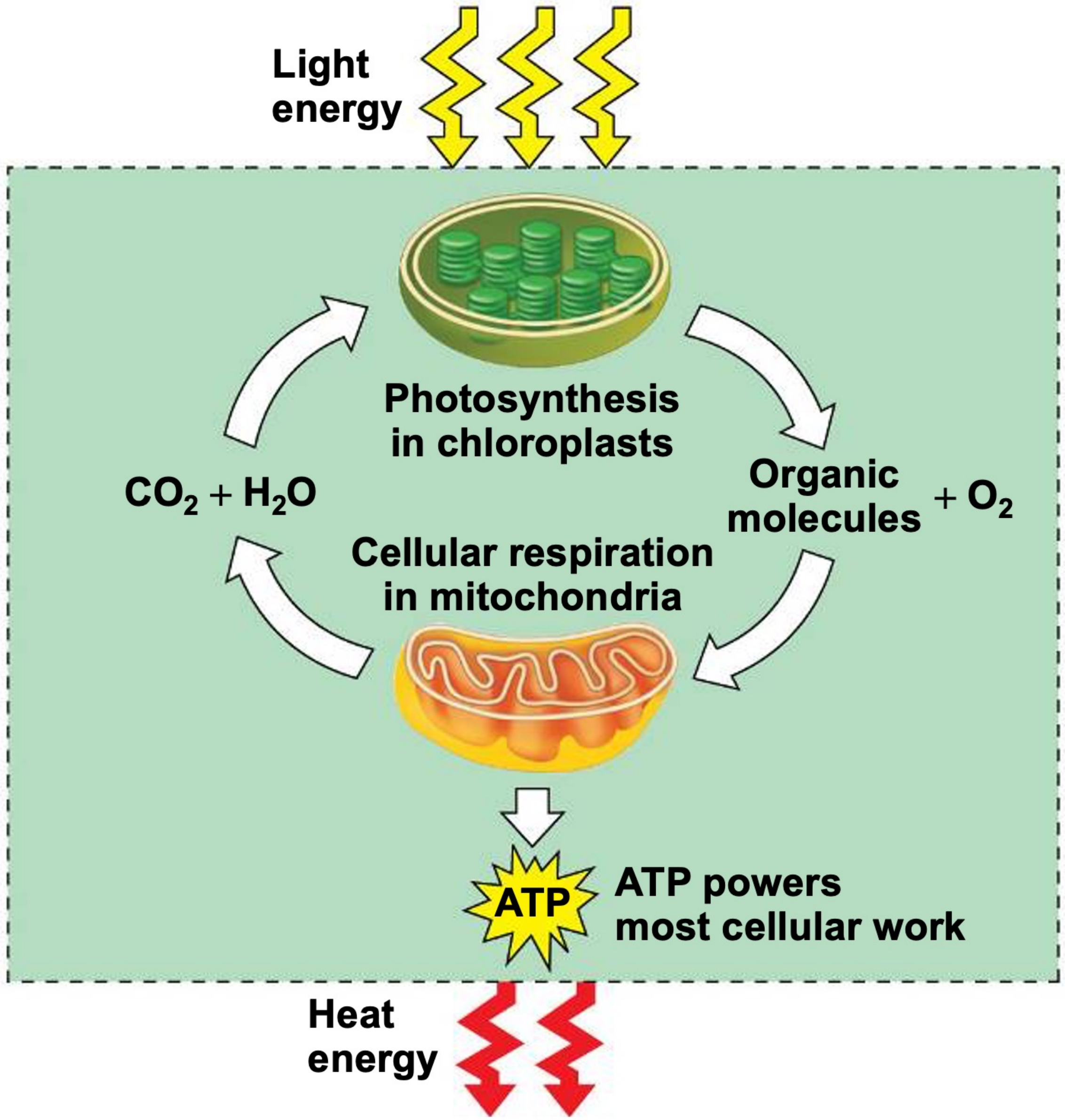
Carbohydrate Metabolism

Outline

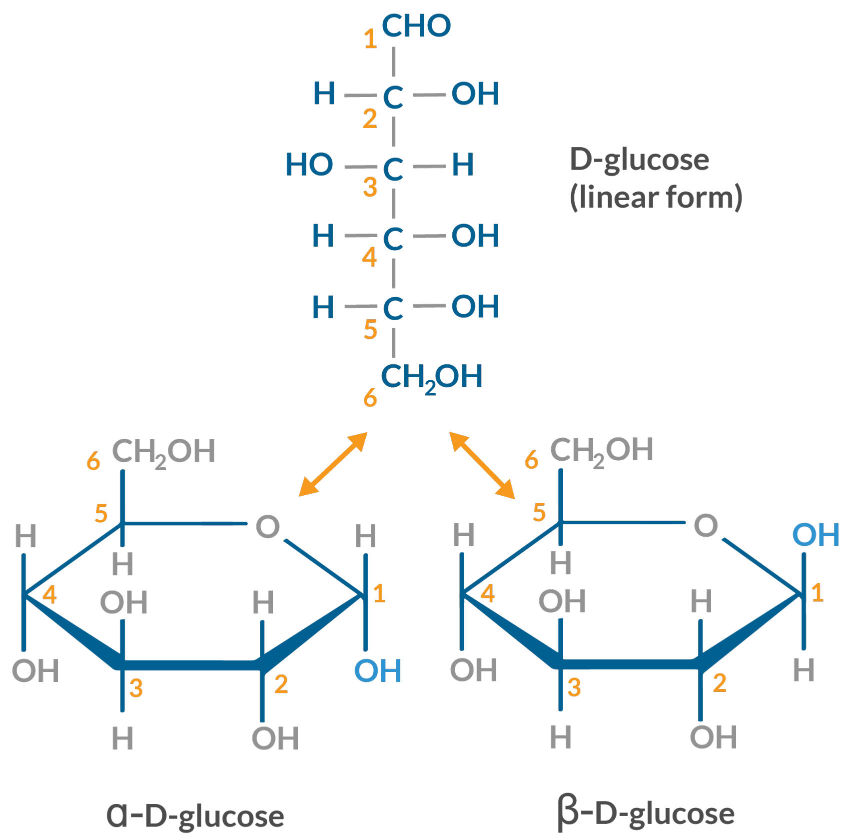
- Introduction
- Respiration
- Photosynthesis



Introduction

Definition

Carbohydrate metabolism comprises the enzymatic pathways responsible for the synthesis, degradation, and interconversion of carbohydrate molecules, integrating energy production with biosynthetic demands.



葡萄糖

Glucose = central metabolic substrate

Introduction

Both processes occur simultaneously but are tightly regulated

Feature	Catabolism	Anabolism
Function	Breakdown	Synthesis
Energy	Produces ATP	Consumes ATP
Example	Glycolysis	Glycogenesis
Redox	$NAD^+ \rightarrow NADH$	NADPH used

Introduction

Biological Significance

Carbohydrates are both fuel and building blocks

1. Energy Production

- ❖ Glucose to ATP via:
  - ✓ Glycolysis (cytosol)
  - ✓ Cellular respiration (mitochondria)
- ❖ Can function:
  - ✓ Anaerobically (fast, low yield)
  - ✓ Aerobically (slow, high yield)

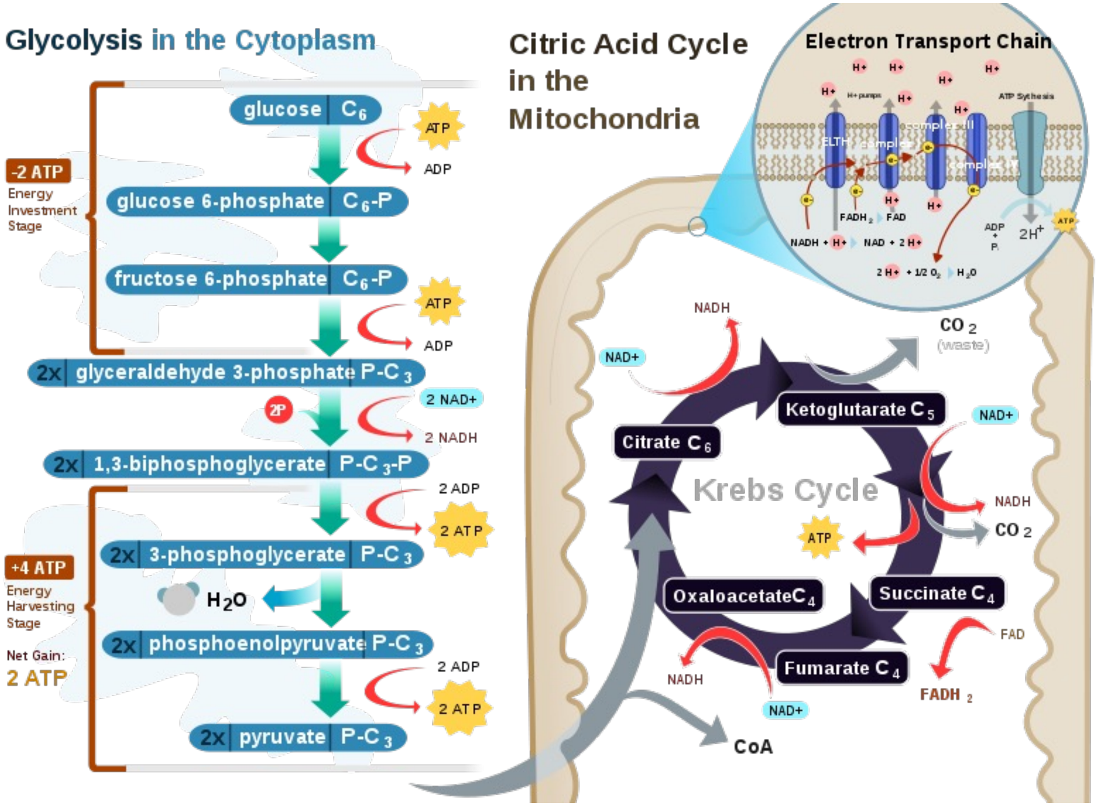
2. Carbon Skeleton Supply

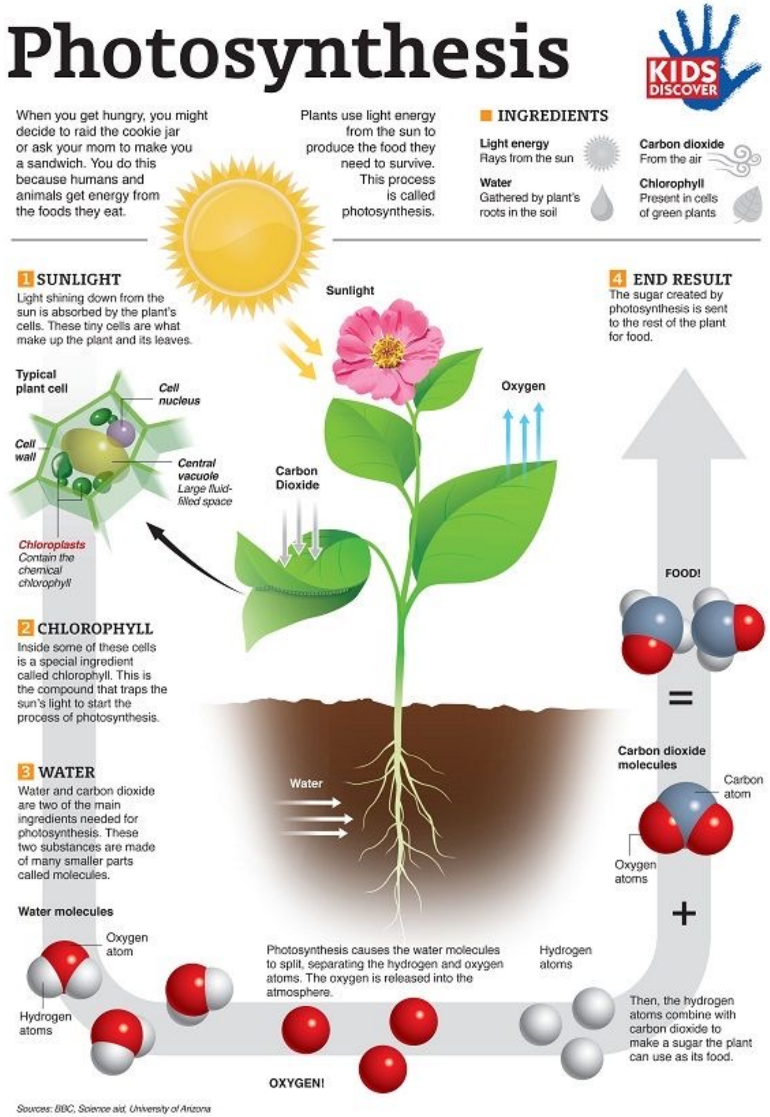
- ❖ Provides intermediates for:
  - ✓ Amino acids
  - ✓ Lipids
  - ✓ Nucleotides

Carbohydrates = **carbon backbone donors**

Introduction

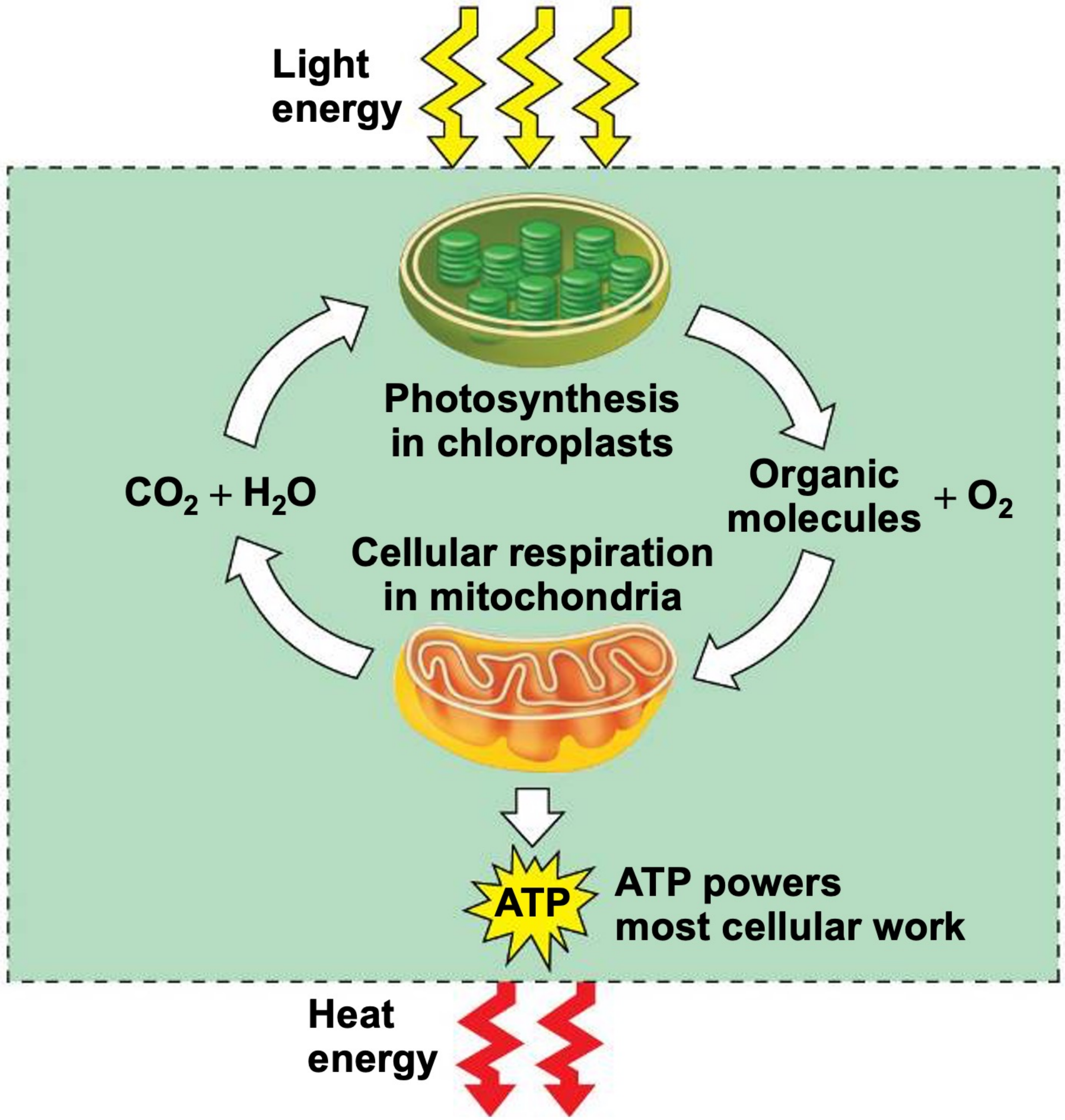
Respiration





Outline

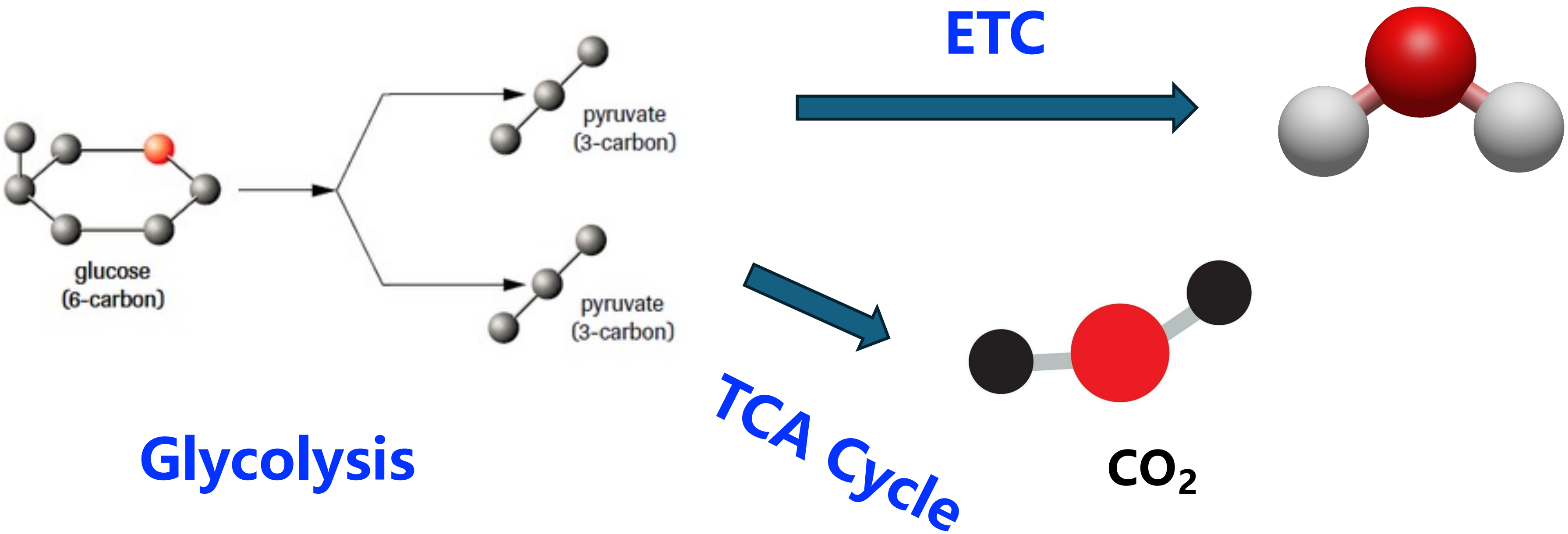
- Introduction
- Respiration
- Photosynthesis



Respiration

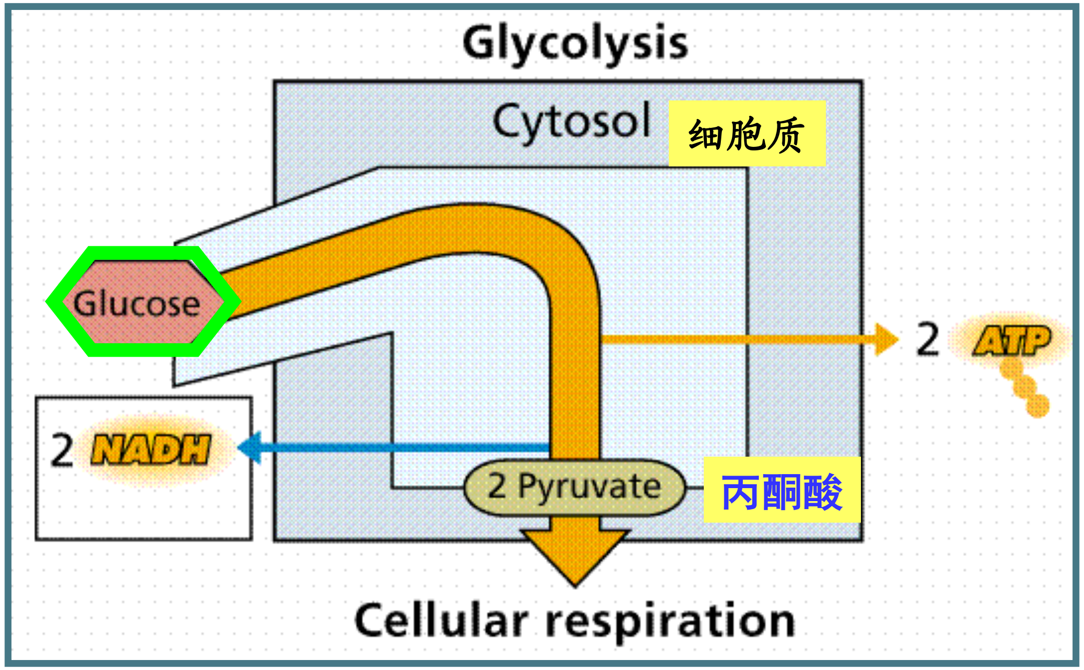
Concept

Respiration refers to the process in which organic molecules within living cells are gradually oxidized, under the catalysis of enzymes, resulting in the release of energy.



Glycolysis/糖酵解

Glycolysis is a cytosolic pathway in which glucose is converted to pyruvate, yielding ATP and NADH.



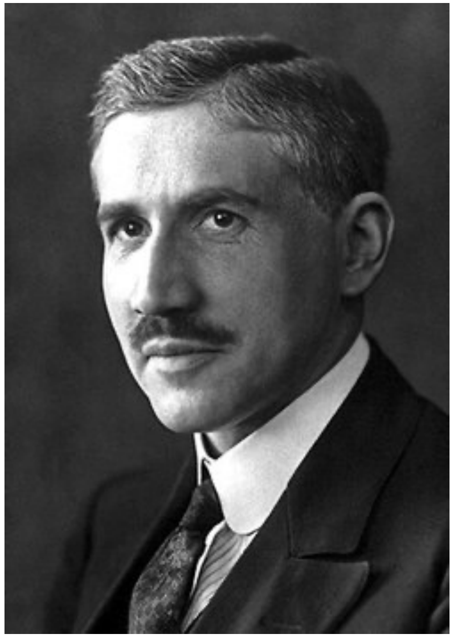
G → 2Pyruvate + 2NADH + $2H^{+}$+ 2ATP

Glycolysis/糖酵解

It also known as the Embden–Meyerhof Pathway (EMP).

Eduard Buchner

First analyzed glucose by the non-cellular fermentation experiments during the 1890s.



In the 1920s Otto **Meyerhof** linked together some of the many individual pieces of glycolysis discovered by others

1930s, Gustav **Embden** proposed a detailed, step-by-step outline of glycolysis

Glycolysis/糖酵解

I. Chemical Reactions of the Glycolysis

II. Physiological Significance of the Glycolysis

III. Regulation of the Glycolysis

Chemical Reactions of the Glycolysis

Overview

- Glycolysis consists of **10 enzymatic steps**
- Occurs in the **cytosol**
- Can be divided into **three phases**:

1. **Energy Investment (2 ATP consumed)**
2. **Cleavage (C6 breaks into 2 C3)**
3. **Energy Payoff (4 ATP + 2 NADH produced)**

Investment phase (1–2)

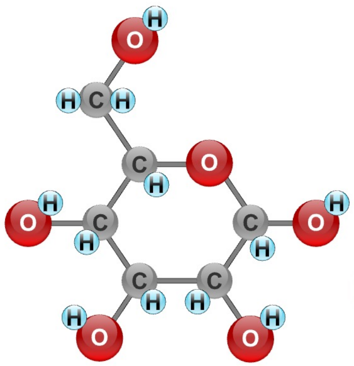
Payoff phase (3)

己糖的磷酸化（消耗2分子ATP）、**磷酸己糖的裂解**、**3-磷酸甘油醛生成丙酮酸**

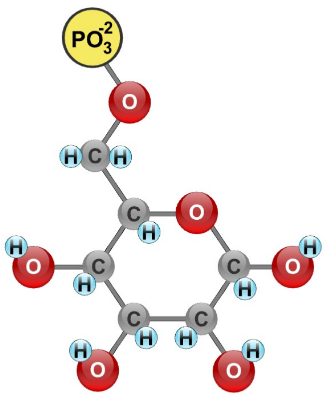
Chemical Reactions of the Glycolysis

Phase 1: Energy Investment

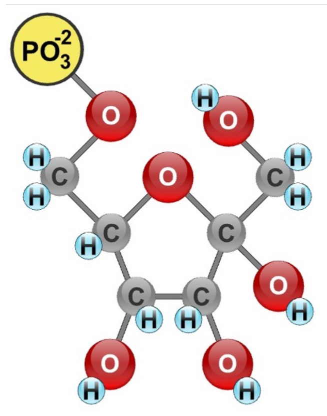
Glucose → (ATP → ADP; Hexokinase, Mg^{++}, 己糖激酶) → G-6-P (葡萄糖-6-磷酸) ⇄ (Phosphoglucose isomerase, 磷酸己糖异构酶) ⇄ F-6-P (果糖-6-磷酸) → (ATP → ADP; Phosphofructokinase, 磷酸果糖激酶) → F-1,6-P (1,6-二磷酸果糖)



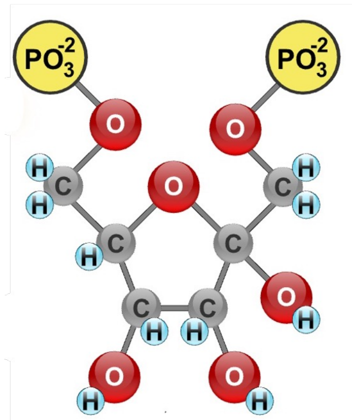
Glucose



Glucose 6-phosphate



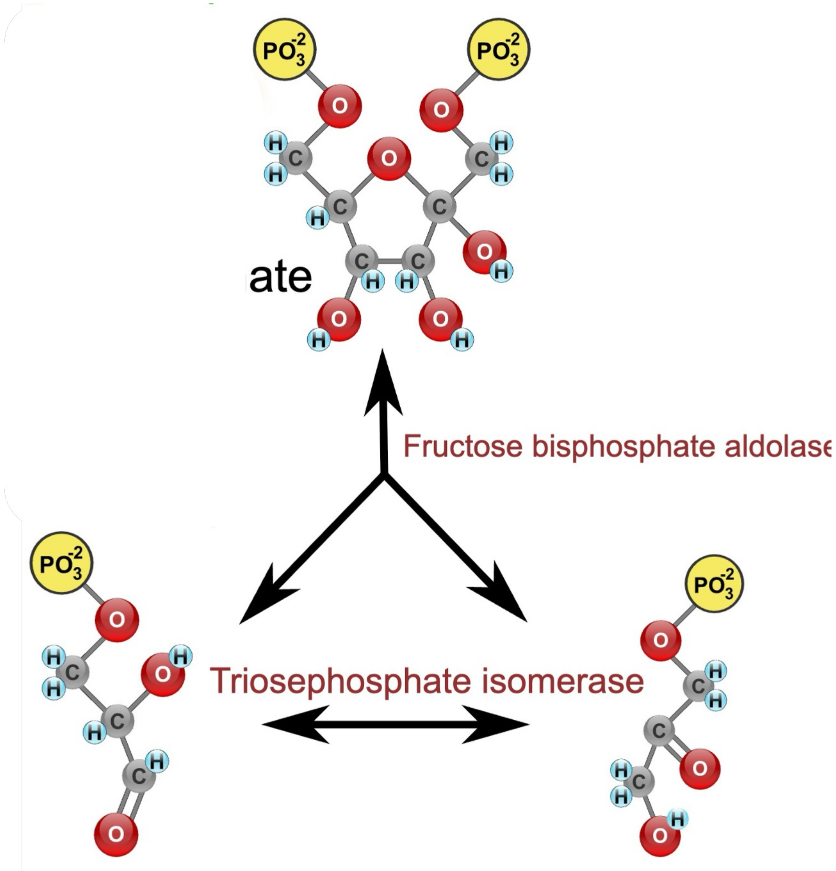
Fructose 6-biphosphate



Fructose 1,6-biphosphate

Chemical Reactions of the Glycolysis

Phase 2: Cleavage (C6 breaks into 2 C3)



1,6-二磷酸果糖 F-1,6-P

醛缩E

磷酸二
羟丙酮
DHAP
(96%)

磷酸丙糖
异构E

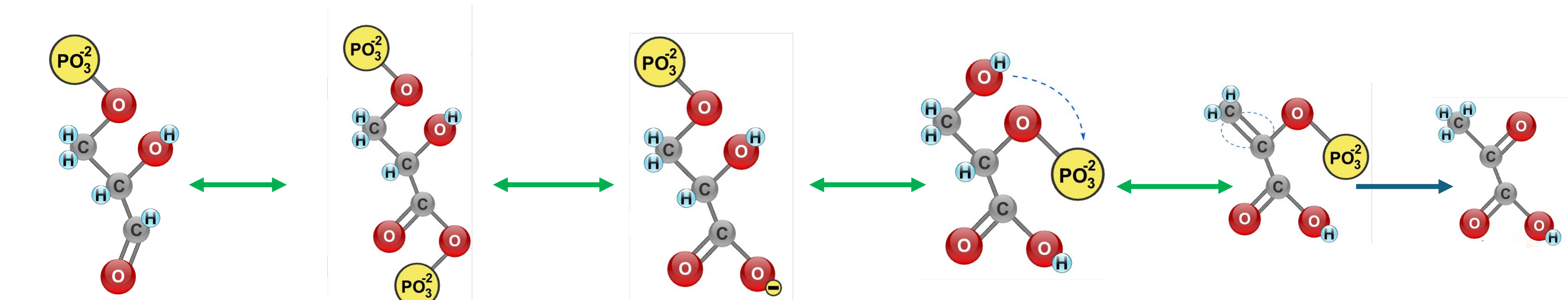
甘油醛
3-磷酸
G-3-P
(4%)

Chemical Reactions of the Glycolysis

Phase 3: Energy Payoff

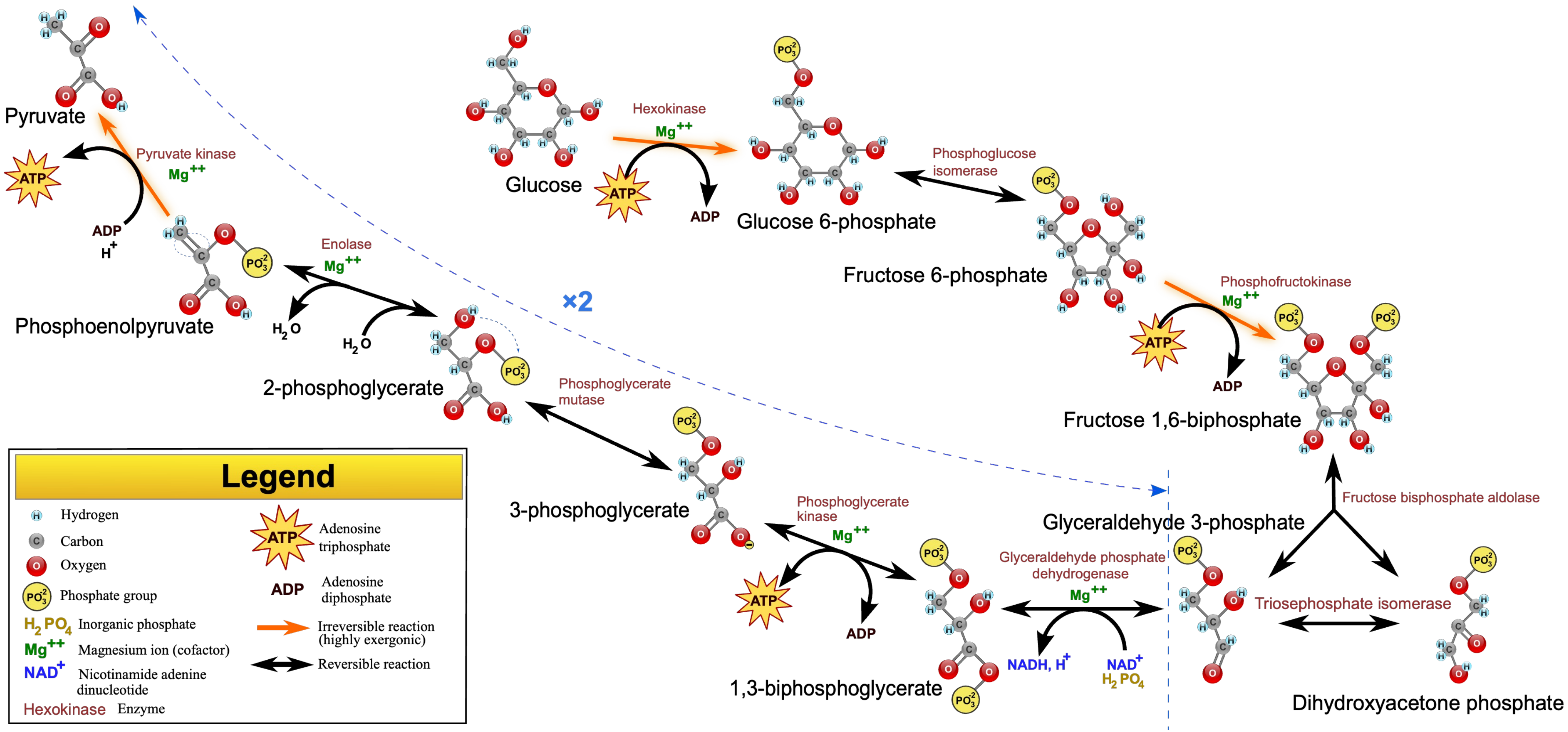
G-3-P ⇄ 1,3-DPGA ⇄ 3-PGA ⇄ 2-PGA ⇄ PEP → Pyr

- G-3-P ⇄ 1,3-DPGA (NAD^+ + Pi → NADH + H^+): Glyceraldehyde -3-phosphate dehydrogenase, 3-磷酸甘油醛脱氢酶
- 1,3-DPGA ⇄ 3-PGA (ADP → ATP): Phosphoglycerate kinase, Mg^{++}, 磷酸甘油酸激酶
- 3-PGA ⇄ 2-PGA: Phosphoglycerate mutase, 磷酸甘油酸变位酶
- 2-PGA ⇄ PEP (H_2O): Enolase, Mg^{++}, 烯醇化酶
- PEP → Pyr (ADP → ATP): Pyruvate kinase, Mg^{++}, 丙酮酸激酶



Glyceraldehyde 3-phosphate 3-磷酸甘油醛 | 1,3-biphosphoglycerate 1,3-二磷酸甘油酸 | 3-phosphoglycerate 3-磷酸甘油酸 | 2-phosphoglycerate 2-磷酸甘油酸 | Phosphoenolpyruvate 磷酸烯醇式丙酮酸 | Pyruvate 丙酮酸

Overview of Glycolysis



Overview of Glycolysis

$$G + 2\ Pi + 2\ NAD^{+} + 2\ ADP$$

↓

$$2\ \begin{array}{c} CH_3 \\ | \\ C{=}O \\ | \\ COOH \end{array} + 2\ H_2O + 2\ ATP + 2\ NADH + 2\ H^{+}$$

Key Features of Glycolysis

1. Phosphoryl Transfer Reactions (Kinases)

磷酸基团转移反应

G + ATP → G-6-P + ADP (Hexokinase 己糖激酶)

F-6-P + ATP → F-1,6-P + ADP (Phosphofructokinase-1 磷酸果糖激酶)

2 1,3-DPGA + 2 ADP ⇌ 2 3-PGA + 2 ATP (Phosphoglycerate kinase 磷酸甘油酸激酶)

2 PEP + 2 ADP → 2 Pyr + 2 ATP (Pyruvate kinase 丙酮酸激酶)

Key Features of Glycolysis

2. Isomerization Reactions (Isomerases)

异构反应

(1) Phosphoglucose isomerase

Glucose−6−phosphate (G−6−P) ⇔ Fructose−6−phosphate (F−6−P)

(2) Triose phosphate isomerase

Dihydroxyacetone phosphate (DHAP) ⇔ Glyceraldehyde−3−phosphate (G−3−P)

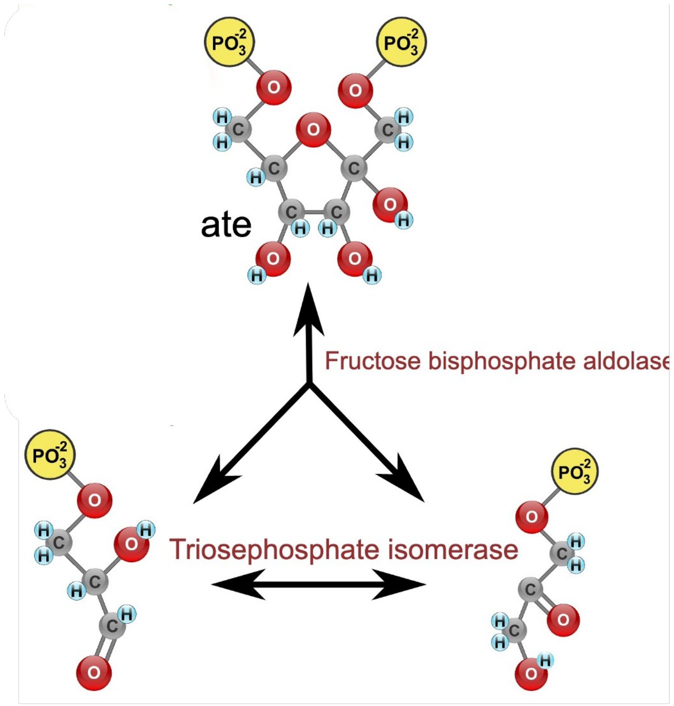
(3) Phosphoglycerate mutase

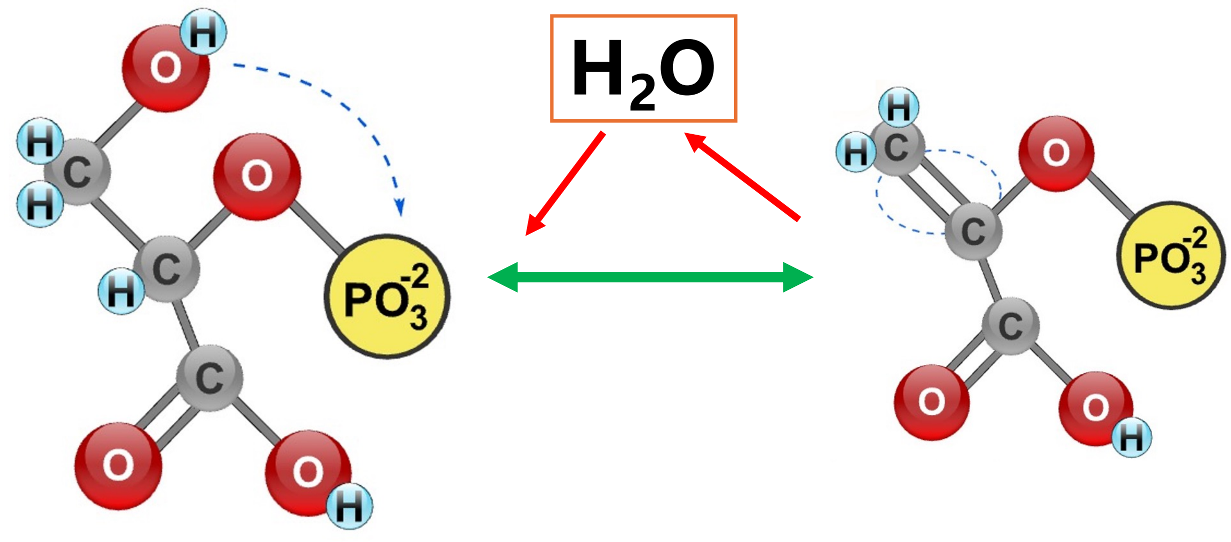
2 3−phosphoglycerate ⇔ 2 2−phosphoglycerate

Key Features of Glycolysis

3. Cleavage and Dehydration Reactions

裂合反应





Key Features of Glycolysis

4. Oxidation–Reduction Reaction

氧化还原反应

$$2\ \text{G-3-P} + 2\text{Pi} \xrightarrow{\text{3-磷酸甘油醛脱氢酶}} 2\ \text{1,3-DPGA}$$

$$2\text{NAD}^+ \rightarrow 2\text{NADH} + 2\text{H}^+$$

Physiological Roles of Glycolysis

1. Source of Cellular Energy

- One glucose yields **2 ATP**
- Under **anaerobic conditions**:
  - ✓ Glycolysis is the **primary source of ATP** (e.g., muscle during intense exercise)
- Under **aerobic conditions**:
  - ✓ NADH is oxidized via the **electron transport chain** can produce **~3–5 additional ATP**

生物能量的来源之一

2. Source of Metabolic Intermediates

- Glycolytic intermediates serve as precursors for:
  - ✓ **Pyruvate → Acetyl-CoA → Lipid synthesis**
  - ✓ **3-carbon intermediates → Amino acids**

中间产物是合成其它物质的原料

3. Link to Gluconeogenesis

- Glycolysis contains three irreversible steps
- Other reactions are reversible

糖异生作提供基本途径

Physiological Roles of Glycolysis

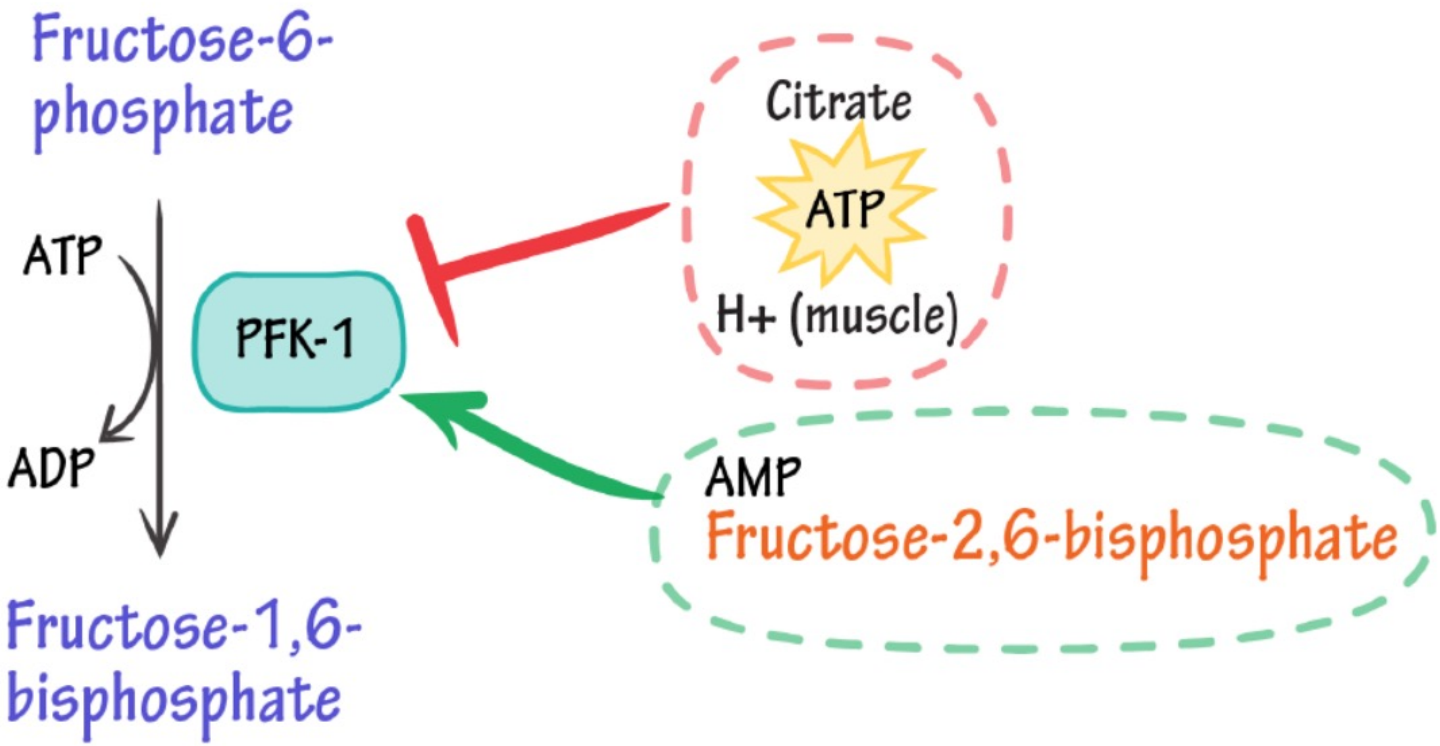
Three Irreversible Steps (Key Control Points)/三个不可逆反应

Glycolysis is regulated by cellular energy status (ATP/AMP ratio)

Enzyme	Activators	Inhibitors
PFK-1 *Rate-limiting step*	AMP, ADP, Fructose-2,6-bisphosphate	ATP, Citrate, H^+
Hexokinase	—	Glucose-6-phosphate
Pyruvate kinase	Fructose-1,6-bisphosphate	ATP, Alanine, Acetyl-CoA

Physiological Roles of Glycolysis

High ATP decreases the affinity of PFK for fructose-6-phosphate, reducing the rate of glycolysis



Fate of Pyruvate / 丙酮酸去向

Pyruvate produced from glycolysis has **two major metabolic fates**:

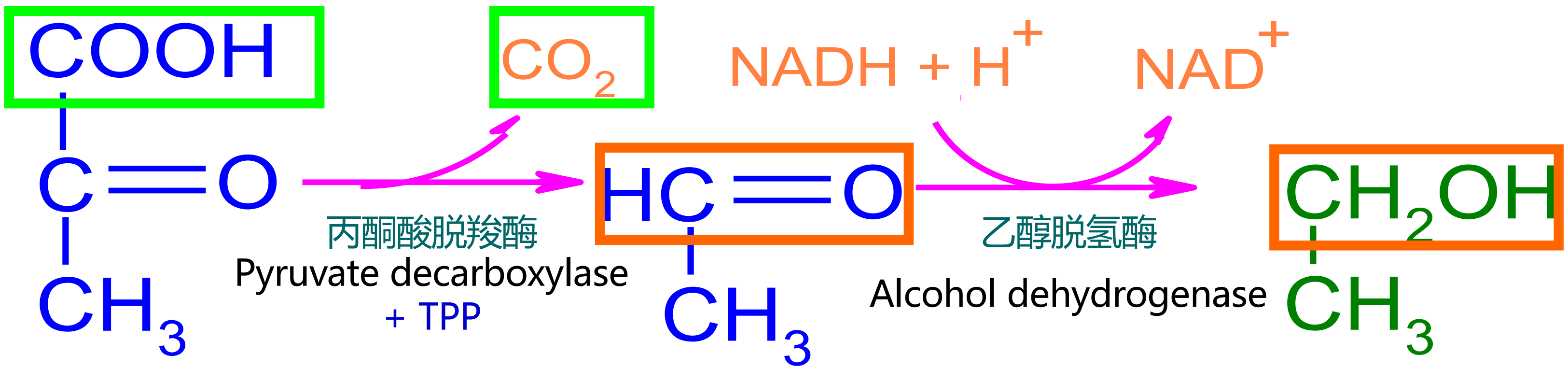
1. Anaerobic Conditions

- ❖ Lactate fermentation
- ❖ Alcohol fermentation

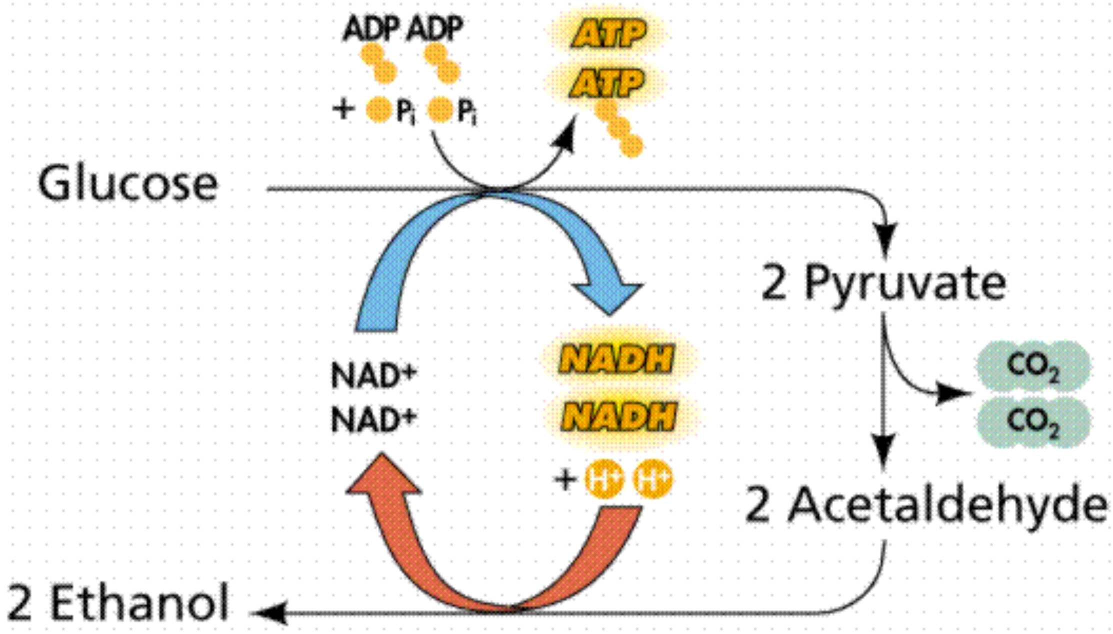
2. Aerobic Conditions

- ❖ Pyruvate enters the mitochondrial matrix
- ❖ Converted to acetyl-CoA
- ❖ Enters the TCA cycle

Fate of Pyruvate / 丙酮酸去向



TPP：焦磷酸硫胺素 /Vitamin B1



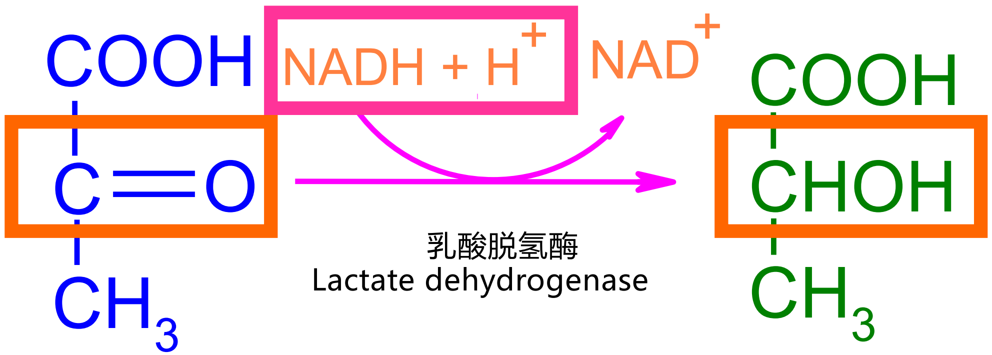
Alcohol fermentation

酒精发酵

Fate of Pyruvate / 丙酮酸去向

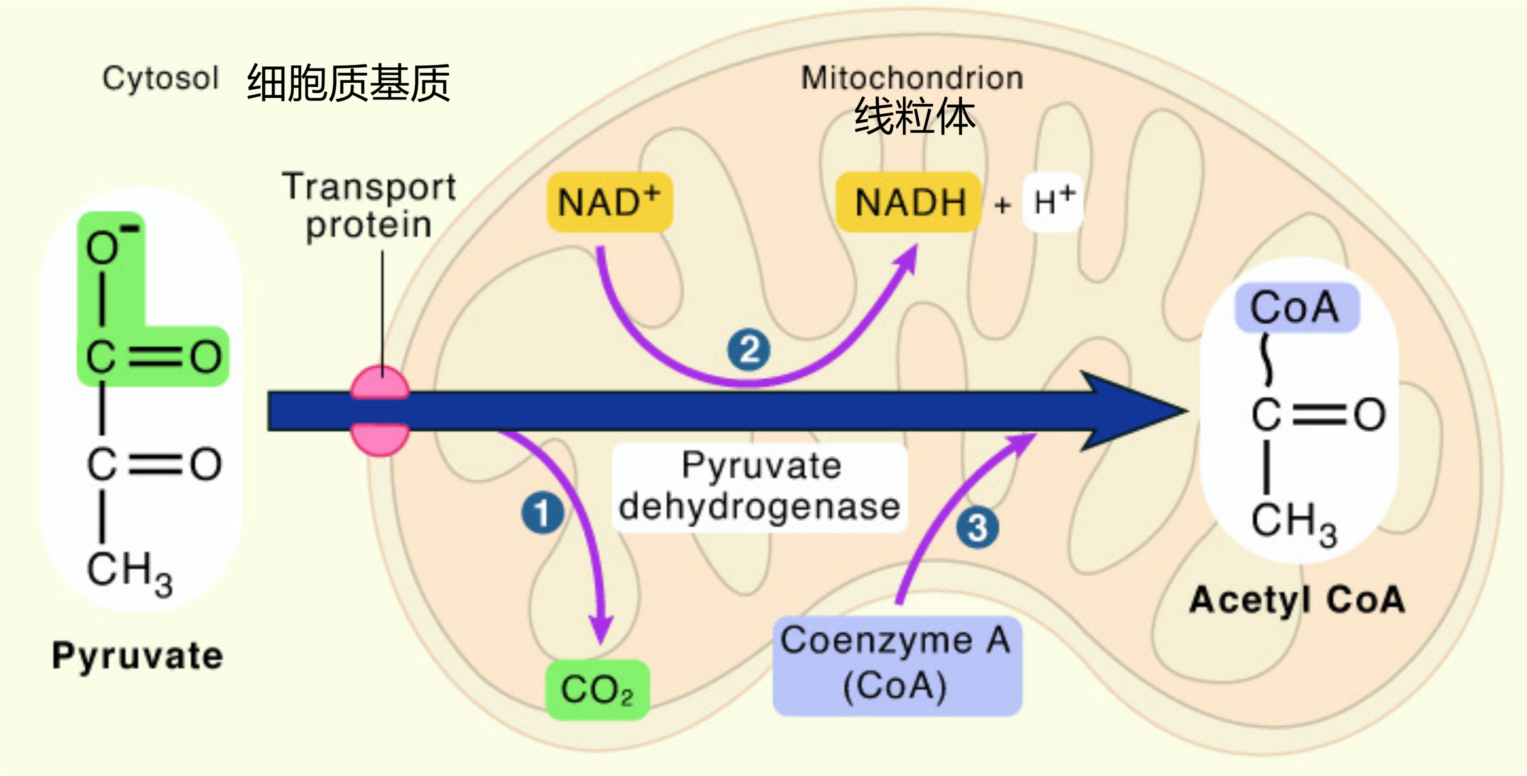
Lactate fermentation

乳酸发酵



Fate of Pyruvate / 丙酮酸去向

Pyruvate Oxidation /有氧降解



1. Carboxyl group gets removed, forming CO_2
2. NAD^+ gets reduced to NADH
3. Coenzyme A gets attached to acetate, forming acetyl CoA

Fate of Pyruvate / 丙酮酸去向

Pyruvate Oxidation /有氧降解

Pyruvate + CoA + NAD^+

Pyruvate dehydrogenase complex (PDH)

丙酮酸脱氢酶系

乙酰辅酶A

Acetyl-CoA + CO_2 + NADH

TCA

PDH Complex Components

- **E1**: Pyruvate dehydrogenase
- **E2**: Dihydrolipoyl transacetylase
- **E3**: Dihydrolipoyl dehydrogenase

Cofactors

- **TPP (Vitamin B1)**
- **Lipoic acid / 硫辛酸**
- **CoA (Vitamin B5) /辅酶A**
- **FAD (Vitamin B2) / 黄素腺嘌呤二核苷酸**
- **NAD^+ (Vitamin B3)/ 烟酰胺腺嘌呤二核苷酸**

TCA cycle / 三羧酸循环

The tricarboxylic acid cycle (TCA cycle), also known as the citric acid cycle/柠檬酸循环, Krebs cycle, Szent–Györgyi–Krebs cycle, is a series of biochemical reactions that release the energy stored in nutrients through acetyl-CoA oxidation.

