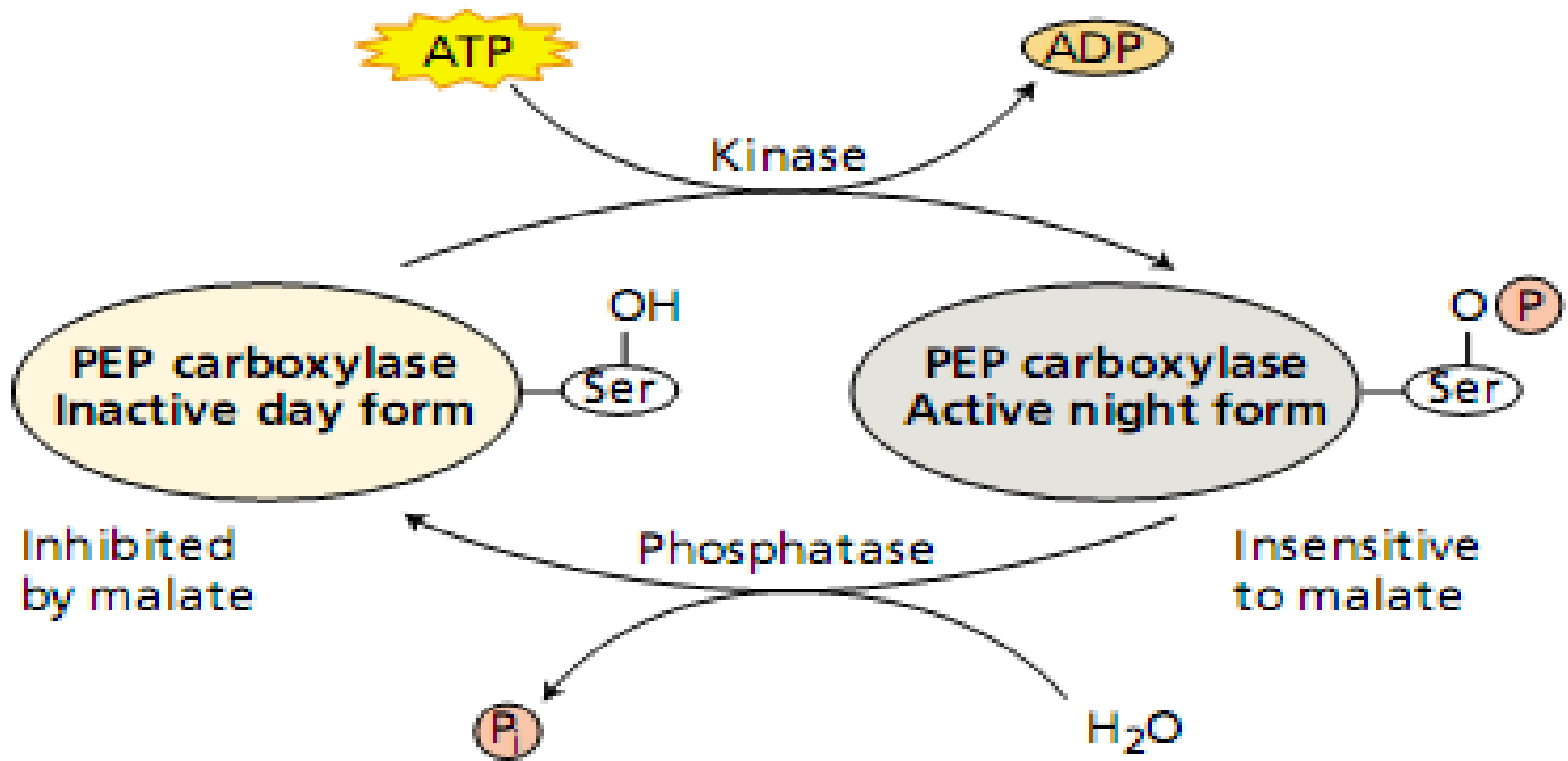
In Hot, Dry Climates, the C₄ Cycle Reduces Photorespiration and Water Loss

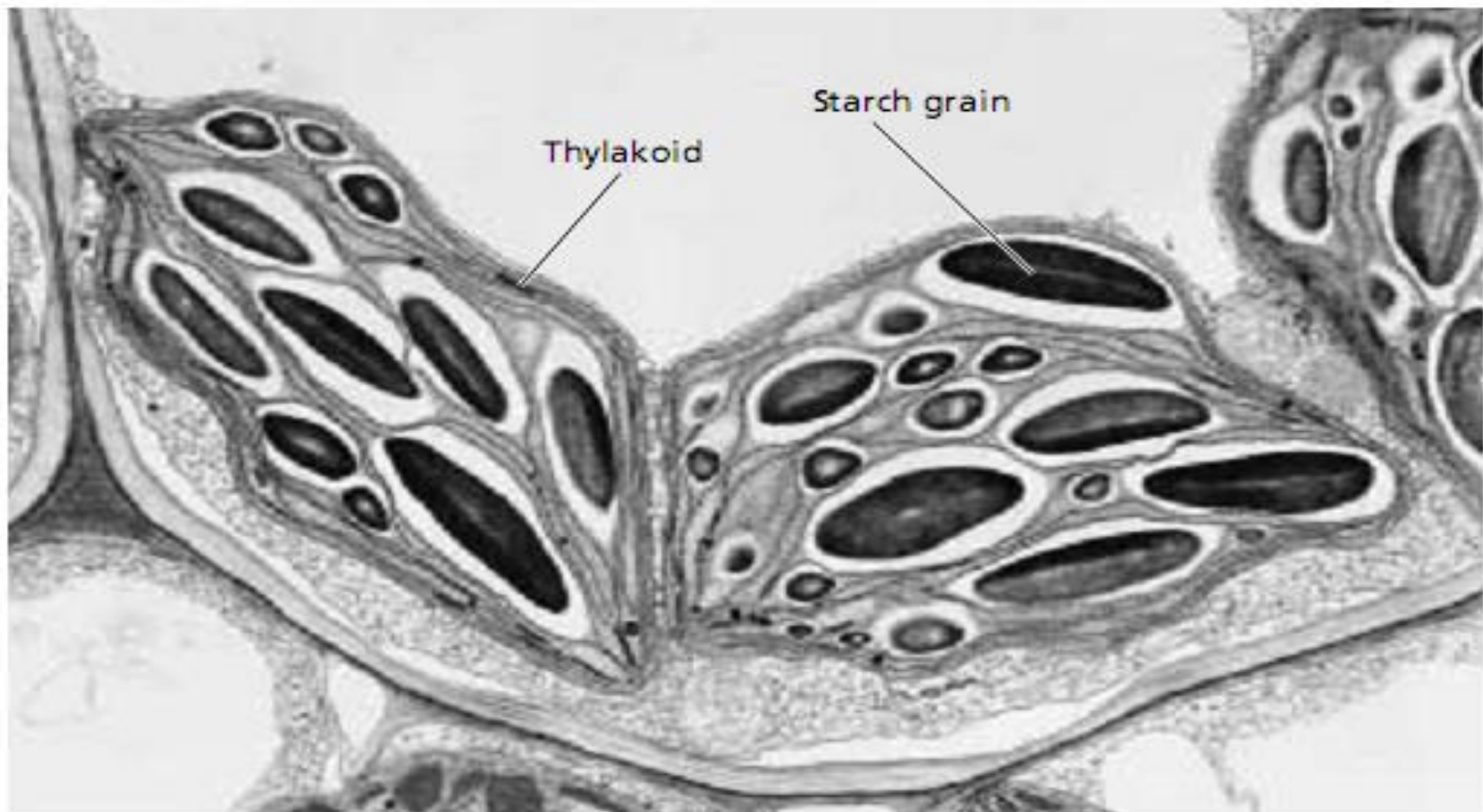
Dark: Stomata opened



Light: Stomata closed







Thylakoid

Starch grain

Transport of organic solutes

Xylem – transports water and minerals from the root system to the aerial portions of the plant.

Phloem – translocates the products of Ps from mature leaves to areas of growth & storage, including the roots.

The cells of phloem that conduct sugars & other organic materials are called sieve elements

Phloem tissue consists of SE, CC, parenchyma cells and in some cases fibers, sclerids & laticifers

SE are directly involved in translocation

1686 – Marcell Malpighi (Italian Anatomist) – girdling expt.

1928 - T.G. Mason & E.J. Maskell – Ts not affected, sugar transport blocked

Radioactive P,S, H^{3+} (Tritium), Cl, Ca, strontium, rubidium, K & C - ^{18}O , ^{15}N & ^{13}C are also used – applied by 1) reverse flap technique

3) removal of cuticle by abrasion

Detection system - autoradiography

Conclusion of above expts.

