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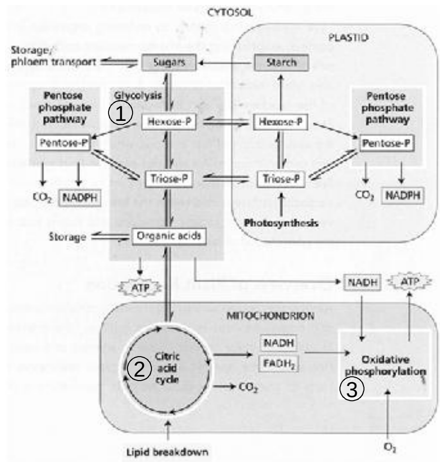
# LECT 6. RESPIRATION




**Cellular respiration** is **critical** for the **survival** of most organisms due to its role in the provision of metabolic energy (ATP)

# COMPETENCIES

Students, after mastering materials of the present lecture, should be able:

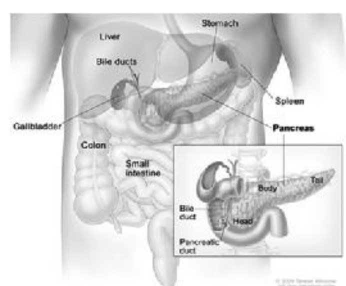
1. To explain the process of respiration (the oxidation of substrates particularly carbohydrates or the synthesis of metabolic energy used for plant growth and maintenance)
2. To explain reactions, enzymes and products involved the respiration
3. To explain specifically glycolysis, gluconeogenesis, pentose phosphate pathway, citric acid cycle and oxidative phosphorylation.

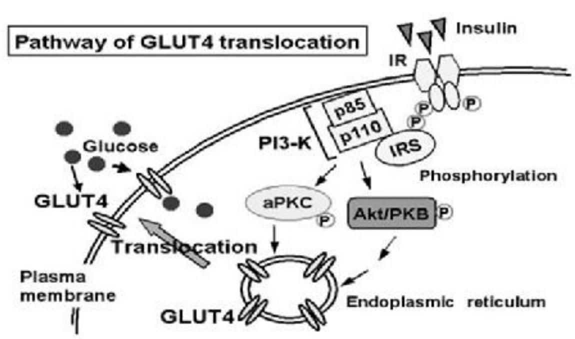
# LECTURE FLOW

1. INTRODUCTION
   - Definition
   - Site of Respiration
   - Electron Carriers
   - Stage of Respiration
2. GLYCOLYSIS
   - Initial Phase
   - Energy-Conserving Phase
   - Gluconeogenesis
   - Fermentation
   - Oxidative Pentose Phosphate Pathway
3. CITRIC ACID CYCLE
   - Discovery
   - Mithochondria
   - Pyruvate Oxidation
4. OXIDATIVE PHOSPHOTYLATION
   - Electron Transport Chain
   - Multiprotein Complexes
   - ATP Synthesis

**Glucose is t**he most commonly cited substrate of respiration

**Glucose** serves as the primary energy source for the brain and is also a source of energy for cells throughout the body




Blood glucose is normally maintained between 70 mg/dl and 110 mg

**GUT4**: glucose transporters (protrein)

http://www.ans.kobe-u.ac.jp/english/gakka/seibutsukinou/seibutu.html

*What is respiration ?*

# 1. INTRODUCTION

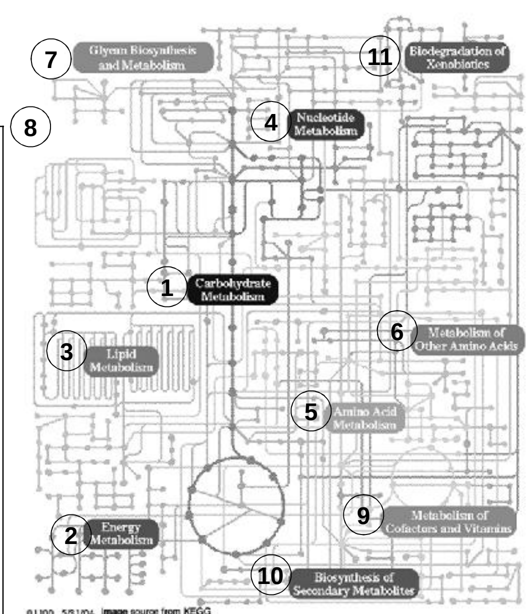
## 1. Definition

- Photosynthesis provides the organic building blocks that plants (and nearly all other organisms) depend on.
- **Respiration** is the process whereby the energy stored in carbohydrates, produced during photosynthesis, is released in a controlled manner for cellular use.
- The energy (free energy) released during respiration is incorporated into a form (ATP) that can be readily utilized for the growth, development and maintenance of the plant.
- At the same time it generates many carbon precursors for biosynthesis.
- Therefore, respiration is tightly coupled to other pathways (Fig. 1).