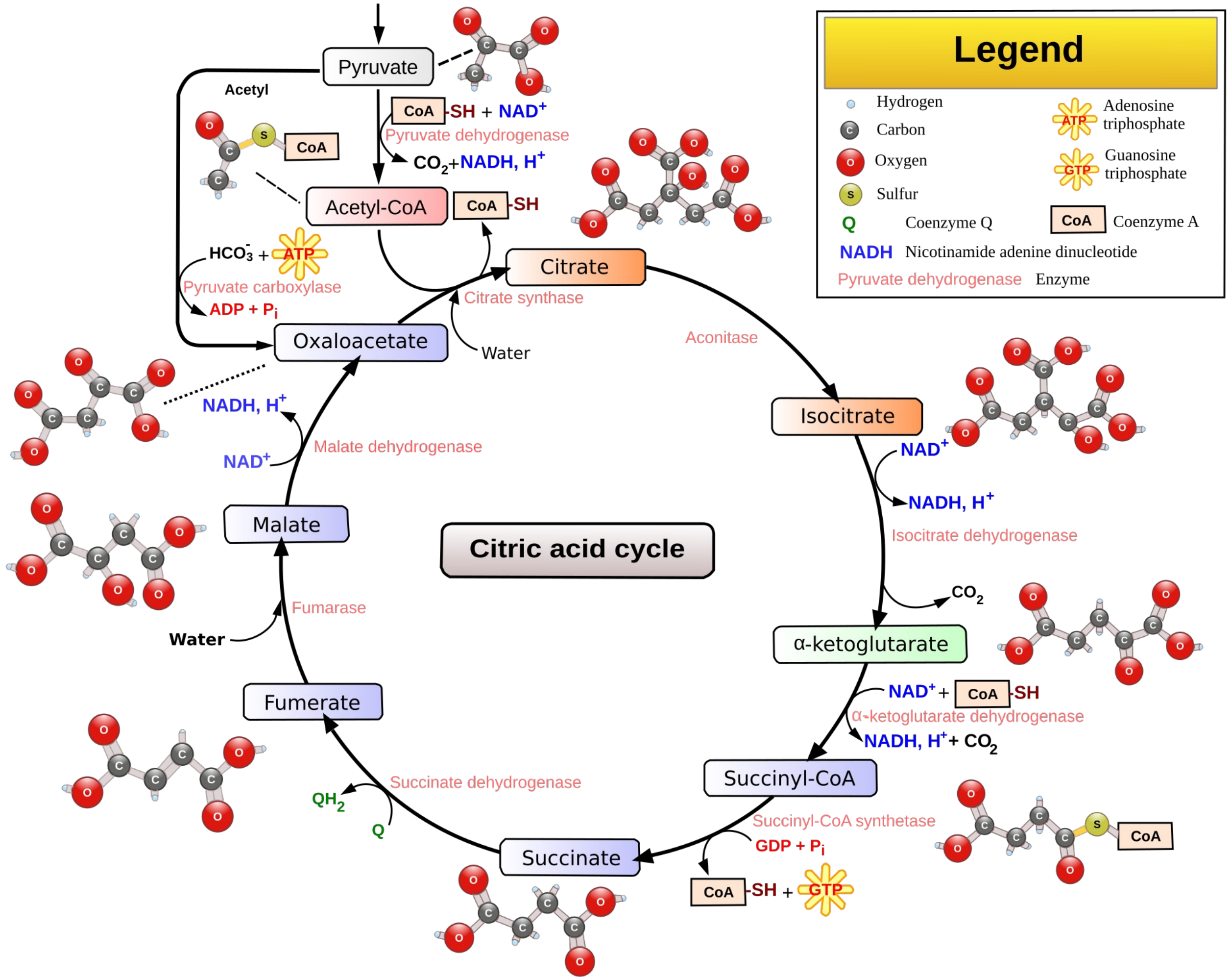
Nobel Prize in Physiology or Medicine 1953

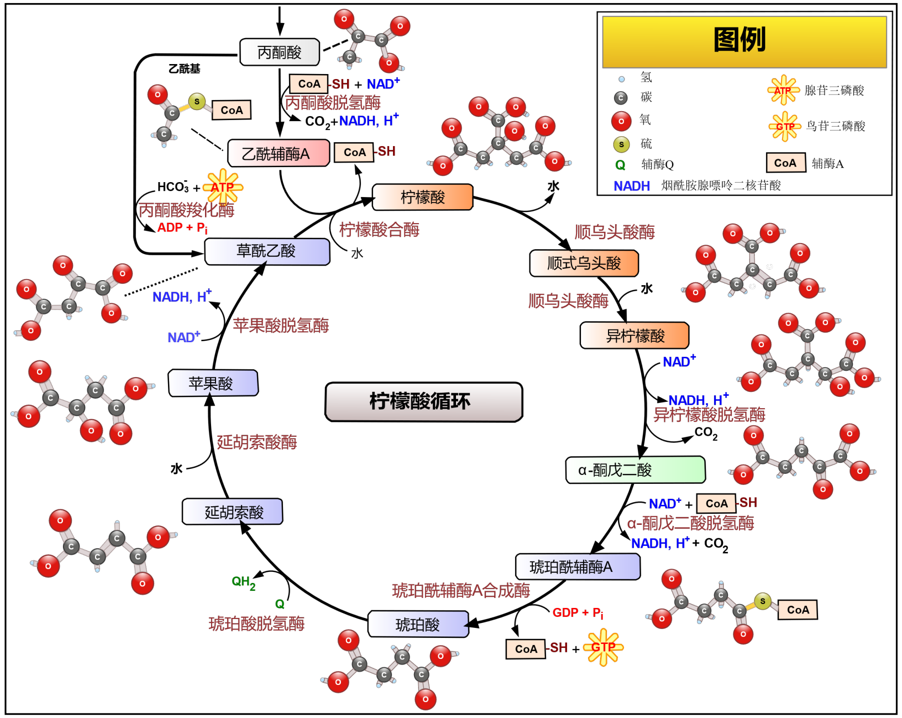
Photo from the Nobel Foundation archive.
Hans Adolf Krebs

Photo from the Nobel Foundation archive.
Fritz Albert Lipmann

The Nobel Prize in Physiology or Medicine 1953 was divided equally between Hans Adolf Krebs "for his discovery of the citric acid cycle" and Fritz Albert Lipmann "for his discovery of co-enzyme A and its importance for intermediary metabolism"

TCA cycle / 三羧酸循环





TCA cycle / 三羧酸循环

$$Acetyl\text{-}CoA + 3\ NAD^+ + FAD + GDP + Pi$$

↓

$$2CO_2 + CoASH + 3\ NADH + 3H^+ + FADH_2 + GTP$$

- Complete Oxidation of Carbon (Two carbons from acetyl-CoA generate 2 CO_2)
- Generation of Reducing Equivalents (3 NADH + 1 $FADH_2$)
- 1 GTP (≈ ATP equivalent) per cycle
- Four Oxidation Steps
  - ✓ 3 NAD^+-dependent reactions
  - ✓ 1 FAD-dependent reaction

TCA cycle / 三羧酸循环

Four Oxidation Steps

A. Isocitrate/异柠檬酸 → α-Ketoglutarate/ α-酮戊二酸

- Enzyme: **Isocitrate dehydrogenase** /异柠檬酸脱氢酶
- Produces: **CO_2 ,NADH, H^+**

B. α-Ketoglutarate → Succinyl-CoA / 琥珀酰CoA

- Enzyme: **α-Ketoglutarate dehydrogenase complex** / α-**酮戊二酸脱氢酶系**
- Requires: **CoA-SH, NAD^+**
- Produces: **CO_2， NADH， H^+**

C. Succinate → Fumarate

- Enzyme: Succinate dehydrogenase
- Produces: $FADH_2$

D. Malate → Oxaloacetate

- Enzyme: Malate dehydrogenase
- Produces: NADH + H^+

TCA cycle / 三羧酸循环

Energy Yield of the TCA Cycle

1. Substrate-Level Phosphorylation

$$\text{Succinyl-CoA} + \text{GDP} + P_i \rightarrow \text{Succinate} + \text{GTP} + \text{CoA-SH}$$

- ❑ Enzyme: **Succinyl-CoA synthetase**
- ❑ **GTP ≈ ATP equivalent**

2. Total Energy Yield (per Acetyl-CoA)

- ❑ 3 NADH → 3 × 2.5 ATP = 7.5 ATP
- ❑ 1 $FADH_2$ → 1 × 1.5 ATP = 1.5 ATP
- ❑ 1 GTP → 1 ATP

10 ATP per cycle

TCA cycle / 三羧酸循环

Physiological Roles of the TCA Cycle

1. Central Pathway of Energy Metabolism

- ❑ Major pathway for **oxidation of carbohydrates**
- ❑ Final common pathway for:
  - ○ **Lipids** (via acetyl-CoA)
  - ○ **Proteins** (via amino acid catabolism)

2. Amphibolic Pathway/物质代谢枢纽

- ❑ TCA cycle is both:
  - ○ **Catabolic** (energy production)
  - ○ **Anabolic** (biosynthesis)

3. Source of Carbon Skeletons

- ❑ **Pyruvate → glucose (gluconeogenesis)**
- ❑ **Acetyl-CoA → fatty acids**
- ❑ **α-Ketoglutarate → amino acids**
- ❑ **Oxaloacetate → amino acids / glucose**

TCA cycle / 三羧酸循环

Allosteric Regulation

Enzyme	Activators	Inhibitors
Citrate synthase 柠檬酸合成酶	—	ATP, NADH, citrate, succinyl-CoA
Isocitrate dehydrogenase 异柠檬酸脱氢酶	ADP	ATP, NADH
α-Ketoglutarate dehydrogenase	—	NADH, succinyl-CoA, ATP

Isocitrate dehydrogenase plays as the rate-limiting step enzyme

Summary of TCA

What is the TCA Cycle?

- ❖ Central pathway in the **mitochondrial matrix**
- ❖ Oxidizes **acetyl-CoA** → **CO_2**

Key Features

- ❖ Occurs in mitochondria
- ❖ Requires oxygen indirectly
- ❖ Generates reducing equivalents (NADH, $FADH_2$)

Regulation by Key Enzymes:

- ❖ Citrate synthase
- ❖ **Isocitrate dehydrogenase (rate-limiting)**
- ❖ α-Ketoglutarate dehydrogenase

Core Functions

1. Energy Production (Indirect)

- 3 NADH + 1 $FADH_2$ + 1 GTP per cycle

2. Complete Oxidation of Carbon

3. Metabolic Hub (Amphibolic)

- Integrates metabolism of Carbohydrates, Lipids, Proteins

4. Source of Biosynthetic Precursors

- Amino acids (α-KG, OAA)
- Fatty acids (acetyl-CoA)
- Gluconeogenesis (OAA)

Anaplerotic Reactions of the TCA Cycle

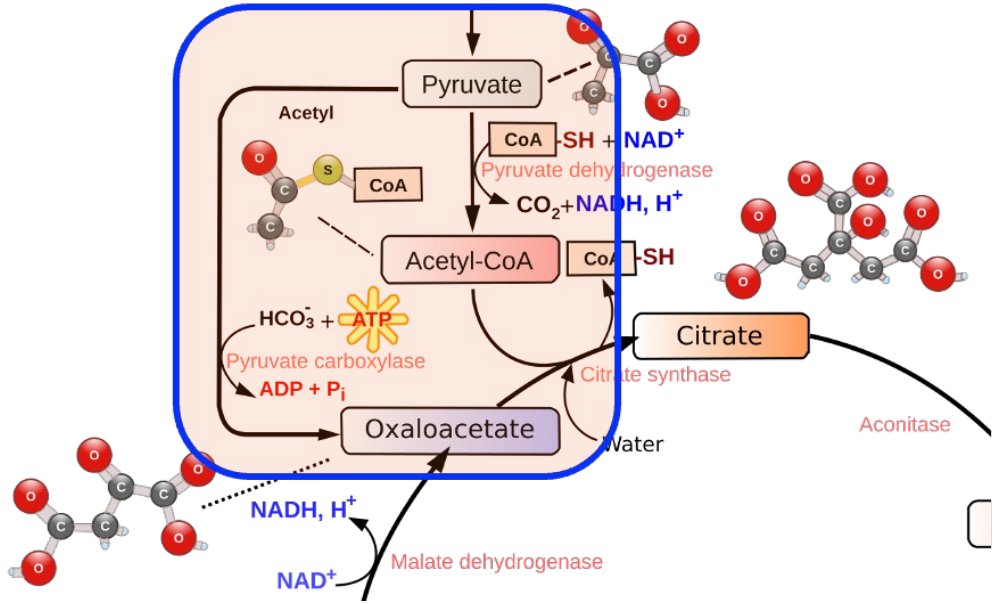
Anaplerotic Reactions

Purpose: Replenish oxaloacetate (OAA) in the TCA cycle

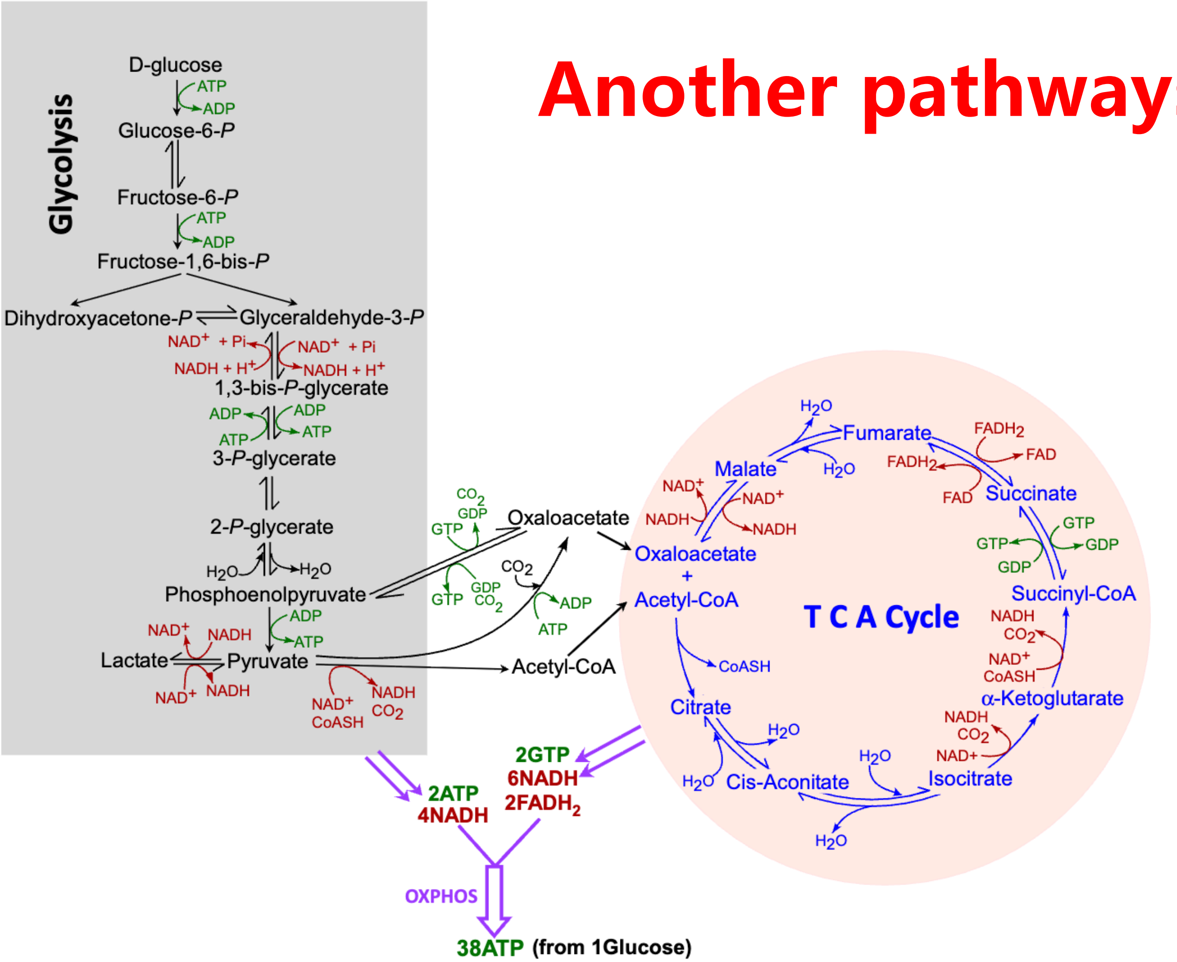
$$\text{Pyruvate} + CO_2 + \text{ATP} \xrightarrow[\text{丙酮酸羧化酶}]{\text{Pyruvate carboxylase}} \text{Oxaloacetate (OAA)} + \text{ADP} + \text{Pi}$$

Physiological Significance

- Maintains **TCA cycle function**
- Required when intermediates are used for **biosynthesis** (amino acids, glucose)



Pentose Phosphate Pathway /磷酸戊糖途径



Another pathways?

Bernard Leonard Horecker

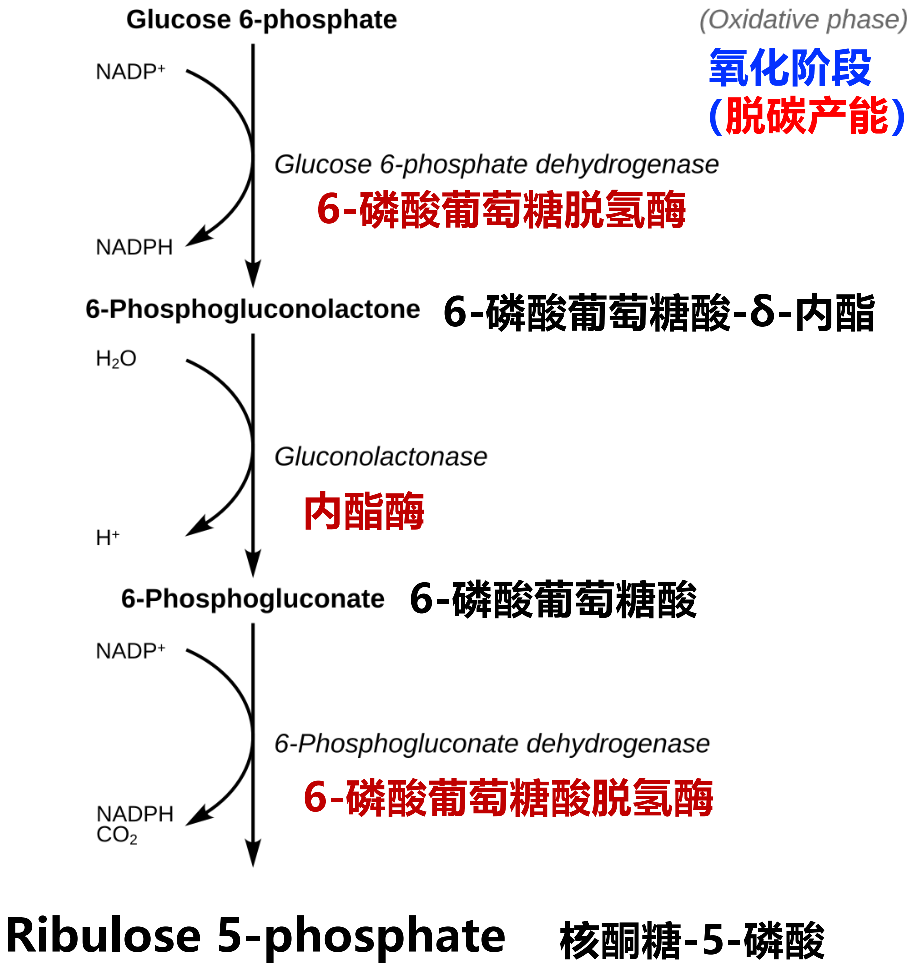
The **pentose phosphate pathway** (**PPP**, also called the phosphogluconate pathway)

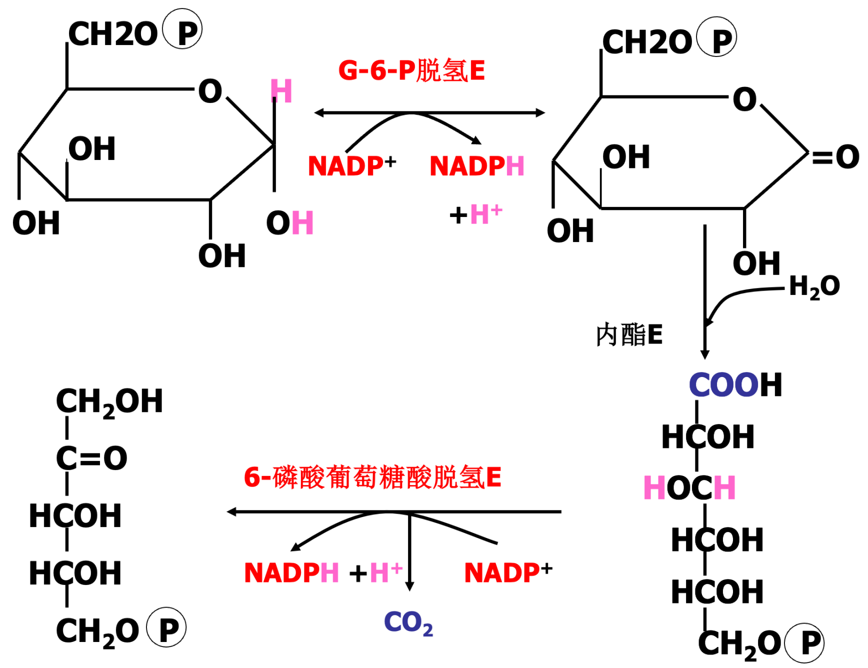
Pentose Phosphate Pathway /磷酸戊糖途径

PPP is a metabolic pathway parallel to glycolysis. It generates NADPH and pentoses (five-carbon sugars) as well as ribose 5-phosphate, a precursor for the synthesis of nucleotides.

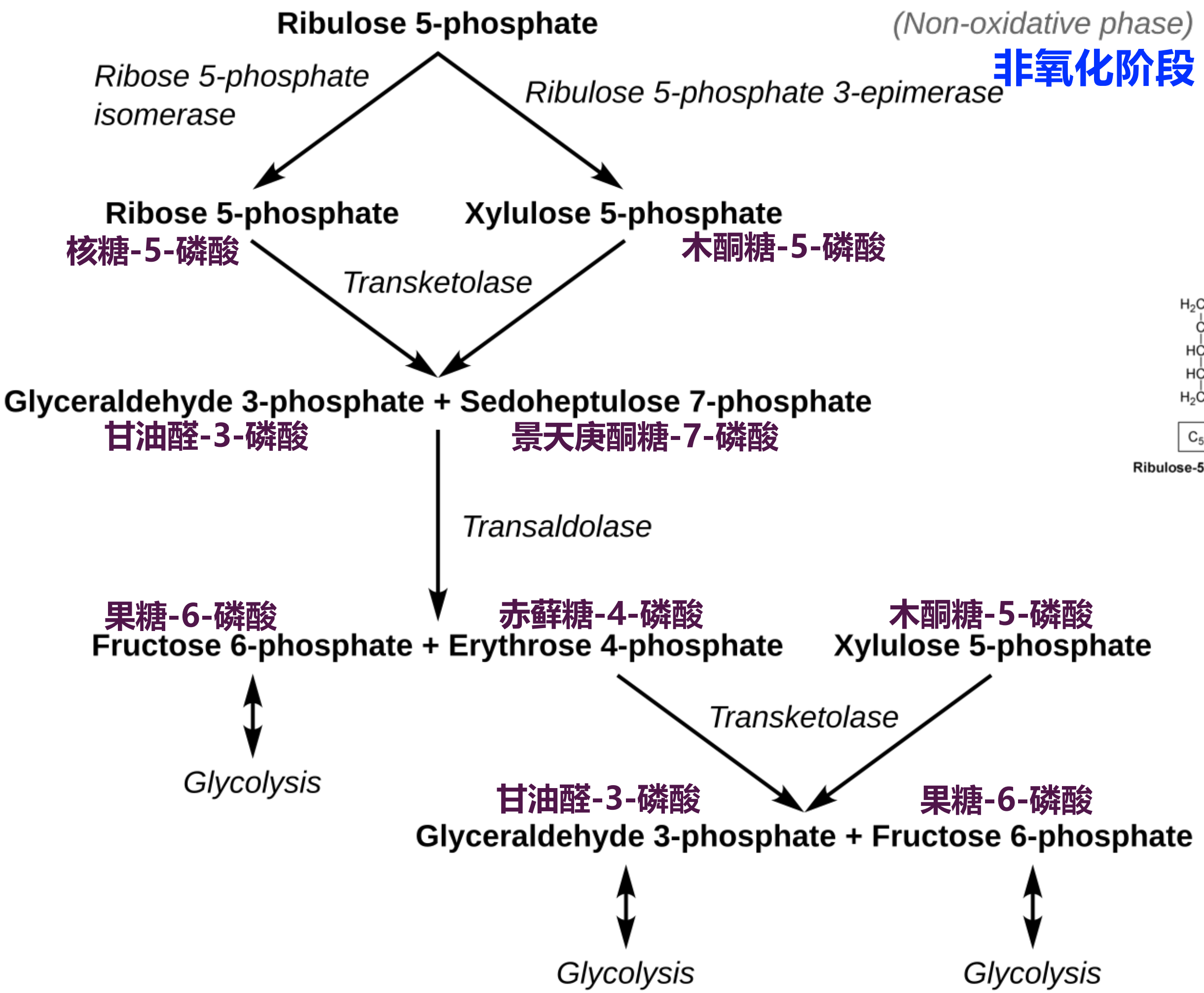
- Occurs in the **cytosol**
- Starts from **glucose-6-phosphate (G6P)**

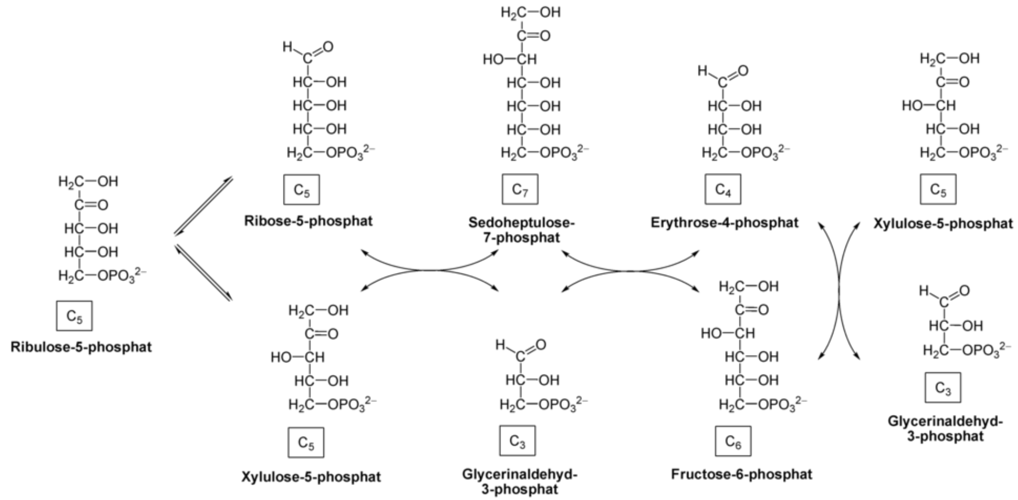
Pentose Phosphate Pathway





Pentose Phosphate Pathway





Pentose Phosphate Pathway

6 G-6-P + 12 $NADP^+$ + 6 H_2O

↓ 氧化阶段

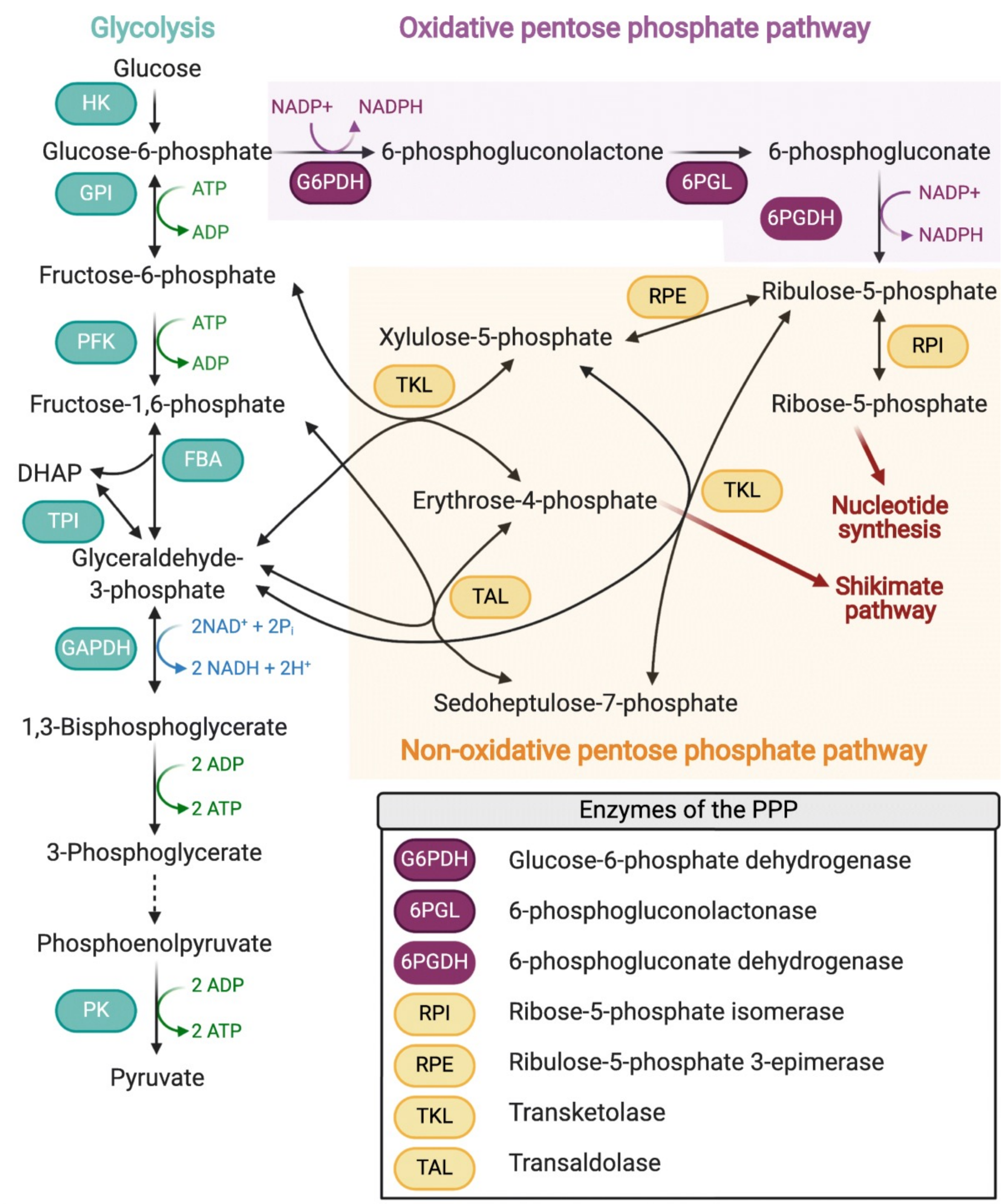
6 CO_2 + 6 Ru-5-P + 12NADPH•H^+

+

H_2O

↓ 非氧化阶段

5 G-6-P + Pi



PPP vs Glycolysis–TCA Pathway

Feature	**PPP**	**Glycolysis**
Location	Cytosol	Cytosol
Starting substrate	Glucose-6-phosphate	Glucose
Oxidation mode	Direct oxidative decarboxylation	Stepwise oxidation
Coenzyme	$NADP^+$	NAD^+
ATP production	None	Yes
Main products	NADPH, Ribose-5-P	ATP, NADH, Pry

Physiological Roles of PPP

1. Production of NADPH (Reducing Power)

- Provides **NADPH** for **Fatty acid, Cholesterol, Nucleotide synthesis**
- Maintains **redox balance (GSSG → 2 GSH)**
- Supports **detoxification and antioxidant defense**

2. Biosynthetic Functions

- **Ribose-5-phosphate** can be used in nucleotide and coenzyme synthesis (NAD^+, FAD)
- **Erythrose-4-phosphate (E4P)** is important for aromatic amino acids (Tyr, Phe, Trp)

3. Metabolic Integration

- Intermediates (e.g., **G3P, F6P**) connect with **Glycolysis (EMP)**

4. Special Roles

- Provides reducing power for **Nitrate/nitrite reduction (plants, bacteria)**
- Linked to **photosynthesis**

Regulation of the PPP

Oxidative Phase (Rate-Limiting Step)

- ❑ Enzyme: **Glucose-6-phosphate dehydrogenase (G6PD)**
- ❑ Regulation:
  - ✓ **Activated by $NADP^+$**
  - ✓ **Inhibited by NADPH**

Non-oxidative Phase

- ❑ **Reversible reactions**
- ❑ Driven by **substrate availability**
- ❑ Excess **ribose-5-phosphate (R5P)** can be converted to:
  - ✓ **Fructose-6-phosphate (F6P)**
  - ✓ **Glyceraldehyde-3-phosphate (G3P)**

Summary of PPP

What is PPP?

- ❖ Cytosolic pathway of **glucose-6-phosphate metabolism**
- ❖ Alternative to glycolysis

Core Functions

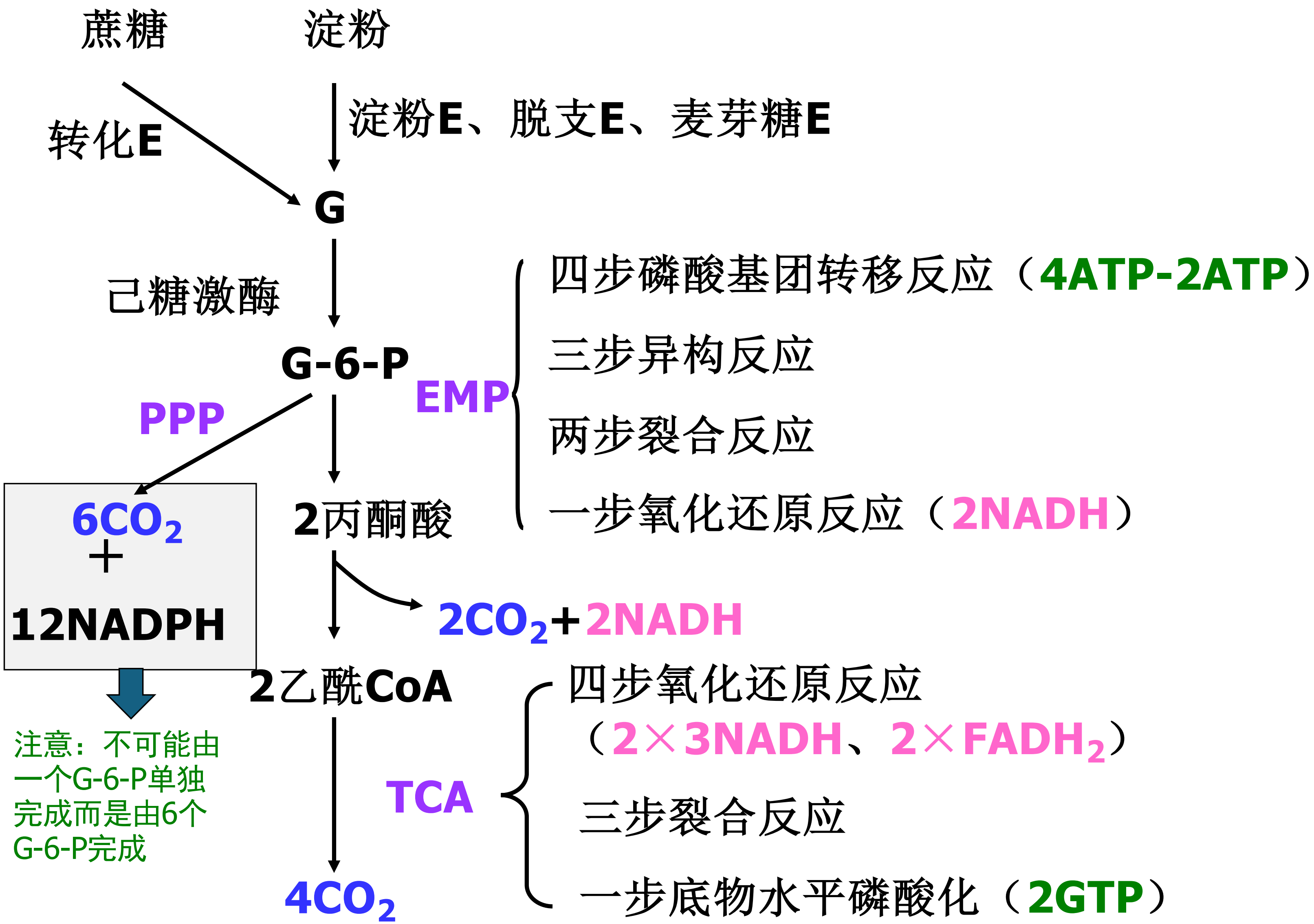
- ❖ **NADPH Production**
- ❖ **Ribose-5-Phosphate Production**
- ❖ **Carbon Rearrangement**

Key Features

- ❖ **No ATP production**
- ❖ **Oxidative phase (irreversible)**
- ❖ **Non-oxidative phase (reversible)**

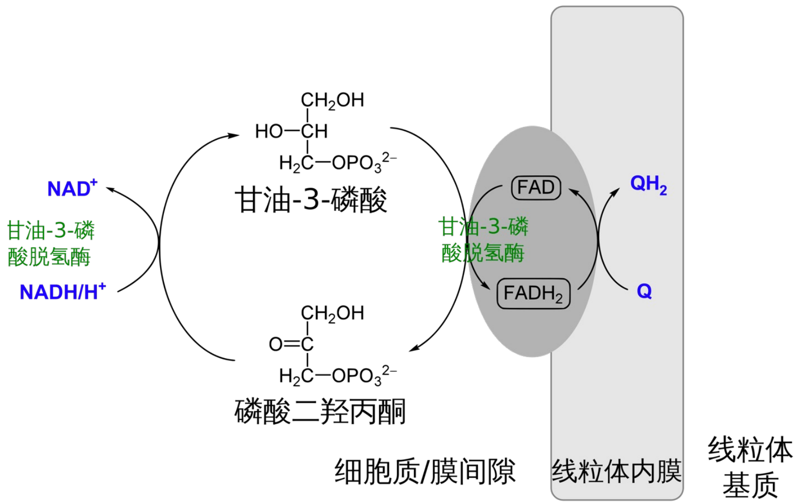
Regulation

- ❖ **Rate-limiting enzyme: G6PD**
- ❖ **NADPH inhibits / $NADP^+$ activates**


蔗糖
淀粉
转化E
淀粉E、脱支E、麦芽糖E
G
己糖激酶
G-6-P
PPP
EMP
四步磷酸基团转移反应（4ATP-2ATP）
三步异构反应
两步裂合反应
一步氧化还原反应（2NADH）
6CO2
＋
12NADPH
2丙酮酸
2CO2+2NADH
2乙酰CoA
注意：不可能由一个G-6-P单独完成而是由6个G-6-P完成
TCA
四步氧化还原反应
（2×3NADH、2×FADH2）
三步裂合反应
一步底物水平磷酸化（2GTP）
4CO2

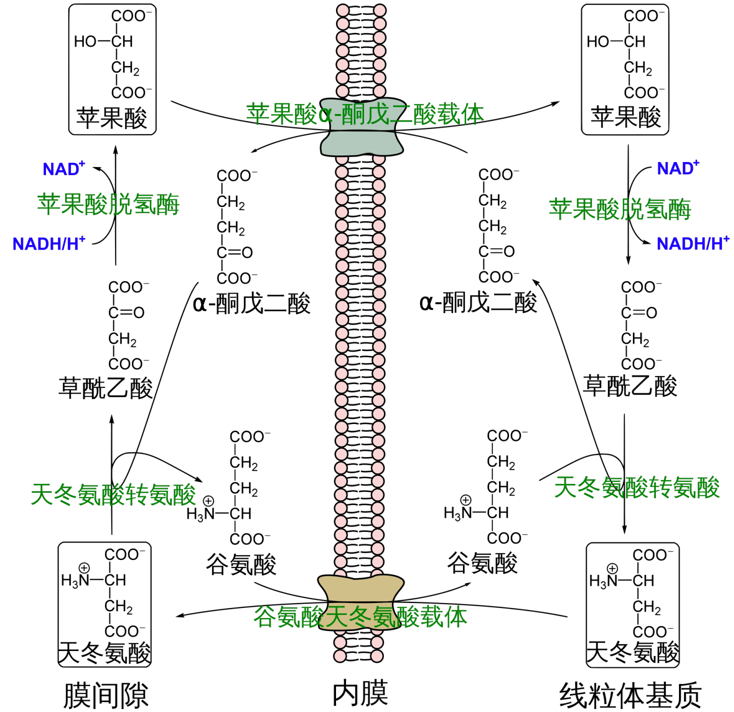
Fate of NADH Produced in Glycolysis

Glycerol-3-Phosphate Shuttle
磷酸甘油穿梭



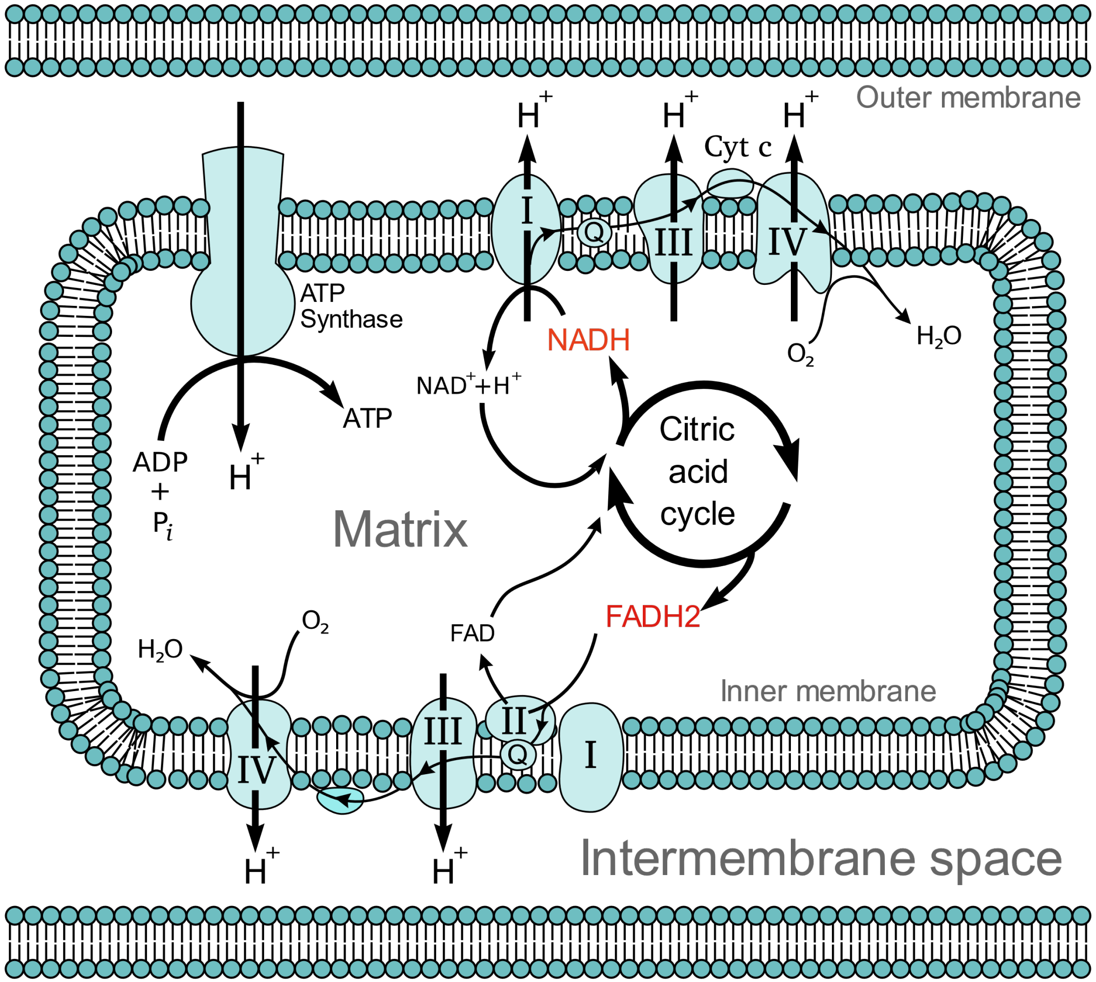
NADH → $FADH_2$

Malate-Aspartate Shuttle
苹果酸穿梭



NADH → NADH

$G + O_2 \longrightarrow CO_2 + H_2O + ATP$



Biological Oxidation

生物氧化

Biological Oxidation

Biological oxidation refers to the process in which organic molecules are oxidized within living cells through enzyme-catalyzed reactions, with the released energy conserved in the form of ATP.

Key Features

- Occurs in **living cells**
- Involves **enzyme-catalyzed redox reactions**
- Energy from NADH/$FADH_2$ is used for **ATP synthesis**

Biological Oxidation

Characteristics of Biological Oxidation

- Occurs under **mild conditions**
  - ✓ physiological temperature
  - ✓ near-neutral pH
- Proceeds via **stepwise enzyme-catalyzed reactions**
- Energy is **released gradually**
- Energy is conserved in **high-energy molecules (ATP, NADH)**

Biological Oxidation

Characteristics of Biological Oxidation

Feature	**Biological Oxidation**	**Combustion / 燃烧**
Conditions	Mild (physiological)	High temperature
Process	Stepwise, enzyme-controlled	One-step reaction
Energy release	Gradual, conserved	Rapid, lost as heat
Energy form	ATP, NADH	Heat
CO_2 formation	Decarboxylation reactions	Direct oxidation

Biological Oxidation

Types of Oxidation in Biological Systems

- **Loss of Electrons / 失电子**

$$Fe^{2+} \rightarrow Fe^{3+} + e^{-}$$

- **Loss of Hydrogen / 脱氢 (Most Important)**

$$\text{Substrate} \rightarrow \text{Oxidized product} + 2H^{+} + 2e^{-}$$

Catalyzed by **dehydrogenases (NAD^{+}, FAD)**

- **Gain of Oxygen / 加氧**

$$RH + \frac{1}{2}O_2 \rightarrow ROH$$

Biological Oxidation

Formation of Water in Biological Oxidation

Step 1: Oxidation (Loss of Electrons)

$$AH_2 \rightarrow A + 2\,H^+ + 2\,e^-$$

Step 2: Electron Transfer

Electron Transport Chain (ETC), and Energy is released stepwise

Step 3: Reduction (Gain of Electrons)

$$\frac{1}{2}\,O_2 + 2\,H^+ + 2e^- \rightarrow H_2O$$

Biological Oxidation

O_2 is the final electron acceptor

Biological Oxidation	Combustion
❖ Oxidation and reduction are **separated**	❖ Oxidation and reduction occur **simultaneously**
❖ Electrons transferred via **carriers**	❖ Direct electron transfer to O_2
❖ Energy released **gradually** → **conserved as ATP**	❖ Energy released **instantly** → **heat**

Biological Oxidation

High-Energy Compounds

High-energy compounds are molecules that, upon hydrolysis or group transfer, release a large amount of free energy (large negative ΔG°')

Energy is released due to:

- ❖ Relief of **electrostatic repulsion**
- ❖ Formation of **more stable products**
- ❖ **Resonance stabilization**

"High-energy bond" does NOT mean unstable bond!

Example: ATP

Biological Oxidation

Electron Transport Chain (ETC)

The ETC is a series of electron carriers located in the inner mitochondrial membrane that transfer electrons from NADH and $FADH_2$ to O_2

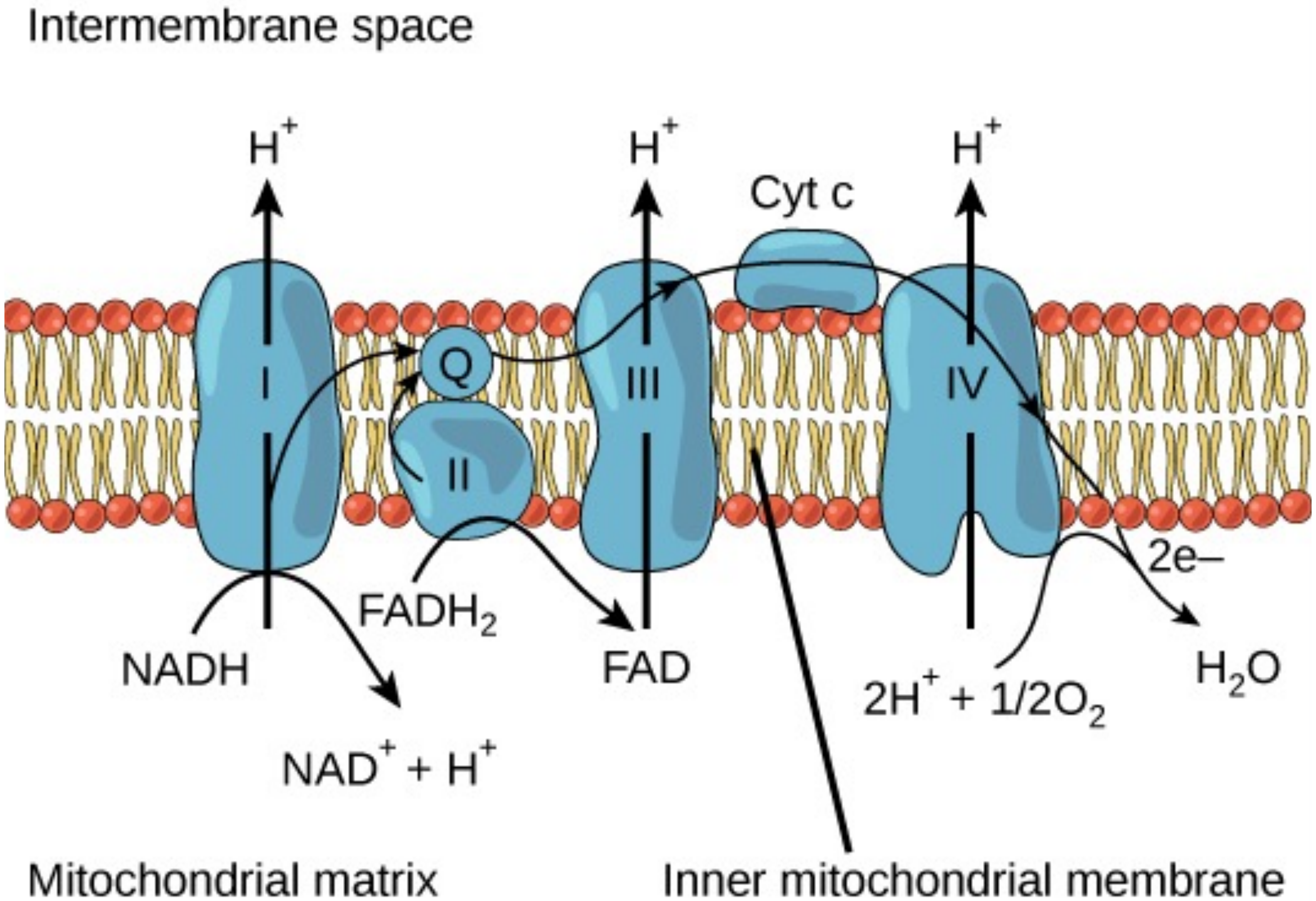
Electrons flow: NADH/$FADH_2$ → ETC → O_2 → H_2O

NADH → Complex I

$FADH_2$ → Complex II

Biological Oxidation

Electron Transport Chain (ETC)

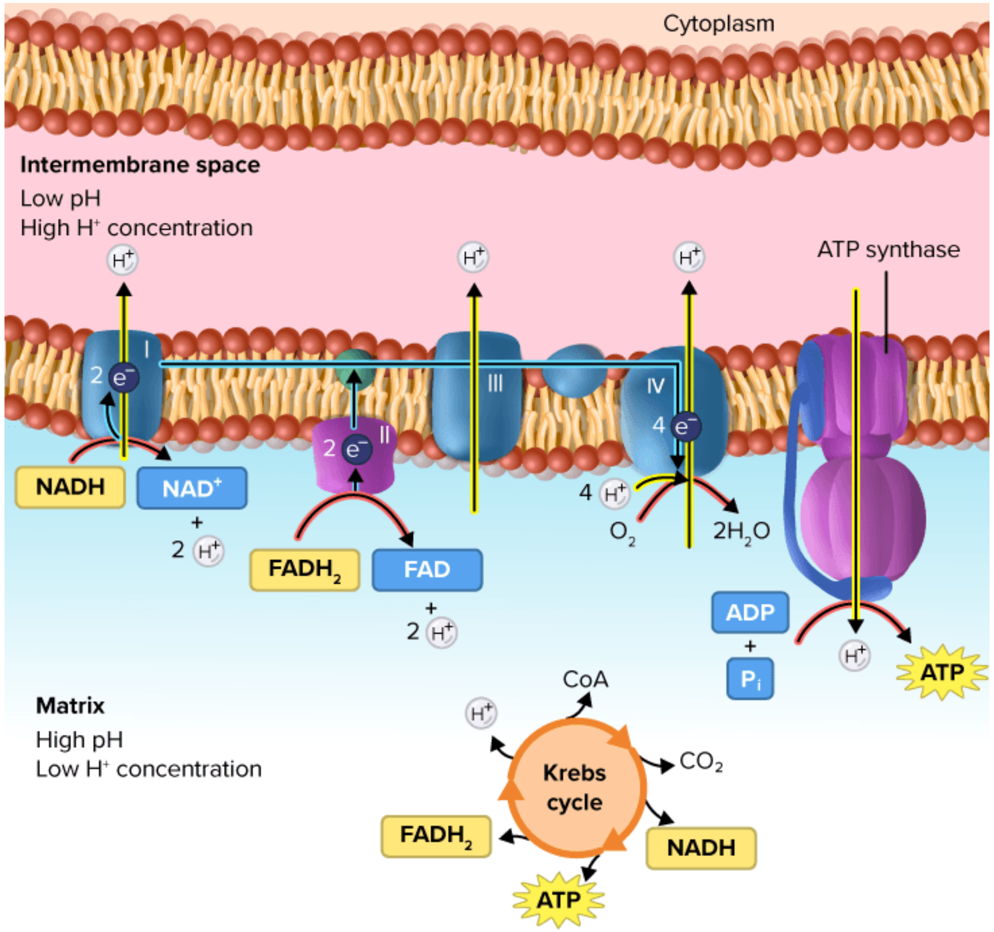


ETC Complexes

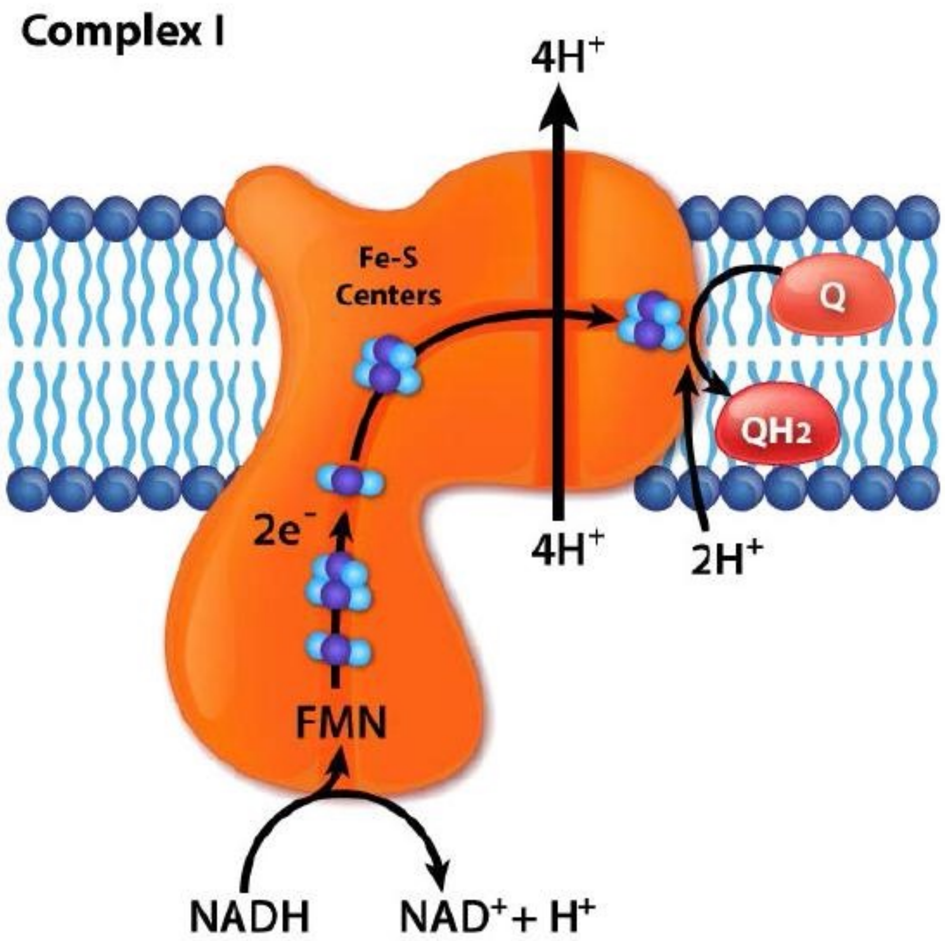
- ❖ **Located in the inner mitochondrial membrane**
- ❖ **Organized as four functional complexes (I–IV)**

❖ Four Complexes

- Complex I – NADH dehydrogenase
- Complex II – Succinate dehydrogenase
- Complex III – Cytochrome bc_1 complex
- Complex IV – Cytochrome c oxidase



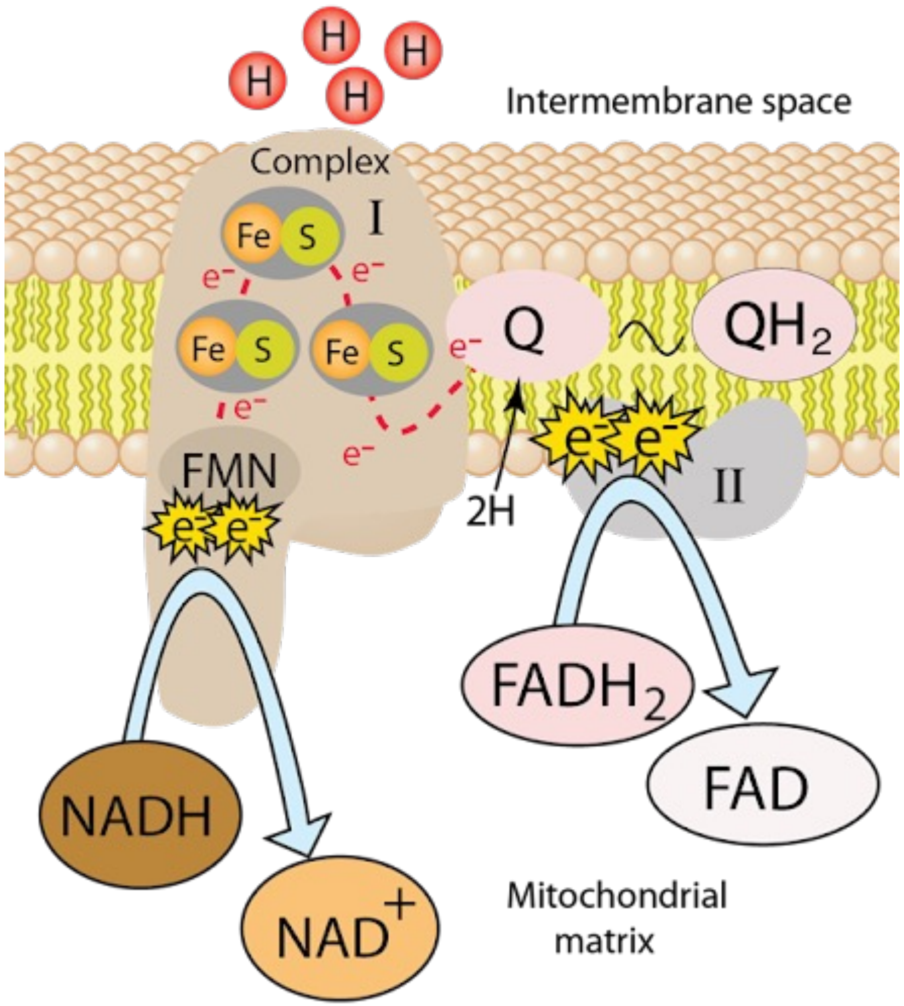
Complex I: NADH Dehydrogenase NADH-CoQ还原酶



Components

- ❖ FMN (flavin mononucleotide)
- ❖ Iron–sulfur (Fe–S) clusters

Complex I: NADH Dehydrogenase NADH-CoQ还原酶



- **Transfers electrons:**

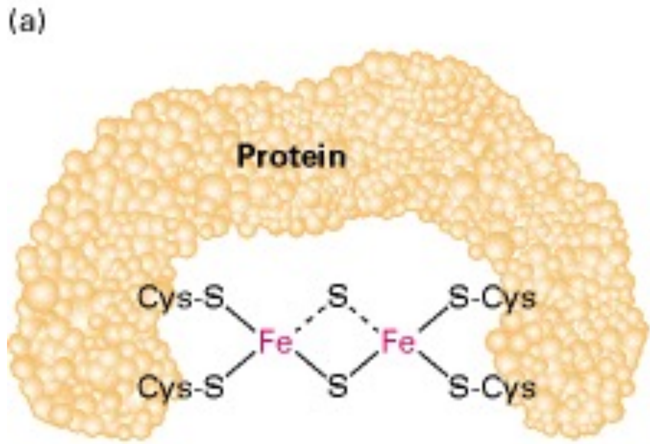
  NADH→FMN→Fe−S→CoQ

- **Pumps protons:**

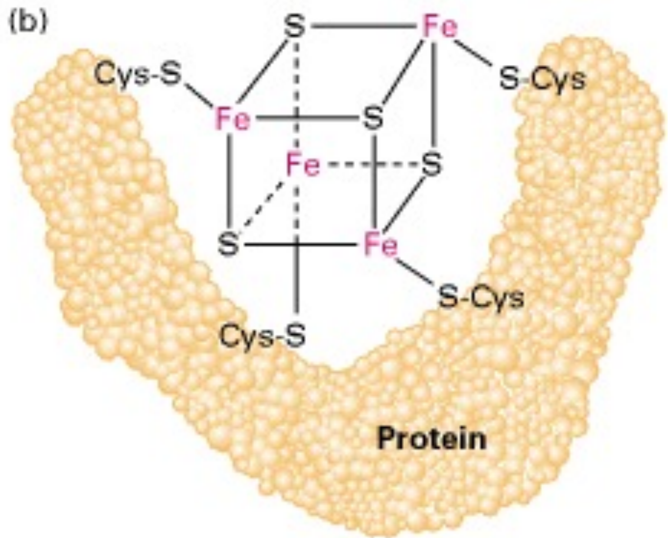
  4 H^+ from matrix → intermembrane space

Complex I: NADH Dehydrogenase NADH-CoQ还原酶

Iron–Sulfur Clusters (Fe–S Centers)



