Chapter 6

BIOENERGETICS

STUDENTS'LEARNING OUTCOMES

After studying this chapter, the students will be able to:

- Explain the role of light, carbon dioxide and water in photosynthesis.
- Identify the two general kinds of photosynthetic pigments (carotenoids and chlorophylls).
- Describe the roles of photosynthetic pigments in the absorption and conversion of light energy.
- Differentiate between the absorption spectra of chlorophyll 'a' and 'b'.
- Draw the molecular structure of chlorophyll.
- Describe the arrangements of photosynthetic pigments in the form of photosystem-I and II.
- Describe the events of non-cyclic photophosphorylation and outline the cyclic photophosphorylation.
- Draw the Z-scheme for explaining the events the light dependent reactions.
- Explain the Calvin cycle.
- Develop a flow chart for explaining the events of light reactions.
- Describe the features of ATP that make it suitable as the universal energy currency.
- Describe the synthesis and breakdown of ATP.
- Describe the four stages in aerobic respiration in eukaryotic cells:
- Explain the process of anaerobic respiration in terms of glycolysis and conversion of pyruvate into lactic acid or ethanol.
- Outline the events of glycolysis (naming the reactants and products of each step).
- Describe the link reaction, including the role of coenzyme A.
- Outline the Krebs cycle (naming the reactants and products of each step).
- Describe the role of NAD and FAD in cellular respiration.
- Explain that passage of electrons through electron transport chain highlighting the oxidation and reduction reactions (details of carriers are not required).
- Describe chemiosmosis and relate it to electron transport chain.
- Explain why the energy yield from respiration in aerobic conditions is much greater than the energy yield from respiration in anaerobic conditions.

Every living organism, from the smallest bacterium to the largest whale, is driven by energy. This energy fuels their growth, reproduction, and daily survival, making it a fundamental aspect of life. But where does this energy come from? How is it harnessed and utilized by cells to perform countless activities essential for life? The answer lies in the fascinating field of bioenergetics.

Nearly all the energy used by living organisms on Earth comes from photosynthesis. Plants, algae, and certain bacteria capture sunlight and convert it into chemical energy, forming the base of the food chain.

Bioenergetics is the study of how energy flows through living systems. It explores the processes through which cells store and expend energy. The processes of photosynthesis and respiration help to understand some of the principles of bioenergetics. Photosynthesis acts as an energy–capturing while respiration as an energy-releasing process.

ATP: The Energy Currency of Cells

Cells use a special energy currency for their reactions. This currency is actually a **nucleotide** called **adenosine triphosphate (ATP).** When cells store energy, they make ATP. When cells need energy, they break ATP. A molecule of ATP has three subunits **i.e. adenine,** (a nitrogen containing base); **ribose** (a five-carbon sugar) and three **phosphate** groups.

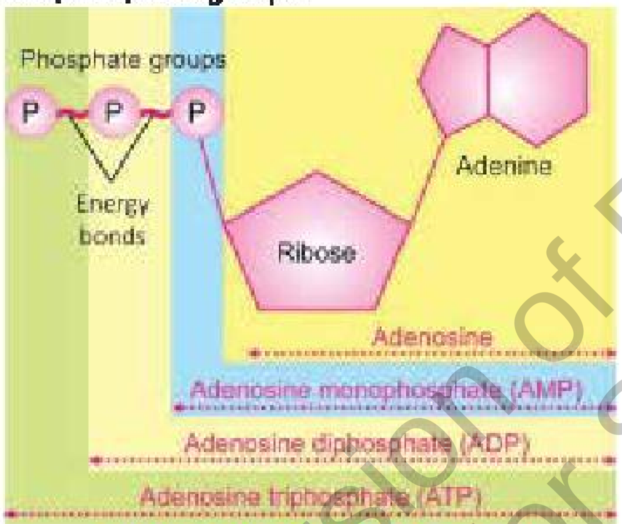


Figure 6.1: Molecular structure of ATP

ATP was discovered in 1929 by **Karl Lohmann.**
In 1941, the Nobel prize winner, **Fritz Lipmann** proposed that ATP is the main energy-transfer molecule in the cell.

The covalent bonds between two phosphates are high-energy bonds. When one of these bonds is broken, inorganic phosphate (Pi) separates and energy is released. The breaking of one phosphate bond releases about 7.3 kcal (7,300 calories) per mole of ATP.

$$ATP + H_2O \rightarrow ADP + P_i + \text{energy } (7.3 \text{ kcal/mole})$$

In common energy reactions only the outer P-P high-energy bond breaks. When this happens, ATP becomes **ADP (adenosine diphosphate)** and one Pi is released.

In some cases, ADP is further broken down to **AMP (adenosine monophosphate)** and Pi:

$$ADP + H_2O \rightarrow AMP + P_i + \text{energy } (7.3 \text{ kcal/mole})$$

Cells get energy from the oxidation of food. They store this energy by combining ADP with P_i to form ATP. So, we can summarize that ATP is made during energy-releasing processes and it is broken down during energy-consuming processes. In this way ATP transfers energy between metabolic reactions.

6.1- PHOTOSYNTHESIS

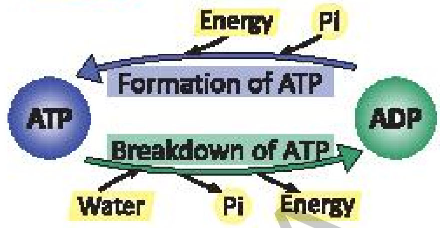


Figure 6.2: ATP-ADP Cycle

Photosynthesis involves the use of light energy that is absorbed and converted into chemical energy by photosynthetic pigments. Photosynthesis in plants can be summarized as:

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

Carbon dioxide, water and light are the reactants while glucose and oxygen are the products. Water appears on both sides of the equation because water is used as reactant in some reactions and released as product in others. However, there is no net yield of water.

Recalling:
Photosynthesis is the process in which the energy-poor inorganic compounds of carbon (i.e., CO_2) are reduced to energy-rich carbohydrates.

Compensation Point: Photosynthesis uses the products of respiration and respiration uses the products of photosynthesis. Photosynthesis occurs only during day time but respiration goes on day and night. During darkness, leaves and other parts respire and utilize oxygen and release carbon dioxide. At dawn and dusk, when light intensity is low, the rate of photosynthesis and respiration may be equal for a short time. Thus, the oxygen released from photosynthesis is just equal to the amount required for cellular respiration. Also, the carbon dioxide released by respiration is just equal to the amount required by photosynthesizing cells. At this moment there is no net gas exchange between leaves and atmosphere. This is termed as compensation point. At noon, when the light intensity increases, the rate of photosynthesis also increases. At this time, there is more requirement of carbon dioxide. Respiration alone cannot supply this carbon dioxide. Similarly, the oxygen produced during photosynthesis is more than the need of the respiring cells. So, the result is the net release of oxygen coupled with the uptake of carbon dioxide.

Role of Light

Light plays a crucial role in photosynthesis, providing the energy required to drive the chemical reactions that transform simple molecules into complex organic compounds. Light energy is absorbed by chlorophyll. The absorbed light energy is converted into chemical energy, which is in turn stored in organic compounds in the form of C-H bond energy. It happens like this;

Plants convert only about 1-2% of the solar energy they receive into chemical energy during photosynthesis. Despite this seemingly low efficiency, this conversion is enough to sustain almost all life on Earth.

Action Spectrum

Photosynthetic pigments absorb different wavelengths of light at different rates. Moreover, the different wavelengths are also differently effective in photosynthesis. The effectiveness of different wavelengths of light is determined in terms of action spectrum. For getting action spectrum of light, a plant is illuminated with different colours of light one by one. While providing each colour, the rate of photosynthesis is measured by measuring the amount of oxygen emitted from leaves. The data is plotted in a graph called action spectrum. The first action spectrum was made by a German biologist, T. W. Engelmann in 1883. He worked on the photosynthetic pigments of *Spirogyra*. When the cells of a filament of *Spirogyra* were illuminated with different wavelengths of light, maximum photosynthesis occurred in the cells which received blue and red spectrum of light and so maximum oxygen was emitted from these cells.

Role of Carbon Dioxide

Sugar is formed by the reduction of CO_2 by using ATP and NADPH. In this way, CO_2 acts as the source of carbon for making sugars. Carbon dioxide enters the leaves through stomata and gets dissolved in water absorbed by the cell walls of mesophyll cells. Stomata are found in large numbers in leaves. The entry of CO_2 into the leaves is dependent upon the opening of stomata.

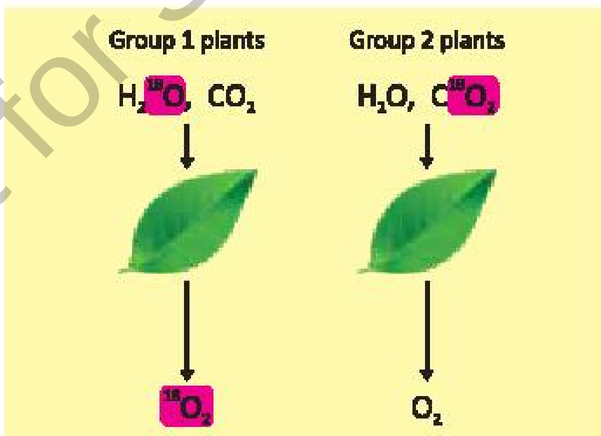
About 10% of total photosynthesis is carried out by terrestrial plants, the rest occurs in oceans, lakes and ponds. Aquatic photosynthetic organisms use dissolved CO_2, bicarbonates and soluble carbonates as carbon source. Land photosynthetic organisms use atmospheric CO_2 as carbon source.

