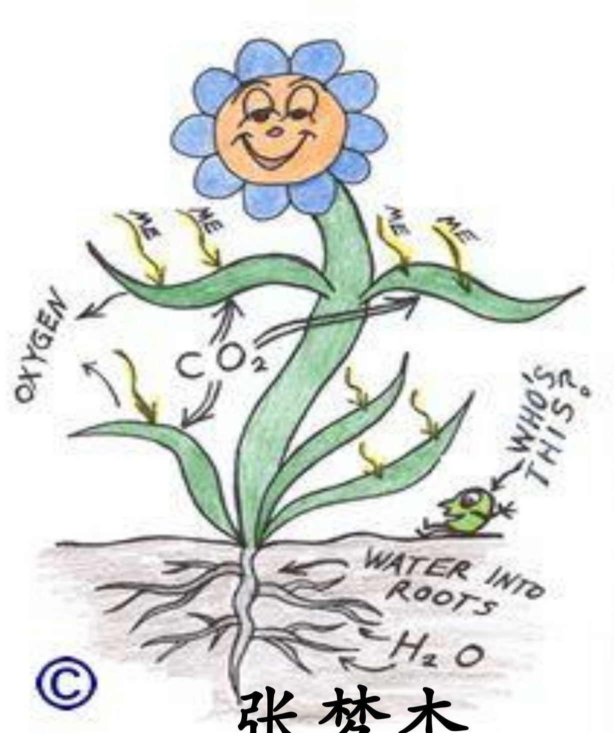
Lecture 6 Photosynthesis
（光合作用）



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- **Introduction**
- **Chloroplasts**
- **Photosynthesis**
  - **Photophosphorylation（光合磷酸化）**
  - **Carbon dioxide fixation（CO_2固定）**
- **Photorespiration（光呼吸）**
- **summary**

1.Introduction to Photosynthesis

Turning sunlight into reduced carbon

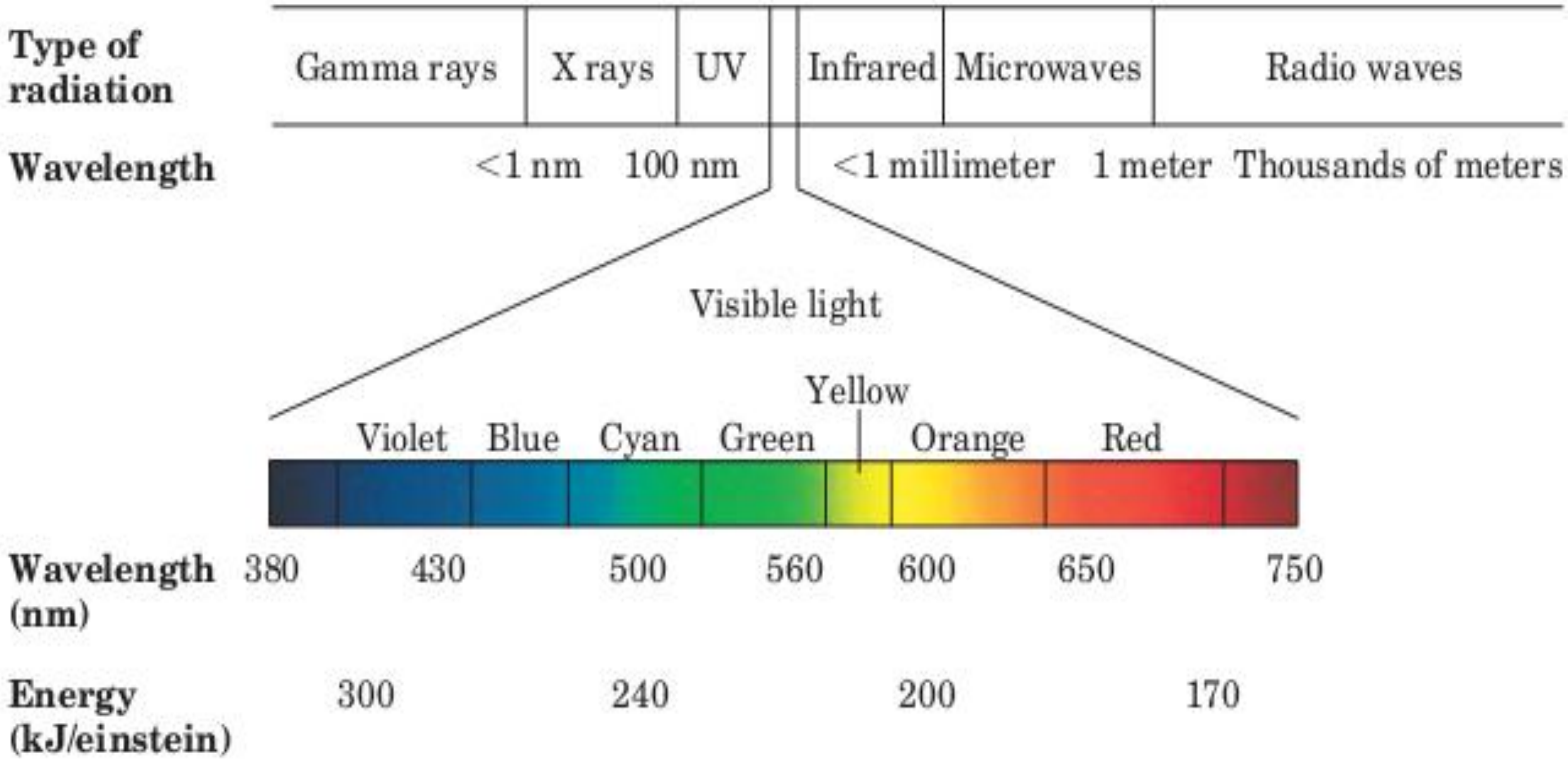
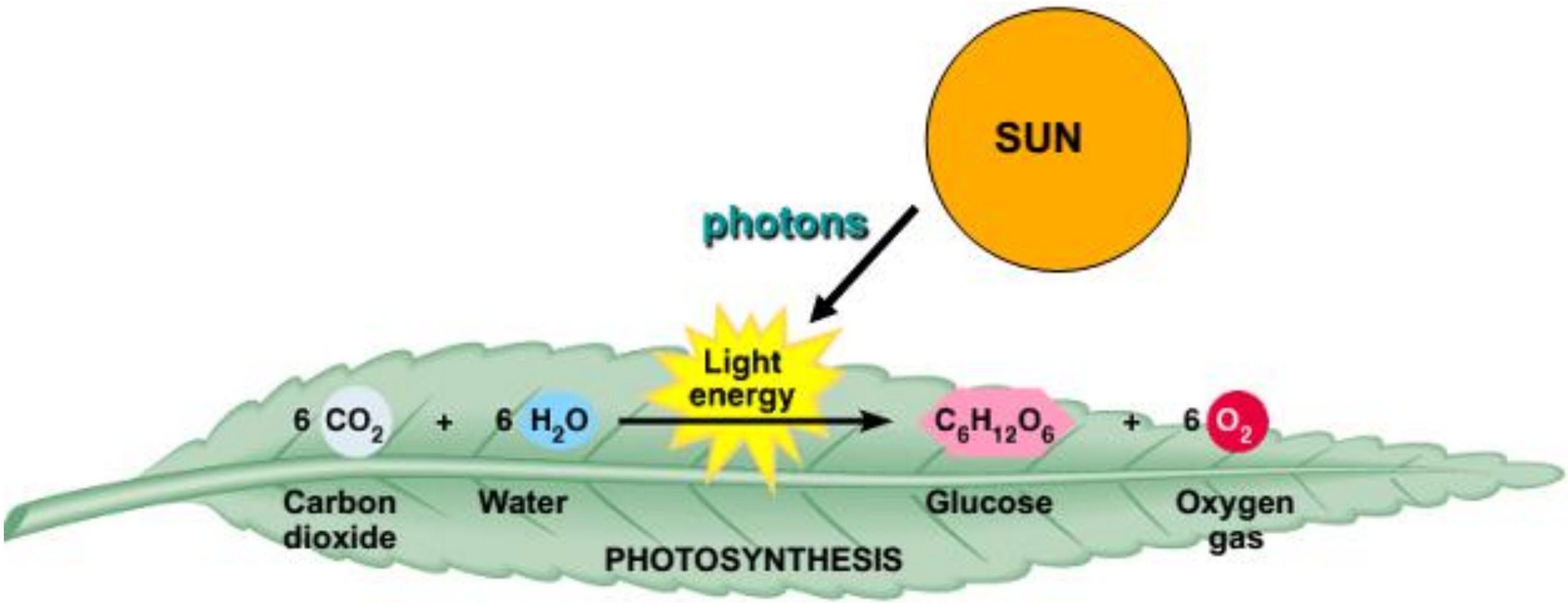
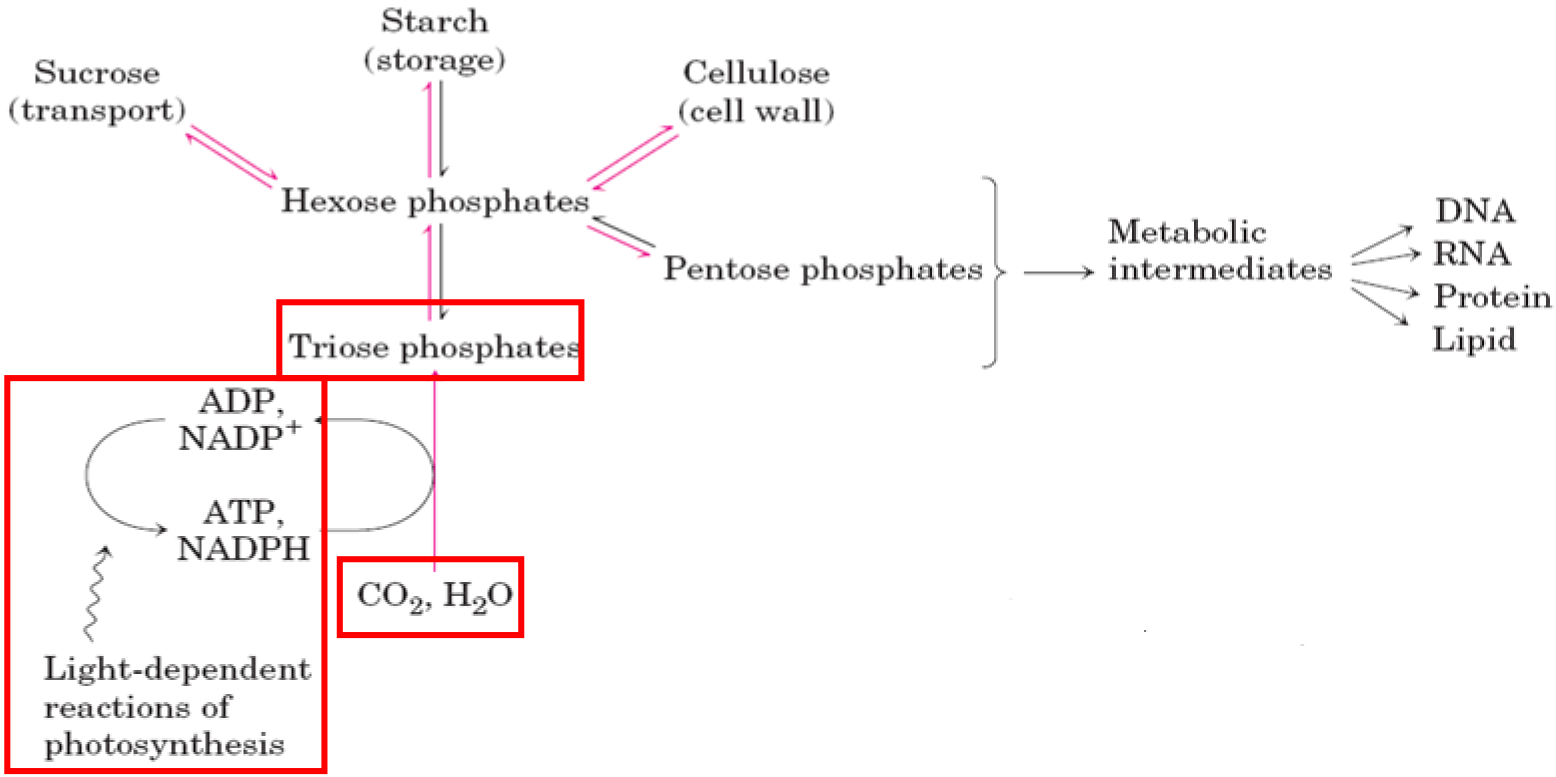


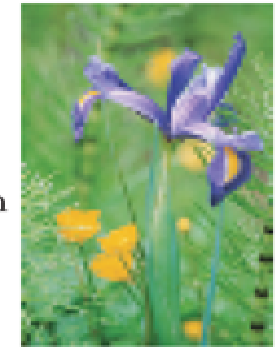
FIGURE 19-39 Electromagnetic radiation. The spectrum of electromagnetic radiation, and the energy of photons in the visible range of the spectrum. One einstein is 6×10^{23} photons.

1 mol ATP ≈ 30kJ

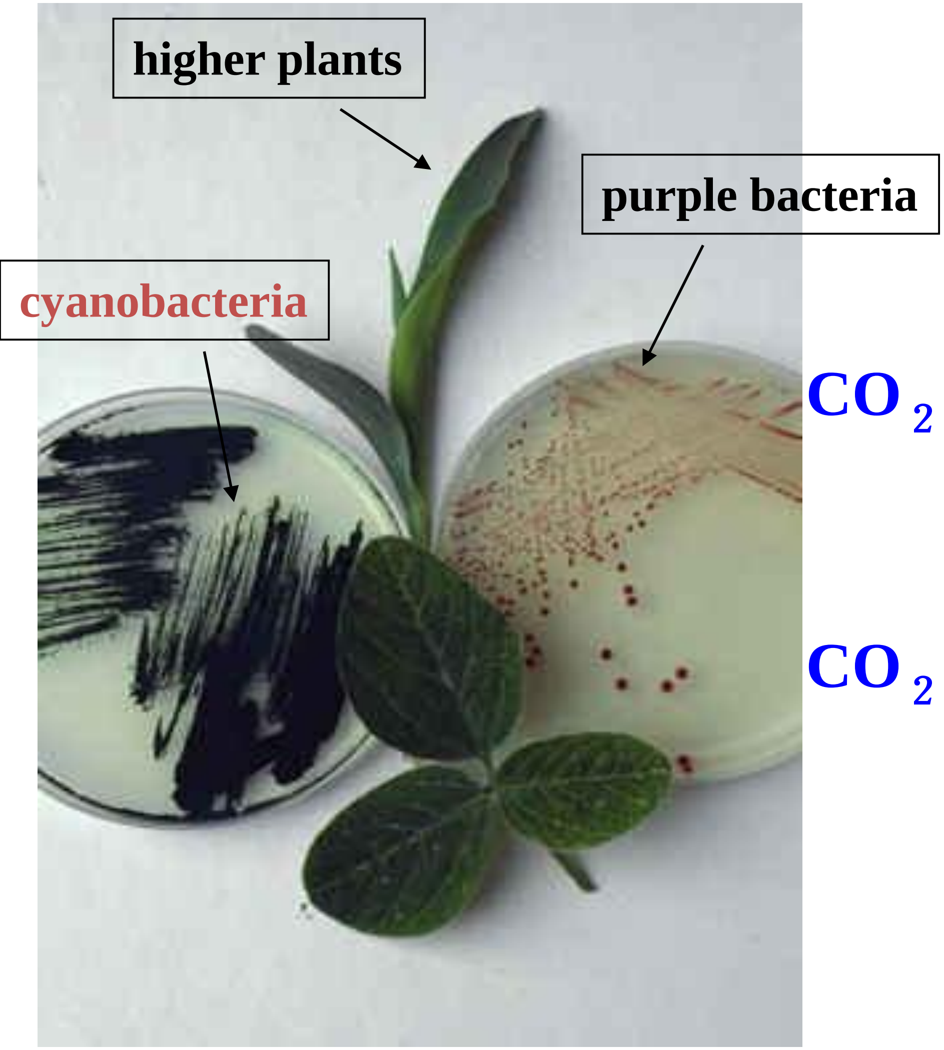
- An anabolic, endergonic, CO_2 requiring process that uses light energy and H_2O to produce organic macromolecules (glucose)