**Chemical Changes: Metabolism (145 pathways)**

1. Carbohydrate Metabolism (17)
2. Energy Metabolism (8)
3. Lipid Metabolism (14)
4. Nucleotide Metabolism (2)
5. Amino Acid Metabolism (16)
6. Metabolism of Other Amino Acids (9)
7. Glycan Biosynthesis and Metabolism (18)
8. Biosynthesis of Polyketides and Nonribosomal Peptides (9)
9. Metabolism of Cofactors and Vitamins (11)
10. Biosynthesis of Secondary Metabolites (21)
11. Biodegradation of Xenobiotics (21)




http://manet.illinois.edu/pathways.php

- From a chemical standpoint, respiration is most commonly expressed in terms of the oxidation of the six-carbon sugar glucose.

$$C_6H_{12}O_6 + 6O_2 + 6H_2O \longrightarrow 6CO_2 + 12H_2O$$

- This equation represents a coupled redox reaction that oxidizes completely glucose to $CO_2$ with **oxygen** serving as the ultimate electron acceptor and reduced to water.
- Glucose is most commonly cited as the substrate for respiration.
- In a functioning plant cell, however, reduced carbon is derived mainly from sources such as the disaccharide **sucrose**, triose phosphates from photosynthesis, fructose-containing polymers (fructans), and other sugars, as well as from lipids (primarily triacylglycerols), organic acids, and on occasion, proteins (Fig. 11.1).

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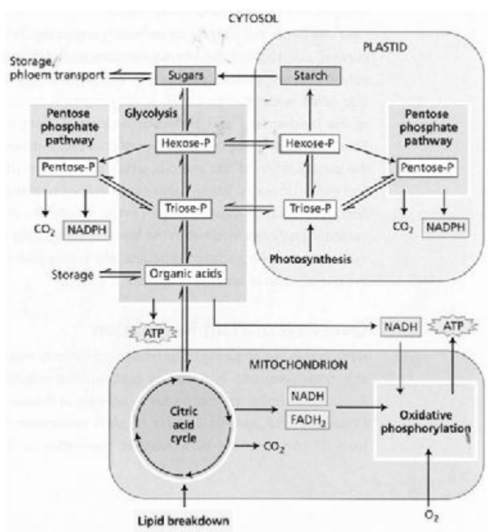
Fig. 11.1 Overview of respiration. Substrates for respiration are generated by other cellular processes and enter the respiratory pathways.




Glycolysis

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- Therefore, plant respiration can be expressed as the oxidation of the 12-carbon molecule sucrose and the reduction of 12 molecules of $O_2$:

$$C_{12}H_{22}O_{11} + 13H_2O \text{ ì } 12CO_2 + 48H^+ + 48e^-$$
$$12O_2 + 48H^+ + 48e^- \text{ ì } 24H_2O$$

giving the following net reaction

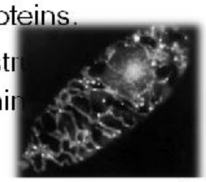
$$C_{12}H_{22}O_{11} + 12O_2 \text{ ì } 12CO_2 + 11H_2O$$

- This reaction is the reversal of the photosynthetic process; it represents a coupled redox reaction in which sucrose is completely oxidized to $CO_2$ while oxygen serves as the ultimate electron acceptor and is reduced to water in the process.
- The change in standard **Gibbs free energy** ($\Delta G^{0\prime}$) for the net reaction is -5760 kJ per mole (342 g) of sucrose oxidized.



## 2. Site of Respiration


1. Cytosol and plastids are involved in the process of respiration.
2. Mitochondria are the main site of ATP synthesis in eukaryote cells and as such are vital for the health and survival of the cell. Numbers of mitochondria per cell vary but usually 100s/cell
3. Mitochondria have some of their own DNA, ribosomes and tRNA; 22 tRNAs & rRNAs (16S and 12S), so mitochondria can make many of their own proteins.
4. The DNA is circular and lies in the matrix in str called "nucleoids". Each nucleoid may contai of the mitochondrial DNA (mtDNA).



## 3. Electron Carriers

- As respiration can be regarded as the redox reactions, then electron carriers are required to support the process.
- Nicotinamide adenine dinucleotide ($NAD^+/NADH$) is an **organic cofactor** (coenzyme) associated with many enzymes that catalyze cellular redox reactions.
- $NAD^+$ is the oxidized form of the cofactor, which undergoes a reversible two-electron reaction that yields NADH (Fig. 11.2):

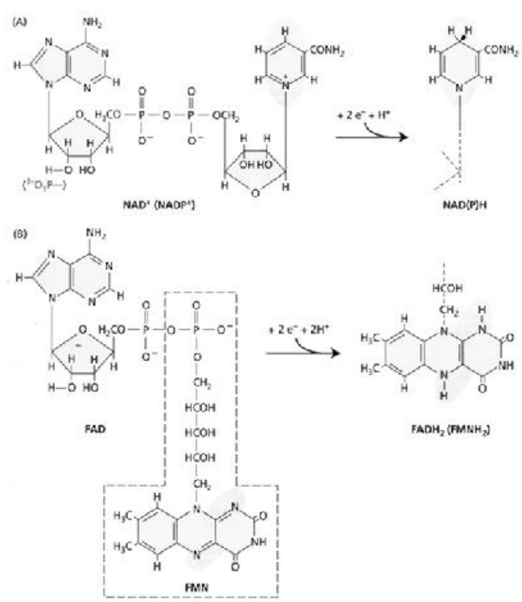
$$\mathbf{NAD^+ + 2\ e^- + H^+ \ \text{ì}\ NADH}$$

- The standard reduction potential for this redox couple is about -320 mV, which makes it a relatively strong reductant (i.e., electron donor).
- NADH is thus a good molecule in which to conserve the free energy carried by the electrons released during the stepwise oxidations of glycolysis and the citric acid cycle.