Neil's hypothesis was based on the investigations on photosynthetic bacteria that make carbohydrate from carbon dioxide, but do not release oxygen.

Role of Water

Water is the source of hydrogen, for the reduction of CO_2 during photosynthesis. Oxygen released during photosynthesis comes from water, and so water is an important source of atmospheric oxygen which most organisms need for aerobic respiration and thus for obtaining energy to live.

In 1930s, **Van Neil** hypothesized that plant splits water as a source of hydrogen, releasing oxygen as a by-product. Neil's hypothesis was later confirmed by scientists during 1940s. An experiment was conducted in which isotopic tracer (^{18}O) of oxygen was used. In laboratory, scientists



Group 1

$$6CO_2 + 12H_2{}^{18}O \longrightarrow C_6H_{12}O_6 + 6H_2O + 6\,{}^{18}O_2$$

Group 2

$$6C^{18}O_2 + 12H_2O \longrightarrow C_6H_{12}{}^{18}O_6 + 6H_2{}^{18}O + 6O_2$$

Figure 6.3: Experiment to prove that water is the source of oxygen released in photosynthesis

prepared water with heavy-oxygen i.e., $H_2{}^{18}O$. They also prepared carbon dioxide with heavy oxygen i.e., $C^{18}O_2$. Experimental green plants in one group were given water $H_2{}^{18}O$ and normal carbon dioxide i.e., $C^{16}O_2$. Plants in the second group were given $C^{18}O_2$ and normal water i.e., $H_2{}^{16}O$. Both plants were given an environment to conduct photosynthesis. Oxygen released during photosynthesis of both plants was collected and tested. It was found that plants of first group produced ^{18}O but the plants of second group produced normal oxygen (^{16}O).

In photosynthesis water is split to release hydrogen. This hydrogen reduces the coenzyme nicotinamide adenine dinucleotide phosphate (NADP) to NADPH. The reduced coenzyme i.e., NADPH serves as the "reducing power" for the reduction of CO_2 to form sugar.

Role of Photosynthetic Pigments

Photosynthetic pigments are present in thylakoid membranes. These pigments capture light energy necessary for photosynthesis. Soe of the pigments are chlorophyll a, chlorophyll b, xanthophylls, carotenes. Different pigments absorb light of different wavelengths (colours). Light behaves like a stream of particles called photons. Pigment molecules absorb one photon at a time.

> Short wavelength photons (blue) have a higher energy than long wavelength (red) photons. More energetic photons (shorter wavelength) promote electrons to higher energy levels.

When a pigment molecule absorbs a photon, its electrons move to higher energy level, So, it becomes energy-rich or excited.

Chlorophylls

Chlorophyll is a lipid molecule. Chlorophylls are of different kinds. Chlorophyll a, b, c and d are found in plants and algae, while the others are found in photosynthetic bacteria and are known as bacteriochlorophylls.

A molecule of chlorophyll consists of two parts i.e., a hydrophilic head and a hydrophobic tail. The head is made of a porphyrin ring, which further consists of four pyrrole rings (5-sided N-containing compounds). The four pyrrole rings are held together by a magnesium atom in the centre. In chlorophyll-a, the second pyrrole ring has methyl (CH_3) group while in chlorophyll-b, it has aldehyde (CHO) group at the same spot. The porphyrin ring of chlorophyll absorbs light. The tail is made of long hydrocarbon chain. It anchors the molecule in the thylakoid membrane.

Chlorophylls absorb mainly violet-blue and orange-red wavelengths of light. Green wavelengths are least absorbed by chlorophylls and are transmitted or reflected.

> Carotenoids, such as beta-carotene, play dual role in photosynthesis. They capture light energy in the blue and green regions of the spectrum and protect the photosynthetic apparatus from damage by excess light.

Accessory Pigments

Accessory pigments include all the pigments, other than chlorophyll-a, which can gather light for photosynthesis. Chlorophyll b is an accessory pigment and others are carotenoids (carotenes and xanthophylls) and phycobilins. Chlorophyll b and carotenoids are found in plants while phycobilins are found in the red algae and cyanobacteria.

When accessory pigments absorb light, they pass on the energy towards chlorophyll a. It is generally believed that the order of transfer of energy in plants is;

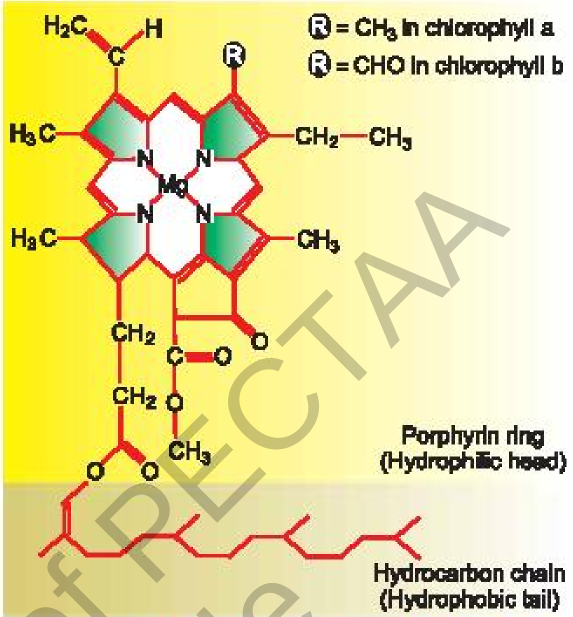


Figure 6.4: Molecular structure of chlorophyll a and chlorophyll b

Carotenoids → Chlorophyll b → Chlorophyll a

Absorption Spectrum

A graph showing different wavelengths absorbed by a pigment, is called absorption spectrum of the pigment. Absorption spectrum of chlorophylls indicates that absorption of blue light (430 nm) and red light (670 nm) is maximum. Absorption peaks of carotenoids are different from those of chlorophylls (Fig 6.5-a). Action spectrum of photosynthesis also shows that blue and red parts lights are the most effective. This means that the action spectrum of photosynthesis coincides with the absorption spectrum of photosynthetic pigments.

Some wavelengths not absorbed by chlorophyll-a are very affectively absorbed by chlorophyll-b and vice-versa. Such differences increase the range of light absorbed by both chlorophylls.

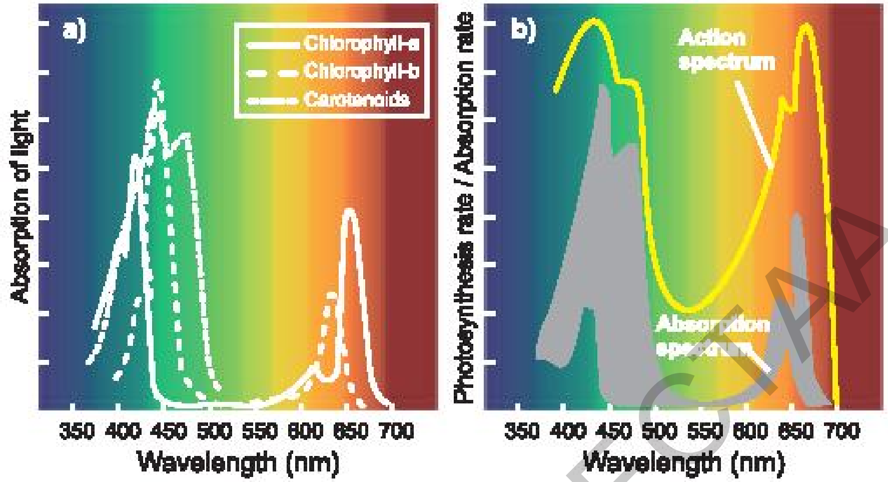


Figure 6.5: (a)-Absorption spectrum; (b)- Action spectrum

Organization of Photosynthetic Pigments (Photosystems)

For efficient absorption and utilization of solar energy, photosynthetic pigments are organized into clusters, called photosystems. These photosystems are embedded in thylakoid membranes of chloroplasts.

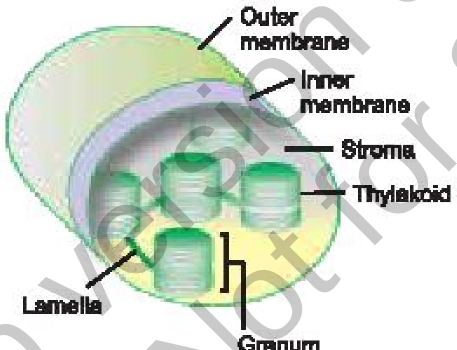


Figure 6.6: Structure of Chloroplast

Photosystems contain photosynthetic pigments and the carriers of electron transport chain. Each photosystem consists of a light gathering **'antenna complex'** and a **'reaction centre'** (Fig 6.7). Antenna complex has many pigment molecules which capture light energy and pass the excitation energy (in the form of high-energy electrons) to the reaction centre. The reaction centre has one or more molecules of chlorophyll-a, which pass the high-energy electrons to a primary electron acceptor. The electron acceptor passes them on to the series of electron carriers, collectively called electron transport chain.

In chloroplast, there are two photosystems, photosystem-I (PS-I) and photosystem-II (PS-II). These are named so in order of their discovery. PS-I has P700 chlorophyll-a molecule in its reaction centre and it absorbs maximum light of 700 nm.

The reaction centre of PS-II has P680 chlorophyll-a, which absorbs best the light of 680 nm.