2Fe-2S



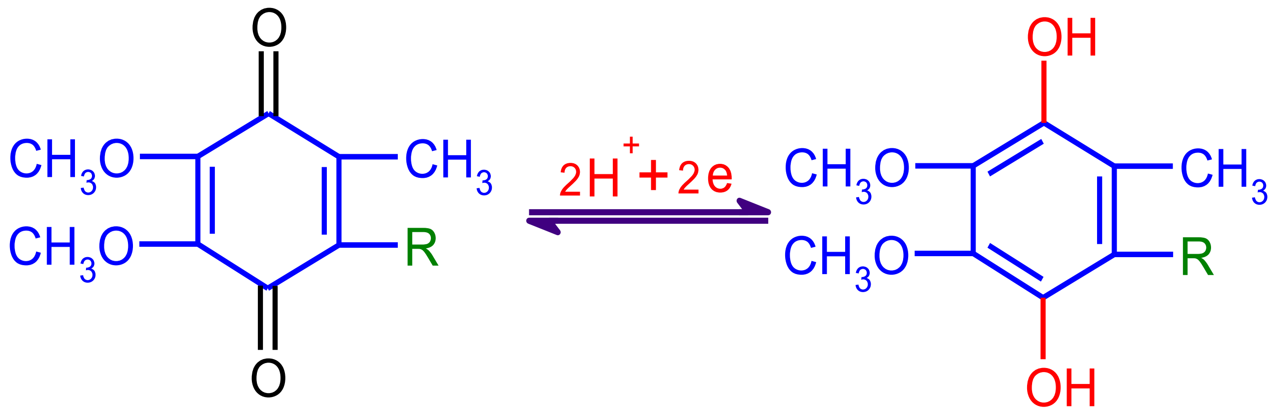
4Fe-4S

$$Fe^{3+} + e^{-} \leftrightarrow Fe^{2+}$$

Complex I: NADH Dehydrogenase NADH-CoQ还原酶

Coenzyme Q (Ubiquinone, CoQ) / 辅酶Q（又称泛醌）

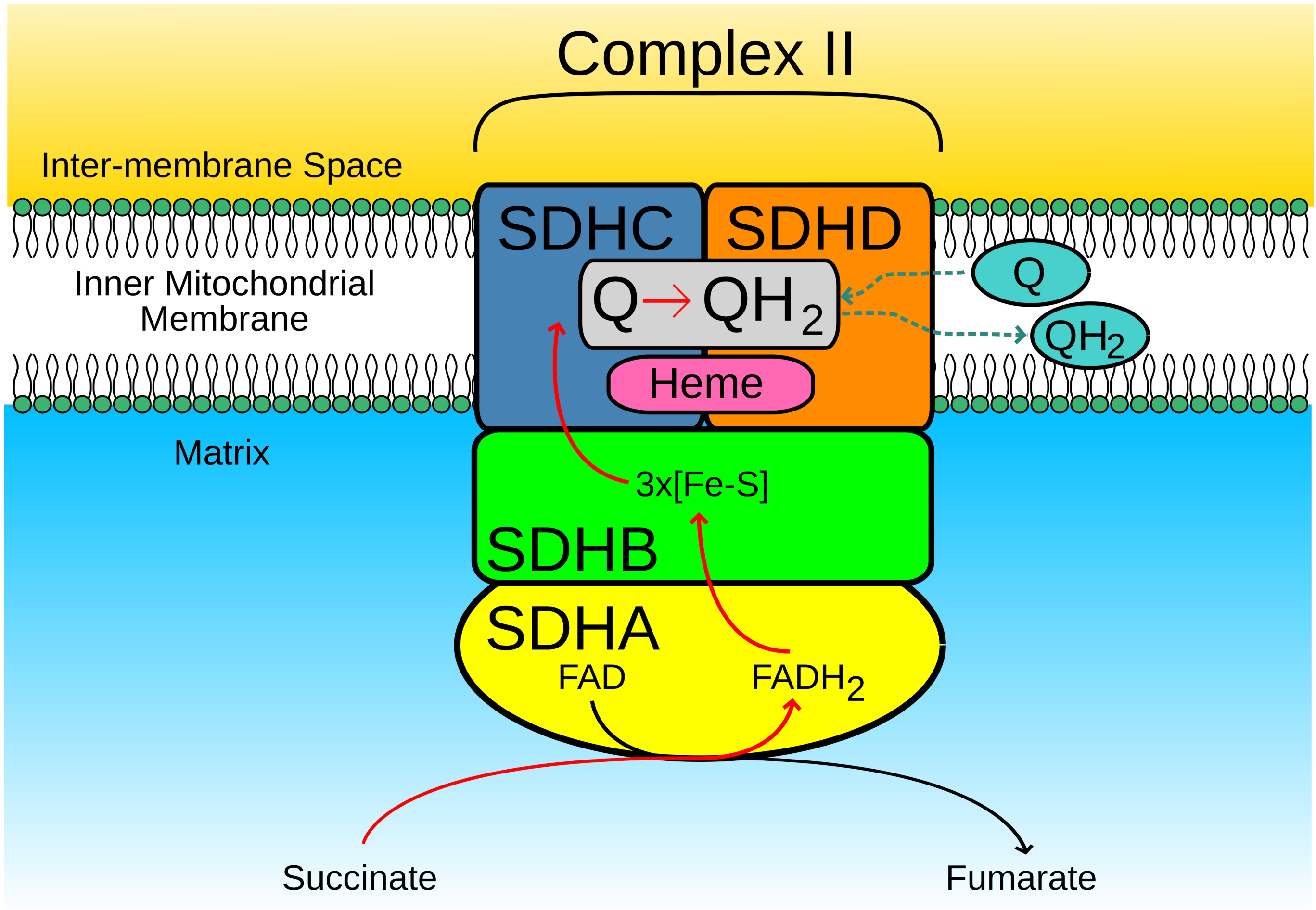
- ❖ **Lipid-soluble quinone / 脂溶性小分子**
- ❖ **Located in the inner mitochondrial membrane**
- ❖ **Mobile electron carrier**



Coenzyme Q

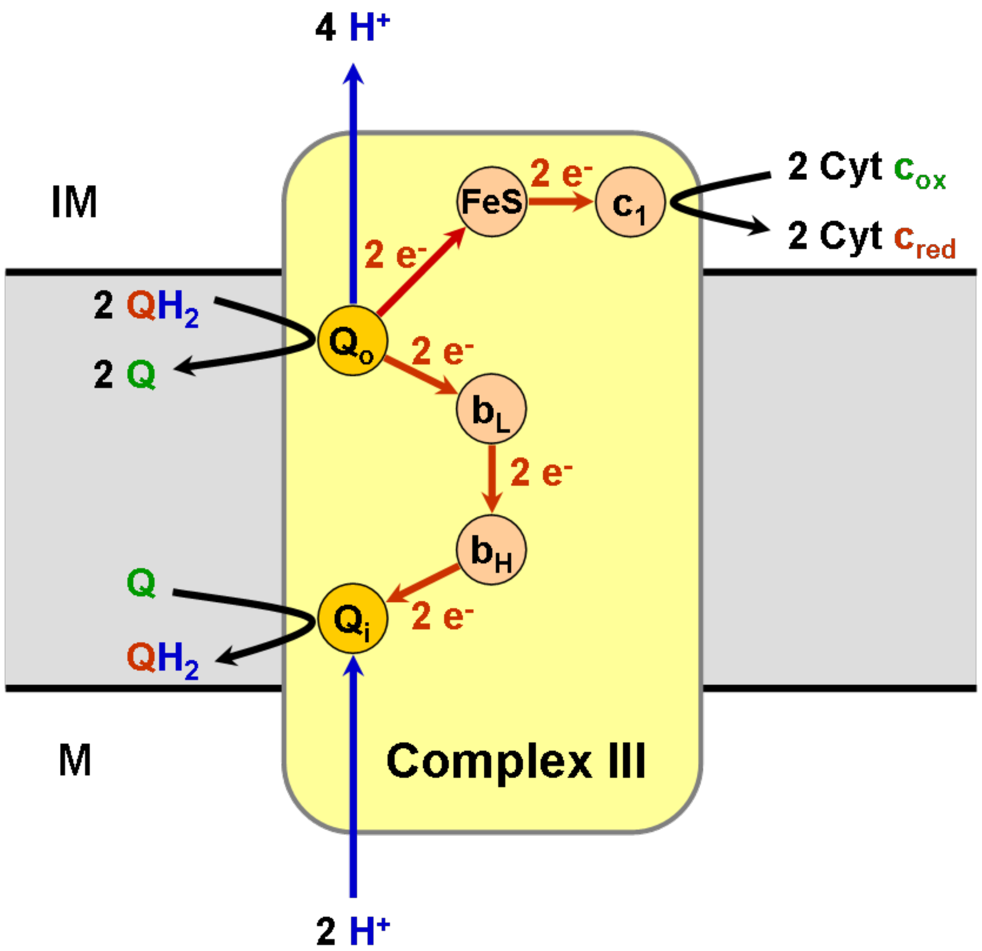
ubiquinol (QH_2)
还原性醌

Complex II: Succinate-coenzyme Q reductase (SQR) 琥珀酸-CoQ还原酶



- **Inner mitochondrial membrane** and active site faces the matrix
- Contains: FAD, Fe–S
- Transfers electrons to CoQ
- **No H^+ pumping**

Complex III: coenzyme Q : cyt c – oxidoreductase 细胞色素C还原酶



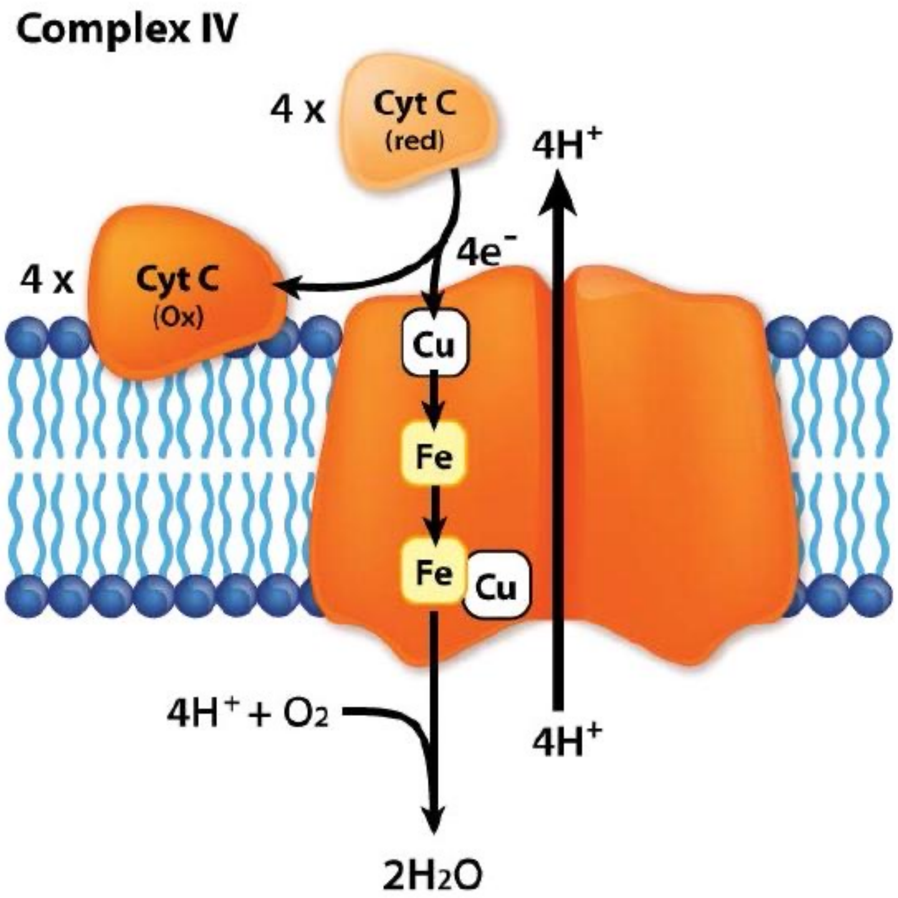
- **Inner mitochondrial membrane**
- **Components**
  - **Cytochrome b**
  - **Cytochrome c_1**
  - **Iron–sulfur (Fe–S) protein**

QH_2→Fe–S→c_1→Cytochrome c

Splits **2 electrons** from QH_2:

- 1 electron → **cytochrome c (one at a time)**
- 1 electron → recycled via **cytochrome b**

Complex IV: cytochrome c oxidase (COX) 细胞色素C氧化酶



- Inner mitochondrial membrane
- Components
  - Cytochromes a and a_3
  - Copper centers (CuA, CuB)
- Pumps 4 H^+ across the membrane (per 4 electrons)

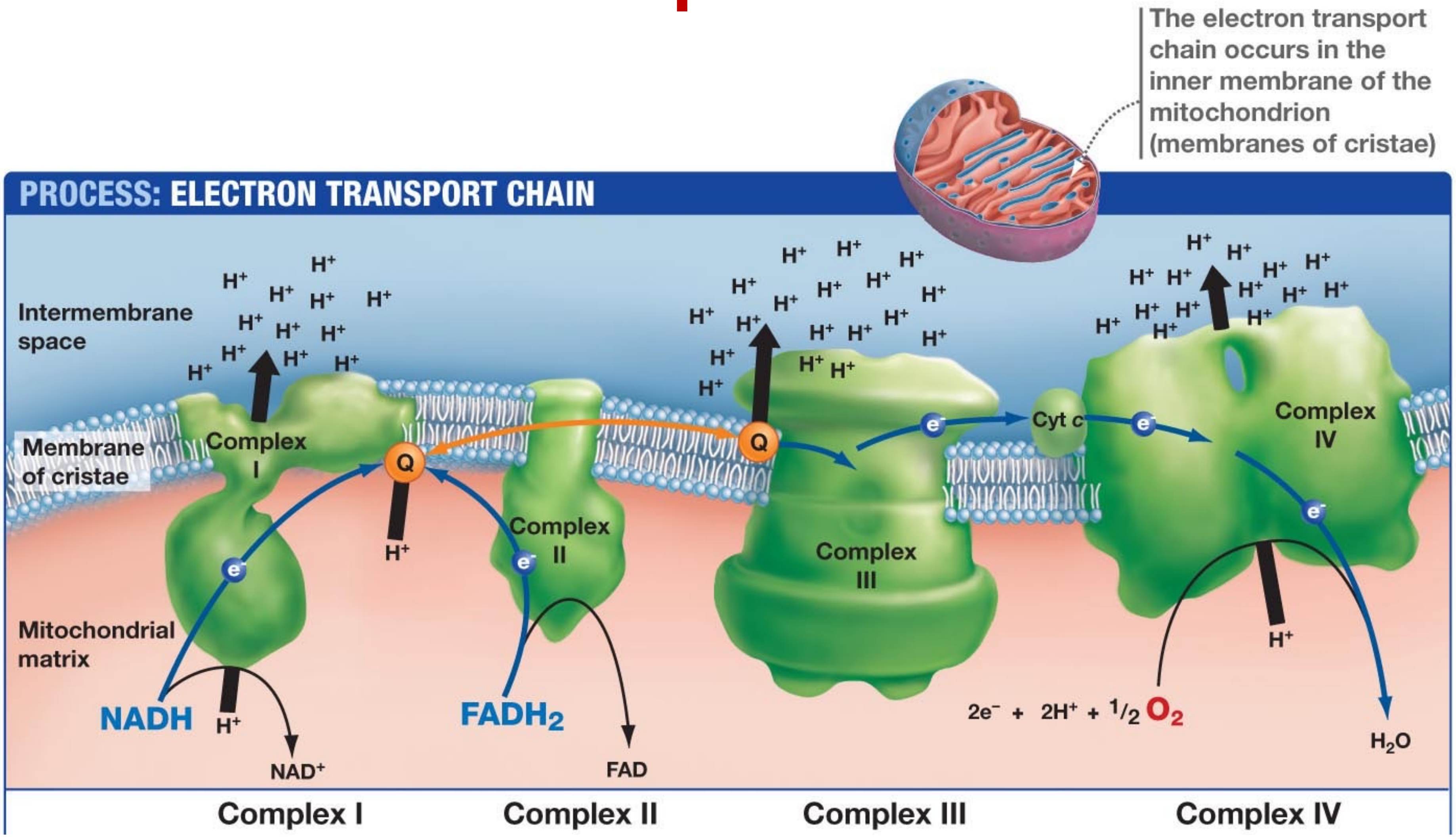
$$O_2 + 4\,H^+ + 4\,e^- \rightarrow 2\,H_2O$$

Features of ETC Complexes

Complex	Name	Electron Source	Electron Transfer	Proton Pumping
I	NADH dehydrogenase	NADH	→ CoQ	Yes
II	Succinate dehydrogenase	$FADH_2$	→ CoQ	**No**
III	Cytochrome bc_1	$CoQH_2$	→ Cytochrome c	Yes
IV	Cytochrome c oxidase	Cytochrome c	→ O_2 → H_2O	Yes

Not all complexes pump protons—this is why NADH and $FADH_2$ yield different ATP.

Electron Transport Chain



Electron Transport Chain

NADH vs $FADH_2$ Entry into ETC

Similarities

- Electrons ultimately transferred to $\mathbf{O_2} \rightarrow \mathbf{H_2O}$
- Occur in the **same electron transport chain**
- Converge at **Coenzyme Q (CoQ)**

Differences

Feature	**NADH**	**$FADH_2$**
Entry point	Complex I	Complex II
Proton pumping	Yes (I, III, IV)	Only III, IV
ATP yield	~2.5 ATP	~1.5 ATP

Electron Transport Chain

How Was ETC Studied?

- ❖ Redox potential (E°') measurement / 氧化还原电位测定
- ❖ Reconstitution of complexes / 复合物重组
- ❖ Spectroscopy (oxidation state changes) / 利用光谱测定组分氧化态
- ❖ Use of inhibitors / 抑制剂

Electron Transport Chain

Redox Potential & Electron Flow

(-0.32) (-0.30) (-0.02) (0.10) (0.00) (0.04) (0.22)

$NADH+H^+ \rightarrow FMN \rightarrow Fe\text{-}S \rightarrow CoQ \rightarrow Cytb \rightarrow Fe\text{-}S \rightarrow Cytc_1$

↓

(0.25) Cytc

↓

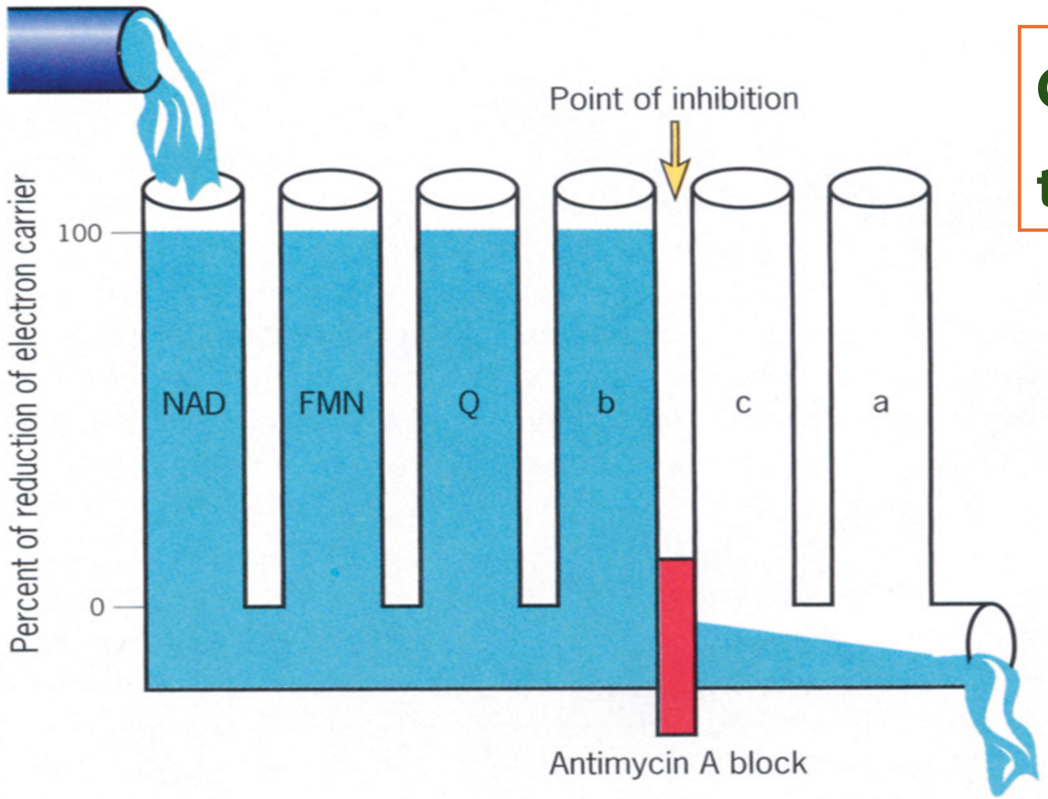
(0.29) $Cytaa_3$

↓

(0.82) O_2

Electron Transport Chain

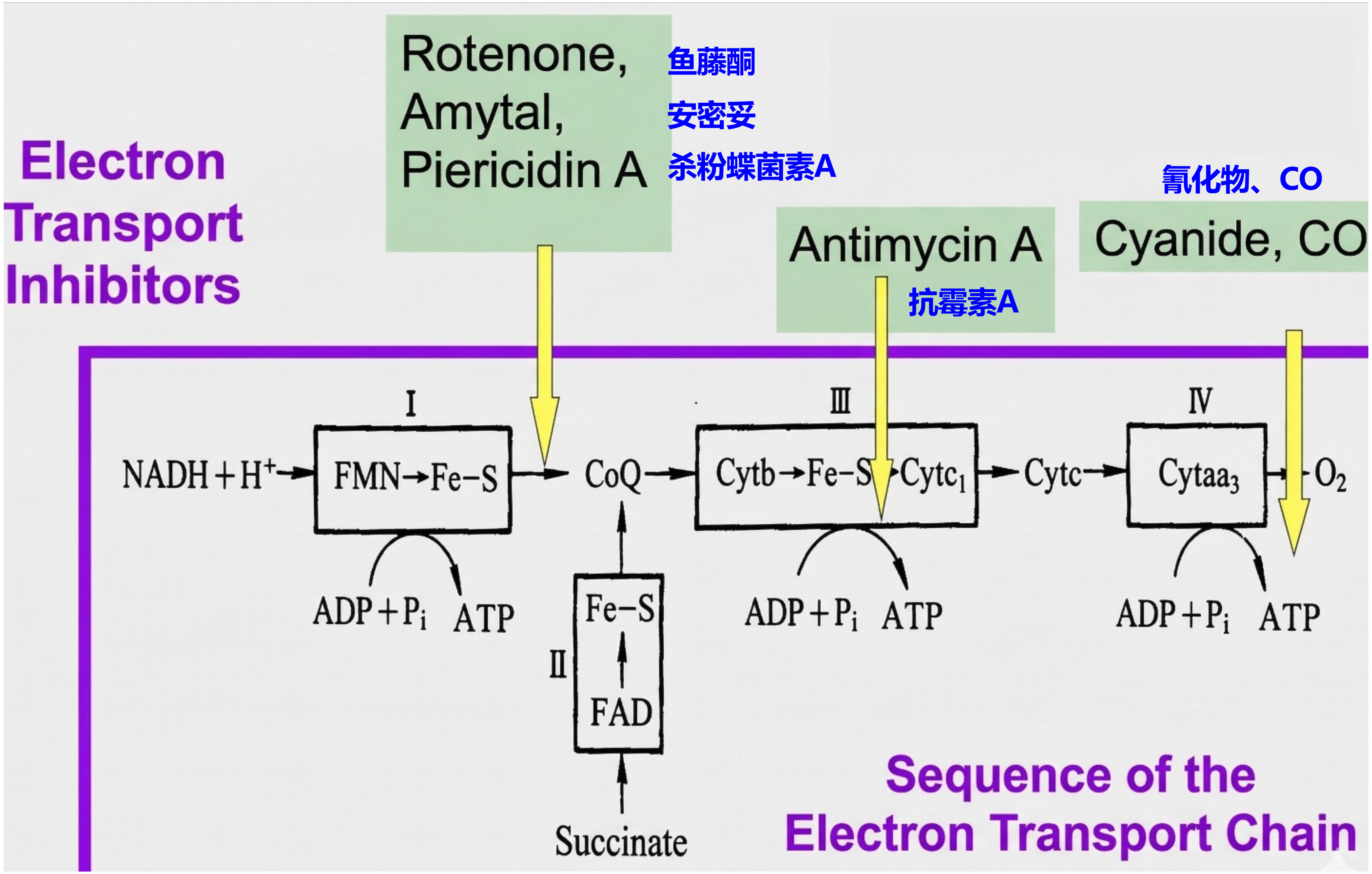
Electron Transport Chain Inhibitors



Compounds that block electron transfer at specific sites in the ETC

- ❖ **Block electron flow**
- ❖ **Upstream → reduced**
- ❖ **Downstream → oxidized**

Electron Transport Chain



Oxidative Phosphorylation

Oxidative phosphorylation is the process in which ATP is synthesized by coupling electron transport to proton gradient formation (chemiosmosis).

Where Does It Occur?

- **Inner mitochondrial membrane**

Main source of ATP in aerobic cells

Electron transport

↓

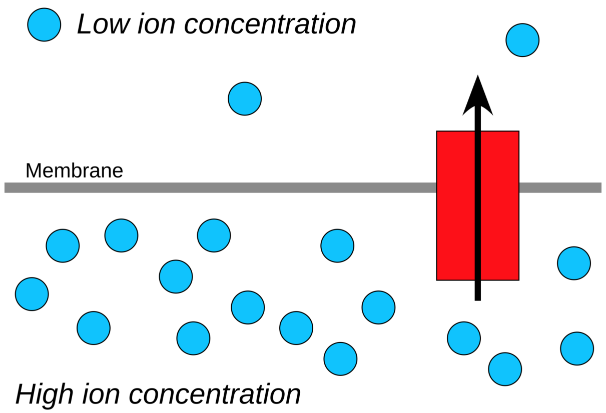
Proton gradient

↓

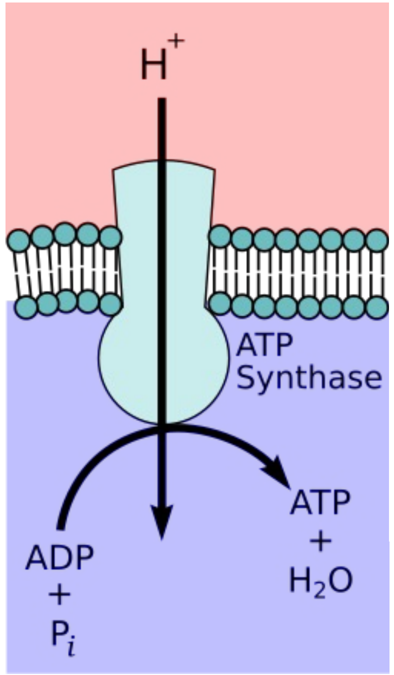
ATP synthesis

Chemiosmotic

Chemiosmotic mechanism of ATP synthesis



Peter Mitchell 1978 Nobel Prize for Chemistry



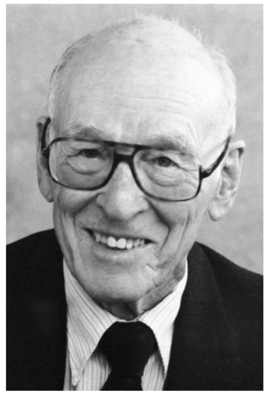


Photo from the Nobel Foundation archive.

Paul D. Boyer

Prize share: 1/4

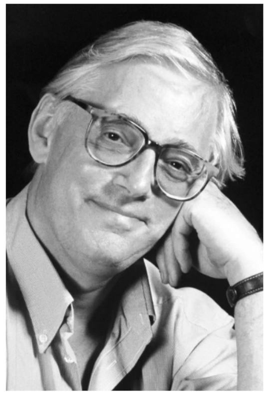


Photo from the Nobel Foundation archive.

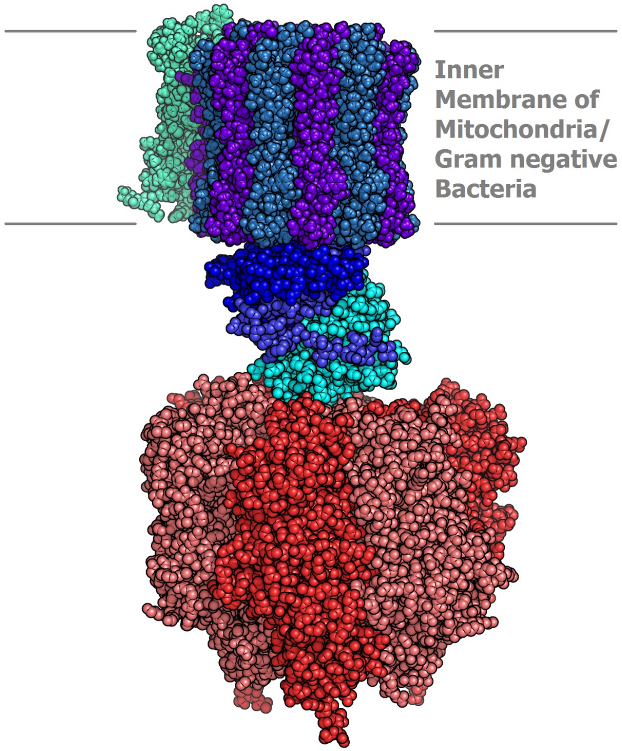
John E. Walker

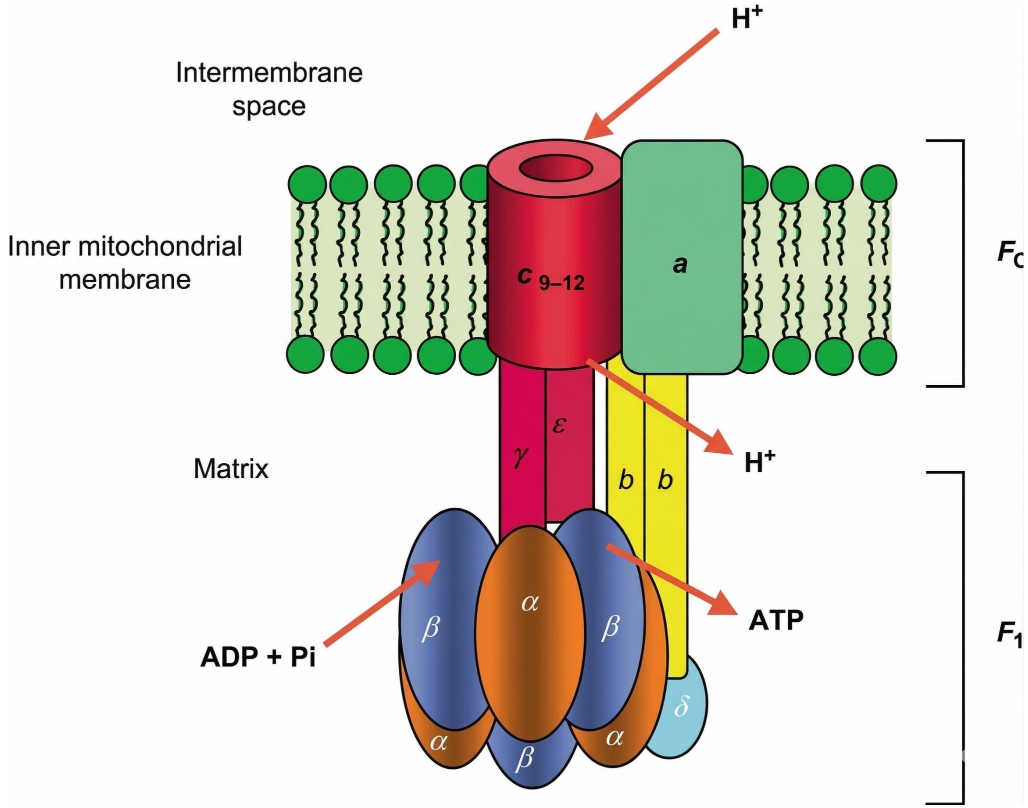
Prize share: 1/4

The Nobel Prize in Chemistry 1997 was divided, one half jointly to Paul D. Boyer and John E. Walker "for their elucidation of the enzymatic mechanism underlying the synthesis of adenosine triphosphate (ATP)"

Chemiosmotic

ATP Synthase Structure





Chemiosmotic

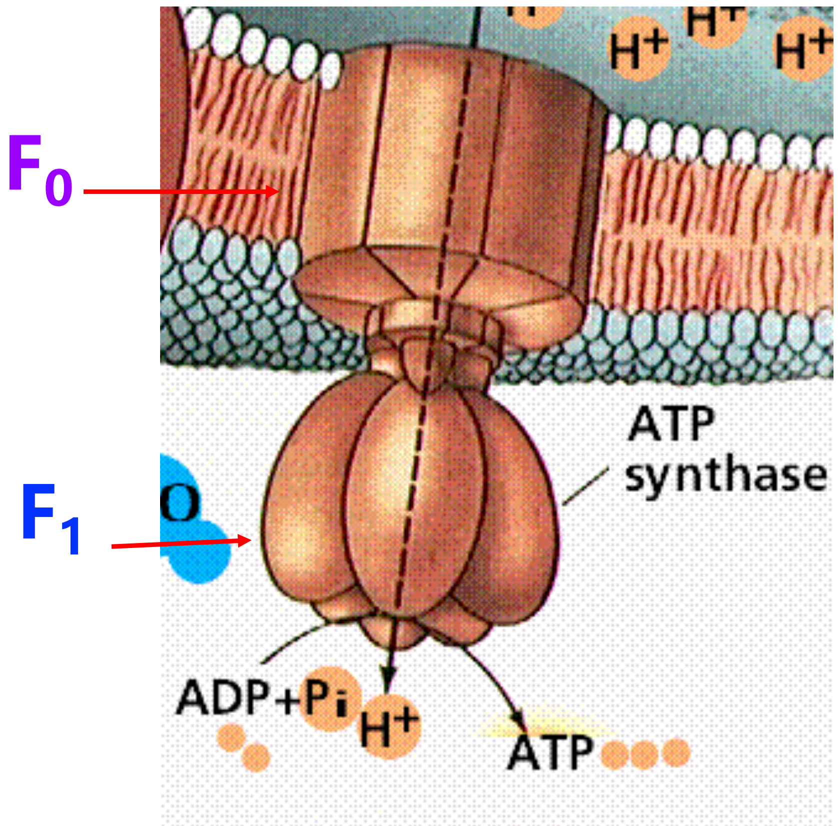
ATP Synthase Structure

F_0 (Membrane Portion)

- Located in Inner mitochondrial membrane
- Function as Proton channel (H^+ flow)

F_1 (Matrix Portion)

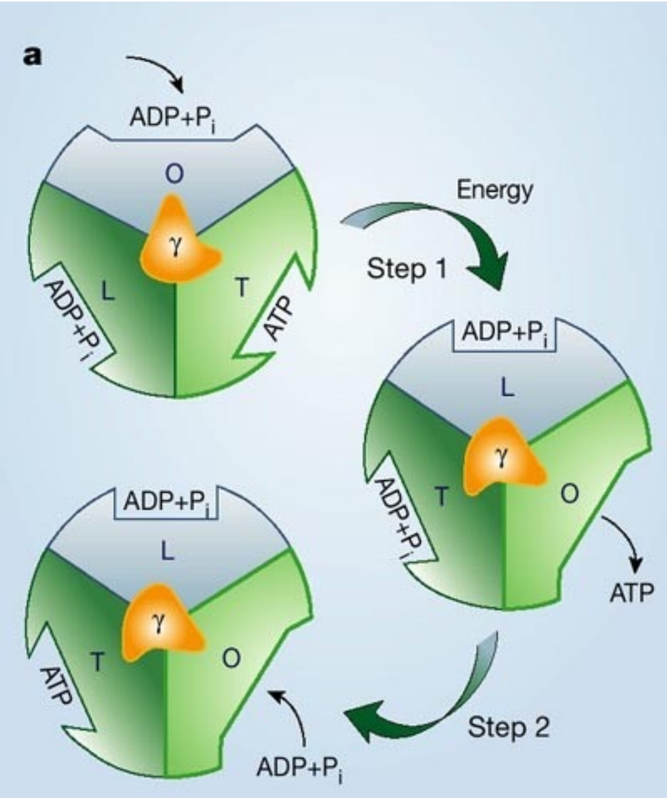
- Extends into Mitochondrial matrix
- Function as Catalytic site for ATP synthesis



Chemiosmotic

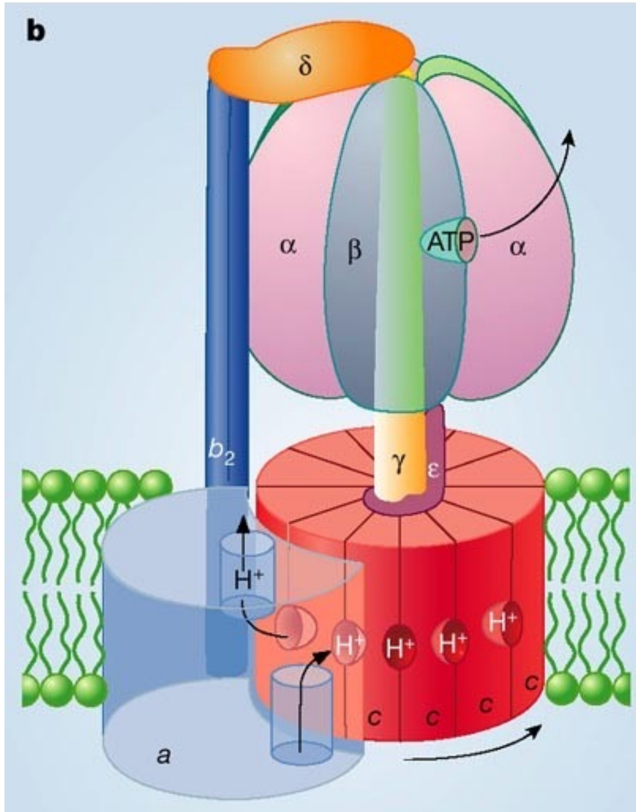
Rotational Catalysis Mechanism

Proposed by **Boyer (1964),** Confirmed by **Walker; shared half of Nobel Prize, 1997**

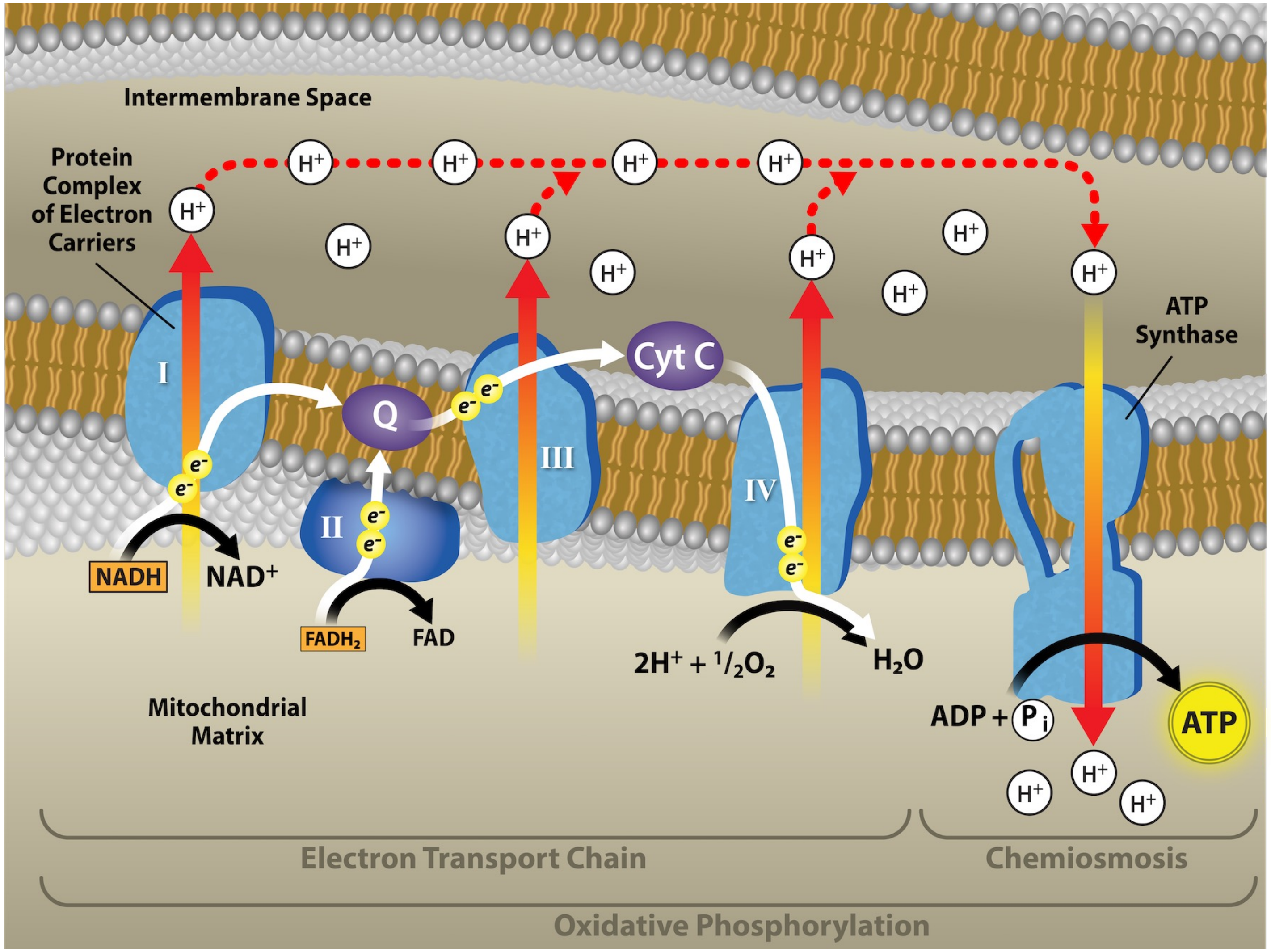


Conformations of β Subunits

- ✓ **O (Open) → releases ATP**
- ✓ **L (Loose) → binds ADP + Pi**
- ✓ **T (Tight) → synthesizes ATP**



Coupling of Electron Transport and Chemiosmotic



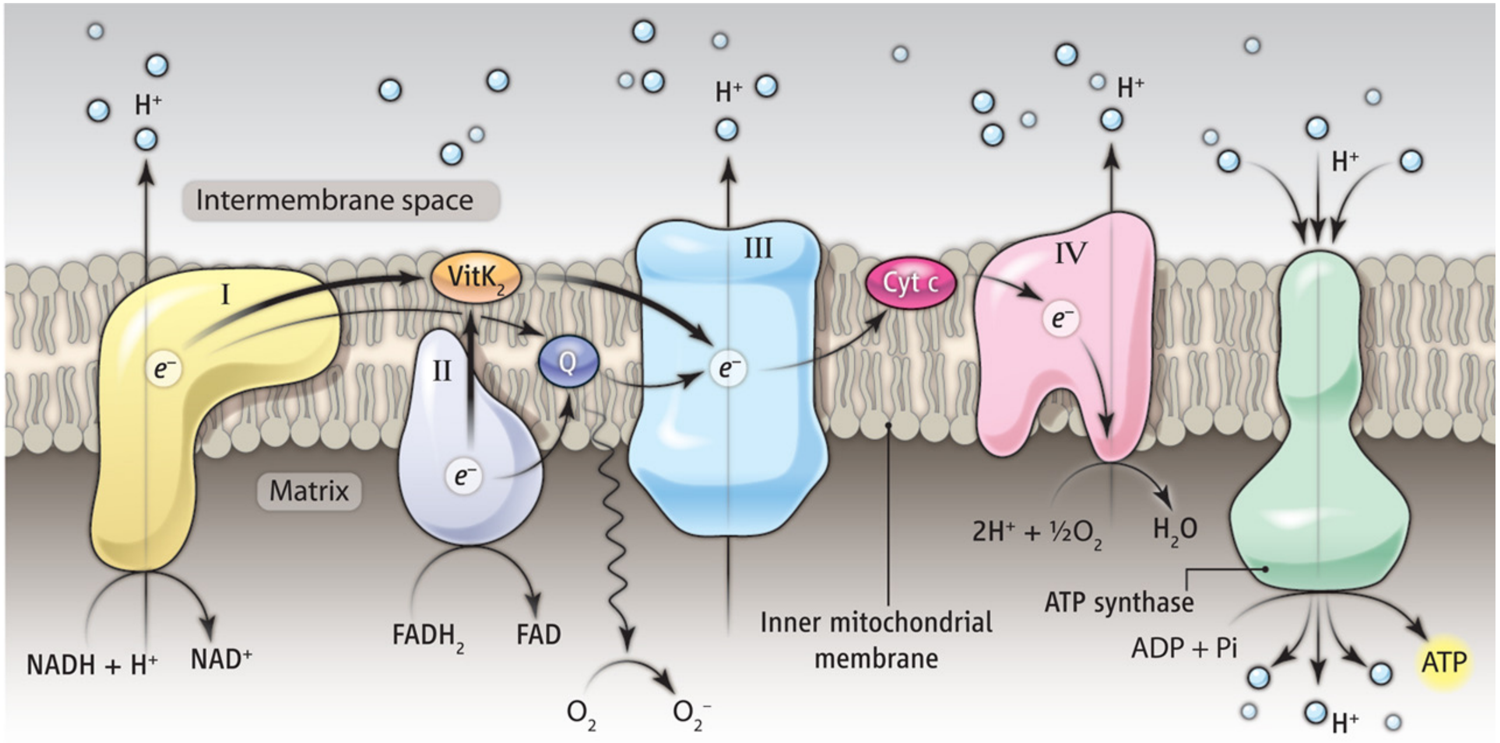
Coupling of Electron Transport and Chemiosmotic

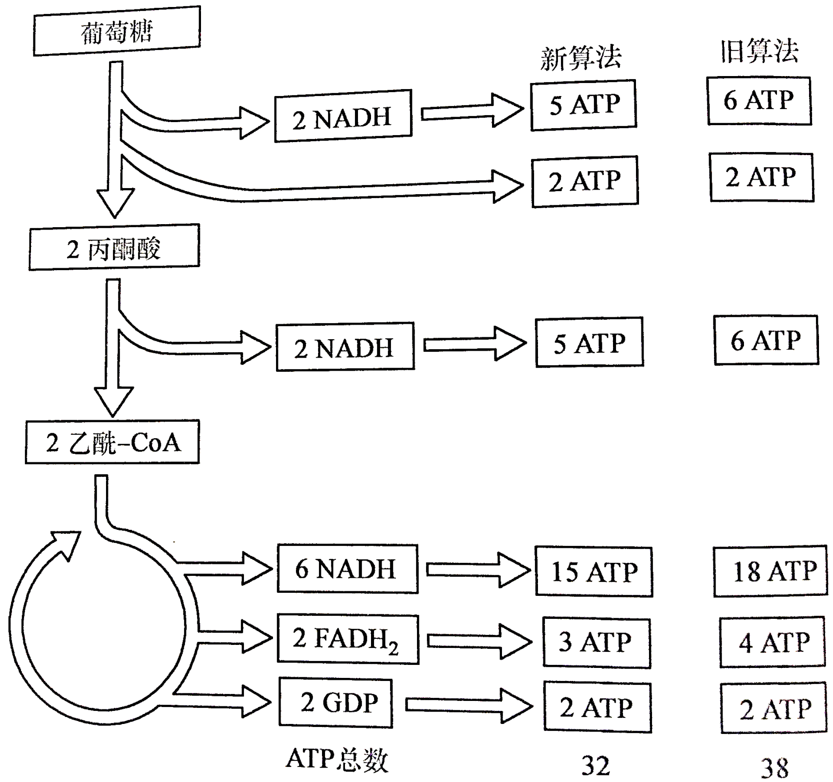
P/O Ratio: Number of ATP molecules produced per pair of electrons transferred to O_2. **ATP yield depends on where electrons enter the ETC**

P/O Ratio

NADH → 2.5 ATP

$FADH_2$ → 1.5 ATP

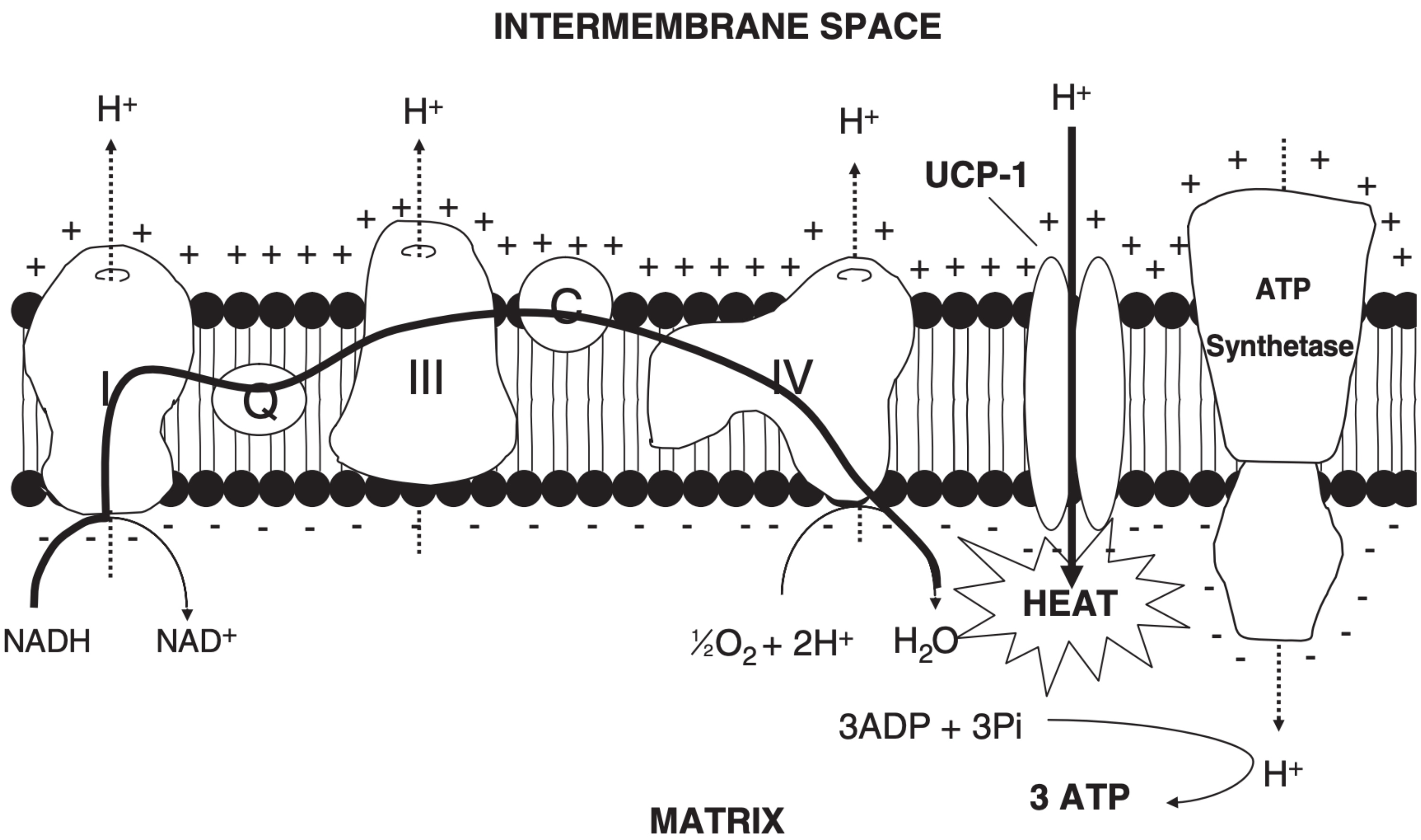




$$G + 10NAD^+ + 2FAD + 4ADP + 4Pi \longrightarrow 6CO_2 + 10NADH + 10H^+ + 2FADH_2 + 4ATP$$

Uncoupling and Inhibition of Oxidative Phosphorylation

- ❖ Do NOT block electron transport
- ❖ Disrupt the proton gradient
- ❖ Energy released as heat



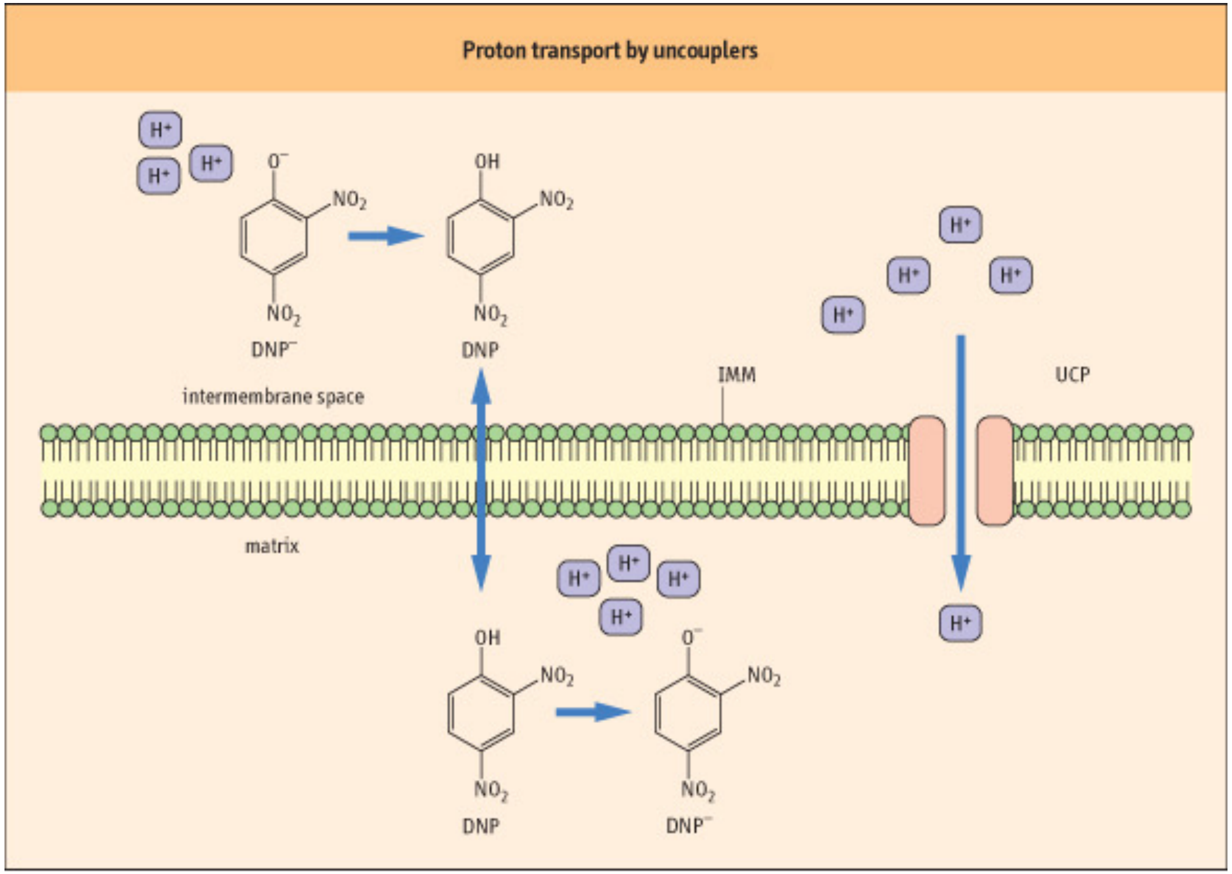
Uncoupling of Oxidative Phosphorylation

Newborn mammals (brown adipose tissue)

Hibernating animals (e.g., bears)

ETC ON, ATP OFF → Heat produced

Inhibition of Oxidative Phosphorylation



Uncoupler: DNP (2,4-Dinitrophenol)

2,4-二硝基苯酚

Mechanism

- DNP acts as a protonophore
- Carries H^+ across the inner mitochondrial membrane

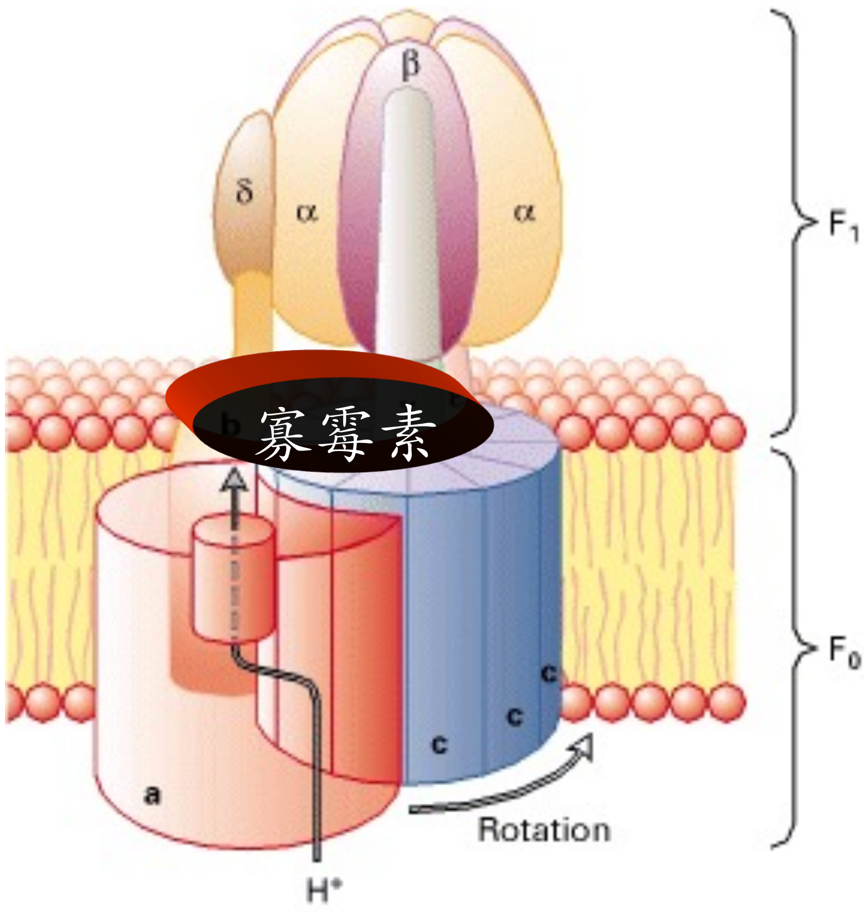
Inhibition of Oxidative Phosphorylation

Target: ATP Synthase

Example: Oligomycin / 寡霉素

Mechanism

- ❖**Binds to F_0 subunit**
- ❖**Blocks proton channel , and H^+ cannot flow back into matrix**



Respiration from Carbohydrate Catabolism perspective

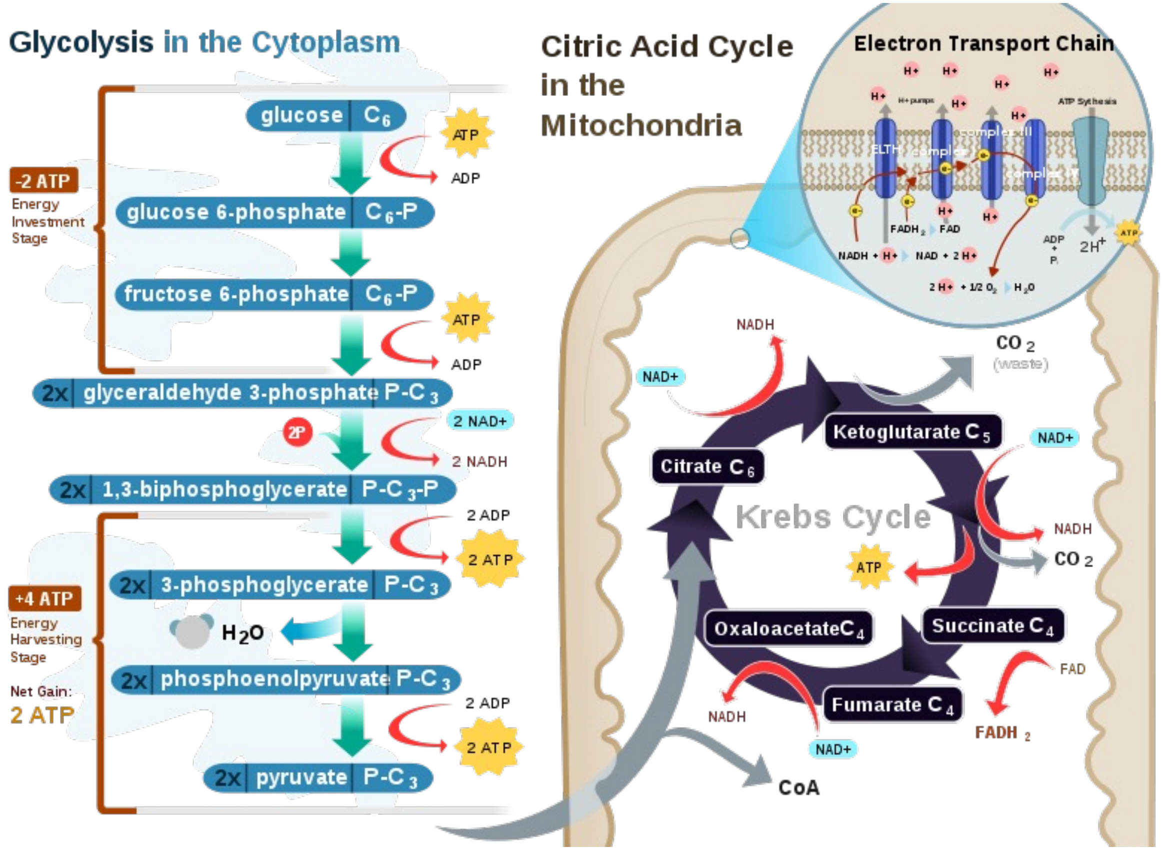
Cellular Respiration

❖ **Occurs in:**

- Cytosol (glycolysis)
- Mitochondria (TCA + ETC)

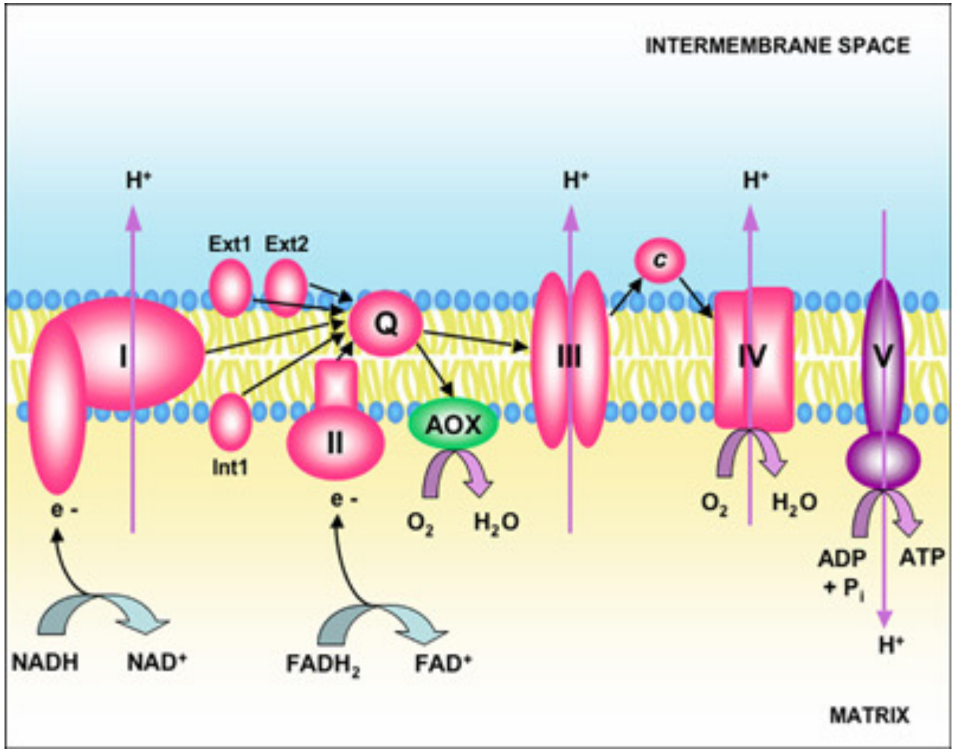
❖ **Functions:**

- ATP production
- NADH/$FADH_2$ generation
- Metabolic integration



Respiration in Plant Physiology

Respiration is the process by which organic molecules are oxidized to generate ATP, producing CO_2 and H_2O under aerobic conditions.



