CHAPTER 19
Oxidative Phosphorylation and Photophosphorylation

Key topics:

– Electron-transport chain in mitochondria
– Capture of light energy in photosynthesis
– Building up the proton-motive force
– Synthesis of ATP in mitochondria and chloroplasts
Energy from reduced fuels is used to synthesize ATP in animals

- Carbohydrates, lipids, and amino acids are the main reduced fuels for the cell
- Electrons from reduced fuels are transferred to reduced cofactors \( \text{NADH} \) or \( \text{FADH}_2 \)
- In oxidative phosphorylation, energy from \( \text{NADH} \) and \( \text{FADH}_2 \) are used to make ATP
Energy Flow in Cellular Respiration

Figure 16-1
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Electrons from the reduced cofactors NADH and FADH$_2$ are passed to proteins in the respiratory chain.

In eukaryotes, oxygen is the ultimate electron acceptor for these electrons.

Energy of oxidation is used to phosphorylate ADP.
Oxidative Phosphorylation

Stage 3
Electron transfer and oxidative phosphorylation

NADH, FADH$_2$ (reduced e$^-$ carriers)

Respiratory (electron-transfer) chain

$\text{2H}^+ + \frac{1}{2} \text{O}_2$ -> H$_2$O

ADP + P$_i$ -> ATP

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Photophosphorylation

• In photosynthetic organisms light causes charge separation between a pair chlorophyll molecules.

• Energy of the oxidized and reduced chlorophyll molecules is used to drive synthesis of ATP.

• Water is the source of electrons that are passed via a chain of protein transporters to the ultimate electron acceptor, NADP$^+$.

• Oxygen is the byproduct of water oxidation.
Chemiosmotic Theory

- ADP + P\textsubscript{i} \rightarrow ATP is Highly Thermodynamically Unfavorable
- How do we make it possible?
- Phosphorylation of ADP is not a result of a direct reaction between ADP and some high-energy phosphate carrier
- Energy needed to phosphorylate ADP is provided by the flow of protons down the electrochemical gradient
- The energy released by electron transport is used to transport protons against the electrochemical gradient
Chemiosmotic energy coupling requires membranes

- The proton gradient needed for ATP synthesis can be stably established across a membrane that is impermeable to ions
  - Plasma membrane in bacteria
  - Inner membrane in mitochondria
  - Thylakoid membrane in chloroplasts
- Membrane must contain proteins that couple the "downhill" flow of electrons in the electron-transfer chain with the "uphill" flow of protons across the membrane
- Membrane must contain a protein that couples the "downhill" flow of protons to the phosphorylation of ADP
Chemiosmotic Theory

(a) Mitochondrion
1. Reduced substrate (fuel) donates $e^-$.
2. Electron carriers pump $H^+$ out as electrons flow to $O_2$.
3. Energy of $e^-$ flow stored as electrochemical potential.
4. ATP synthase uses electrochemical potential to synthesize ATP.

(b) Chloroplast
1. Light converts $H_2O$ to a good $e^-$ donor.
2. Electron carriers pump $H^+$ in as electrons flow to NADP$^+$.
3. Energy of $e^-$ flow stored as electrochemical potential.
4. ATP synthase uses electrochemical potential to synthesize ATP.

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Structure of a Mitochondrion

Double membrane leads to four distinct compartments:

1. Outer Membrane:
   - Relatively porous membrane allows passage of metabolites

2. Intermembrane Space (IMS):
   - similar environment to cytosol
   - higher proton concentration (lower pH)

3. Inner Membrane
   - Relatively impermeable, with proton gradient across it
   - Location of electron transport chain complexes
   - Convolutions called Cristae serve to increase the surface area

4. Matrix
   - Location of the citric acid cycle and parts of lipid and amino acid metabolism
   - Lower proton concentration (higher pH)
Structure of a Mitochondrion