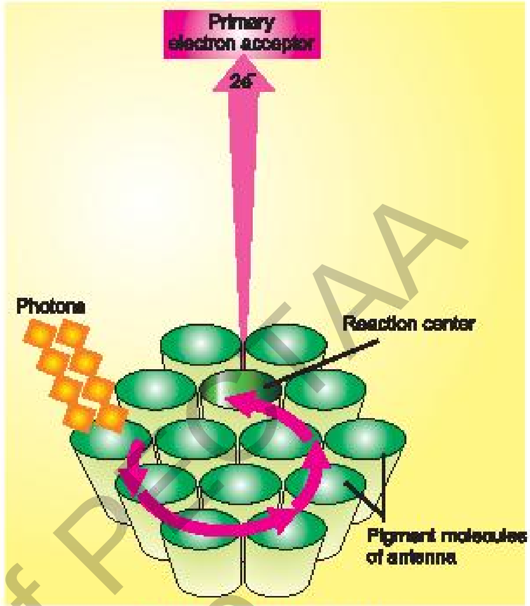


Figure 6.7: Photosystem

Mechanism of Photosynthesis

Photosynthesis is a redox (oxidation-reduction) process. As indicated in the photosynthesis equation below, when water molecules are split apart, they are actually oxidized (they lose electrons and hydrogen ions) and yield oxygen. Meanwhile, CO_2 is reduced to sugar as electrons and hydrogen ions are added to it. In this way oxidation and reduction go hand in hand.

Reduction ($CO_2 \rightarrow C_6H_{12}O_6$); Oxidation ($H_2O \rightarrow O_2$)

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

However, it is not a simple, single-step process. Rather, it is a complex metabolic pathway consisting of a series of reactions. The light-dependent reactions take place on the thylakoid membranes of the grana while the light-independent reactions take place in the stroma of the chloroplasts. Figure 6.8 shows the summary of these reactions.

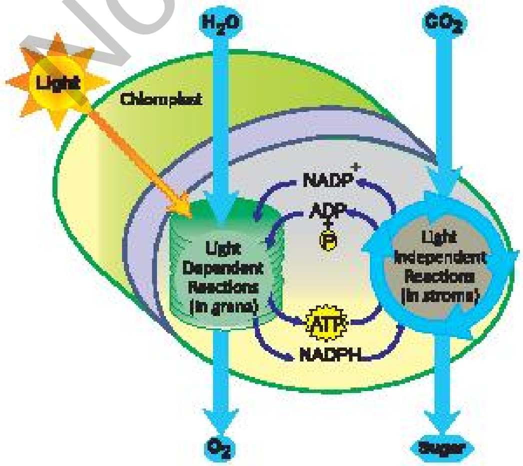


Figure 6.8: Overview of photosynthesis

1- Light- Dependent Reactions

During light dependent reactions, light energy is absorbed and converted into chemical energy, which is in the form of reducing and assimilating powers i.e., NADPH and ATP.
Light independent reactions use NADPH and ATP for the reduction CO_2 and thus store chemical energy in the form of C-H bond energy

The key events in the light-dependent reactions of photosynthesis are (1) the absorption of light energy by photosynthetic pigments, (2) the excitation of electrons by that energy, and (3) the formation of ATP and NADPH.

The formation of ATP is the most important step of light-dependent reactions. It is called photophosphorylation. This process is either non-cyclic photophosphorylation or cyclic photophosphorylation.

a)- Non -Cyclic Photophosphorylation

It is the usual way of the production of ATPs during light-dependent reactions. In non-cyclic pathway, both photosystems i.e., PS-I and PS-II participate and two electron chains are involved (Fig. 6.9). It happens in the following way.

1- **Absorption of light by PS-II:** When light falls on PS-II, the energy level of chlorophyll molecules of its antenna centre rises. Two excited electrons move from them and pass to different chlorophyll molecules. The excited electrons reach P680 chlorophyl present in the reaction centre. Due to energy boost of P680 chlorophyll, its two excited electrons pass to the primary electron acceptor of photosystem-II. Due to it, an electron "hole" is created in p680 chlorophyll, which has become a strong oxidizing agent.

The oxygen produced during photolysis is the main source of atmospheric oxygen.

2- **Photolysis of water:** The electron "hole" in chlorophyll molecule is filled by the electrons from water. When water molecule reacts with oxidized chlorophyll in PS-II, it breaks into two hydrogen ions, an oxygen atom (which immediately combines with another oxygen to form O_2), and two electrons. These two electrons fill the "hole" in P680 chlorophyll. This water splitting step of photosynthesis is called **photolysis**.

3- **Electron flow from PS-II to PS-I:** In step 1, the photoexcited electrons of P680 chlorophyll were received by primary electron acceptor of PS-II. Now, these electrons pass to PS-I via an electron transport chain of PS-II. This chain consists of electron carriers called plastoquinone (PQ), cytochrome complex, and plastocyanin (PC). As electrons move down the chain, their energy goes on decreasing and is used by thylakoid membrane to produce ATP through the process of chemiosmosis.

4- **Absorption of light by PS-I:** In the next step light energy is absorbed by PS-I. The energy level of its chlorophyll molecules boosts to very hight level. The excited electrons of P700 chlorophyll of the reaction centre pass to the primary electron acceptor of PS-I. The electrons coming from PS-II fill the electron "hole" of P700 chlorophyll of PS-I.

5- **Electron flow from PS-I to $NADP^+$:** The primary electron acceptor of PS-I passes the photoexcited electrons to a second electron transport chain. These electrons are received by ferredoxin (FD). An enzyme NADP reductase transfers these electrons from FD to $NADP^+$. When $NADP^+$ gets two electrons and an H^+ ion, it is reduced to NADPH. This reaction stores the high-energy electrons in NADPH.

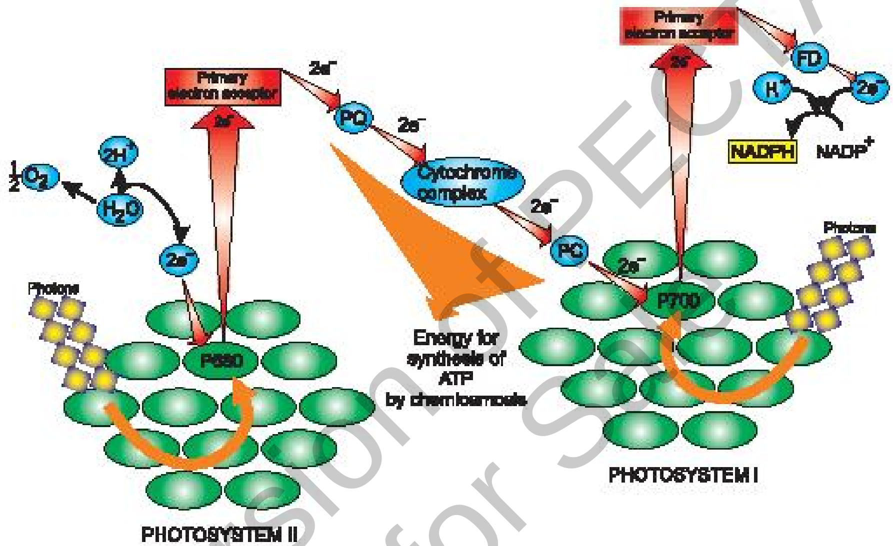


Figure 6.9: Light-dependent reactions (noncyclic photophosphorylation)

So, the light energy gets converted into chemical energy (ATP and NADPH). The zigzag path taken by electrons through PS-II and PS-II and electron transport chains, is called **Z-scheme**

b)- Cyclic Photophosphorylation

Under certain conditions, photoexcited electrons of PS-I take an alternative path called cyclic electron flow. This path uses PS-I but not PS-II. These electrons cycle-back from primary electron acceptor of PS-I to P700 chlorophyll via the electron transport chain. There is no production of NADPH and no release of oxygen. Cyclic flow however generates ATP (Fig 6.10). It happens when Calvin cycle slows down and NADPH accumulates in chloroplast.

Chemiosmosis

During light-dependent reactions when electrons are transferred to the series of carriers of electron transport chain, it results in oxidation and reduction reactions. A carrier is oxidized when it loses electrons and next carrier is reduced when it gets electrons. Electrons lose energy during this carrier-to-carrier transport. Chemiosmosis is the mechanism in which thylakoid membranes couple these redox reactions with the synthesis of ATPs.

How does chemiosmosis use the energy released from electrons to synthesize ATP? Actually, this energy is spent for the active transport of H^+ ions from the stroma of chloroplast to its inner compartment (lumen). In this way many H^+ ions are deposited in the lumen. This H^+ ion gradient in lumen has potential energy. The H^+ ions diffuse back from lumen in stroma (from higher concentration in lumen to lower concentration). While diffusing, they pass through a special protein of the membrane of thylakoid cells. This protein is an enzyme called ATP synthase. This enzyme uses the energy yielded from the flow of H^+ ions to make a bond between ADP and inorganic phosphate (Pi). So, ADP is converted into ATP and energy is packed in it (Fig 6.11).

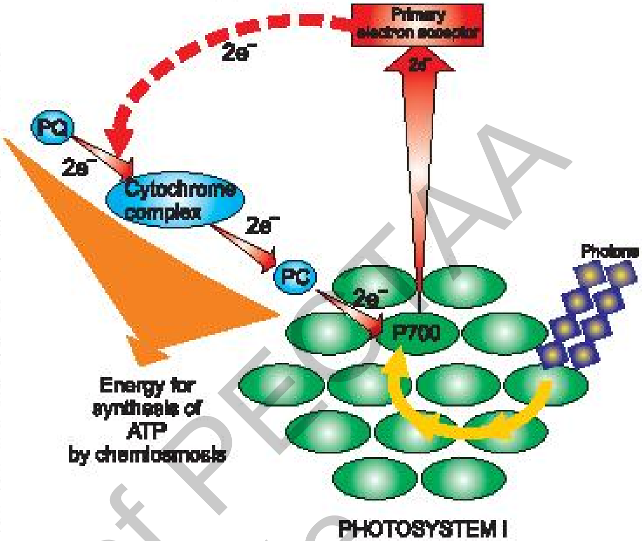


Figure 6.10: Cyclic Photophosphorylation

> The electron transport chains in mitochondria and chloroplasts generate ATP by the same mechanism of chemiosmosis.

