is available in soil. Thus, nitrogen is a limiting nutrient for both natural and agricultural eco-systems. Nitrogen exists as two nitrogen atoms joined by a very strong triple covalent bond (N ≡ N). The process of conversion of nitrogen (N_2) to ammonia is termed as **nitrogen-fixation.** In nature, lightning and ultraviolet radiation provide enough energy to convert nitrogen to nitrogen oxides (NO, NO_2, N_2O). Industrial combustions, forest fires, automobile exhausts and power-generating stations are also sources of atmospheric nitrogen oxides. Decomposition of organic nitrogen of dead plants and animals into ammonia is called ammonification. Some of this ammonia volatilises and re-enters the atmosphere but most of it is converted into nitrate by soil bacteria in the following steps:

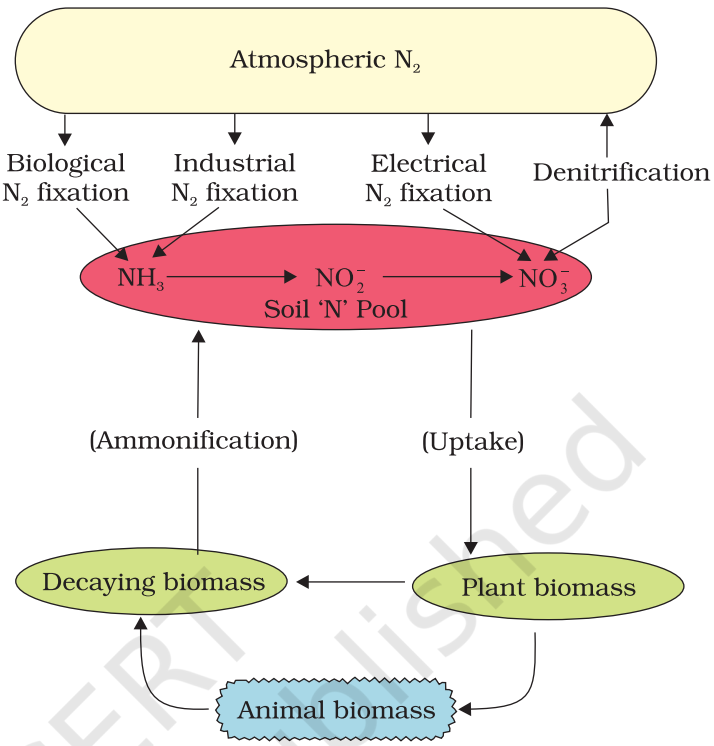


Figure 12.3 The nitrogen cycle showing relationship between the three main nitrogen pools – atmospheric soil, and biomass

$$2NH_3 + 3O_2 \longrightarrow 2NO_2^- + 2H^+ + 2H_2O \quad \text{.... (i)}$$

$$2NO_2^- + O_2 \longrightarrow 2NO_3^- \quad \text{..... (ii)}$$

Ammonia is first oxidised to nitrite by the bacteria *Nitrosomonas* and/or *Nitrococcus*. The nitrite is further oxidised to nitrate with the help of the bacterium *Nitrobacter*. These steps are called **nitrification** (Figure 12.3). These nitrifying bacteria are **chemoautotrophs**.

The nitrate thus formed is absorbed by plants and is transported to the leaves. In leaves, it is reduced to form ammonia that finally forms the amine group of amino acids. Nitrate present in the soil is also reduced to nitrogen by the process of denitrification. Denitrification is carried by bacteria *Pseudomonas* and *Thiobacillus*.

12.6.2 Biological Nitrogen Fixation

Very few living organisms can utilise the nitrogen in the form N_2, available abundantly in the air. Only certain prokaryotic species are capable of fixing nitrogen. Reduction of nitrogen to ammonia by living organisms is

called **biological nitrogen fixation.** The enzyme, nitrogenase which is capable of nitrogen reduction is present exclusively in prokaryotes. Such microbes are called N_2- fixers.

$$N \equiv N \xrightarrow{\text{Nitrogenase}} NH_3$$

The nitrogen-fixing microbes could be free-living or symbiotic. Examples of free-living nitrogen-fixing aerobic microbes are *Azotobacter* and *Beijernickia* while *Rhodospirillum* is anaerobic and *Bacillus* free-living. In addition, a number of cyanobacteria such as *Anabaena* and *Nostoc* are also free-living nitrogen-fixers.

Symbiotic biological nitrogen fixation

Several types of symbiotic biological nitrogen fixing associations are known. The most prominent among them is the legume-bacteria relationship. Species of rod-shaped *Rhizobium* has such relationship with the roots of several legumes such as alfalfa, sweet clover, sweet pea, lentils, garden pea, broad bean, clover beans, etc. The most common association on roots is as nodules. These nodules are small outgrowths on the roots. The microbe, *Frankia,* also produces nitrogen-fixing nodules on the roots of non-leguminous plants (e.g., Alnus). Both *Rhizobium* and *Frankia* are free-living in soil, but as symbionts, can fix atmospheric nitrogen.