(a) ATP synthase $(F_0 F_1)$
Cristae

Outer membrane
Freely permeable to small molecules and ions

Inner membrane
Impermeable to most small molecules and ions, including $H^+$
Contains:
- Respiratory electron carriers (Complexes I-IV)
- ADP-ATP translocase
- ATP synthase $(F_0 F_1)$
- Other membrane transporters

Matrix
Contains:
- Pyruvate dehydrogenase complex
- Citric acid cycle enzymes
- Fatty acid $\beta$-oxidation enzymes
- Amino acid oxidation enzymes
- DNA, ribosomes
- Many other enzymes
- ATP, ADP, $P_i$, $Mg^{2+}$, $Ca^{2+}$, $K^+$
- Many soluble metabolic intermediates

Figure 19-2
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Electron-transport chain complexes contain a series of electron carriers

- Each complex contains multiple redox centers consisting of:
  - Flavin Mononucleotide (FMN) or Flavin Adenine Dinucleotide (FAD)
    - Initial electron acceptors for Complex I and Complex II
    - Can carry two electrons by transferring one at a time
  - Cytochromes a, b or c
  - Iron-sulfur cluster
Cytochromes

- One electron carriers
- Iron coordinating porphoryin ring derivatives
- a, b or c differ by ring additions
Iron-Sulfur Clusters

- One electron carriers
- Coordinating by cysteines in the protein
- Containing equal number of iron and sulfur atoms

Figure 19-5
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Coenzyme Q or Ubiquinone

- **Ubiquinone** is a lipid-soluble conjugated dicarbonyl compound that **readily accepts electrons**
- Upon accepting two electrons, **it picks up two protons** to give an alcohol, ubiquinol
- Ubiquinol can freely diffuse in the membrane, **carrying electrons with protons** from one side of the membrane to another side
- Coenzyme Q is a mobile electron carrier transporting electrons from Complexes I and II to Complex III
Coenzyme Q or Ubiquinone

Ubiquinone (Q) (fully oxidized)

Semiquinone radical (•QH)

Ubiquinol (QH₂) (fully reduced)
**TABLE 19–2** Standard Reduction Potentials of Respiratory Chain and Related Electron Carriers

<table>
<thead>
<tr>
<th>Redox reaction (half-reaction)</th>
<th>$E^\circ , (V)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$2H^+ + 2e^- \longrightarrow H_2$</td>
<td>$-0.414$</td>
</tr>
<tr>
<td>$NAD^+ + H^+ + 2e^- \longrightarrow NADH$</td>
<td>$-0.320$</td>
</tr>
<tr>
<td>$NADP^+ + H^+ + 2e^- \longrightarrow NADPH$</td>
<td>$-0.324$</td>
</tr>
<tr>
<td>$\text{NADH dehydrogenase (FMN)} + 2H^+ + 2e^- \longrightarrow \text{NADH dehydrogenase (FMNH}_2\text{)}$</td>
<td>$-0.30$</td>
</tr>
<tr>
<td>Ubiquinone $+ 2H^+ + 2e^- \longrightarrow$ ubiquinol</td>
<td>$0.045$</td>
</tr>
<tr>
<td>Cytochrome $b$ $(\text{Fe}^{3+}) + e^- \longrightarrow$ cytochrome $b$ $(\text{Fe}^{2+})$</td>
<td>$0.077$</td>
</tr>
<tr>
<td>Cytochrome $c_1$ $(\text{Fe}^{3+}) + e^- \longrightarrow$ cytochrome $c_1$ $(\text{Fe}^{2+})$</td>
<td>$0.22$</td>
</tr>
<tr>
<td>Cytochrome $c$ $(\text{Fe}^{3+}) + e^- \longrightarrow$ cytochrome $c$ $(\text{Fe}^{2+})$</td>
<td>$0.254$</td>
</tr>
<tr>
<td>Cytochrome $a$ $(\text{Fe}^{3+}) + e^- \longrightarrow$ cytochrome $a$ $(\text{Fe}^{2+})$</td>
<td>$0.29$</td>
</tr>
<tr>
<td>Cytochrome $a_3$ $(\text{Fe}^{3+}) + e^- \longrightarrow$ cytochrome $a_3$ $(\text{Fe}^{2+})$</td>
<td>$0.35$</td>
</tr>
<tr>
<td>$\frac{1}{2}O_2 + 2H^+ + 2e^- \longrightarrow H_2O$</td>
<td>$0.8166$</td>
</tr>
</tbody>
</table>