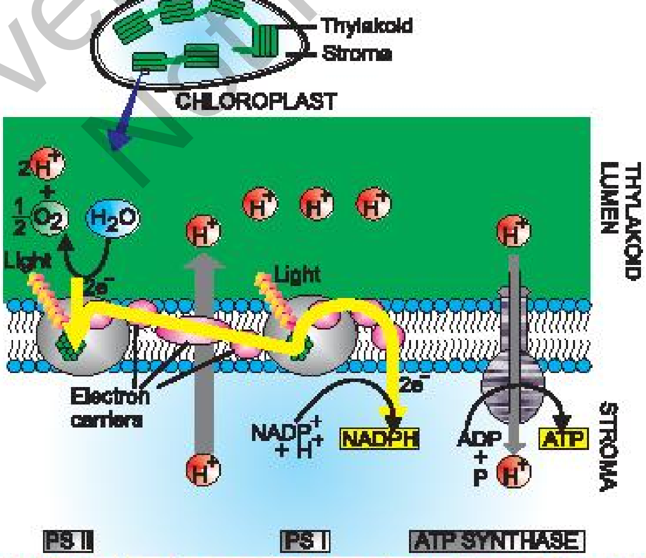


Figure 6.11: Electron transport chain and chemiosmosis in chloroplast

2- Light-Independent Reactions

Light-independent reactions are a series of reactions which happen in the stroma of chloroplast. These reactions use carbon from CO_2, energy from ATP, and hydrogen ions from NADPH to construct energy-rich sugar molecules. These are also called **dark reactions.** These reactions can occur in the absence as well as in the presence of light, as long as ATP and NADPH are available (Fig 6.11). The Calvin cycle is divided into the following phases.

The details of dark reactions were discovered by **Melvin Calvin** and his colleagues at the University of California. That is why, the dark reactions are also called the Calvin cycle. Calvin was awarded Nobel Prize in 1961 for this work.

Phase I: Carbon Fixation

Carbon fixation refers to the initial incorporation of CO_2 into organic material. An enzyme known as ribulose biphosphate carboxylase (or Rubisco; probably the most abundant protein on Earth) combines three molecules of CO_2 with three molecules of a five-carbon sugar named ribulose biphosphate (RuBP). It results in the formation of six molecules of a three–carbon compound called 3–phosphoglyceric acid (3-PGA) or 3-phosphoglycerate.

> Since the product of initial carbon fixation is a three–carbon compound, the Calvin cycle is also known as C-3 pathway.

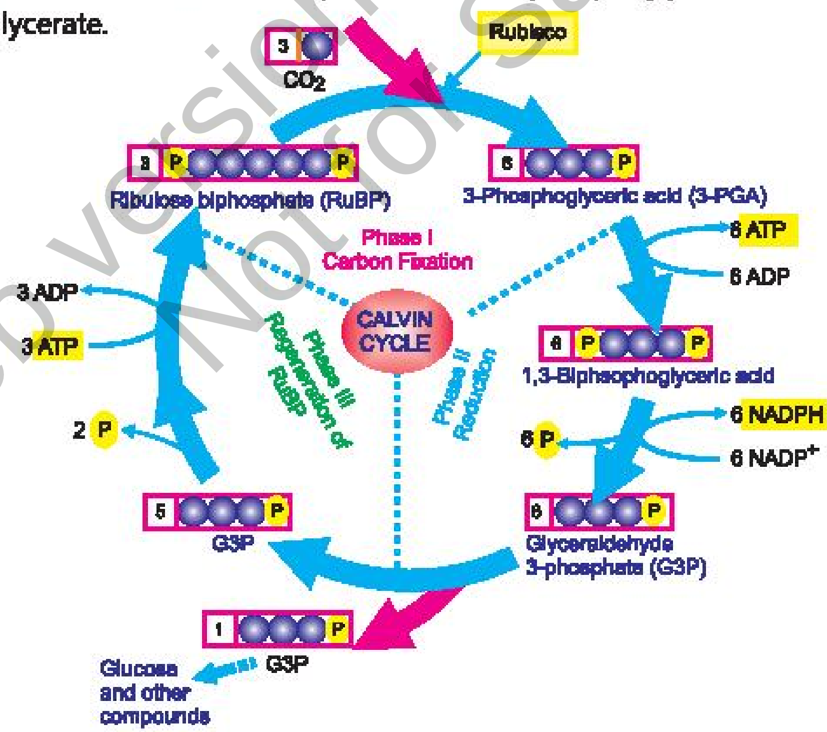


Figure 6.12: The Calvin cycle

Phase II: Reduction

In this phase, six phosphate groups are taken from six ATPs and added to molecules of 3-PGA. In this way, each 3-PGA changes into 1,3-biphsophoglyceric acid. Each 1,3-biphsophoglyceric acid is then reduced to Glyceraldehyde 3-phosphate (G3P). NADPH provides hydrogen for this reduction. During this step, phosphate groups are also detached from 1,3-biphsophoglyceric acid.

> G3P is the same three-carbon sugar which is formed in glycolysis (first phase of cellular respiration) by the splitting of glucose.

In this way, six molecules of G3P are produced, out of which one molecule leaves the cycle. It combines with another G3P and makes glucose, which may be then converted to other carbohydrates.

Phase III: Regeneration of RuBp

Through a series of reactions, five molecules of G3P are converted into three molecules of Ribulose phosphate (RuP). One phosphate group is added to each RuP to make three molecules of RuBP by using three ATPs of light reactions. These RuBP receive CO_2 again, and the cycle continues.

6.2. CELLULAR RESPIRATION

Cellular respiration is the universal process by which organisms break down complex carbon containing compounds (e.g., glucose) to get useable energy. Cellular respiration can be summarized as:

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

> The exchange of CO_2 and O_2 between the organism and its environment is called external respiration or breathing. Cellular respiration is the process by which energy is made available to cells in a step-by-step oxidation of food in the cells.

You can see that the arrangement of atoms in glucose has more stored energy while there is much less energy in the arrangement of atoms in CO_2 and H_2O. The reason is that there are many C-H bonds in glucose but there are no such bonds in CO_2 and H_2O.

The basic events in cellular respiration in all cells are much similar. Almost all cells in all organisms use glucose as energy source. That is why, glucose is known as respiratory fuel. There are two main types of cellular respiration:

> Many of the reactions that occur in your cells also occur in the cells of frog, mice, planaria, mushrooms and radishes.

1. Anaerobic respiration (fermentation) takes place in the absence of oxygen.
2. Aerobic respiration takes place in the presence of oxygen.

In the first step of both these types, glucose is split into two molecules of pyruvic acid ($C_3H_4O_3$) in a process called glycolysis. The next reactions of pyruvic acid are different in anaerobic and aerobic respiration.

Mechanism of Anaerobic Respiration

Anaerobic respiration happens in many microorganisms and in some cells of higher plants. It also happens in the muscle cells of vertebrates. In anaerobic respiration, glucose is not completely oxidized. This type of respiration yields relatively small amount of energy from glucose molecule. As a result of anaerobic respiration, one glucose molecule yields only two ATPs (only about 2% of the energy present in glucose). The energy in two ATPs is equivalent to 14.6 kcal.

Anaerobic respiration consists of glycolysis followed by the reduction of pyruvic acid by NADH to either lactic acid or alcohol and CO_2 i.e., it may again be classified as;

a- Alcoholic Fermentation: In primitive prokaryotic cells (bacteria) and in some eukaryotic cells such as yeast, pyruvic acid is further broken down by alcoholic fermentation into alcohol (C_2H_5OH) and CO_2.

$$\underset{\text{Pyruvic acid}}{2(C_3H_4O_3)} \longrightarrow \underset{\text{Ethyl alcohol}}{2(C_2H_5OH)} + 2CO_2$$

b- Lactic acid Fermentation: In lactic acid fermentation, each pyruvic acid molecule is converted into lactic acid $C_3H_6O_3$ in the absence of oxygen gas.

$$\underset{\text{Pyruvic acid}}{2(C_3H_4O_3)} \xrightarrow{4H} \underset{\text{Lactic acid}}{2(C_3H_6O_3)}$$

This form of anaerobic respiration occurs in muscle cells of humans and other animals. It happens during extreme physical activities, when oxygen cannot be transported to the cells as rapidly as it is needed. Many bacteria also use lactic acid fermentation to get energy.