Uproot any one plant of a common pulse, just before flowering. You will see near-spherical outgrowths on the roots. These are nodules. If you cut through them you will notice that the central portion is red or pink. What makes the nodules pink? This is due to the presence of leguminous haemoglobin or leg-haemoglobin.

Nodule Formation

Nodule formation involves a sequence of multiple interactions between *Rhizobium* and roots of the host plant. Principal stages in the nodule formation are summarised as follows:

Rhizobia multiply and colonise the surroundings of roots and get attached to epidermal and root hair cells. The root-hairs curl and the bacteria invade the root-hair. An infection thread is produced carrying the bacteria into the cortex of the root, where they initiate the nodule formation in the cortex of the root. Then the bacteria are released from the thread into the cells which leads to the differentiation of specialised nitrogen fixing cells. The nodule thus formed, establishes a direct vascular connection with the host for exchange of nutrients. These events are depicted in Figure 12.4.

The nodule contains all the necessary biochemical components, such as the enzyme nitrogenase and leghaemoglobin. The enzyme nitrogenase is a Mo-Fe protein and catalyses the conversion of atmospheric nitrogen to ammonia, (Figure 12.5) the first stable product of nitrogen fixation.

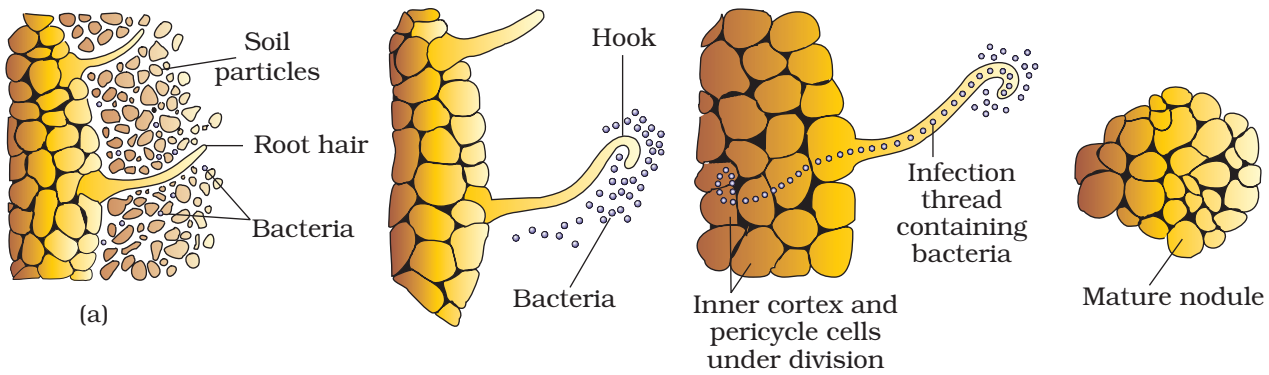


Figure 12.4 Development of root nodules in soyabean : (a) *Rhizobium* bacteria contact a susceptible root hair, divide near it, (b) Successful infection of the root hair causes it to curl, (c) Infected thread carries the bacteria to the inner cortex. The bacteria get modified into rod-shaped bacteroids and cause inner cortical and pericycle cells to divide. Division and growth of cortical and pericycle cells lead to nodule formation, (d) A mature nodule is complete with vascular tissues continuous with those of the root

The reaction is as follows:

$$N_2 + 8e^- + 8H^+ + 16ATP \longrightarrow 2NH_3 + H_2 + 16ADP + 16P_i$$

The enzyme nitrogenase is highly sensitive to the molecular oxygen; it requires anaerobic conditions. The nodules have adaptations that ensure that the enzyme is protected from oxygen. To protect these enzymes, the nodule contains an oxygen scavenger called leg-haemoglobin. It is interesting to note that these microbes live as aerobes under free-living conditions (where nitrogenase is not operational), but during nitrogen-fixing events, they become anaerobic (thus protecting the nitrogenase enzyme). You must have noticed in the above reaction that the ammonia synthesis by nitrogenease requires a