Starch
(storage)
Sucrose
(transport)
Cellulose
(cell wall)
Hexose phosphates
Pentose phosphates
Metabolic
intermediates
DNA
RNA
Protein
Lipid
Triose phosphates
ADP,
NADP+
ATP,
NADPH
CO2, H2O
Light-dependent
reactions of
photosynthesis



Start point



$$CO_2 + 2H_2O \rightarrow (CH_2O) + O_2 + H_2O$$

$$CO_2 + 2H_2S \rightarrow (CH_2O) + 2S + H_2O$$

- 1931 C.B.Van Niel： equation for photosynthesis

$$CO_2 + 2H_2A \rightarrow (CH_2O) + 2A + H_2O$$

History of Photosynthesis

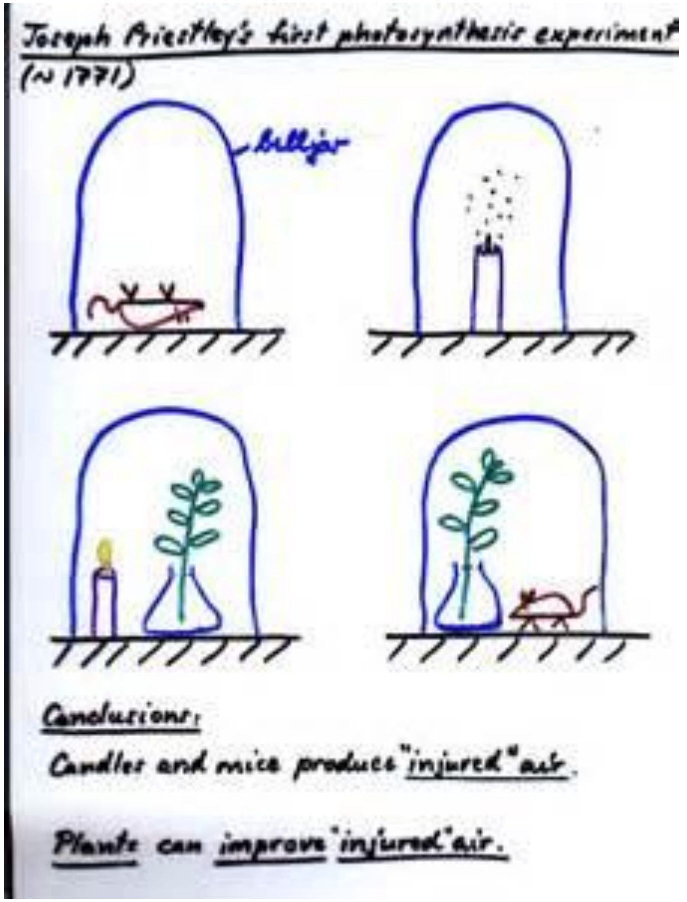
- Does the increase in mass of a plant come from the air? The soil? The Water?
- Early research focused on the overall process
- Later researchers investigated the detailed chemical pathways

Van Helmont's Experiment 1643

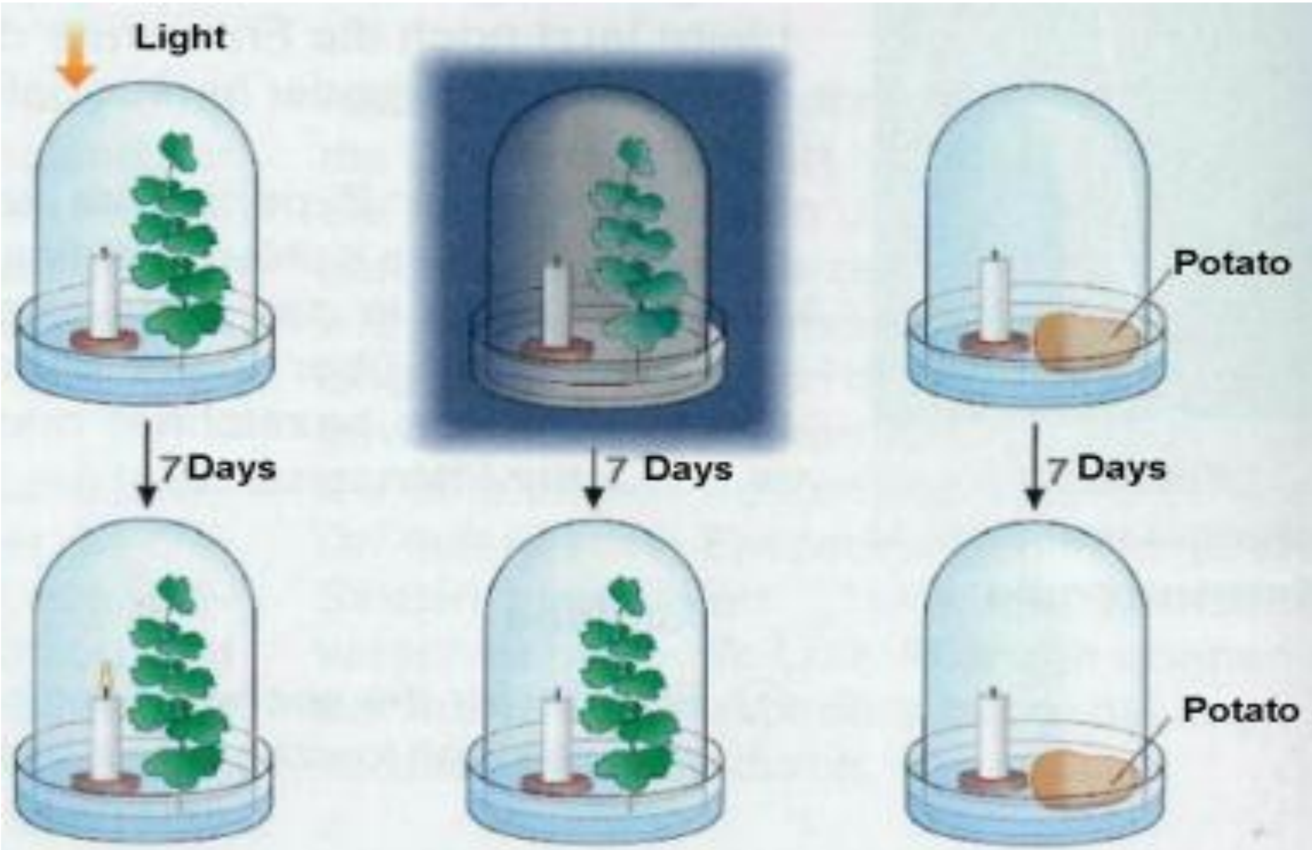
- Plant： 2.27kg→ 75 kg in 5 years
- Soil： 90kg → 90 kg
- Concluded mass came from water

Priestley's Experiment 1771

- **Burned candle in bell jar until it went out.**
- **Placed sprig of mint in bell jar for a few days.**
- **Candle could be relit and burn.**
- **Concluded plants released substance (O_2) necessary for burning.**



Ingenhousz's Experiment 1779



- **Light** was necessary for plant to produce the "burning gas"

Julius Robert Mayer 1845

- Proposed that plant can convert light energy into chemical energy

Samuel Rubin & Martin Kamen 1941

- Used isotopes to determine that the oxygen comes from water in photosynthesis

RUBIN

KAMEN

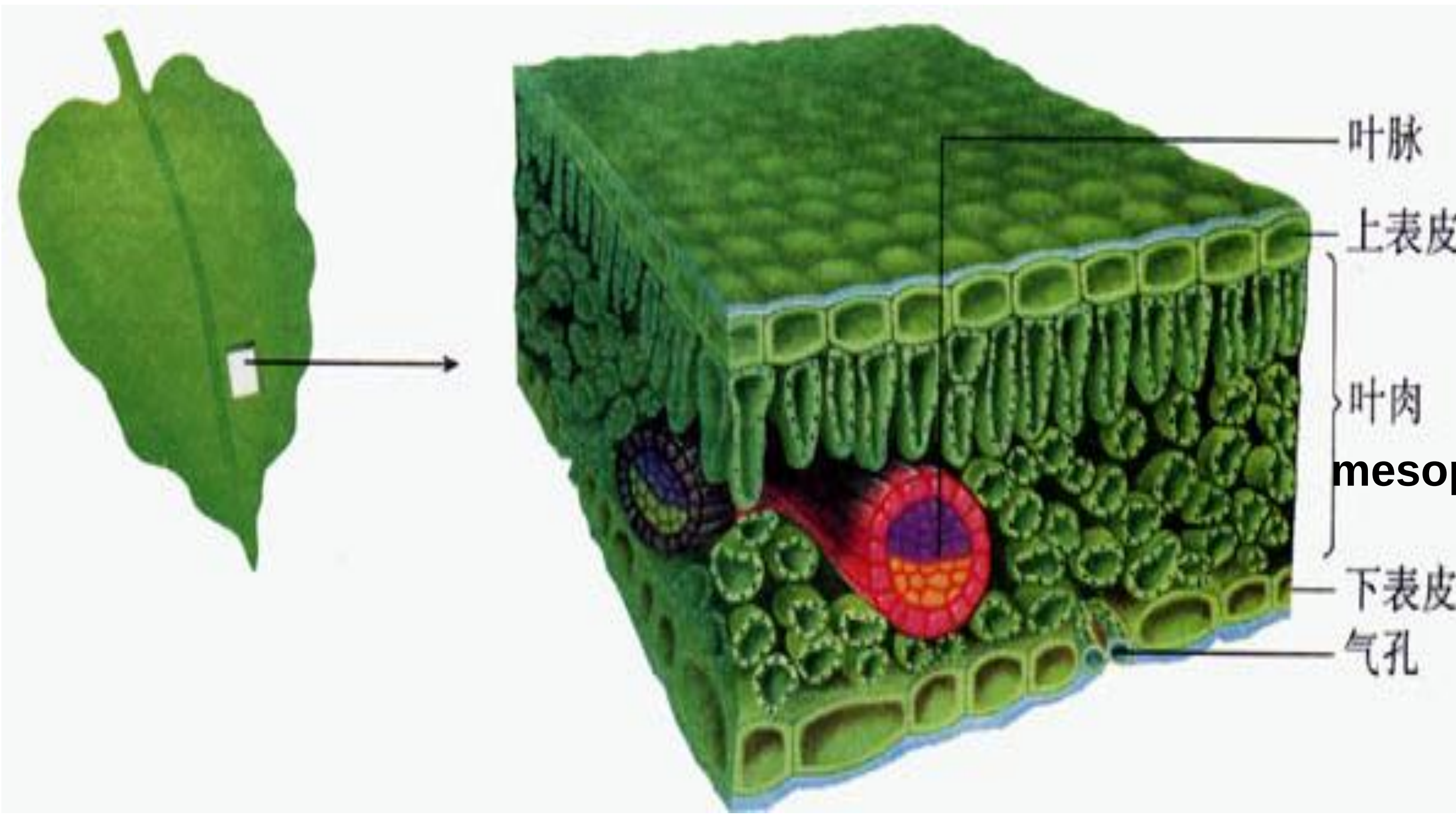
Melvin Calvin 1948

- First to trace the path that $CO_2 \rightarrow$ glucose
- **Calvin Cycle** or **light independent reaction** or **dark reaction**

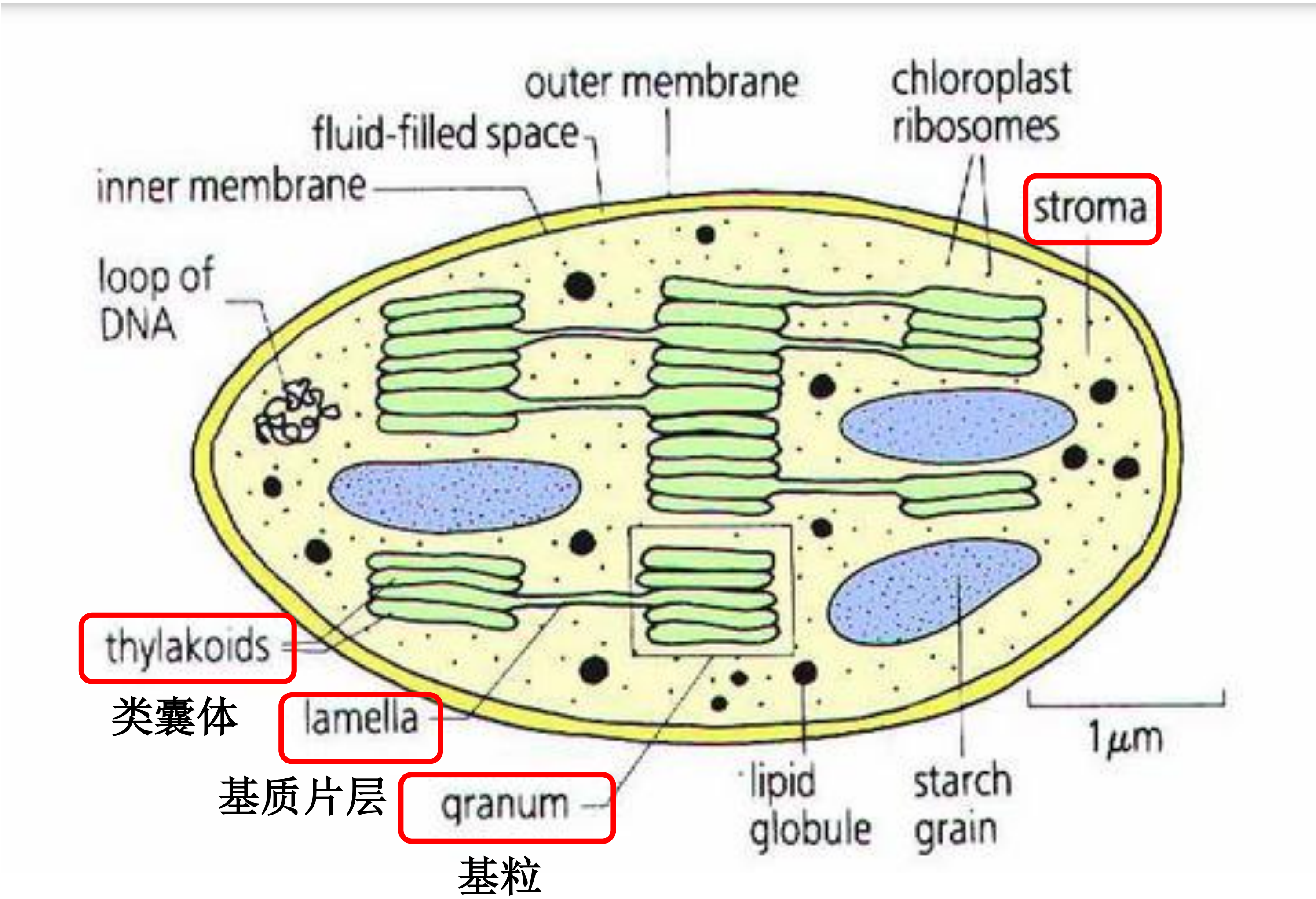
Rudolph Marcus (1992 Nobel)

- First to describe the electron transport chain
- **Marcus theory** of **electron transfer reactions** in 1956

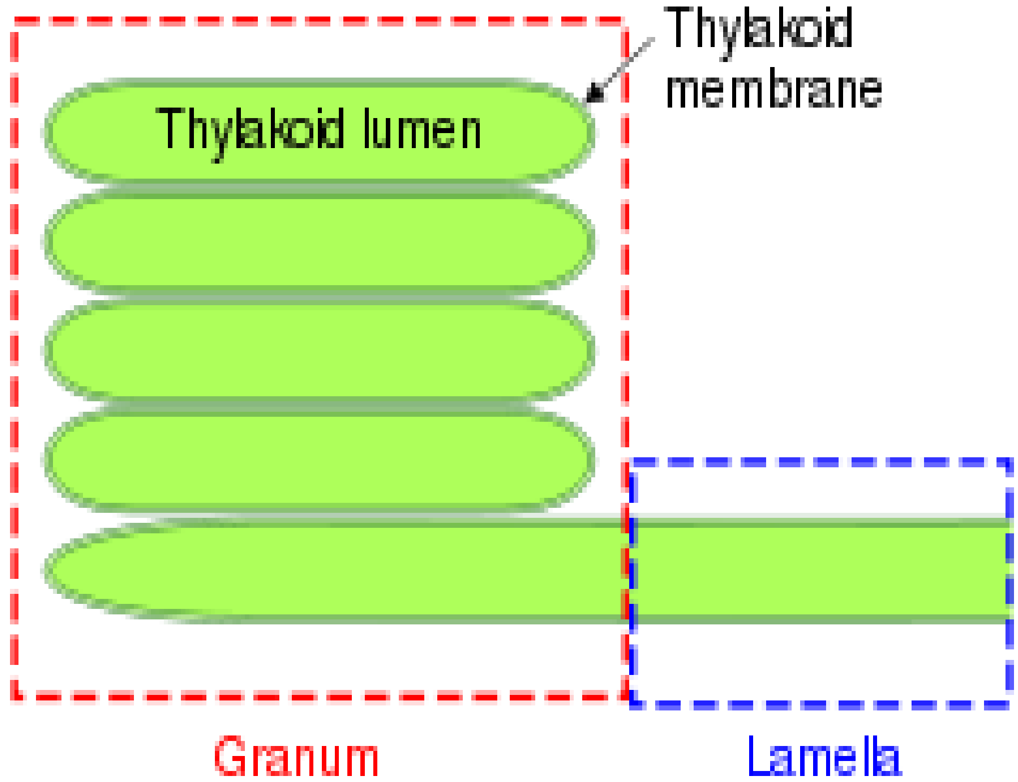
2.Where does photosynthesis take place?