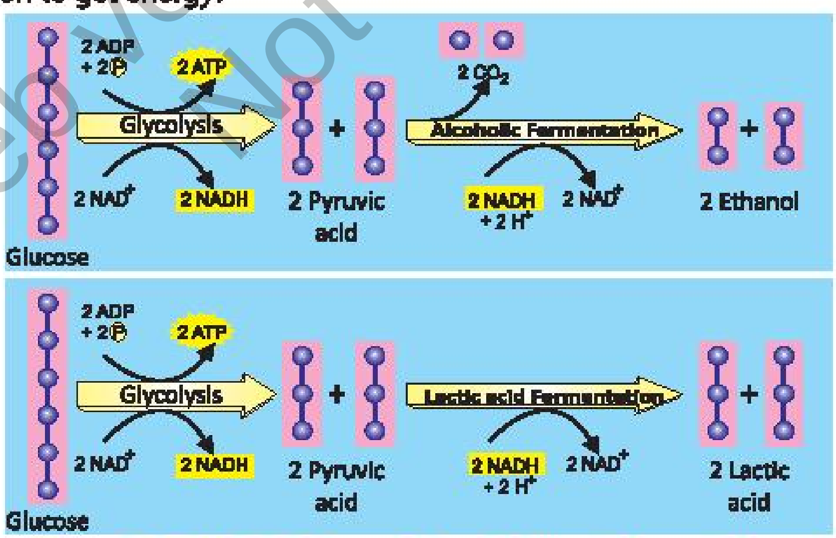


Figure 6.13: Alcoholic fermentation and lactic acid fermentation

Mechanism of Aerobic Respiration

When life evolved on planet Earth free O_2 was not available. So, only anaerobic respiration was possible. But with the evolution of photosynthesis on Earth, molecular oxygen accumulated slowly in the atmosphere. The presence of free oxygen made evolution of aerobic respiration possible.

The complete breakdown of glucose molecule occurs only in aerobic respiration. During aerobic respiration, glucose is broken down to pyruvic acid which is then completely oxidized to CO_2 and water and all the energy stored in its C-H bonds, is released.

Cellular respiration is a continuous process, but for study purposes we can divide it into four main stages.

1- Glycolysis
2- Pyruvic acid oxidation
3- Krebs cycle or citric acid cycle
4- Electron transport chain and Chemiosmosis

Glycolysis occurs in the cytosol and oxygen is not essential for this stage. The other three stages occur within mitochondria where the presence of oxygen is essential (Fig 6.14).

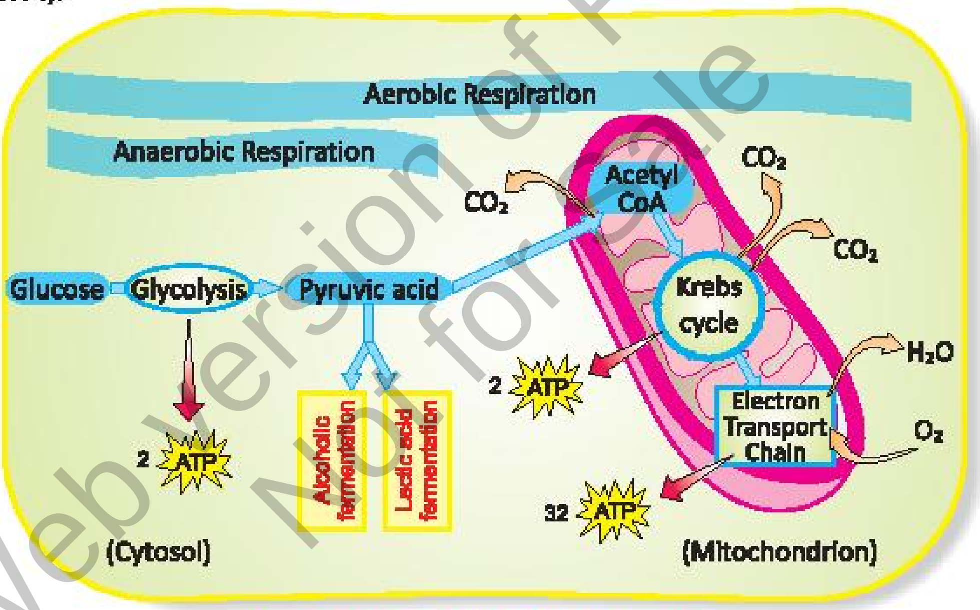


Figure 6.14: Overview of cellular respiration

Stage 1: Glycolysis

Glycolysis is the breakdown of glucose into two molecules of pyruvic acid. Glycolysis takes place in both types of respiration i.e., anaerobic and aerobic. The breakdown of glucose takes place in a series of steps, each catalysed by a specific enzyme (Fig 6.15). All these enzymes are found dissolved in the cytosol. In addition to the enzymes, ATP and coenzyme NAD^+ (nicotinamide adenine dinucleotide) are also essential. Glycolysis involves following reactions.

Preparatory Phase

It involves the expenditure of energy and the breakdown of glucose. It consists of the following steps:

1. A phosphate group is transferred from ATP to glucose. As a result, glucose changes into glucose 6-phosphate.
2. Glucose 6-phosphate is converted into its isomer called fructose 6-phosphate.
3. Another ATP molecule transfers a second phosphate group to fructose 6-phosphate. So, it becomes fructose 1, 6-biphosphate.
4. Fructose 1, 6-biphosphate is highly reactive and breaks into two molecules of three-carbon intermediates i.e., glyceraldehyde 3-phosphate (G3P) and dihydroxy acetone phosphate (DAP). These are inter-converted and result in two molecules of G3P.

Oxidative Phase

It involves the removal of hydrogen from G3P and packing of released energy in the form of ATP. It consists of the following steps:

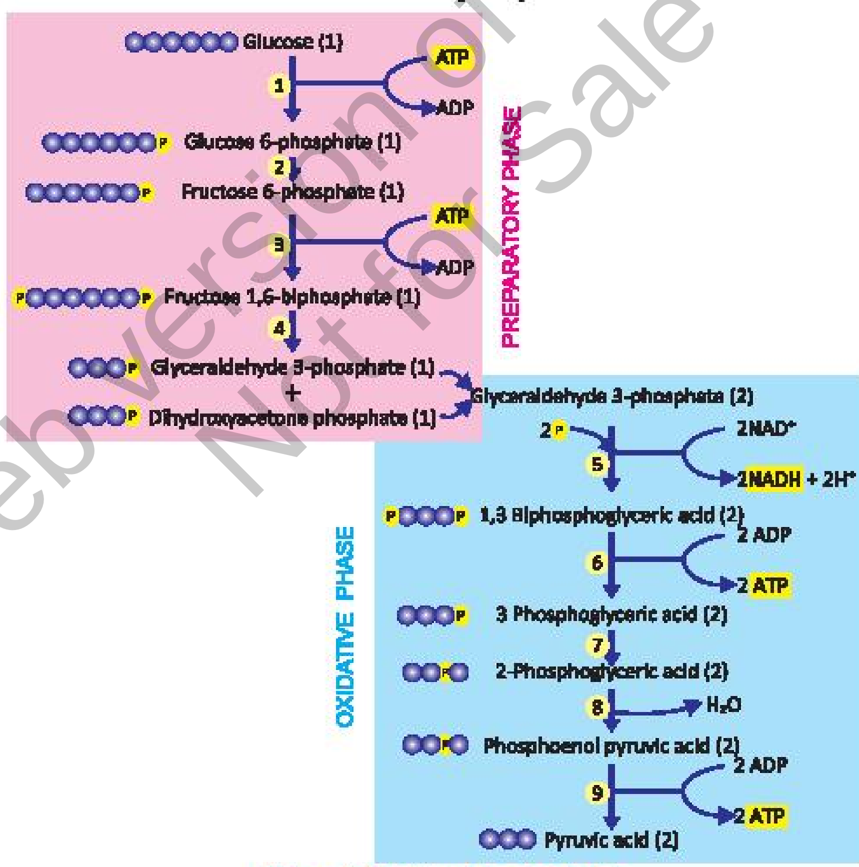


Figure 6.15: Steps in glycolysis

1. Each G3P is oxidized to its acidic form. In this step, two hydrogen atoms (containing two high-energy electrons) are removed from G3P and transferred to NAD^+. At the same time, an inorganic phosphate group is also added to G3P. It results in a molecule of 1, 3-biphosphoglyceric acid (1,3-BPGA).
2. The phosphate group is transferred from 1,3-BPGA to ADP. So, 1,3-BPGA changes into 3-phosphoglyceric acid (3-PGA). A molecule of ATP is also formed in this step.
3. 3-PGA is converted to 2-phosphoglyceric acid (2-PGA).
4. 2-PGA is dehydrated (water removed) into phosphoenol pyruvic acid (PEP).
5. PEP gives up its high energy phosphate to convert a second molecule of ADP to ATP. As a result, PEP is changed into pyruvic acid.

Stage 2: Pyruvic acid Oxidation

Pyruvic acid does not directly participate in Krebs cycle. It has to go through the following changes before entering the Krebs cycle.

> Glucose enters cells from the tissue fluid by passive transport using a specific glucose carrier. This carrier can be controlled (gated) by hormones such as insulin.

> Pyruvic acid can also be turned back into glucose by reversing glycolysis. This is called gluconeogenesis.

1. A molecule of carbon dioxide is removed from pyruvic acid. So, it changes into acetaldehyde.
2. Acetaldehyde is oxidized (hydrogen is removed) to make acetyl group. A molecule of NAD^+ is reduced to NADH.
3. Acetyl group combines with coenzyme-A (CoA) to form acetyl-CoA (Fig 6.16).

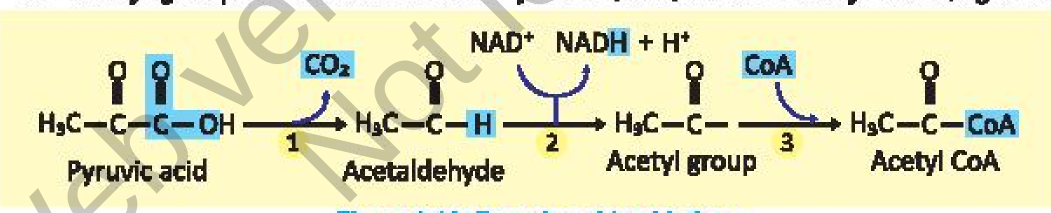


Figure 6.16: Pyruvic acid oxidation

Stage 3: Krebs Cycle

Acetyl-CoA now enters a cyclic series of chemical reactions during which oxidation process is completed (Fig 6.17). Much of this cycle was worked out by a British biochemist, Sir Hans Krebs so it is called the Krebs cycle. It is also called the citric acid cycle, after the six-carbon citric acid molecule formed in its first step. All steps of the citric acid cycle occur in mitochondria. It involves following reactions.