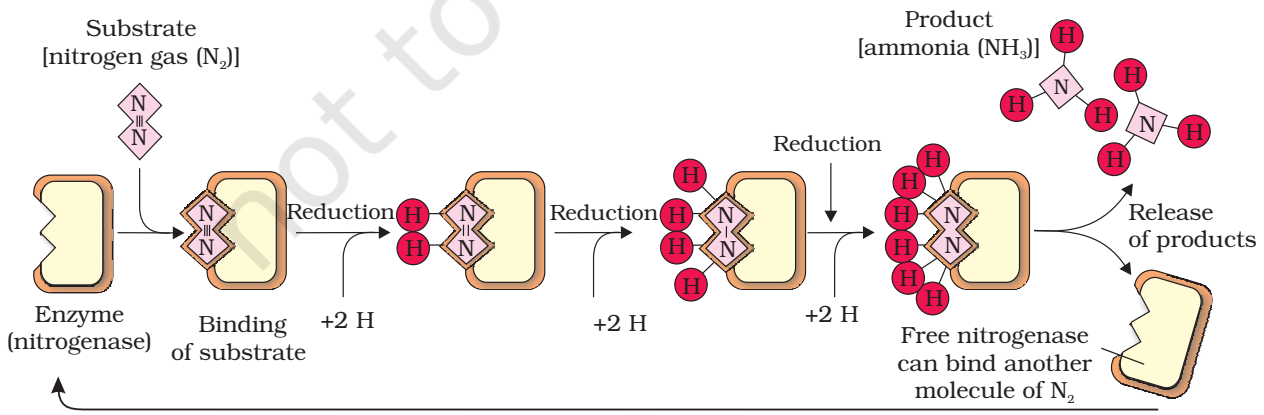


Figure 12.5 Steps of conversion of atmospheric nitrogen to ammonia by nitrogenase enzyme complex found in nitrogen-fixing bacteria

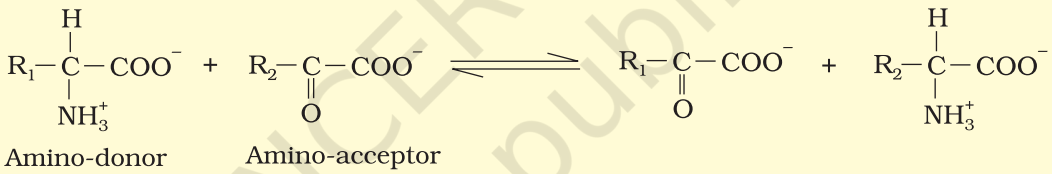
very high input of energy (8 ATP for each NH_3 produced). The energy required, thus, is obtained from the respiration of the host cells.

Fate of ammonia: At physiological pH, the ammonia is protonated to form NH_4^+ (ammonium) ion. While most of the plants can assimilate nitrate as well as ammonium ions, the latter is quite toxic to plants and hence cannot accumulate in them. Let us now see how the NH_4^+ is used to synthesise amino acids in plants. There are two main ways in which this can take place:

(i) **Reductive amination :** In these processes, ammonia reacts with α-ketoglutaric acid and forms glutamic acid as indicated in the equation given below :

$$\alpha - \text{ketoglutaric acid} + NH_4^+ + NADPH \xrightarrow[\text{Dehydrogenase}]{\text{Glutamate}} \text{glutamate} + H_2O + NADP$$

(ii) **Transamination :** It involves the transfer of amino group from one amino acid to the keto group of a keto acid. Glutamic acid is the main amino acid from which the transfer of NH_2, the amino group takes place and other amino acids are formed through transamination. The enzyme **transaminase** catalyses all such reactions. For example,



The two most important amides – asparagine and glutamine – found in plants are a structural part of proteins. They are formed from two amino acids, namely aspartic acid and glutamic acid, respectively, by addition of another amino group to each. The hydroxyl part of the acid is replaced by another NH_2^- radicle. Since amides contain more nitrogen than the amino acids, they are transported to other parts of the plant via xylem vessels. In addition, along with the transpiration stream the nodules of some plants (e.g., soyabean) export the fixed nitrogen as ureides. These compounds also have a particularly high nitrogen to carbon ratio.

SUMMARY

Plants obtain their inorganic nutrients from air, water and soil. Plants absorb a wide variety of mineral elements. Not all the mineral elements that they absorb are required by plants. Out of the more than 105 elements discovered so far, less than 21 are essential and beneficial for normal plant growth and development. The elements required in large quantities are called macronutrients while those required in less quantities or in trace are termed as micronutrients. These elements are either essential constituents of proteins, carbohydrates, fats, nucleic acid etc.,

and/or take part in various metabolic processes. Deficiency of each of these essential elements may lead to symptoms called deficiency symptoms. Chlorosis, necrosis, stunted growth, impaired cell division, etc., are some prominent deficiency symptoms. Plants absorb minerals through roots by either passive or active processes. They are carried to all parts of the organism through xylem along with water transport.

Nitrogen is very essential for the sustenance of life. Plants cannot use atmospheric nitrogen directly. But some of the plants in association with N_2-fixing bacteria, especially roots of legumes, can fix this atmospheric nitrogen into biologically usable forms. Nitrogen fixation requires a strong reducing agent and energy in the form of ATP. N_2-fixation is accomplished with the help of nitrogen-fixing microbes, mainly *Rhizobium*. The enzyme nitrogenase which plays an important role in biological N_2 fixation is very sensitive to oxygen. Most of the processes take place in anaerobic environment. The energy, ATP, required is provided by the respiration of the host cells. Ammonia produced following N_2 fixation is incorporated into amino acids as the amino group.