- 1) water with its dissolved minerals moves primarily upward through xylem tissues
- 2) Assimilates, move over relatively long distances primarily through sieve tubes in the phloem
- 3) Assimilates move from source to sink

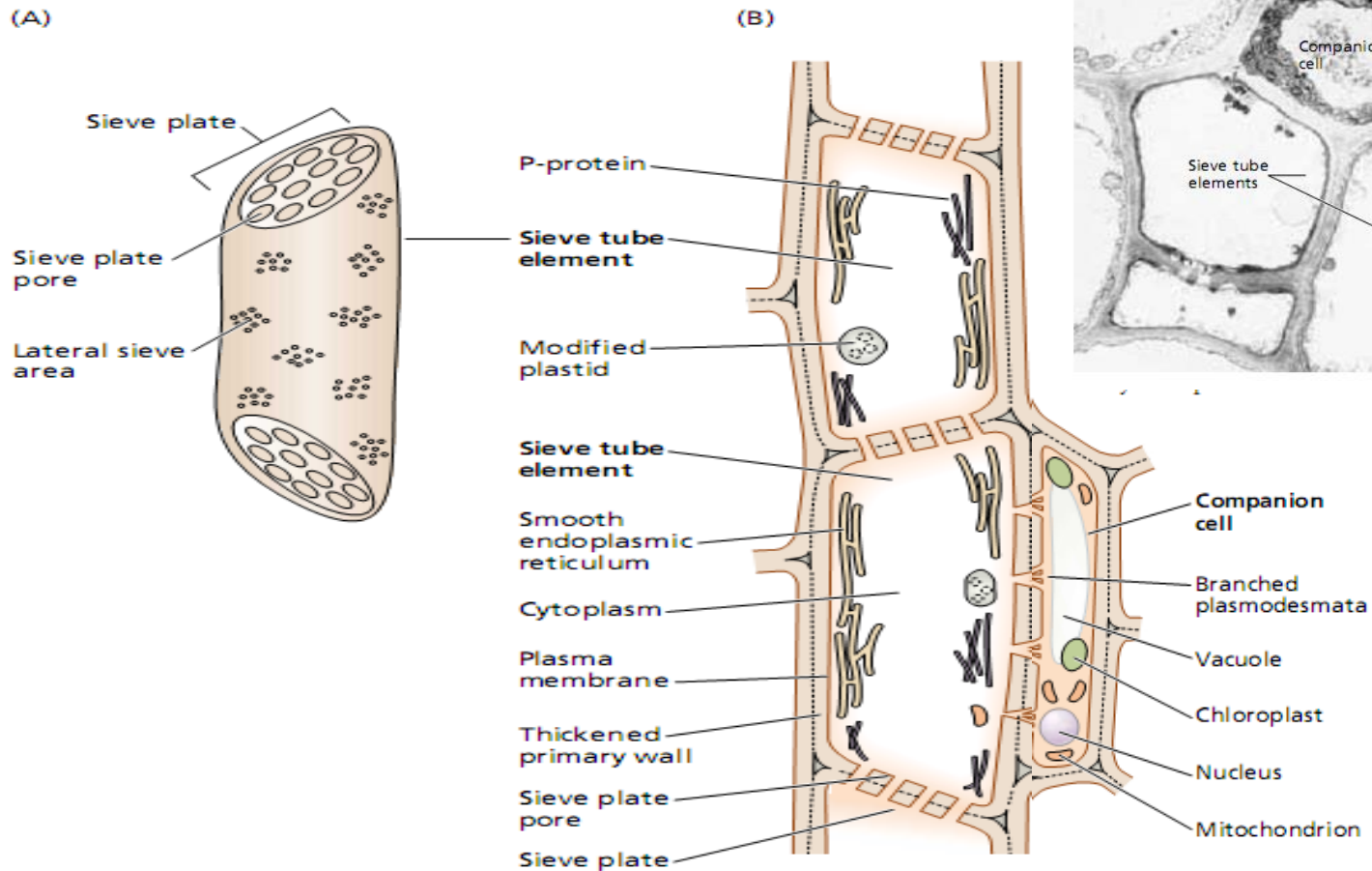
Source – leaves, exporting storage organ, cotyledons and endosperm cells of seeds

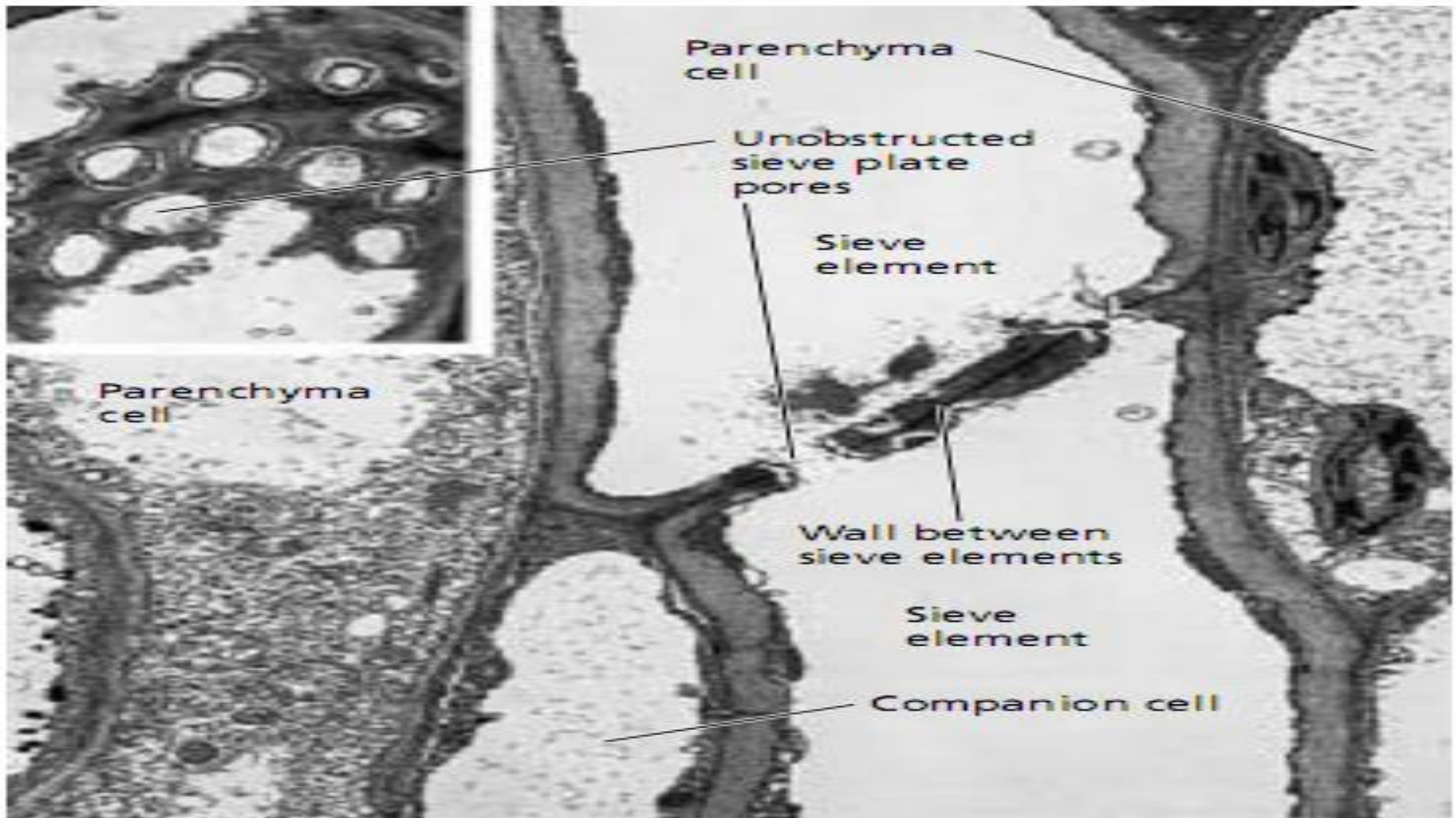
Sink – growing, storing or metabolizing tissue

- Expts. – girdle between growing shoot and leaf branch

gravity does not control this flow from source to sink

Mature sieve tube element





SE & CC

SE & CC are formed by the division of a single mother cell.- plasmodesmatal connections exist between them

Functions of CC - 1) protein synthesis (which is lost from SE during differentiation)