> The release of carbon dioxide takes place before oxygen is involved. It is therefore not true to say that respiration turns oxygen into carbon dioxide. It is more correct to say that respiration turns glucose into carbon dioxide, and oxygen into water.

1. Acetyl-CoA splits into CoA and acetyl group. The acetyl group combines with a four-carbon molecule, oxaloacetic acid. As a result, a six-carbon citric acid is formed.
2. Citric acid undergoes an oxidative decarboxylation reaction. It is decarboxylated (releasing a molecule of CO_2) and then oxidized (reducing an NAD^+ to NADH). So, a five-carbon molecule called alpha-ketoglutaric acid is formed.
3. Alpha-ketoglutaric acid undergoes further oxidation and decarboxylation. It results in the formation of a four-carbon molecule i.e., succinic acid. Succinic acid joins with CoA and makes succinyl CoA.

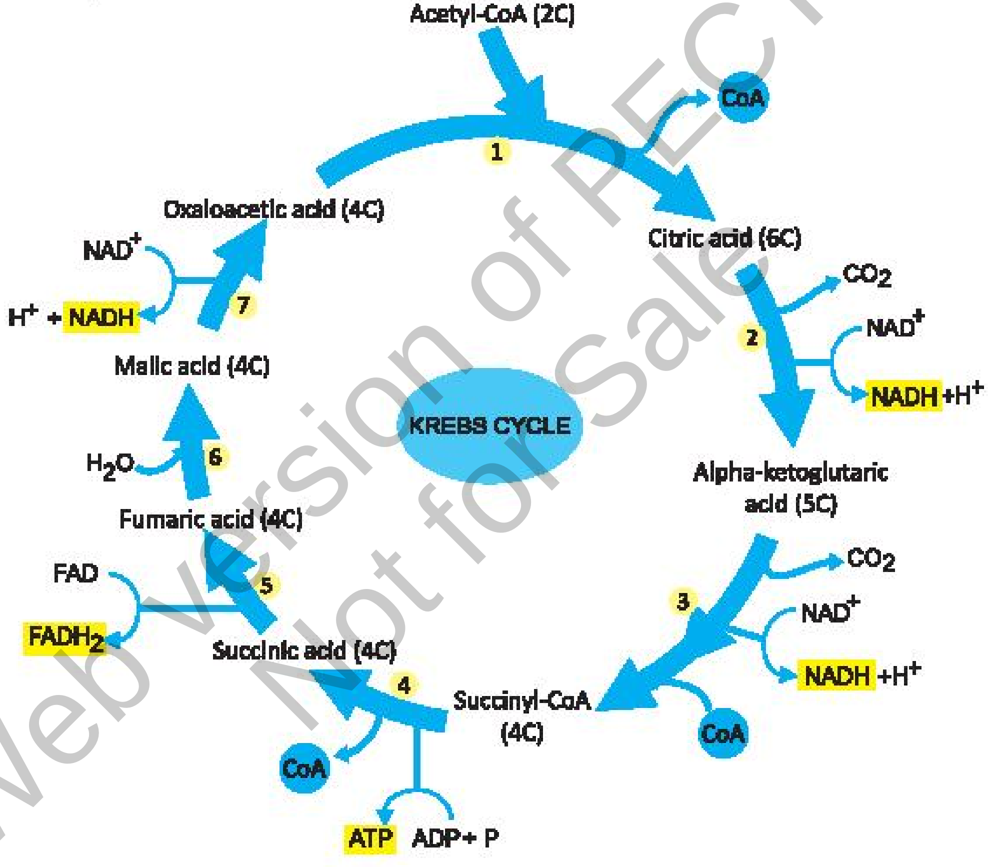


Figure 6.17: Krebs cycle

4. The bond between succinic acid and CoA is a high-energy linkage. It again splits into CoA and succinic acid. The energy released in this reaction, is used in making a molecule of ATP.
5. Succinic acid is oxidized to fumaric acid. When its two hydrogen atoms are removed, the free energy is not enough to reduce NAD+. So, a different

electron acceptor i.e., the coenzyme flavin adenine dinucleotide (FAD) is used and is reduced to FADH2.

6. In order to regenerate oxaloacetic acid, a molecule of water added to fumaric acid and it is changed to malic acid.
7. Malic is oxidized to produce oxaloacetic acid. The hydrogen and electrons released from malic acid convert an NAD+ to NADH. This completes the cycle and oxaloacetic acid is now free to bind another molecule of acetyl CoA to initiate the cycle.

Stage 4: Electron Transport Chain and Chemiosmosis

In electron transport chain the electrons are transferred from the reduced coenzymes i.e., NADH and $FADH_2$ to a series of electron carriers and finally to oxygen. After getting the electrons, the oxygen attaches with hydrogen ions and forms water (Fig. 6.18).

You have seen that in redox reactions electrons and hydrogen ions are removed from substrates and transferred to coenzymes NAD^+ and FAD.

The transfer of electrons to the series of carriers of electron transport chain results in oxidation and reduction reactions i.e., a carrier is oxidized when it loses electrons and next carrier is reduced when it gets electrons. Electrons loose energy during this carrier-to-carrier transport. Chemiosmosis is the mechanism in which membranes are used to couple these redox reactions with the synthesis of ATPs.

Pathway of electrons: The electron transport chain of respiration is built in the inner membrane of the mitochondrion. At the start of electron transport chain, NADH is oxidized and the released electrons are taken up by coenzyme Q. If $FADH_2$ is also to be oxidized, its electrons also move to coenzyme Q. The reduced CoQ transports electrons to cytochrome 'b' which in turn transports them to cytochrome 'c'. Cytochrome 'c' then transports electrons to cytochrome 'a' complex (a complex of two cytochromes). This complex transports electrons to an atom of oxygen that is present at the bottom end of the chain.

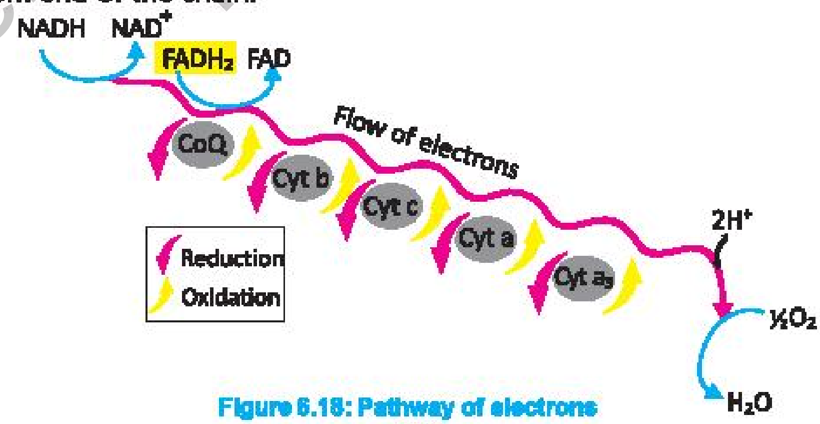


Figure 6.18: Pathway of electrons

Synthesis of ATP: As redox occurs, the energy released from the electrons is used for the active transport of H^+ ions from one side (the matrix of mitochondrion) of the membrane to the other (the inter-membrane space). In this way, many H^+ ions are deposited in the inter-membrane space. The resulting H^+ ion gradient stores potential energy. The H^+ ions diffuse back along their concentration gradient from the inter-membrane space to the matrix (Fig. 6.19).