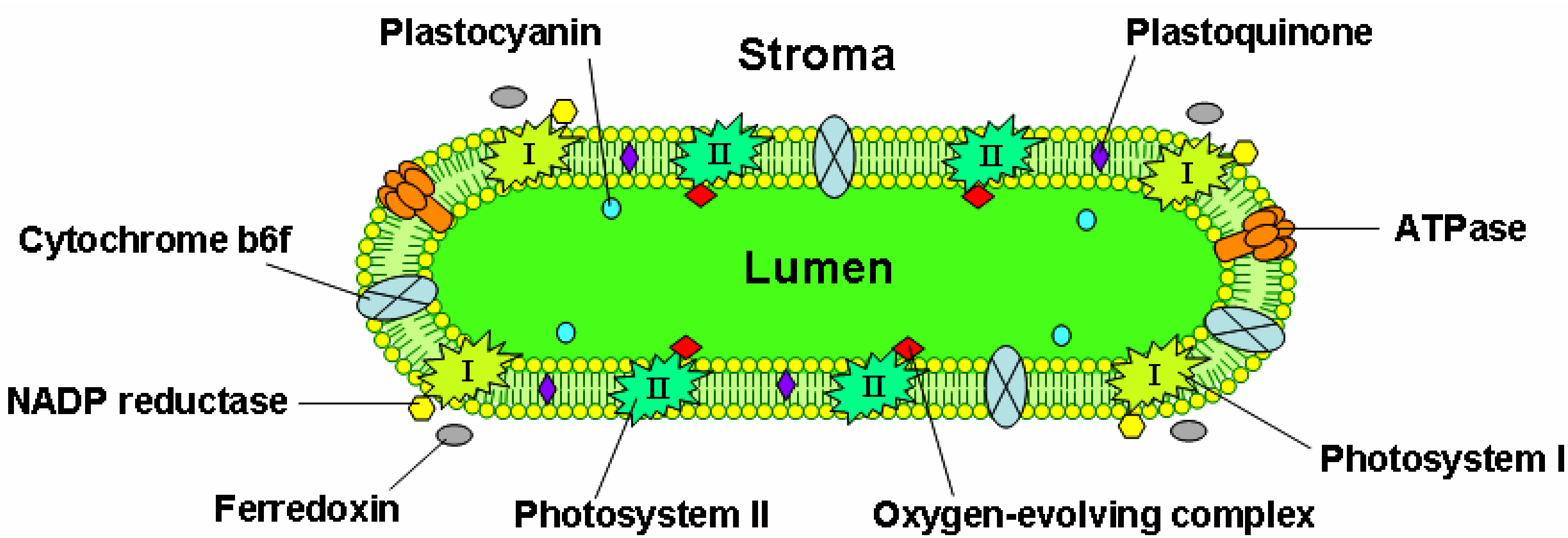


Chloroplast（叶绿体）



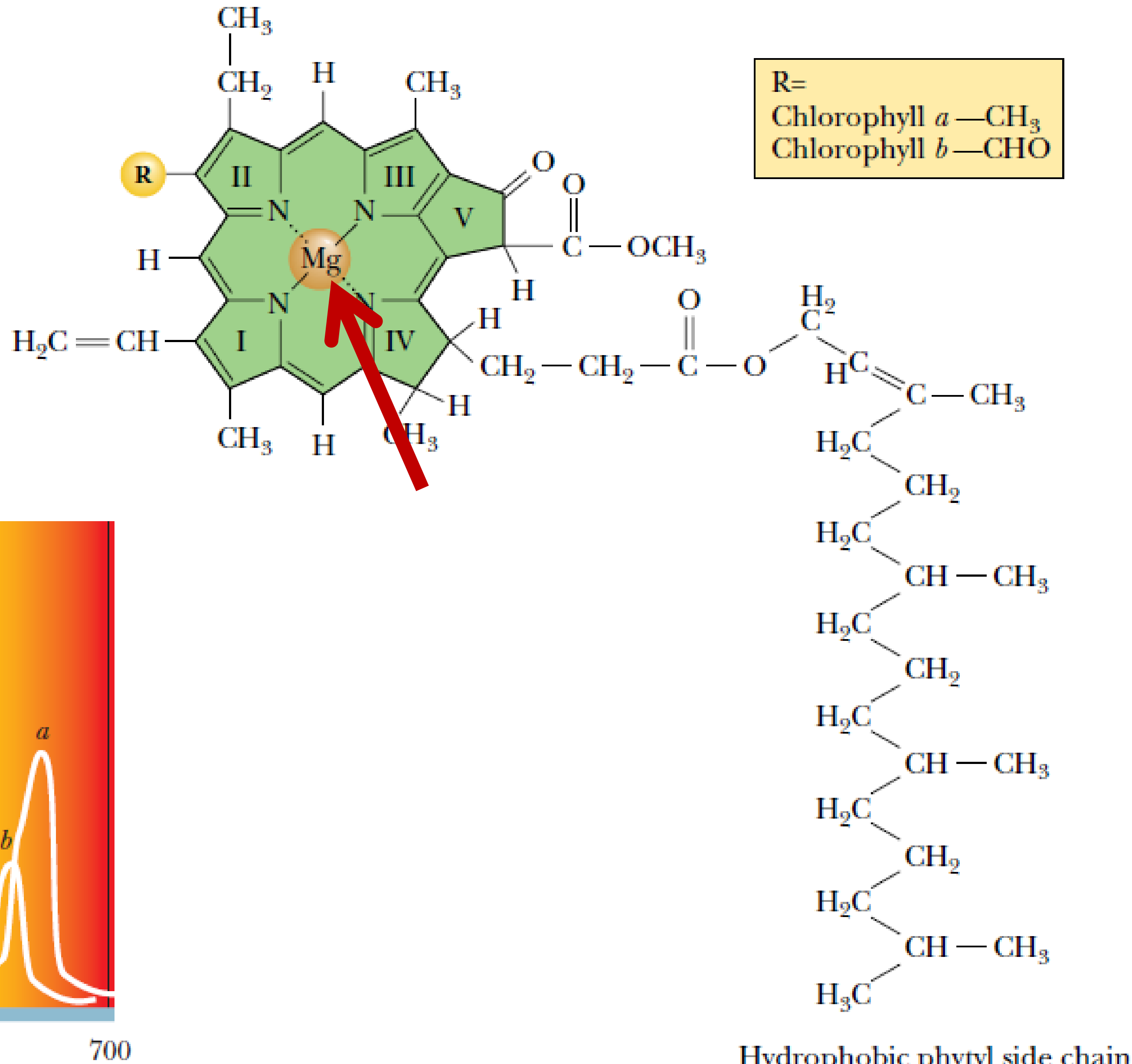
Thylakoid
（类囊体）





Chloroplast Pigments

- Chlorophyll a
- Chlorophyll b
- Carotenoids（类胡萝卜素）
- Xanthophyll（叶黄素）



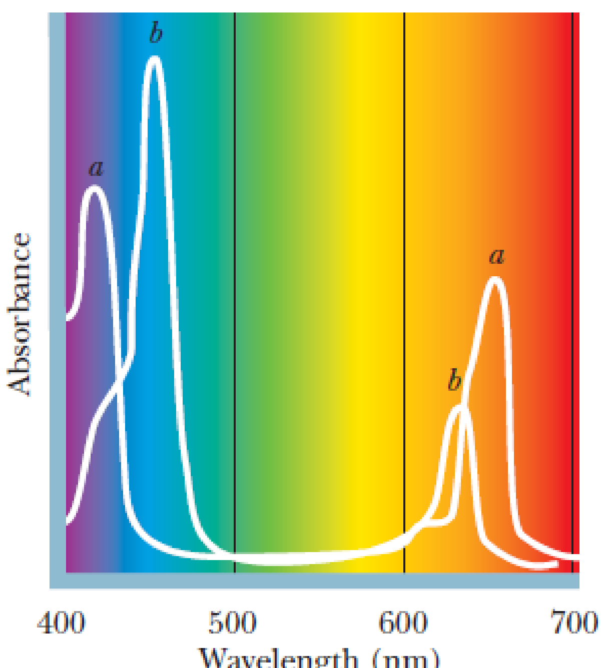


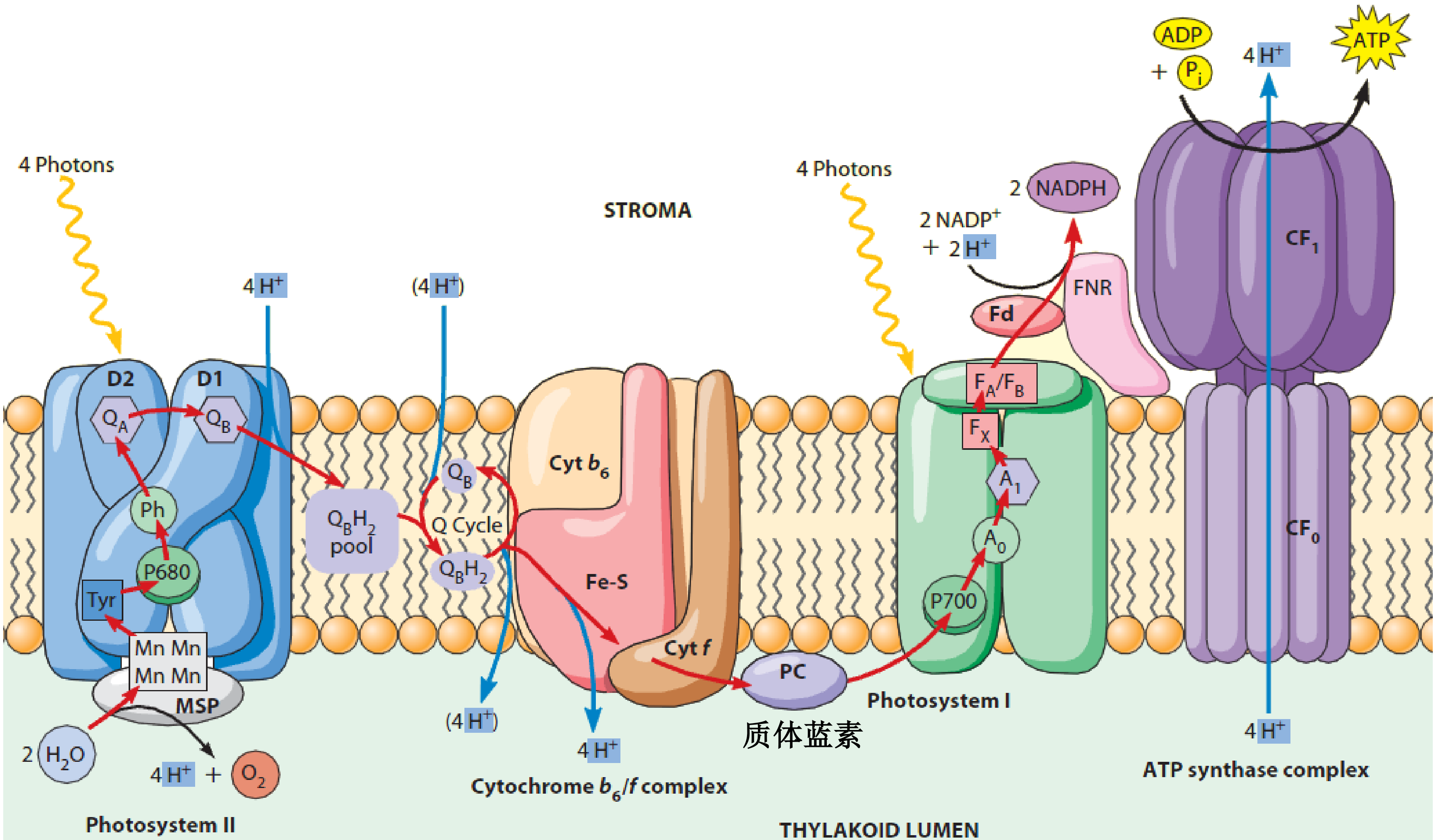
FIGURE 22.6 • Absorption spectra of chlorophylls *a* and *b*.