3) supply ATP

4) transport Ps products from producing cells to SE

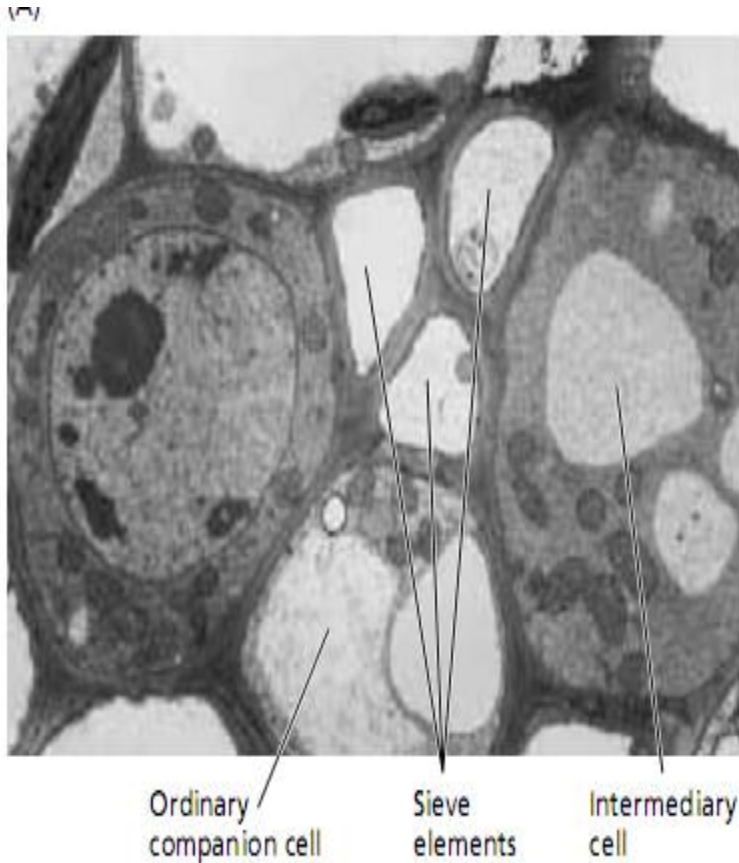
CC are of 3 types

1) ordinary CC - few plasmodesmatal connections to the surrounding cells

2) transfer cell - with finger like wall ingrowths, particularly on cell walls that face away from the sieve element (increases surface area of pm, thus increasing the potential for taking up solutes from apoplast to cell wall space.

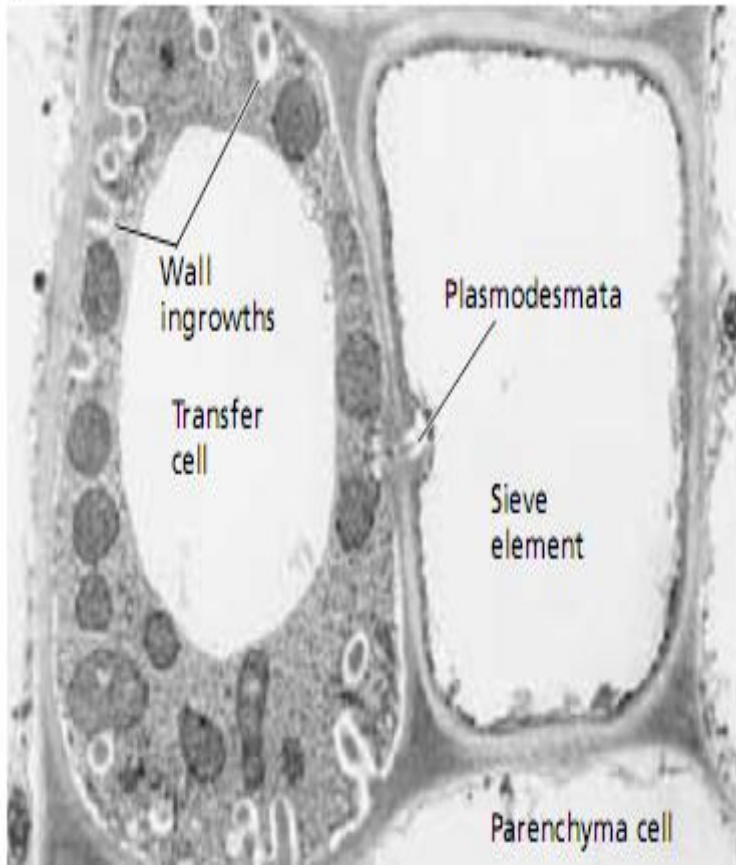
3) Intermediary cell – numerous plasmodesmatal connections- suited for taking solutes via cytoplasmic connections

3 different types of companion cells



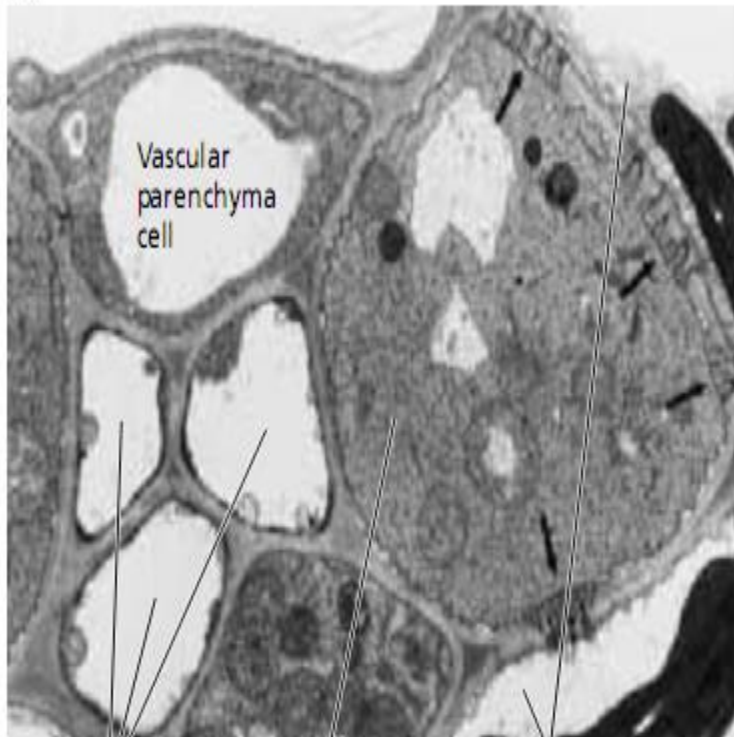
- Ordinary companion have chloroplasts with well-developed thylakoids and a cell wall with a smooth inner surface.
- Few plasmodesmata connect this type of companion cell to any of the surrounding cells except its own sieve element.

(B)



- Transfer cells are similar to ordinary companion cells, except for the development of fingerlike wall ingrowths, particularly on the cell walls that face away from the sieve element
- the ordinary companion cell and the transfer cell are specialized for taking up solutes from the apoplast or cell wall space.

(C)



- Intermediary cells appear well suited for taking up solutes via cytoplasmic connections. Intermediary cells have numerous plasmodesmata connecting them to surrounding cells, particularly to the bundle sheath cells.

Materials translocated in phloem

- sucrose, A.A, hormones & some inorganic ions

Phloem sap can be collected and analyzed

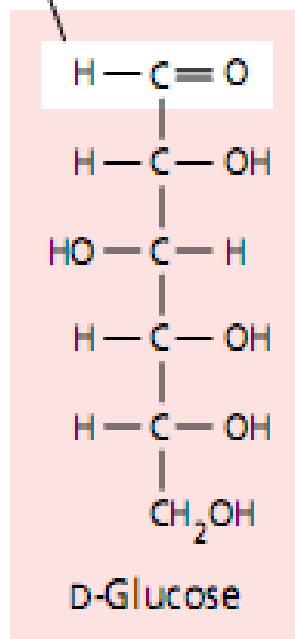
- 1) A cut in the SE - apply EDTA to chelate Ca, an activator of callose synthase - disadvantage - contaminated phloem sap
- 2) Use of ting syringe
- 3) Stylet of aphid

Sugars are translocated in non reducing form

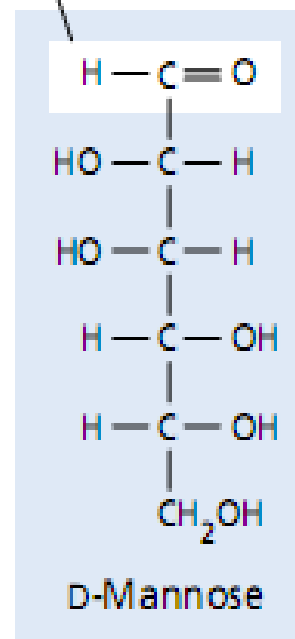
(A) Reducing sugars, which are not generally translocated in the phloem

The reducing groups are aldehyde (glucose and mannose) and ketone (fructose) groups.