EXERCISES

1. 'All elements that are present in a plant need not be essential to its survival'. Comment.
2. Why is purification of water and nutrient salts so important in studies involving mineral nutrition using hydroponics?
3. Explain with examples: macronutrients, micronutrients, beneficial nutrients, toxic elements and essential elements.
4. Name at least five different deficiency symptoms in plants. Describe them and correlate them with the concerned mineral deficiency.
5. If a plant shows a symptom which could develop due to deficiency of more than one nutrient, how would you find out experimentally, the real deficient mineral element?
6. Why is that in certain plants deficiency symptoms appear first in younger parts of the plant while in others they do so in mature organs?
7. How are the minerals absorbed by the plants?
8. What are the conditions necessary for fixation of atmospheric nitrogen by *Rhizobium*. What is their role in N_2-fixation?
9. What are the steps involved in formation of a root nodule?
10. Which of the following statements are true? If false, correct them:
    (a) Boron deficiency leads to stout axis.
    (b) Every mineral element that is present in a cell is needed by the cell.
    (c) Nitrogen as a nutrient element, is highly immobile in the plants.
    (d) It is very easy to establish the essentiality of micronutrients because they are required only in trace quantities.

Chapter 13

Photosynthesis in Higher Plants

All animals including human beings depend on plants for their food. Have you ever wondered from where plants get their food? Green plants, in fact, have to make or rather synthesise the food they need and all other organisms depend on them for their needs. The green plants make or rather synthesise the food they need through photosynthesis and are therefore called autotrophs. You have already learnt that the autotrophic nutrition is found only in plants and all other organisms that depend on the green plants for food are heterotrophs. Green plants carry out 'photosynthesis', a physico-chemical process by which they use light energy to drive the synthesis of organic compounds. Ultimately, all living forms on earth depend on sunlight for energy. The use of energy from sunlight by plants doing photosynthesis is the basis of life on earth. Photosynthesis is important due to two reasons: it is the primary source of all food on earth. It is also responsible for the release of oxygen into the atmosphere by green plants. *Have you ever thought what would happen if there were no oxygen to breath?* This chapter focusses on the structure of the photosynthetic machinery and the various reactions that transform light energy into chemical energy.

13.1 What do we Know?

Let us try to find out what we already know about photosynthesis. Some simple experiments you may have done in the earlier classes have shown that chlorophyll (green pigment of the leaf), light and CO_2 are required for photosynthesis to occur.

You may have carried out the experiment to look for starch formation in two leaves – a variegated leaf or a leaf that was partially covered with black paper, and exposed to light. On testing these leaves for the presence of starch it was clear that photosynthesis occurred only in the green parts of the leaves in the presence of light.

Another experiment you may have carried out where a part of a leaf is enclosed in a test tube containing some KOH soaked cotton (which absorbs CO_2), while the other half is exposed to air. The setup is then placed in light for some time. On testing for the presence of starch later in the two plants of the leaf, you must have found that the exposed part of the leaf tested positive for starch while the portion that was in the tube, tested negative. This showed that CO_2 was required for photosynthesis. *Can you explain how this conclusion could be drawn?*

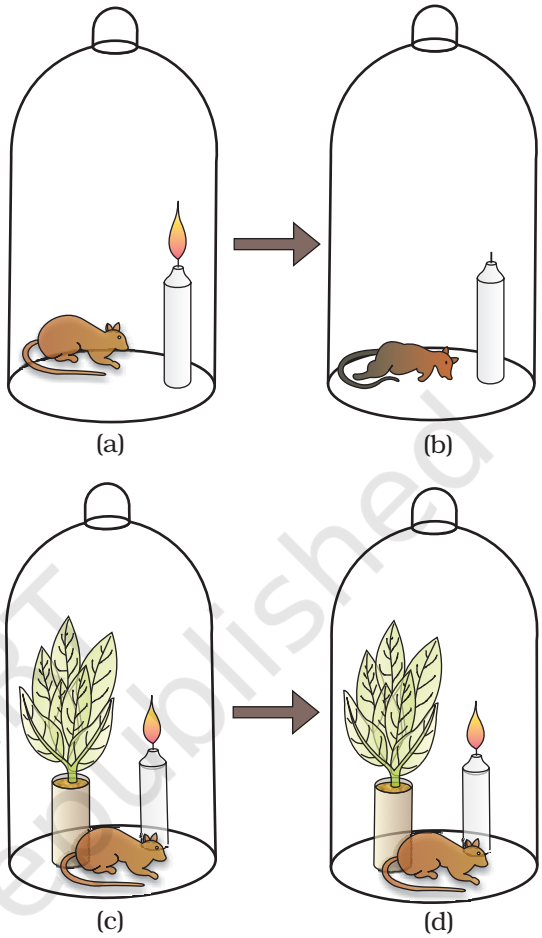


Figure 13.1 Priestley's experiment

13.2 EARLY EXPERIMENTS

It is interesting to learn about those simple experiments that led to a gradual development in our understanding of photosynthesis.