Fig. 11.2 Structures and reactions of the major electron-carrying nucleotides involved in respiratory bioenergetics.

(A) Reduction of $NAD(P)^+$ to NAD(P)H. The hydrogen (in red) in $NAD^+$ is replaced by a phosphate group (also in red) in $NADP^+$.
(B) Reduction of FAD to $FADH_2$. FMN is identical to the flavin part of FAD and is shown in the dashed box. Blue shaded areas show the portions of the molecules that are involved in the redox reaction.



## 4. Stage of Respiration

- The cells mobilize the large amount of free energy released in the oxidation of sucrose in a series of step-by-step reactions to prevent damage (incineration) of cellular structures.
- These reactions can be grouped into four major processes:
  1. **glycolysis**,
  2. the **oxidative pentose phosphate pathway**,
  3. the **citric acid cycle**, and
  4. **oxidative phosphorylation.**
- These pathways do not function in isolation, but exchange metabolites at several levels.



# 2. GLYCOLYSIS

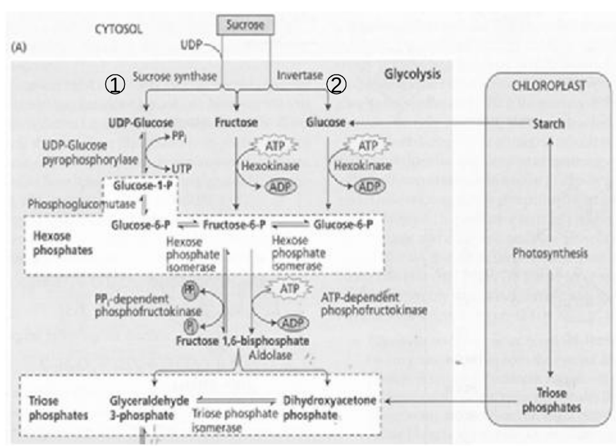
## 1. Initial Phase

- Glycolysis (from the Greek words glykos, “sugar,” and lysis, ”splitting") occurs in all living organisms (prokaryotes and eukaryotes).
- The principal reactions associated with the classic glycolytic pathway in plants are almost identical to those in animal cells (Fig. 11.3).
- In animals, the substrate of glycolysis is glucose, and the end product is pyruvate.
- Sucrose (not glucose) can be argued to be the true sugar substrate for plant respiration as the fact that:
  - sucrose is the major translocated sugar in most plants, and is therefore the form of carbon that most nonphotosynthetic tissues import.

- Substrates from different sources are channeled into triose phosphate (Fig. 11.3).
- In the early steps of glycolysis, sucrose is split into its two monosaccharide units—glucose and fructose—which can readily enter the glycolytic pathway.
- Two pathways for the splitting of sucrose are known in plants, both of which also take part in the unloading of sucrose from the phloem:
  1. Sucrose synthase pathway. Sucrose synthase, located in the cytosol, combines sucrose with UDP to produce fructose and UDP-glucose.
  2. Invertase pathway. *Invertases* present in the cell wall, vacuole, or cytosol hydrolyze sucrose into its two component hexoses (glucose and fructose).
- Four molecules of triose phosphates are formed for each molecule of sucrose that is metabolized which requires 4 ATP.



Fig. 11.3 Initial reactions of plant glycolysis and fermentation.




(A) **In the main glycolytic pathway, sucrose is oxidized via hexose phosphates and triose phosphates to the organic acid pyruvate**, but plants also carry out alternative reactions. All the enzymes included in this figure have been measured at levels sufficient to support the respiration rates observed in intact plant tissues, and flux through the pathway has been observed in vivo.

## 2. Energy-Conserving Phase

- Energy-conserving phase of glycolysis occur in the reactions converting triose phosphate to pyruvate as the end product.
- In the first and reactions, $NAD^+$ is reduced to NADH by glyceraldehyde-3-phosphate dehydrogenase, and ATP is synthesized in the reaction catalyzed by phosphoglycerate kinase and pyruvate kinase.
- An alternative end product, phosphoenolpyruvate, can be converted to malate for mitochondrial oxidation or storage in the vacuole.
- NADH can be reoxidized during fermentation by either lactate dehydrogenase or alcohol dehydrogenase.
- For each sucrose entering the pathway, four ATPs are generated by this reaction—one for each molecule of 1,3—bisphosphoglycerate.

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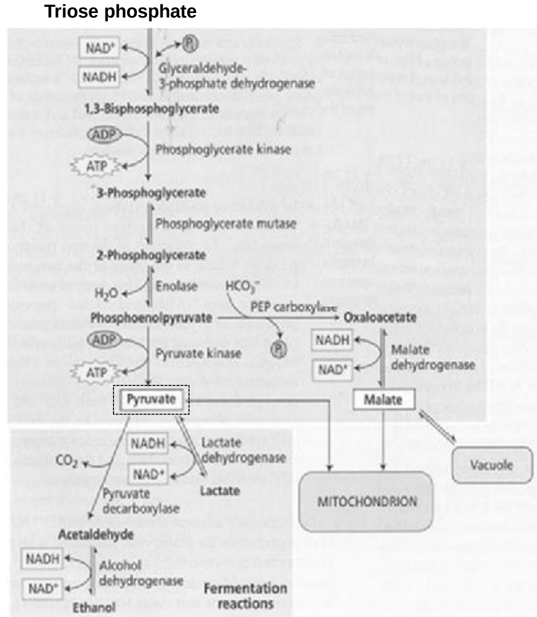
Fig. 11.3 Energy-conserving phase of glycolysis starting from the conversion of triose phosphate to 1,3-Biphosphoglycerate with pyruvate as the end product, but fermentation takes place under anaerobic conditions with Ethanol or Lactate as the end products