Table 19-2
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Free Energy of Electron Transport

Reduction Potential \( (E) \)
\[
\Delta E^o' = E^o'_{(e^- \text{ acceptor})} - E^o'_{(e^- \text{ donor})}
\]

\[
\Delta G^o' = -nF\Delta E^o'
\]
For negative \( \Delta G \) need positive \( \Delta E \)
\[
E_{(\text{acceptor})} > E_{(\text{donor})}
\]

Electrons are transferred from lower (more negative) to higher (more positive) reduction potential.

Free Energy released is used to pump proton, storing this energy as the electrochemical gradient
<table>
<thead>
<tr>
<th>Enzyme complex/protein</th>
<th>Mass (kDa)</th>
<th>Number of subunits*</th>
<th>Prosthetic group(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>I  NADH dehydrogenase</td>
<td>850</td>
<td>43 (14)</td>
<td>FMN, Fe-S</td>
</tr>
<tr>
<td>II  Succinate dehydrogenase</td>
<td>140</td>
<td>4</td>
<td>FAD, Fe-S</td>
</tr>
<tr>
<td>III Ubiquinone:cytochrome c oxidoreductase</td>
<td>250</td>
<td>11</td>
<td>Hemes, Fe-S</td>
</tr>
<tr>
<td>Cytochrome c^i</td>
<td>13</td>
<td>1</td>
<td>Heme</td>
</tr>
<tr>
<td>IV  Cytochrome oxidase</td>
<td>160</td>
<td>13 (3–4)</td>
<td>Hemes; Cu\textsubscript{A}, Cu\textsubscript{B}</td>
</tr>
</tbody>
</table>

*Number of subunits in the bacterial equivalents in parentheses.

^Cytochrome c is not part of an enzyme complex; it moves between Complexes III and IV as a freely soluble protein.

Table 19-3
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Flow of Electrons from Biological Fuels into the Electron-Transport Chain
NADH:ubiquinone oxidoreductase, a.k.a. Complex I

- One of the largest macro-molecular assemblies in the mammalian cell
- Over 40 different polypeptide chains, encoded by both nuclear and mitochondrial genes
- NADH binding site in the matrix side
- Noncovalently bound flavin mononucleotide (FMN) accepts two electrons from NADH
- Several iron-sulfur centers pass one electron at a time toward the ubiquinone binding site
NADH:Ubiquinone oxidoreductase is a proton pump

- Transfer of two electrons from NADH to ubiquinone is accompanied by a transfer of protons from the matrix (N) to the intermembrane space (P).
- Experiments suggest that about four protons are transported per one NADH.

\[ \text{NADH} + \text{Q} + 5\text{H}^+_{\text{N}} = \text{NAD}^+ + \text{QH}_2 + 4 \text{H}^+_{\text{P}} \]

- Reduced coenzyme Q picks up two protons.
- Protons are transported by proton wires:
  - A series of amino acids that undergo protonation and deprotonation to get a net transfer of a proton from one side of a membrane to another.
Succinate Dehydrogenase, a.k.a. Complex II

- FAD accepts two electrons from succinate
- Electrons are passed, one at a time, via iron-sulfur centers to ubiquinone, which becomes reduced QH$_2$
- Does not transport protons

\[ \Delta G^{\circ} = 0 \text{ kJ/mol} \]
Complex II

Intermembrane space (P side)
Phosphatidylethanolamine

Matrix (N side)
Heme b

QH₂
Ubiquinone
Fe-S centers

Figure 19-10
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Ubiquinone: Cytochrome c Oxidoreductase, a.k.a. Complex III