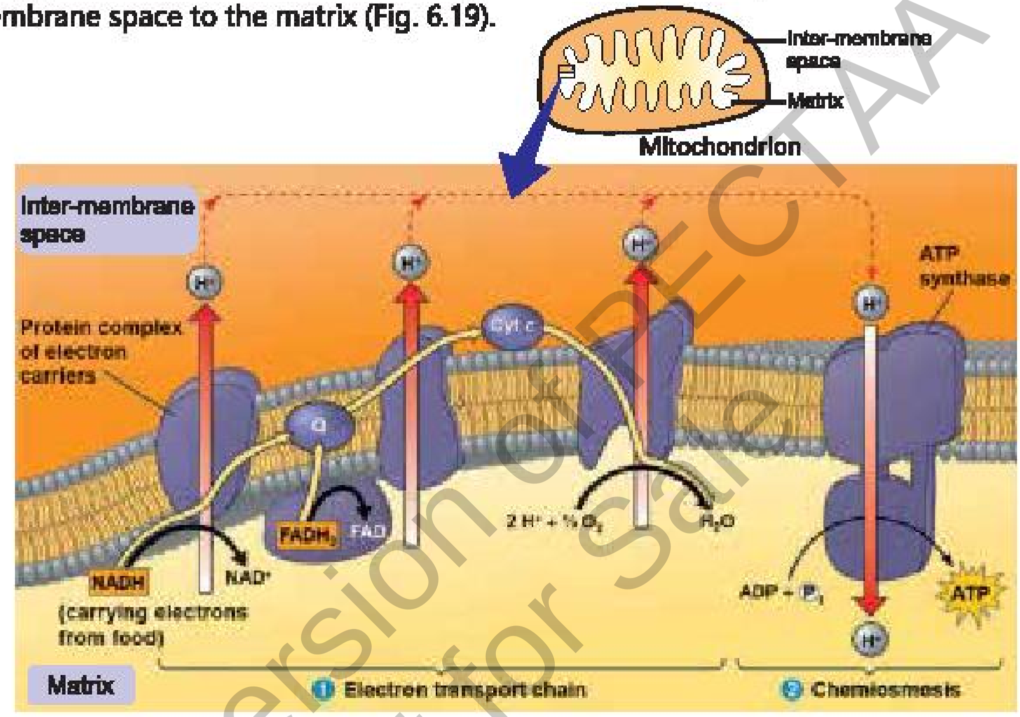
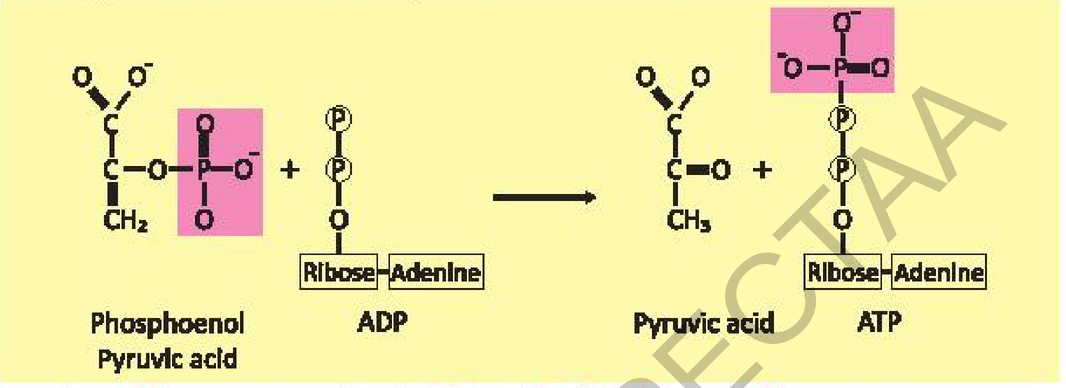


Figure 6.19: Electron transport chain and chemiosmosis in mitochondrion

On their way they pass through a special protein known as ATP synthase. As the H^+ ions move through this protein, their flow drives the synthesis of ATP (Fig 5.19). Oxidation of one molecule of NADH in electron transport chain produces three ATP. While oxidation of one $FADH_2$ produces two ATP. At the end, the two hydrogen ions are taken by the oxygen atom which has also taken two electrons to form water.

Substrate-level Phosphorylation

Cells generate ATP by phosphorylation i.e. adding a phosphate group to ADP. A cell has two ways to do this: chemiosmotic phosphorylation (chemiosmosis) and substrate-level phosphorylation. Substrate-level phosphorylation is much simpler than chemiosmosis. It does not involve any membrane or electron transport chain. In this process, an enzyme transfers a phosphate group from an organic substrate molecule to ADP. The products are a new organic molecule and a molecule of ATP. For example; during the last step of glycolysis, an enzyme transfers phosphate group from phosphoenol pyruvic (PEP) acid to ADP. As a result, ADP becomes ATP and PEP is changed into pyruvic acid. Substrate-level phosphorylation accounts for only a small percentage of the ATP that a cell generates. This reaction can be shown as:



Overview of the energy extracted from the Oxidation of Glucose

The NADH and $FADH_2$ produced during glycolysis and Krebs cycle pass on their energy-rich electrons to the electron transport chain and ATPs are produced.

- The NADH molecule generated in the Krebs cycle causes the production of three ATP molecules, during chemiosmosis.

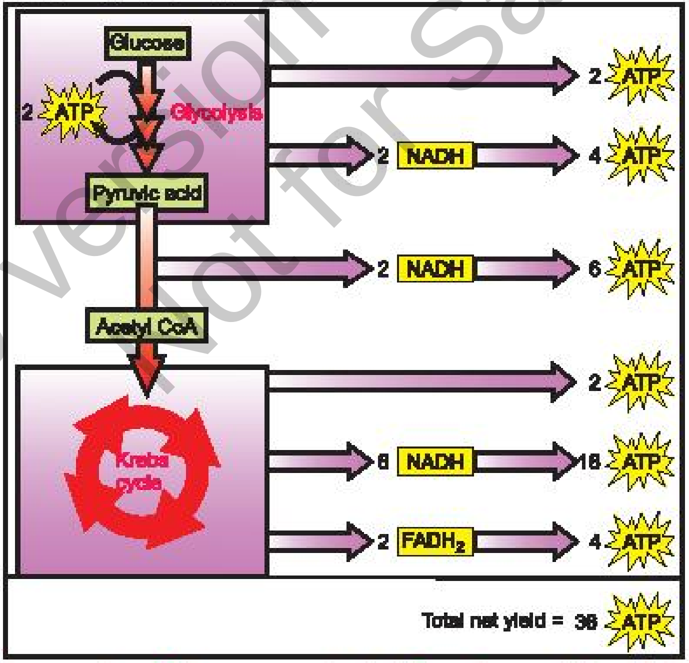


Figure 6.20: An overview of the energy extracted from the aerobic oxidation of glucose

- Glycolysis takes place in cytoplasm and the NADH, produced during glycolysis, have to be transported across the mitochondrial membrane. It costs one ATP molecule per NADH. Thus, each NADH of glycolysis produces two ATP molecules in the final balance sheet instead of three.

- Each $FADH_2$ molecule leads to the production of two ATP molecules.

In this way, aerobic oxidation of glucose yields a net profit of 36 ATP molecules. While during the glycolysis of anaerobic oxidation only 2 ATP molecules are generated. Thus, aerobic oxidation is 18 times more efficient than anaerobic (Fig 6.20).

Other Organic Moleculesas fuel for Cellular Respiration

Free glucose molecules are not common in our diet. Rather, we consume sucrose and other disaccharides, starch, and fats and proteins. Proteins may also be used as fuel but they must be digested to their constituent amino acids. Typically, a cell uses most of the amino acids to make its own proteins. Some amino acids are de-aminated (amino group detached) and then are converted to other organic compounds. These compounds are usually converted to pyruvic acid, acetyl CoA, or the organic acids in the Krebs cycle, and their energy is converted to ATP.

Lipids are excellent cellular fuel because they contain many carbon-hydrogen bonds. They are first hydrolysed into glycerol and fatty acids. Glycerol is converted to glyceraldehyde 3-phosphate, an intermediate in glycolysis, while the fatty acids are changed into acetyl CoA. In this way both the fatty acids and the glycerol enter cellular respiration.

6.3 - PHOTORESPIRATION

The respiratory activity that occurs in green cells in the presence of light resulting in release of carbon dioxide is termed as photorespiration. It needs oxygen and produce CO_2 and H_2O like aerobic respiration. However, ATP is not produced during photorespiration.

Recalling:
During carbon fixation, rubisco combines three molecules of CO_2 with three molecules of RuBP and makes six molecules of 3–phosphoglyceric acid (3-PGA).

Mechanism of Photorespiration

We know that RuBP carboxylase (rubisco) catalyses the addition of CO_2 to RuBP to make phosphoglyceric acid (phosphoglycerate), which is further reduced to form glucose. However, when the relative concentration of CO_2 decreases and there is more oxygen in leaf cells, rubisco adds O_2 in RuBP instead of CO_2. It results in the breakdown of RuBP into two molecules i.e., one phosphoglycerate and one phosphoglycolate (a two-carbon molecule).

Phosphoglycolate is converted into glycolate, which moves from chloroplast to peroxisome. Here, it is metabolized to glyoxylate by using O_2. This reaction also produces toxic hydrogen peroxide (H_2O_2). Glyoxylate is then converted to glycine, which is transported to mitochondrion. Here, two molecules of glycine form a molecule of serine. Serine is then transported to peroxisome. Here, it is converted to glycerate. From peroxisome, glycerate moves to chloroplast, where it is changed to phosphoglycerate which can re-enter Calvin cycle.

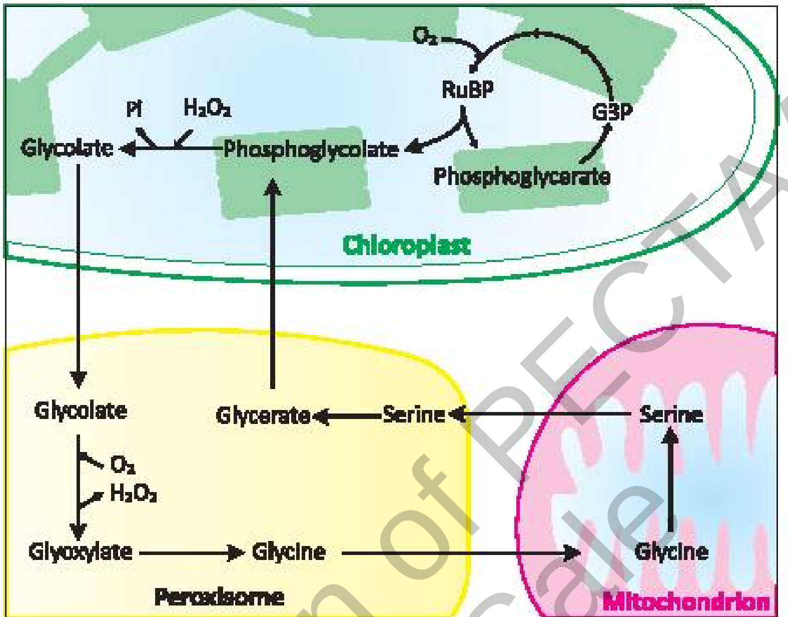


Figure 6.21: Reactions of photorespiration

Disadvantages of Photorespiration

Plants that use Calvin cycle to fix carbon are called C-3 plants. When photorespiration occurs in these plants, they lose between a 25% to 50% of their fixed carbon. It results in reduction in their yields. The rate of photorespiration also depends on temperature. At higher temperatures the oxidative activity of rubisco increases than its carbon fixing activity. In tropical climates, especially those in which the temperature is often above 28 °C, the problem is a severe and it has a major negative impact on agricultural yields.