Triose phosphate

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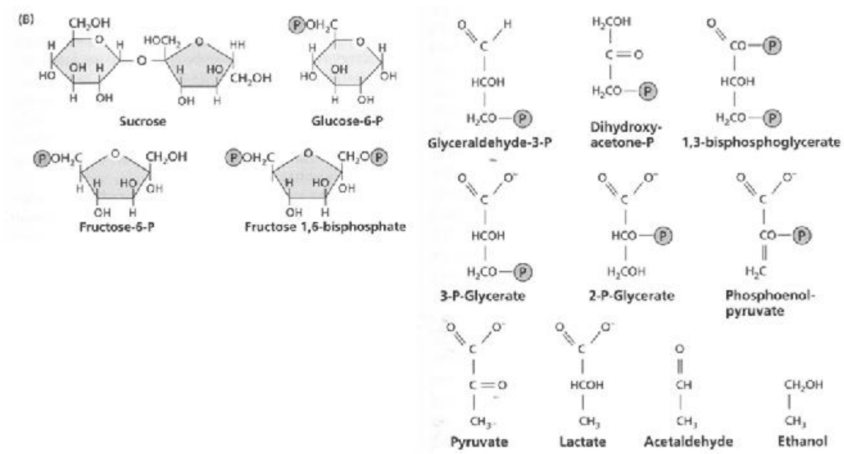
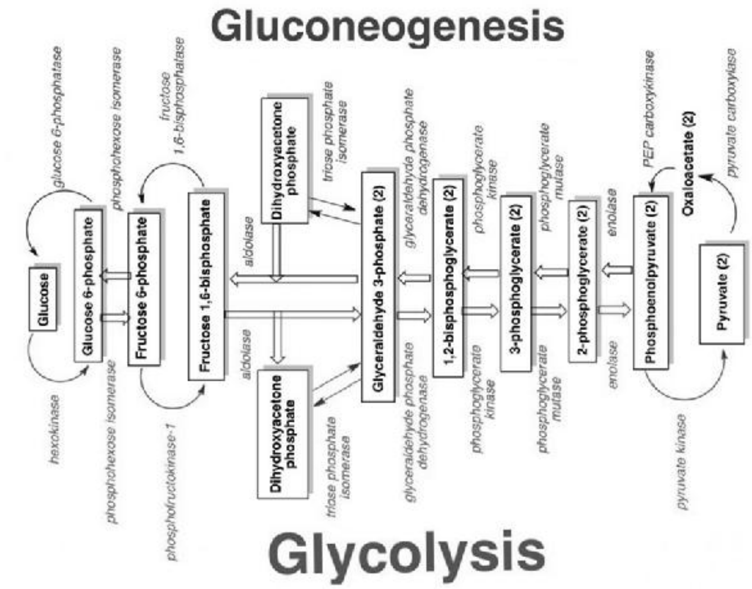



(B) The structures of the carbon intermediates. P, phosphate group.



## 3. Gluconeogenesis

- Organisms can operate the glycolytic pathway in the opposite direction to synthesize sugars from organic acids which process is known as **gluconeogenesis**.
- Gluconeogenesis is particularly important in the seeds of plants (such as the castor oil plant *Ricinus communis* and sunflower) that store a significant quantity of their carbon reserves in the form of oils (triacylglycerols).
- After such a seed germinates, much of the oil is converted by gluconeogenesis into sucrose, which is then used to support the growing seedling.
- In the initial phase of glycolysis, gluconeogenesis overlaps with the pathway for synthesis of sucrose from photosynthetic triose phosphate.

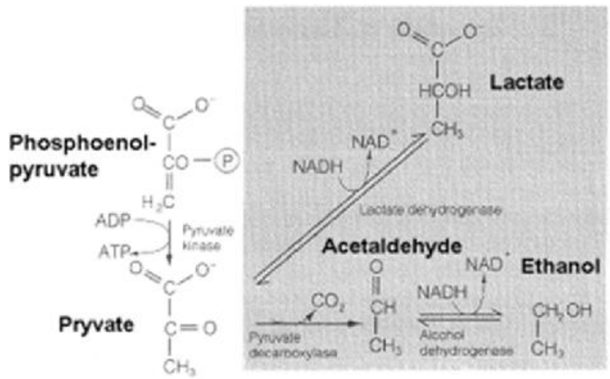





# 4. Fermentation

- Oxidative phosphorylation does not function in the absence of oxygen.
- Glycolysis thus cannot continue to operate because the cell's supply of $NAD^+$ is limited and once all the $NAD^+$ becomes tied up in the reduced state (NADH), the catalytic activity of glyceraldehyde-3-phosphate dehydrogenase comes to a halt.
- To overcome this limitation, plants and other organ-isms can further metabolize pyruvate by carrying out one or more forms of **fermentation** (Fig. 11.3).
- Alcoholic fermentation is common in plants, although more widely known from brewer's yeast.
- Two enzymes, pyruvate decarboxylase and alcohol dehydrogenase, act on pyruvate, ultimately producing ethanol and $CO_2$ and oxidizing NADH in the process.