- Uses two electrons from QH$_2$ to reduce two molecules of cytochrome c
- Additionally contains iron-sulfur clusters, cytochrome $bs$, and cytochrome $cs$
- The Q cycle results in four additional protons being transported to the IMS
Complex III

Figure 19-11
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The Q Cycle

- Experimentally, four protons are transported across the membrane per two electrons that reach CytC
- Two of the four protons come from QH₂
- The Q cycle provides a good model that explains how two additional protons are picked up from the matrix
- Two molecules of QH₂ become oxidized, releasing protons into the IMS
- One molecule becomes rereduced, thus a Net transfer of four protons per reduced Coenzyme Q
The Q Cycle

\[
\begin{align*}
\text{QH}_2 + Q + \text{cyt c}_1 (\text{oxidized}) & \longrightarrow QH_2 + Q^- + 2H^+_N + \text{cyt c}_1 (\text{oxidized}) \\
Q + Q^- + 2H^+_p + \text{cyt c}_1 (\text{reduced}) & \longrightarrow Q + 2H^+_p + \text{QH}_2 + \text{cyt c}_1 (\text{reduced})
\end{align*}
\]

Net equation: \( \text{QH}_2 + 2 \text{cyt c}_1 (\text{oxidized}) + 2H^+_N \longrightarrow Q + 2 \text{cyt c}_1 (\text{reduced}) + 4H^+_p \)

Figure 19-12
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The Q Cycle: Cycle 1

\[
\begin{align*}
QH_2 + Q + \text{cyt } c_1 \text{ (oxidized)} & \rightarrow \\
Q + 'Q^- + 2H_p^+ + \text{cyt } c_1 \text{ (reduced)}
\end{align*}
\]

Figure 19-12
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The Q Cycle: Cycle 2

\[
\begin{align*}
\text{QH}_2 + Q + \text{cyt c}_1 \text{ (oxidized)} & \rightarrow \text{QH}_2 + 'Q' + 2H_p^+ + \text{cyt c}_1 \text{ (reduced)} \\
Q + 'Q' + 2H_p^+ + \text{cyt c}_1 \text{ (reduced)} & \rightarrow \text{Q} + 2H_p^+ + \text{QH}_2 + \text{cyt c}_1 \text{ (oxidized)}
\end{align*}
\]

Net equation: \[
\text{QH}_2 + 2 \text{ cyt c}_1 \text{ (oxidized)} + 2H_N^+ \rightarrow \text{Q} + 2 \text{ cyt c}_1 \text{ (reduced)} + 4H_p^+
\]
Cytochrome c

- The second mobile electron carrier
- A soluble heme-containing protein in the intermembrane space
- Heme iron can be either ferrous (Fe$^{3+}$, oxidized) or ferric (Fe$^{2+}$, reduced)
- Cytochrome c carries a single electron from the cytochrome $bc_1$ complex to cytochrome oxidase
Cytochrome c absorbs visible light

- Intense Soret band near 400 nm absorbs blue light and gives cytochrome c an intense red color
- Cytochromes are named by the position of their longest-wavelength (α) peak
Cytochrome Oxidase, a.k.a. Complex IV

- Mammalian cytochrome oxidase is a membrane protein with 13 subunits
- Contains two heme groups: $a$ and $a_3$
- Contains copper ions
  - $Cu_A$: two ions that accept electrons from Cyt c
  - $Cu_B$: bonded to heme $a_3$ forming a binuclear center that transfers four electrons to oxygen
Cytochrome oxidase passes electrons to $O_2$

- Four electrons are used to reduce one oxygen molecule into two water molecules.
- Four protons are picked up from the matrix in this process.
- Four additional protons are passed from the matrix to the intermembrane space.
Electron flow through Complex IV

Figure 19-14
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Multiple complexes associate together to form a respirasome