3. Photosynthesis

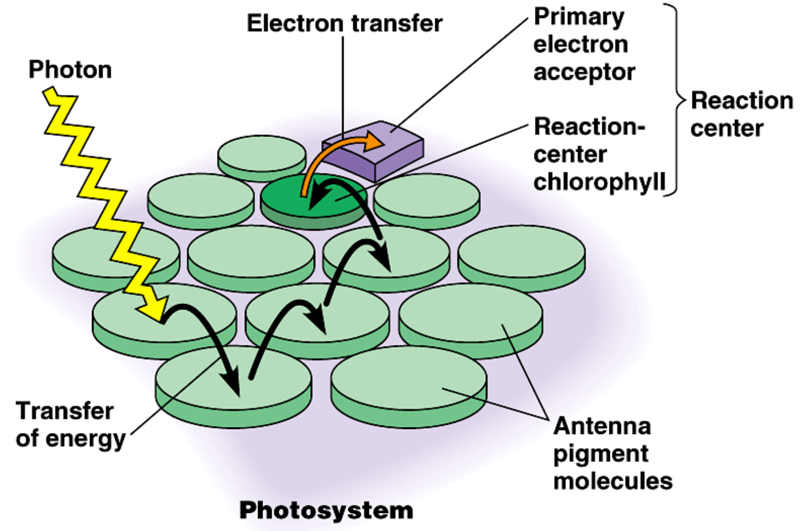
•The **light reactions** ---- **thylakoid（类囊体） membranes** **electrons** from **H_2O** through a series of membrane-bound carriers, producing **NADPH** and **ATP**.（ **light dependent reaction**）

• The **carbon-assimilation reactions** ---- **Chl stroma（基质）** reduce CO_2 with NADPH and ATP. （dark reaction，**light independent reaction** ）

3.1 Light reactions



Photosystem I



- >200 **chlorophyll a**, little **chlorop**
- Carotenoid（类胡萝卜素）with protein
- A pair of special **chlorophyll a** cal
- Primary electron acceptor called **A_0**

Photosystem II

- **Chlorophyll a,** small amount of **chlorophyll b**
- ß-carotene with protein
- A pair of special **chlorophyll a** called **P680**
- Primary electron acceptor called **pheophytin**（褐藻素）

The Stucture of PS Ⅱ

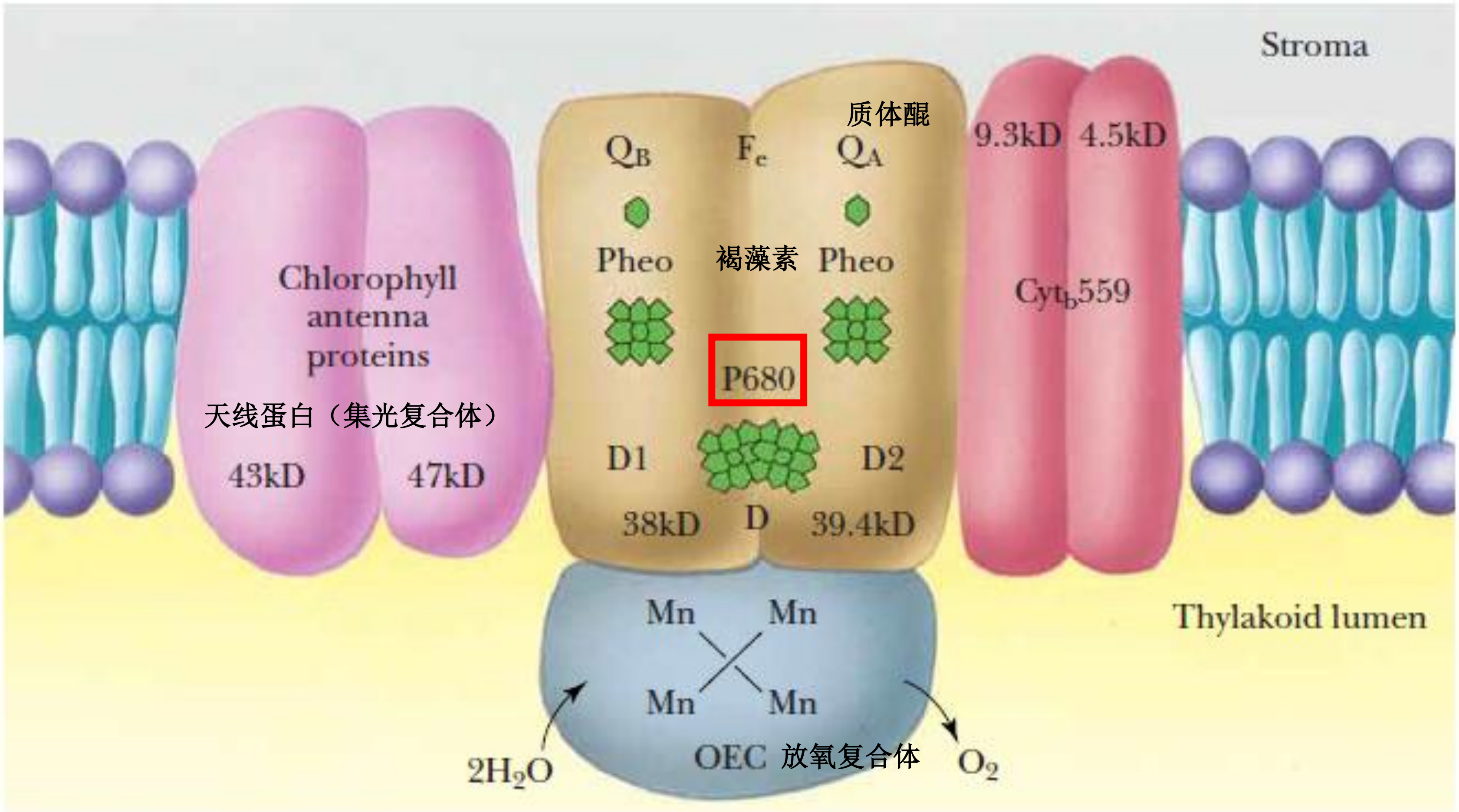
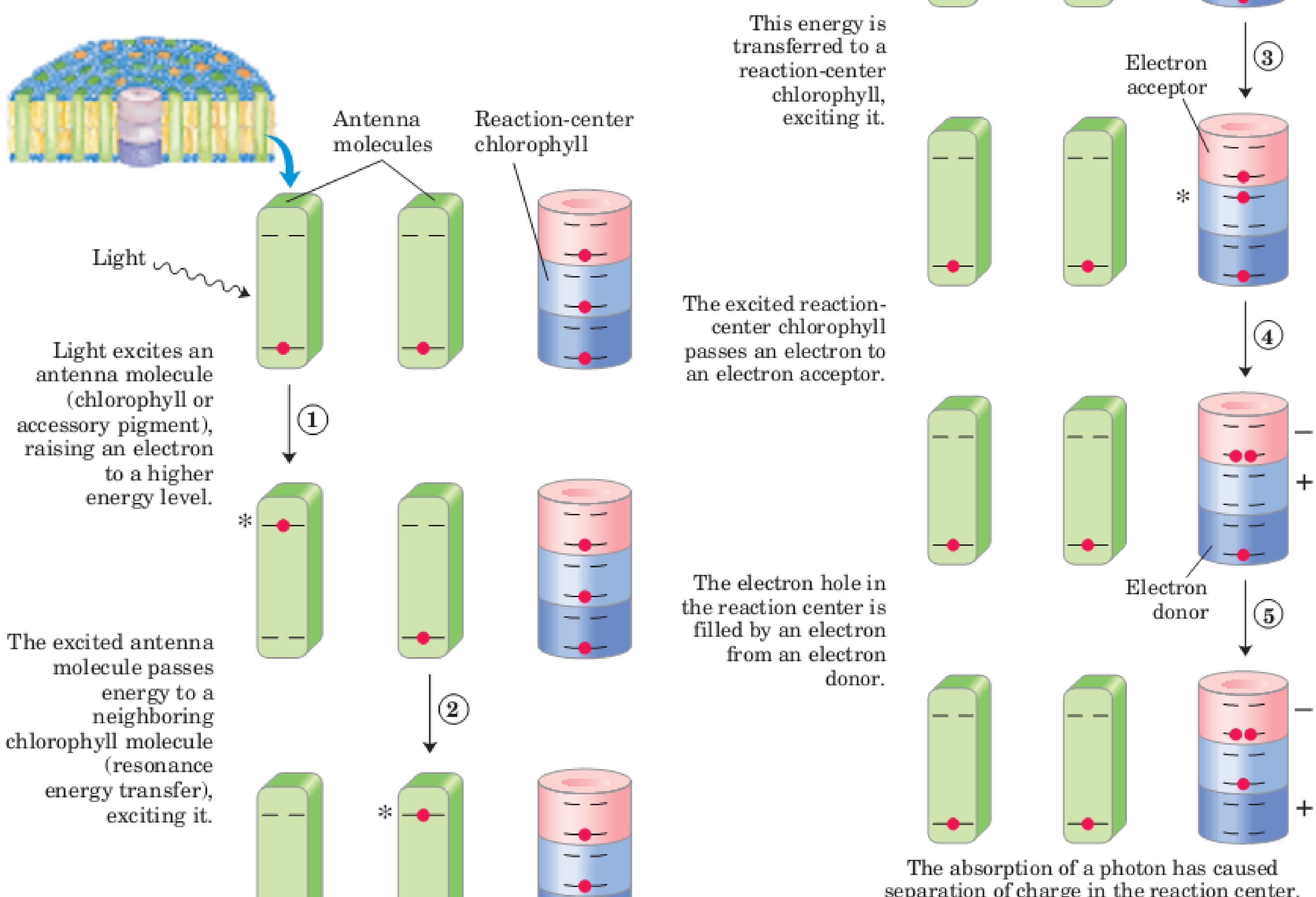
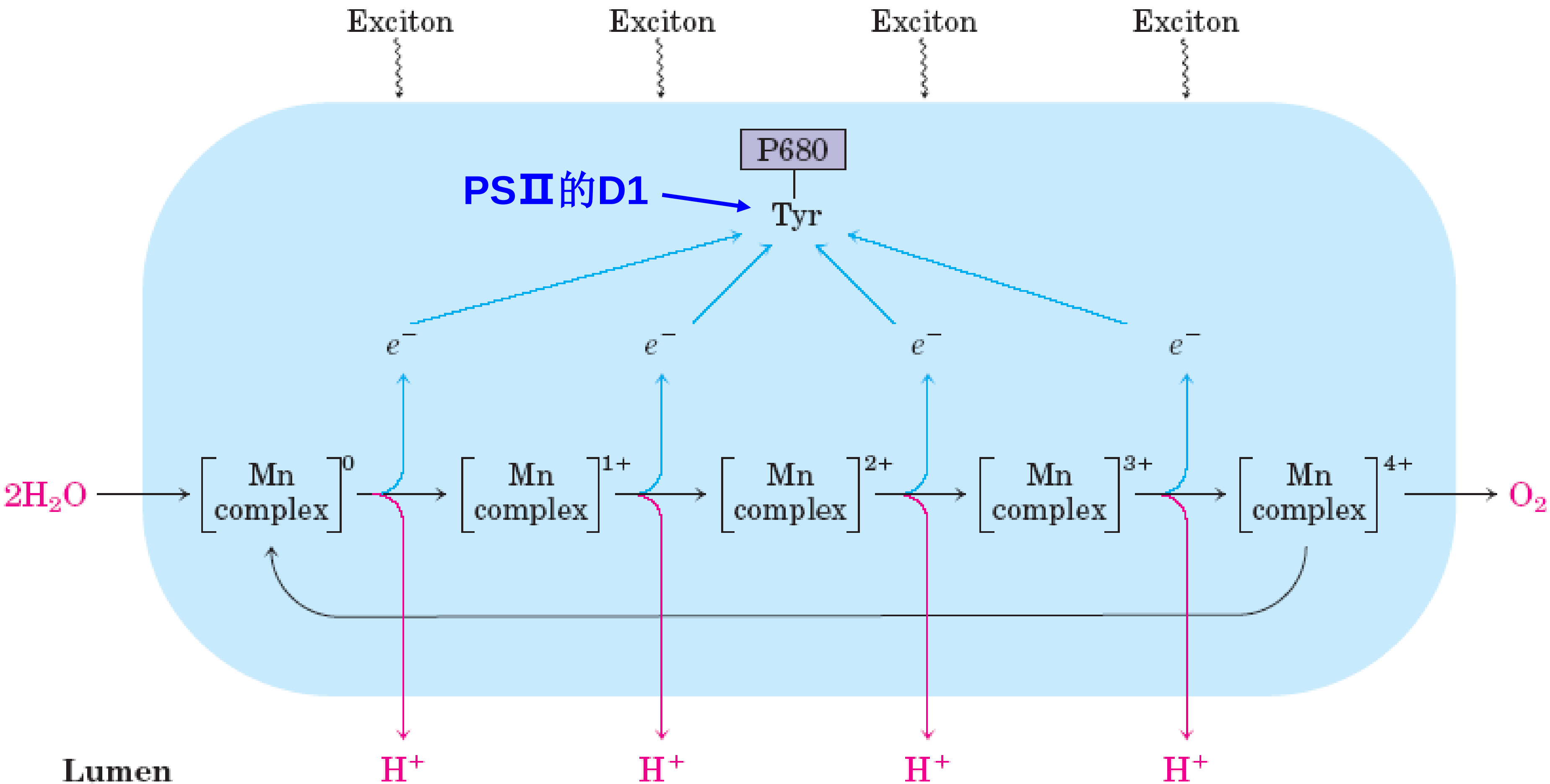


FIGURE 22.19 • The molecular architecture of PSII. The core of the PSII complex consists of the two polypeptides (D1 and D2) that bind P680, pheophytin (Pheo), and the quinones, Q_A and Q_B. Additional components of this complex include cytochrome b_{559}, two additional intrinsic proteins (47 and 43 kD) that serve an accessory light-harvesting function, and an extrinsic protein complex that is essential to O_2 evolution.

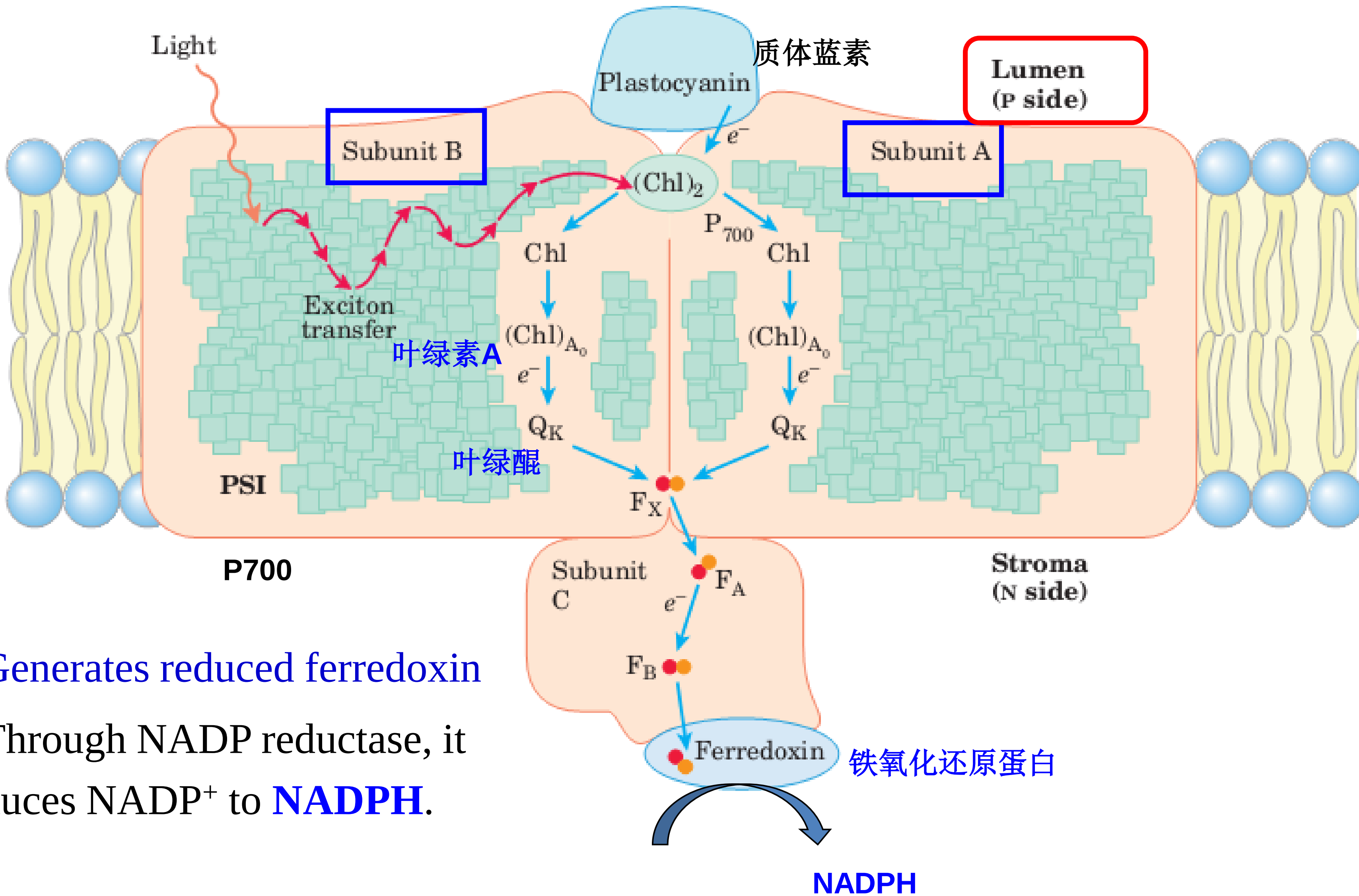


initiates an oxidation-reduction chain



Oxygen-evolving complex （放氧复合体）

The Stucture of PS Ⅰ



- Generates reduced ferredoxin
- Through NADP reductase, it reduces $NADP^+$ to **NADPH**.