- In lactic acid fermentation (common in mammalian muscle, but also found in plants), the enzyme lactate dehydrogenase uses NADH to reduce pyruvate to lactate, thus regenerating $NAD^+$.
- In plant roots in flooded soils—glycolysis (fermentation) can be the main source of energy for cells.





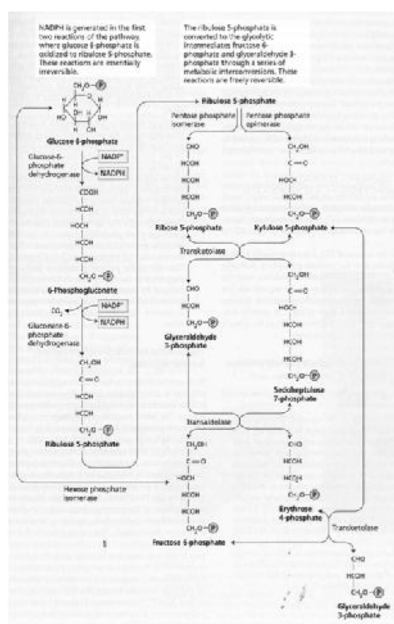

- *Efficiency* is defined here as the energy conserved as ATP relative to the energy potentially available in a molecule of sucrose.
- The standard free-energy change ($\Delta G°'$) for the complete oxidation of sucrose to $CO_2$ is -5760 kJ $mol^{-1}$. The $\Delta G°'$ for the synthesis of ATP is 32 kJ mol'1.
- However, under the nonstandard conditions that normally exist in both mammalian and plant cells, the synthesis of ATP requires an input of free energy of approximately 50 kJ $mol^{-1}$.
- With ethanol or lactate as the final product, the efficiency of fermentation is only about 4%.
- Most of the energy available in sucrose remains in the ethanol or lactate.

## 5. Oxidative Pentose Phosphate Pathway

- The oxidation of sugars in plant cells can be also accomplished via the oxidative pentose phosphate (**PP**) pathway , also known as the hexose monophos-phate shunt (HMS), can also this task (Fig. 11.4).
- The reactions are carried out by soluble enzymes present in the cytosol and in plastids.
- Under most conditions, the pathway in plastids predominates over that in the cytosol (Dennis *et al*. 1997).
- Studies of the release of $CO_2$ from isotopically labeled glucose indicate that the PP pathway accounts for **10-25%** of the glucose breakdown, with the rest occurring mainly via glycolysis.



Fig. 11.4 Reactions of the oxidative pentose phosphate pathway in plants. The first two reactions—which are oxidizing reactions—are essentially irreversible. They supply NADPH to the cytoplasm and to plastids in the absence of photosynthesis. The downstream part of the pathway is reversible (as denoted by double-headed arrows), so it can supply five-carbon substrates for biosynthesis even when the oxidizing reactions are inhibited; for example, in chloroplasts in the light.



- The oxidative PP pathway plays several roles in plant metabolism:
  - *NADPH supply in the cytosol*. This NADPH drives reductive steps associated with biosynthetic and defensive reactions that occur in the cytosol and is a substrate for reactions that remove reactive oxygen species (ROS).
  - *NADPH supply in plastids*. In nongreen plastids, such as amyloplasts in the root, and in chloroplasts functioning in the dark, the PP pathway is a major supplier of NADPH.
  - *Supply of substrates for biosynthetic processes.* In most organisms, the PP pathway produces ribose 5-phosphate, which is a precursor of the ribose and deoxyribose needed in the synthesis of nucleic acids. In plants, however, ribose appears to be synthesized by another, as yet unknown, pathway (Sharples and Fry 2007). Another intermediate in the PP pathway, the four-carbon erythrose 4—phosphate, combines with PEP in the initial reaction that produces plant phenolic compounds, including aromatic amino acids and the precursors of lignin, flavonoids, and phytoalexins.

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# 4. CITRIC ACID CYCLE

## 1. Discovery

- During the 19th century, biologists discovered that in the absence of air, cells produce ethanol or lactic acid, whereas in the presence of air, cells consume $O_2$ and produce $CO_2$ and $H_20$.
- In 1937 the German-born British biochemist Hans A. Krebs reported the discovery of the citric acid cycle—also called the tricarboxylic acid cycle or Krebs cycle.
- This discovery explained how pyruvate is broken down into $CO_2$ and $H_2O$, and highlighted the key concept of cycles in metabolic pathways.
- For his discovery, Hans Krebs was awarded the Nobel Prize in physiology or medicine in 1953.

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### 3. Mitochondria

- The breakdown of sucrose into pyruvate releases less than 25% of the total energy in sucrose; the remaining energy is stored in the four molecules of pyruvate. The next two stages of respiration (the citric acid cycle and oxidative phosphorylation) take place within an organelle enclosed by a double membrane, the **mitochondrion** (plural *mitochondria*).
- In electron micrographs, plant mitochondria usually look spherical or rod-like (Fig. 11.5) with 0.5 to 1.0 μm in diameter and up to 3 μm in length (Douce 1985).
- The number of mitochondria per plant cell varies; it is usually directly related to the metabolic activity of the tissue, reflecting the mitochondrial role in energy metabolism.