Figure 19-15
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Summary of the Electron Flow in the Respiratory Chain

Figure 19.16
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Summary of Electron Transport

• Complex I → Complex IV

\[ 1\text{NADH} + 11\text{H}^{+}_{(N)} + \frac{1}{2}\text{O}_2 \rightarrow \text{NAD}^+ + 10\text{H}^{+}_{(P)} + \text{H}_2\text{O} \]

• Complex II → Complex IV

\[ \text{FADH}_2 + 6\text{H}^{+}_{(N)} + \frac{1}{2}\text{O}_2 \rightarrow \text{FAD} + 6\text{H}^{+}_{(P)} + \text{H}_2\text{O} \]

Difference in number of protons transported reflects differences in ATP synthesized.
Reactive oxygen species can damage biological macromolecules.

Figure 19-18
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Proton-Motive Force

• The proteins in the electron-transport chain created the **electrochemical proton gradient** by one of three means:
  – actively transport protons across the membrane
    • Complex I and Complex IV
  – Chemically remove protons from the matrix
    • Reduction of CoQ and reduction of oxygen
  – Release protons into the intermembrane space
    • Oxidation of QH₂
Proton-Motive Force

\[ \text{P side} \]
\[ [H^+]_P = C_2 \]

\[ \text{N side} \]
\[ [H^+]_N = C_1 \]

\[ \Delta G = RT \ln \left( \frac{C_2}{C_1} \right) + Z \Delta \varepsilon \psi \]
\[ = 2.3RT \Delta p \text{H} + \varepsilon \Delta \psi \]
Chemiosmotic Model for ATP Synthesis

- **Electron transport** sets up a proton-motive force
- Energy of proton-motive force **drives synthesis of ATP**

---

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Consequently, electron transport is coupled to ATP synthesis

• As described, ATP synthesis requires electron transport
• But electron transport also requires ATP synthesis
Mitochondrial ATP Synthase Complex

• Contains two functional units:
  - $F_1$
    • Soluble complex in the matrix
    • Individually catalyzes the hydrolysis of ATP
  - $F_0$
    • Integral membrane complex
    • Transports protons from IMS to matrix, dissipating the proton gradient
    • Energy transferred to $F_1$ to catalyze phosphorylation of ADP
Mitochondrial ATP Synthase Complex

Apoptosome causes dimerization of procaspase-9, creating active caspase-9 dimers.

Caspase-9 catalyzes proteolytic activation of caspase-3 and caspase-7.

These caspases lead to the death and resorption of the cell.

Figure 19-39 part 2
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The $F_1$ catalyzes $\text{ADP} + P_i \rightleftharpoons \text{ATP}$

- Hexamer arranged in three $\alpha\beta$ dimers
- Dimers can exist in three different conformations:
  - Open: empty
  - Loose: binding ADP and $P_i$
  - Tight: catalyzes ATP formation and binds product
Binding-Change Model
Coupling Proton Translocation to ATP Synthesis

- Proton translocation causes a rotation of the $F_0$ subunit and the central shaft $\gamma$
- This causes a conformational change within all the three $\alpha\beta$ pairs
- The conformational change in one of the three pairs promotes condensation of ADP and $P_i$ into ATP
Evidence of Rotation
Transport of ADP and $P_i$ into the Matrix
Malate-Aspartate Shuttle

Figure 19-31
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<table>
<thead>
<tr>
<th>Process</th>
<th>Direct product</th>
<th>Final ATP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glycolysis</td>
<td>2 NADH (cytosolic)</td>
<td>3 or 5*</td>
</tr>
<tr>
<td></td>
<td>2 ATP</td>
<td>2</td>
</tr>
<tr>
<td>Pyruvate oxidation (two per glucose)</td>
<td>2 NADH (mitochondrial matrix)</td>
<td>5</td>
</tr>
<tr>
<td>Acetyl-CoA oxidation in citric acid cycle (two per glucose)</td>
<td>6 NADH (mitochondrial matrix)</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>2 FADH$_2$</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>2 ATP or 2 GTP</td>
<td>2</td>
</tr>
<tr>
<td><strong>Total yield per glucose</strong></td>
<td></td>
<td><strong>30 or 32</strong></td>
</tr>
</tbody>
</table>