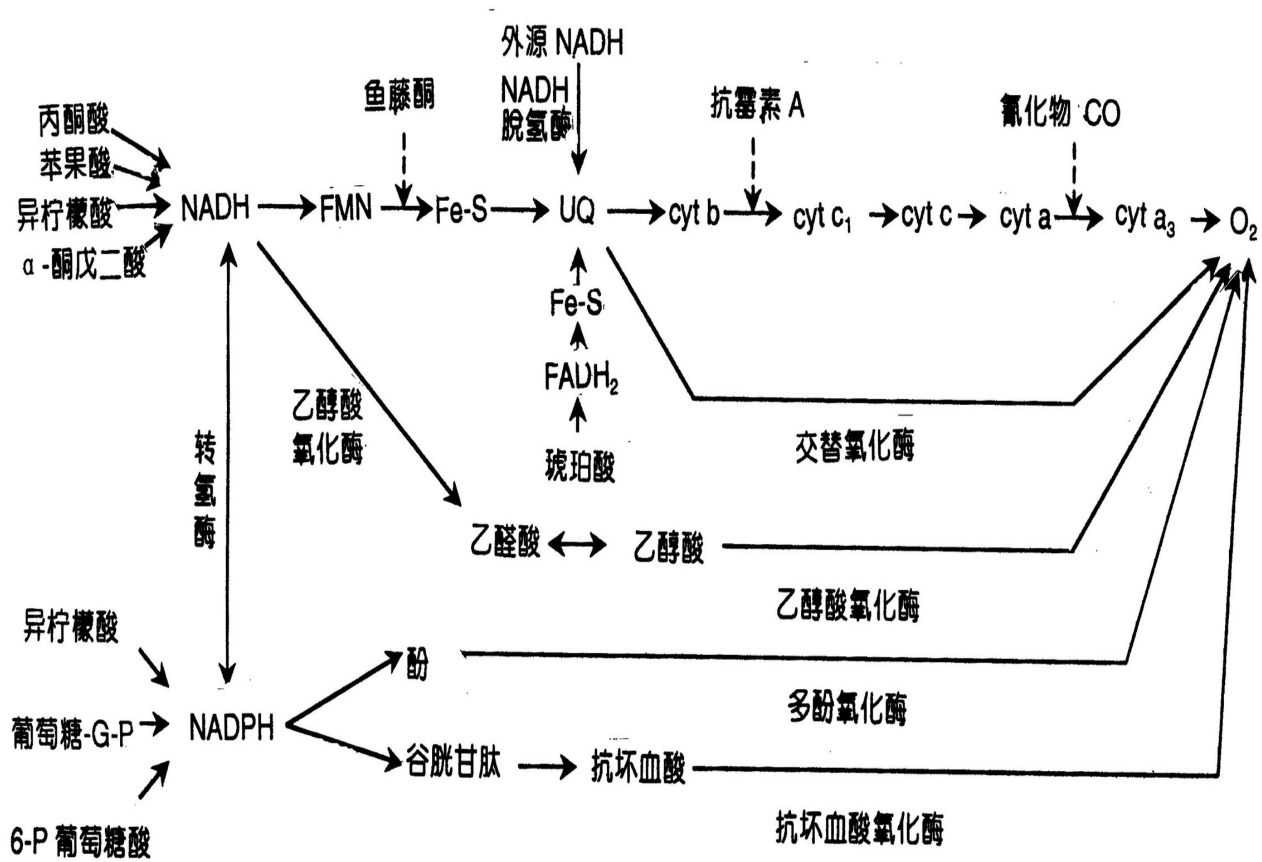
Plant-Specific Feature：Alternative oxidase (AOX) pathway

交替途径(抗氰呼吸)

Electrons bypass Complex III & IV and transferres directly to O_2 via AOX

Respiration in Plant Physiology

Plant Respiratory Electron Pathways



Respiration in Plant Physiology

Measurement of Respiration in Plant Physiology

Respiration Rate: Amount of **CO_2 released** or **O_2 consumed** per unit time and mass

Respiratory Quotient (RQ)/ 呼吸商:

$$RQ=\frac{CO_2\ \text{produced}}{O_2\ \text{consumed}}$$

Indicates **Respiratory substrate** and **Oxygen availability**

Respiration in Plant Physiology

Measurement of Respiration in Plant Physiology

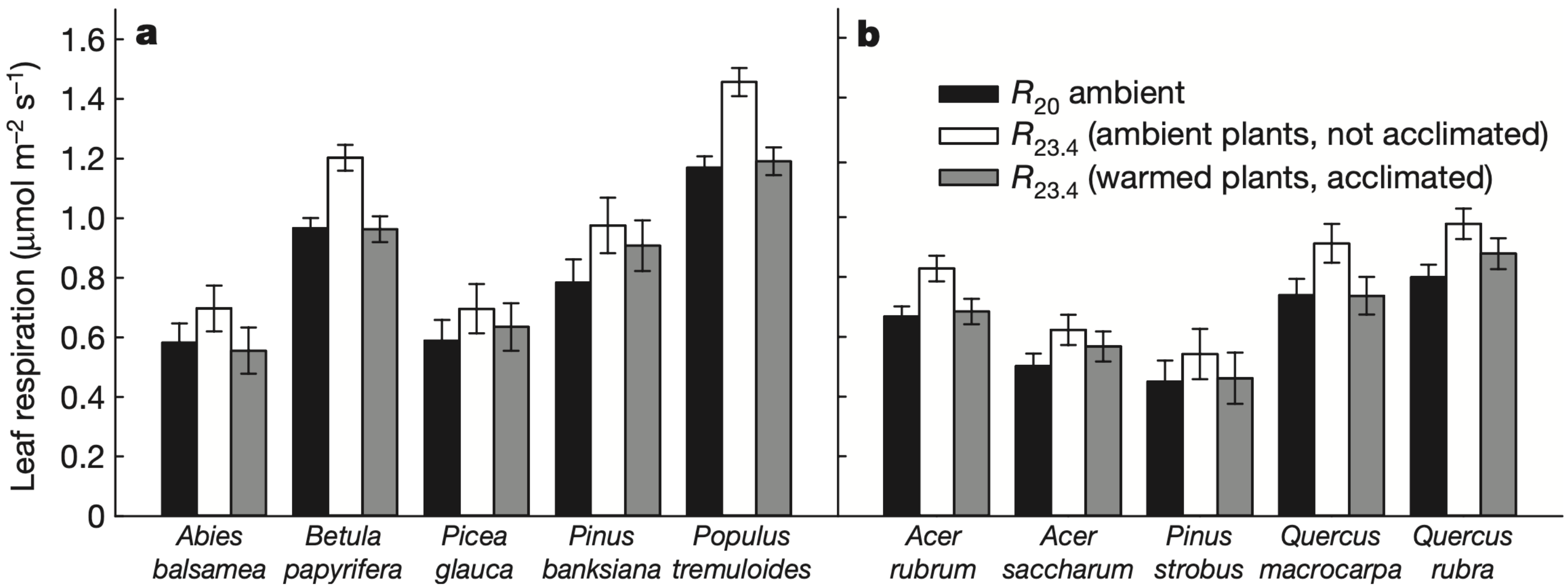
RQ is influenced by both substrate and oxygen availability

Substrate	RQ	Explanation
Carbohydrates	≈ 1.0	Balanced oxidation
Lipids	< 1	More O_2 required
Proteins	< 1	Similar to lipids
Organic acids	> 1	Less O_2 needed

Respiration in Plant Physiology

Internal Factors Affecting Respiration Rate

1. Plant species



Respiration in Plant Physiology

Internal Factors Affecting Respiration Rate

2. Different Among Organs

- **Young, actively growing tissues → high respiration rate**
- **Reproductive organs > vegetative organs**
  - ✓ Highest in: pollen, developing flowers

Example (Apple)

•Young shoots > stems > roots

(Reflects **metabolic activity)**

Respiration in Plant Physiology

Internal Factors Affecting Respiration Rate

3. Effect of Developmental Stage

- ❖ Young tissues → high respiration
- ❖ Mature tissues → moderate
- ❖ Senescent tissues → decline

4. Physical Factors

- ❖ Water content
- ❖ Substrate availability
- ❖ Enzyme activity
- ❖ Mitochondrial function

Respiration in Plant Physiology

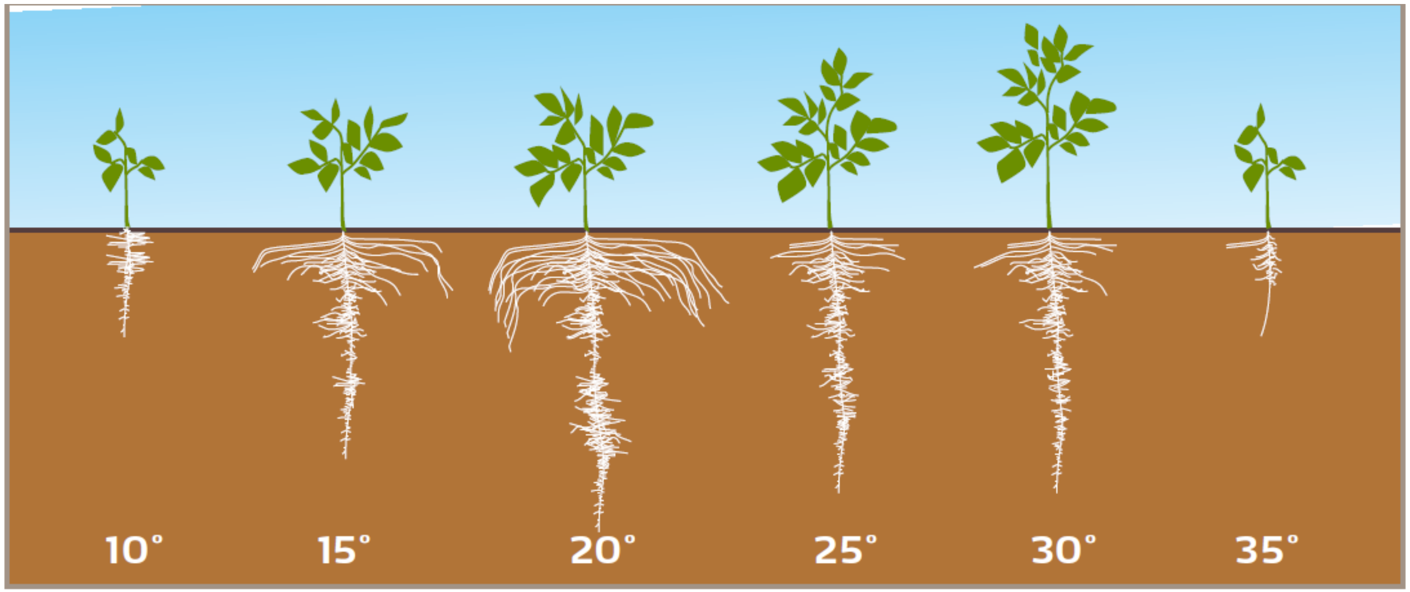
Environment Factors Affecting Respiration Rate

1. Temperature

Both extremes reduce respiration efficiency

- Low Temperature Respiration slows; but may continue even below 0°C (cold-adapted plants)

- High Temperature increase respiration at short-term; but may cause enzyme denaturation and membrane damage, then declines respiration



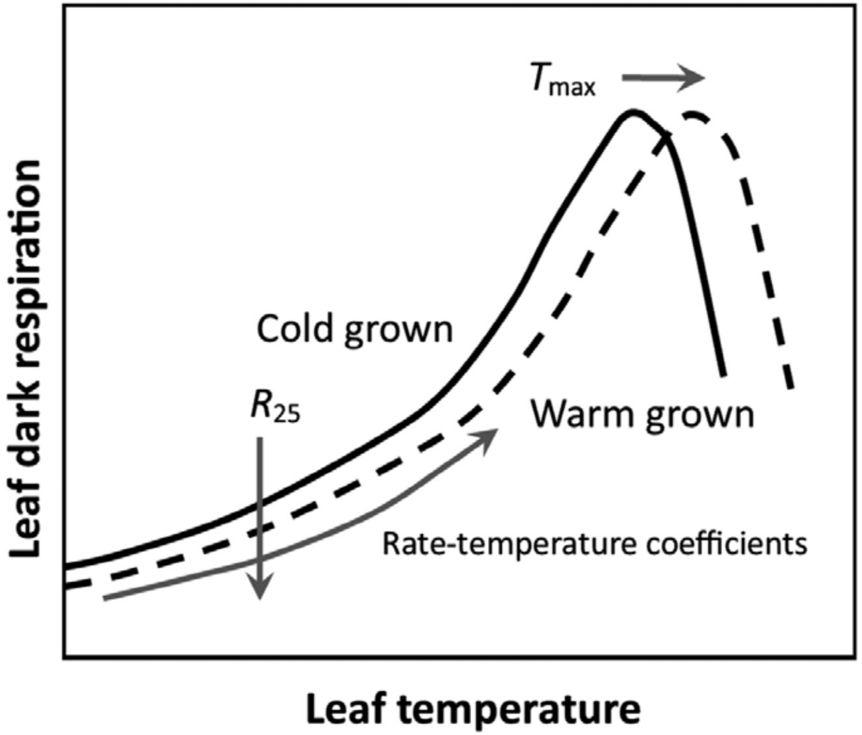
Respiration in Plant Physiology

Environment Factors Affecting Respiration Rate

1. Temperature

Optimum Temperature

- **Temperature at which respiration rate is maximal under steady conditions**
- **Typically 25–35°C (temperate plants)**



Respiration in Plant Physiology

Environment Factors Affecting Respiration Rate

1. Temperature

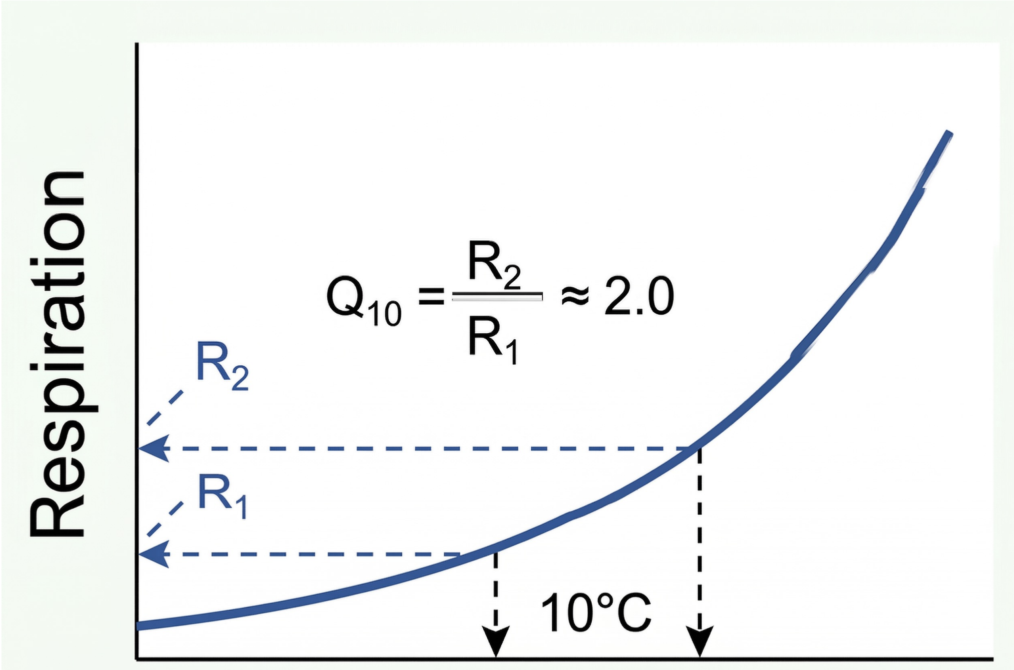
Temperature Coefficient (Q_{10}):

Respiration roughly doubles per 10°C increase (within limits).

$$Q_{10} = \frac{\text{Rate at } T+10}{\text{Rate at } T}$$

Typical Values: 2–2.5 (0–35°C)

Q10: 温度系数



Respiration in Plant Physiology

Environment Factors Affecting Respiration Rate

2. Oxygen

Oxygen availability determines both rate and pathway

1. Oxygen and Respiration Rate

- O_2 is the final electron acceptor
- When O_2 becomes limiting, the respiration rate decreases

2. Oxygen and Respiration Type

- At high O_2, Aerobic respiration dominates
- At Low O_2, Anaerobic respiration increases

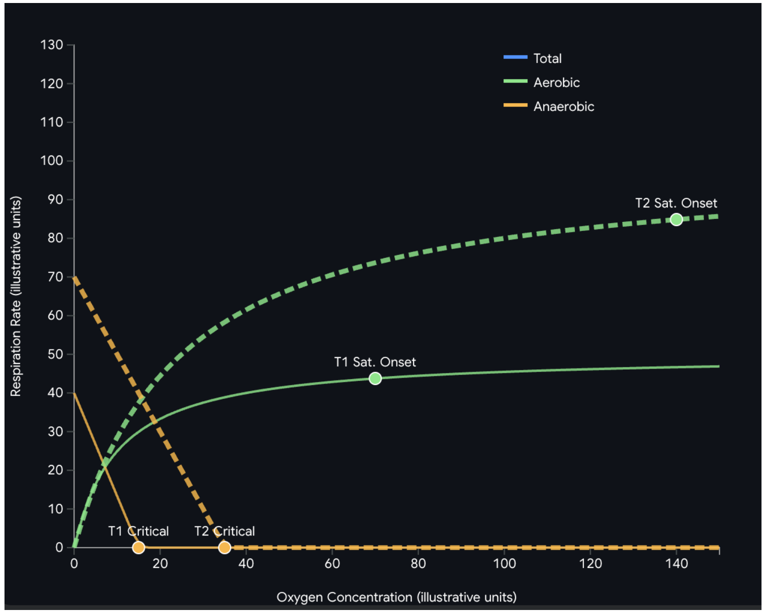
Respiration in Plant Physiology

Environment Factors Affecting Respiration Rate

2. Oxygen

Oxygen–Respiration Relationship

Critical Oxygen Concentration / 无氧呼吸的消失点: the minimum O_2 level at which anaerobic respiration disappears



Oxygen Saturation Point/氧饱和点: O_2 level beyond which respiration rate no longer increases

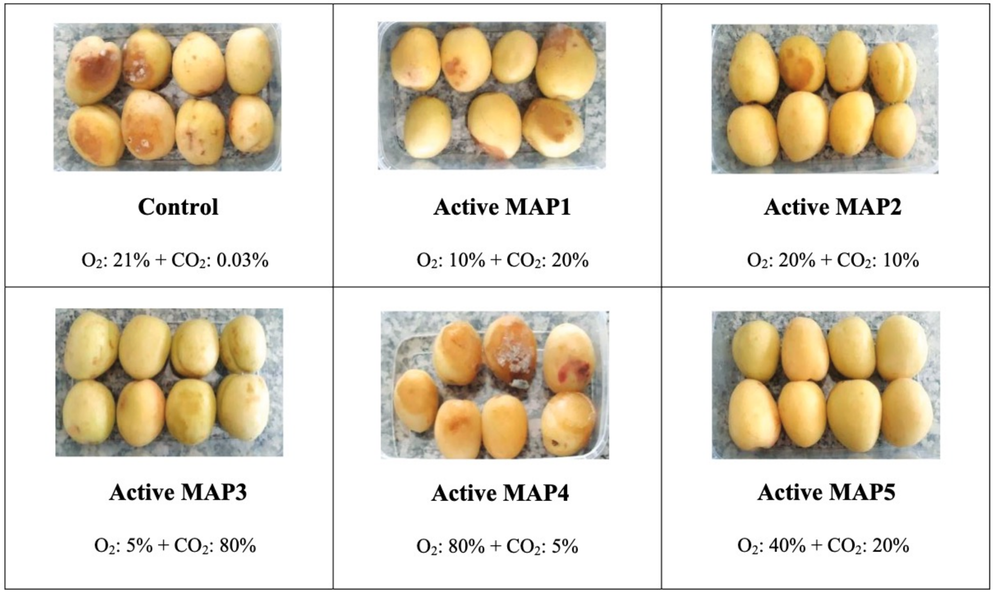
Respiration in Plant Physiology

Environment Factors Affecting Respiration Rate

3. CO_2

Increasing CO_2 Inhibits respiration

- ❖ Slows decarboxylation reactions
- ❖ Alters cellular pH
- ❖ Limits gas diffusion



Very high → toxic effects

High CO_2 used in fruit storage

Respiration in Plant Physiology

Environment Factors Affecting Respiration Rate

3. Water

General Trend：Respiration rate increase with water content

Dry vs Hydrated Tissue

❖ Dry seeds → **very low respiration**

❖ After hydration → **rapid increase**

Drought Response

❖ Early drought increase respiration

❖ Severe/prolonged drought decline respiration

Respiration in Plant Physiology

Environment Factors Affecting Respiration Rate

4. Mechanical Injury

Observation: Mechanical injury increases respiration rate

- ❖ Loss of cellular compartmentalization, and substrates contact enzymes
- ❖ Activation of oxidative enzymes
- ❖ Induction of Wound respiration
- ❖ Increased demand for repair and biosynthesis

Respiration in Agriculture

Respiration in Seed Maturation and Storage

During Maturation

- **High respiration:**
  - ✓ supports **biosynthesis**
  - ✓ supports **dry matter accumulation**

During Storage

Respiration must be minimized to minimalize

- **nutrient loss**
- **viability decline**
- **heat accumulation**

Control Measures

- **Low temperature**
- **Low moisture**
- **Low O_2 / controlled atmosphere**

Respiration in Agriculture

Respiration in Fruit Development and Storage

Development

Respiration supports:

- growth
- metabolism

Ripening (Climacteric fruits)

- Respiration increases sharply/Climacteric rise

Storage

- Goal: reduce respiration

Methods:

- Low temperature
- Controlled atmosphere (↑CO_2, ↓O_2)

Respiration in Agriculture

Respiration and Crop Productivity

Positive Role

- ❖ Provides ATP
- ❖ Provides biosynthetic intermediates

Negative Role

- ❖ Consumes photosynthates (carbon loss)

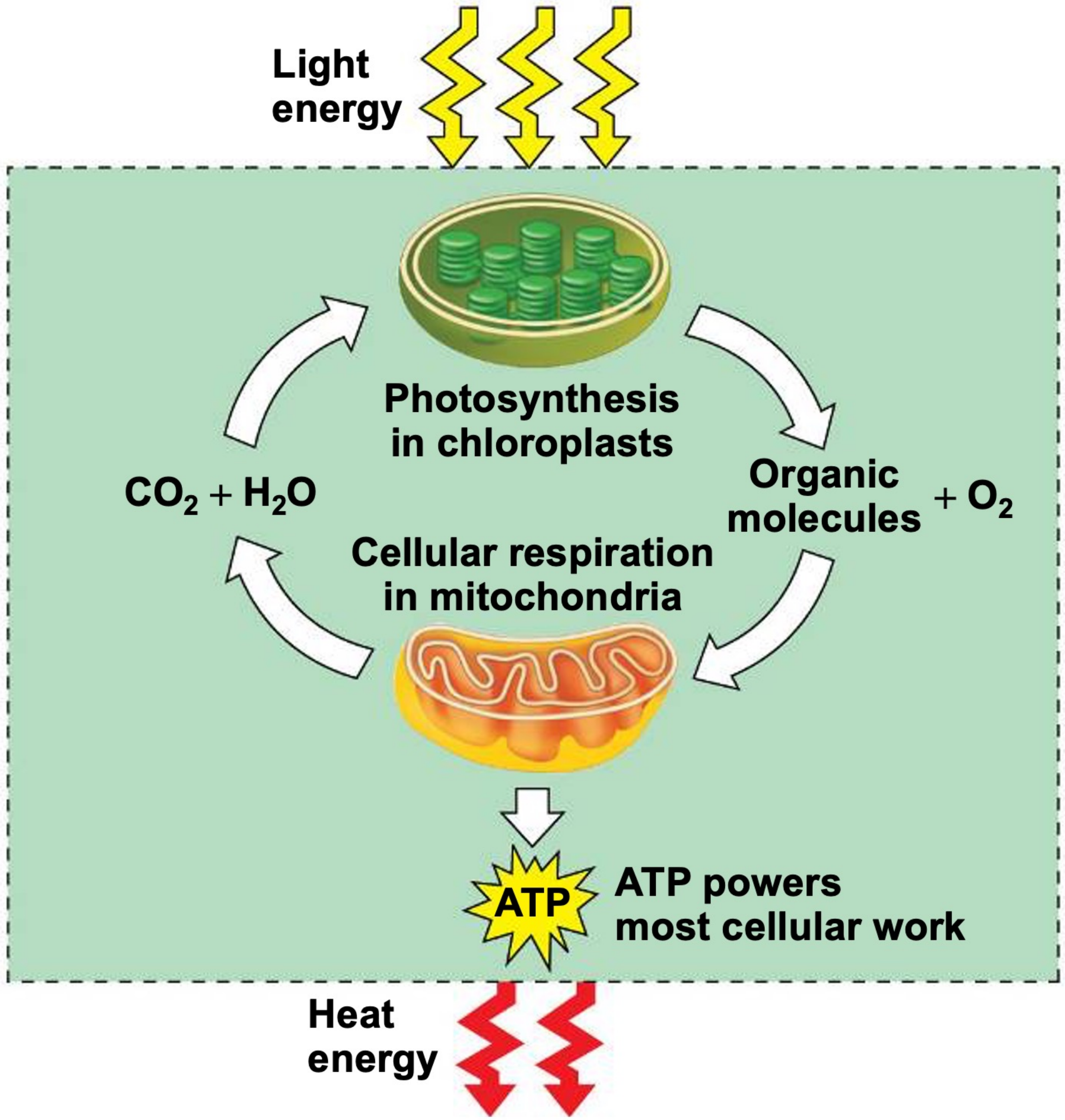
Agronomic Implication

- ❖ Optimize conditions to reduce unnecessary respiration and improve carbon use efficiency

Balance between photosynthesis and respiration

Outline

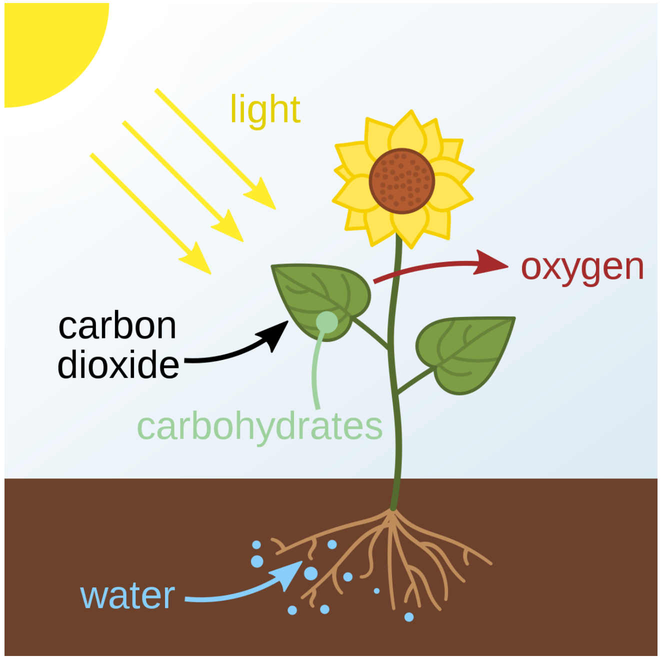
- Introduction
- Respiration
- **Photosynthesis**



What is photosynthesis?

- Photosynthesis, was from the Greek φῶς, *phōs*, "light", and σύνθεσις, *synthesis*, "putting together".

Conversion of light energy into chemical energy stored in organic molecules.



What is photosynthesis?

The most famous and falsest chemical equation

$$6CO_2 + 6H_2O \xrightarrow[Enzymes]{Light} C_6H_{12}O_6 + 6O_2$$

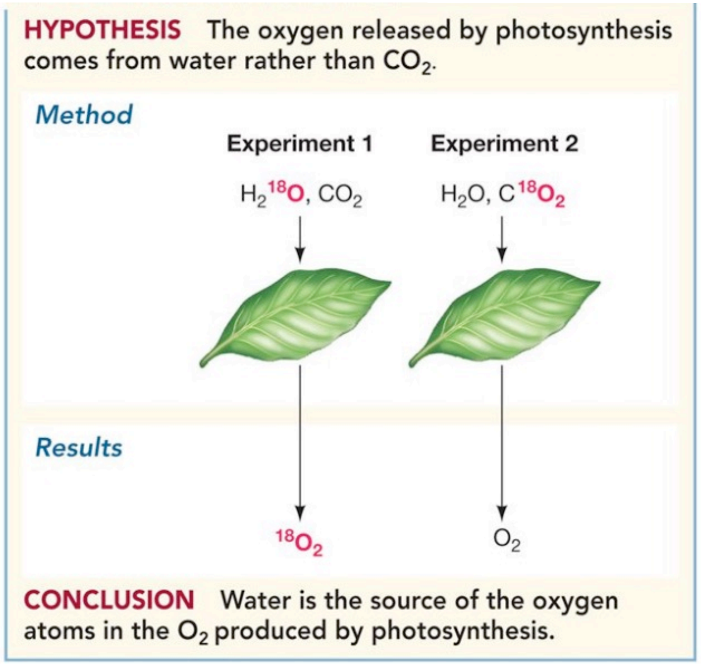
- Glucose is NOT the primary photosynthetic product
- The O of O_2 is from water

Discovery of Photosynthesis

- **1771–1772 — Joseph Priestley (UK)**
  Demonstrated that plants can restore "injured air" (now understood as replenishing oxygen, O_2) that had been depleted by combustion or respiration.
- **1779 — Jan Ingenhousz (Netherlands)**
  Showed that only the green parts of plants produce oxygen, and only in the presence of light. Established the **light dependency** of photosynthesis.
- **1782 — Jean Senebier (Switzerland)**
  Demonstrated that carbon dioxide (CO_2) is required for photosynthesis and is consumed during the process. Linked **CO_2 uptake with oxygen production**.
- **1864 — Julius von Sachs (Germany)**
  Observed that starch accumulates in chloroplasts under light conditions. Provided evidence that **photosynthesis produces carbohydrates** (stored as starch).
- **1941 — Samuel Ruben et al. (USA)**
  Used isotopic labeling ($H_2{}^{18}O$) to show that the oxygen (O_2) released in photosynthesis originates from water, not CO_2. Established **water as the source of evolved oxygen** via photolysis.

Discovery of Photosynthesis

$$6CO_2 + 6H_2O \xrightarrow[Enzymes]{Light} C_6H_{12}O_6 + 6O_2$$



Ruben and Kamen 1941

$$12H_2O \rightarrow 24H^+ + 24e^- + 6O_2$$

$$6CO_2 + 24H^+ + 24e^- \rightarrow C_6H_{12}O_6 + 6H_2O$$

$$6CO_2 + 12H_2O \xrightarrow[Enzymes]{Light} C_6H_{12}O_6 + 6O_2 + 6H_2O$$

Concept of Photosynthesis

❖ **Carbon Assimilation (碳同化作用)**

The process by which autotrophic organisms incorporate inorganic carbon (CO_2) into organic molecules. In plants, this occurs primarily via the **Calvin cycle**.

❖ **Photosynthesis (光合作用)**

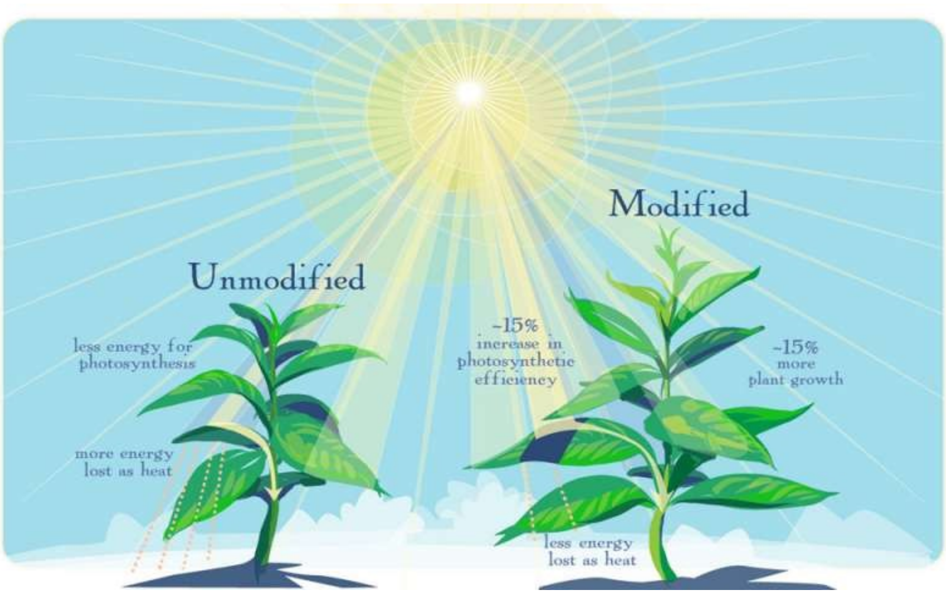
Photosynthesis is the process by which photoautotrophic organisms (plants, algae, and cyanobacteria) use light energy to convert carbon dioxide (CO_2) and water (H_2O) into energy-rich organic compounds, releasing oxygen (O_2) as a byproduct.

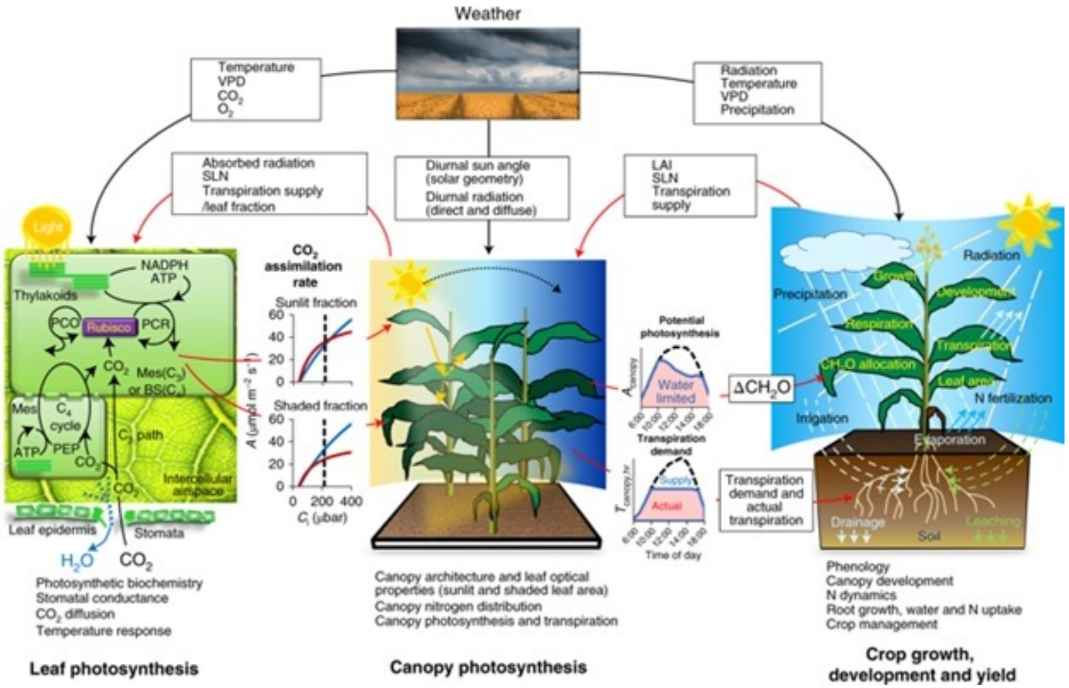
Importance of Photosynthesis

➢Food

Form the base of nearly all food chains.

Can you think of a food that is NOT somehow tracked back to photosynthetic process?





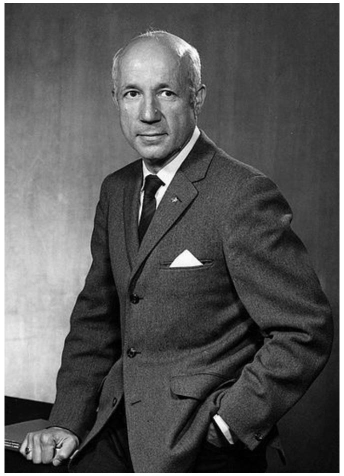
Importance of Photosynthesis

➢ **Fresh air**

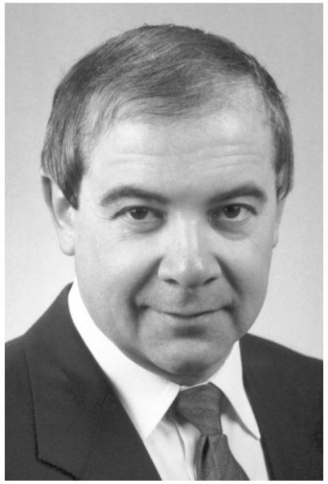
Removes carbon dioxide from, and adds oxygen to, the atmosphere

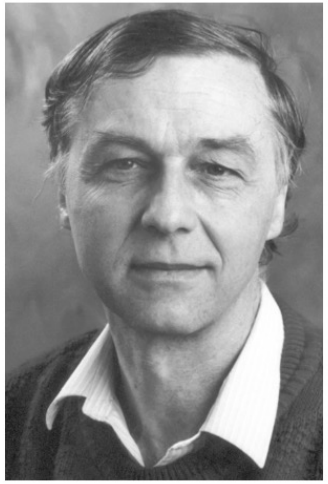
Importance of Photosynthesis

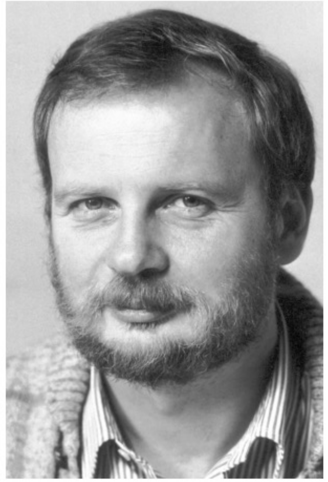
Richard Willstätter
1915



Melvin Calvin
(1961)







Johann Deisenhofer Robert Huber Hartmut Michel
1988

Barbara McClintock
1983

- **历史上授予植物学学家的诺贝尔奖非常少，至今仅有四项诺贝尔“科学奖”是授予植物科学家的。其中三项是光合作用相关研究。**
- **另外，Norman Borlaug因绿色革命获1970和平奖。**

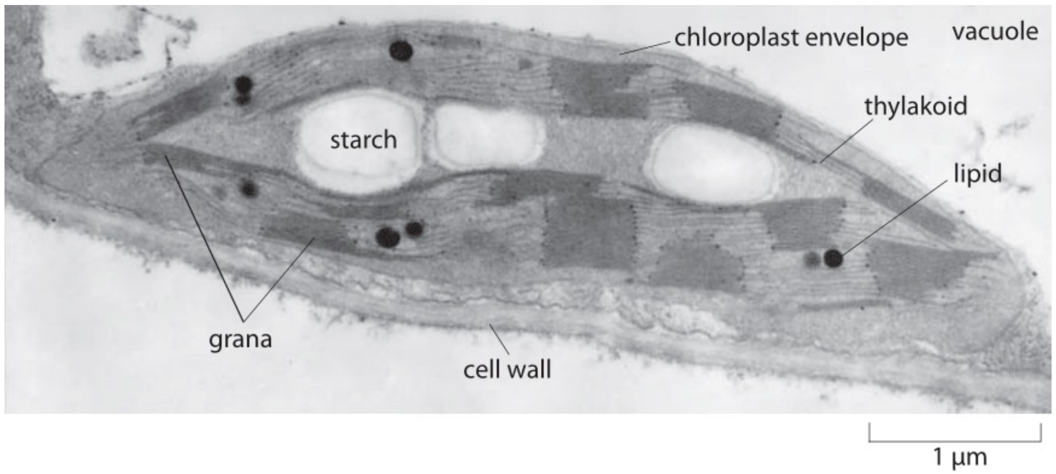
注: 光合作用相关的诺贝尔奖共14项；Govindjee et al., 2004, Photosyn Res

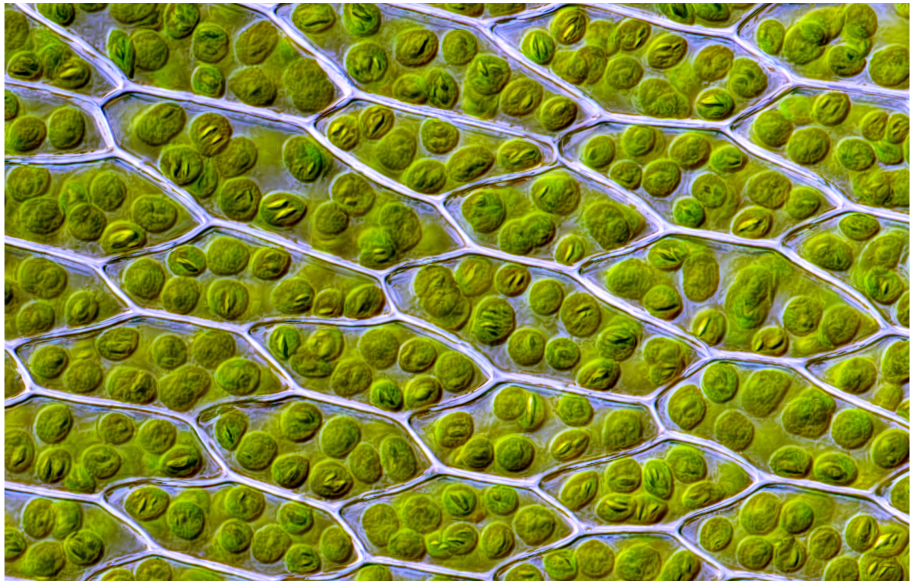
Where Does Photosynthesis Occur?

Photosynthesis occurs in **specialized cellular structures**, with clear spatial organization:

❖ In eukaryotic photoautotrophs (plants and algae), photosynthesis occurs in the **chloroplast** / 叶绿体.

❖ In prokaryotic photoautotrophs (cyanobacteria), photosynthesis occurs on **internal membrane systems** (no chloroplast).





Where Does Photosynthesis Occur?

Structure and Function of the Chloroplast

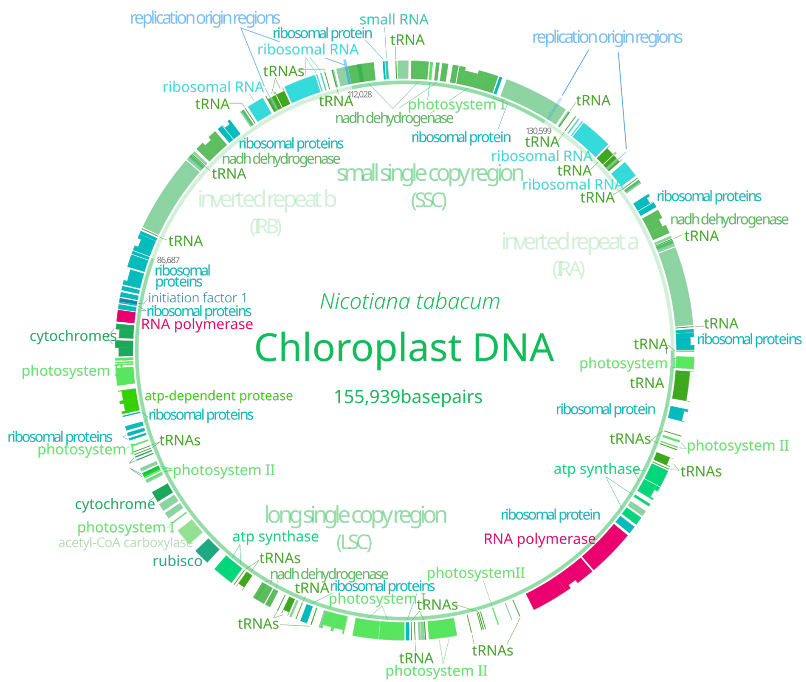
❖ Chloroplasts are typically:

- **5–10 µm in diameter**, **~2–3 µm thick**
- Present in **dozens to hundreds per cell**

❖ Chloroplasts contain:

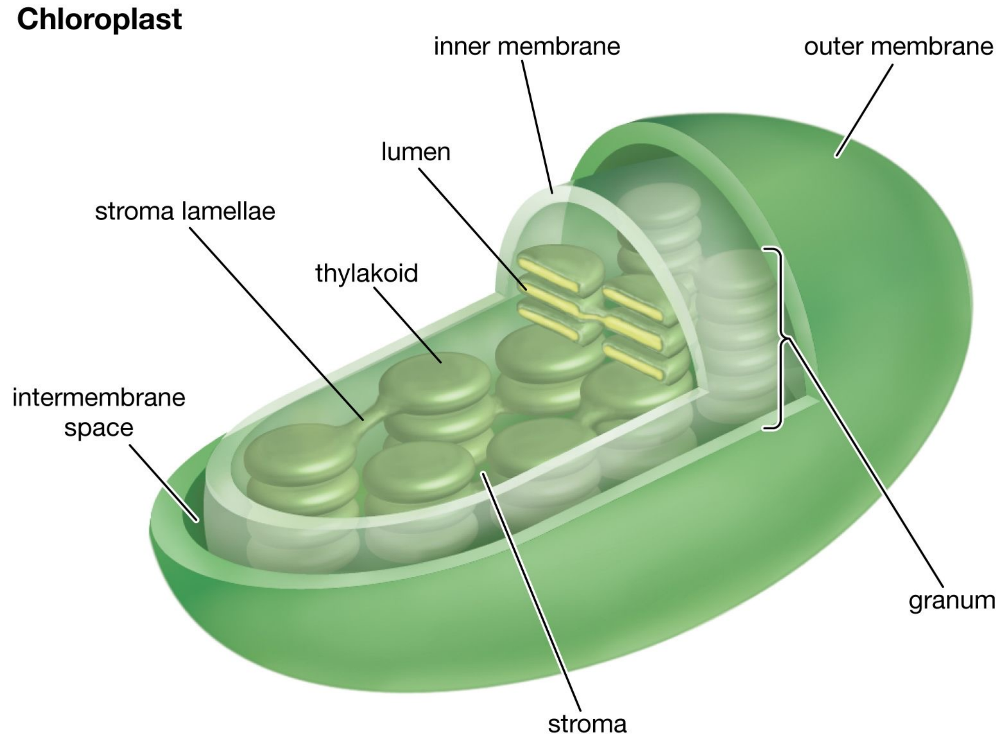
- Their own **DNA and ribosomes**
- Partial capacity for **protein synthesis**

❖ Supports the **endosymbiotic theory**/内共生理论**,** which claims chloroplasts originated from ancestral cyanobacteria.



Where Does Photosynthesis Occur?

Structure and Function of the Chloroplast

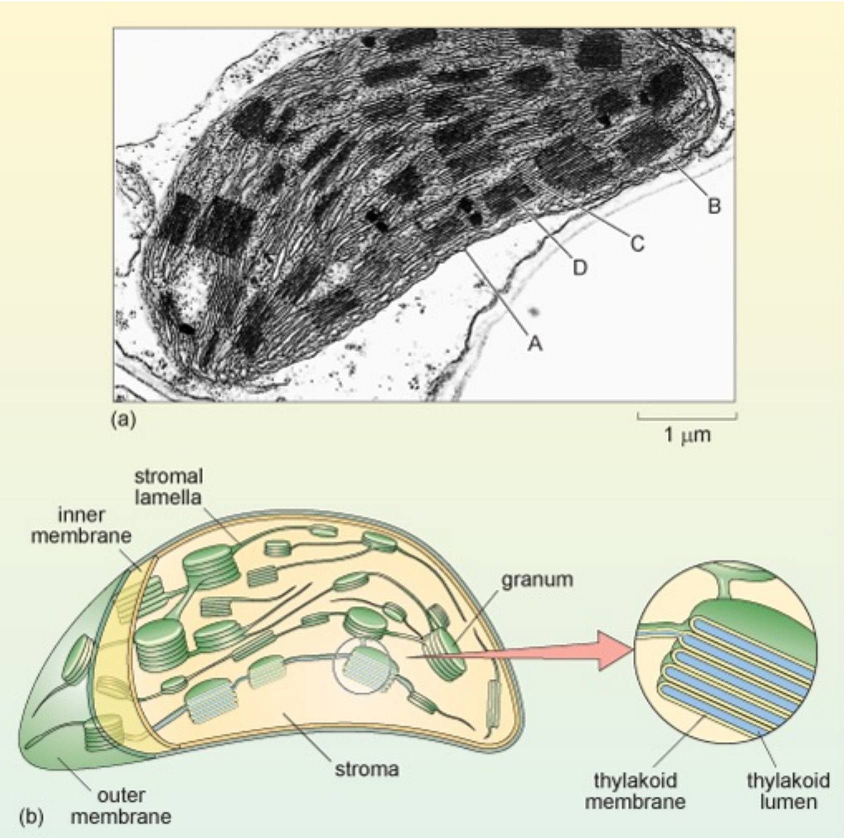


Envelope Membranes

- **Outer membrane / 外被膜**:
  - ✓ Relatively permeable (non-selective to small molecules and ions)
- **Inner membrane / 内被膜**:
  - ✓ Highly **selective**
  - ✓ Regulates transport via specific carriers

Where Does Photosynthesis Occur?

Structure and Function of the Chloroplast

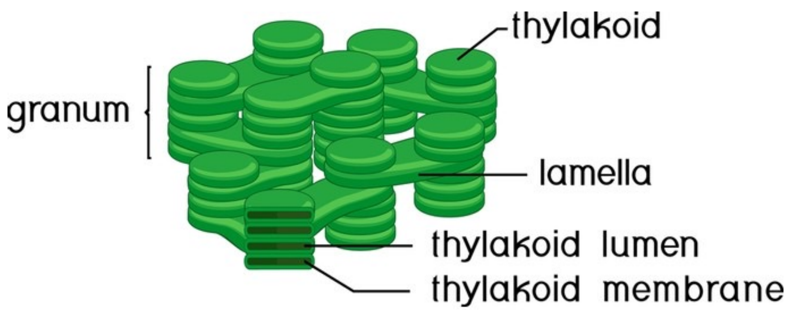


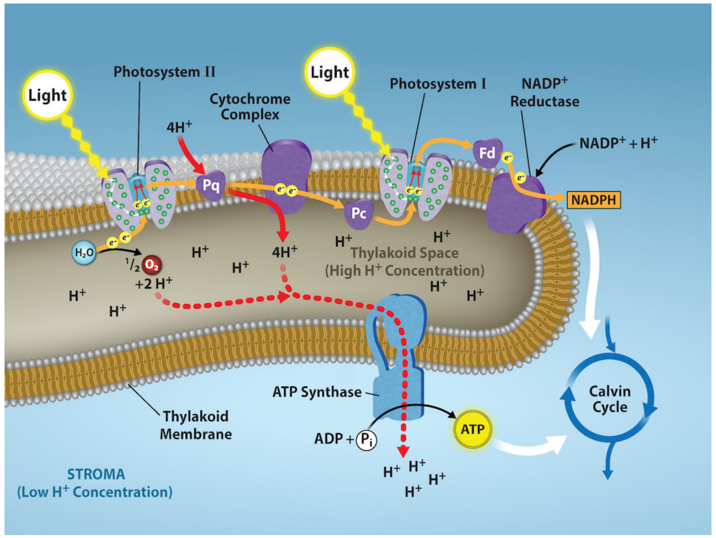
Stroma（基质）

- ❖ Protein-rich matrix containing:
  - **Calvin cycle enzymes**
  - DNA, RNA, ribosomes
  - Starch granules, metabolites
- ❖ Site of **carbon fixation and biosynthesis**

Where Does Photosynthesis Occur?

Structure and Function of the Chloroplast



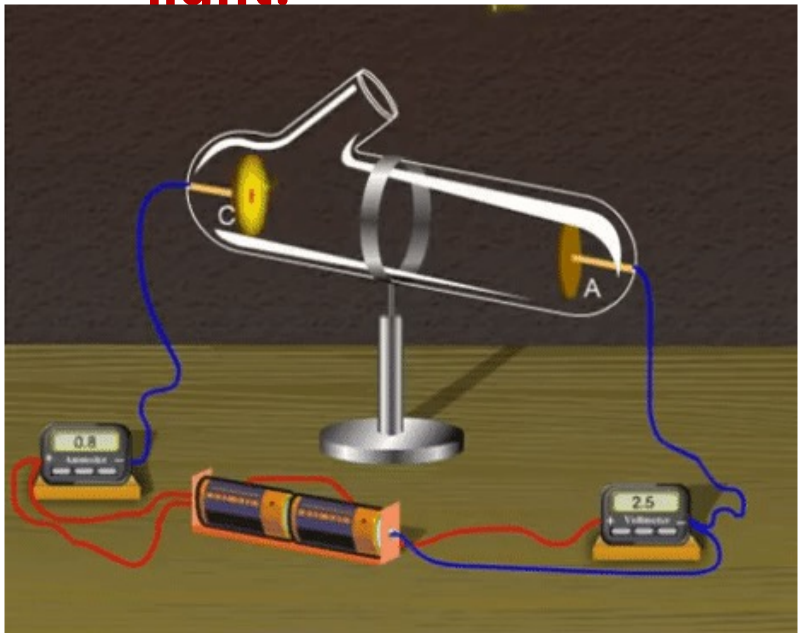


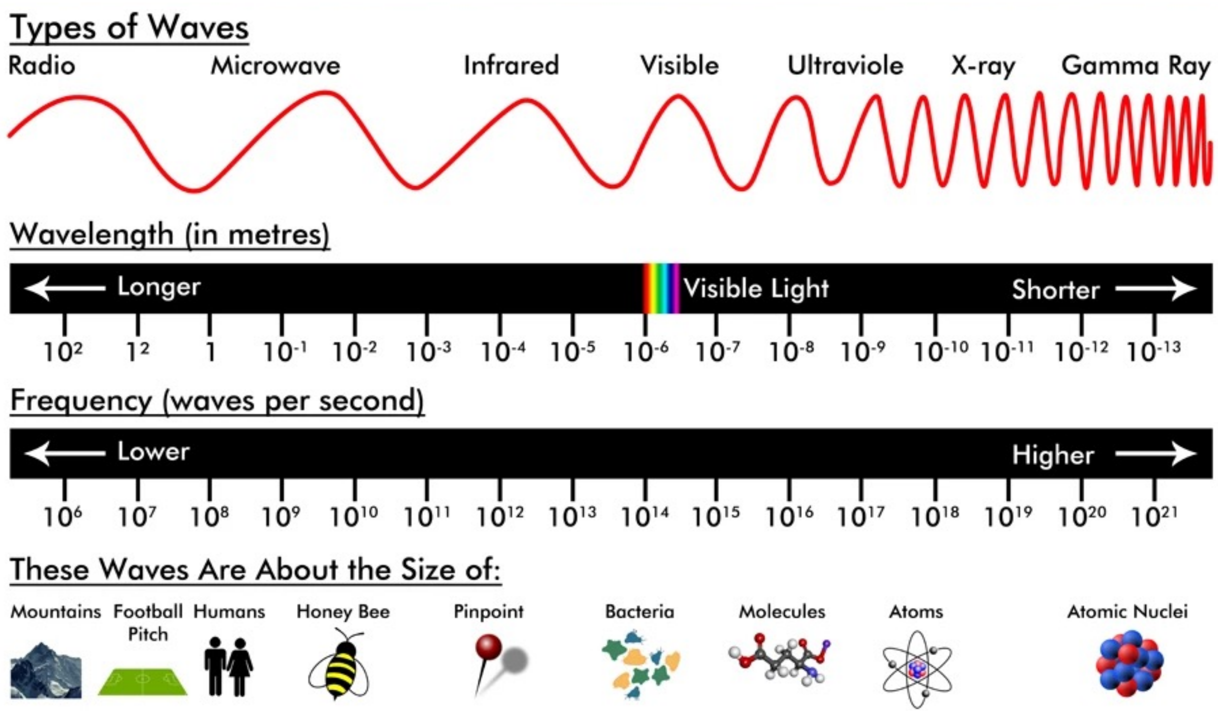
Thylakoid System (类囊体系统)

- Flattened membrane sacs and can be organized into
  - ✓ Grana/基粒(stacked thylakoids)
  - ✓ Stroma lamellae /间质 (unstacked connections)
- Thylakoid membrane = Photosynthetic membrane
  - ✓ Photosystems (PSII, PSI)
  - ✓ Electron transport chain
  - ✓ ATP synthase

Light absorption

What is light?





Wave–particle duality is the concept in quantum mechanics that every particle or quantum entity may be described as either a particle or a wave.