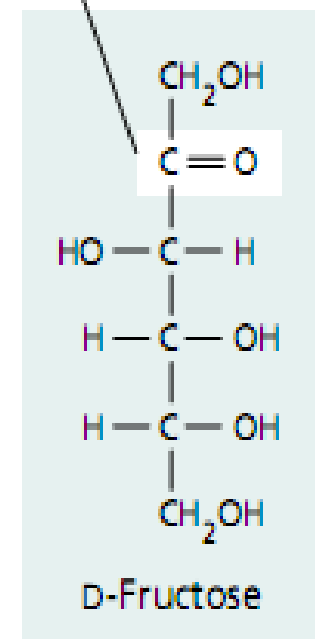
Aldehyde



Aldehyde

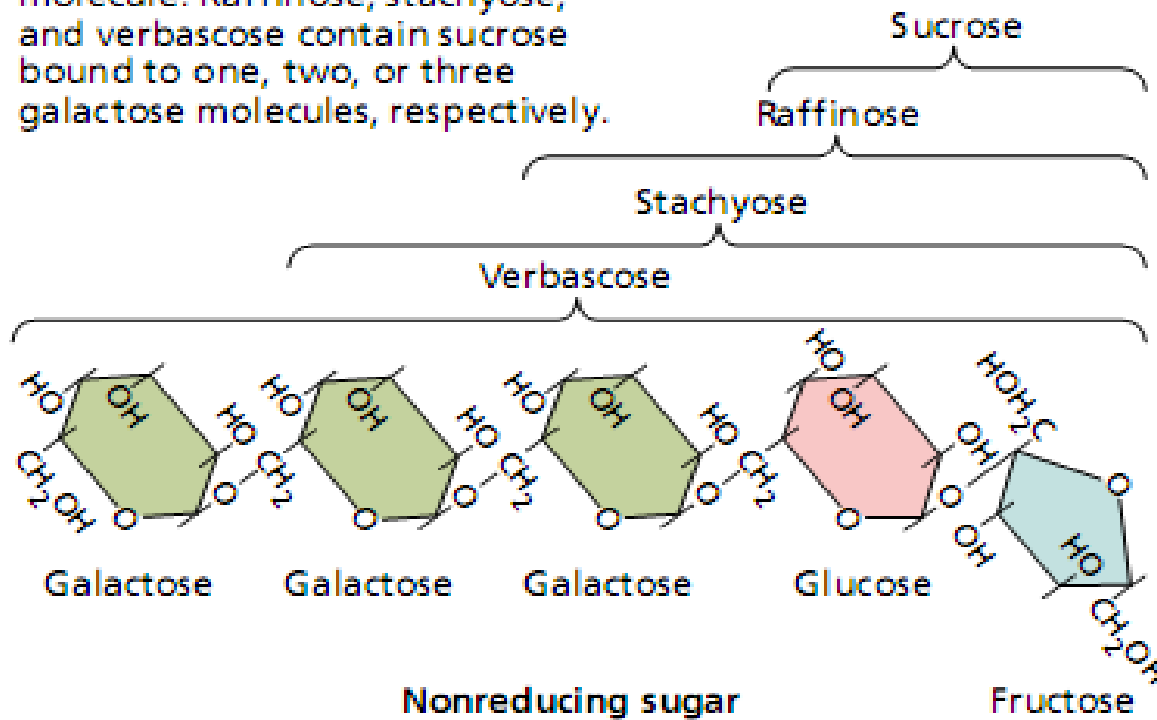


Ketone

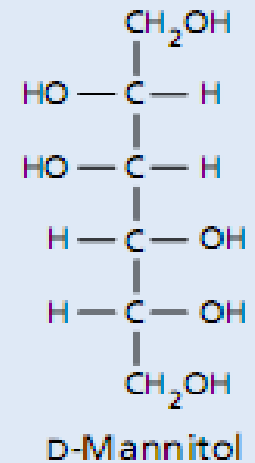


(B) Compounds commonly translocated in the phloem

Sucrose is a disaccharide made up of one glucose and one fructose molecule. Raffinose, stachyose, and verbascose contain sucrose bound to one, two, or three galactose molecules, respectively.

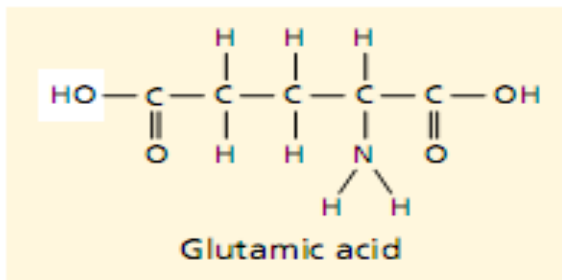


Mannitol is a sugar alcohol formed by the reduction of the aldehyde group of mannose.

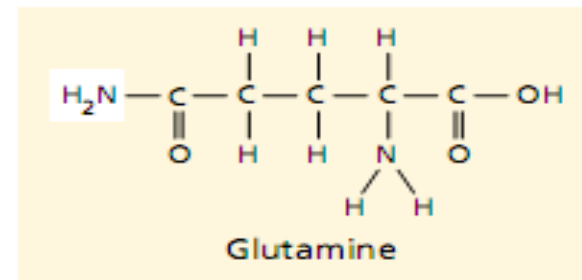


Sugar alcohol

Glutamic acid, an amino acid, and glutamine, its amide, are important nitrogenous compounds in the phloem, in addition to aspartate and asparagine.

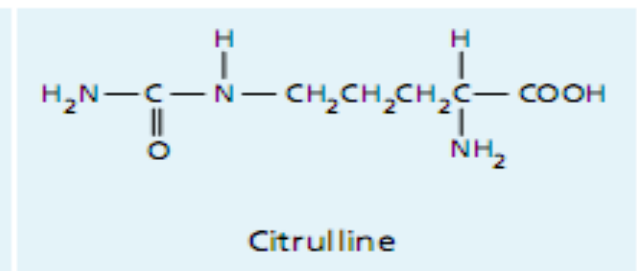
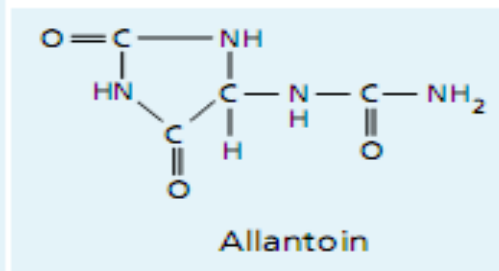
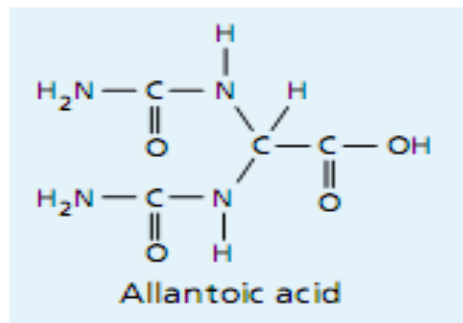


Amino acid



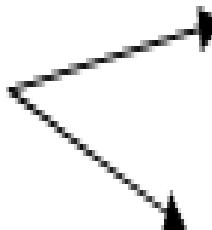
Amide

Species with nitrogen-fixing nodules also utilize ureides as transport forms of nitrogen.