Joseph Priestley (1733-1804) in 1770 performed a series of experiments that revealed the essential role of air in the growth of green plants. Priestley, you may recall, discovered oxygen in 1774. Priestley observed that a candle burning in a closed space – a bell jar, soon gets extinguished (Figure 13.1 a, b, c, d). Similarly, a mouse would soon suffocate in a closed space. He concluded that a burning candle or an animal that breathe the air, both somehow, damage the air. But when he placed a mint plant in the same bell jar, he found that the mouse stayed alive and the candle continued to burn. Priestley hypothesised as follows: Plants restore to the air whatever breathing animals and burning candles remove.

Can you imagine how Priestley would have conducted the experiment using a candle and a plant? Remember, he would need to rekindle the candle to test whether it burns after a few days. *How many different ways can you think of to light the candle without disturbing the set-up?*

Using a similar setup as the one used by Priestley, but by placing it once in the dark and once in the sunlight, Jan Ingenhousz (1730-1799) showed that sunlight is essential to the plant process that somehow purifies the air fouled by burning candles or breathing animals. Ingenhousz in an elegant experiment with an aquatic plant showed that in bright sunlight, small bubbles were formed around the green parts while in the dark they did not. Later he identified these bubbles to be of oxygen. Hence he showed that it is only the green part of the plants that could release oxygen.

It was not until about 1854 that Julius von Sachs provided evidence for production of glucose when plants grow. Glucose is usually stored as starch. His later studies showed that the green substance in plants (chlorophyll as we know it now) is located in special bodies (later called chloroplasts) within plant cells. He found that the green parts in plants is where glucose is made, and that the glucose is usually stored as starch.

Now consider the interesting experiments done by T.W Engelmann (1843 – 1909). Using a prism he split light into its spectral components and then illuminated a green alga, *Cladophora*, placed in a suspension of aerobic bacteria. The bacteria were used to detect the sites of O_2 evolution. He observed that the bacteria accumulated mainly in the region of blue and red light of the split spectrum. A first action spectrum of photosynthesis was thus described. It resembles roughly the absorption spectra of chlorophyll *a* and *b* (discussed in section 13.4).

By the middle of the nineteenth century the key features of plant photosynthesis were known, namely, that plants could use light energy to make carbohydrates from CO_2 and water. The empirical equation representing the total process of photosynthesis for oxygen evolving organisms was then understood as:

$$CO_2 + H_2O \xrightarrow{\text{Light}} [CH_2O] + O_2$$

where $[CH_2O]$ represented a carbohydrate (e.g., glucose, a six-carbon sugar).

A milestone contribution to the understanding of photosynthesis was that made by a microbiologist, Cornelius van Niel (1897-1985), who, based on his studies of purple and green bacteria, demonstrated that photosynthesis is essentially a light-dependent reaction in which hydrogen from a suitable oxidisable compound reduces carbon dioxide to carbohydrates. This can be expressed by:

$$2H_2A + CO_2 \xrightarrow{\text{Light}} 2A + CH_2O + H_2O$$

In green plants H_2O is the hydrogen donor and is oxidised to O_2. Some organisms do not release O_2 during photosynthesis. When H_2S, instead is the hydrogen donor for purple and green sulphur bacteria, the 'oxidation' product is sulphur or sulphate depending on the organism and not O_2. Hence, he inferred that the O_2 evolved by the green plant comes from H_2O, not from carbon dioxide. This was later proved by using radioisotopic techniques. The correct equation, that would represent the overall process of photosynthesis is therefore:

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

where $C_6 H_{12} O_6$ represents glucose. The O_2 released is from water; this was proved using radio isotope techniques. Note that this is not a single

reaction but description of a multistep process called photosynthesis. *Can you explain why twelve molecules of water as substrate are used in the equation given above?*

13.3 WHERE DOES PHOTOSYNTHESIS TAKE PLACE?

You would of course answer: in 'the green leaf' or 'in the chloroplasts', based on what you earlier read in Chapter 8. You are definitely right. Photosynthesis does take place in the green leaves of plants but it does so also in other green parts of the plants. *Can you name some other parts where you think photosynthesis may occur?*

You would recollect from previous unit that the mesophyll cells in the leaves, have a large number of chloroplasts. Usually the chloroplasts align themselves along the walls of the mesophyll cells, such that they get the optimum quantity of the incident light. *When do you think the chloroplasts will be aligned with their flat surfaces parallel to the walls? When would they be perpendicular to the incident light?*

You have studied the structure of chloroplast in Chapter 8. Within the chloroplast there is membranous system consisting of grana, the stroma lamellae, and the matrix stroma (Figure 13.2). There is a clear division of labour within the chloroplast. The membrane system is responsible for trapping the light energy and also for the synthesis of ATP and NADPH. In stroma, enzymatic reactions synthesise sugar, which in turn forms starch. The former set of reactions, since they are directly light driven are called **light reactions** (photochemical reactions). The latter are not directly light driven but are dependent on the products of light reactions (ATP and NADPH). Hence, to distinguish the latter they are called, by convention, as **dark reactions** (carbon reactions). However, this should not be construed to mean that they occur in darkness or that they are not light-dependent.