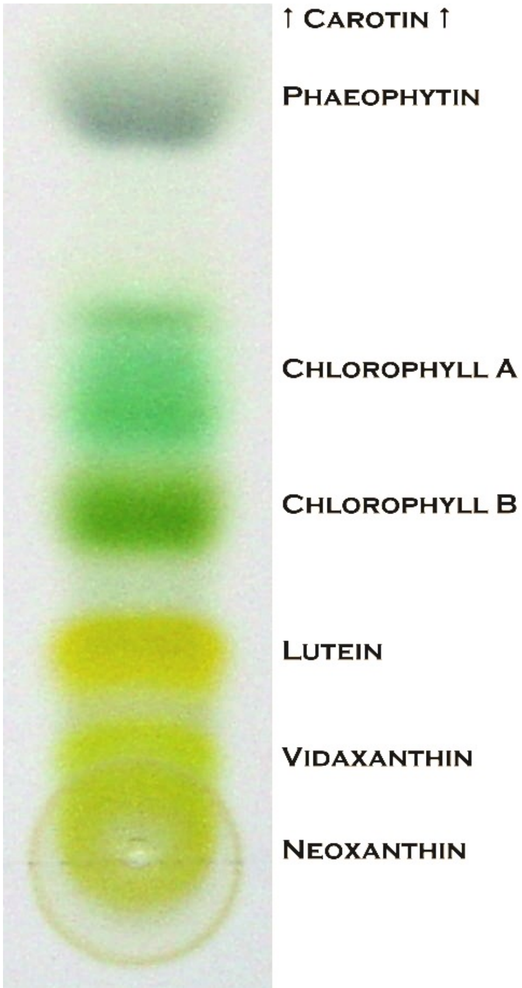
Light absorption

Plant pigment vs photosynthetic pigment

Light absorption

Photosynthetic pigments

- **Photosynthetic Pigments (光合色素)**
  Pigments that absorb light energy and participate in photosynthesis
- **Major classes include**:
  - Chlorophylls (叶绿素)
  - Carotenoids (类胡萝卜素) — including carotenes and xanthophylls (叶黄素类)
  - Phycobilins (藻胆素) in cyanobacteria and red algae



Light absorption

Photosynthetic pigments

1. Chlorophylls

- Main types: **Chlorophyll a, Chlorophyll b**
- Structure:
  - ✓ **Porphyrin ring**(卟啉环) with central **Mg^{2+}**
  - ✓ Hydrophobic **phytol tail** (植醇) (anchors in membrane)
- Function:
  - ✓ Primary pigments in **reaction centers**
  - ✓ Absorb mainly **blue and red light**

叶绿素 a

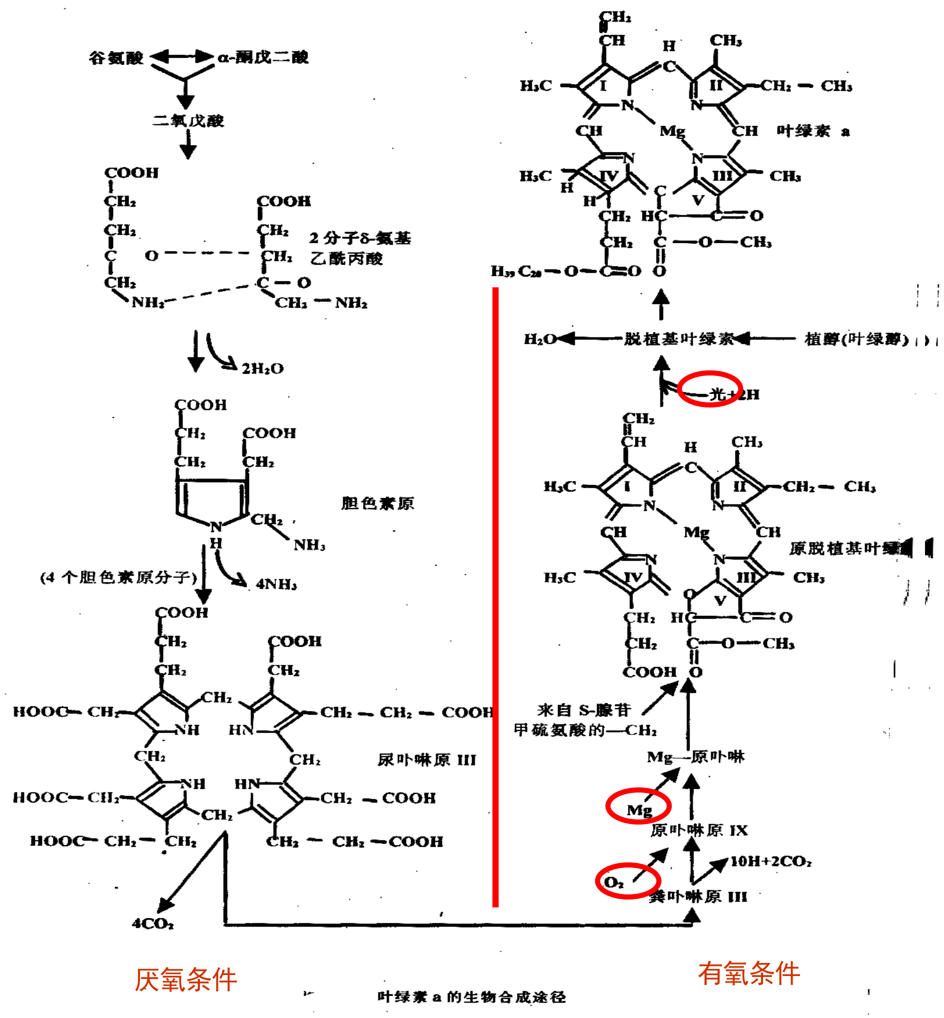
Chl a: $C_{55}H_{72}O_5N_4Mg$

Chl b: $C_{55}H_{70}O_6N_4Mg$

Light absorption

Photosynthetic pigments

Chlorophyll biosynthesis is a tetrapyrrole (四吡咯) pathway, sharing early steps with heme (血红素) synthesis, then diverging toward Mg-containing chlorophyll.



Light absorption

Photosynthetic pigments

Factors Affecting Chlorophyll Biosynthesis

- ❖ Light is required for conversion of protochlorophyllide/原叶绿酸酯 to chlorophyllide/叶绿素酸酯
- ❖ In darkness:
  - ✓ Seedlings become etiolated (黄化; yellow, elongated)
  - ✓ Chlorophyll synthesis is blocked at protochlorophyllide

Light absorption

Photosynthetic pigments

Factors Affecting Chlorophyll Biosynthesis

叶绿素的形成受遗传因素控制，如水稻、玉米的白化苗以及花卉中的斑叶不能合成叶绿素。有些病毒也能引起斑叶。

- Chlorophyll biosynthesis is regulated by nuclear and plastid genes
- Examples:
  - ✓ Albino/白化 mutants cannot synthesize chlorophyll
  - ✓ Variegated leaves/斑叶 defective chloroplast development

Light absorption

Photosynthetic pigments

Factors Affecting Chlorophyll Biosynthesis

Temperature

- Minimum: ~2–4 °C
- Maximum: ~40 °C
- Optimum: 20–30 °C

Water deficit

- Inhibits enzyme activity
- Reduces precursor availability
- Can accelerate chlorophyll degradation

Mineral Nutrition

- N, Mg → structural components
- Fe, Cu, Mn, Zn → enzyme cofactors

Oxygen and Redox Conditions

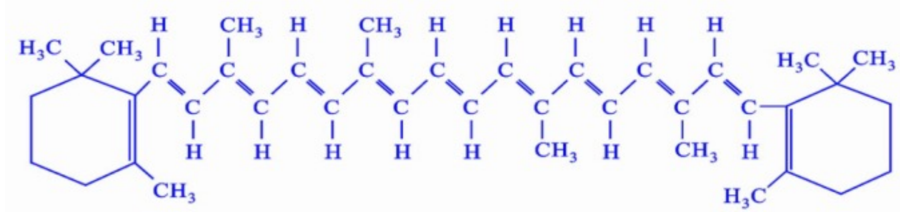
- Certain oxidative steps in tetrapyrrole synthesis
- Excess light and O_2 cause photooxidation
- Leads to chlorophyll damage via ROS

Light absorption

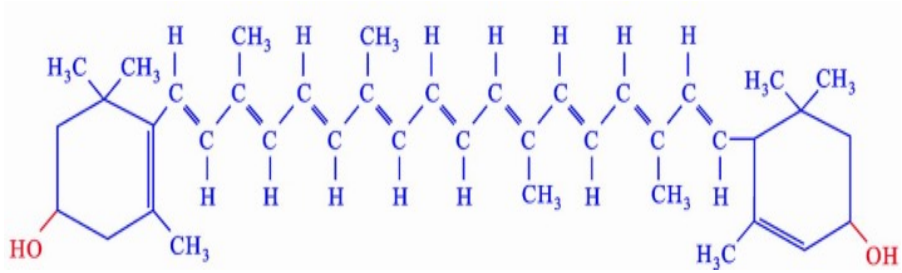
Photosynthetic pigments

2. Carotenoids

- Two subgroups:
  - **Carotenes** / 胡萝卜素 (e.g., β-carotene)
  - **Xanthophylls** / 叶黄素类 (e.g., lutein, violaxanthin, neoxanthin)
- Chemical feature:
  - Long chains of **conjugated double bonds**
- Functions:
  - Accessory light absorption (blue-green region)
  - **Photoprotection** (quenching excess energy, preventing ROS damage)



β- 胡萝卜素 ($C_{40}H_{56}$)

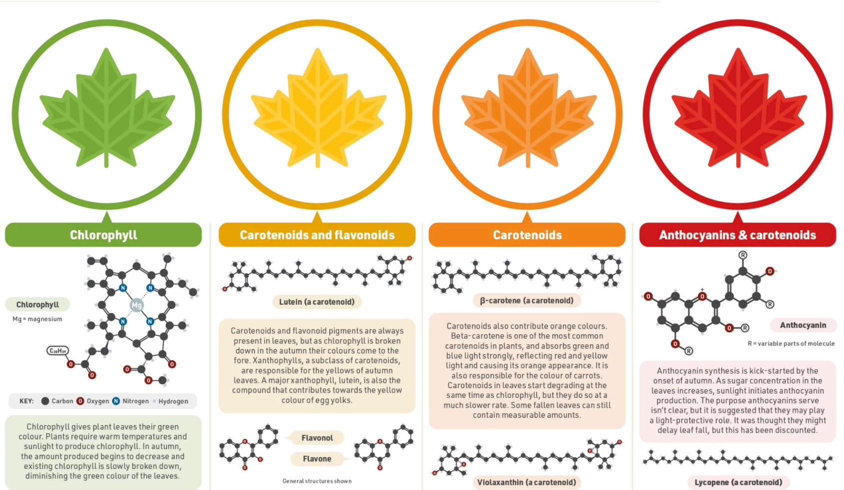


叶 黄 素 ($C_{40}H_{56}O_2$)

Light absorption

2. Carotenoids

Under normal conditions **Chlorophyll : Carotenoids ≈ 3 : 1**



- ❖ Yellow Leaves (Carotenoid Dominance) occurs during autumn, stress conditions, leaf senescence
- ❖ Mechanism:
  - Chlorophyll degrades rapidly
  - Carotenoids remain relatively stable

- ❖ Red Leaves (anthocyanin accumulation), occurs during autumn (cold nights and light exposure), sometimes in young leaves or stress conditions
- ❖ Synthesis of anthocyanins/花青素 (NOT photosynthetic pigments)

Light absorption

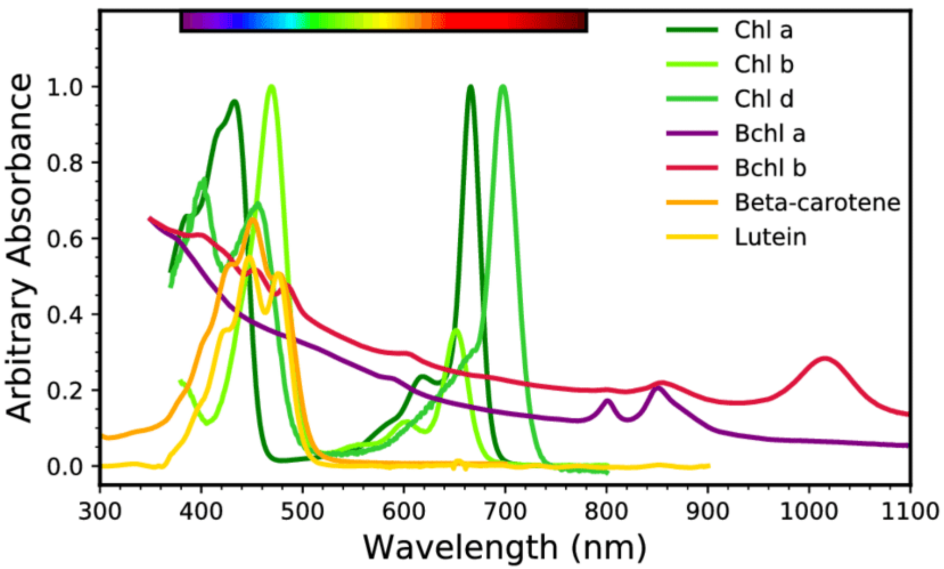
Photosynthetic pigments

3. Phycobilins / 藻胆素

- Found in cyanobacteria, red algae
- Water-soluble pigments
- Organized in phycobilisomes

Light absorption

Absorption spectrum



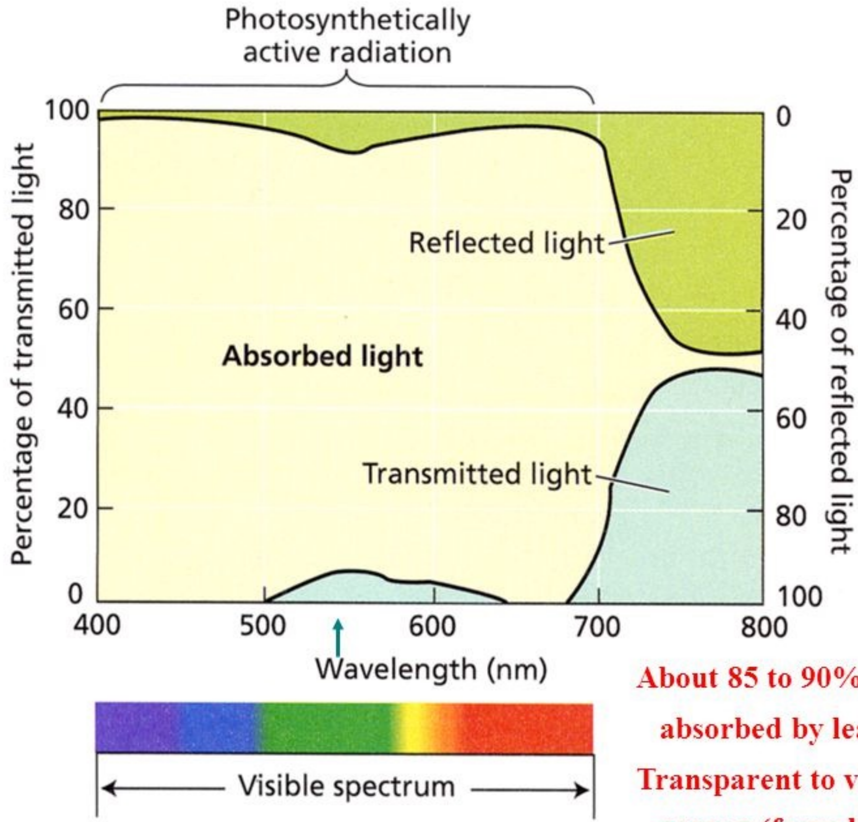


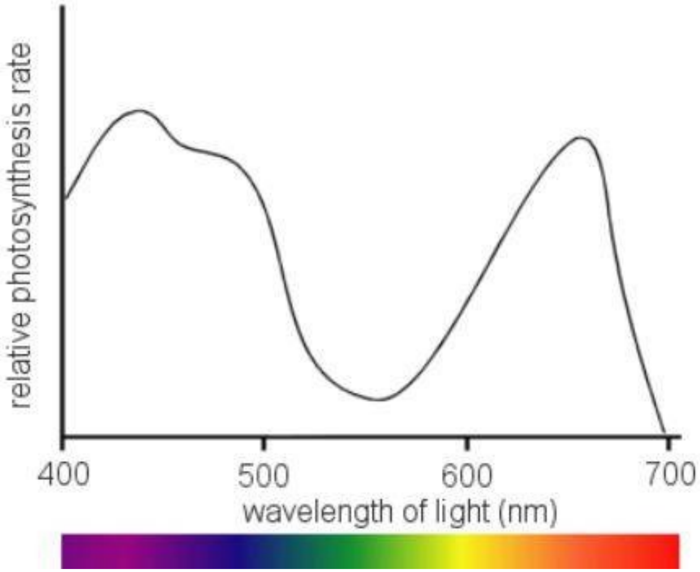
FIGURE 9.3

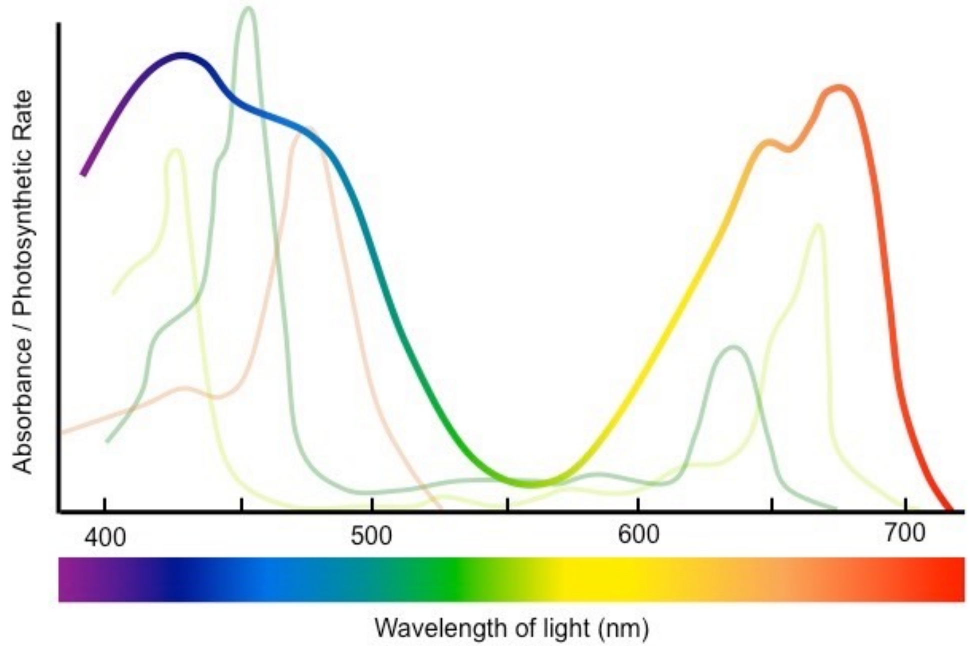
About 85 to 90% of PAR is absorbed by leaf

Transparent to visible light and convex (focus light) at epidermal cells

Light absorption

Action spectrum





- **Absorption spectrum** is the range of wavelengths that can be absorbed by a pigment
- **Action spectrum** means the wavelengths of light trigger photosynthesis

Light absorption

搜狐

《Science》：新型光合作用被发现，有望改写教科书！

近日，科研人员发现了新型光合作用。该发现改变了人们对光合作用基本原理的认识，甚至可能改写课本。 这一发现为我们搜寻外星生命量身定制了 ...

Jun 17, 2018

科技日报

新型光合作用可利用近红外光-国际-中国科技网首页

研究负责人、帝国理工学院生命科学学院的比尔·卢瑟福教授认为： "这种新型光合作用改变了我们对标准光合作用'内核'的认识，是一项改写教科书的 ...

Jun 19, 2018

Photochemistry beyond the red limit in chlorophyll f–containing photosystems

Dennis J. Nürnberg[1,*], Jennifer Morton[2], Stefano Santabarbara[3], Alison Telfer[1], Pierre Joliot[4], Laura A. Antonaru[1], Alexand...

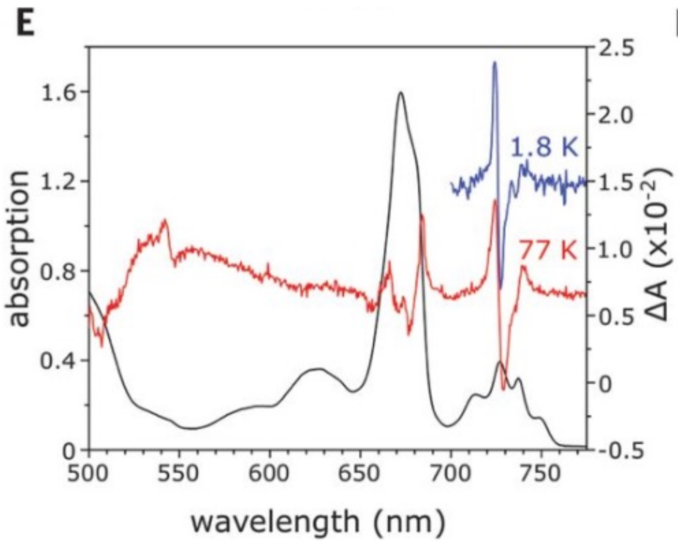
+ See all authors and affiliations

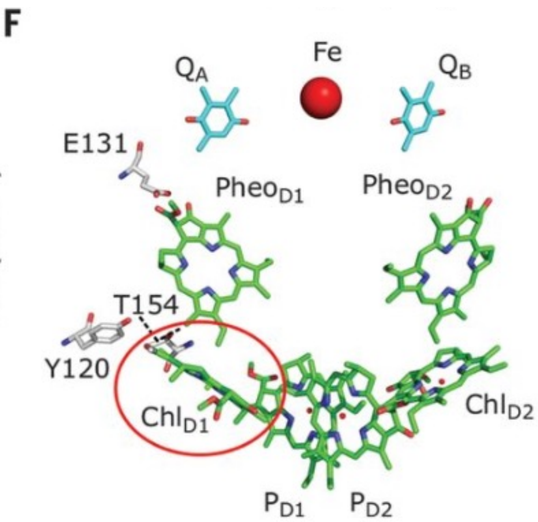
Science 15 Jun 2018:
Vol. 360, Issue 6394, pp. 1210-1213
DOI: 10.1126/science.aar8313

Science

新型光合作用可利用近红外光

2018-06-19 09:54:02 来源: 科技日报 作者: 记者刘霞





或将改写教科书 为农作物改良提供新思路

科技日报北京6月18日电 （记者刘霞）据美国《每日科学》网站报道，根据近日发表于《科学》杂志上的一篇论文，英国帝国理工学院牵头的一个国际科研团队发现，在阴暗环境下生存的蓝藻内，存在一种新型光合作用。与目前地球上占主导地位的利用红光的光合作用不同，新光合作用利用的是近红外光。该发现不仅改变了人们对光合作用基本原理的认识，甚至还可能改写课本。

研究人员解释，目前我们所知的光合作用是通过叶绿素-a来收集光线，并利用光能制造有用的生化物质和氧气。由于叶绿素-a存在于已知的所有植物、藻类及蓝藻中，因此人们普遍认为，红光的能量为光合作用设置了“红光限制”——在产生氧气的化学过程中需要的最少能量。

然而科研团队发现，一些在低能量的近红外光下生长的蓝藻，使用叶绿素-f来进行光合作用，打破了叶绿素-a一统天下的局面——这就是超越“红光限制”的光合作用。

人们此前曾发现，另一种蓝藻（Acaryochloris）也可进行超越“红光限制”的光合作用。但由于其仅发生在单一物种内，且生长地特殊，故被认为是孤例。最新发现的基于叶绿素-f的光合作用则代表了第三种广泛存在的光合作用。

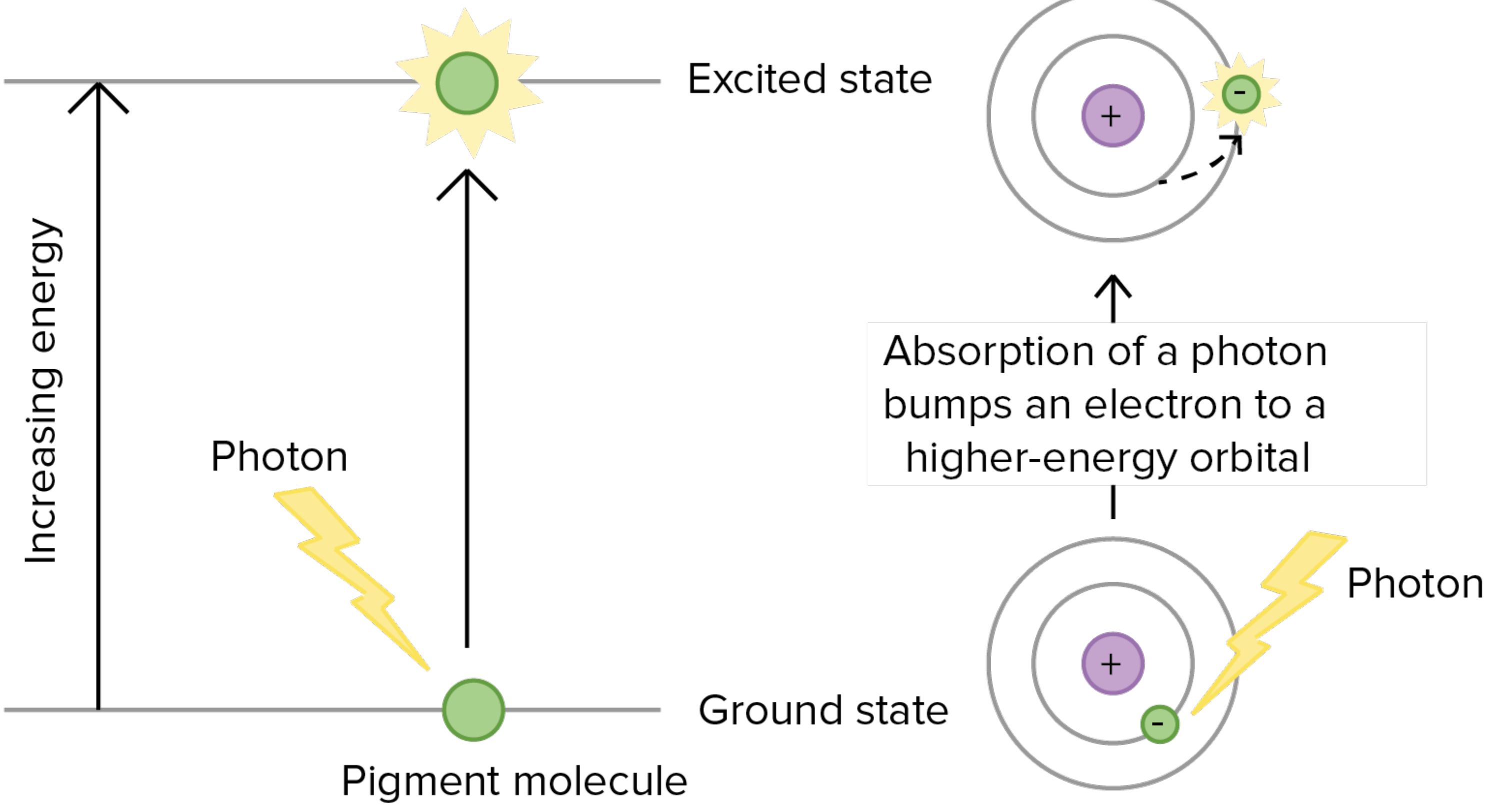
研究人员指出，这种光合作用只存在于特殊的红外光丰富的阴暗环境中，正常光照环境仍是标准红光形式光合作用的“天下”。此外有人认为，超越“红光限制”会导致更严重的光损伤。但新研究表明，在稳定的阴暗环境中，光损伤并非问题。

研究负责人、帝国理工学院生命科学学院的比尔·卢瑟福教授认为：“这种新型光合作用改变了我们对标准光合作用‘内核’的认识，是一项改写教科书的发现。”

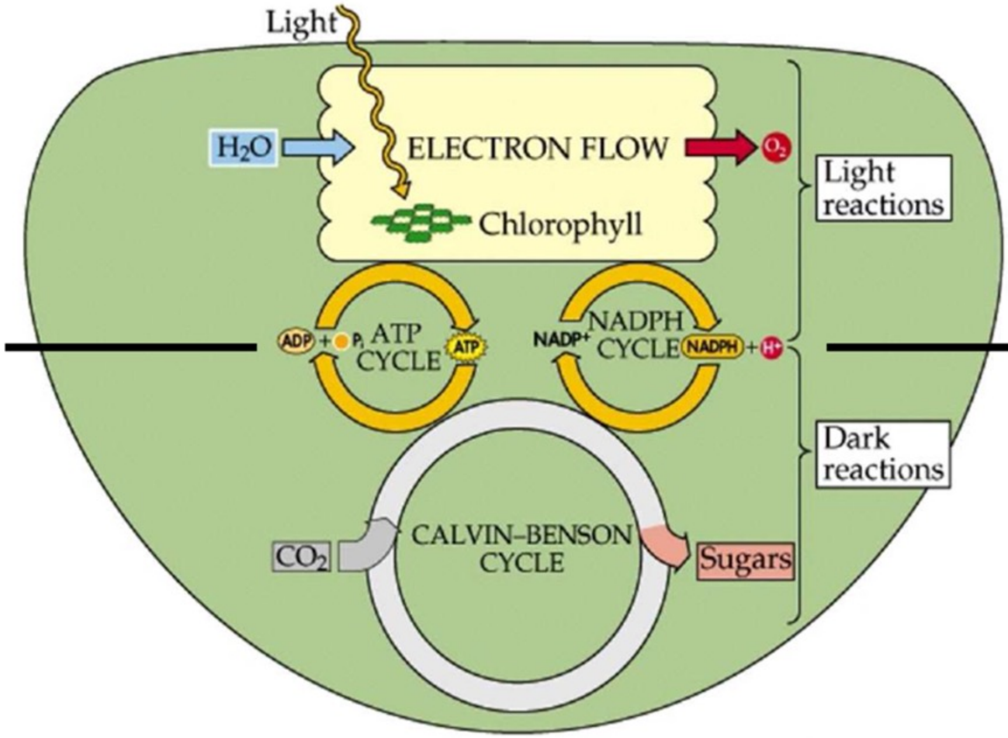
研究人员还表示，新发现也为搜寻外星生命提供了新思路。此外，研究这些蓝藻如何保护自己免受光的亮度变化所导致的损伤，有助于发现更好的作物改良方法。

Light absorption

Light capture



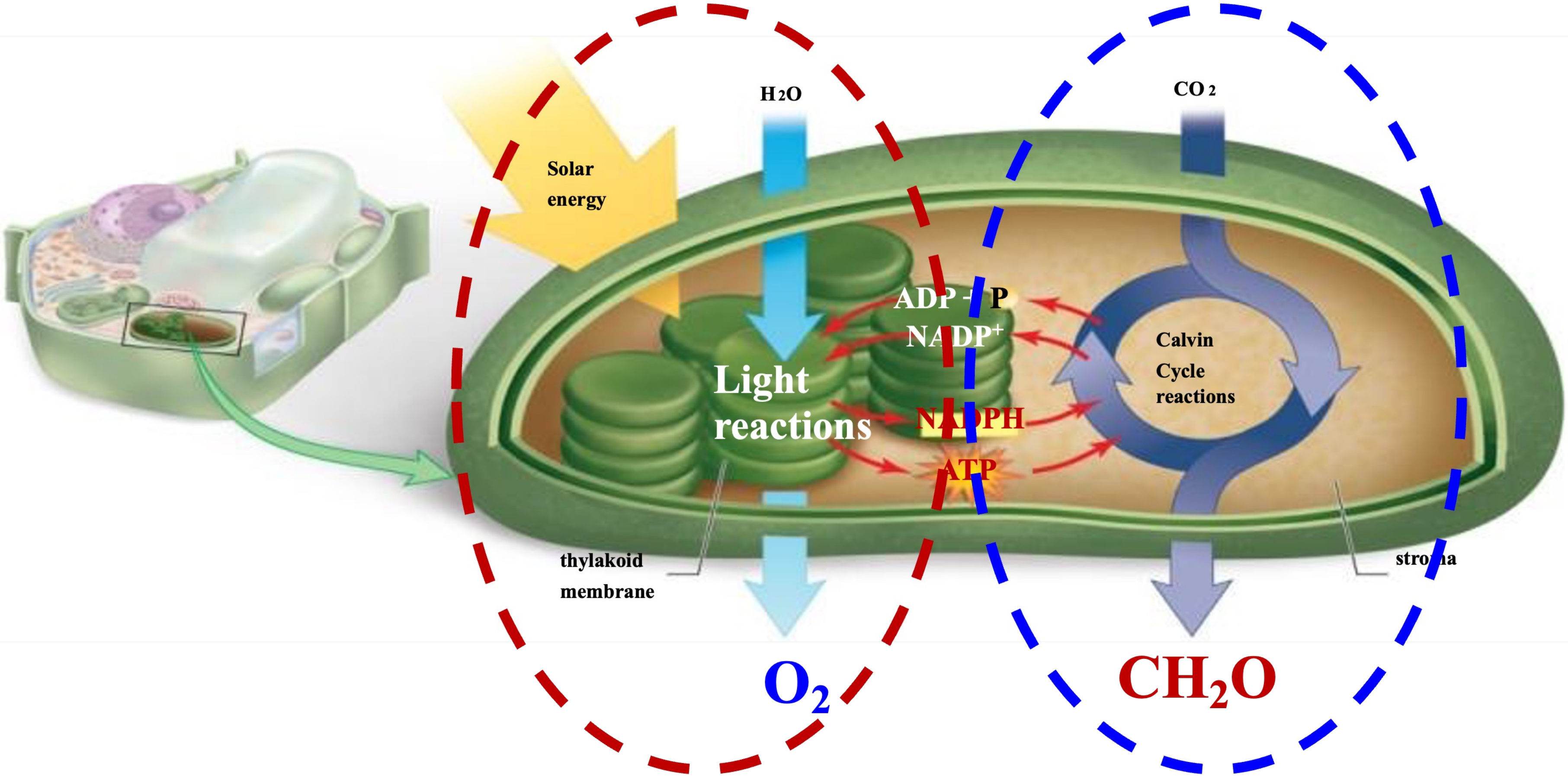
A two(=multi)part photosynthetic process:



1) **Light-dependent reactions**
PHOTOCHEMISTRY.
Light energy captured by chlorophyll is (PARTLY) used for ATP and NADPH synthesis from ADP and $NADP^+$.

2) **Light-independent reactions**
. **BIOCHEMISTRY**.
ATP and NADPH are used to reduce and fix CO_2 generating sugars in the C-B-B cycle.

Photosynthetic Reactions



Where Is Light Absorbed in Photosynthesis?

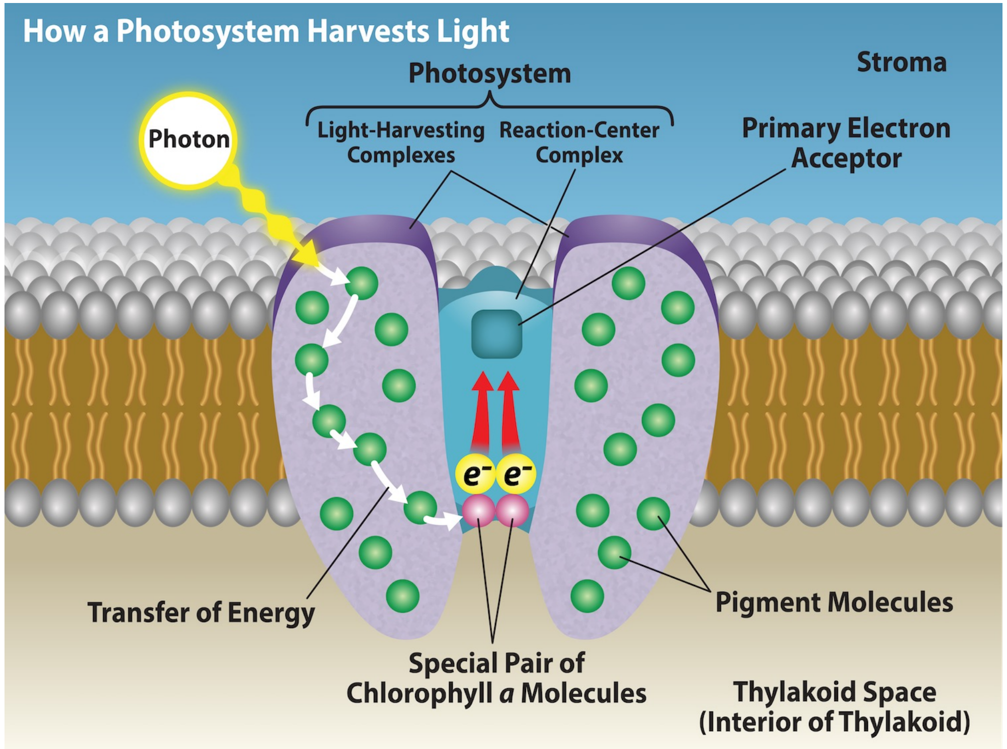
- **Chlorophyll does not function freely, but non-covalently bound to proteins forming pigment–protein complexes (叶绿素蛋白复合体)**
- **These complexes are embedded in the thylakoid membrane**
- **Two major categories:**
  - Chlorophyll a protein complexes (CP) / 叶绿素a蛋白复合体
  - Chlorophyll a/b protein complexes (light-harvesting complexes, LHC) / 叶绿素a/b蛋白复合体

Where Is Light Absorbed in Photosynthesis?

Pigment–Protein Complexes

Chlorophyll a protein complexes (CP)

- ❖ Associated with **reaction centers**
  - ✓ **CPI → Photosystem I (PSI) core**
  - ✓ **CPa → Photosystem II (PSII) core**
- ❖ Contain mainly **chlorophyll a**
- ❖ Directly involved in **photochemistry**



Chlorophyll a/b protein complexes (LHC)

- ❖ Surround reaction centers
- ❖ Contain chlorophyll a, chlorophyll b and carotenoids
- ❖ Absorb light across a broad spectrum
- ❖ Transfer **excitation energy to the reaction center**

Where Is Light Absorbed in Photosynthesis?

Pigment–Protein Complexes

Component	Function	Pigment Composition
Antenna complex (LHC)	Light capture	Chl a, Chl b, carotenoids
Reaction center (CP)	Charge separation	Chl a (special pair)

Photosynthetic Unit

A **photosynthetic unit** is the **smallest functional unit** in the thylakoid membrane capable of:

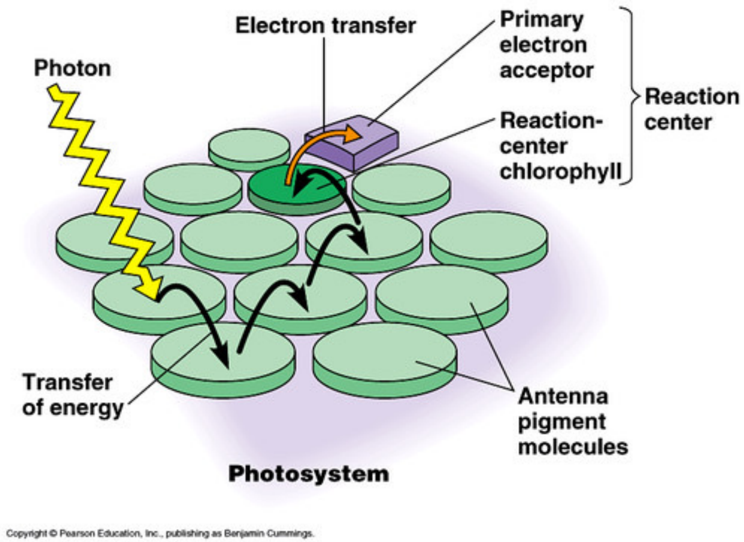
- ❖ Absorbing light
- ❖ Transferring excitation energy
- ❖ Performing primary photochemistry

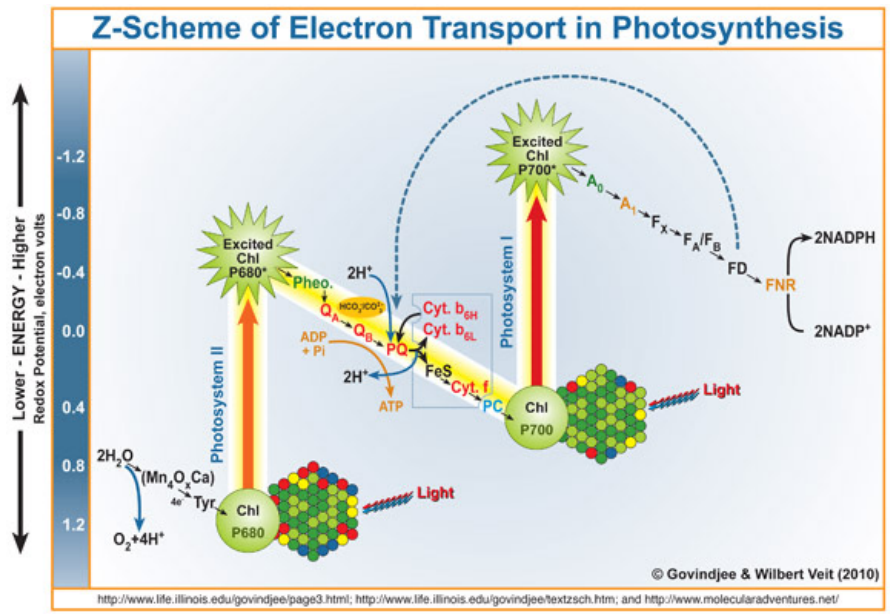
Photosynthetic Unit = **LHC** (Antenna) + **CP** (Reaction Center)

A photosynthetic unit consists of an LHC antenna system functionally coupled to a CP core complex, enabling one photochemical event per absorbed photon.

Photosynthetic Unit

Photosystem	LHC Type	CP Type	Reaction Center
PSII	LHCII	CPa	P680
PSI	LHCI	CPI	P700





Photosynthetic Unit

Reaction Center (Core of Photochemistry)

- **Special pair chlorophyll a**
  - ✓ **PSII: P680**
  - ✓ **PSI: P700**
- **Primary electron donor (P)**
- **Primary electron acceptor (A)**
- **Secondary electron donor (D)**

Component	Role	Example
Primary donor (P)	Excited chlorophyll	P680(PSII), P700(PSI)
Primary acceptor (A)	First electron acceptor	PSII: pheophytin; PSI: A_0 (chlorophyll)
Secondary donor (D)	Replaces lost electron	PSII: H_2O (via OEC); PSI: plastocyanin

Primary Reaction (原初反应)

The **primary reaction** is the initial photochemical event in photosynthesis in which **excitation energy, delivered from the antenna (LHC), is converted into stable chemical energy via charge separation in the reaction center (CP).**

❖ **Characteristics:**

- **Extremely fast** (~picoseconds)
- **Temperature-independent** (photophysical process)
- **High quantum efficiency (~1 under optimal conditions)**

❖ **Process:**

- Excitation of reaction center chlorophyll
- Charge separation
- Electron transferred to primary acceptor

Primary Reaction (原初反应)

$$D \cdot P \cdot A \xrightarrow{h\upsilon} D \cdot P^* \cdot A \longrightarrow D \cdot P^+ \cdot A^- \longrightarrow D^+ \cdot P \cdot A^-$$

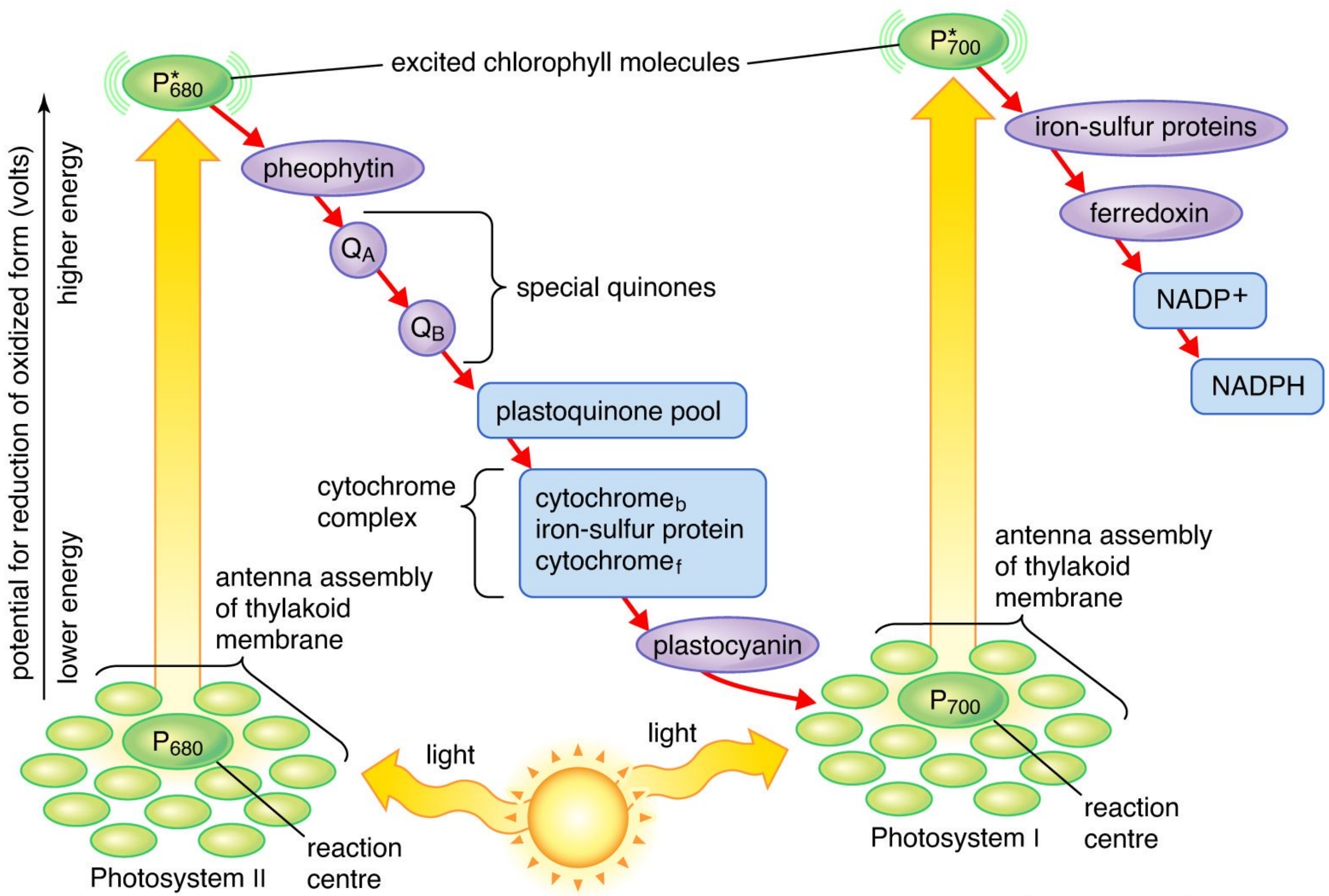
Level	Donor	Acceptor	Meaning
Primary (immediate)	P680 / P700	Primary acceptor (A)	First charge separation
Secondary (chain)	Electron carriers	Next carriers	Electron transport chain
Ultimate (overall)	H_2O	$NADP^+$	Net photosynthetic flow

Energy Transfer in Antenna Pigments

- ❖ Antenna pigments absorb photons and become excited.
- ❖ The excitation energy is transferred to neighboring pigments via:
  - ✓ **Exciton transfer** / 激子传递
  - ✓ **Resonance energy transfer (FRET-like mechanism) / 共振传递**

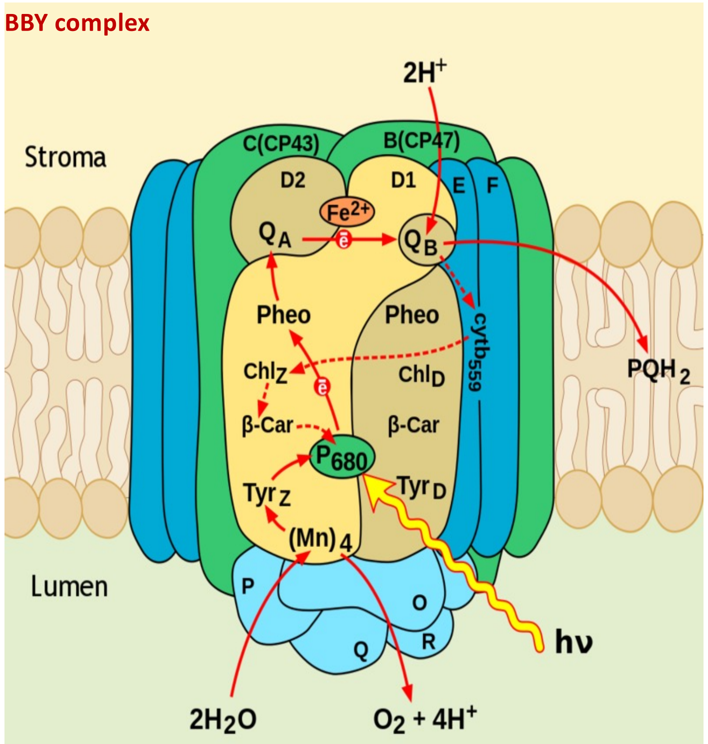
An exciton is a quasi-particle representing an excited state consisting of an electron–hole pair, capable of transferring energy without transferring net charge.

Photosynthetic electron pathway



Photosynthetic electron pathway

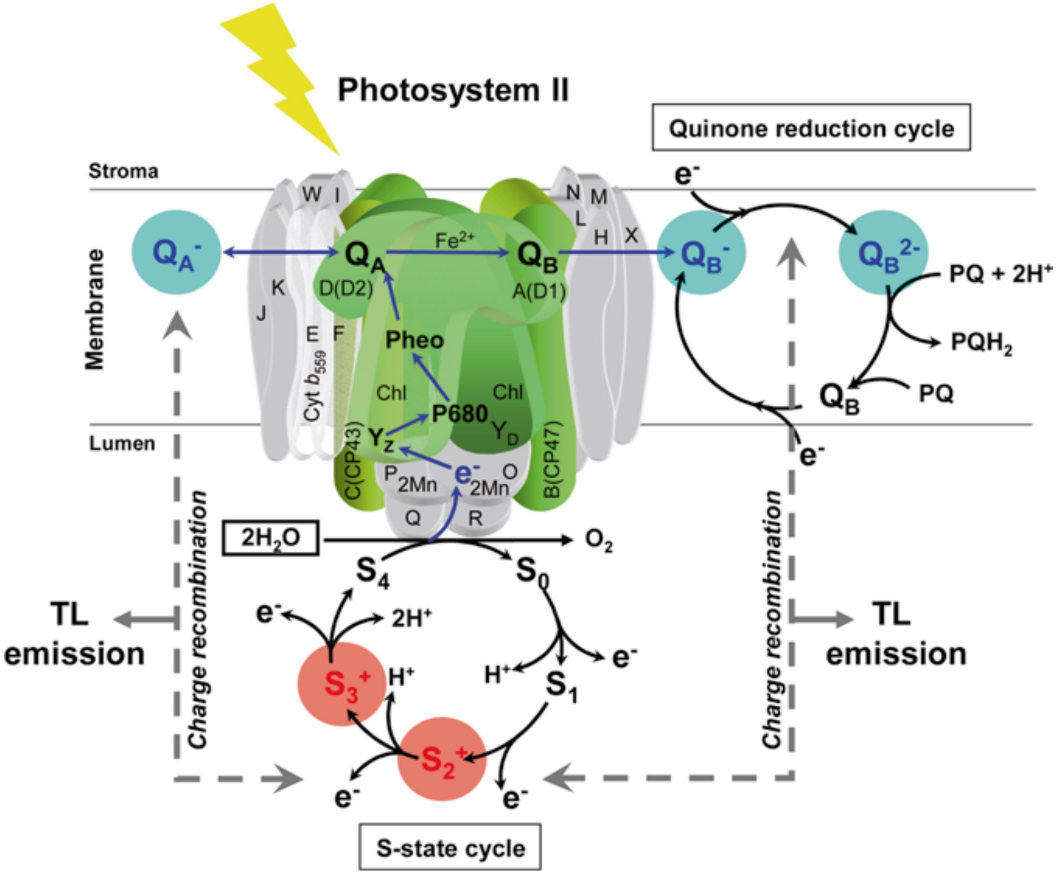
Photosystem II (PSII) Complex



- ❖ Also known as the BBY complex (core PSII reaction center preparation)
- ❖ Located in the thylakoid membrane (mainly grana)
- ❖ Approximate size: ~17–20 nm
- ❖ Central function: Initiates electron flow by oxidizing water and reducing plastoquinone
- ❖ Reaction center: P680 (bound by D1 and D2)
- ❖ Primary acceptor: Pheophytin (Pheo)/去镁叶绿素
- ❖ Secondary acceptors：Q_A, Q_B (plastoquinones)

Photosynthetic electron pathway

Photosystem II (PSII) Complex



Primary Reaction in PSII

1. Light excites **P680 → P680***
2. Electron transferred to **pheophytin (Pheo)**
3. Then to **Q_A → Q_B → plastoquinone (PQ → PQH_2)**

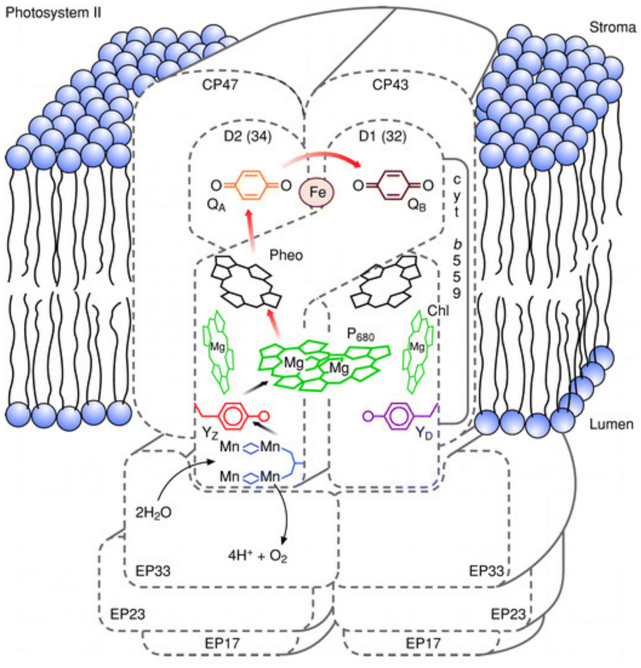
Electron Replacement

1. $P680^+$ is highly oxidizing
2. Re-reduced via:
    1. Y_Z (or $tyr_{z;}$ tyrosine residue)
    2. Then Mn cluster extracts electrons from H_2O

Photosynthetic electron pathway

Photosystem II (PSII) Complex

Oxygen-evolving complex (OEC) / 放氧复合体



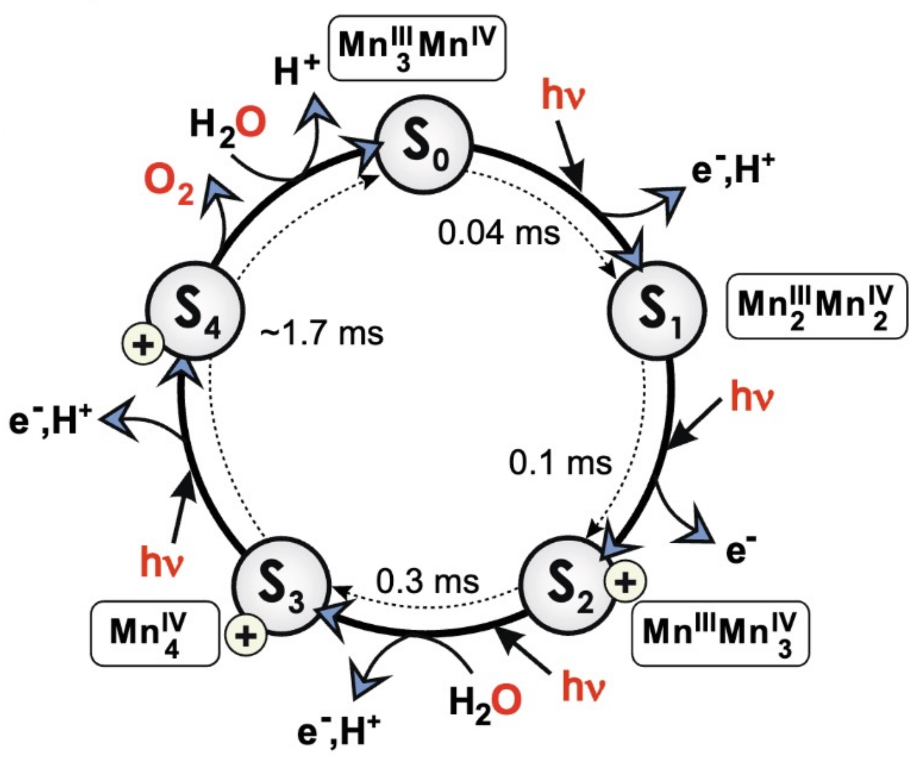
Biology 2402, Introduction to Botany, University of Arkansas at Little Rock (www.ualr.edu/botany/)

Water Splitting (OEC)

- ❖ Located on **lumen side**
- ❖ Contains: **Mn_4Ca cluster** / 锰稳定蛋白
- ❖ Extract electrons from water to replace electrons lost by $P680^+$
  - ✓ **O_2 (released)**
  - ✓ **Protons (H^+) into lumen**

Photosynthetic electron pathway

Photosystem II (PSII) Complex



OEC: Kok Cycle (S-State Cycle)

By Kok (1970)

- The OEC cycles through five oxidation states:

  $S_0 \rightarrow S_1 \rightarrow S_2 \rightarrow S_3 \rightarrow S_4$

- Each step is driven by one photon absorbed by P680

Photosynthetic electron pathway

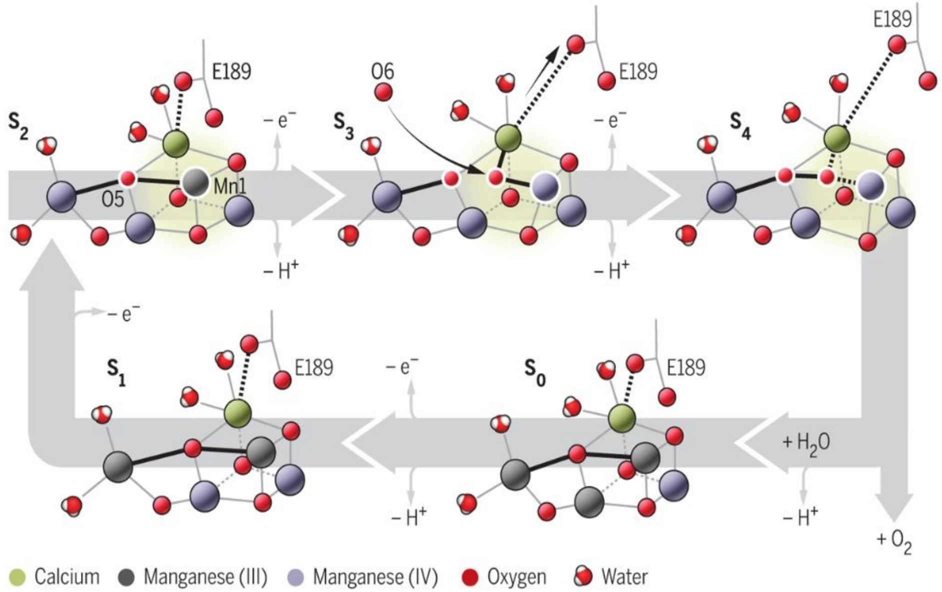
Photosystem II (PSII) Complex

RESEARCH ARTICLE

An oxyl/oxo mechanism for oxygen-oxygen coupling in PSII revealed by an x-ray free-electron laser

Michihiro Suga[1,2,*,†], Fusamichi Akita[1,2,*], Keitaro Yamashita[3,‡], Yoshiki Nakajima[1], Go Ueno[3], Hongjie Li[1,4], Takahiro Yaman...
+ See all authors and affiliations

Science 18 Oct 2019:
Vol. 366, Issue 6463, pp. 334-338
DOI: 10.1126/science.aax6998



Photosynthetic electron pathway

Plastoquinone (PQ；质体醌): Mobile Electron and Proton Carrier

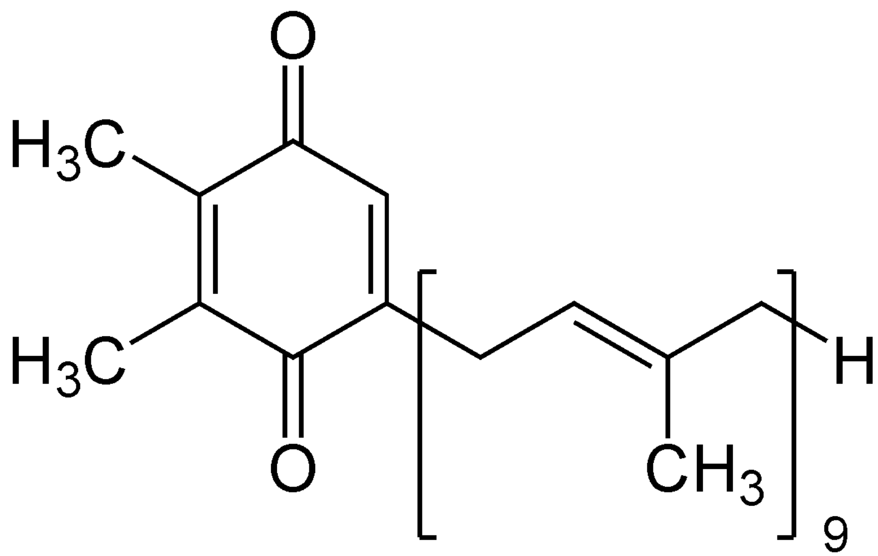
❖ Plastoquinone (PQ) is a lipid-soluble quinone located in the thylakoid membrane.