Ureides

deposition of P (phloem) protein & callose seals damaged SE

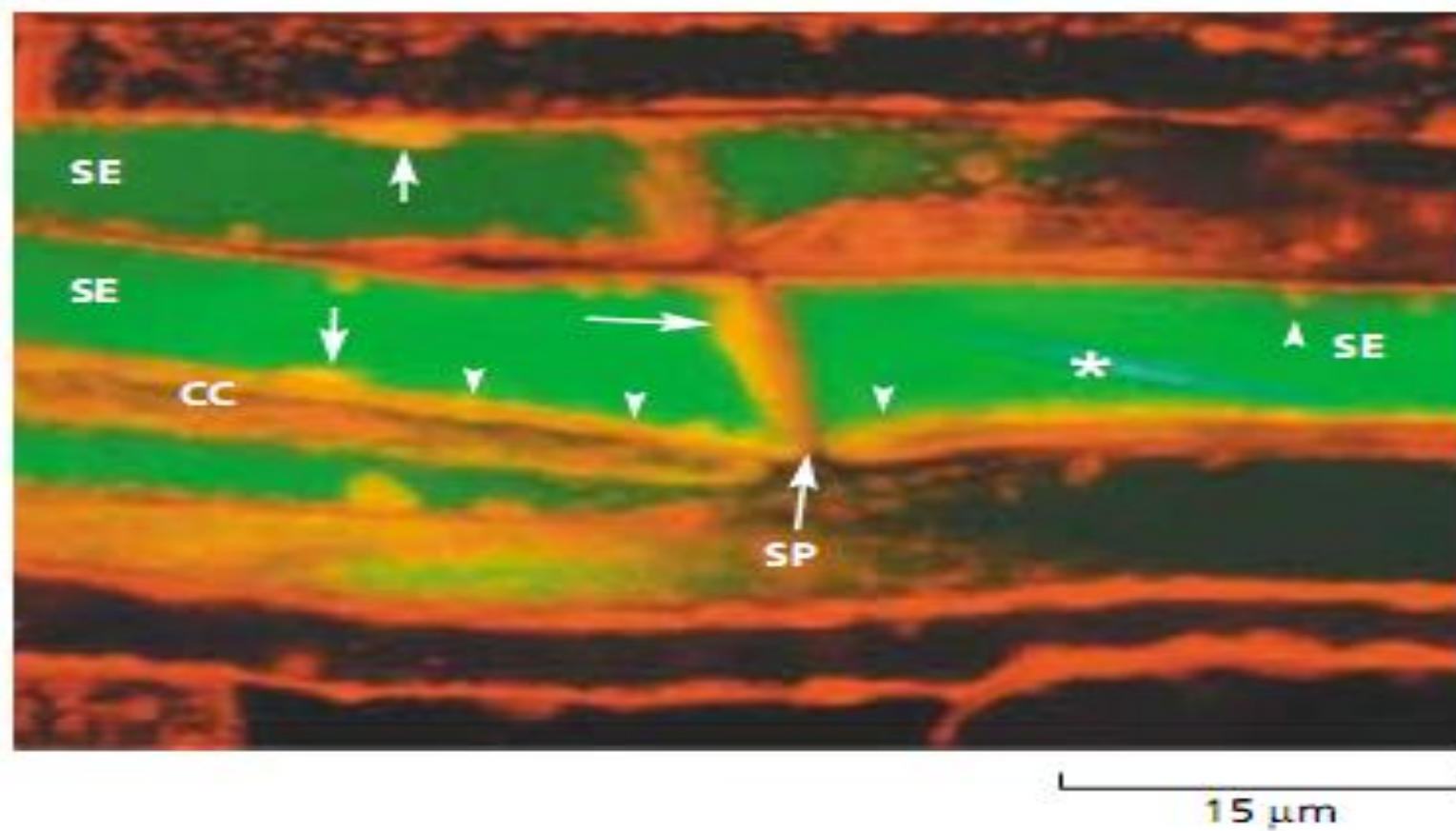
P proteins 

PP2 – phloem lectin

-both are synthesized in CC and transported via plasmodesmata to SE

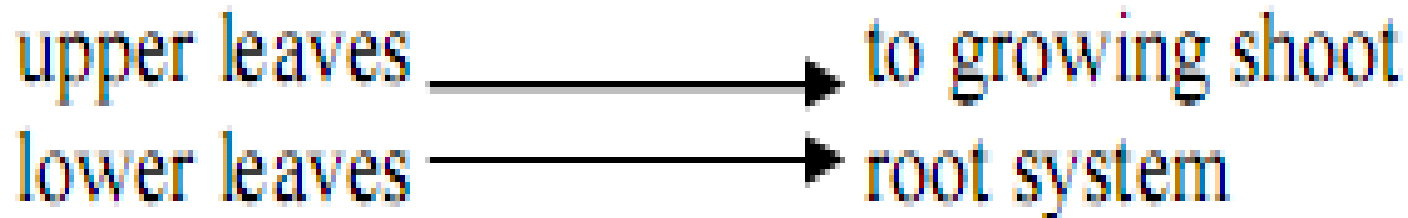
- it seals off damaged SE - plugs the sieve plate pores
- Sieve tubes, under very high internal TP
- A longer term solution of the damage problem is production of callose

(B)



Source to Sink pathways follow anatomical and developmental patterns:

a) proximity



b) Development

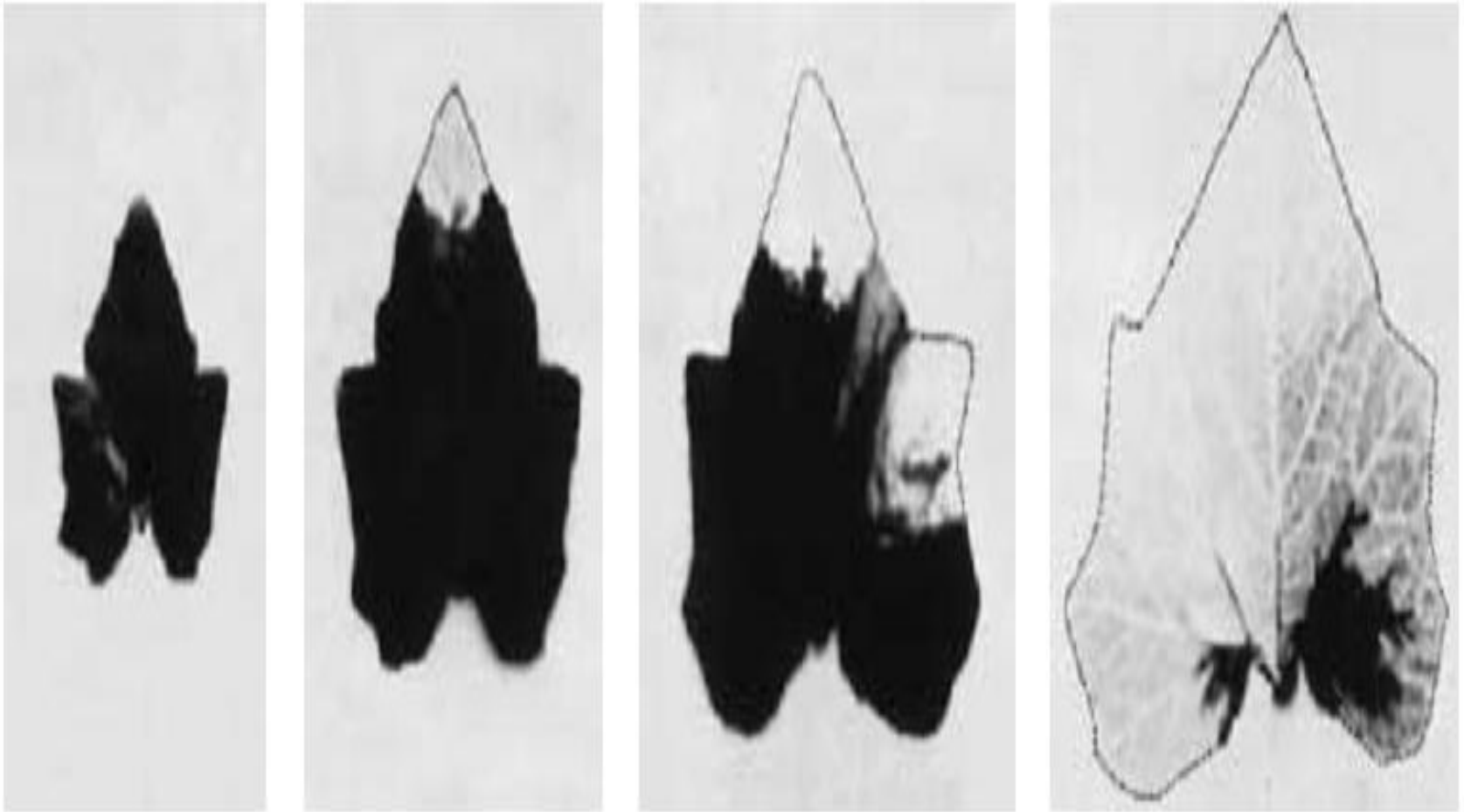
Major sinks – Shoot and root

Shift in sink – during fruit development

c) Vascular connections

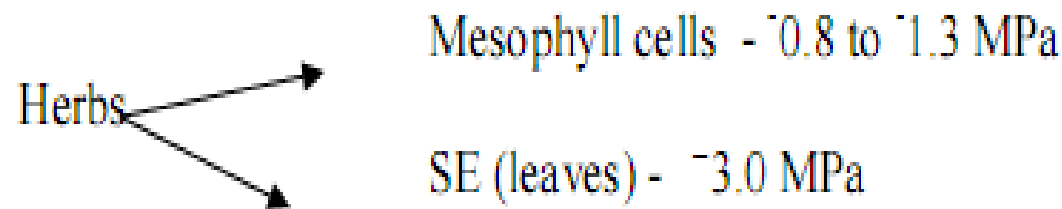
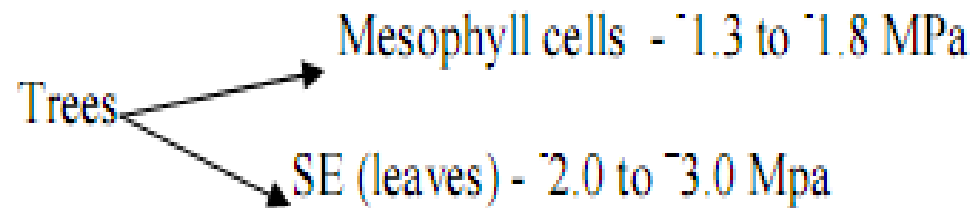
d) Altering translocation pathways

Autoradiographs of a leaf of summer squash (*Cucurbita pepo*), showing the transition of the leaf from sink to source status.