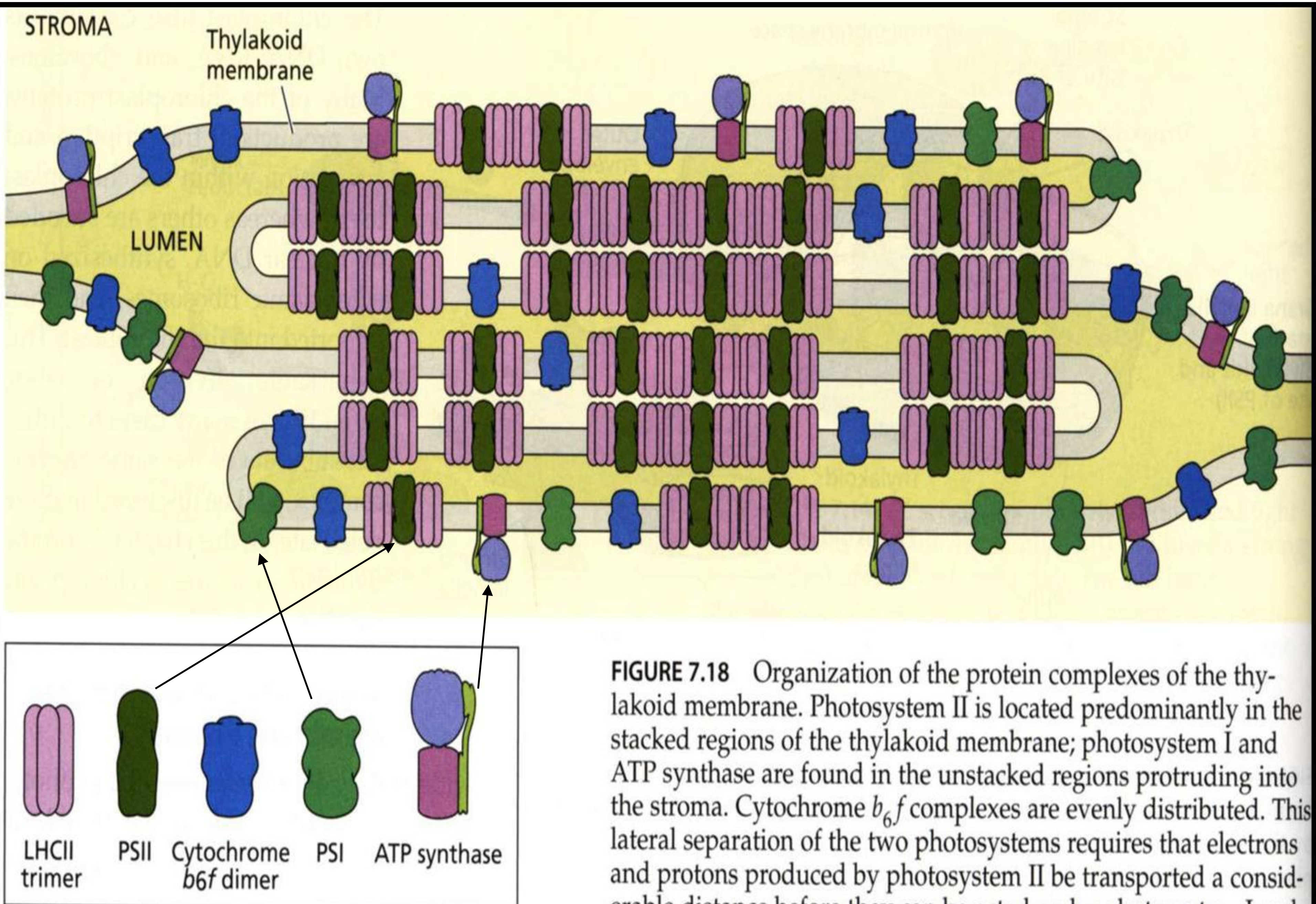
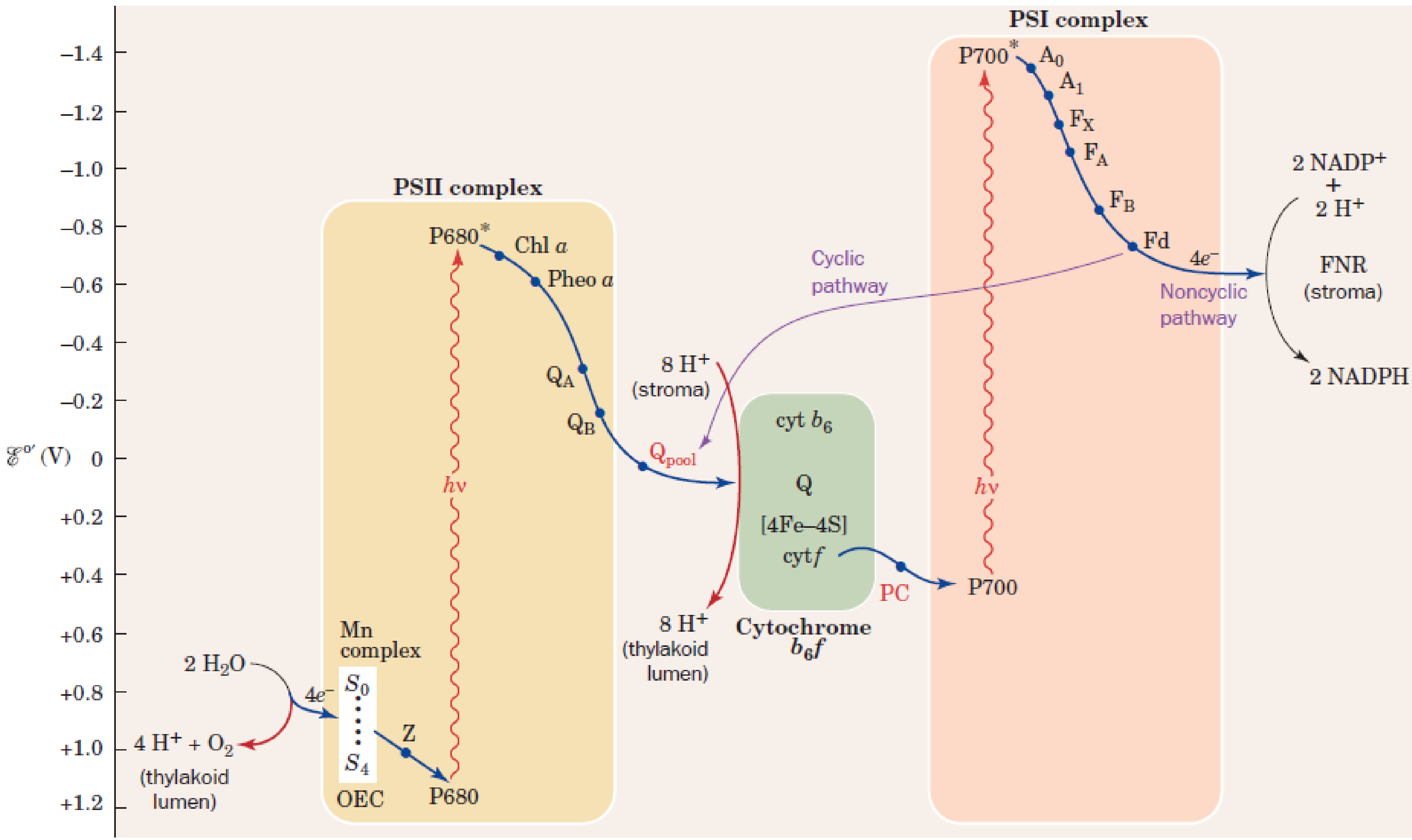


FIGURE 7.18 Organization of the protein complexes of the thylakoid membrane. Photosystem II is located predominantly in the stacked regions of the thylakoid membrane; photosystem I and ATP synthase are found in the unstacked regions protruding into the stroma. Cytochrome b_6f complexes are evenly distributed. This lateral separation of the two photosystems requires that electrons and protons produced by photosystem II be transported a considerable distance before they can be acted on by photosystem I and the ATP-coupling enzyme. (After Allen and Forsberg 2001.)

Plant "z-scheme" photosystems I and II



Photophosphorylation

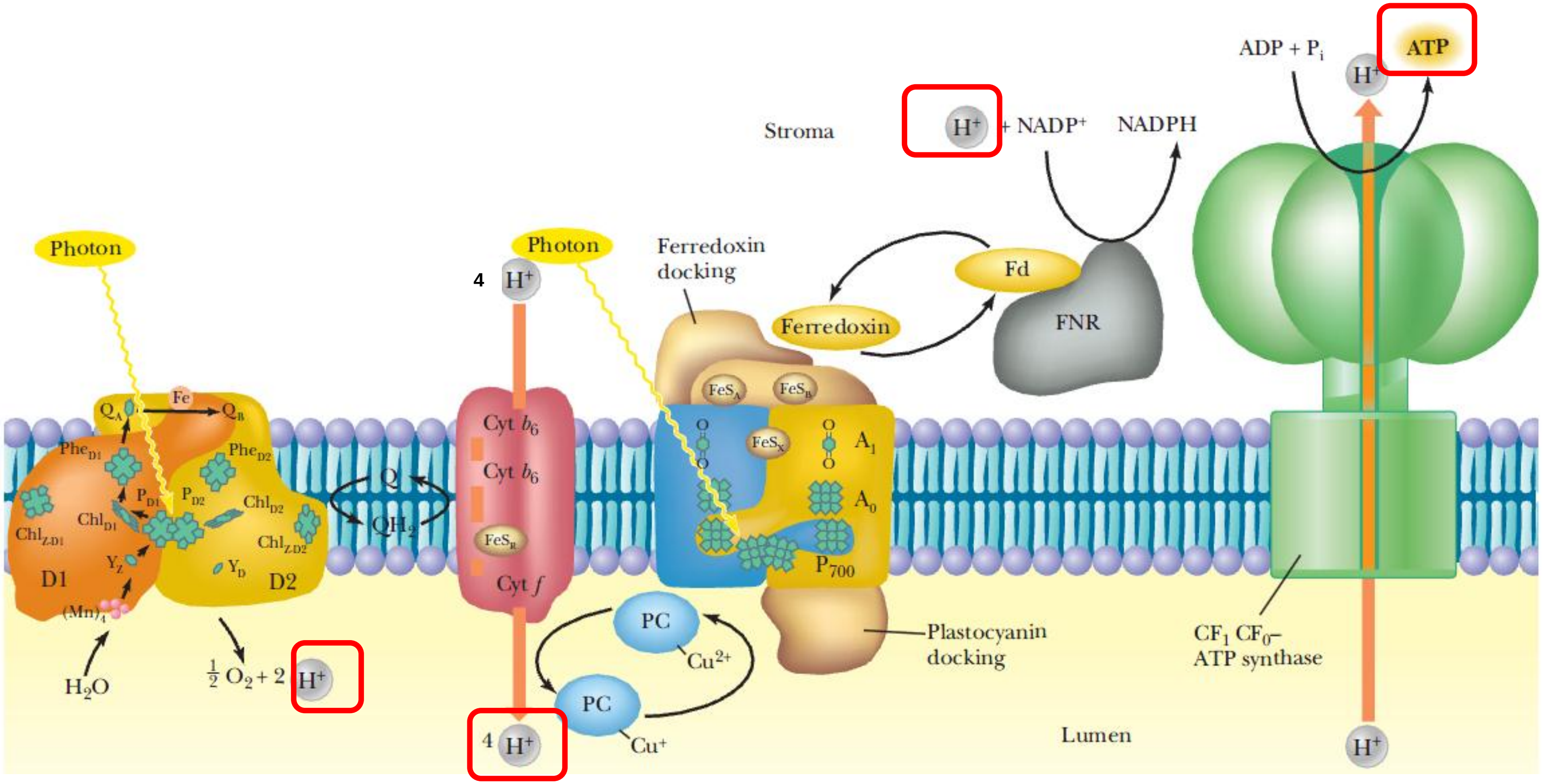
★ ADP + Pi $\xrightarrow{\text{light}}$ ATP

★ Non-cyclic & cyclic photophosphorylation

★ The mechanism is similar to that of oxidative phosphorylation

How the Light Reactions Generate ATP and NADPH?

Noncyclic Photophosphorylation (非环式光合磷酸化)



- Photoexcitation of PS I and PS II leads Q → QH_2
- **H_2O splitting by PS II**
- oxidation of **QH_2** by the ***cytb6f*** leads to **H^+** across the membrane

Cyclic Photophosphorylation（环式光合磷酸化）

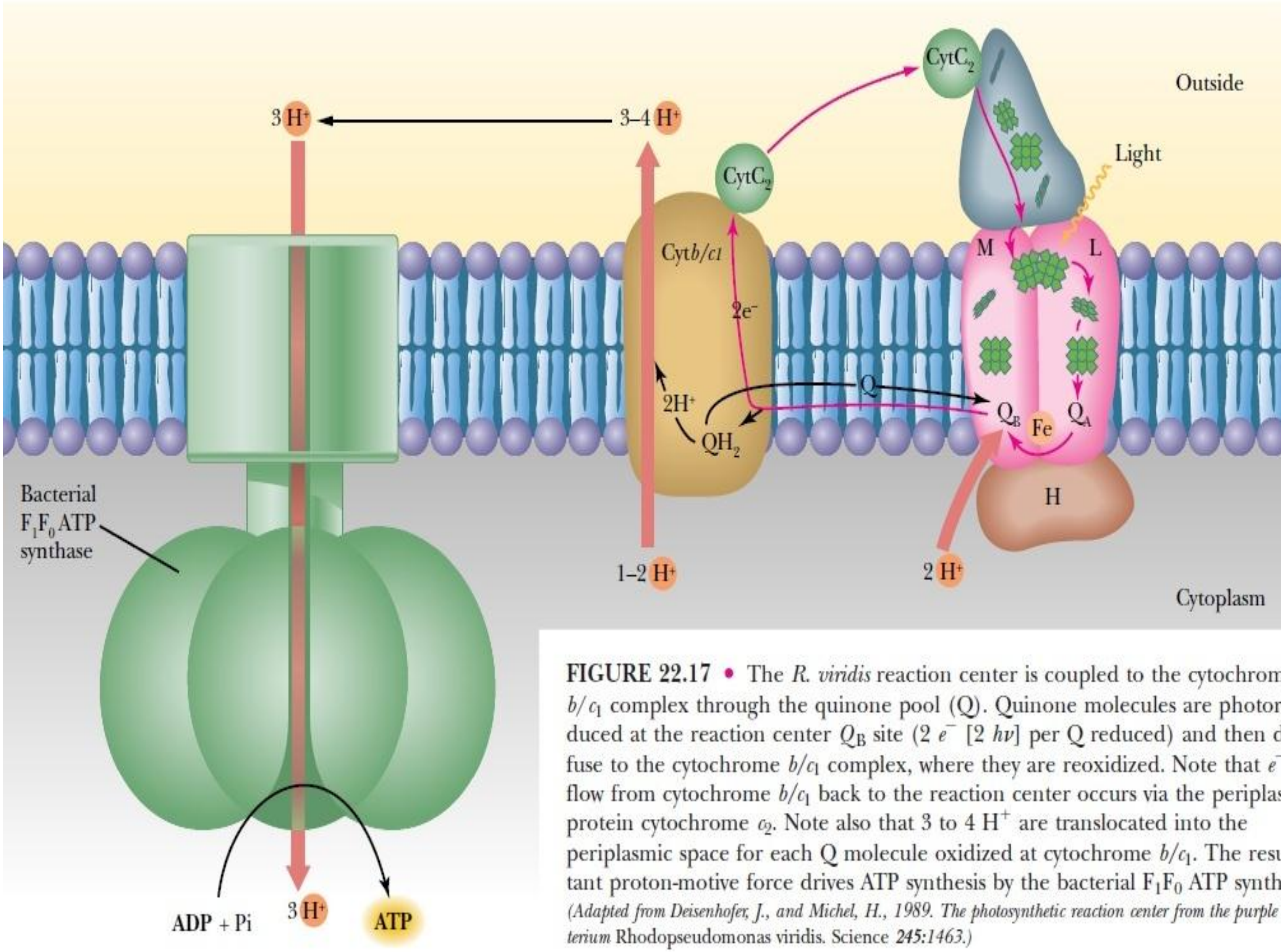
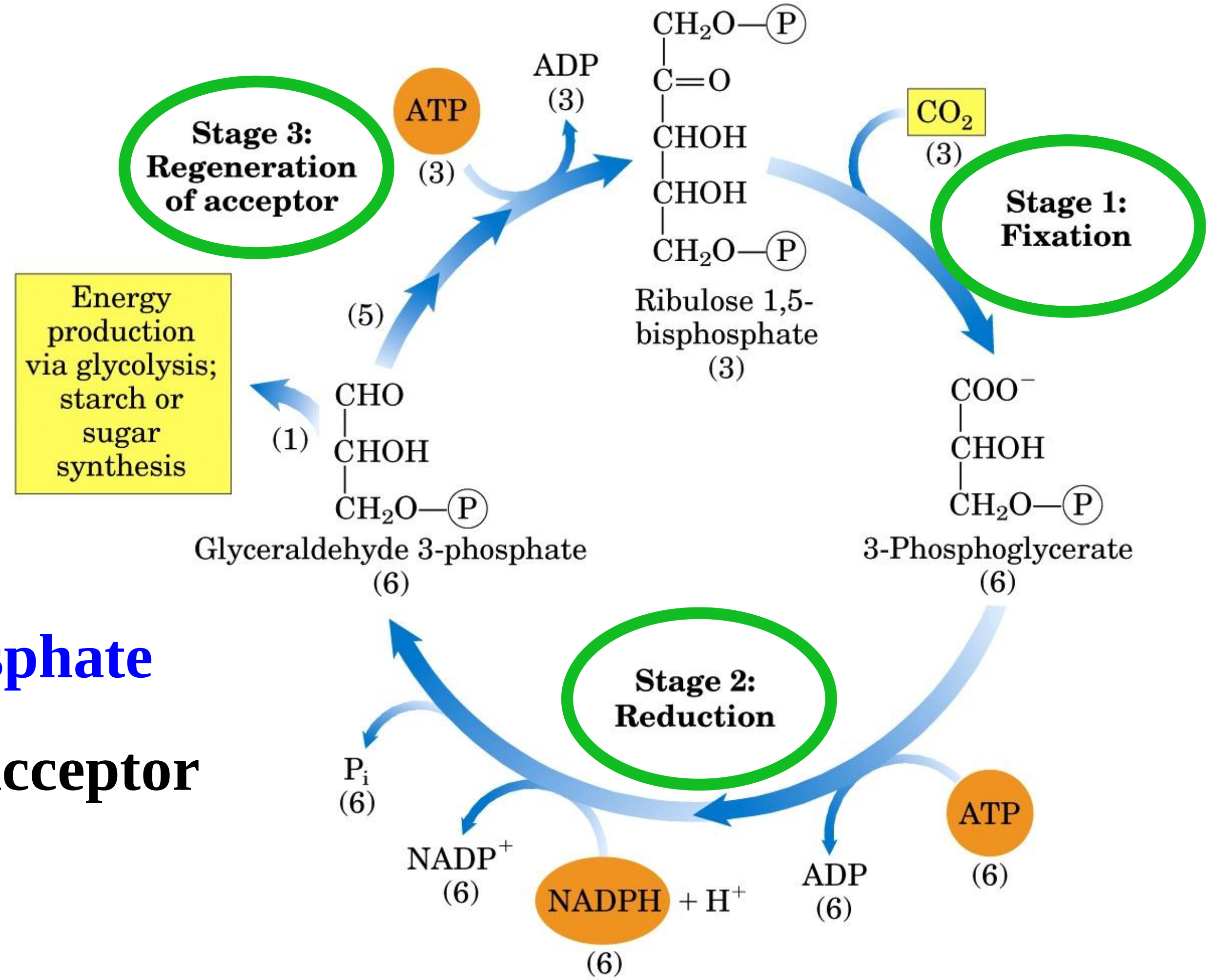