❖ Functions as a mobile carrier of:

- Electrons (e^-)
- Protons (H^+)

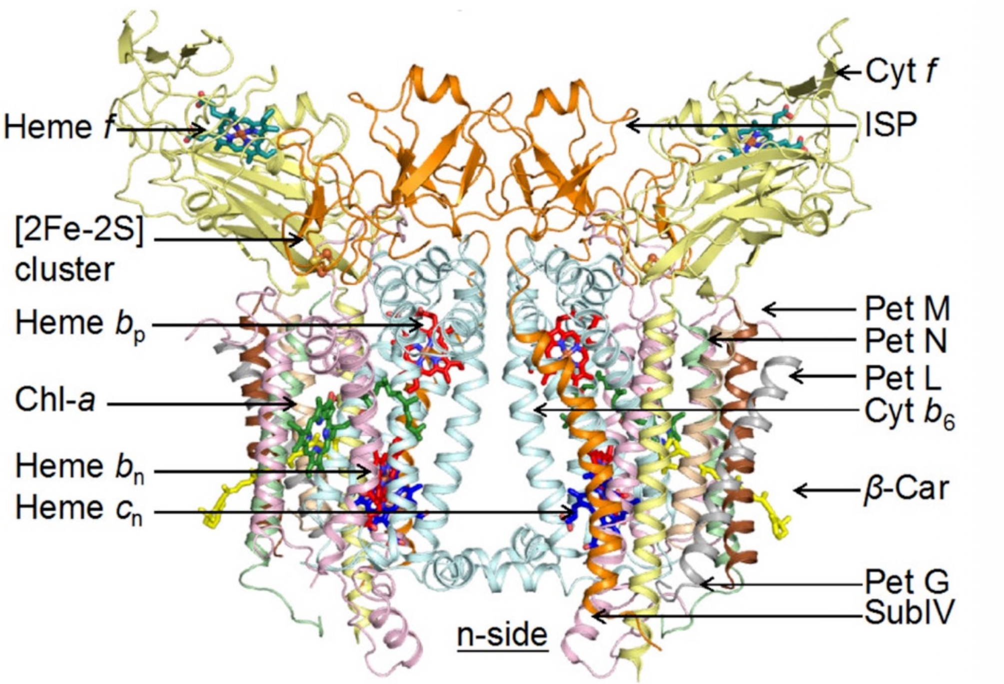
❖ Links Photosystem II (PSII) to the cytochrome b_6f complex / 细胞色素b_6f

❖ Reduced form: PQH_2 (plastoquinol, 还原态醌), PQH^- (plastosemiquinone; 半醌)



Photosynthetic electron pathway

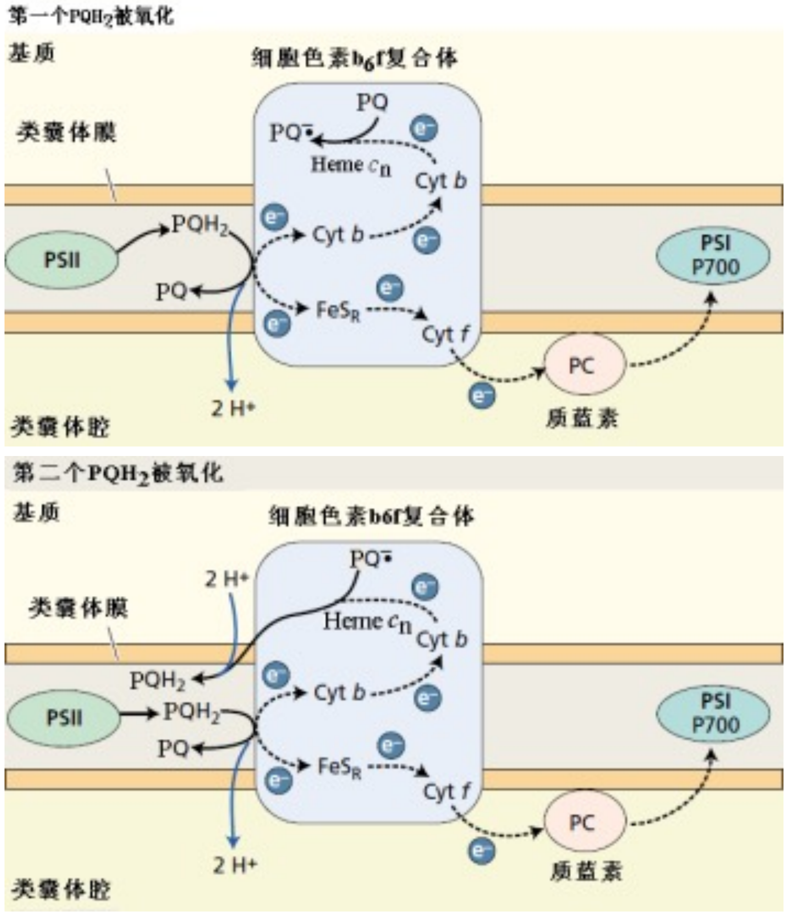
Cytochrome b_6f Complex



- ❖ Located in the thylakoid membrane
- ❖ Functions as:
  - ✓ Electron transfer intermediate
  - ✓ Proton translocation system
- ❖ Electron Flow Through Cyt b_6f
  - ✓ Input: PQH_2 (from PSII)
  - ✓ Output: Plastocyanin (PC) → PSI

Photosynthetic electron pathway

Cytochrome b_6f Complex



Q-Cycle Mechanism

First PQH_2 Oxidation (at Q_o site)

❖ $PQH_2 \rightarrow PQ + 2e^- + 2H^+$ (to lumen)

❖ Electron split:

- ✓ Path 1: Rieske → Cyt f → PC → PSI (P700)
- ✓ Path 2: Cyt b_6 → Q → reduces PQ → PQH^-

Second PQH_2 Oxidation

❖ Repeats same process:

- ❖ Another $2H^+$ released into lumen
- ❖ Second electron: reduces $PQH^- \rightarrow PQH_2$

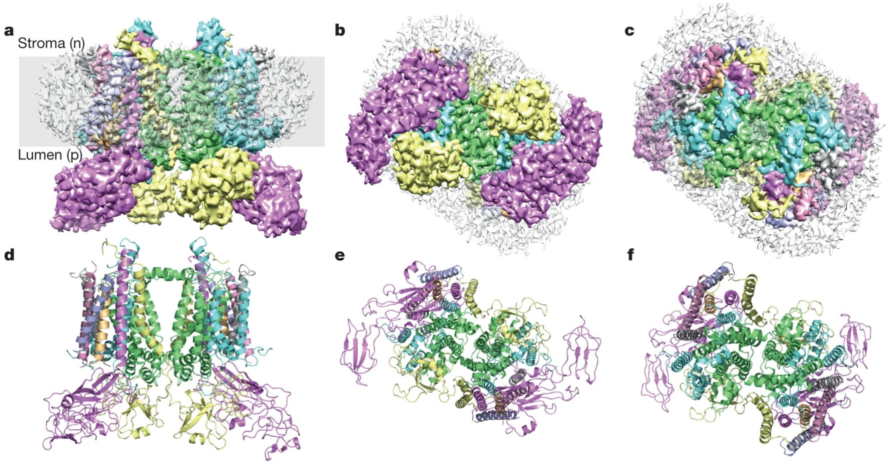
❖ Requires: $2H^+$ uptake from stroma

nature

Article | Published: 13 November 2019

Cryo-EM structure of the spinach cytochrome b_6f complex at 3.6 Å resolution

Lorna A. Malone, Pu Qian, Guy E. Mayneord, Andrew Hitchcock, David A. Farmer, Rebecca F. Thompson, David J. K. Swainsbury, Neil A. Ranson, C. Neil Hunter ✉ & Matthew P. Johnson ✉



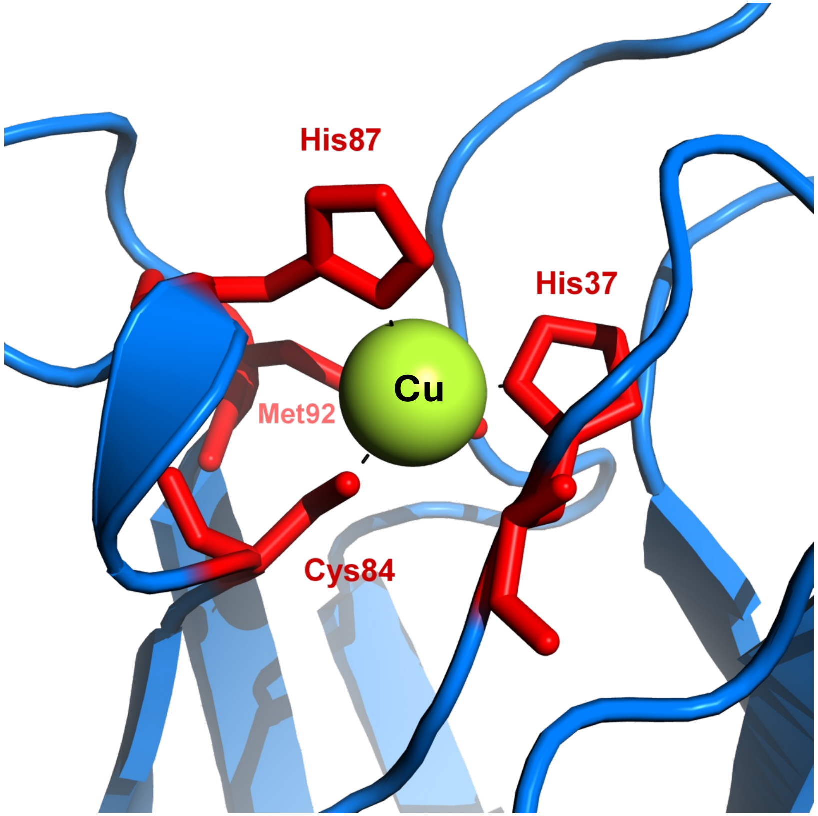
Key Photosynthesis Complex Viewed in Spinach

Findings fuel hopes for improved food-crop efficiency

Dr. Matt Johnson, reader in Biochemistry at the University of Sheffield and one of the supervisors of the study added: "Cytochrome b6f is the **beating heart** of photosynthesis which plays a crucial role in regulating photosynthetic efficiency.

Photosynthetic electron pathway

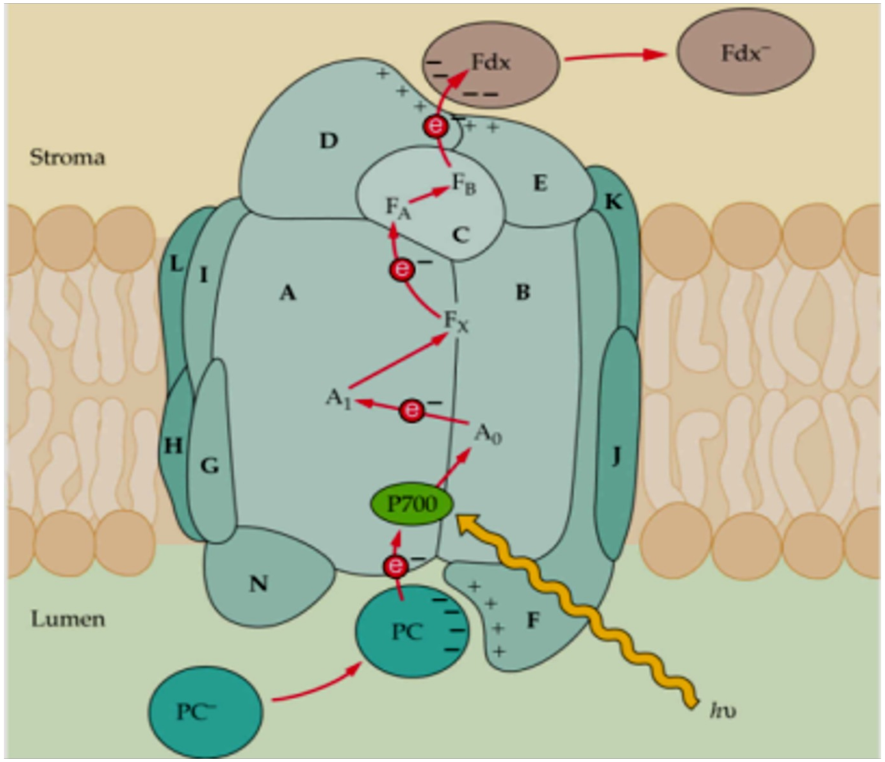
Plastocyanin (PC): Mobile Electron Carrier to PSI 质蓝素



- ❖ Plastocyanin (PC) is a small, soluble copper-containing protein
- ❖ Located in the thylakoid lumen
- ❖ Functions as a mobile electron carrier
- ❖ Redox states:
  - ✓ **Cu^{+} (reduced form)**
  - ✓ **Cu^{2+} (oxidized form)**

Photosynthetic electron pathway

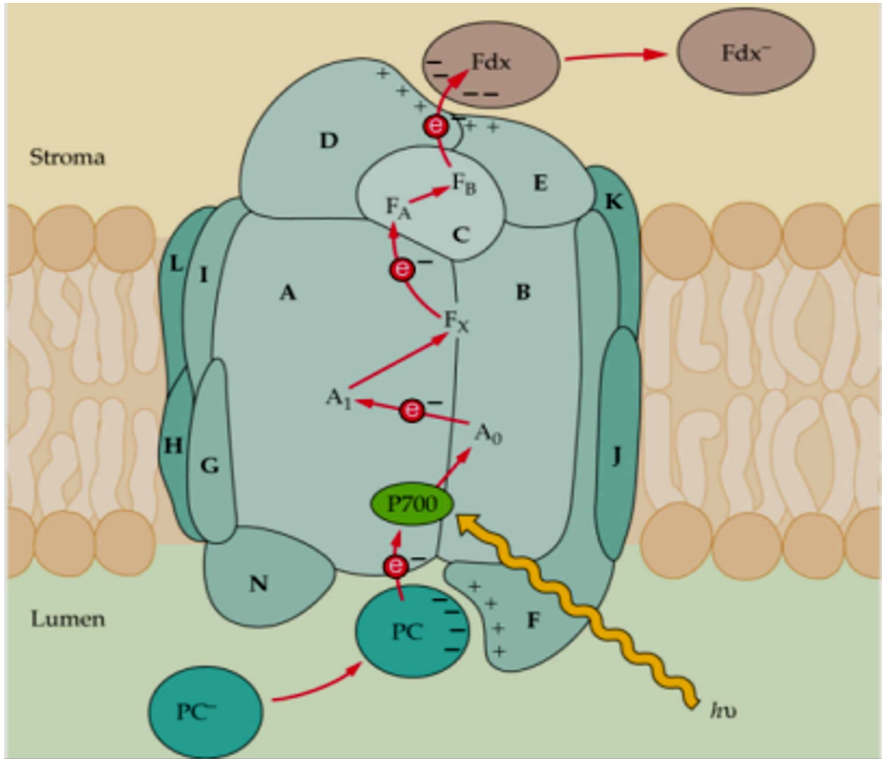
Photosystem I (PSI): Light Reaction and NADP⁺ Reduction



- ❖ PSI is a large pigment–protein complex embedded in the thylakoid membrane
- ❖ Enriched in stroma lamellae (non-appressed regions)
- ❖ Convert light energy into reducing power (NADPH)
- ❖ Reaction center: P700
- ❖ Electron carriers:
  - ✓ A_0 (chlorophyll a), primary acceptor
  - ✓ A_1 (phylloquinone/维生素K)
  - ✓ Fe–S clusters (F_x, F_a, F_b)

Photosynthetic electron pathway

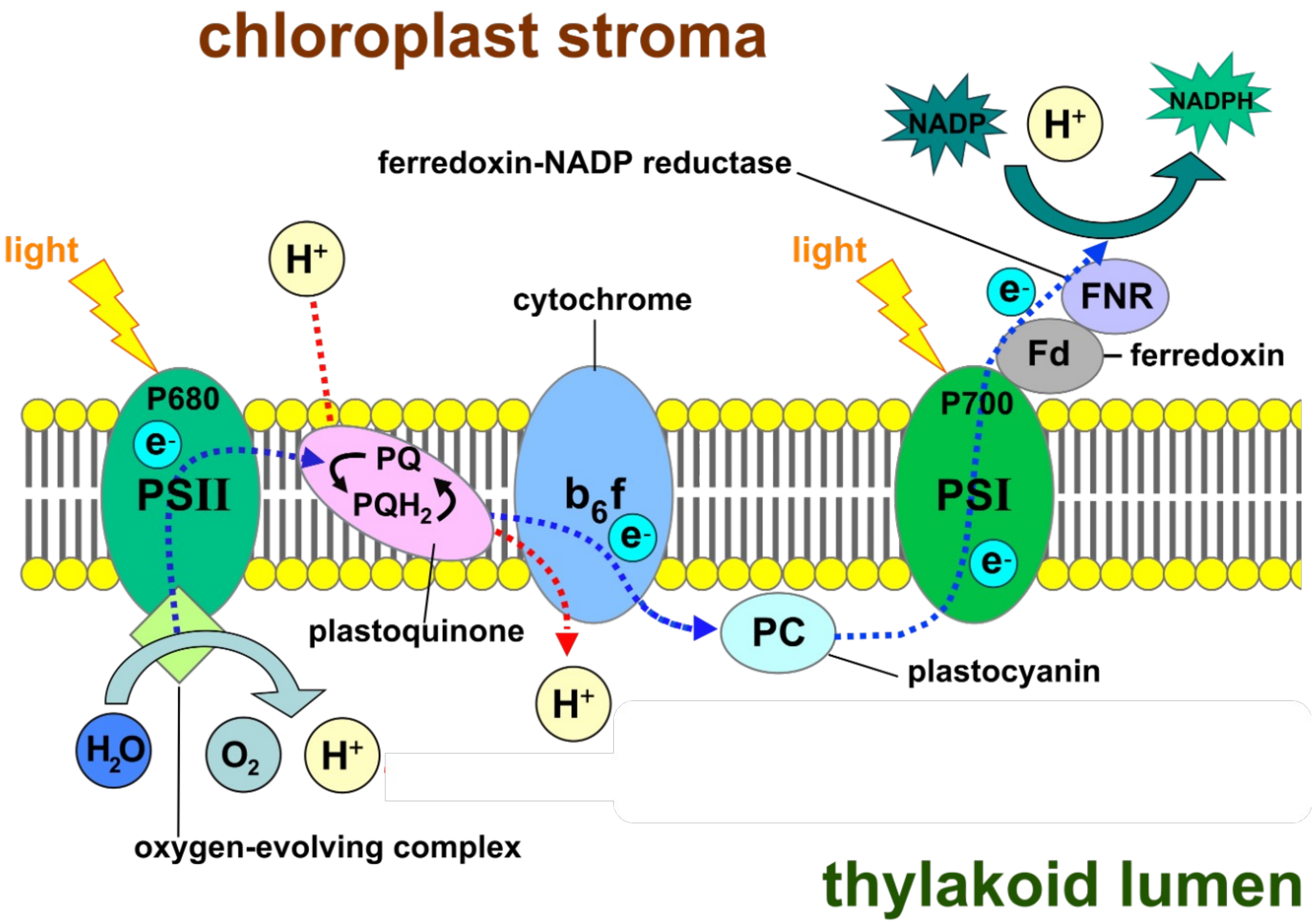
Photosystem I (PSI): Light Reaction and NADP⁺ Reduction



- P700⁺ is reduced by **Plastocyanin (PC)**
- Electrons exit PSI via Ferredoxin (Fd)
- Then Ferredoxin–NADP⁺ reductase (FNR) catalyzes:

$$NADP^{+} + 2e^{-} + H^{+} \rightarrow NADPH$$

Photosynthetic electron pathway



Photosynthetic electron pathway

Photosynthetic electron transport operates in three modes:

1. **Linear (noncyclic) electron flow / 非环式电子传递**
2. **Cyclic electron flow / 环式电子传递**
3. **Pseudocyclic electron flow (Mehler reaction / 米歇尔反应) / 假环式电子传递**

Photosynthetic electron pathway

Linear (noncyclic) electron flow

H_2O→PSⅡ→PQ→Cytb_6/f→PC→PS Ⅰ→Fd→FNR→$NADP^+$

For 4 electrons transferred:

- 2 H_2O split → 1 O_2 released
- 2 $NADP^+$ → 2 NADPH
- ~8 H^+ accumulated in lumen
- ATP produced via chemiosmosis

Key Features

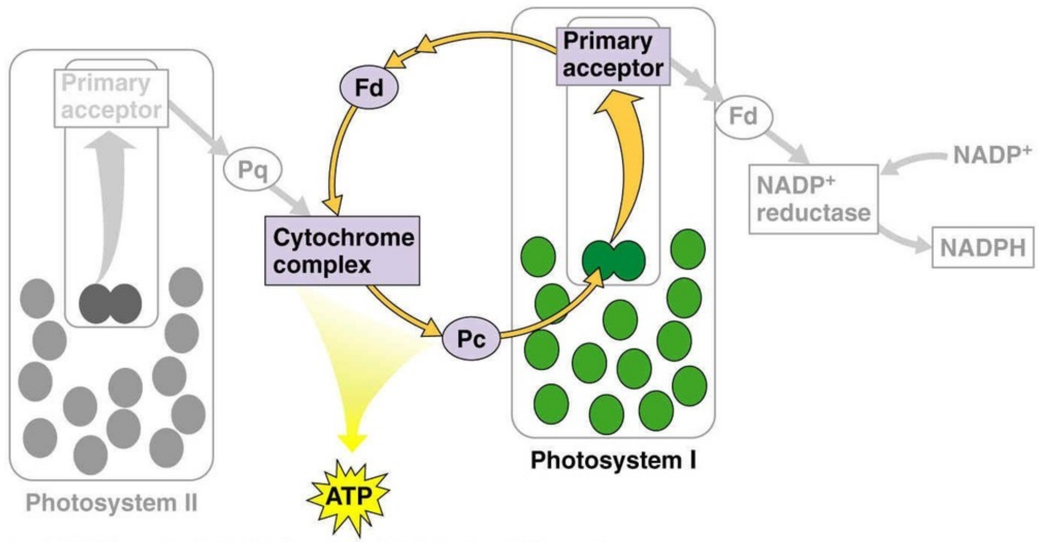
- Involves both PSII and PSI
- 8 photons → 1 O_2
- Produces: ATP + NADPH + O_2

Photosynthetic electron pathway

Cyclic Electron Flow (Around PSI)

PS I →Fd→(NADPH→PQ)→Cytb6/f→PC→PS I

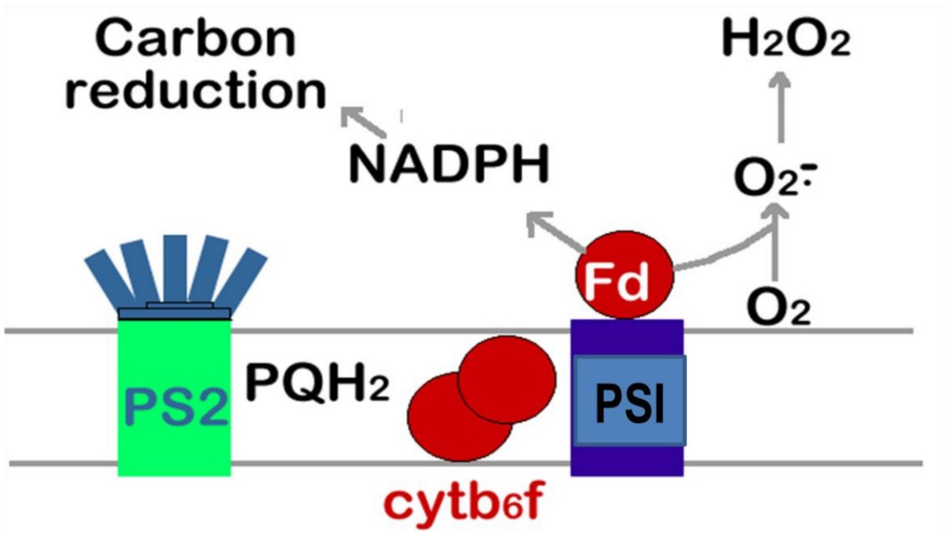
- **Produce ATP only**
- **No NADPH production and O_2 evolution**
- **Balances ATP/NADPH ratio**
- **Activated when:**
  - ✓ **NADPH is abundant**
  - ✓ **ATP demand is high**



Photosynthetic electron pathway

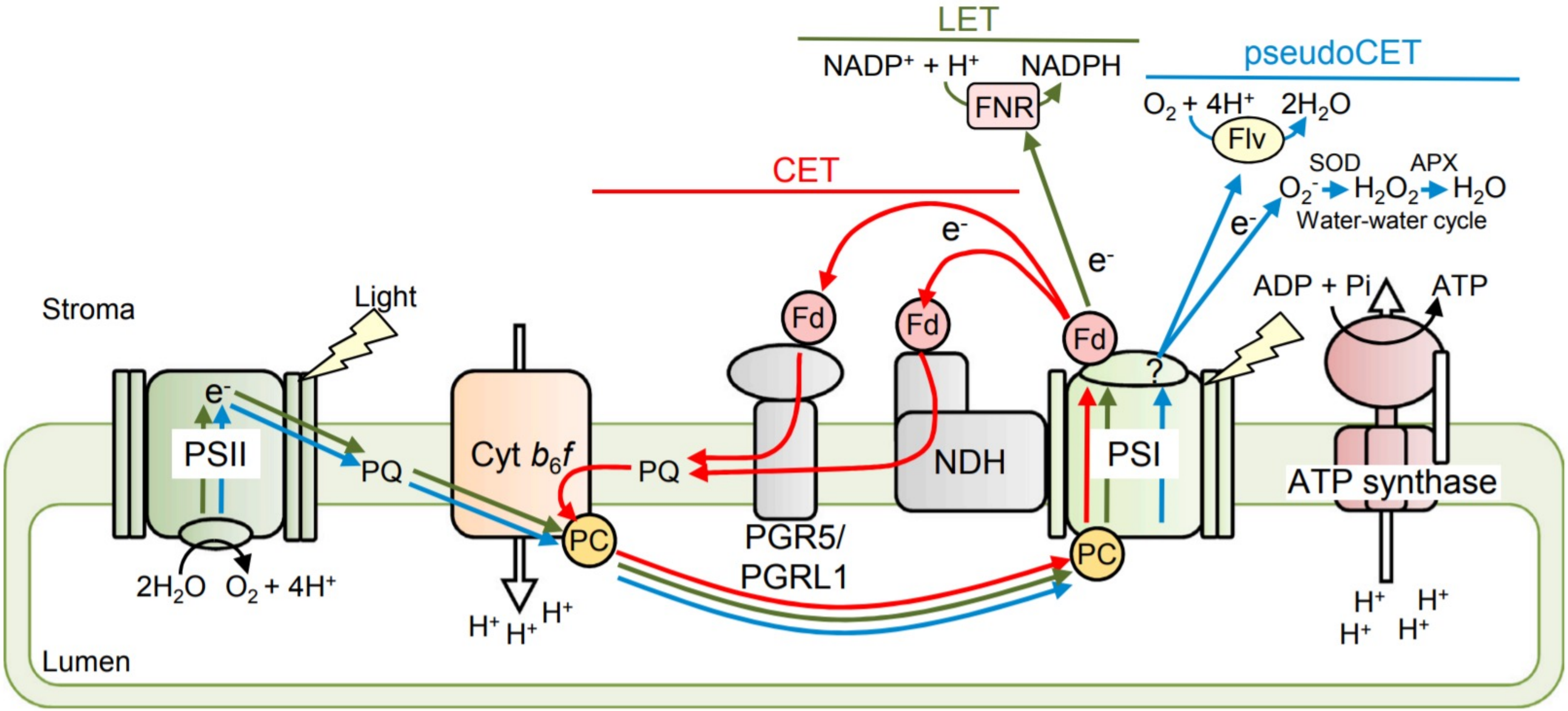
Pseudocyclic Electron Flow (Mehler Reaction)

H_2O→PSⅡ→PQ→Cytb6/f→PC→PS Ⅰ →Fd→O2

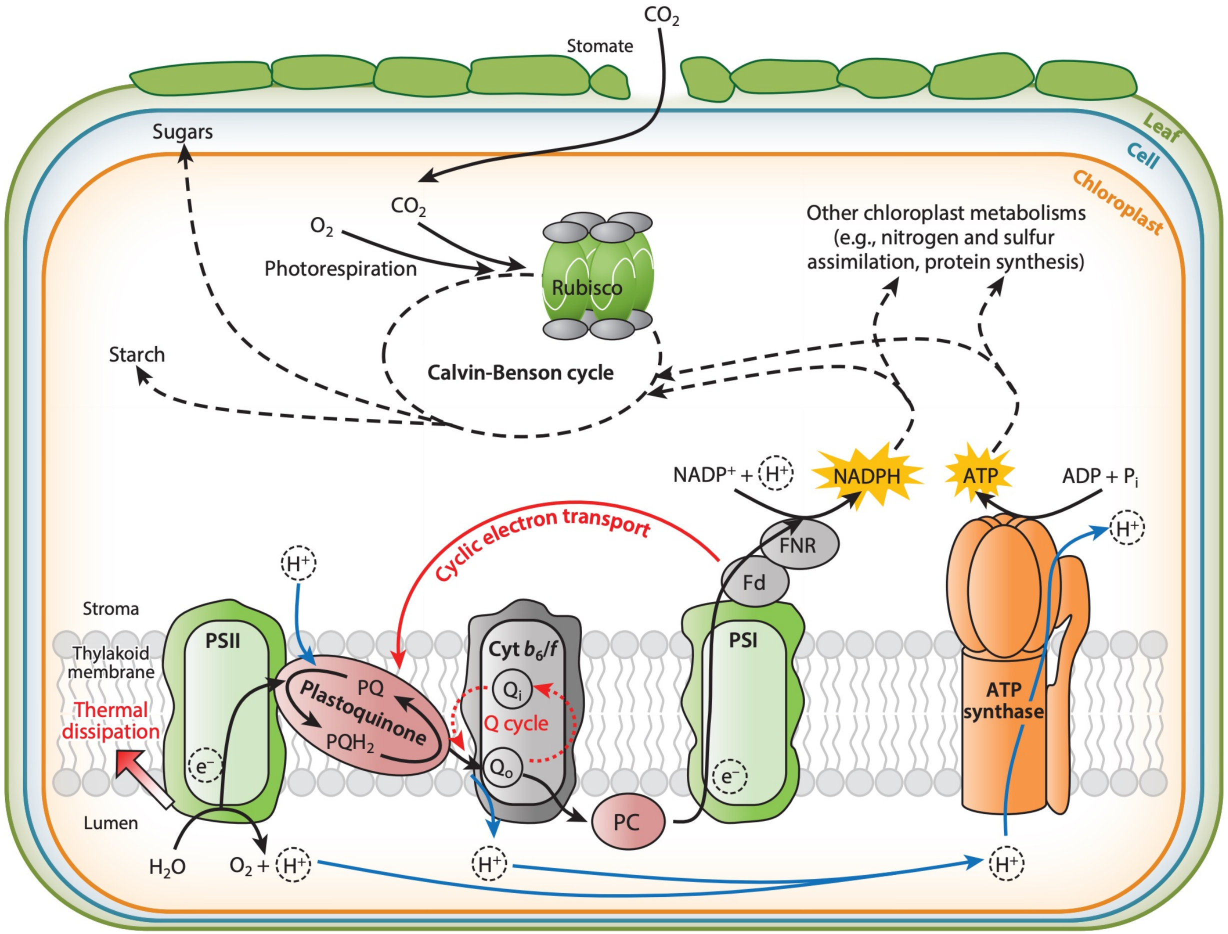


- ❖ No NADPH produced
- ❖ O_2 is consumed (not produced overall)
- ❖ Produces: Reactive oxygen species (ROS) (e.g., superoxide O_2^-)
- ❖ Can contribute indirectly to: Proton gradient → ATP formation

Photosynthetic electron pathway



Photophosphorylation /光合磷酸化



The process by which light-driven electron transport generates a proton gradient across the thylakoid membrane, which is then used to synthesize ATP from ADP and Pi via ATP synthase.

Protons (H^+) accumulate in the thylakoid lumen via:

1. Water splitting (PSII)
2. Plastoquinone (PQ cycle)
3. Cytochrome b_6f (Q-cycle)

Photophosphorylation /光合磷酸化

Types of Photophosphorylation

(1) Noncyclic Photophosphorylation

- Pathway: **PSII + PSI**
- Produces: **ATP, NADPH**, O_2
- The Main pathway for photosynthesis

(2) Cyclic Photophosphorylation

- Pathway: **PSI only**
- Produces: **ATP only**
- Adjusts **ATP/NADPH balance**

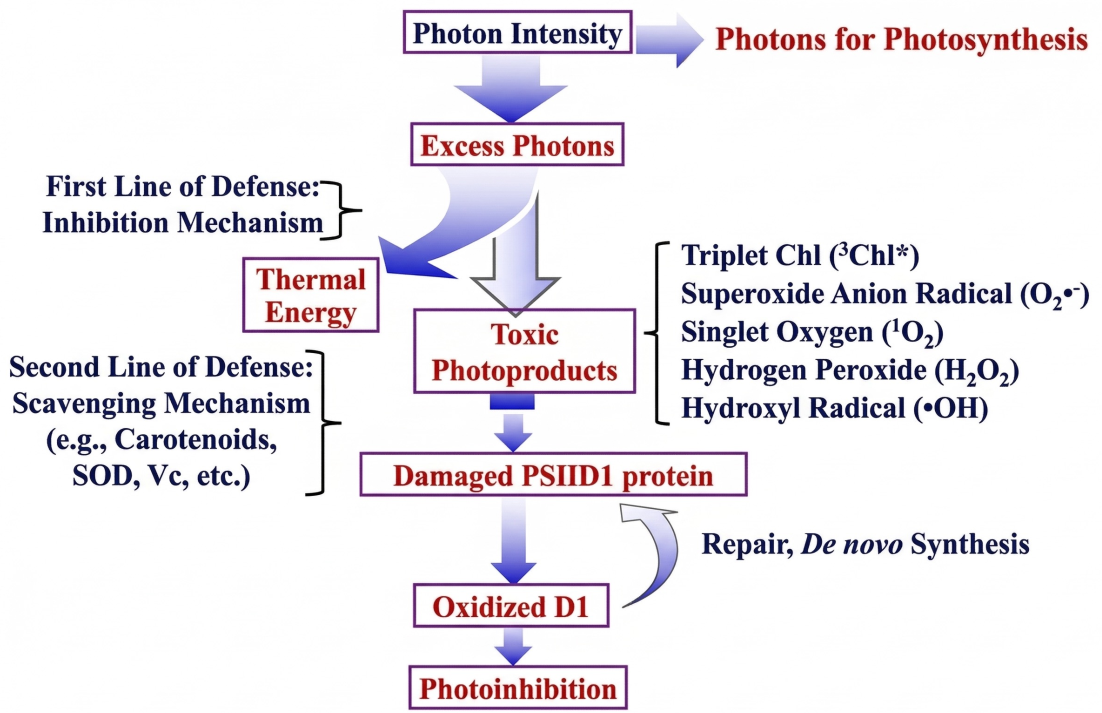
(3) Pseudocyclic photophosphorylation

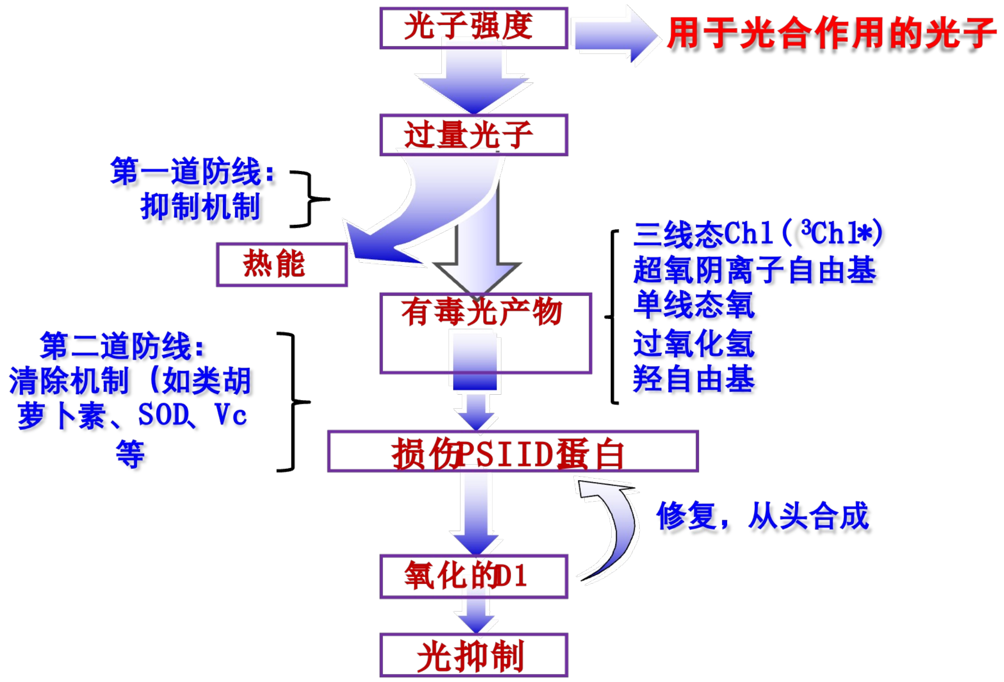
- Pathway: **PSII + PSI**
- Produces: **ATP only**
- Photoprotection

Photophosphorylation /光合磷酸化

Pathway	Electron Acceptor	Products	Function
Linear	$NADP^+$	ATP, NADPH, O_2	Main pathway
Cyclic	PSI loop	ATP only	Energy balance
Pseudocyclic	O_2	ATP (indirect), ROS	Photoprotection

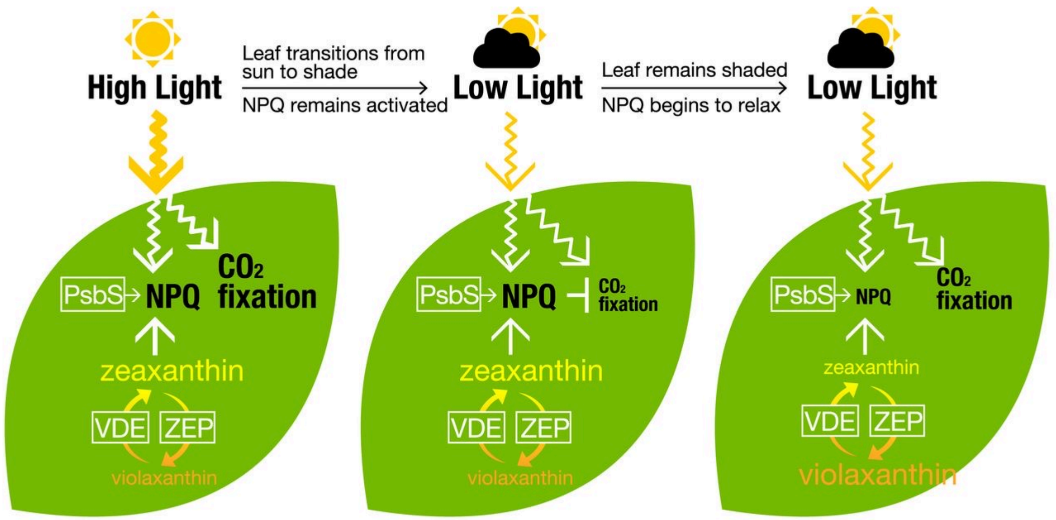
Light Energy Distribution and Photoprotection





Light reaction and crop improvement

Improving photosynthesis and crop productivity by accelerating recovery from photoprotection

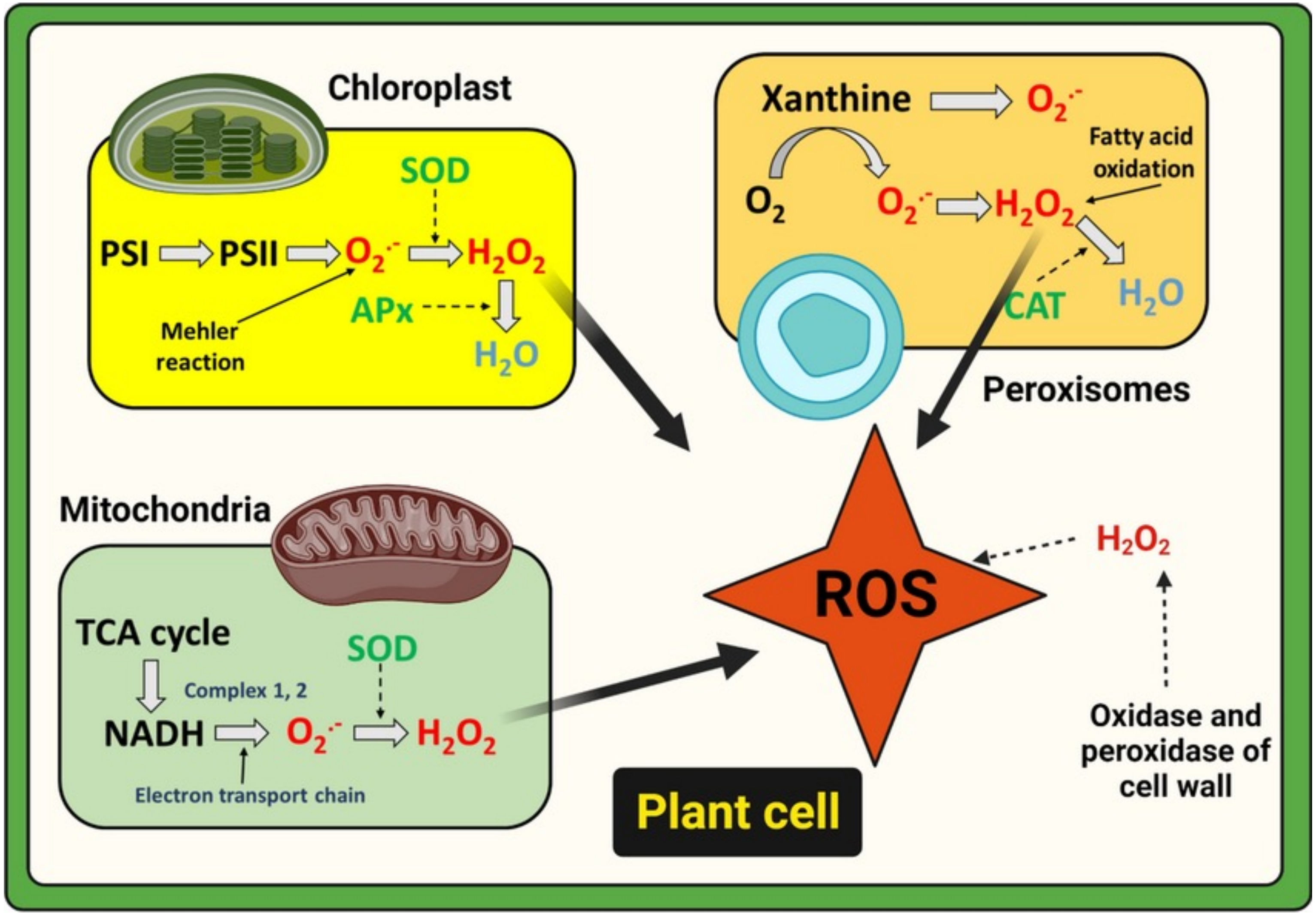


ZEP speeds up NPQ relaxation
VDE balances ZEP activity during NPQ induction
PsbS adjusts NPQ level to maintain WT amplitude

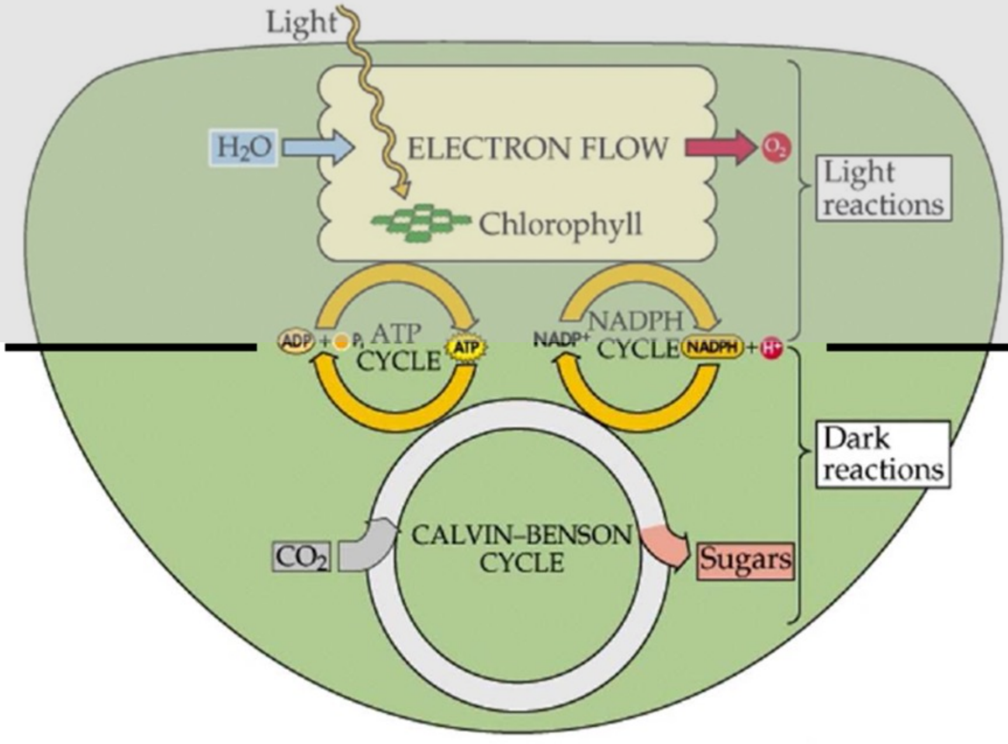
2016 Science, 10.1126/science.aai8878

2022 Science, 10.1126/science.adc9831

Sources of Reactive Oxygen Species (ROS) in Plants



A two(=multi)part photosynthetic process:



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PHOTOCHEMISTRY.
Light energy captured by chlorophyll is (PARTLY) used for ATP and NADPH synthesis from ADP and $NADP^+$.

2) **Light-independent reactions**
. **BIOCHEMISTRY**.
ATP and NADPH are used to reduce and fix CO_2 generating sugars in the C-B-B cycle.

Carbon Assimilation in Photosynthesis

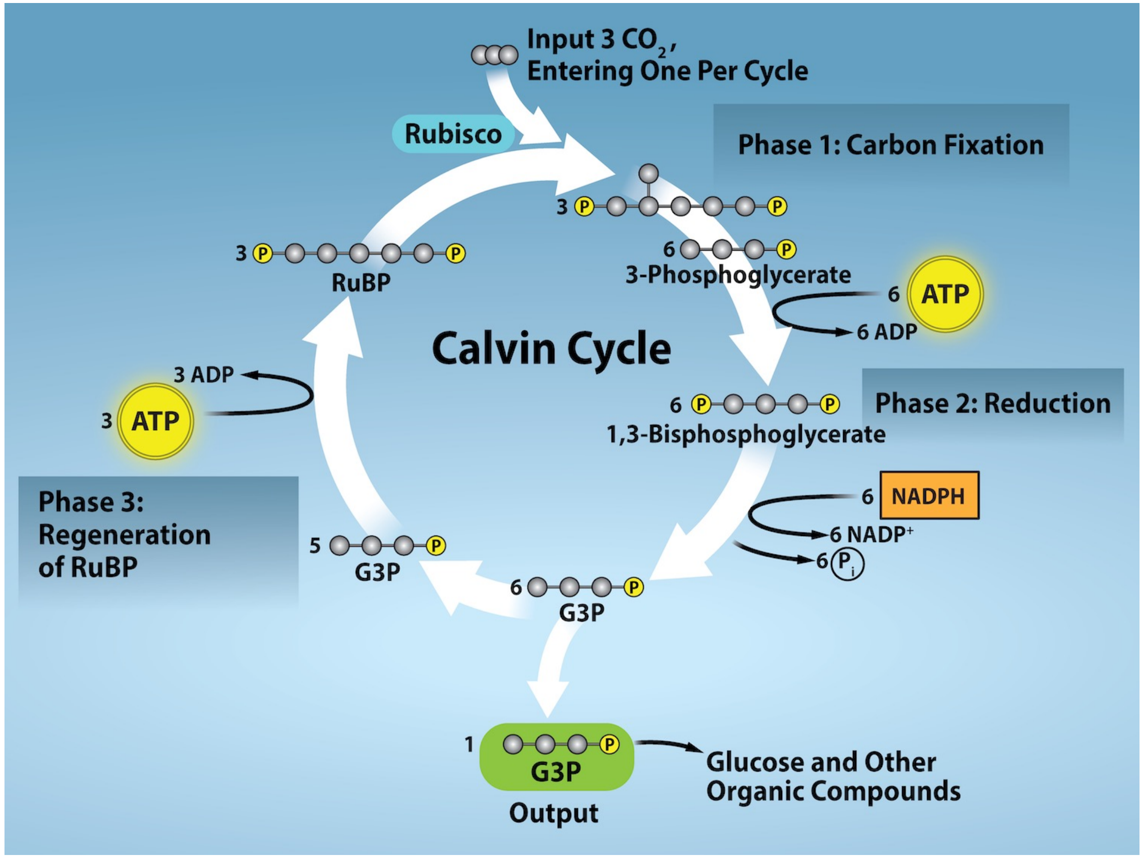
- ❖ Carbon assimilation (CO_2 assimilation): The process by which plants use ATP and NADPH (from light reactions) to convert CO_2 into carbohydrates.
- ❖ Occurs in: Chloroplast stroma

Major Carbon Fixation Pathways

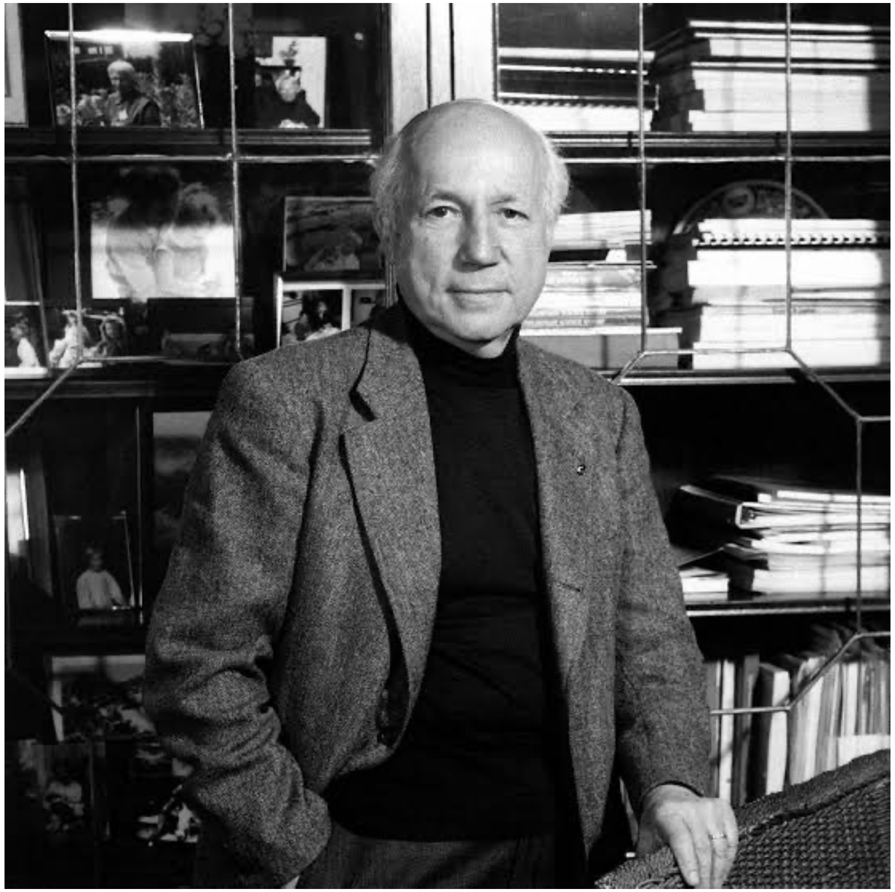
- ❑ **C_3 pathway (Calvin cycle)** (most common)
- ❑ **C_4 pathway**
- ❑ **CAM pathway**

The C_3 Pathway (Calvin–Benson Cycle)

A photosynthetic carbon fixation pathway in which ribulose-1,5-bisphosphate (RuBP) acts as the CO_2 acceptor, and the first stable product formed is the three-carbon compound 3-phosphoglycerate (PGA).