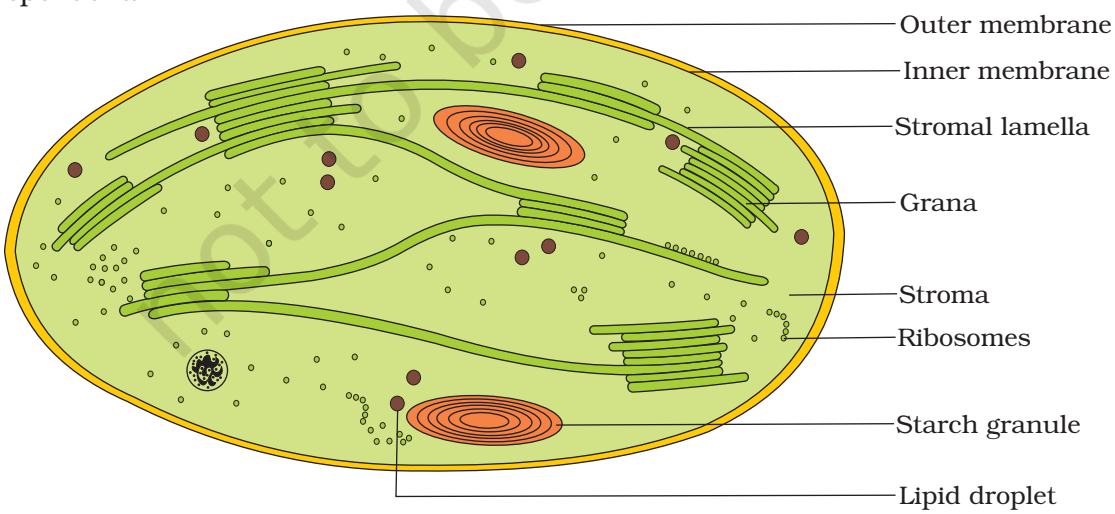


Figure 13.2 Diagrammatic representation of an electron micrograph of a section of chloroplast

13.4 How many Types of Pigments are Involved in Photosynthesis?

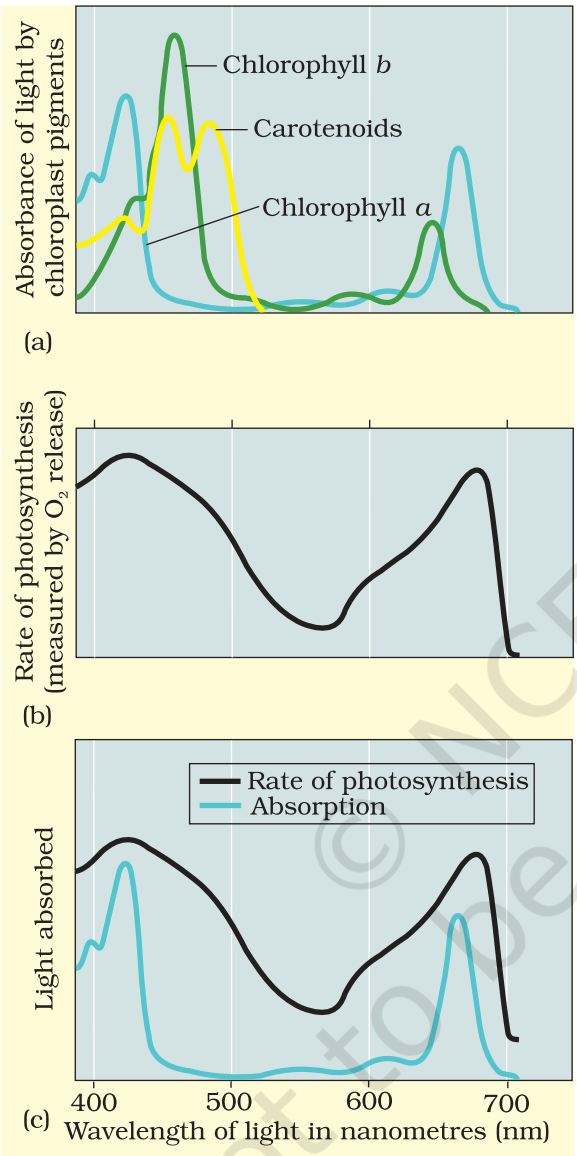


Figure 13.3a Graph showing the absorption spectrum of chlorophyll *a*, *b* and the carotenoids

Figure 13.3b Graph showing action spectrum of photosynthesis

Figure 13.3c Graph showing action spectrum of photosynthesis superimposed on absorption spectrum of chlorophyll *a*

Looking at plants have you ever wondered why and how there are so many shades of green in their leaves – even in the same plant? We can look for an answer to this question by trying to separate the leaf pigments of any green plant through paper chromatography. A chromatographic separation of the leaf pigments shows that the colour that we see in leaves is not due to a single pigment but due to four pigments: **Chlorophyll *a*** (bright or blue green in the chromatogram), **chlorophyll *b*** (yellow green), **xanthophylls** (yellow) and **carotenoids** (yellow to yellow-orange). Let us now see what roles various pigments play in photosynthesis.