FIGURE 22.17 • The *R. viridis* reaction center is coupled to the cytochrome b/c_1 complex through the quinone pool (Q). Quinone molecules are photoreduced at the reaction center Q_B site (2 e^- [2 $h\nu$] per Q reduced) and then diffuse to the cytochrome b/c_1 complex, where they are reoxidized. Note that e^- flow from cytochrome b/c_1 back to the reaction center occurs via the periplasmic protein cytochrome c_2. Note also that 3 to 4 H$^+$ are translocated into the periplasmic space for each Q molecule oxidized at cytochrome b/c_1. The resultant proton-motive force drives ATP synthesis by the bacterial F_1F_0 ATP synthase. *(Adapted from Deisenhofer, J., and Michel, H., 1989. The photosynthetic reaction center from the purple bacterium* Rhodopseudomonas viridis. Science *245:1463.)*

3.2 Carbon dioxide fixation

- In C3 plants, all processes occur in the **mesophyll cells**.

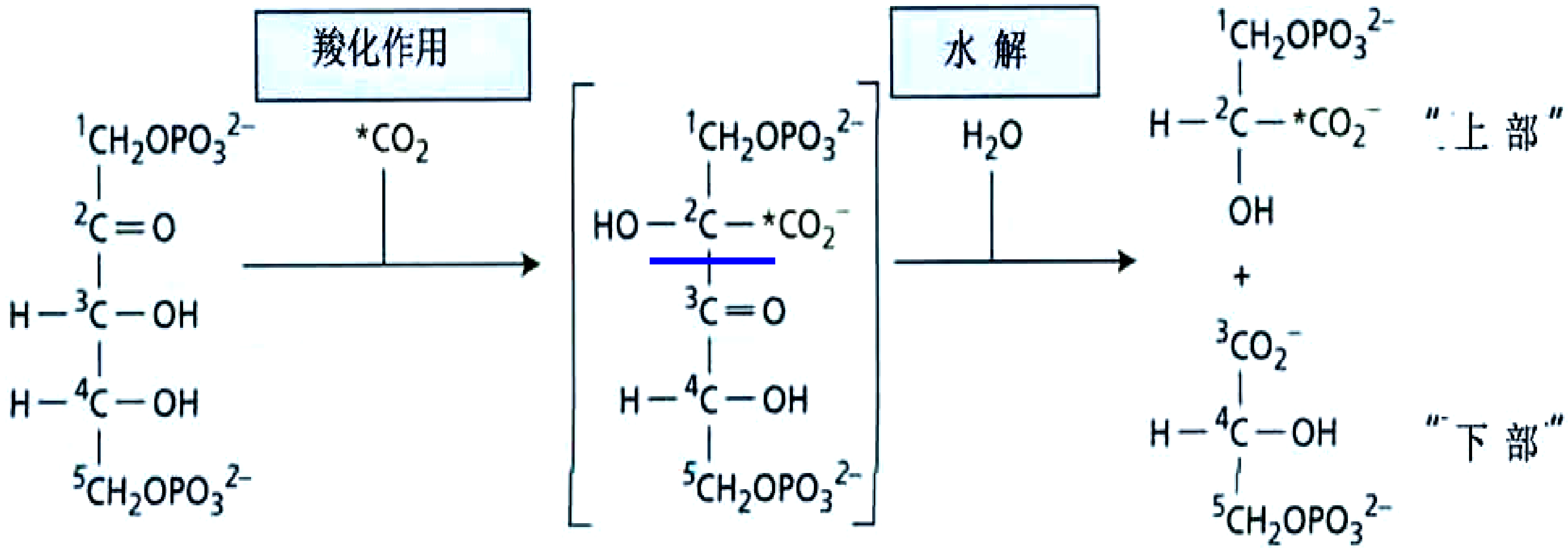


- **Ribulose-1,5-Bisphosphate**

（RuBP） is the CO_2 acceptor

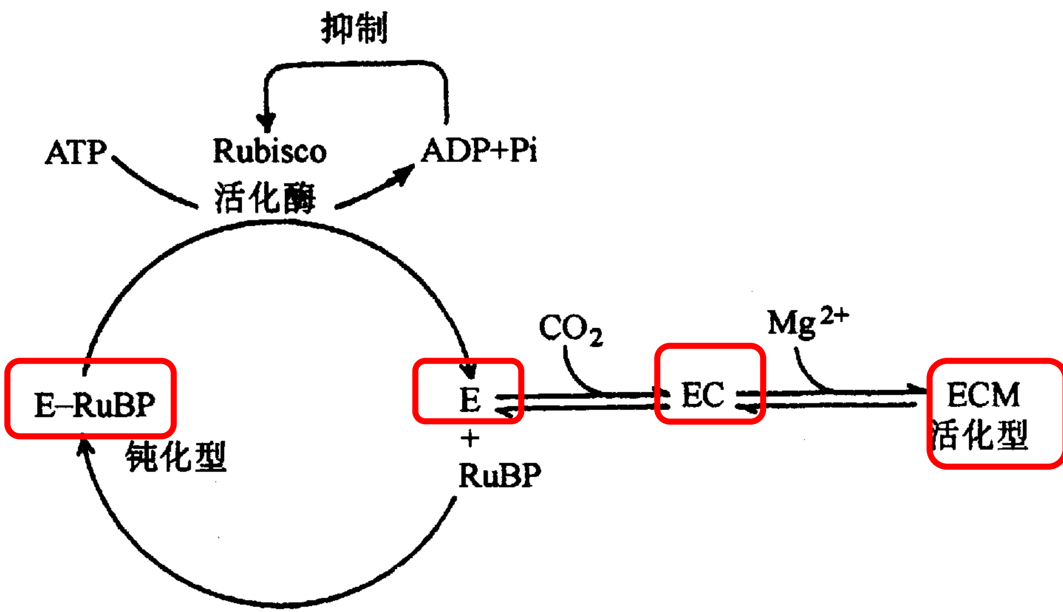
(1) carboxylation phase (羧化阶段)

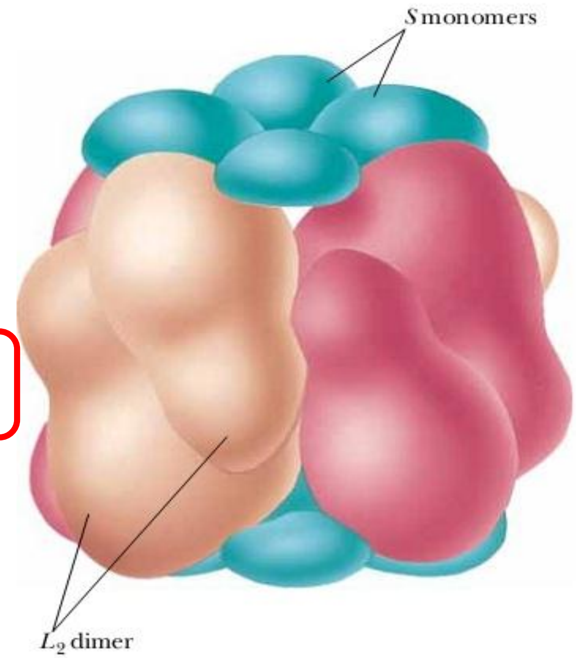
Ribulose-1,5-Bisphosphate Carboxylase/Oxygenase （**Rubisco**）



1，5- 二磷酸 - 核酮糖　　2- 羧基 -3- 酮基阿拉糖醇 -1，5- 二磷酸　　3，磷酸甘油酸

（是一种暂时的与酶结合不稳定的中间产物）





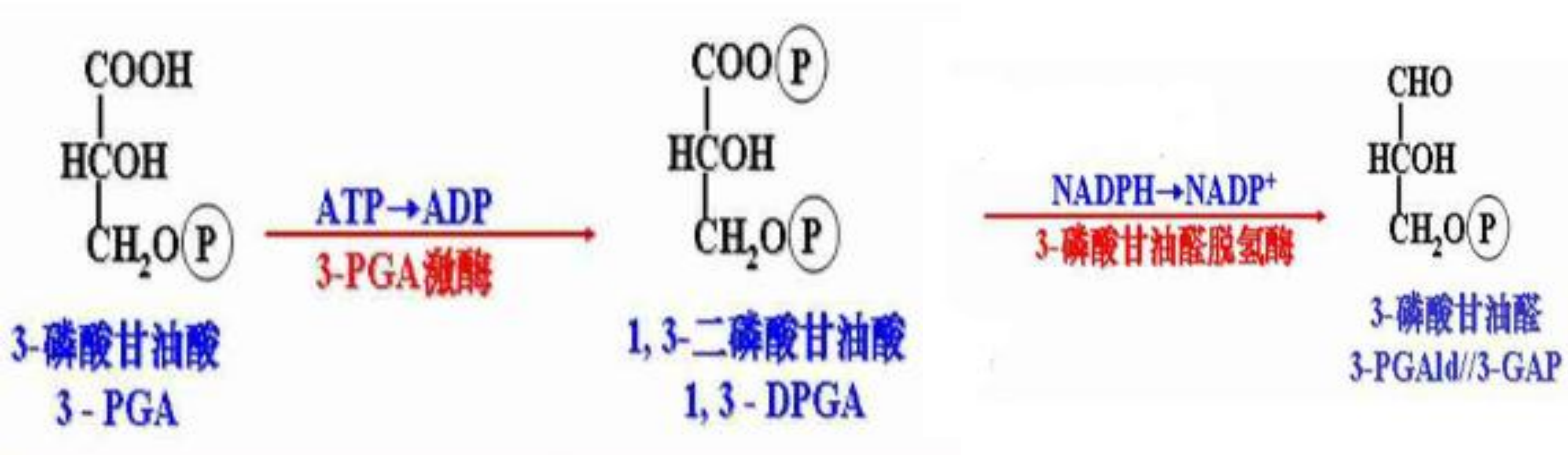
Ribulose-1,5-Bisphosphate Carboxylase

（8L+8S subunits）

(2) reduction phase (还原阶段)

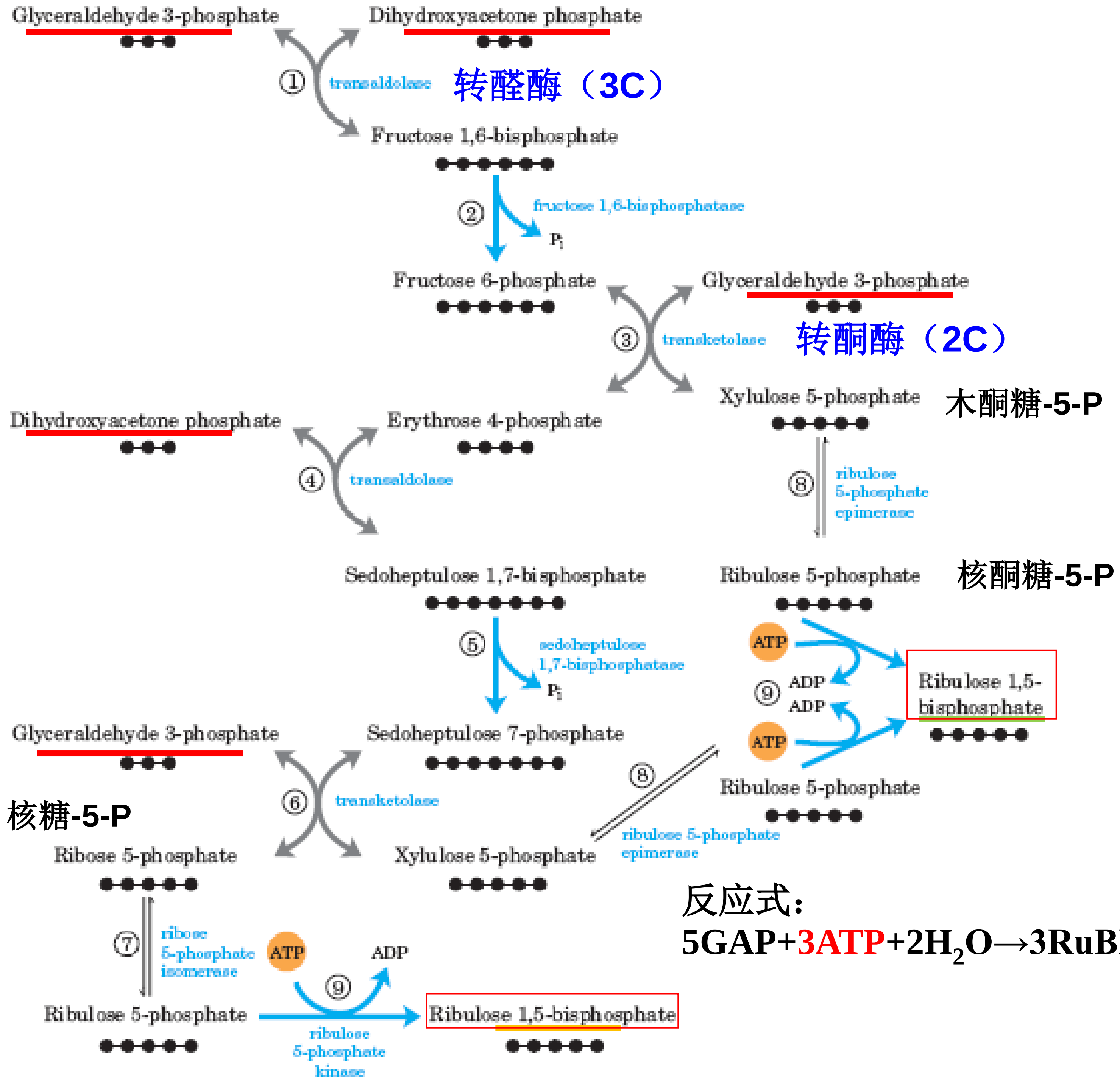
PGA+ATP+NADPH+ H^+→→GAP+ADP+$NADP^+$ + Pi