Discovery



Nobel Prize in Chemistry 1961

Photo: Berkeley, CA. Nobel Foundation archive

Melvin Calvin

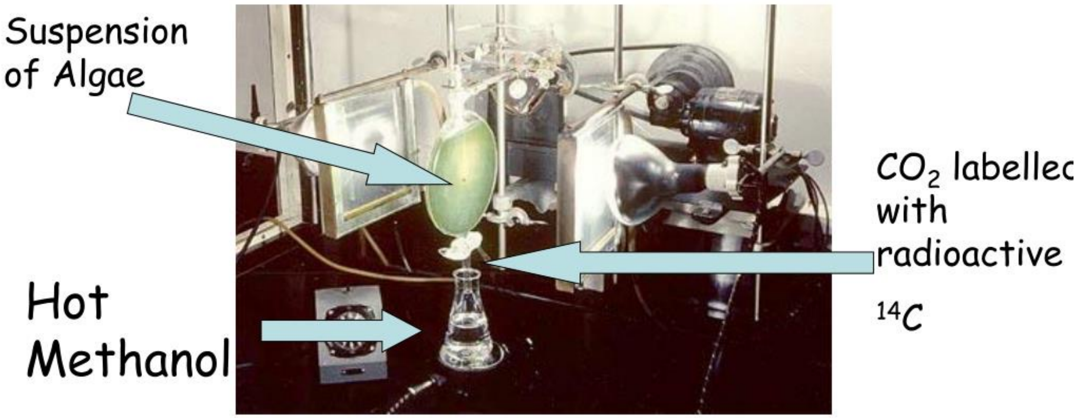
Prize share: 1/1

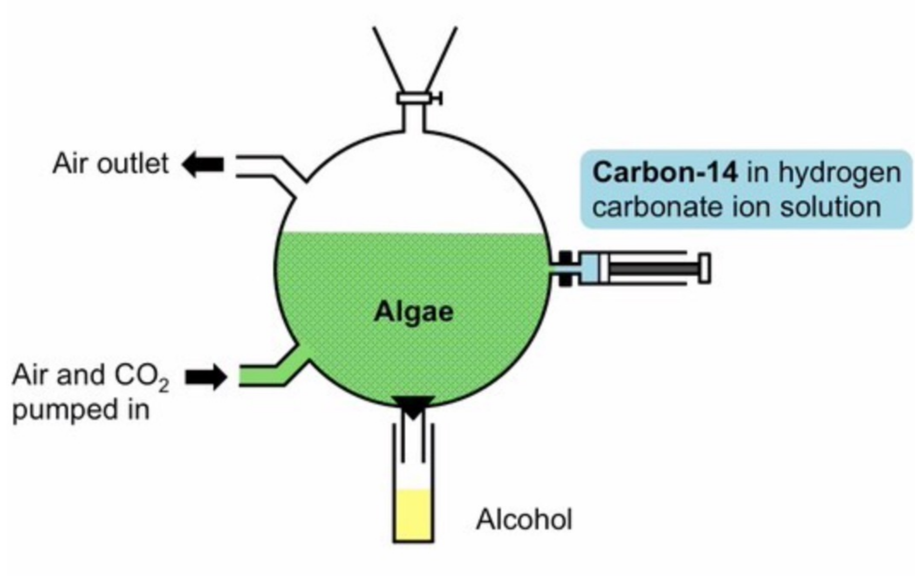
The Nobel Prize in Chemistry 1961 was awarded to Melvin Calvin "for his research on the carbon dioxide assimilation in plants"

Melvin Calvin, (1911-1997)

Discovery

Calvin's Experiment – the light independent reaction of photosynthesis

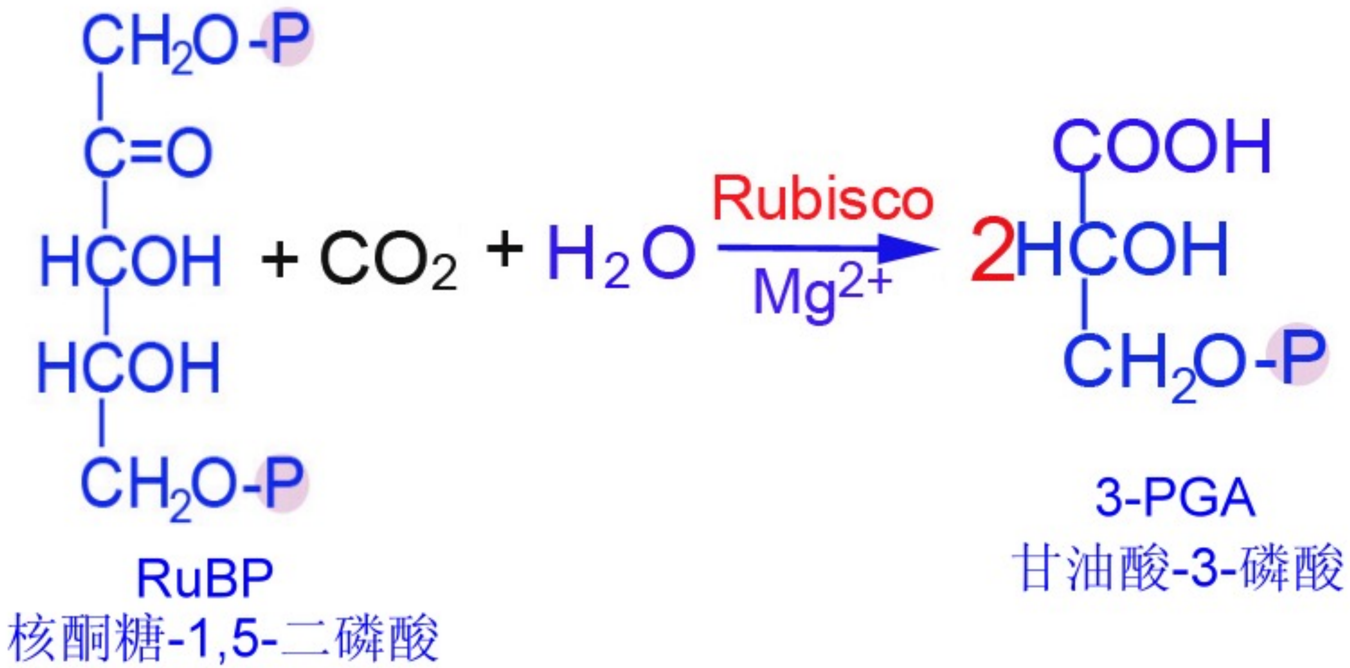




- Step 1: Expose algae to **$^{14}CO_2$ under light**
- Step 2: Stop reaction rapidly using **hot methanol (quenching)**
- Step 3: Analyze labeled compounds via **chromatography**

The C_3 Pathway (Calvin–Benson Cycle)

Step 1: CO_2 Fixation / CO_2 固定



Ribulose 1,5-bisphosphate

3-Phosphoglycerate

PGA contains 3 Carbon atoms, and this defines the pathway as C3

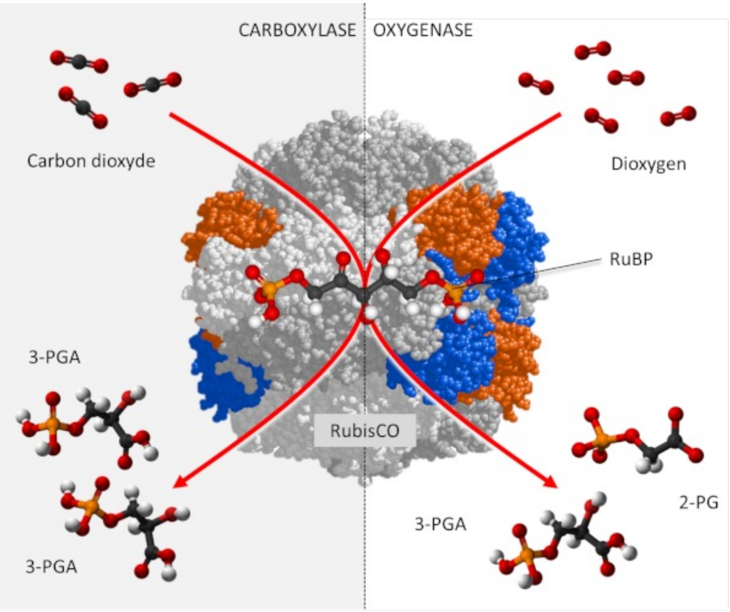
The C_3 Pathway (Calvin–Benson Cycle)

Step 1: CO_2 Fixation / CO_2 固定

RuBisCO: Ribulose-1,5-bisphosphate carboxylase/oxygenase

L_8S_8 complex (16 subunits)

- ❖ Large subunits (L, ~55–56 kDa), which encoded by chloroplast genome, and contain active sites
- ❖ Small subunits (S, ~14 kDa), which encoded by nuclear genome, plays as Regulatory/structural role

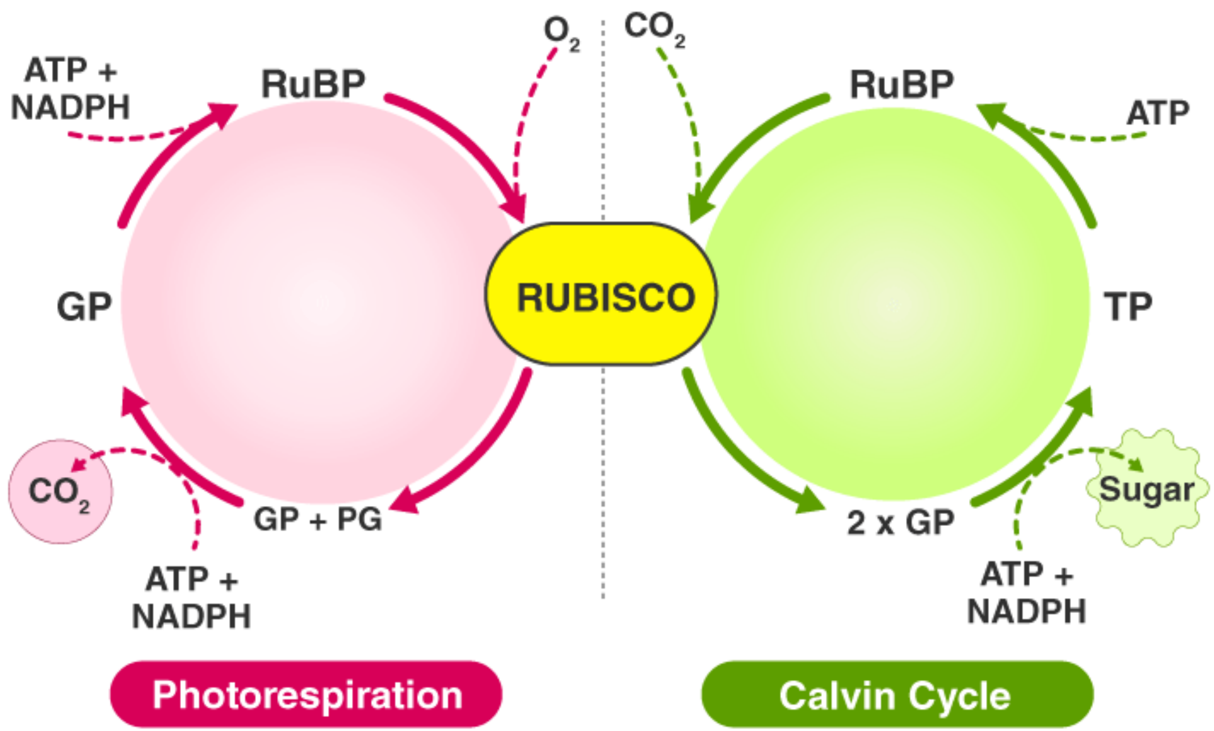


RuBisCO accounts for >40% of soluble leaf protein

The C_3 Pathway (Calvin–Benson Cycle)

Step 1: CO_2 Fixation / CO_2 固定

RuBisCO: Ribulose-1,5-bisphosphate carboxylase/oxygenase



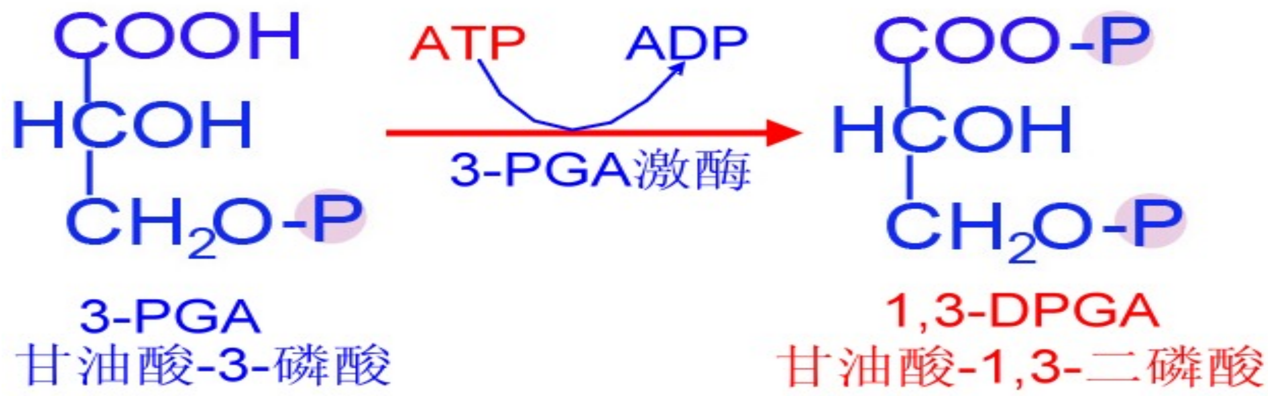
Carboxylase Activity

vs

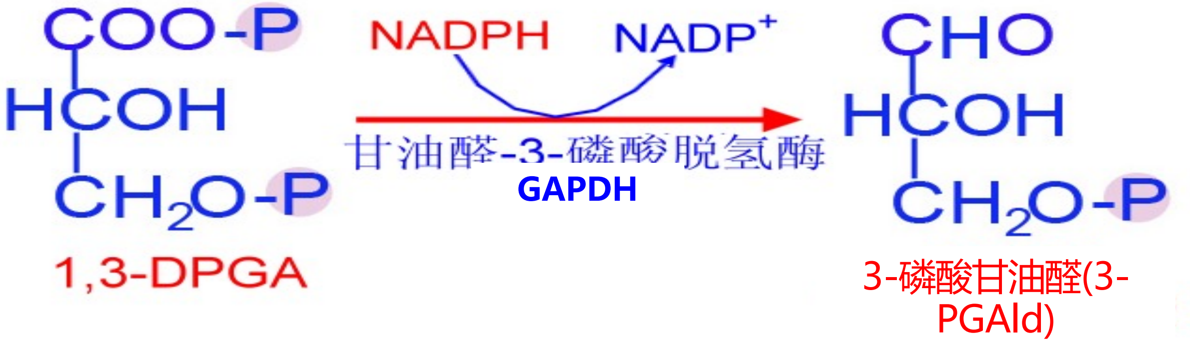
Oxygenase Activity

The C_3 Pathway (Calvin–Benson Cycle)

Step 2: Reduction / 还原



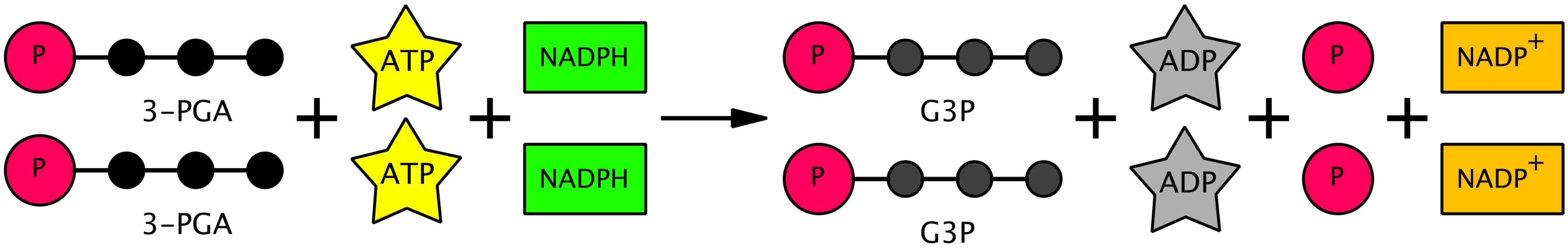
3-Phosphoglycerate **1,3-Bisphosphoglycerate**



1,3-Bisphosphoglycerate **Glyceraldehyde 3-phosphate**

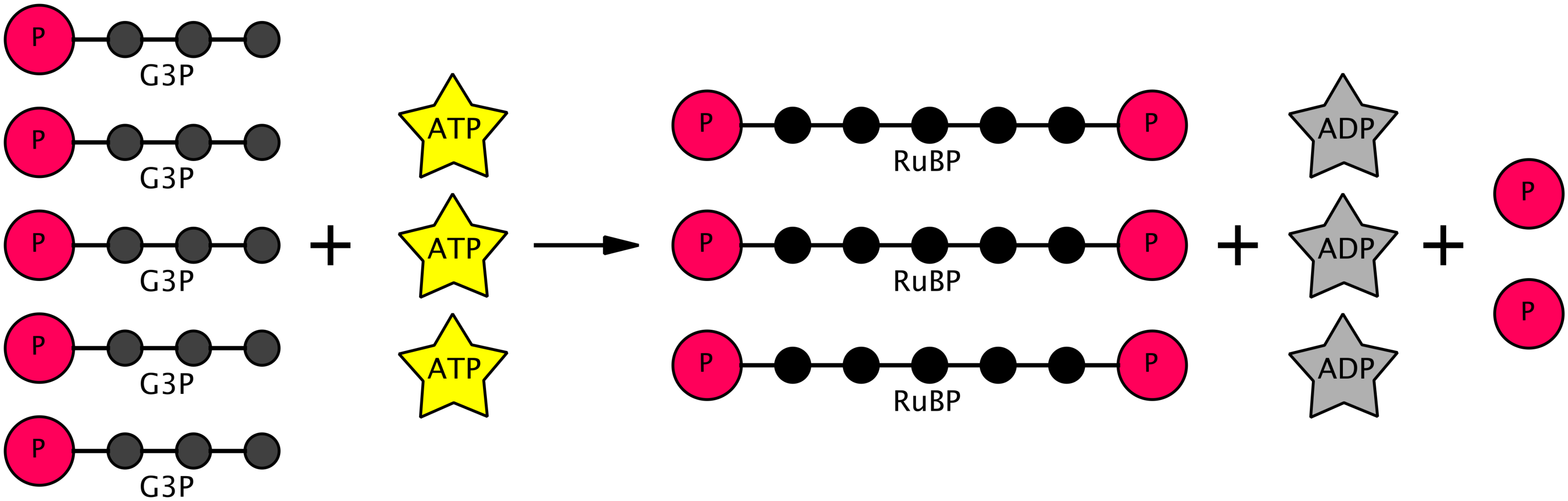
The C_3 Pathway (Calvin–Benson Cycle)

Step 2: Reduction / 还原



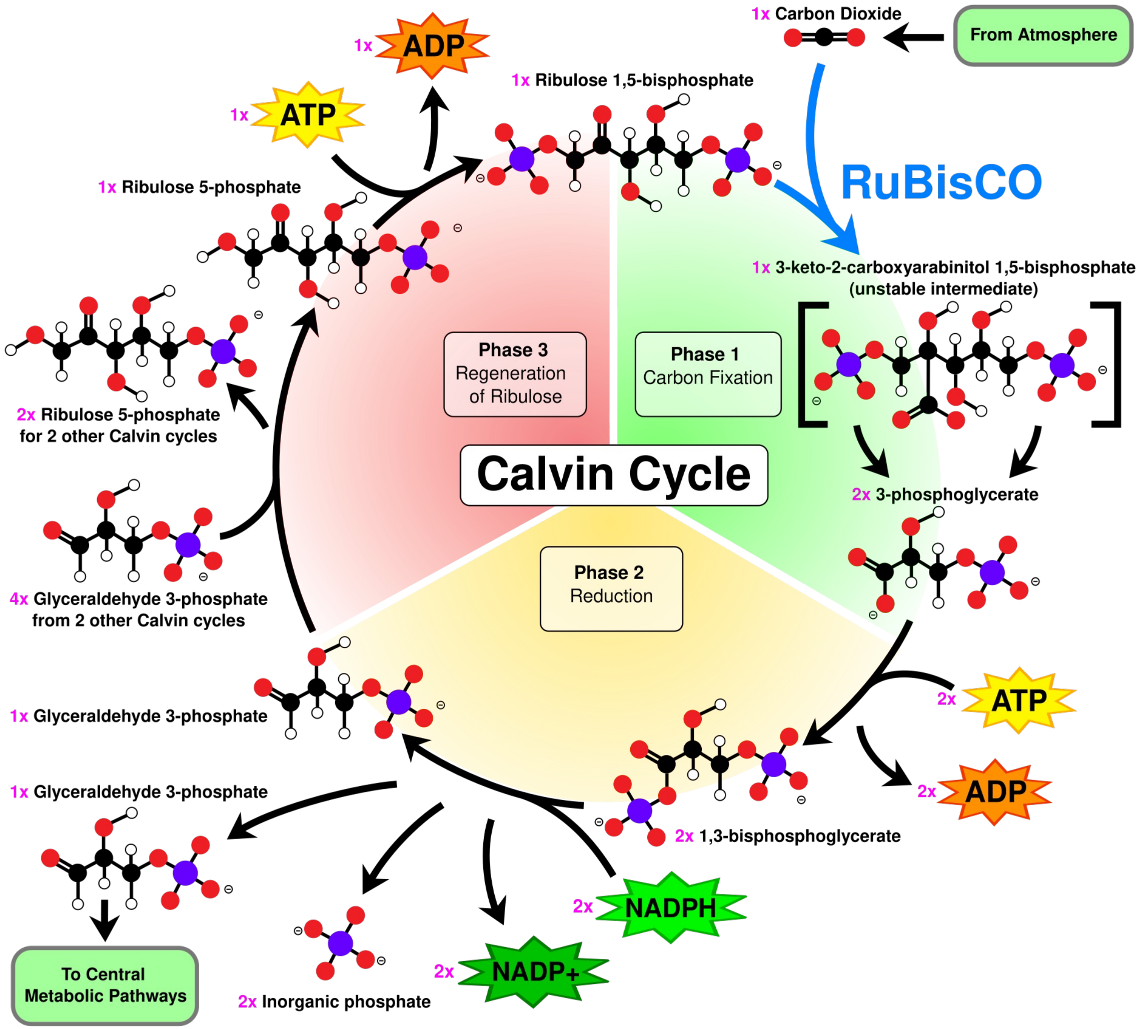
The C_3 Pathway (Calvin–Benson Cycle)

Step 3: RuBP Regeneration / RuBP 再生



Five G3P molecules produce three RuBP molecules, using up three molecules of ATP.

The C_3 Pathway (Calvin–Benson Cycle)



- ❖ **6C sugars ($C6H12O6$) are not products of the Calvin cycle!**
- ❖ The carbohydrate products of the Calvin cycle are three-carbon sugar phosphate molecules, or "triose phosphates", namely, glyceraldehyde-3-phosphate (G3P)

The sum of reactions in the Calvin cycle

$3\ CO_2 + 6\ NADPH + 9\ ATP + 6\ H^+$

$\downarrow$

$G3P + 6\ NADP^+ + 9\ ADP + 3\ H_2O + 8\ Pi$

- For every 1 mol CO_2 assimilated, the Calvin cycle consumes: **3 mol ATP + 2 mol NADPH**
- Reduction of 3 mol CO_2 produces: 1 mol triose phosphate as net output.

Regulation of the C_3 Pathway (Calvin Cycle)

1. Autocatalytic Regulation (Self-Regulation)/ 自动催化调节

- ❖ The cycle maintains a steady-state pool of intermediates (especially RuBP)
  - ✓ Regeneration of RuBP ensures continuous CO_2 fixation
  - ✓ Flux depends on: Availability of intermediates and enzyme activities

2. Light Regulation/ 光调节 (关键调控机制)

- ❖ Light reactions pump H^+ into lumen (pH increase)
- ❖ Counter-ion movement from lumen into stroma (Mg^{2+} increase)
- ❖ Key Light-Activated Enzymes: RuBisCO (via RuBisCO activase), GAPDH, FBPase (fructose-1,6-bisphosphatase), and SBPase

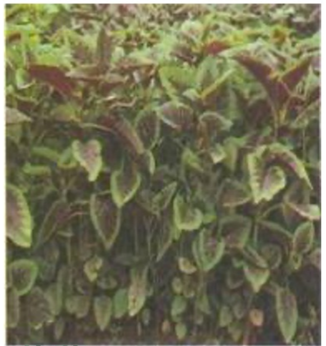
3. Regulation of Triose Phosphate Export / 光合产物输出速率的调节

- ❖ Triose phosphate/phosphate translocator (TPT): Exports G3P/DHAP to cytosol and Imports Pi into chloroplast

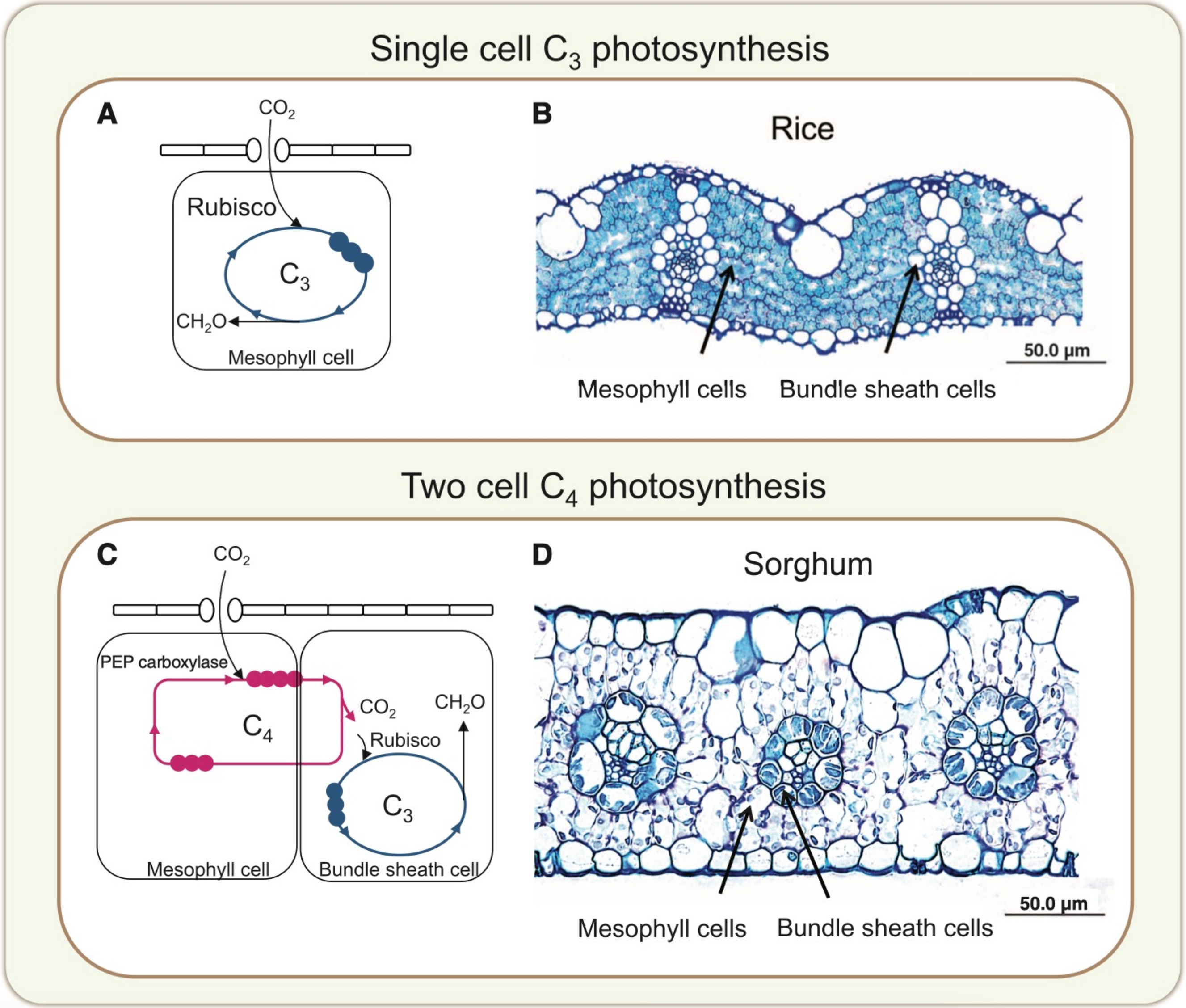
C_4 Pathway (Hatch–Slack pathway)

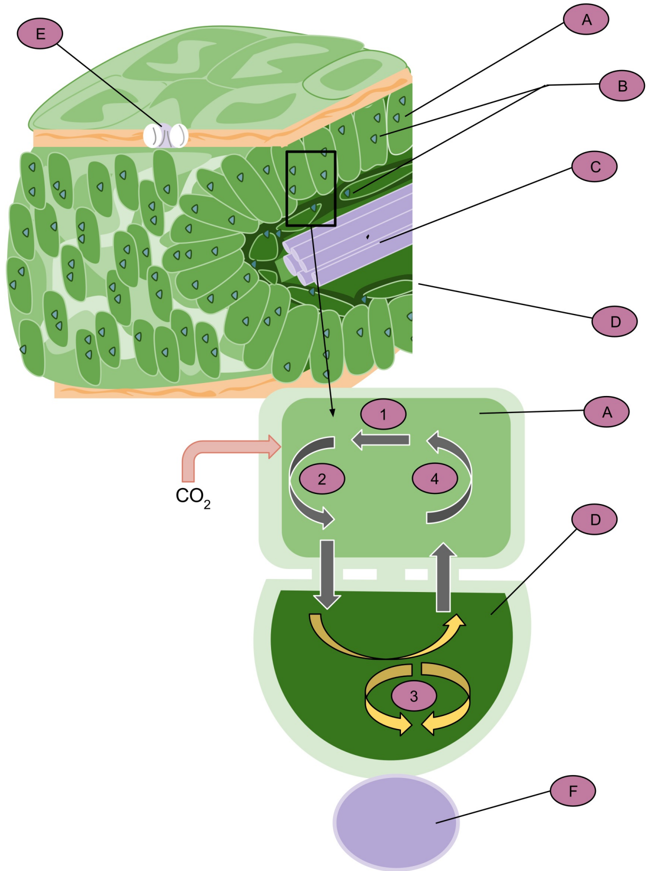
A photosynthetic carbon fixation pathway in which phosphoenolpyruvate (PEP) acts as the initial CO_2 acceptor, forming a four-carbon compound (oxaloacetate, OAA), followed by transport and decarboxylation to supply CO_2 to the Calvin cycle.

甘蔗(sugarcane)



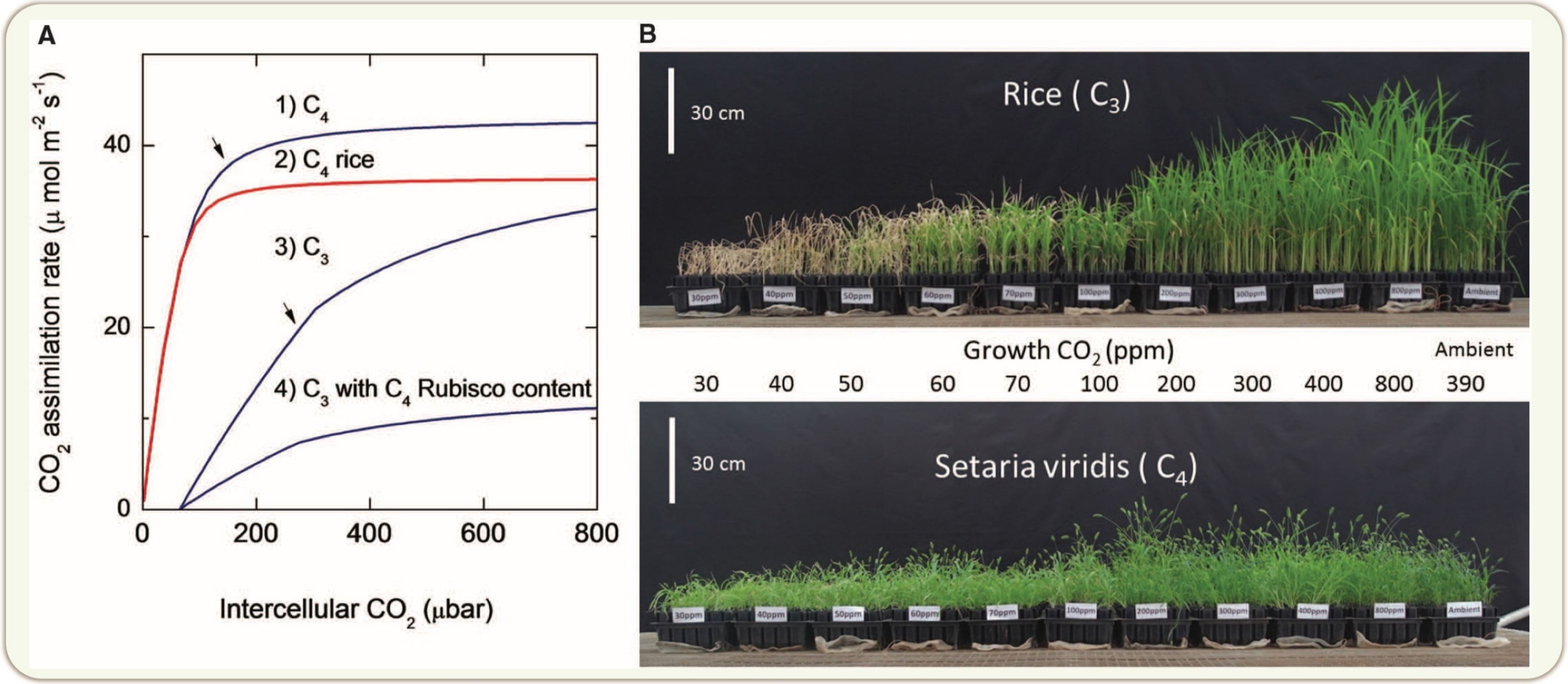
苋菜(amaranth)





Caemmerer et al., 2012

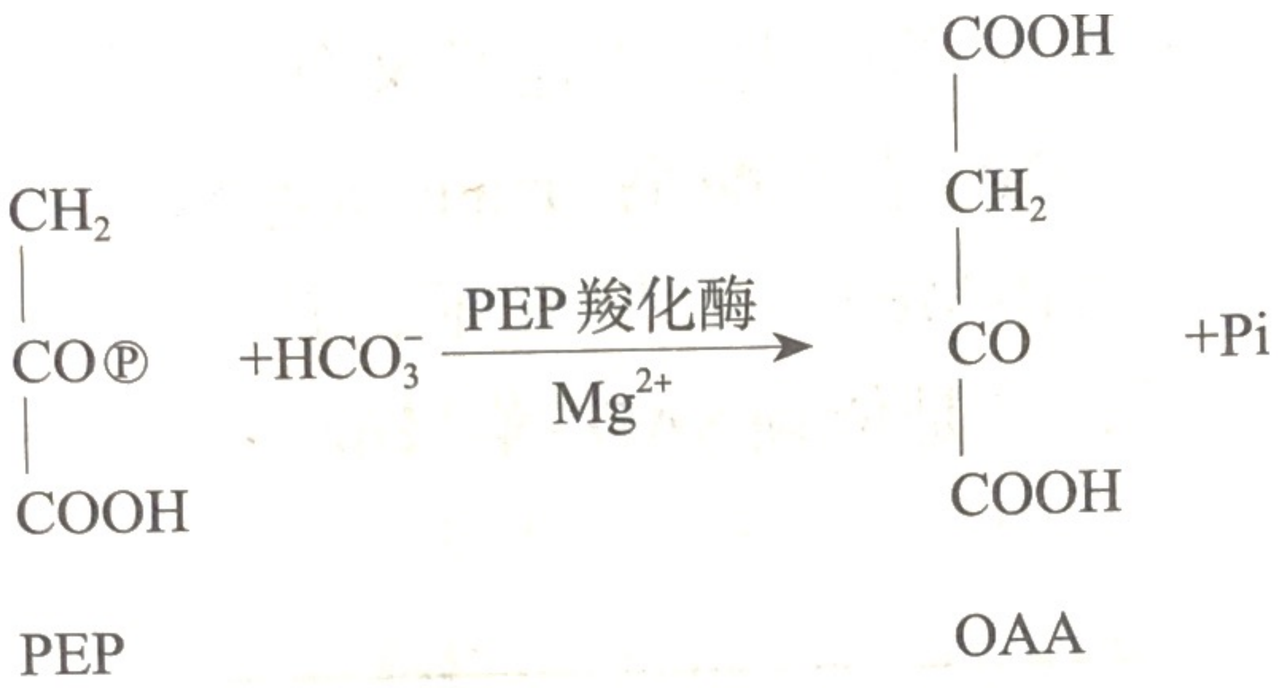
Plant Metabolism



Caemmerer et al., 2012

C_4 Pathway (Hatch–Slack pathway)

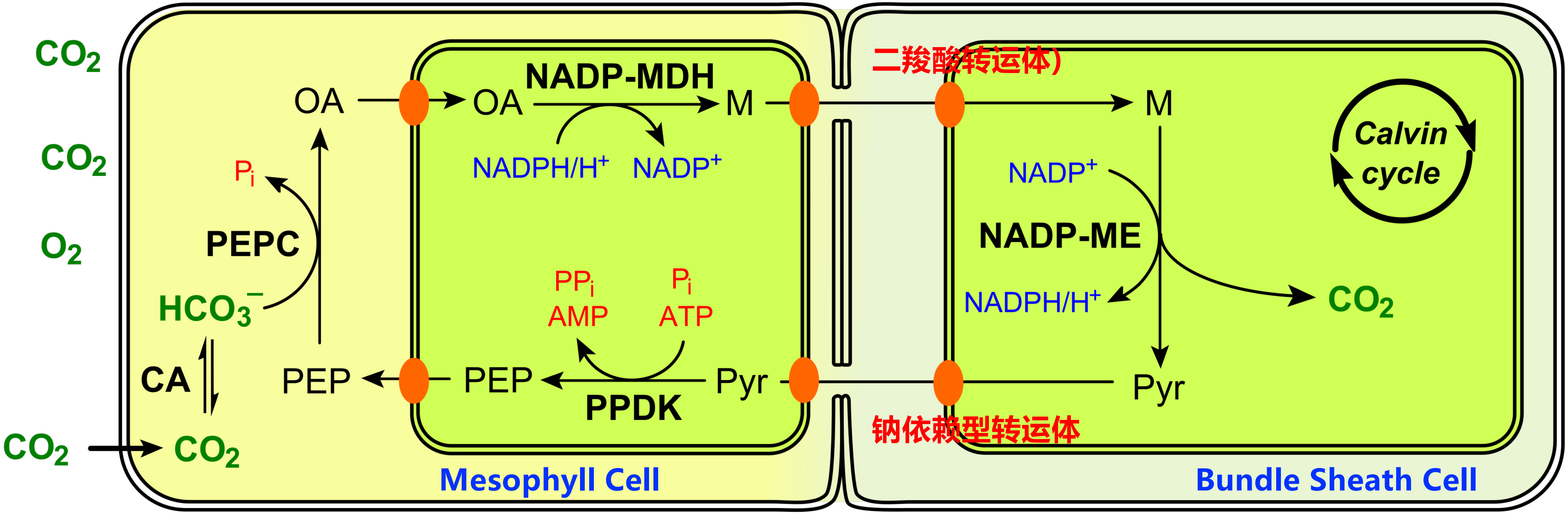
Step 1: CO_2 Fixation in Mesophyll



C_4 Pathway (Hatch–Slack pathway)

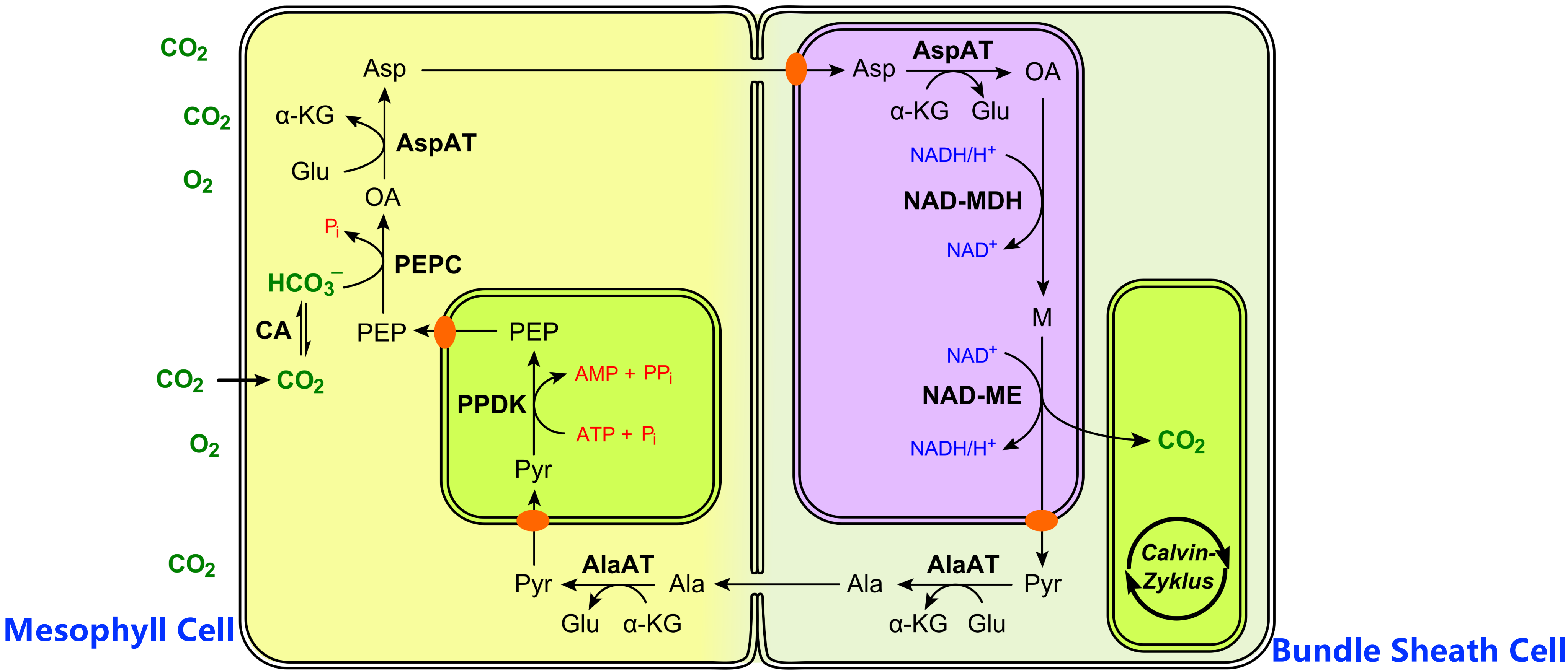
NADP-ME / NADP-苹果酸酶型

Corn, Sugarcane, Sorghum



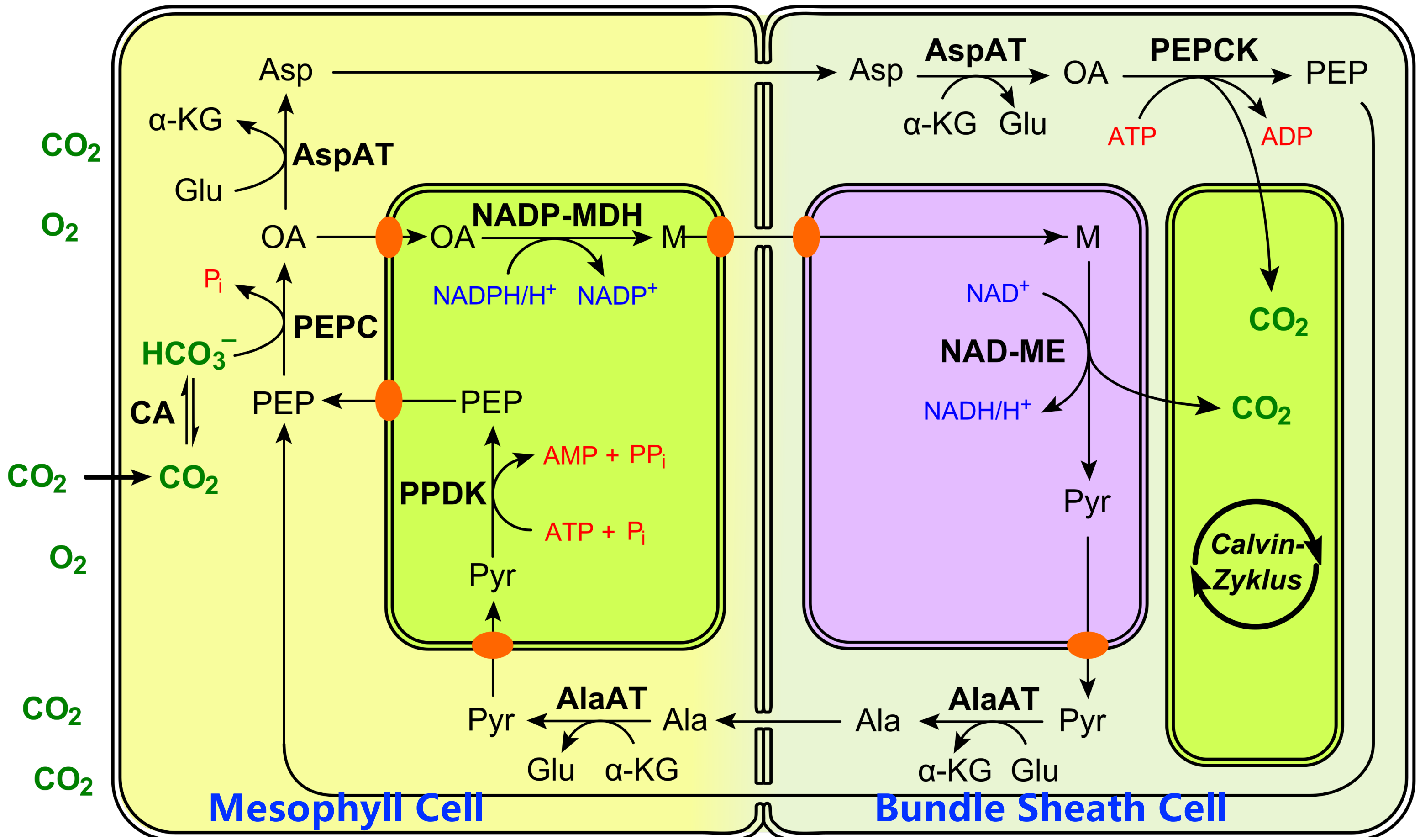
C_4 Pathway (Hatch–Slack pathway)

NAD-ME / NAD - 苹果酸酶型



C_4 Pathway (Hatch–Slack pathway)

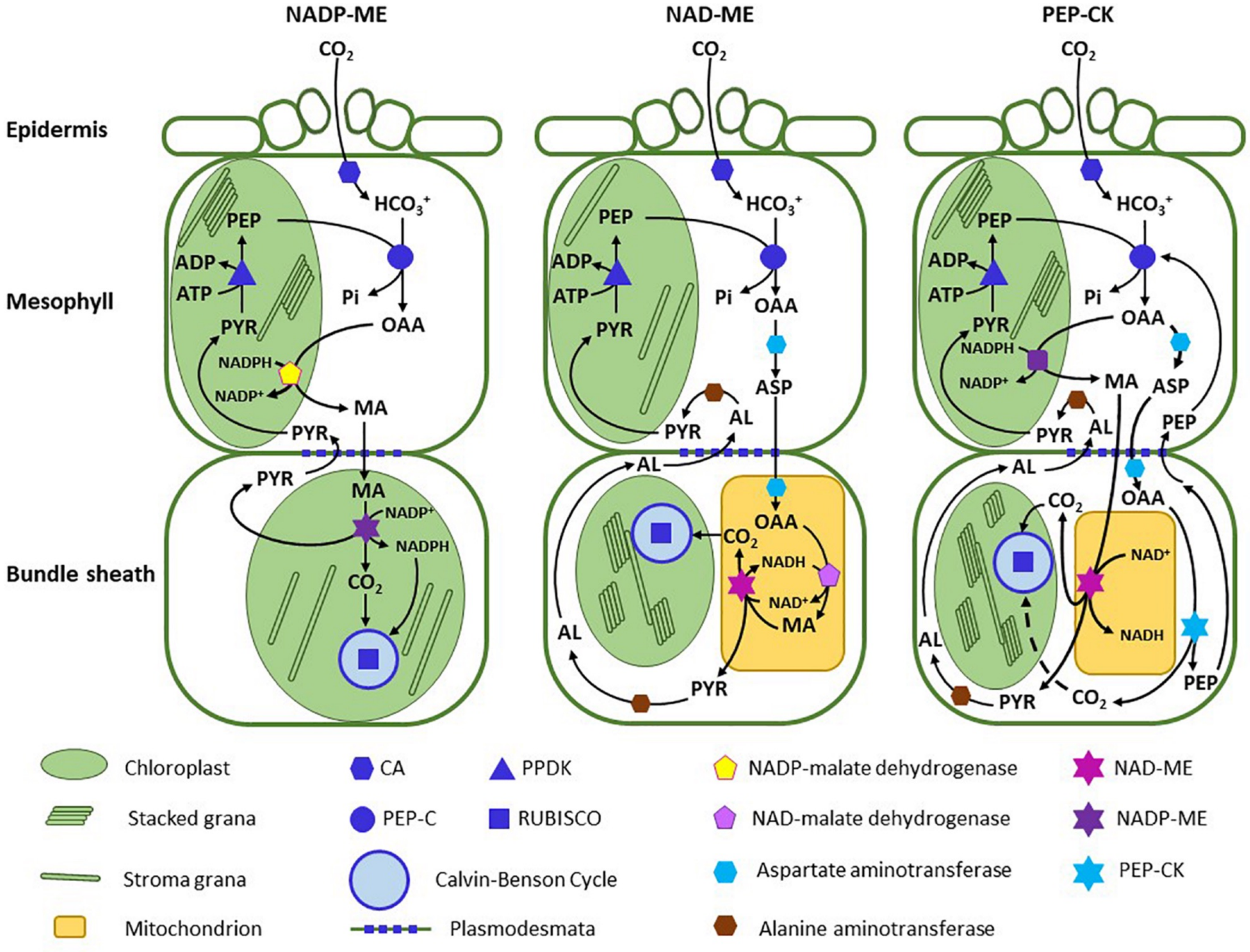
PEPCK / PEP羧化激酶型



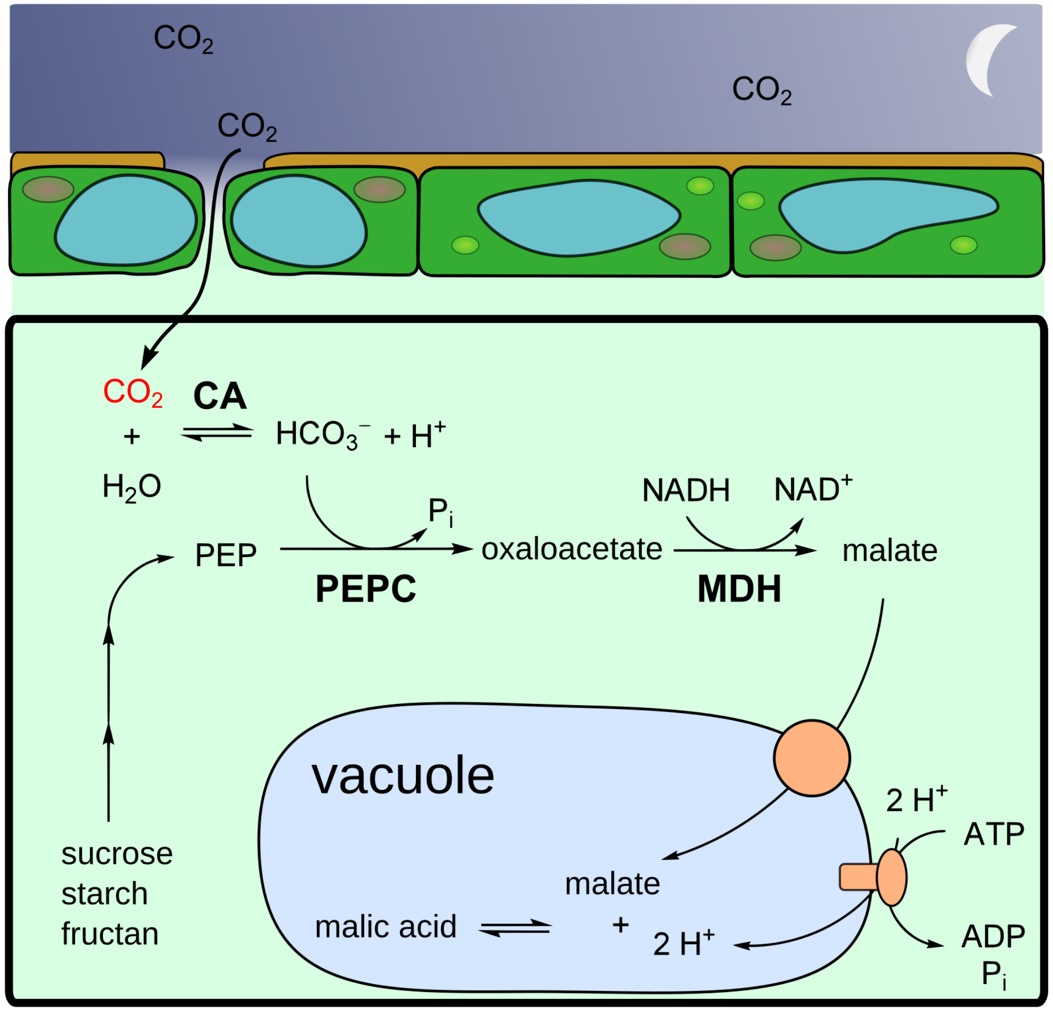
C_4 Pathway (Hatch–Slack pathway)

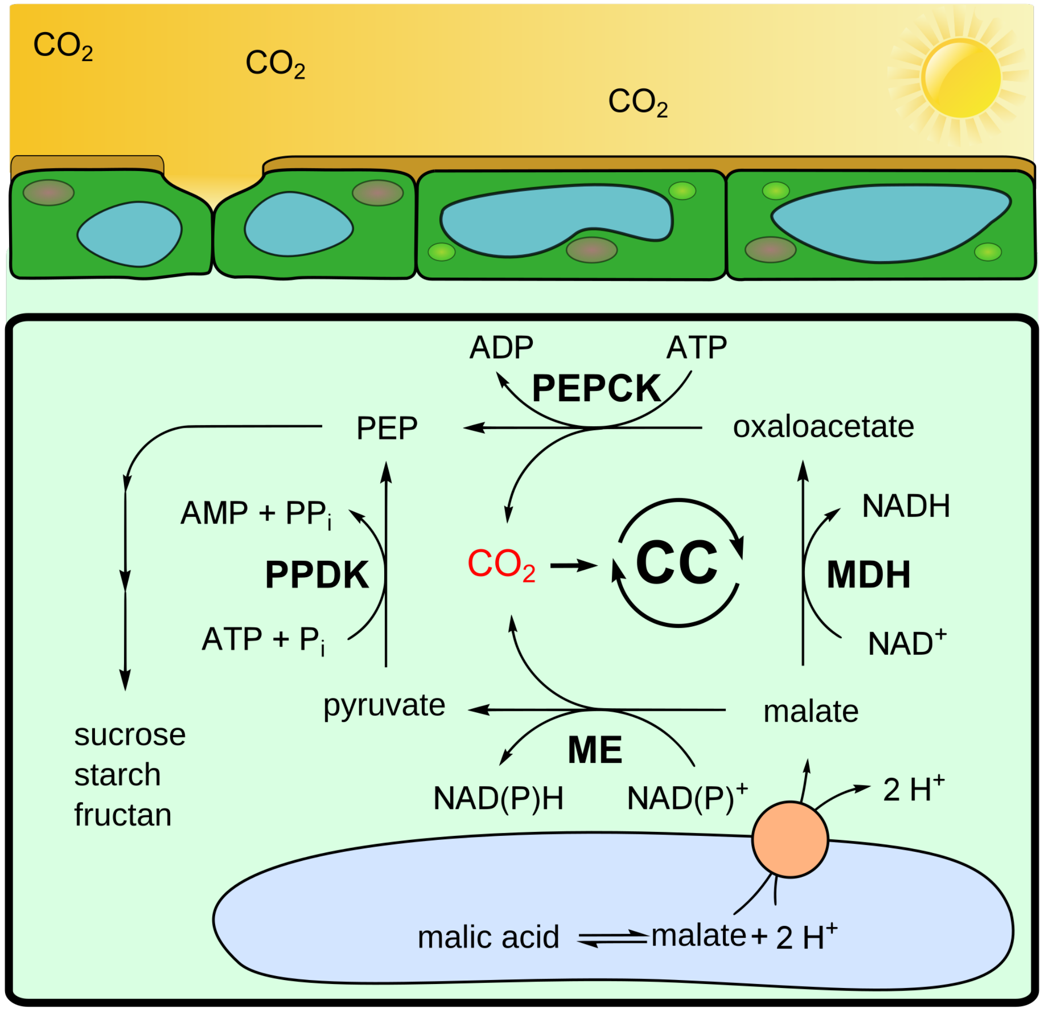
Subtype	BSC release CO_2
NADP-ME	Mal → Mal —叶绿体→ Pyr + CO_2 ($NADP^+$ → NADPH)
NAD-ME	Asp → Mal —线粒体→ Pyr + CO_2 (NAD^+ → NADH)
PEPCK	Asp → OAA —细胞质→ PEP + CO_2 (ATP → ADP)

C_4 Pathway (Hatch–Slack pathway)



CAM photosynthesis / 景天科酸代谢途径

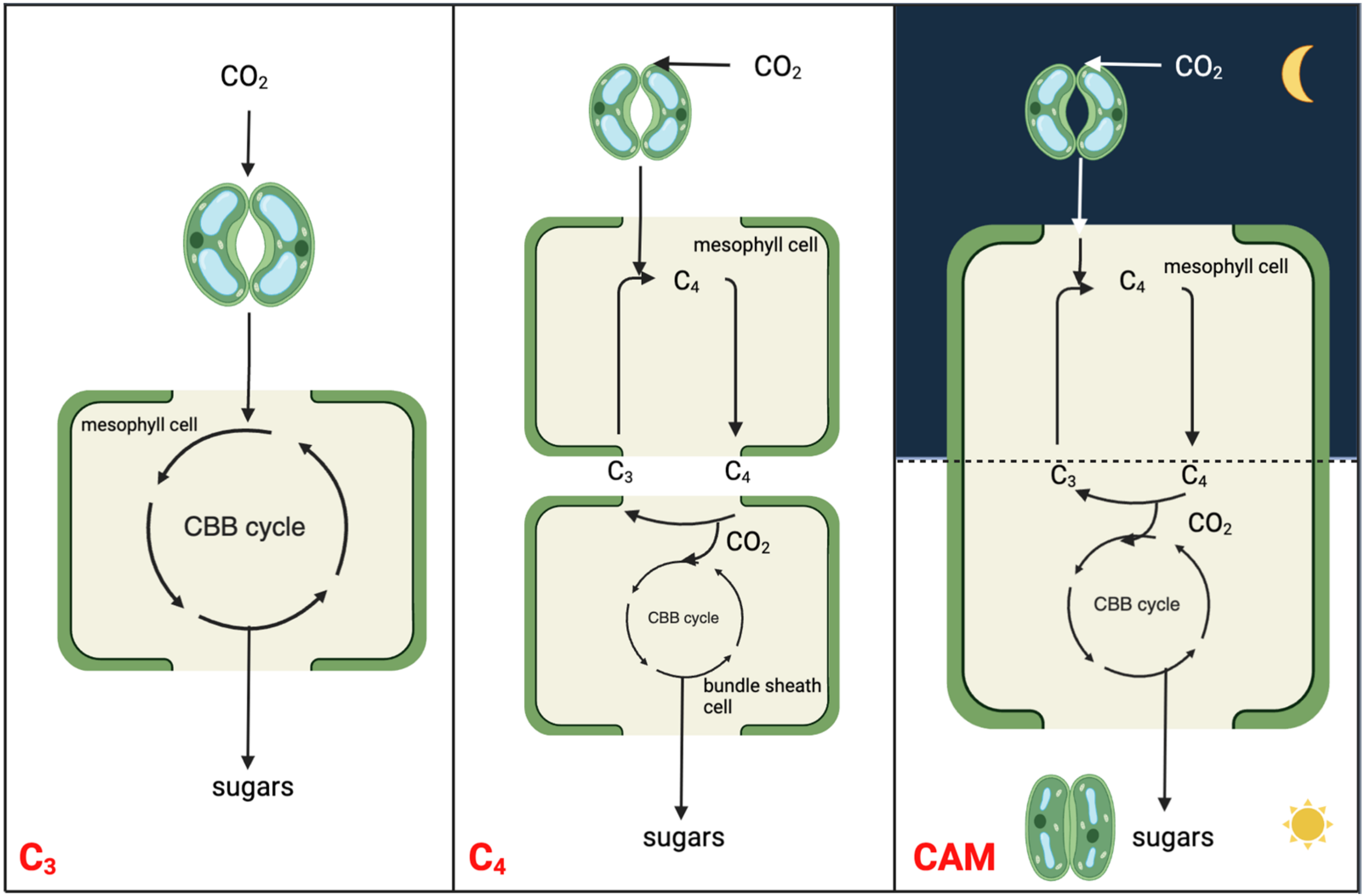




CAM photosynthesis / 景天科酸代谢途径

- **During the night**, CAM plants have their stomata open, which allows CO_2 to enter and be fixed as organic acids by a PEP reaction similar to the C_4 pathway. The resulting Mal are stored in vacuoles for later use.

- **During the day**, the stomata close to conserve water, and the CO_2-storing organic acids are released from the vacuoles of the mesophyll cells. An enzyme in the stroma of chloroplasts releases the CO_2, which enters into the Calvin cycle so that photosynthesis may take place.

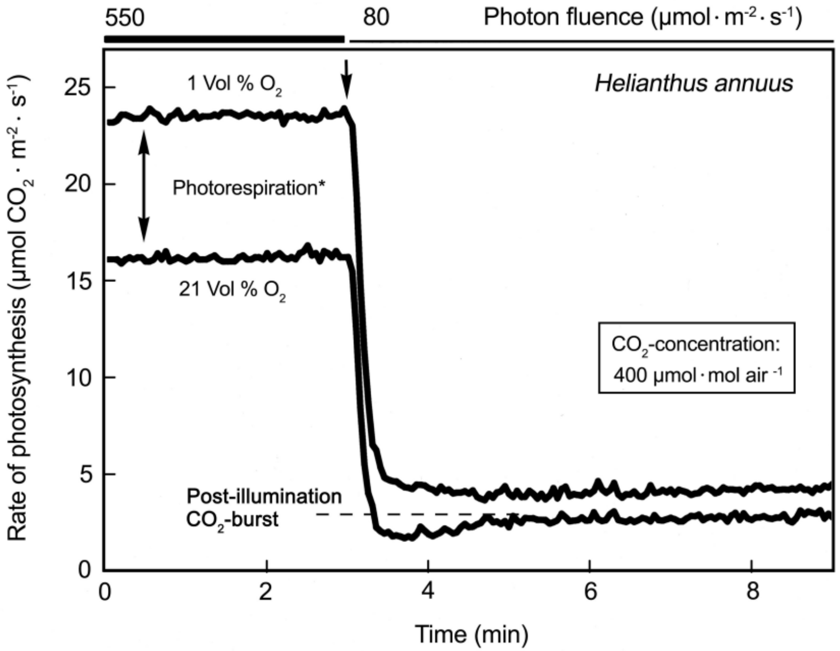


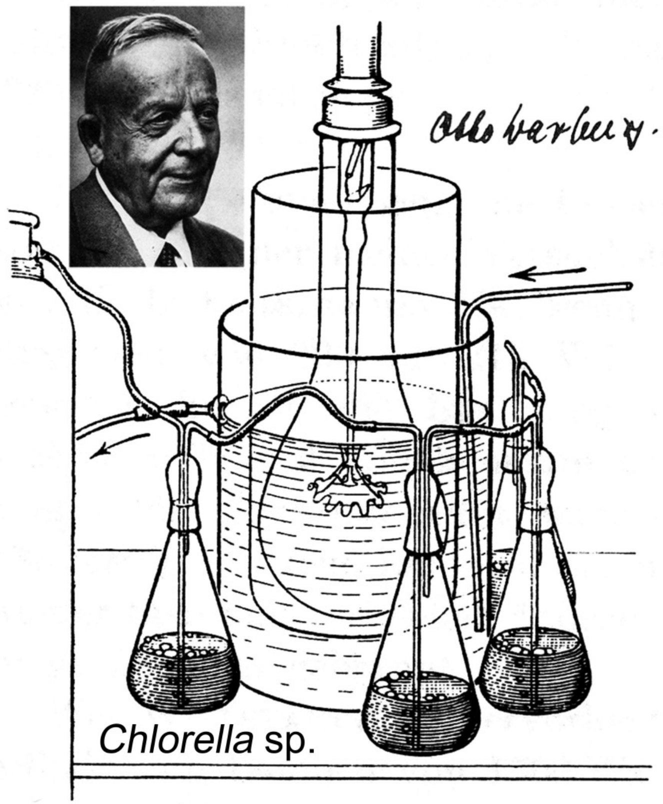
CO_2
mesophyll cell
CBB cycle
sugars
C_3
CO_2
mesophyll cell
C_4
C_3
C_4
CO_2
CBB cycle
bundle sheath cell
sugars
C_4
CO_2
mesophyll cell
C_4
C_3
C_4
CO_2
CBB cycle
sugars
CAM

Comparison of photosynthetic pathways

Feature	C_3 Plants	C_4 Plants	C_3–C_4 Intermediates	CAM Plants
Bundle Sheath Cells (BSC)	Poorly developed	Well developed	Moderately developed	Poorly developed
Chloroplasts in BSC	Absent (or very few)	Present	Present	Generally absent; cells rich in mitochondria
Leaf Anatomy	Mesophyll cells loosely arranged; **no Kranz anatomy**	Mesophyll cells tightly arranged around BSC; **Kranz anatomy present**	BSC present but thinner cell walls than C_4 plants	Large vacuoles in mesophyll cells
Special Structural Feature	No spatial separation of processes	Clear spatial separation (mesophyll vs bundle sheath)	Partial characteristics of both C_3 and C_4	Temporal separation (night/day metabolism)

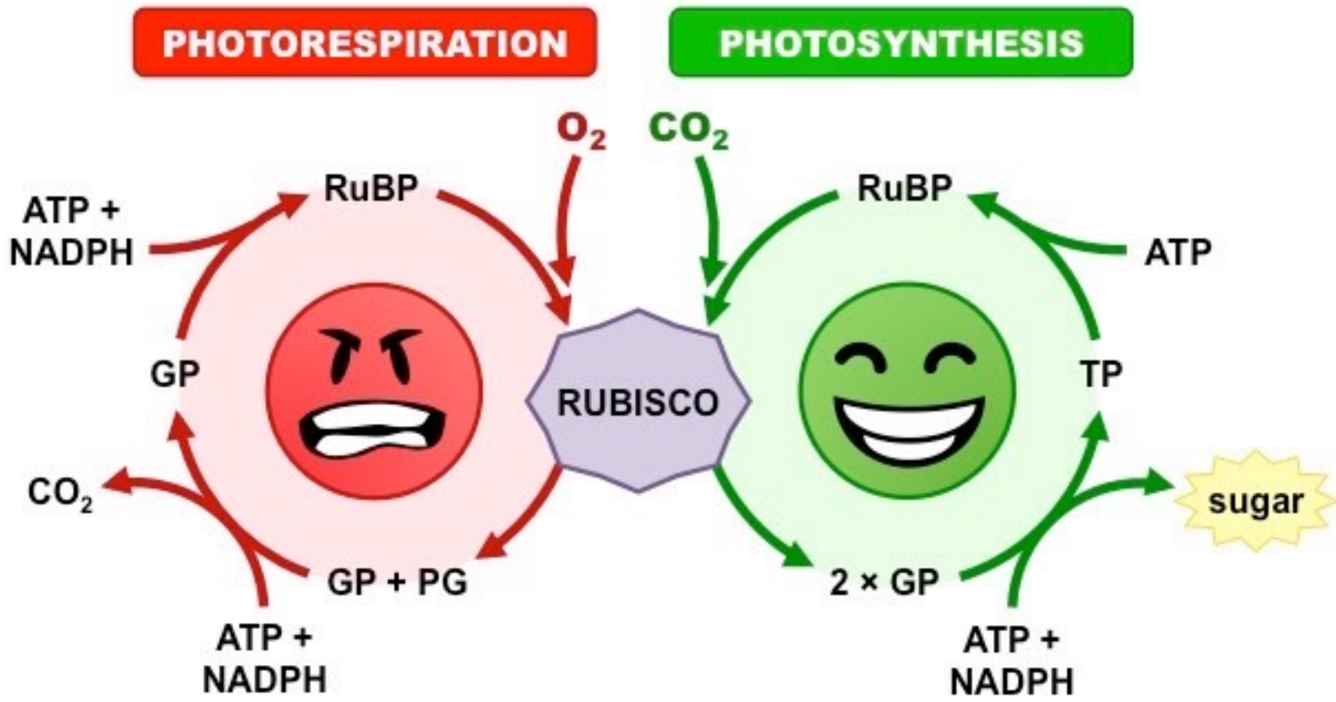
1920, Otto Warburg discovered that in liquid cultures of unicellular green algae (Chlorella sp.) molecular oxygen (O_2) exerts an inhibitory effect on photosynthesis. It is late known due to photorespiration / 光呼吸.