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Fig.11.5 Structure of plant mitochondria. (A) Three-dimensional representation of a mitochondrion, showing the invaginations of the inner membrane, called cristae, as well as the locations of the matrix and intermembrane space (see also Figure 11.9). (B) Electron micrograph of mitochondria in a mesophyll cell of broad bean (*Vicia faba*). Typically, individual mitochondria are 1 to 3 um long in plant cells, which means that they are substantially smaller than nuclei and plastids. (B from Gunning and Steer 1996.)

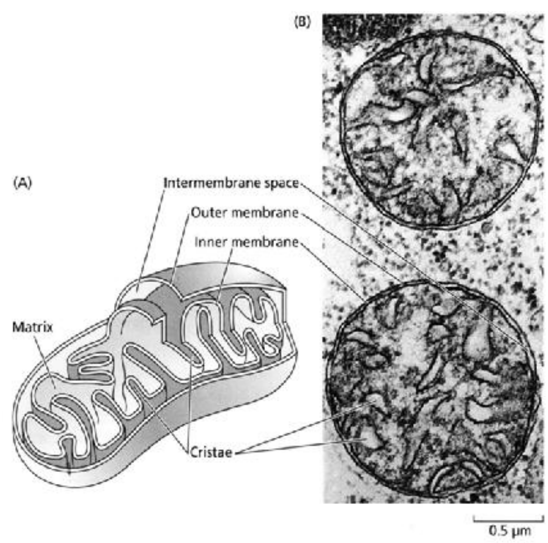


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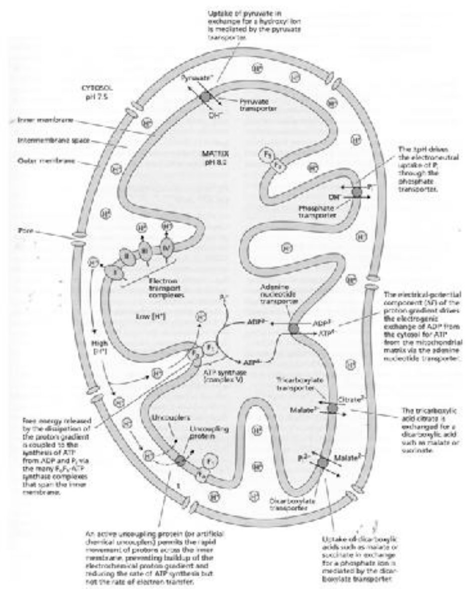
Fig. 11.9 Transmembrane transport in plant mitochondria. An electrochemical proton gradient, $\Delta\mu_{H+}$, consisting of an electrical potential component ($\Delta E$, -200 mV, negative inside) and a chemical potential component ($\Delta pH$, alkaline inside), is established across the inner mitochondrial membrane during electron trans- port, as outlined in the text. Specific metabolites are moved across the inner membrane by specialized proteins called transporters or carriers. (After Douce 1985.)






- Plant mitochondria have two membranes:
  - a smooth **outer membrane** completely surrounds a highly invaginated **inner membrane**.
  - The invaginations of the inner membrane are known as cristae (singular crista).
  - The region between the two mitochondrial membranes is known as the intermembrane space.
  - The compartment enclosed by the inner membrane is referred to as the mitochondrial matrix.
- The lipid fraction of both membranes is primarily made up of phospholipids:
  - 80% of which are either phosphatidylcholine or phosphatidylethanolamine.
  - About 15% is diphosphatidylglycerol (also called cardiolipin), which occurs in cells only in the inner mitochondrial membrane.

# 5. OXIDATIVE PHOSPHORYLATION

## 1. Electron Transport Chain

- For each molecule of sucrose oxidized through glycolysis and the citric acid cycle,
  - 4 molecules of NADH are generated in the cytosol, and 16 molecules of NADH plus 4 molecules of $FADH_2$ (associated with succinate dehydrogenase) are generated in the mitochondrial matrix.
  - These reduced compounds must be reoxidized, or the entire respiratory process will come to a halt.
- The electron transport chain catalyzes a transfer of two electrons from NADH (or $FADH_2$) to oxygen, the final electron acceptor of the respiratory process.



## 2. Pyruvate Oxidation

- Pyruvate enters the mitochondrion and is oxidized via the citric acid cycle (Fig. 11.6).
- The products of pyruvate oxidation are and produces NADH, $CO_2$, and acetyl-CoA, in which the acetyl group derived from pyruvate is linked by a thioester bond to a cofactor, coenzyme A.