3−磷酸甘油酸　　　　　　　　　　　　甘油醛-3-磷酸



(3) regeneration phase (再生阶段)

GAP（甘油醛-3-磷酸）→　**RuBP**（核酮糖-1,-5-二磷酸）



反应式：

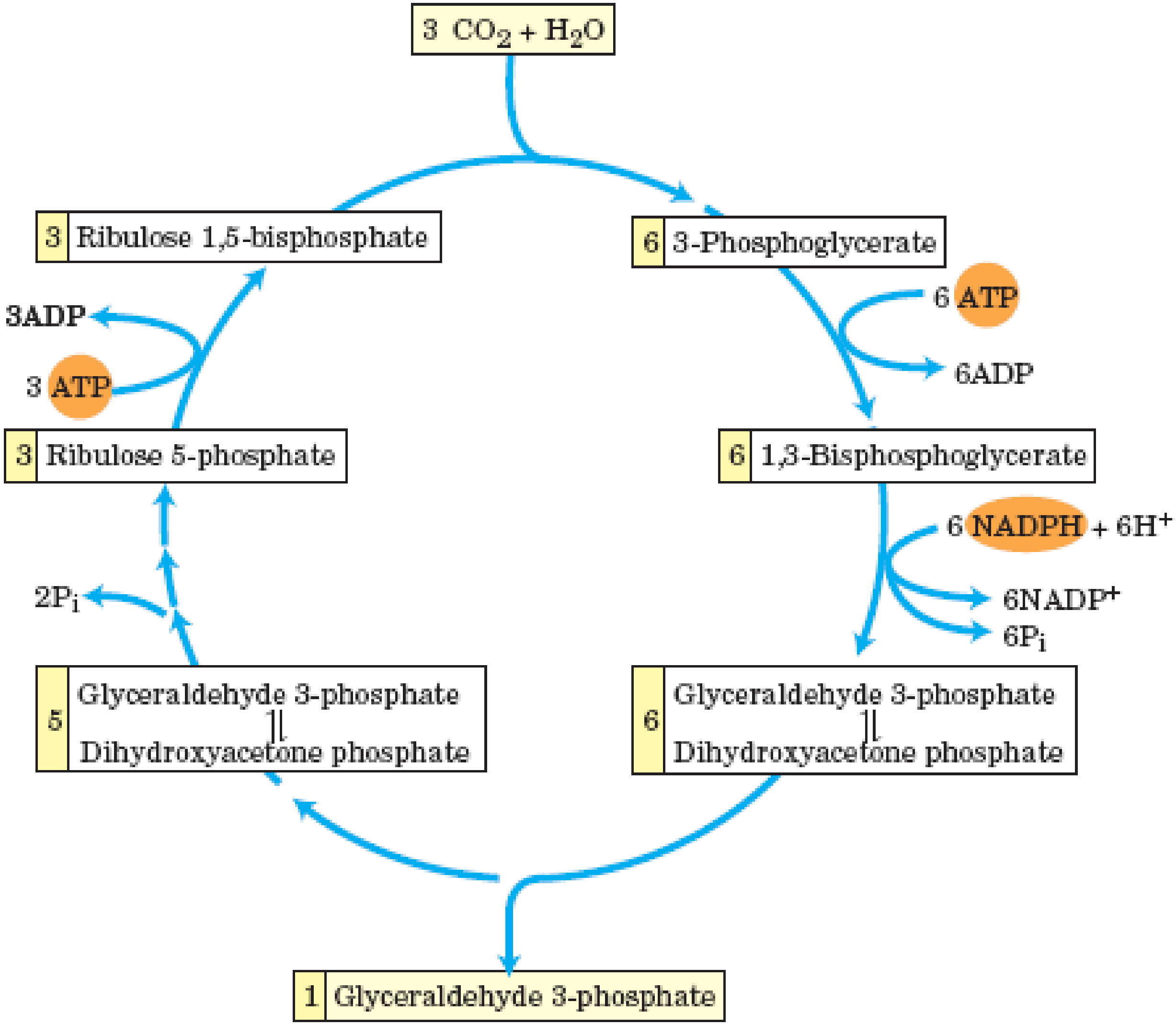
$$5GAP+3ATP+2H_2O \rightarrow 3RuBP+3ADP+2Pi+3H^+$$

The Calvin Cycle Series of Reactions

Reactions 1 through 15 constitute the cycle that leads to the formation of one equivalent of glucose. The enzyme catalyzing each step, a concise reaction, and the overall carbon balance is given. Numbers in parentheses show the numbers of carbon atoms in the substrate and product molecules. Prefix numbers indicate in a stoichiometric fashion how many times each step is carried out in order to provide a balanced net reaction.

1. Ribulose bisphosphate carboxylase: 6 CO_2 + 6 H_2O + 6 RuBP $\longrightarrow$ 12 3-PG	6(1) + 6(5) $\longrightarrow$ 12(3)
2. 3-Phosphoglycerate kinase: 12 3-PG + 12 ATP $\longrightarrow$ 12 1,3-BPG + 12 ADP	12(3) $\longrightarrow$ 12(3)
3. $NADP^+$-glyceraldehyde-3-P dehydrogenase: 12 1,3-BPG + 12 NADPH $\longrightarrow$ 12 $NADP^+$ + 12 G3P + 12 P_i	12(3) $\longrightarrow$ 12(3)
4. Triose-P isomerase: 5 G3P $\longrightarrow$ 5 DHAP	5(3) $\longrightarrow$ 5(3)
5. Aldolase: 3 G3P + 3 DHAP $\longrightarrow$ 3 FBP	3(3) + 3(3) $\longrightarrow$ 3(6)
6. Fructose bisphosphatase: 3 FBP + 3 H_2O $\longrightarrow$ 3 F6P + 3 P_1	3(6) $\longrightarrow$ 3(6)
7. Phosphoglucoisomerase: 1 F6P $\longrightarrow$ 1 G6P	1(6) $\longrightarrow$ 1(6)
8. Glucose phosphatase: 1 G6P + 1 H_2O $\longrightarrow$ 1 GLUCOSE + 1 P_i	1(6) $\longrightarrow$ 1(6)
The remainder of the pathway involves regenerating six RuBP acceptors (= 30 C) from the leftover two F6P (12 C), four G3P (12 C), and two DHAP (6 C).	
9. Transketolase: 2 F6P + 2 G3P $\longrightarrow$ 2 Xu5P + 2 E4P	2(6) + 2(3) $\longrightarrow$ 2(5) + 2(4)
10. Aldolase: 2 E4P + 2 DHAP $\longrightarrow$ 2 sedoheptulose-1,7-bisphosphate (SBP)	2(4) + 2(3) $\longrightarrow$ 2(7)
11. Sedoheptulose bisphosphatase: 2 SBP + 2 H_2O $\longrightarrow$ 2 S7P + 2 P_i	2(7) $\longrightarrow$ 2(7)
12. Transketolase: 2 S7P + 2 G3P $\longrightarrow$ 2 Xu5P + 2 R5P	2(7) + 2(3) $\longrightarrow$ 4(5)
13. Phosphopentose epimerase: 4 Xu5P $\longrightarrow$ 4 Ru5P	4(5) $\longrightarrow$ 4(5)
14. Phosphopentose isomerase: 2 R5P $\longrightarrow$ 2 Ru5P	2(5) $\longrightarrow$ 2(5)
15. Phosphoribulose kinase: 6 Ru5P + 6 ATP $\longrightarrow$ 6 RuBP + 6 ADP	6(5) $\longrightarrow$ 6(5)
Net: 6 CO_2 + 18 ATP + 12 NADPH + 12 H^+ + 12 H_2O $\longrightarrow$ glucose + 18 ADP + 18 P_i + 12 $NADP^+$	6(1) $\longrightarrow$ 1(6)

Stoichiometry of CO_2 assimilation in the Calvin cycle



$6CO_2$

12NADPH

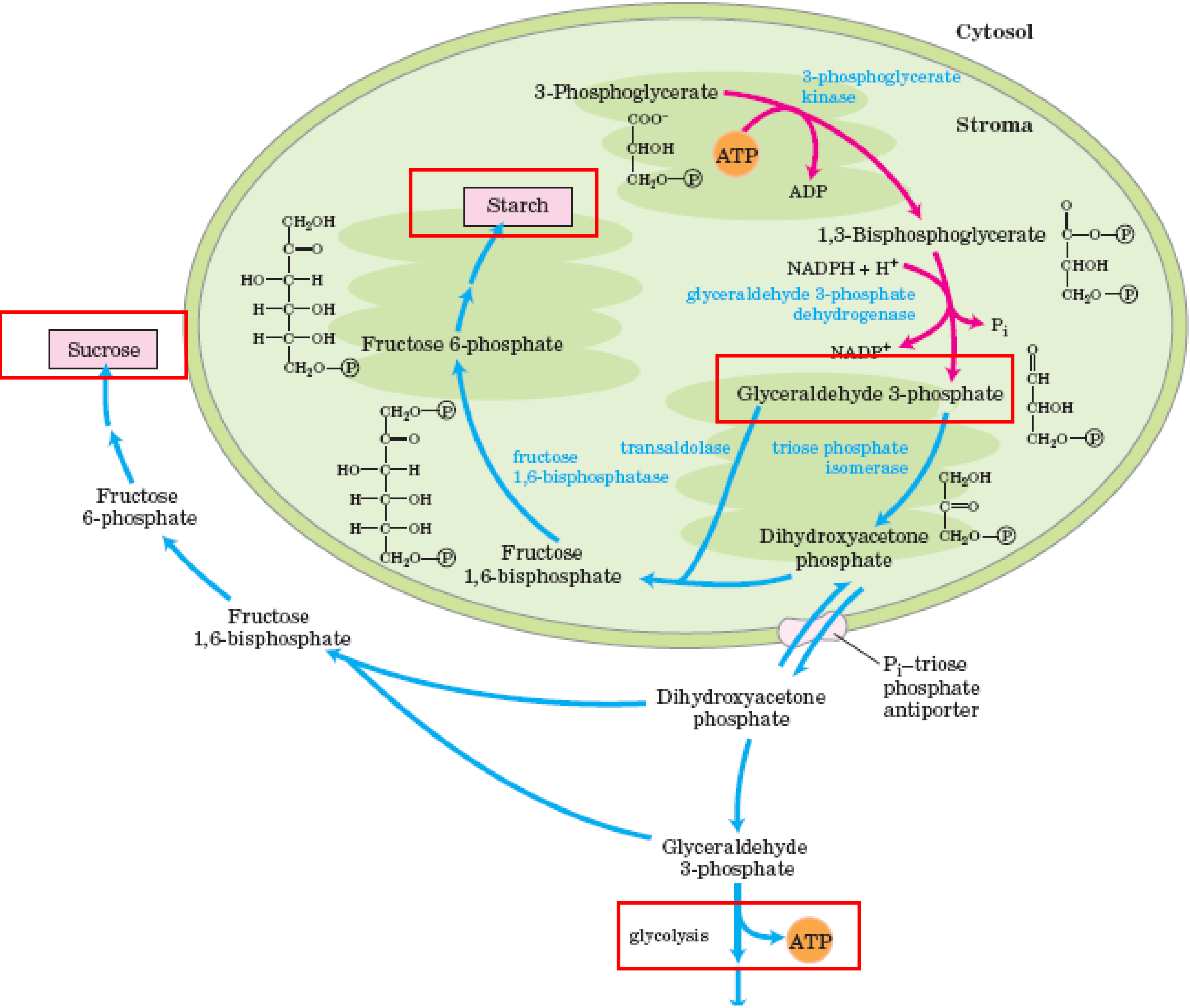
18ATP

1Glc

fates of glyceraldehyde 3-phosphate（3-P-甘油醛）

- The most is recycled to ribulose 1,5-bisphosphate
- “extra” glyceraldehyde 3-phosphate

- As a source of energy
- Be converted to sucrose（蔗糖） for transport
- Be stored in the chloroplast as starch



Cytosol
Stroma
3-Phosphoglycerate
3-phosphoglycerate kinase
ATP
ADP
1,3-Bisphosphoglycerate
NADPH + H+
glyceraldehyde 3-phosphate dehydrogenase
P_i
NADP+
Glyceraldehyde 3-phosphate
triose phosphate isomerase
transaldolase
Dihydroxyacetone phosphate
Fructose 1,6-bisphosphate
fructose 1,6-bisphosphatase
Fructose 6-phosphate
Starch
Sucrose
Fructose 6-phosphate
Fructose 1,6-bisphosphate
Dihydroxyacetone phosphate
P_i–triose phosphate antiporter
Glyceraldehyde 3-phosphate
glycolysis
ATP

4. Photorespiration（光呼吸）

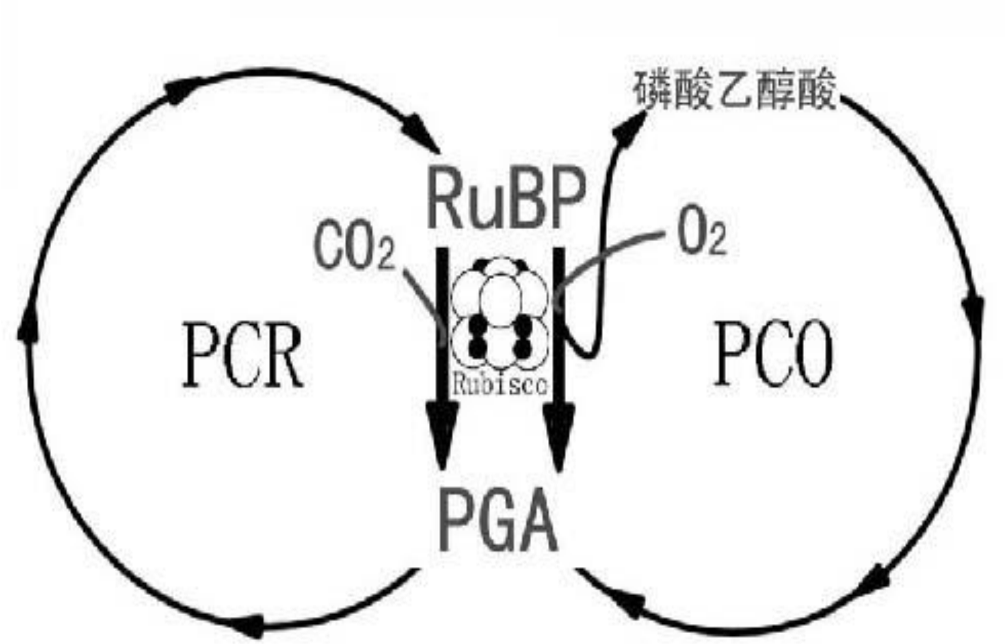
- **mitochondrial respiration**, substrates→CO_2 + H_2O.
- **photorespiration** （in plants）
  - consumes O_2 and produces CO_2
  - is driven by light.