Phloem loadings

From chloroplasts to SE



The process in which sugars are raised to high conc. In phloem cells close to source (Ps cells) is called Phloem loading

1st step: triose phosphate (Chloroplast) → sucrose (Day) (Cytosol)

2nd step: Sucrose
Starch → glucose → sucrose (night)
Mesophyll cell → vicinity of SE (of small vein) - called short distance transport

3rd step: (SE loading) From vicinity → SE & CC → Sink
long distance transport (export)

Photosynthate moves from mesophyll cells to SE via apoplast or symplast:

- 1) transport sugars are found in apoplast
- 2) sucrose supplied exogenously accumulates in the SE & CC
- 3) inhibitor of sucrose transporter (PCMBS) inhibits sucrose uptake from apoplast

-In apoplast pathway, sucrose uptake requires metabolic energy

SE loading uses sucrose-H⁺ symport

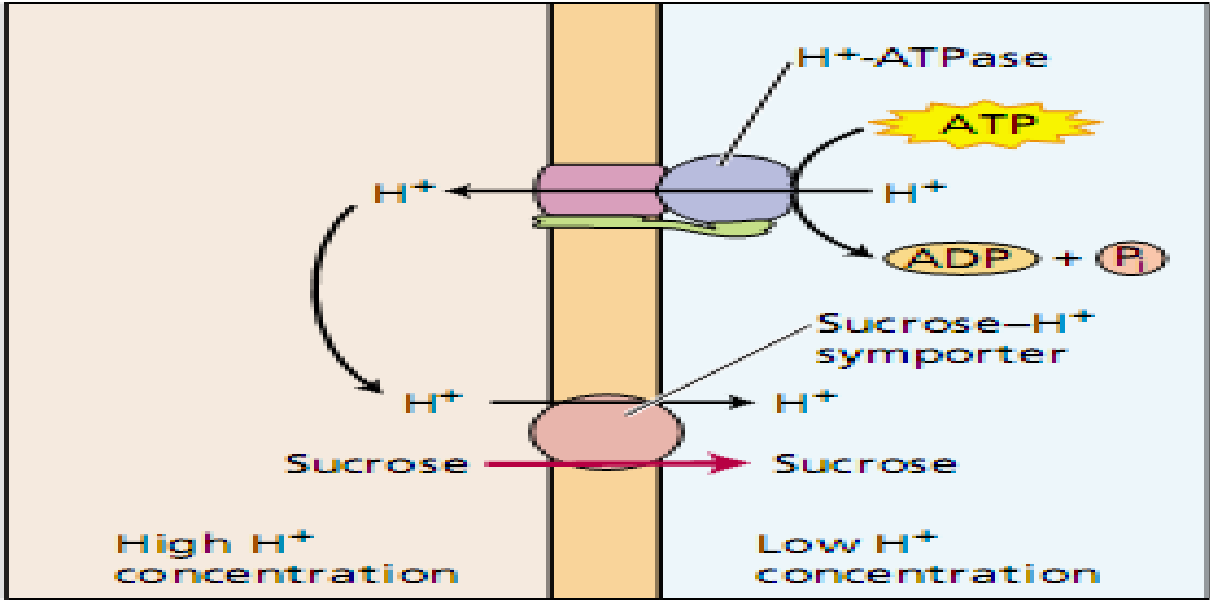
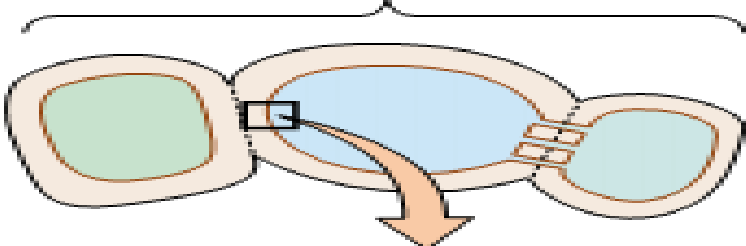
- 1) pri. Active transport - direct utilization of ATP
- 2) sec. Active transport - H⁺ gradient establishment - sucrose-H⁺ symport (SUC2) (SUT1)

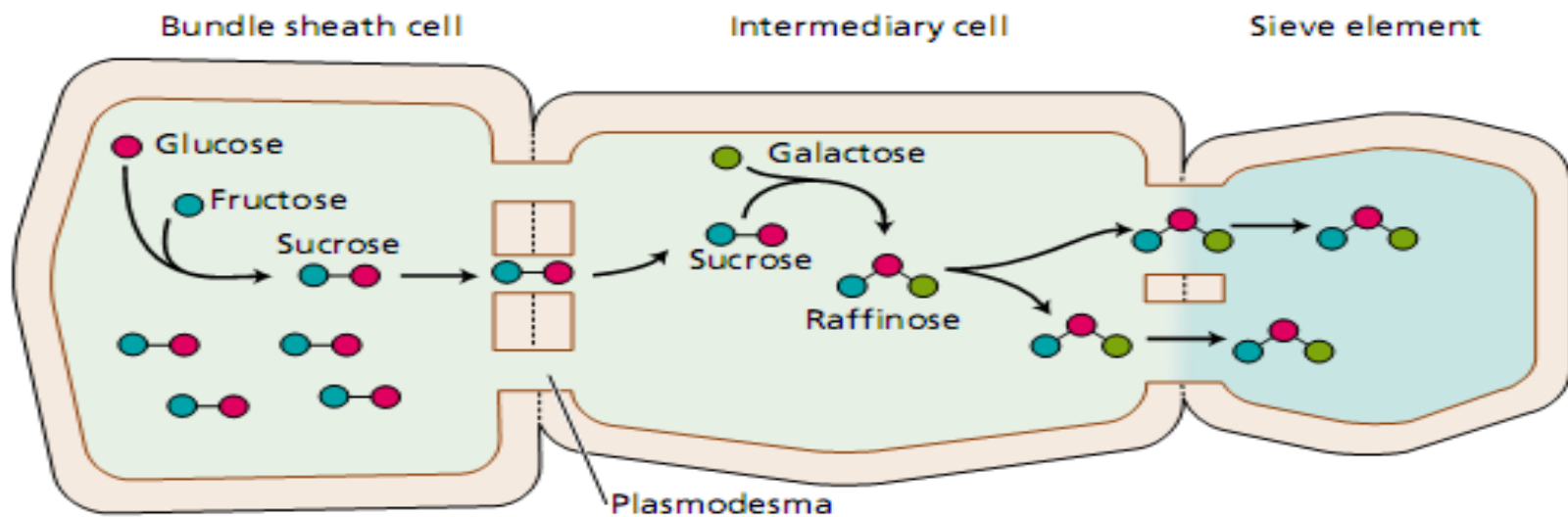
- sucrose from apoplast \longrightarrow SE by sucrose H⁺ symporter
↓
influenced by
1) TP (solute potential) of SE
2) High apoplastic concentration of sucrose

-Phloem loading appears to be symplastic in plants with intermediary cells:

- Is specific and selective - explained by polymer trapping model

Sieve element-companion cell complex





Sucrose, synthesized in the mesophyll, diffuses from the bundle sheath cells into the intermediary cells through the abundant plasmodesmata.

In the intermediary cells, raffinose (and stachyose) are synthesized from sucrose and galactose, thus maintaining the diffusion gradient for sucrose. Because of their larger sizes, they are not able to diffuse back into the mesophyll.

Raffinose and stachyose are able to diffuse into the sieve elements. As a result, the concentration of transport sugar rises in the intermediary cells and the sieve elements.