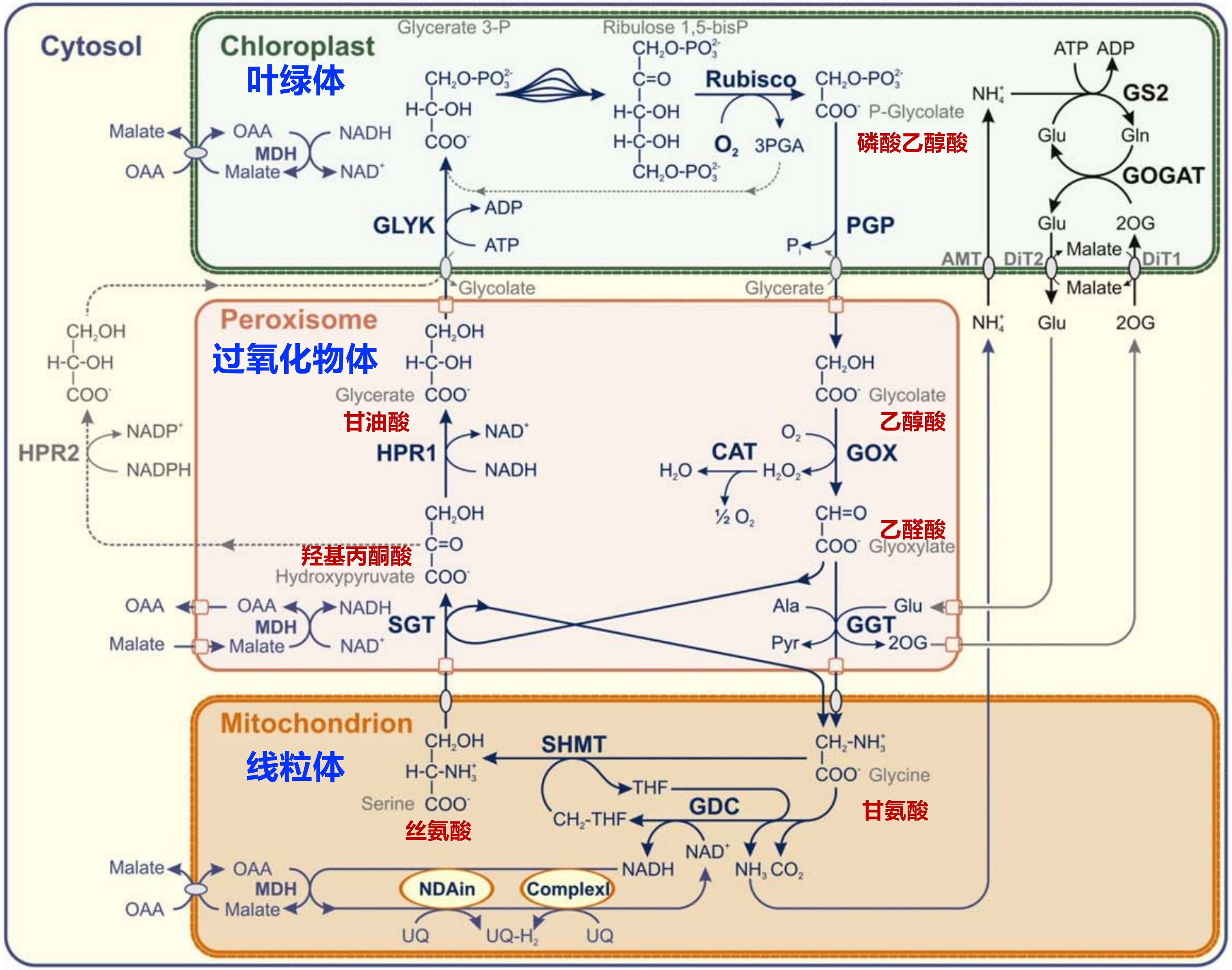




Photorespiration

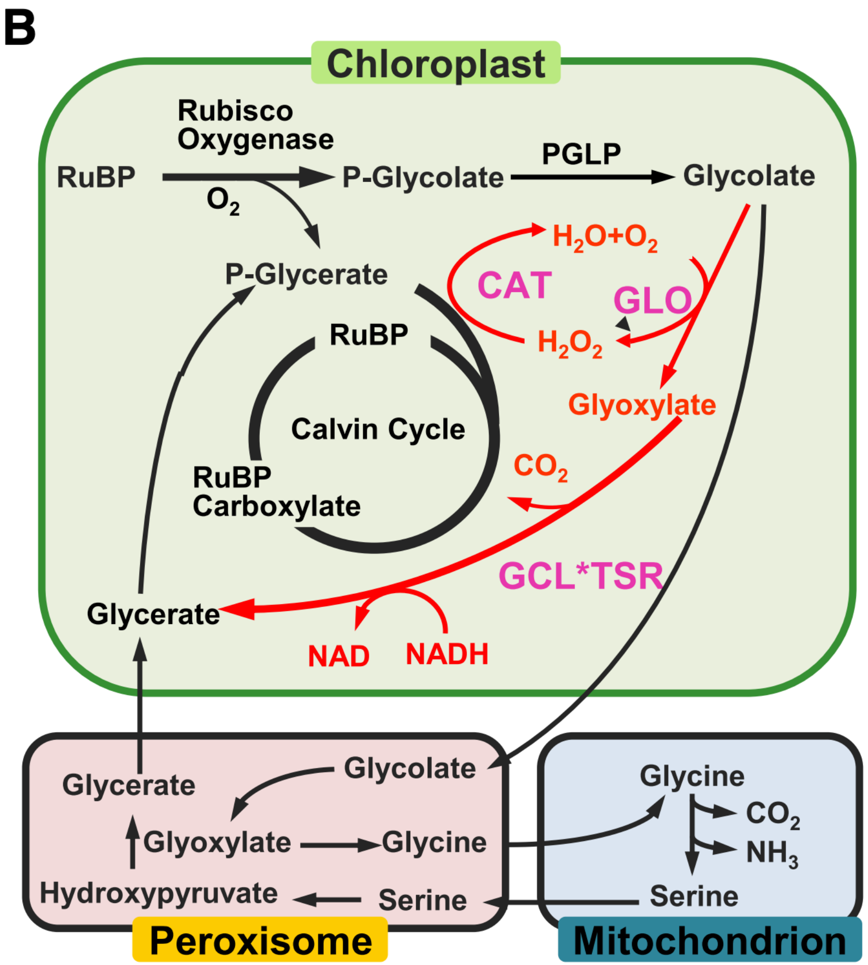
A light-dependent metabolic process in which RuBisCO oxygenates RuBP, leading to O_2 consumption and CO_2 release, without production of sugars.





- Photorespiration involves **three organelles**: **Chloroplast, Peroxisome, Mitochondrion**
- **O_2 consumption** occurs in **chloroplast and peroxisome**
- **CO_2 release** occurs mainly in **mitochondria**
- **Carbon Loss:** For every **2 glycolate molecules 1 CO_2 released** (**25%**)

Photorespiratory pathway redesign



彭新湘教授

Photorespiration

Physiological Functions of Photorespiration

- **Removes 2-phosphoglycolate (toxic metabolite)**
- **Maintenance of C_3 Cycle Operation under stresses**
- **Photoprotection: Consumes excess ATP and NADPH**
- **Link to Nitrogen Metabolism: Produces Glycine (Gly), Serine (Ser), and other amino acids**

Photosynthesis in plant physiology

❖ **Photosynthetic Rate** (光合速率): the amount of CO_2 assimilated or O_2 evolved per unit time per unit leaf area.

❖ **Net vs Gross Photosynthesis**

$$P_{net} = P_{gross} - \text{Respiration}$$

❖ **Photosynthetic Productivity (NAR):** The amount of dry matter produced per unit leaf area per unit time over longer periods.

The photosynthetic equation:

Based on this equation, how could the rate of photosynthesis be measured?

Provides the carbon to produce organic compounds during the Calvin Cycle

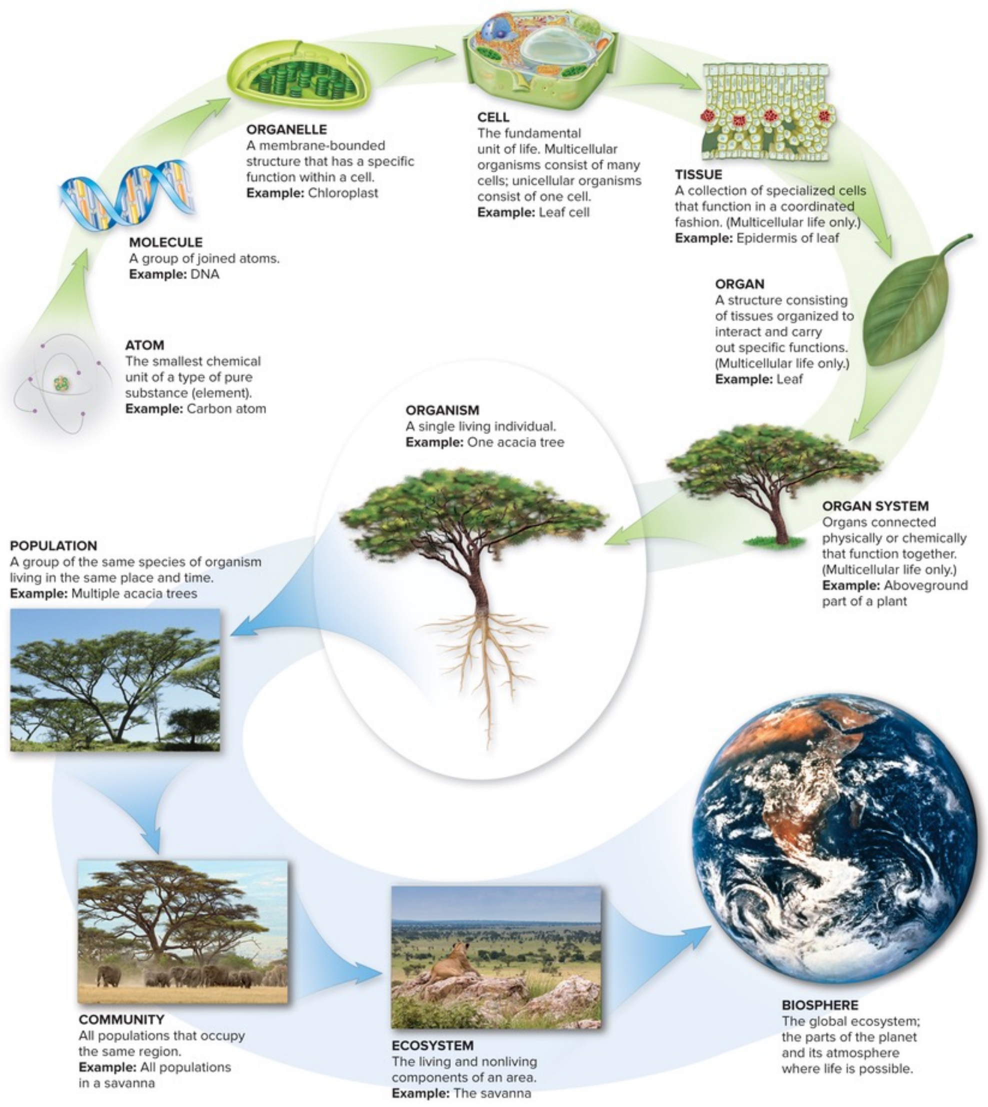
The organic compound ultimately produced during the Calvin Cycle

$$6\ H_2O + 6\ CO_2 \xrightarrow{\text{light}} 6\ O_2 + C_6H_{12}O_6$$

Split during the light reactions to replace electrons lost from PSII

Excites electrons during the light reactions

Produced as a byproduct of the splitting of water during the light reactions



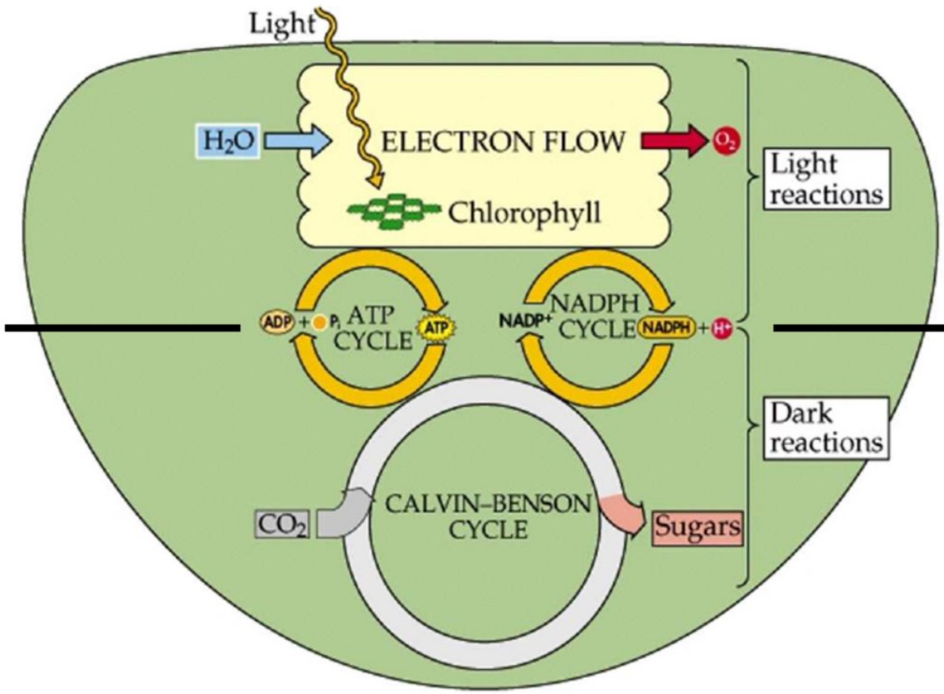
Chemistry or biochemistry approaches in tubes or *in vitro*

We focus on Leaf to canopy scales *in vivo*

Modeling (next part) or Remote sensing

How can we study these two parts of the photosynthesis process *in vivo*?

Chlorophyll fluorescence

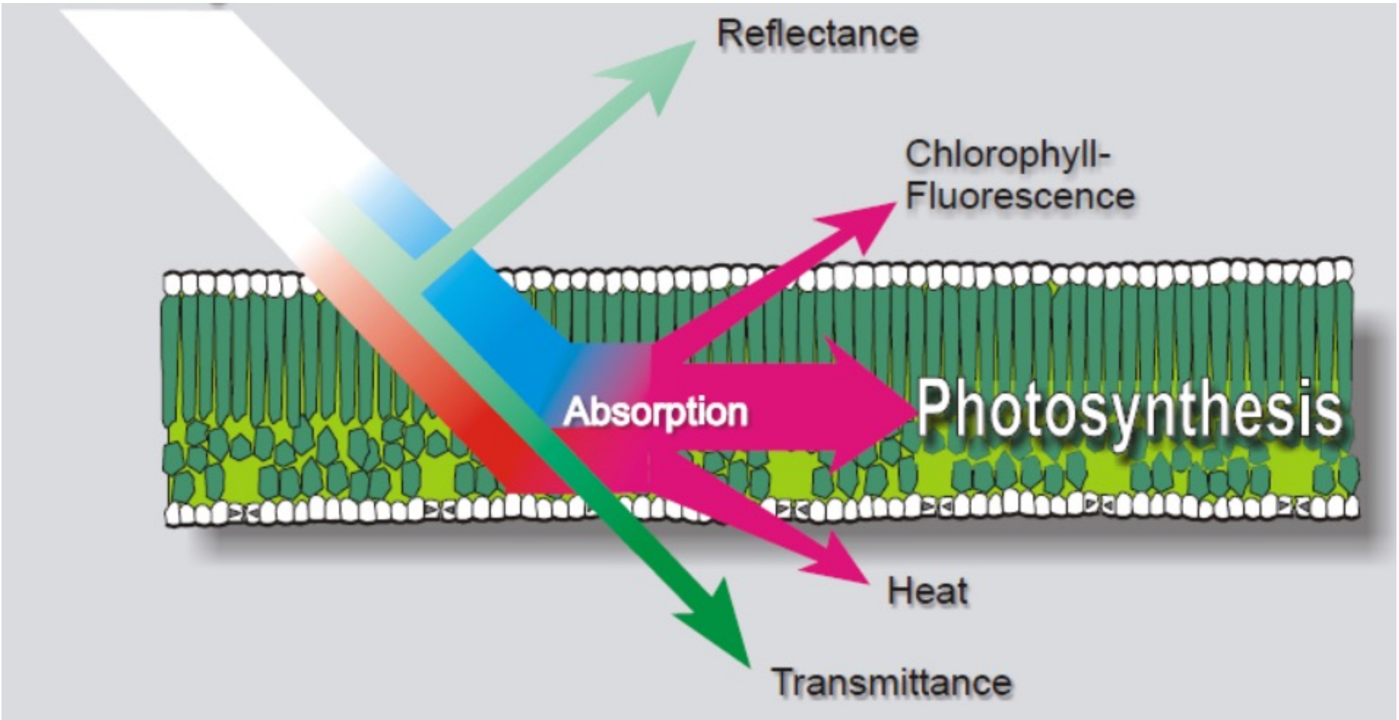


1) **Light-dependent reactions**
PHOTOCHEMISTRY.
Light energy captured by chlorophyll is (PARTLY) used for ATP and NADPH synthesis from ADP and $NADP^+$.

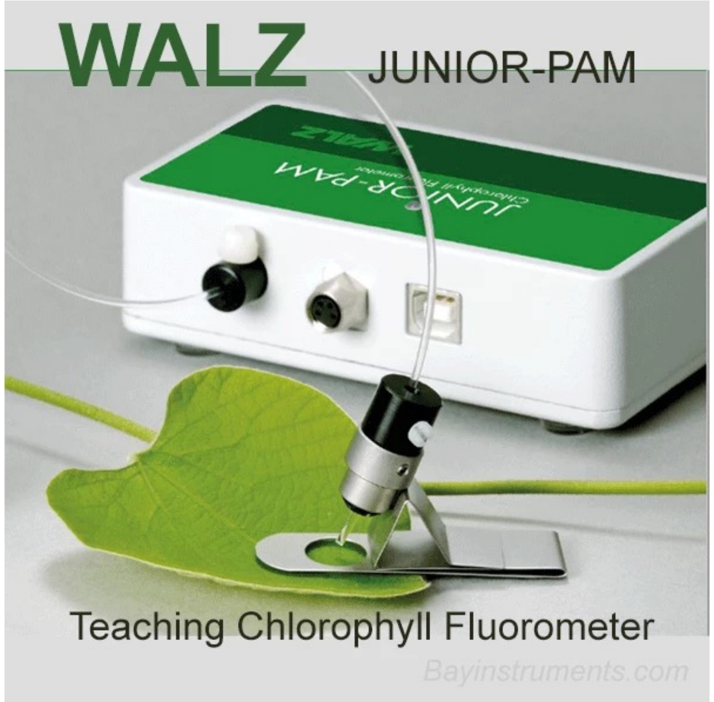
2) **Light-independent reactions**
. **BIOCHEMISTRY**.
ATP and NADPH are used to reduce and fix CO_2 generating sugars in the C-B-B cycle.

Gas exchange

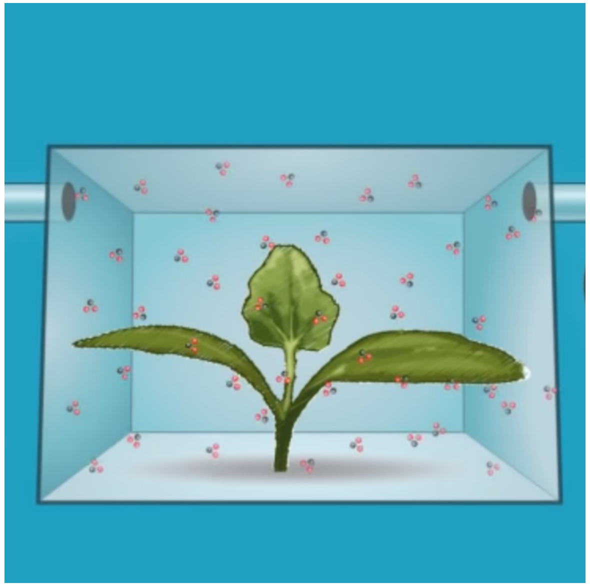
Light absorption index

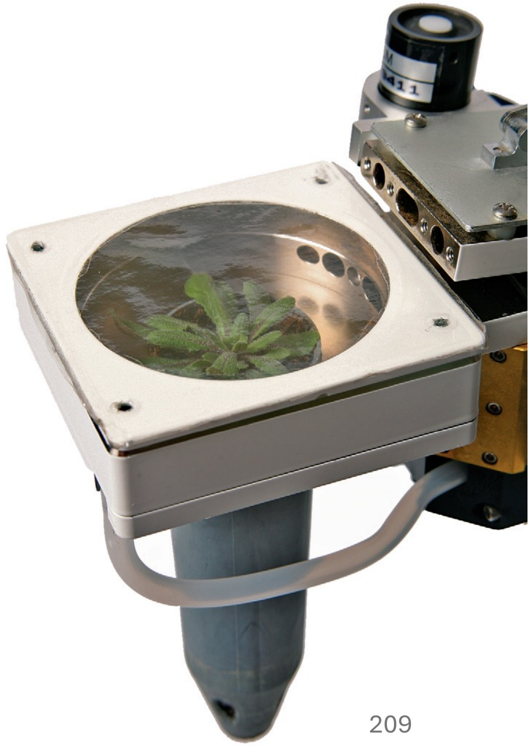


f (Photochemistry
Heat dissipation
Intensity of excitation)


WALZ
JUNIOR-PAM
Teaching Chlorophyll Fluorometer
Bayinstruments.com


WALZ
DUAL PAM 100
P700 and Chlorophyll Fluorescence Measurment

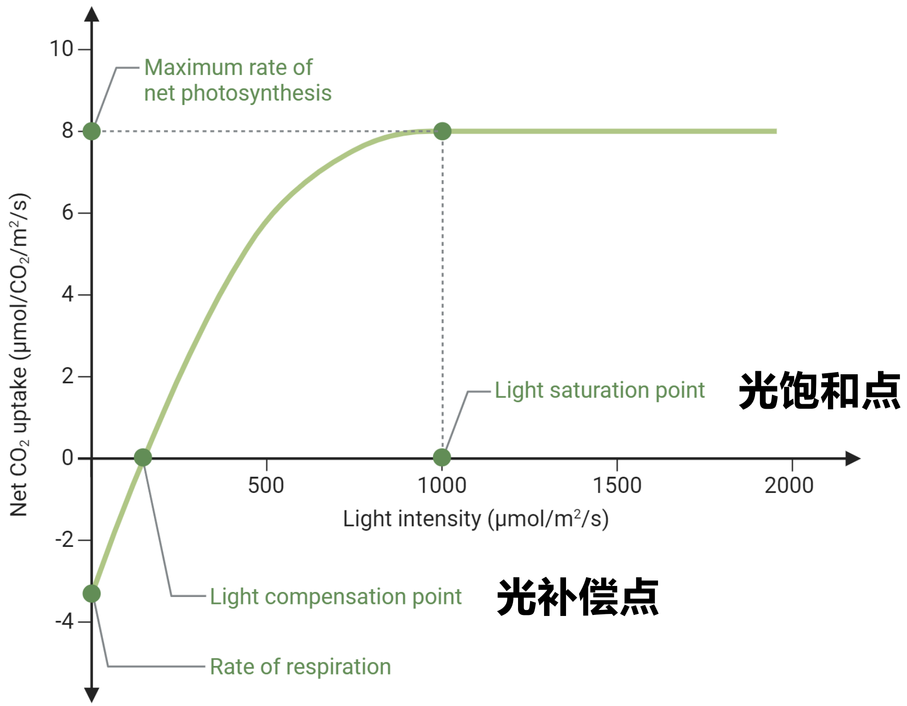




How much CO_2 consumed in unit of time is the net photosynthetic rate (typically normalized by leaf area).

Photosynthesis in plant physiology

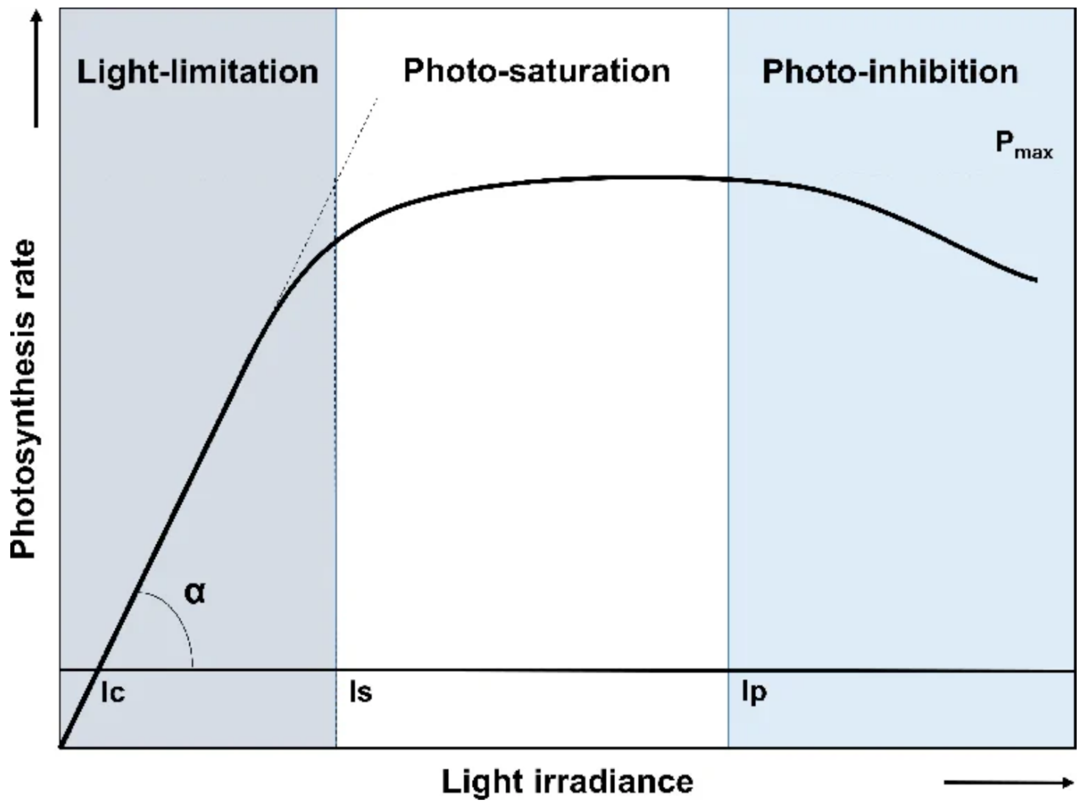
Photosynthetic Light Response Curve
Light Intensity and Plant Activity



Light Intensity

- Light is a primary factor controlling **photosynthetic rate**
- **Light Compensation Point (光补偿点):** The light intensity at which Photosynthesis = Respiration
- **Light Saturation Point (光饱和点):** The light intensity at which photosynthetic rate reaches maximum

Photosynthesis in plant physiology



Light Intensity

- **Photoinhibition**: A decrease in photosynthetic efficiency caused by excess light energy exceeding the capacity of photochemical utilization and protective mechanisms.
- **Primarily occurs in PSII**, and under special conditions (e.g., low temperature + light stress), PSI can also be affected

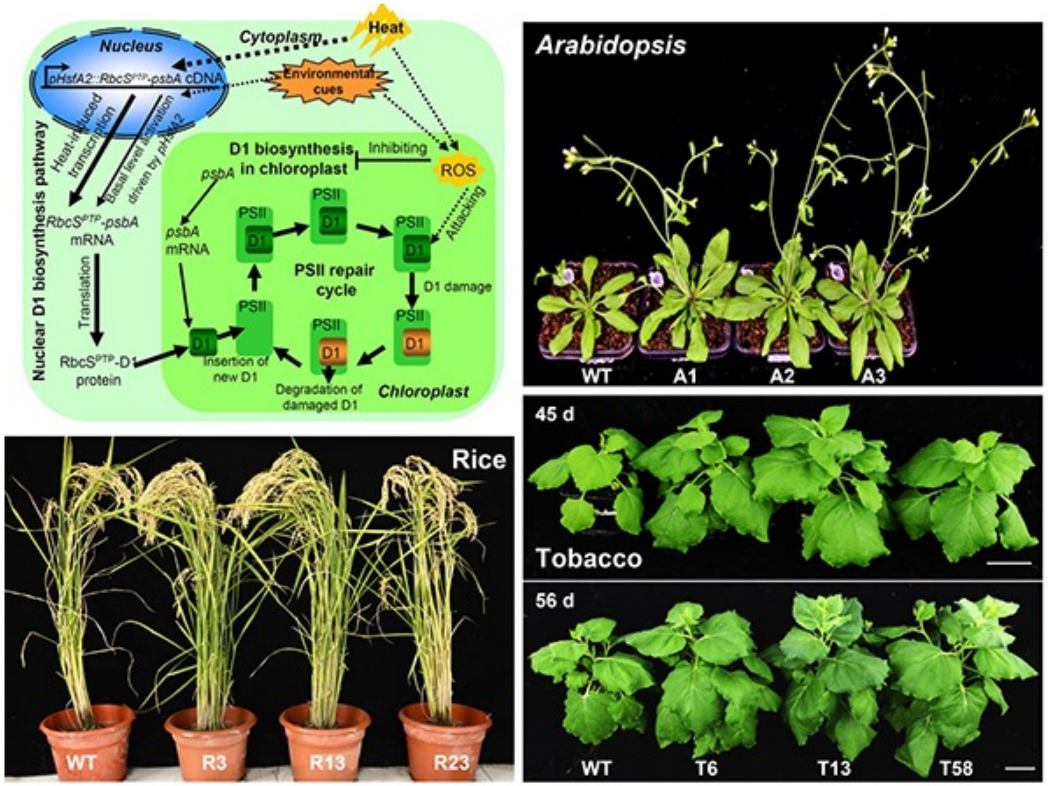
ARTICLES
https://doi.org/10.1038/s41477-020-0629-z

nature plants

Check for updates

Nuclear-encoded synthesis of the D1 subunit of photosystem II increases photosynthetic efficiency and crop yield

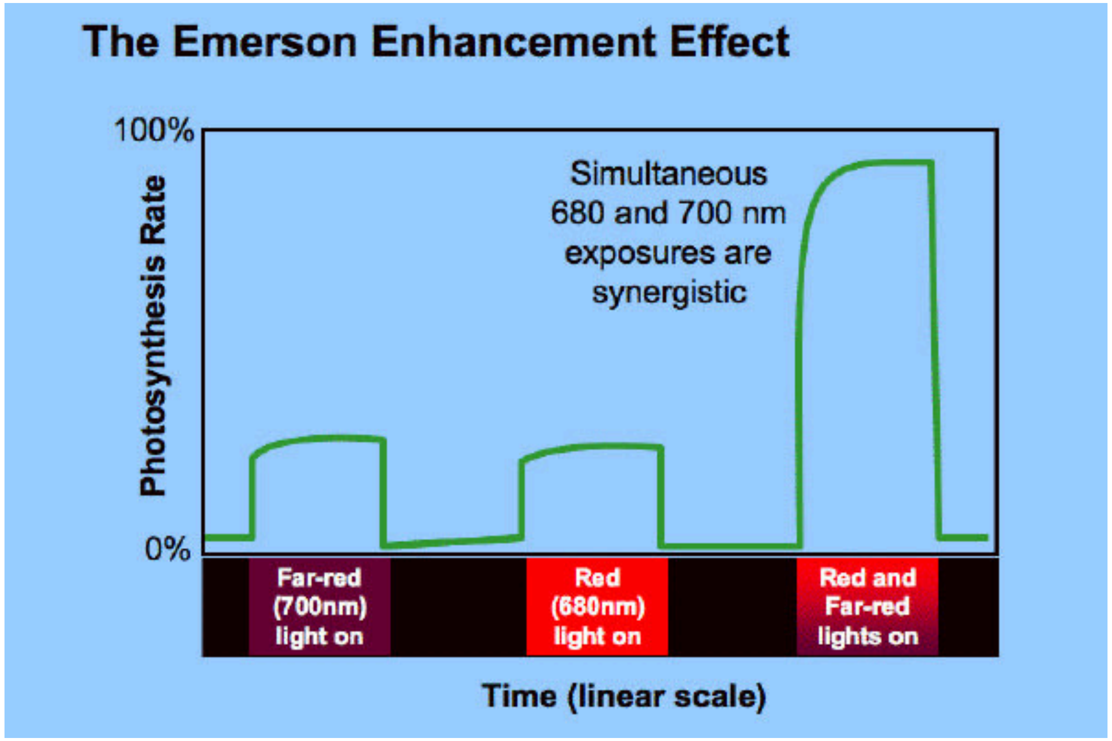
Juan-Hua Chen[1,2,3], Si-Ting Chen[1,3], Ning-Yu He[1], Qing-Long Wang[1], Yao Zhao[1,2], Wei Gao[1,2] and Fang-Qing Guo[1]✉



Photosynthesis in plant physiology

Light quality

Emerson Enhancement Effect (爱默生效应)



Observation (Emerson, 1957)

- Red light (~650 nm) → moderate photosynthesis
- Far-red light (~700 nm) → low photosynthesis
- **Both together → much higher than sum**

Photosynthesis in plant physiology

Light quality

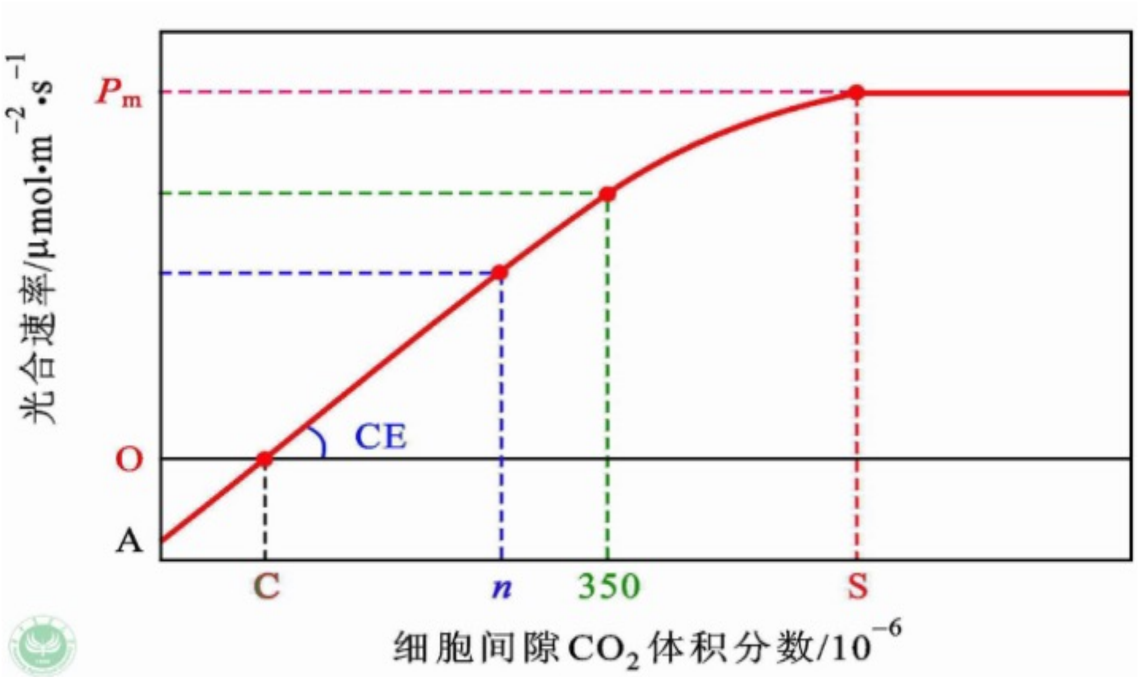
Red Drop Phenomenon (红降现象)

When wavelength > 685 nm (far-red light), the photosynthetic efficiency drops sharply

- **Quantum Yield (量子产额):** The number of O_2 molecules evolved (or CO_2 molecules fixed) per photon absorbed. Typical value is ~1/8 to 1/10 O_2 per photon
- **Quantum Requirement (量子需要量):** The number of photons required to produce 1 O_2, or Fix 1 CO_2. Typical value is 8–10 photons

Photosynthesis in plant physiology

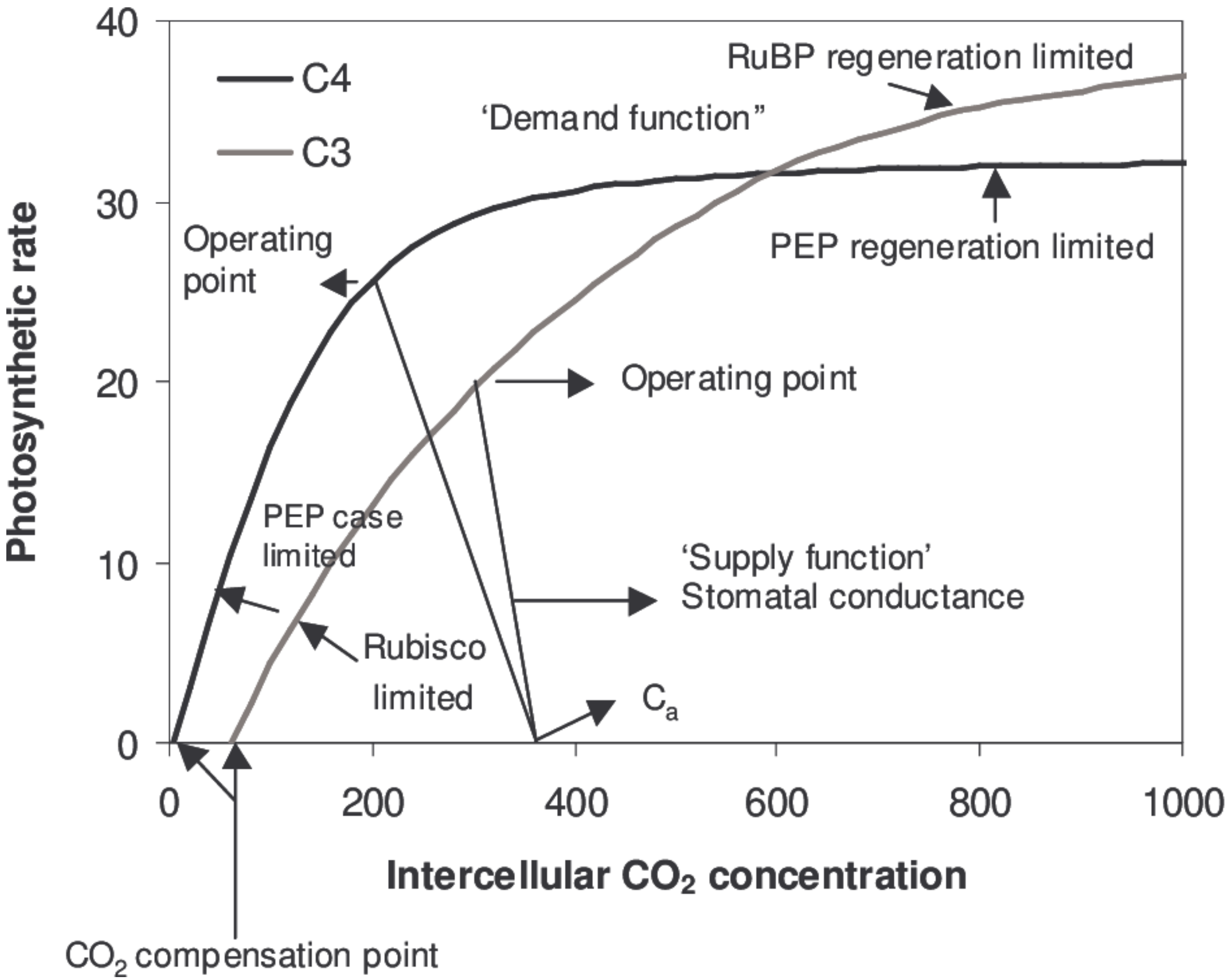
CO_2



- ❖ Carboxylation Efficiency (CE): Initial slope of CO_2 response curve
- ❖ CO_2 Compensation Point
- ❖ CO_2 Saturation Point
- ❖ Maximum Photosynthetic Rate (P_m)

Photosynthetic CO_2 response curves (A-Ci curves)

Photosynthesis in plant physiology



CO_2

C_4 plants:

- ❖ Lower CO_2 compensation point
- ❖ Higher efficiency at low CO_2

C_3 plants:

- ❖ Higher compensation point
- ❖ Stronger CO_2 limitation

Photosynthesis in plant physiology

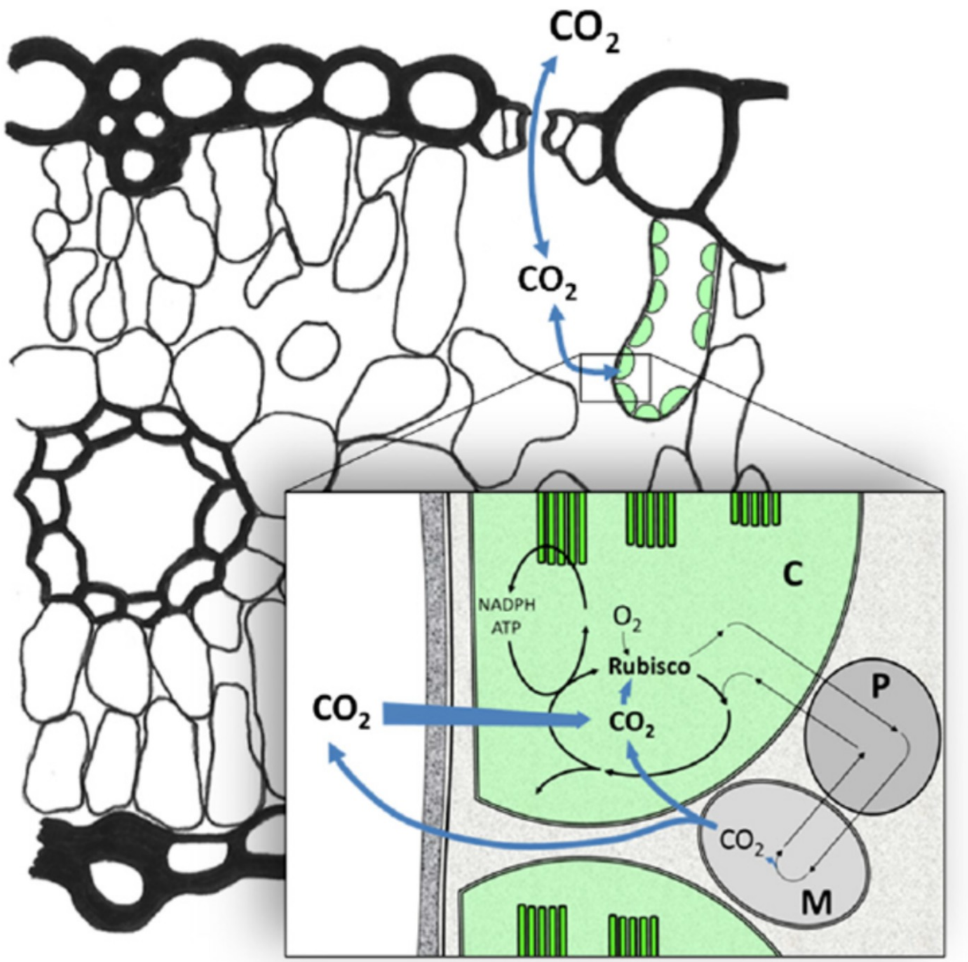
CO_2

Route of CO_2 Entry in C3

Atmosphere → Stomata → Intercellular space → Cytosol → Chloroplast stroma

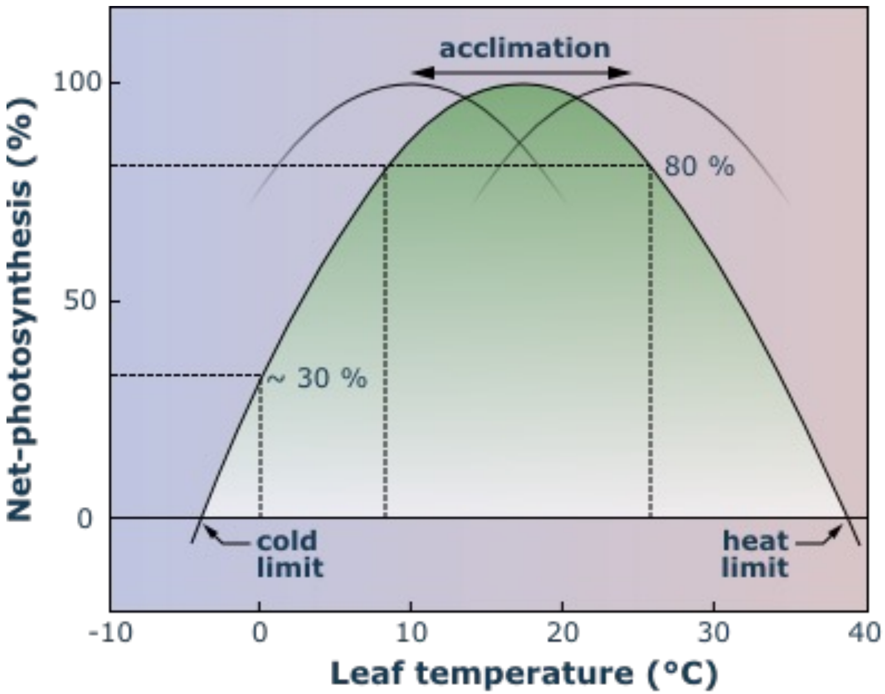
Limiting Factors

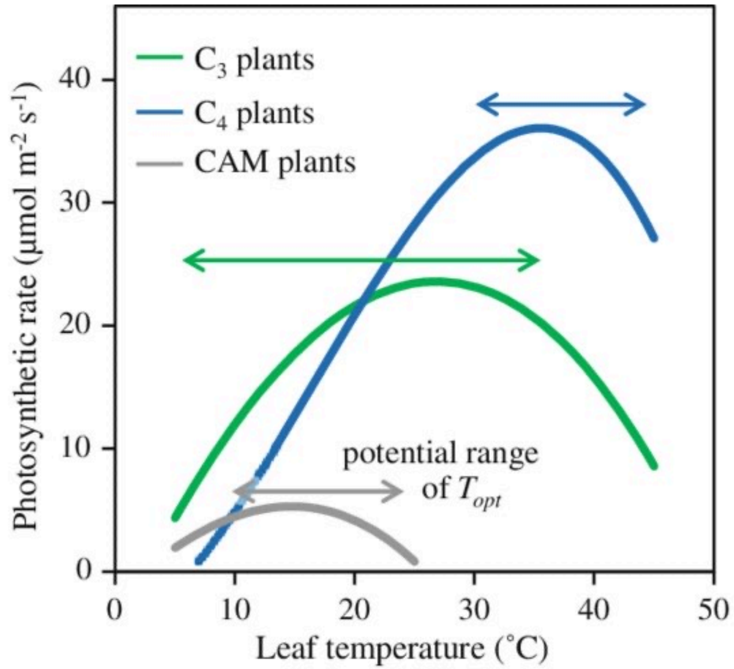
- ❖ **Concentration gradient**
- ❖ **Diffusion resistance:**
  - ✓ Stomatal resistance
  - ✓ Mesophyll resistance



Photosynthesis in plant physiology

Temperature





Photosynthesis in plant physiology

Temperature

Parameter	Typical Range (C_3 plants)	Definition	Physiological Basis
Minimum temperature (Tmin)	~2–4 °C	Lowest temperature at which photosynthesis can occur	Enzyme activity extremely low; metabolic processes slow
Optimum temperature (Topt)	~20–30 °C	Temperature at which photosynthesis is maximal	Balance of enzyme activity, CO_2 fixation, and low photorespiration
Maximum temperature (Tmax)	~40–45 °C	Highest temperature at which photosynthesis can proceed	Enzyme denaturation, membrane instability, high respiration

Photosynthesis in plant physiology

Mineral Nutrition

Element Group	Elements	Function in Photosynthesis
Structural components	N, P, S, Mg	Chlorophyll, proteins, membranes
Electron transport	Fe, Cu	Components of electron carriers (cytochromes, plastocyanin)
Energy metabolism	Pi	ATP, NADPH, metabolic intermediates
Water splitting	Mn, Cl	Essential for oxygen-evolving complex (OEC)
Regulation	K, Ca	Stomatal movement, metabolite transport

Photosynthesis in plant physiology

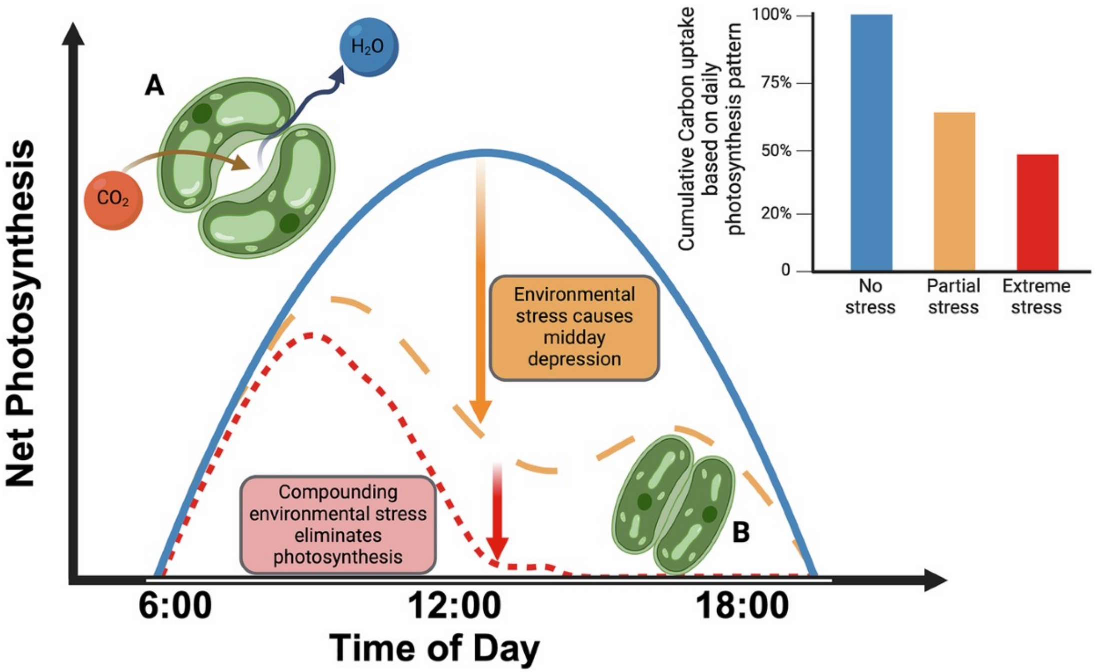
Water stress

Only a very small fraction of water is used directly in photosynthesis ~1% (for photolysis in PSII). Therefore, water affects photosynthesis mainly **indirectly.**

- **Stomatal Closure**
- **Reduced Assimilate Transport**
- **Damage to Photosynthetic Apparatus**
- **Reduced Leaf Area**

Photosynthesis in plant physiology

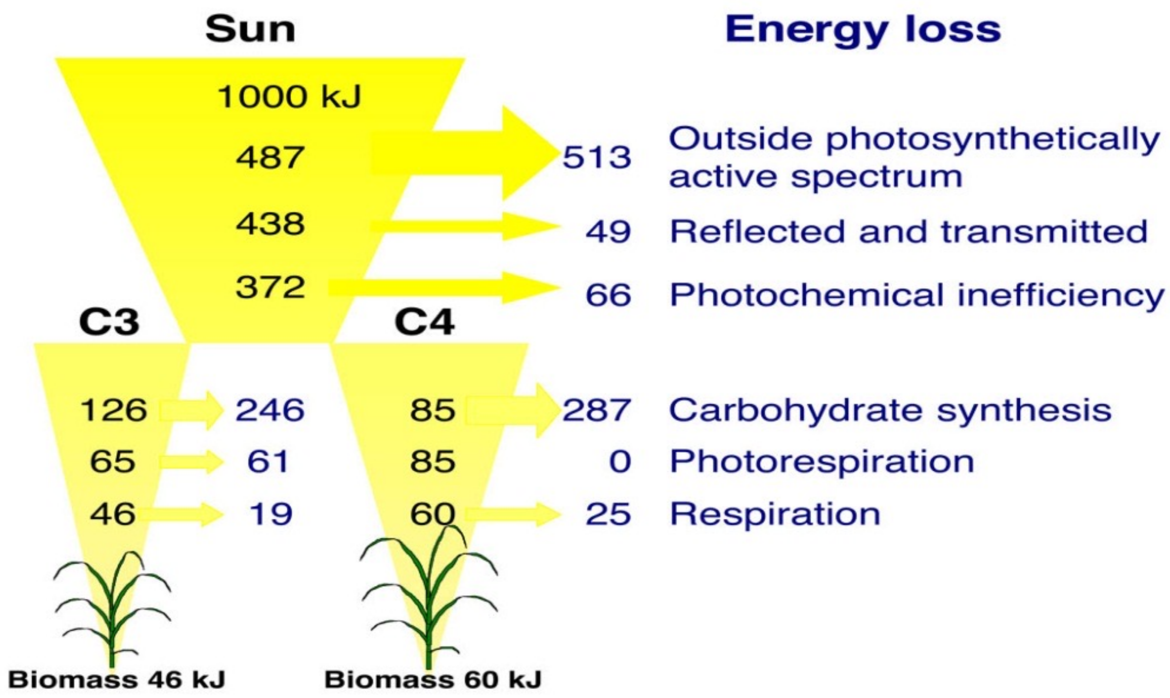
Diurnal Patterns



- ❖ **Normal Conditions — Single Peak Curve**
- ❖ **Stress Conditions — Double Peak Curve (Midday Depression)**
  - ✓ A temporary decline in photosynthetic rates around noon, despite high light intensity.

Photosynthesis on crop yield improvement

Light Use Efficiency (LUE)/ 光能利用效率 is the percentage of incident solar energy that is converted into chemical energy stored in plant biomass over a given time and land area.



Photosynthesis on crop yield improvement

Why Is Light Use Efficiency Low?

Factor	Description	Impact on Photosynthesis
Light leakage (>50%)	Large fraction of solar radiation not absorbed by canopy	Reduced available energy
Light saturation & waste	Light exceeds photosynthetic capacity (PAR up to 1800–2000 μmol m^{-2} s^{-1} vs saturation ~540–900)	Excess energy dissipated (heat, NPQ)
Environmental constraints	Suboptimal temperature, water, nutrients	Limits biochemical processes
Respiration losses	Carbon lost via maintenance and growth respiration	Reduces net biomass accumulation

Photosynthesis on crop yield improvement

Radiation Use Efficiency (RUE) / 辐射利用效率

RUE is the ratio of biomass accumulation (dry matter) to absorbed photosynthetically active radiation (PAR) over a given period.

Plant Type	RUE Range ($g \cdot MJ^{-1}$)
C_3 plants	~0.85 – 3.0
C_4 plants	Up to ~4.8

Photosynthesis on crop yield improvement

Biomass = Photosynthetic production − Respiratory losses

Photosynthetic production = Photosynthetic capacity
×
Photosynthetic duration
×
Photosynthetic area

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Review

Perspectives of improving rice photosynthesis for higher grain yield

Dongliang Xiong

National Key Laboratory of Crop Genetic Improvement, Hubei Hongshan Laboratory, MARA Key Laboratory of Crop Ecophysiology and Farming System in the Middle Reaches of the Yangtze River, College of Plant Science and Technology, Huazhong Agricultural University, Wuhan, Hubei 430070, China

A R T I C L E I N F O

Keywords:
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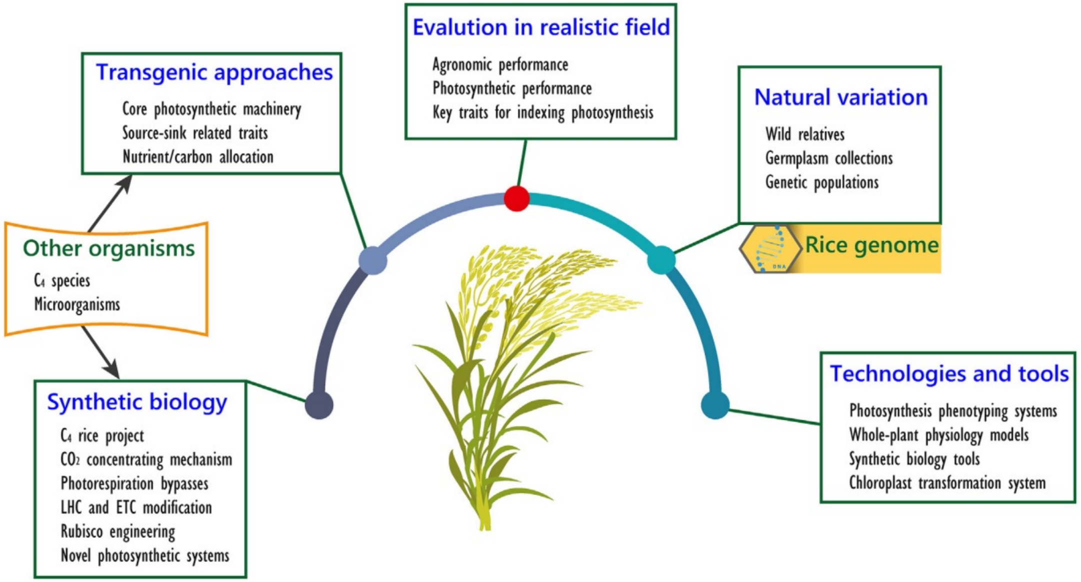
Sink-source relationships



Trends in Plant Science

CellPress
REVIEWS

Opinion

Increasing Photosynthesis: Unlikely Solution For World Food Problem

Thomas R. Sinclair,[1,*] Thomas W. Rufty,[1] and Ramsey S. Lewis[1]

Increasing the photosynthesis rate of plants has been recently revitalized as an approach for increasing grain crop yields and solving world food crises. The idea that photosynthesis is the key to increasing grain crop yields is not new. Considerable research in the 1970s and 1980s showed that carbon input was not limiting for crop growth and yield. Instead, the availability and uptake of water and nutrients were found to be critical for increasing grain yield, and that conclusion still applies today. In this Opinion article, nitrogen limitation is given particular attention because of its quantitative linkage with vegetative and reproductive growth and its essential role as a quantitative component of seeds.

Photosynthesis Rate and Grain Yield

Recent publications [1–3] and a steady stream of articles in the popular press [4–12] suggest that new discoveries in photosynthesis research will lead to increased crop yields and provide the solution to global food shortages. The logic for this conclusion has been enunciated for decades and often stated as a 'truism':

Thomas Sinclair

Adjunct Professor
Crop Physiology & Ecology
Adjunct Faculty
trsincla@ncsu.edu
919.513.1620

Carbon accumulation in the absence of additional nitrogen does not increase yield.

Yield increase requires greater nitrogen accumulation, plant nitro-

Homework Assignments

A plant physiologist grows two groups of artificial plant cells under different experimental conditions. Both groups contain chloroplasts, mitochondria, enzymes, carbohydrates, lipids, proteins, and nucleic acids, but their energy-processing systems function differently. In **Model 1**, the chloroplasts are highly active and produce large amounts of glucose and oxygen, but the mitochondria are inefficient and produce ATP slowly. In **Model 2**, the mitochondria produce ATP efficiently, but the chloroplasts capture light energy poorly and synthesize glucose slowly.

✓ **Task 1:** Analyze the distinct roles of **chloroplasts, mitochondria, glucose, oxygen, carbon dioxide, water, and ATP** in supporting energy transformation in the two models.
✓ **Task 2:** Discuss whether a cell with strong **photosynthetic ability** but weak **cellular respiration** should be considered more successful than a cell with efficient ATP production but limited glucose production.
✓ **Task 3:** Suggest how changing one or more factors, such as **light availability, chlorophyll activity, mitochondrial efficiency, enzyme activity, or glucose storage**, could improve the performance of each artificial cell, and explain what new limitations might appear.