-- Reason：Rubisco catalyzes the reaction between ribulose-1,5-bisphosphate with O_2 instead of CO_2

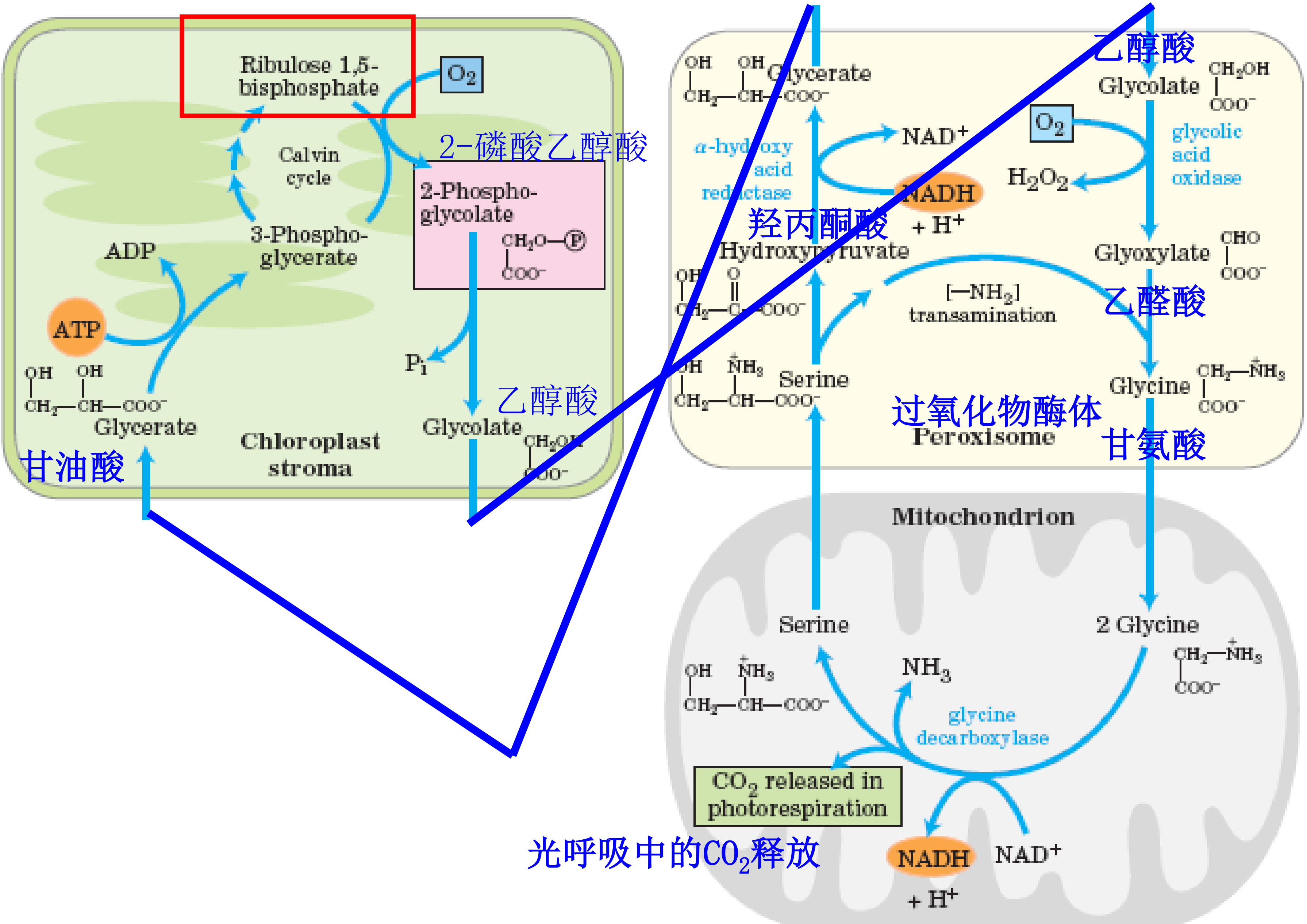
Photorespiration

- Occurs under
  - Intense Light
  - high O_2 concentrations
  - High heat
- Reduces photosynthetic efficiency by 25%
- protect against reactive O_2

ribulose 1,5-bisphosphate carboxylase/oxygenase（ Rubisco）



- Rubisco add O_2 to RuBP→ loss of RuBP（CO_2 acceptor during CO_2 fixation）
- salvaging the carbons from 2-phosphoglycolate（2-磷酸乙醇酸）



The oxygenase reation of rubisco-乙醇酸途径

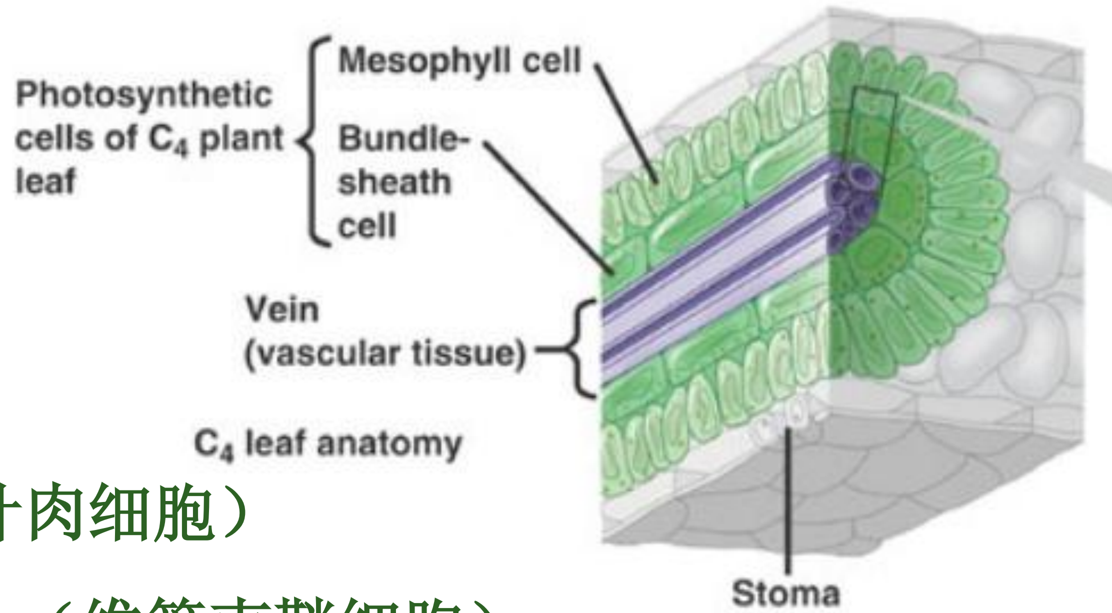
C4 Photosynthesis

*** Both convert CO_2 into a 4 carbon intermediate**

- Plants have developed ways to limit the photorespiration
  - C4 Pathway*
  - CAM Pathway*

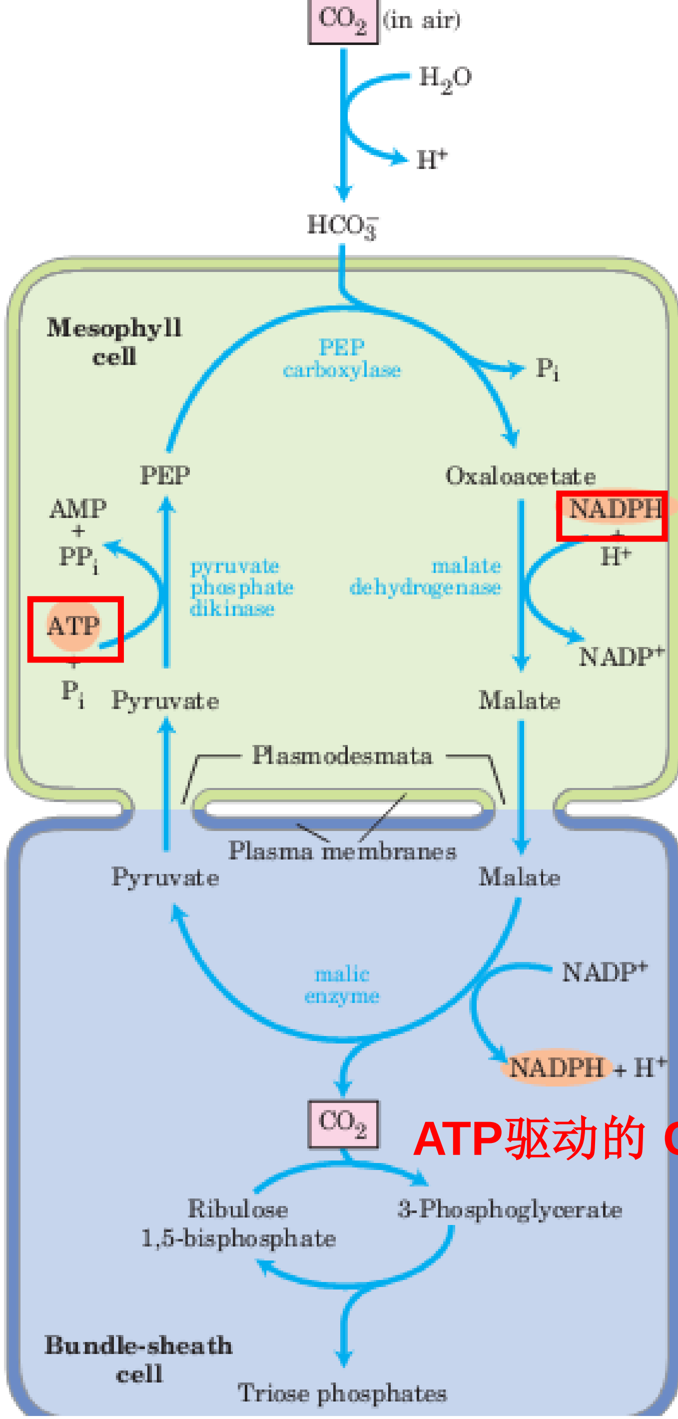
Carbon assimilation（碳同化） in C4 plants

- many plants in the tropics, such as maize玉米, sugarcane甘蔗, and sorghum 高粱



mesophyll cells （叶肉细胞）
bundle-sheath cells （维管束鞘细胞）

- **C4 Plants, CO_2 Fixation and Rubisco Activity Are Spatially Separated**



PEP carboxylase（磷酸烯醇式丙酮酸羧化酶，PEPC)以及与C_4二羧酸生成有关的酶

mesophyll cell （叶肉细胞）

Rubisco等参与C_3途径的酶、乙醇酸氧化酶以及脱羧酶

ATP驱动的 CO_2泵

BSC（维管束鞘细胞）

How does the C4 Pathway limit photorespiration?

- **Bundle sheath cells** are far from the surface – less O_2
- **PEP Carboxylase** doesn't have an affinity for O_2 → allows plant to collect a lot of CO_2 and concentrate it in the bundle sheath cells (**Rubisco**)

Crassulaceanacid metabolism (CAM) Pathway

剑麻

龙舌兰

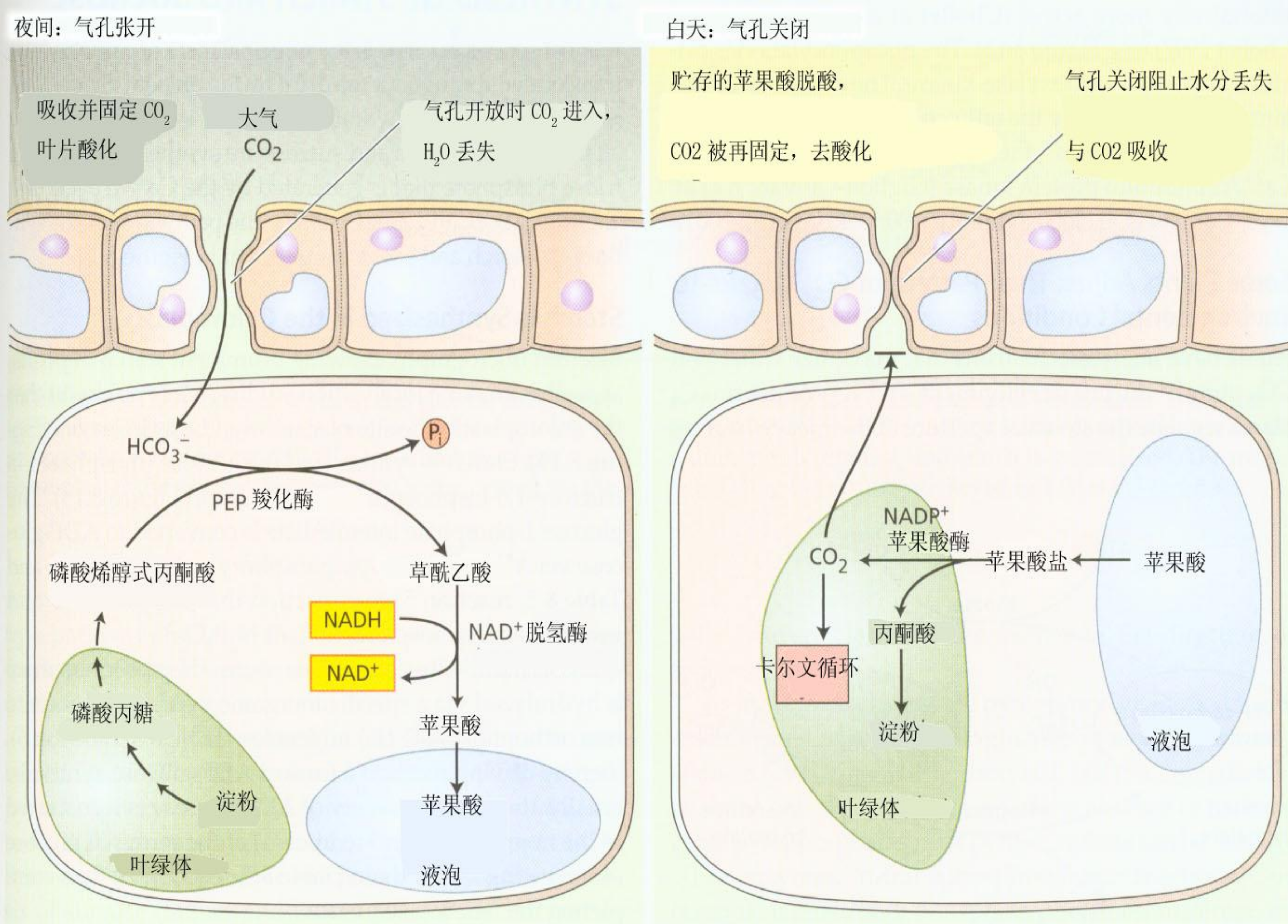
落地生根

芦荟

绯牡丹

昙花

瓦松


夜间：气孔张开
吸收并固定 CO_2
叶片酸化
大气
CO_2
气孔开放时 CO_2 进入，
H_2O 丢失
HCO_3^-
P_i
PEP 羧化酶
磷酸烯醇式丙酮酸
草酰乙酸
NADH
NAD^+
NAD^+ 脱氢酶
磷酸丙糖
苹果酸
淀粉
苹果酸
叶绿体
液泡
白天：气孔关闭
贮存的苹果酸脱酸，
CO2 被再固定，去酸化
气孔关闭阻止水分丢失
与 CO2 吸收
$NADP^+$
苹果酸酶
CO_2
苹果酸盐
苹果酸
丙酮酸
卡尔文循环
淀粉
液泡
叶绿体

summary

- **Photosynthesis in chloroplasts**
  - **Photophosphorylation（光合磷酸化）**
  - **Carbon dioxide fixation（CO_2固定）**
- **Photorespiration（光呼吸）**
  - **C4**
  - **CAM**

思考题

- 什么是光合磷酸化？有哪两种形式？
- 什么是卡尔文循环？每固定1分子葡萄糖需要几分子的ATP和NADPH？
- 热带植物和沙漠植物为了适应环境而特有的CO_2固定方式是什么？
- 什么是光呼吸？
- Where does photosynthesis take place?
- Why would CAM plants close their stomates during the day?