*The number depends on which shuttle system transfers reducing equivalents into the mitochondrion.*

Table 19-5

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Regulation of Oxidative Phosphorylation

• Primarily regulated by substrate availability
  – NADH and ADP/P_i
  – Due to coupling both substrates required for electron transport and ATP synthesis

• Inhibitor of F₁ (IF₁)
  – Prevents hydrolysis of ATP during low oxygen
  – Only active at lower pH, encountered when electron transport it stalled (i.e., low oxygen)

• Inhibition of OxPhos leads to accumulation of NADH
  – Causes feedback inhibition cascade up to PFK-1 in glycoysis
Regulation of Oxidative Phosphorylation

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Light Energy is Converted to ATP in Plant Chloroplasts

- Light reactions:
  - $\text{H}_2\text{O} \rightarrow \text{O}_2$,
  - NADP$^+$ to NADPH,
  - ADP + $P_1$ to ATP,

- Carbon-assimilation reactions:
  - Carbohydrate to CO$_2$.

(a) Chloroplast diagram:
- Outer membrane
- Inner membrane
- Grana (thylakoids)
- Stroma

(b) Enlarged view of chloroplast:

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Figure 19-47
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Various Pigments Harvest the Light Energy

Chlorophyll $a$

- Saturated bond in bacteriochlorophyll

Phytol side chain

β-Carotene

- Unsaturated bond in phycocyanobilin

Phycocyanobilin

Lutein (xanthophyll)

- Saturated bond in bacteriochlorophyll
Photopigments absorb different wavelengths of light

The energy is transferred to the photosynthetic reaction center
Organization of Light-Absorbing Molecules in Chloroplasts

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From Light Energy to Charge Separation

1. Light excites an antenna molecule (chlorophyll or accessory pigment), raising an electron to a higher energy level.

2. The excited antenna molecule passes energy to a neighboring chlorophyll molecule (exciton transfer), exciting it.

3. This energy is transferred to a reaction-center chlorophyll, exciting it.

4. The excited reaction-center chlorophyll passes an electron to an electron acceptor.

5. The electron hole in the reaction center is filled by an electron from an electron donor.

The absorption of a photon has caused separation of charge in the reaction center.

Figure 19-55
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Chloroplasts couple the two types of photosystems found in bacteria.
Photosystem II evolves oxygen
Water-Splitting

(a)

\[ \text{2H}_2\text{O} \rightarrow \text{H}^+ + \text{H}^+ + \text{O}_2 \]

(b)

Figure 19-64

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Photosystem I results in reduced NADPH
Structure of Photosystem I

Figure 19-60bc
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Cytochrome $b_{6}f$ Complex links PS II and I and translocates protons into the lumen.
Organization of photosynthetic machinery in the thylakoid membrane

Figure 19-62a
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Location of phosynthetic machinery in the thylakoid membrane
Light-induced redox reactions cause acidification of lumen

The proton-motive force across the thylakoid membrane drives the synthesis of ATP.
Flow of Protons: Mitochondria, Chloroplasts, Bacteria

- According to endosymbiotic theory, mitochondria and chloroplasts arose from entrapped bacteria
- Bacterial cytosol became mitochondrial matrix and chloroplast stroma
Chapter 19: Summary

In this chapter, we learned:

• The reduced cofactors pass electrons into the electron-transport chain in mitochondria

• The energy of sunlight creates charge separation in the photosynthetic reaction complex

• Stepwise electron transport is accompanied by the directional transport of protons across the membrane against their concentration gradient

• The energy in the electrochemical proton gradient drives synthesis of ATP by coupling the flow of protons via ATP synthase to conformational changes that favor formation of ATP in the active site