-organic acids and hormones enter phloem

- a) by diffusion
- b) by a passive transporter
- c) symplastic movement

-Dvpt of loading capacity

-sink source transition

ex. Young leaf \longrightarrow maturing

-selective loading of sugars: radioactivity study

sucrose and sugar alcohols loaded

Transported solutes: sucrose, raffinose, stachyose & verbascose & sugar alcohols
(mannitol, sorbitol, galacitol, myoinositol)

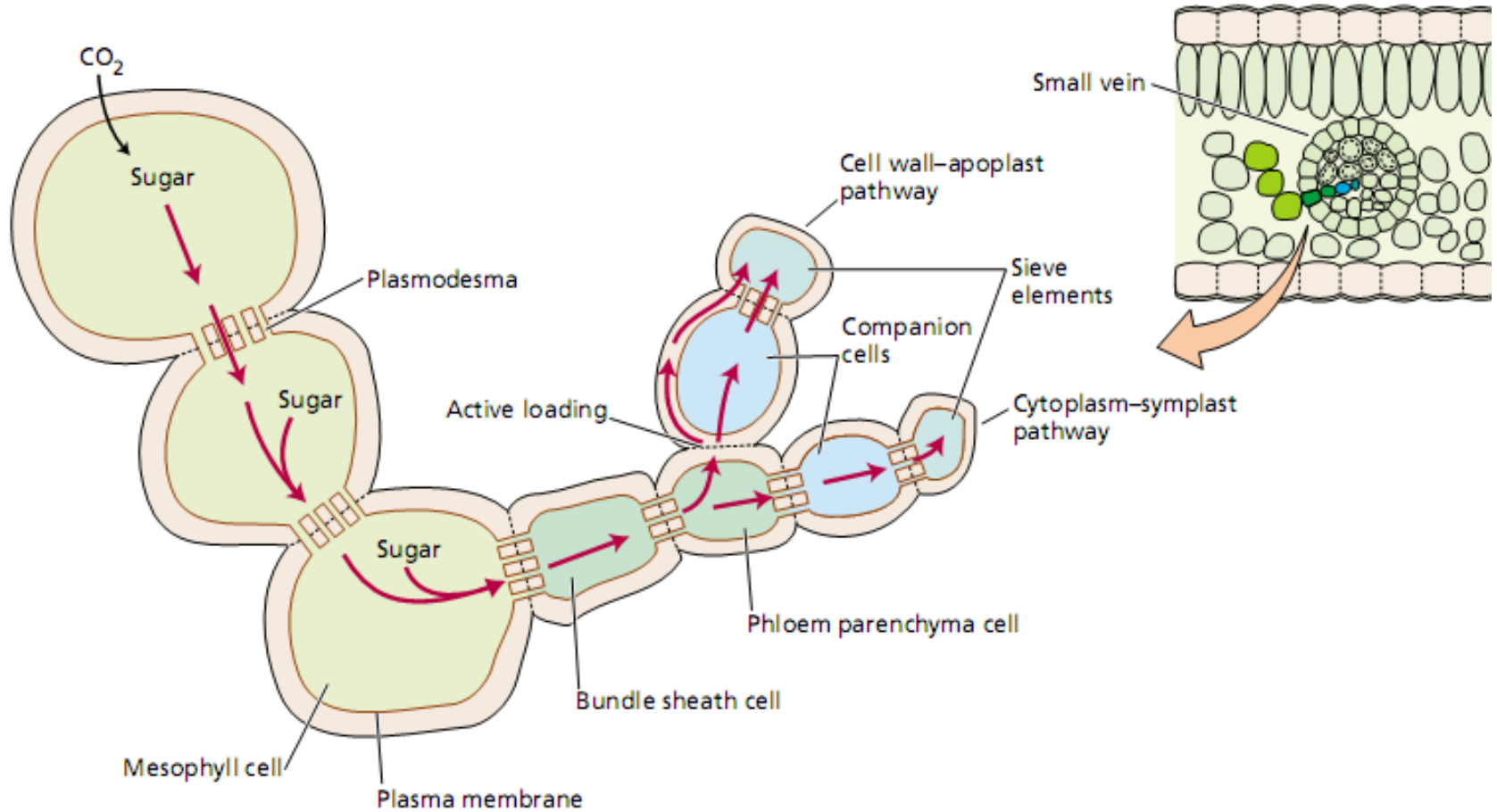
G & F transferred only less to phloem

A carrier in pm recognize the sugars and results in selective loading

Certain a.a are preferentially loaded

Among minerals P & k readily loaded

Schematic diagram of pathways of phloem loading in source leaves



Phloem Unloading

Removal of sucrose & other solutes from SE at the sink - imp. In phloem transport

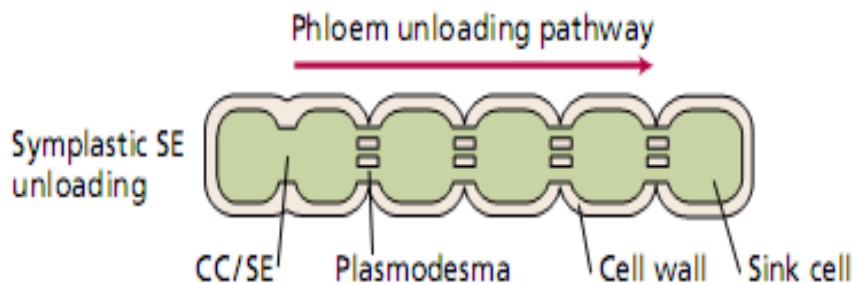
- import takes place in 3 steps
- 1) SE unloading
- 2) short distance transport – into sink
- 3) storage and metabolism

Phloem unloading can be symplastic (in growing regions) or apoplastic (embryo, storage organs – fruits, roots)

Transport into sink tissues depends on metabolic activity:

- symplastic \longrightarrow passive – but energy is required for Rs & biosynthesis reactions- low sucrose conc. In sink cells maintained by Rs or by conversion of sugars into compounds needed for growth or storage
- apoplastic \longrightarrow active - should cross 2 membranes (pm of exporting cell, pm of receiver & tonoplast)
- sugar transport into vacuoles of storage cells accomplished by sucrose-proton gradient.

(A) Symplastic phloem unloading



(B) Apoplastic phloem unloading



Type 1: This phloem unloading pathway is designated apoplastic because one step, transport from the sieve element-companion cell complex to the successive sink cells, occurs in the apoplast. Once the sugars are taken back up into the symplast of adjoining cells, transport is symplastic. This route has not yet been demonstrated in any sink type.

Type 2: This pathway also has an apoplastic step. However, the exit from the sieve element-companion cell complex—that is, sieve element unloading—is symplastic. The apoplastic step occurs later in the pathway. The upper figure (2A) shows an apoplastic step close to the sieve element-companion cell complex; the lower figure (2B), an apoplastic step that is further removed.

The transition of a leaf from sink to source is gradual:

- 1) the symplastic unloading pathway is closed
- 2) leaf synthesizes assimilates, making it available for support
- 3) sucrose synthesizing genes are being expressed
- 4) the sucrose - H^+ symporter activates pm of SE-CC complex

Empty legume ovule method

Pressure in the phloem:

Ex. Aphid feeding

Tapping of sugar palm (10% sucrose, 0.25% mineral salts)

Gradients in the osmotic potential in sieve tube exist, with most negative values at source

To measure pr.

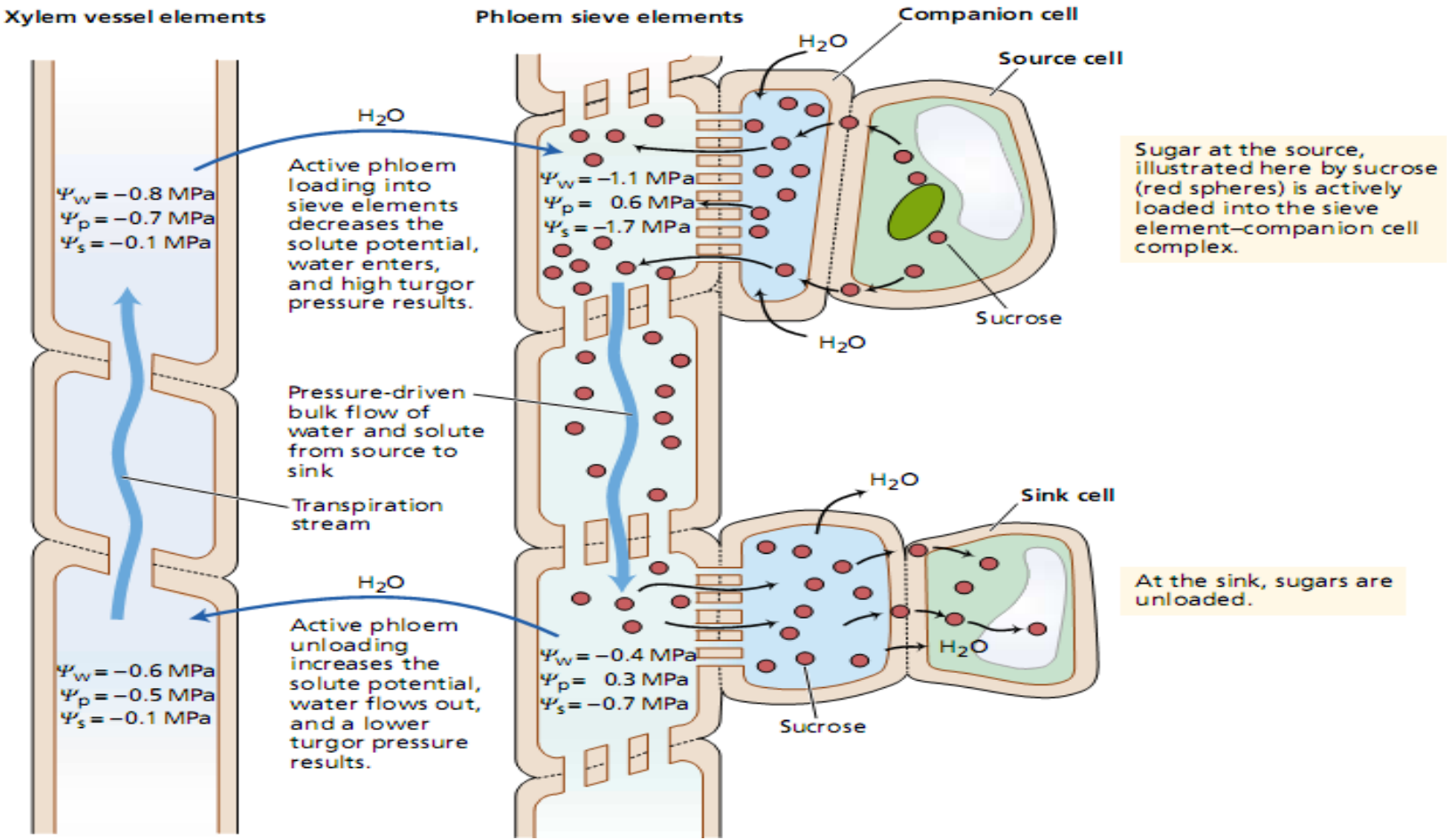
- 1) Pr. Guage at cut palm shoot
- 2) Pr, cuff
- 3) Introducing a glass capillary partially filled with dyed water & sealed at one end and attached to a needle, introduced in P tube