Pigments are substances that have an ability to absorb light, at specific wavelengths. *Can you guess which is the most abundant plant pigment in the world?* Let us study the graph showing the ability of chlorophyll *a* pigment to absorb lights of different wavelengths (Figure 13.3 a). Of course, you are familiar with the wavelength of the visible spectrum of light as well as the VIBGYOR.

From Figure 13.3a can you determine the wavelength (colour of light) at which chlorophyll a shows the maximum absorption? Does it show another absorption peak at any other wavelengths too? If yes, which one?

Now look at Figure 13.3b showing the wavelengths at which maximum photosynthesis occurs in a plant. Can you see that the wavelengths at which there is maximum absorption by chlorophyll *a*, i.e., in the blue and the red regions, also shows higher rate of photosynthesis. Hence, we can conclude that chlorophyll *a* is the chief pigment associated with photosynthesis. *But by looking at Figure 13.3c can you say that there is a complete one-to-one overlap between the absorption spectrum of chlorophyll a and the action spectrum of photosynthesis?*

These graphs, together, show that most of the photosynthesis takes place in the blue and red regions of the spectrum; some photosynthesis does take place at the other wavelengths of the visible spectrum. Let us see how this happens. Though chlorophyll is the major pigment responsible for trapping light, other thylakoid pigments like chlorophyll *b*, xanthophylls and carotenoids, which are called accessory pigments, also absorb light and transfer the energy to chlorophyll *a*. Indeed, they not only enable a wider range of wavelength of incoming light to be utilised for photosyntesis but also protect chlorophyll *a* from photo-oxidation.

13.5 WHAT IS LIGHT REACTION?

Light reactions or the 'Photochemical' phase include light absorption, water splitting, oxygen release, and the formation of high-energy chemical intermediates, ATP and NADPH. Several protein complexes are involved in the process. The pigments are organised into two discrete photochemical **light harvesting complexes** (**LHC**) within the **Photosystem I (PS I)** and **Photosystem II (PS II)**. These are named in the sequence of their discovery, and not in the sequence in which they function during the light reaction. The LHC are made up of hundreds of pigment molecules bound to proteins. Each photosystem has all the pigments (except one molecule of chlorophyll *a*) forming a light harvesting system also called **antennae** (Figure 13.4). These pigments help to make photosynthesis more efficient by absorbing different wavelengths of light. The single chlorophyll *a* molecule forms the **reaction centre.** The reaction centre is different in both the photosystems. In PS I the reaction centre chlorophyll *a* has an absorption peak at 700 nm, hence is called **P700,** while in PS II it has absorption maxima at 680 nm, and is called **P680**.

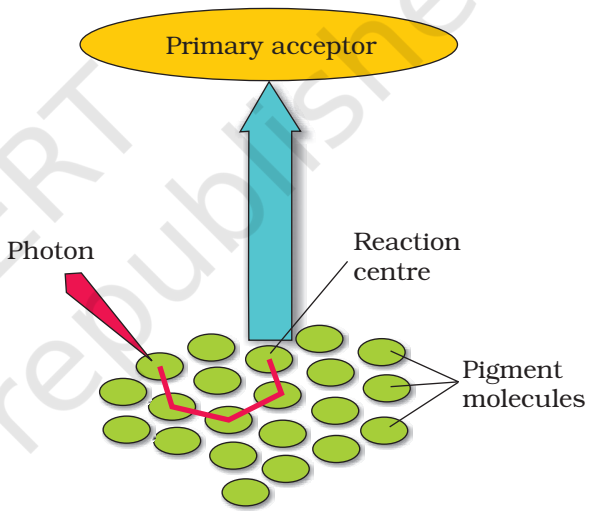


Figure 13.4 The light harvesting complex

13.6 THE ELECTRON TRANSPORT

In photosystem II the reaction centre chlorophyll *a* absorbs 680 nm wavelength of red light causing electrons to become excited and jump into an orbit farther from the atomic nucleus. These electrons are picked up by an electron acceptor which passes them to an **electrons transport**