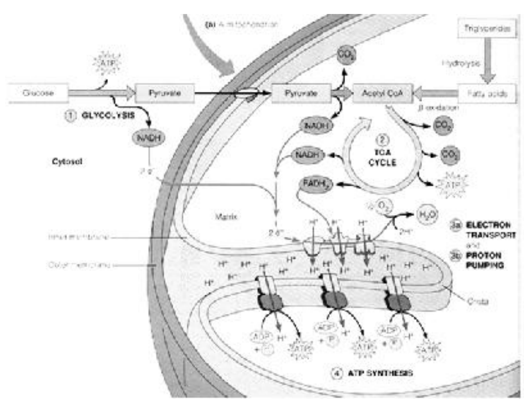
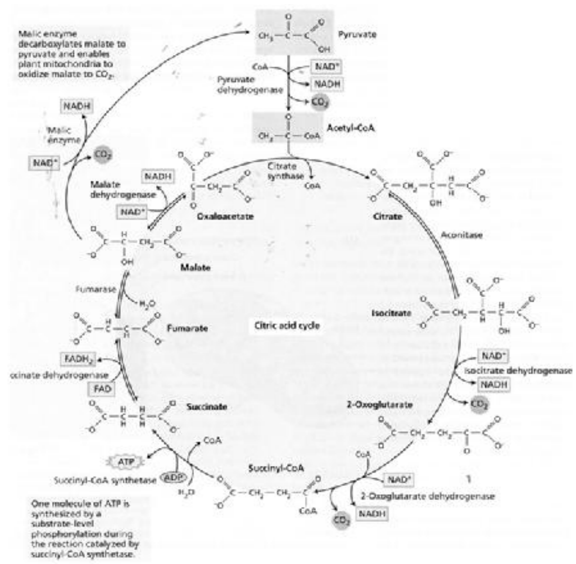


Fig. 11.6 The plant citric acid cycle. The reactions and enzymes of the citric acid cycle are displayed, along with the accessory reactions of pyruvate dehydrogenase and malic enzyme. Pyruvate is completely oxidized to three molecules of $CO_2$. The electrons released during these oxidations are used to reduce four molecules of $NAD^+$ to NADH and one molecule of FAD to $FADH_2$






- For the oxidation of NADH, the reaction can be written as

$$NADH + H^+ + \frac{1}{2} O_2 \rightarrow NAD^+ + H_2O$$

- The role of the electron transport chain is to bring about the oxidation of NADH (and $FADH_2$) and, in the process, utilize some of the free energy released to generate an electrochemical proton gradient, $\Delta\mu_{H+}$, across the inner mitochondrial membrane.
- The electron transport chain (ETC) of plants contains the same set of electron carriers found in the mitochondria of other organisms (Fig. 11.8).
- The individual electron transport proteins are organized into four transmembrane multiprotein complexes (identified as I through IV), all of which are localized in the inner mitochondrial membrane.

- Three of these complexes are engaged in proton pumping (I, III, and IV).

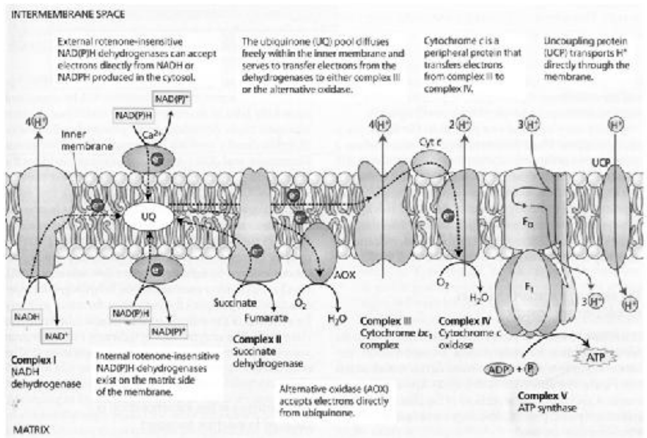



Fig. 11.8 Organization of the electron transport chain and ATP synthesis in the inner membrane of the plant mitochondrion.

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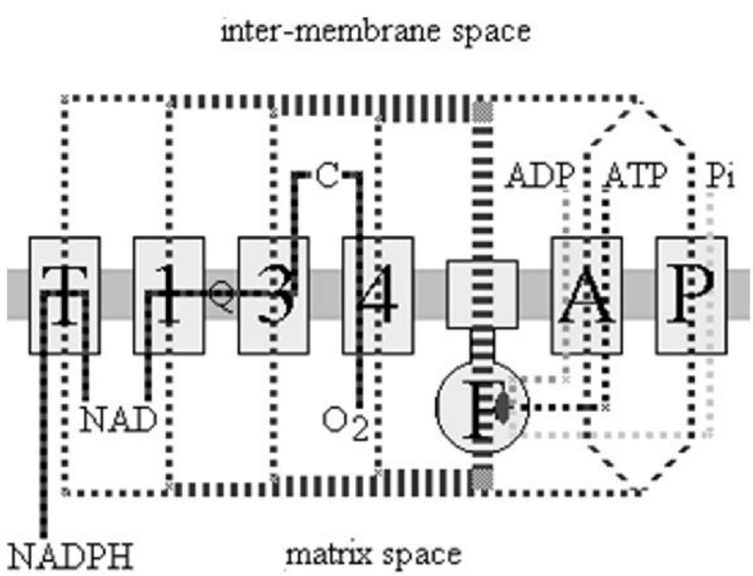


http://www.bmb.leeds.ac.uk/illingworth/oxphos/

## 2. Multiprotein Complexes

- Mitochondria from nearly all eukaryotes contain the four standard protein complexes: I, II, III, and IV.
  1. **COMPLEX I** (NADH DEHYDROGENASE) Electrons from NADH, generated in the mitochondrial matrix during the citric acid cycle, are oxidized by complex I (an **NADH dehydrogenase**).
     - The electron carriers in complex I include a tightly bound cofactor (**flavin mononucleotide**, or **FMN**, which is chemically similar to FAD) and several iron-sulfur centers.
     - **Ubiquinone**, a small lipid-soluble electron and proton carrier, is localized within the inner membrane. It is not tightly associated with any protein, and it can diffuse within the hydrophobic core of the membrane bilayer.
  2. **COMPLEX II** (SUCCINATE DEHYDROGENASE) Oxidation of succinate in the citric acid cycle is catalyzed by this complex, and the reducing equivalents are transferred via $FADH_2$ and a group of iron—sulfur centers to ubiquinone. Complex II does not pump protons.