Phloem Translocation:

The pressure flow mechanism – Ernst Munch – Germany - 1926

Flow of solute on SE is driven by an osmotically generated pr. Gradient between source and sink - established as a consequence of phloem loading at source and unloading at sink.

Pressure-flow model of translocation in the phloem.



Problems with Pr. Flow model

- 1) velocities between 2 points along transport system were highest for ^{14}C -sugars, ^{32}P labeled P moving more slowly and $^3\text{H}_2\text{O}$ moving slowest of all.
 - a) water moves from sieve tubes into surround tissues, while much water moves from these tissues into tubes
 - b) SE contain cytoplasm with organelles – this becomes a reason for solute to metabolize or interact on their route
- 2) It is incompatible with movement of 2 different substances in opposite directions in same sieve tube at same time - Bidirectional transport
 - 1) expt. By applying tracers
 - 2) tracers + dyes - in stylet of aphids
- 3) Participation of ATP
- 4) Flow retardation due to plugging of sieve plates & resistance of plasmodesmata
- 5) participation of cytoplasm is not considered

Requisites for suitable function of Pr. Flow model:

- 1) an osmotic gradient between 2 osmometers
- 2) membranes that allow the establishment of pr. Gradient in response to the established osmotic gradient
- 3) a low resistance pathway between osmometers
- 4) osmometer with the most negative OP being immersed in a solution with a higher water potential than that in the osmometer.

If these conditions are met in plant the pr. Flow model functions as explained in the model.

Assimilate allocation and partitioning

The regulation of the diversion of fixed carbon into the various metabolic pathways is termed allocation

The differential distribution of photoassimilates within the plant is termed partitioning

The fate of fixed carbon in a source cell

- 1) synthesis of storage compounds - starch storers - grasses, fructan is stored
- 2) metabolic utilization
- 3) synthesis of transport compounds

unloaded
↓

- a) storage sinks - accumulated as sucrose/hexose in vacuoles or starch in amyloplasts
- c) growing sinks - sugars utilized for Rs & synthesis of other molecules for growth

The greater the ability of a sink to store or metabolize imported sugars, the greater is its ability to compete for assimilates from source

TP in SE is a means to communicate between source and sink - to coordinate loading & unloading - also chemical messengers (hormones & nutrients - sucrose, K^+ , PO_4^{+})

Increase of yield by increasing Pn not successful - increase in harvest index (ratio of harvest yield to total shoot yield) improves yield.

Sink tissues compete for available translocated assimilate

-a strong sink can deplete the sugar content of SE & thus steepen pr. Gradient, increasing translocation towards itself

$$\text{sink strength} = \text{sink size} \times \text{sink activity}$$

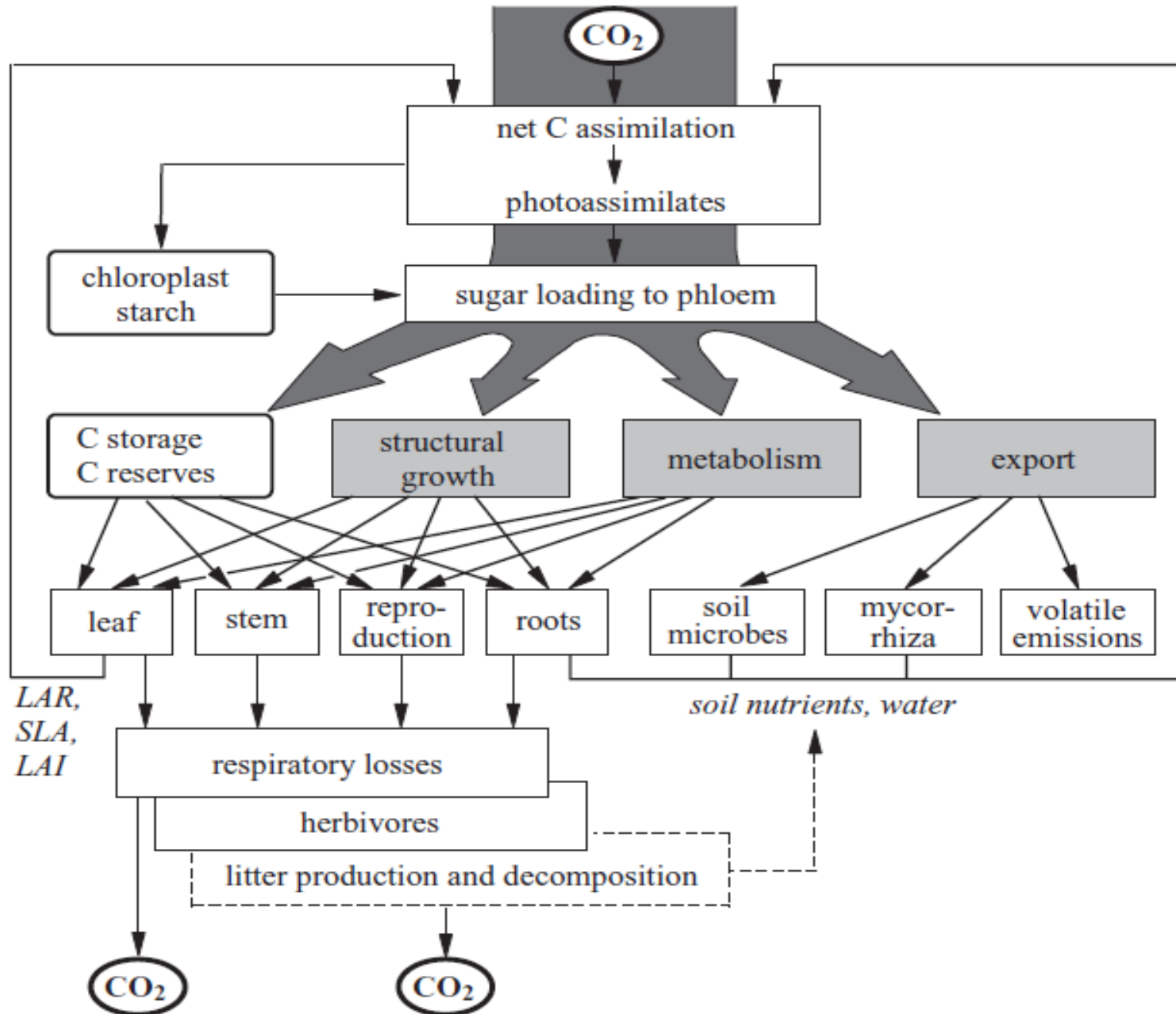
Ps & sink demand

-Ex. Potato tuber removed < Ps

-Regulation of C3 cycle

-Used up in actively growing regions, converted to starch in storage regions.

the fate of carbon in plants



67. The two principal products of photosynthesis are

(a) starch and sucrose

(b) glycerol and glycogen

(c) cellulose and glycogen

(d) glycerol and cellulose

62. Which of the following statements is true about the Krebs (citric acid) cycle and the Calvin (light-independent) cycle?

(a) They both result in a net production of ATP and NADH

(b) They both result in a release of oxygen

(c) They both are carried out by enzymes located within an organelle matrix

7. The major difference in PS-I and PS-II found in Chloroplast are-

- a. Position on lamellae
- b. Chlorophyll a
- c. Position of electron carriers
- d. Energy harvesting

44. In photosynthesis, light energy is utilized in-
- a. Converting ATP into ADP
 - b. CO₂ change into carbohydrate
 - c. ADP converting into ATP
 - d. All of these