When photosynthesis first evolved, there was little oxygen in the atmosphere. So, there was little or no photorespiration. After millions of years, free O_2 accumulated in the atmosphere and competition started between CO_2 and O_2 for the same active site of rubisco. It led to the problem that photorespiration now poses.

Adaptations to the problems of Photorespiration

Plants of warmer climates evolved the following two ways to deal with the problem of photorespiration.

C-4 plants carry out C-4 as well as C-3 photosynthesis.

I. C-4 Photosynthesis

Some plants including grasses (corn, sugarcane and sorghum) and about two dozen other plant groups run a special pathway called C-4 photosynthesis in addition to the normal Calvin cycle. In their leaves, the mesophyll cells have less air spaces. The enzymes of Calvin cycle are more deposited in specialized cells called bundle-sheath cells, which are impermeable to CO_2.

In C-4 photosynthesis, the energy cost for making a glucose molecule is almost double. However, in hot climates, in which photorespiration would otherwise remove more than half of the carbon fixed, it is best compromise available.

During C-4 photosynthesis (Fig 6.22) in mesophyll cells, CO_2, is attached with a 3-carbon molecule called phosphoenol pyruvic acid. It results in the formation of a four-carbon molecule oxaloacetic acid. Due to this first 4-C product, this process is called C-4 photosynthesis and the plants are called C-4 plants. Oxaloacetic acid is then converted to malic acid, by using NADH. Malic acid is transported to an adjacent bundle-sheath cell. Here, malic acid is broken down to pyruvic acid and CO_2. These cells can hold CO_2 in them. So, concentration of CO_2 increases in these cells and they run Calvin cycle instead of photorespiration. Pyruvic acid produced in bundle sheath cells returns to mesophyll cell and is converted again to phosphoenol pyruvic acid b using an ATP.

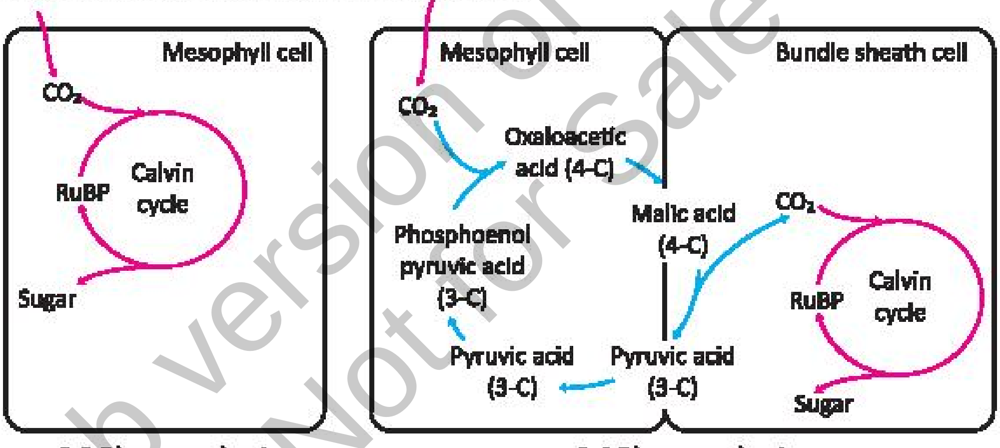
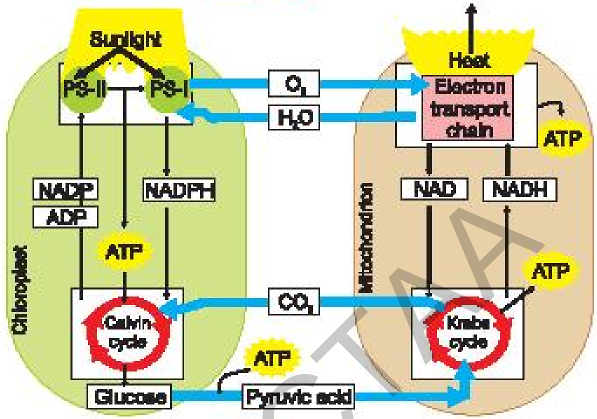


Figure 6.22: C-3 photosynthesis andC-4 photosynthesis

CAM Metabolism

In hot climates, many succulent plants such as *Cacti*, pineapples and some other plant groups perform Crassulaceal acid metabolism or CAM (after the plant family Crassulaceae in which it was first discovered). In these plants, the stomata open during the night and close during the day. Closing stomata during the day prevents water loss and removal of CO_2. So, rate of photorespiration is reduced due to high concentration of carbon dioxide. The carbon dioxide necessary for producing sugar is provided from organic molecules made the night before. Like C-4 plants, these plants use both C-4 and C-3 pathways.

From the given flowchart, build a paragraph that can describe a comparison between photosynthesis and respiration in terms of reactants and products of major steps.



EXERCISE

SECTION 1: MULTIPLE CHOICE QUESTIONS

1- What main process occurs during the dark reaction of photosynthesis?
(a) Release of oxygen
(b) Energy absorption by chlorophyll
(c) Adding of hydrogen to CO_2
(d) Formation of ATP

2- What is TRUE about glycolysis?
(a) It produces no ATP
(b) It takes place only in aerobic respiration
(c) It takes place in the mitochondrion
(d) It reduces 2 molecules of NAD+ for every glucose molecule processed

3- Which of the following are produced by the reactions that occur in the thylakoid and consumed by the reactions that occur in the stroma?
(a) CO2 and H_2O
(b) Glucose and O_2
(c) NADP+ and ADP
(d) ATP and NADPH

4- When deprived of oxygen, yeast cells obtain energy by fermentation, producing CO2, ATP and;
(a) Acetyl CoA
(b) Ethyl alcohol
(c) Lactic acid
(d) Pyruvic acid

5- Conversion of Glucose 6-phosphate into Fructose 6-phosphate is;
(a) Isomerization
(b) Polymerization
(c) Condensation
(d) Phosphorylation

6- In which of the following conversions, ATP is produced?
(a) Alpha ketoglutaric acid into succinyl CoA
(b) Succinyl CoA into succinic acid
(c) Succinic acid into fumaric acid
(d) Fumaric acid into malic acid

7- In electron transport chain, FADH:H produces how many ATPs?
(a) One (b) Two (c) Three (d) Four

8- Which of these is CO_2 acceptor during photosynthesis?
(a) Malic acid (b) Ribulose biphosphate
(c) Oxaloacetic acid (d) Phosphoglyceric acid

9- Which of the following takes the electrons lost by Photosystem I on absorption of light energy?
(a) Ferredoxin (b) Cytochrome (c) Cytochrome a-3 (d) Plastocyanin

10- Photosystem-II makes up the electrons lost due to light excitation by taking up the electrons released from,
(a) Ferredoxin (b) NADPH:H^+
(c) Plastocyanin (d) Photolysis of water

SECTION 2:SHORT QUESTIONS

1- Differentiate between action spectrum and absorption spectrum.
2- How is photosynthesis a redox reaction?
3- Which molecule contributes Oxygen in glucose? Water or carbon dioxide!
4- State the role of CO_2 in photosynthesis.
5- Define electron transport chain.
6- What do you mean by glycolysis?
7- What is the main structural difference between chlorophyll-a and chlorophyll-b?
8- How can a cell synthesize ATP through substrate-level phosphorylation?
9- Can pyruvic acid enter Krebs cycle as such? If not, what changes are made to it before Krebs cycle?
10- Differentiate between C-3 and C-4 photosynthesis.

SECTION 3: LONG QUESTIONS

1- What are photosynthetic pigments and what role they play in the absorption and conversion of light energy?
2- How are the absorption spectra of chlorophyll 'a' and 'b' different?
3- Describe and illustrate how photosynthetic pigments are organized in thylakoid membrane?
4- Describe how the role of water in photosynthesis can be explained through experiment.
5- What are the events that capture light and convert it into chemical energy during light dependent reactions?
6- Illustrate the cyclic photophosphorylation.
7- Describe light independent reactions of photosynthesis in terms of paragraph and illustrate in terms of Calvin cycle.

8- What happens with glucose in anaerobic respiration and how different organisms modify the end products?
9- How is glucose broken down to pyruvic acid in glycolysis?
10- Describe how Krebs cycle is the completion of the oxidation of glycolytic products.
11- Explain the passage of electron through electron transport chain.
12- Define chemiosmosis. How would you relate it with electron transport chain?
13- Through which ways proteins and fats enter cellular respiration?
14- Define photorespiration and present it in proving that "photosynthesis is not perfect".
15- What are the effects of temperature on the oxidative activity of Rubisco?
16- How is the process of C4 photosynthesis an adaptation to deal with the problem of photorespiration?

INQUISITIVE QUESTIONS

1. Why does cellular respiration release energy more efficiently than fermentation?
2. Why is the conversion of glucose into ATP during cellular respiration considered a more efficient use of energy than burning glucose directly?
3. Why might a disruption in either photosynthesis or respiration processes affect global carbon and oxygen cycles?