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3. **COMPLEX III (**CYTOCHROME *bc₁*, COMPLEX**)** Complex III oxidizes reduced ubiquinone (ubiquinol) and transfers the electrons via an iron—sulfur center, two *b*-type cytochromes ($b_{565}$ and $b_{560}$), and a membrane-bound cytochrome *c*1 to cytochrome *c*. Four protons per electron pair are pumped out of the matrix by complex III using a mechanism called the Q-cycle.
   - **Cytochrome *c*** is a small protein loosely attached to the outer surface of the inner membrane and serves as a mobile carrier to transfer electrons between complexes III and IV.
4. **COMPLEX IV** (CYTOCHROME *c* OXIDASE) Complex IV contains two copper centers ($Cu_A$ and $Cu_B$) and cytochromes *a* and $a_3$. This complex is the terminal oxidase and brings about the four-electron reduction of O2 to two molecules of $H_2O$. Two protons are pumped out of the matrix per electron pair.

- Reality may be more complex than the description above implies. Plant respiratory complexes contain a number of plant—specific subunits whose function is still unknown.

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## 3. ATP Synthesis

- In oxidative phosphorylation, the transfer of electrons to oxygen via complexes I, III, and IV is coupled to the synthesis of ATP from ADP and Pi via the $F_0F_1$-ATP synthase (complex V).
  - The number of ATPs synthesized depends on the nature of the electron donor.
  - In experiments conducted on isolated mitochondria, electrons derived from matrix NADH (e.g., generated by malate oxidation) give ADP:O ratios (the number of ATPs synthesized per two electrons transferred to oxygen) of 2.4 to 2.7 (Table 11.1).

**TABLE 11.1**
**Theoretical and experimental ADP:O ratios in isolated plant mitochondria**

| | ADP:0 ratio | |
|---|---|---|
| Substrate | Theoretical[a] | Experimental |
| Malate | 2.5 | 2.4–2.7 |
| Succinate | 1.5 | 1.6–1.8 |
| NADH (external) | 1.5 | 1.6–1.8 |
| Ascorbate | 1.0[b] | 0.8–0.9 |



- On the basis of theoretical ADP:O values, 52 molecules of ATP is estimated to be generated per molecule of sucrose by oxidative phosphorylation.
- The complete aerobic oxidation of sucrose (including substrate- level phosphorylation) results in a total of about 60 ATPs synthesized per sucrose molecule (Table 11.2).

**TABLE 11.2**
**The maximum yield of cytosolic ATP from the complete oxidation of sucrose to $CO_2$ via aerobic glycolysis and the citric acid cycle**

| Part reaction | ATP per sucrose[a] |
|---|---|
| Glycolysis | |
| 4 substrate-level phosphorylations | 4 |
| 4 NADH | 4 × 1.5 = 6 |
| Citric acid cycle | |
| 4 substrate-level phosphorylations | 4 |
| 4 $FADH_2$ | 4 × 1.5 = 6 |
| 16 NADH | 16 × 2.5 = 40 |
| Total | 60 |

## ENERGY PRODUCTION

| Site/Process | Quantity | ADP/O | ATP |
|---|---|---|---|
| • Glycolysis | 2 ATP | | 2 |
| • TCA Cycle | 2 ATP | | 2 |
| • Cytosol | 2 NADH | 2.5 | 5 |
| • Mitochondrial Matrix | 8 NADH | 2.5 | 20 |
| • Mitochondrial Matrix | 2 $FADH_2$ | 1.5 | 3 |
| TOTAL | | | 32 |

**Conversion Efficiency**

**Glucose:**

**(32 x 50.2 kJ/mol)/(2880 kJ/mol )= 55.8%**

**Sucrose:**

**(60 x 50.2 kJ/mol)/(5647 kJ/mol )= 53.3%**

Table. ADP/O ratios in isolated plant mitochondria

| **Substrate** | **ADP/O** |
|---|---|
| NADH (Malate) | 2.4-2.7 |
| NADH (Succinate) | 1.6-1.8 |
| NADH (External) | 1.6-1.8 |
| NADH (Ascorbate)* | 0.8-0.9 |

*Artificial electron donor
ADP/O = number of ATPs synthesized per two electrons transferred to oxygen

**Table 11.2 The maximum yield of cytosolic ATP from the complete oxidation of sucrose to $CO_2$ via aerobic glycolysis and the citric acid cycle**

| Part reaction | ATP per sucrose[a] |
|---|---|
| **Glycolysis** | |
| 4 substrate-level phosphorylations | 4 |
| 4 NADH | 4 x 1.5 = 6 |
| **Citric acid cycle** | |
| 4 substrate-level phosphorylations | 4 |
| 4 FADH2 | 4 X 1.5 = 6 |
| 16 NADH | 16 X 2.5 = 40 |
| TOTAL | **60** |

Note: Cytosolic NADH is assumed oxidized by the external NADH dehydrogenase. The nonphosphorylating pathways are assumed not to be engaged.
[a]Calculated using the theoretical ADP / O values from Table 11.1.
Source: Adapted from Brand 1994.