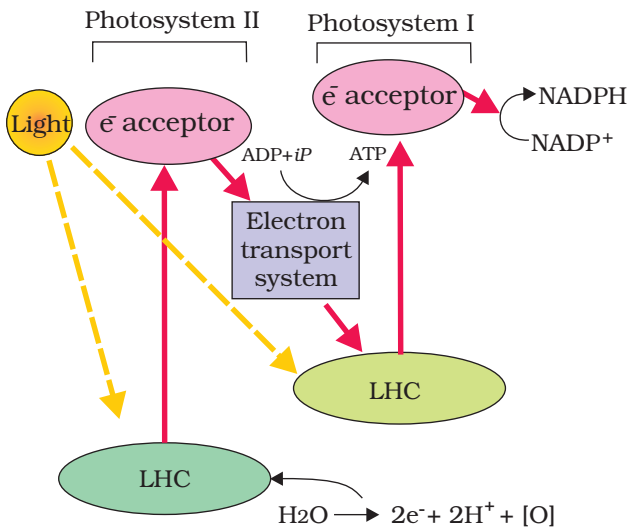


Figure 13.5 Z scheme of light reaction

system consisting of cytochromes (Figure 13.5). This movement of electrons is downhill, in terms of an oxidation-reduction or redox potential scale. The electrons are not used up as they pass through the electron transport chain, but are passed on to the pigments of photosystem PS I. Simultaneously, electrons in the reaction centre of PS I are also excited when they receive red light of wavelength 700 nm and are transferred to another accepter molecule that has a greater redox potential. These electrons then are moved downhill again, this time to a molecule of energy-rich $NADP^+$. The addition of these electrons reduces $NADP^+$ to NADPH + H^+. This whole scheme of transfer of electrons, starting from the PS II, uphill to the acceptor, down the electron transport chain to PS I, excitation of electrons, transfer to another acceptor, and finally down hill to $NADP^+$ reducing it to NADPH + H^+ is called the **Z scheme**, due to its characterstic shape (Figure 13.5). This shape is formed when all the carriers are placed in a sequence on a redox potential scale.

13.6.1 Splitting of Water

You would then ask, *How does PS II supply electrons continuously?* The electrons that were moved from photosystem II must be replaced. This is achieved by electrons available due to splitting of water. The splitting of water is associated with the PS II; water is split into $2H^+$, [O] and electrons. This creates oxygen, one of the net products of photosynthesis. The electrons needed to replace those removed from photosystem I are provided by photosystem II.

$$2H_2O \longrightarrow 4H^+ + O_2 + 4e^-$$

We need to emphasise here that the water splitting complex is associated with the PS II, which itself is physically located on the inner side of the membrane of the thylakoid. *Then, where are the protons and O_2 formed likely to be released – in the lumen? or on the outer side of the membrane?*

13.6.2 Cyclic and Non-cyclic Photo-phosphorylation

Living organisms have the capability of extracting energy from oxidisable substances and store this in the form of bond energy. Special substances like ATP, carry this energy in their chemical bonds. The process through which

ATP is synthesised by cells (in mitochondria and chloroplasts) is named phosphorylation. Photo-phosphorylation is the synthesis of ATP from ADP and inorganic phosphate in the presence of light. When the two photosystems work in a series, first PS II and then the PS I, a process called non-cyclic photo-phosphorylation occurs. The two photosystems are connected through an electron transport chain, as seen earlier – in the Z scheme. Both ATP and NADPH + H^+ are synthesised by this kind of electron flow (Figure 13.5).

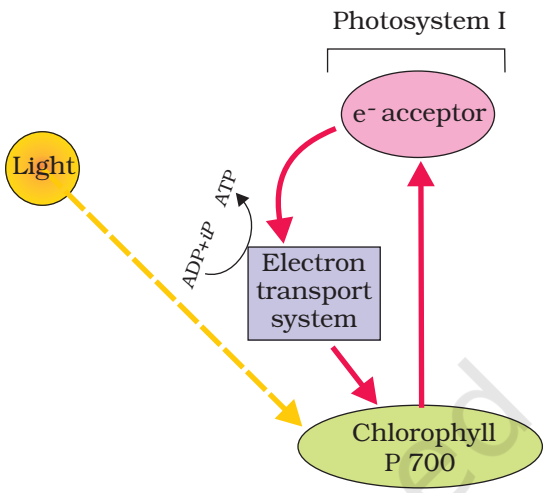


Figure 13.6 Cyclic photophosphorylation

When only PS I is functional, the electron is circulated within the photosystem and the phosphorylation occurs due to cyclic flow of electrons (Figure 13.6). A possible location where this could be happening is in the stroma lamellae. While the membrane or lamellae of the grana have both PS I and PS II the stroma lamellae membranes lack PS II as well as NADP reductase enzyme. The excited electron does not pass on to $NADP^+$ but is cycled back to the PS I complex through the electron transport chain (Figure 13.6). The cyclic flow hence, results only in the synthesis of ATP, but not of NADPH + H^+. Cyclic photophosphorylation also occurs when only light of wavelengths beyond 680 nm are available for excitation.

13.6.3 Chemiosmotic Hypothesis

Let us now try and understand how actually ATP is synthesised in the chloroplast. The chemiosmotic hypothesis has been put forward to explain the mechanism. Like in respiration, in photosynthesis too, ATP synthesis is linked to development of a proton gradient across a membrane. This time these are the membranes of thylakoid. There is one difference though, here the proton accumulation is towards the inside of the membrane, i.e., in the lumen. In respiration, protons accumulate in the intermembrane space of the mitochondria when electrons move through the ETS (Chapter 14).

Let us understand what causes the proton gradient across the membrane. We need to consider again the processes that take place during the activation of electrons and their transport to determine the steps that cause a proton gradient to develop (Figure 13.7).

(a) Since splitting of the water molecule takes place on the inner side of the membrane, the protons or hydrogen ions that are produced by the splitting of water accumulate within the lumen of the thylakoids.

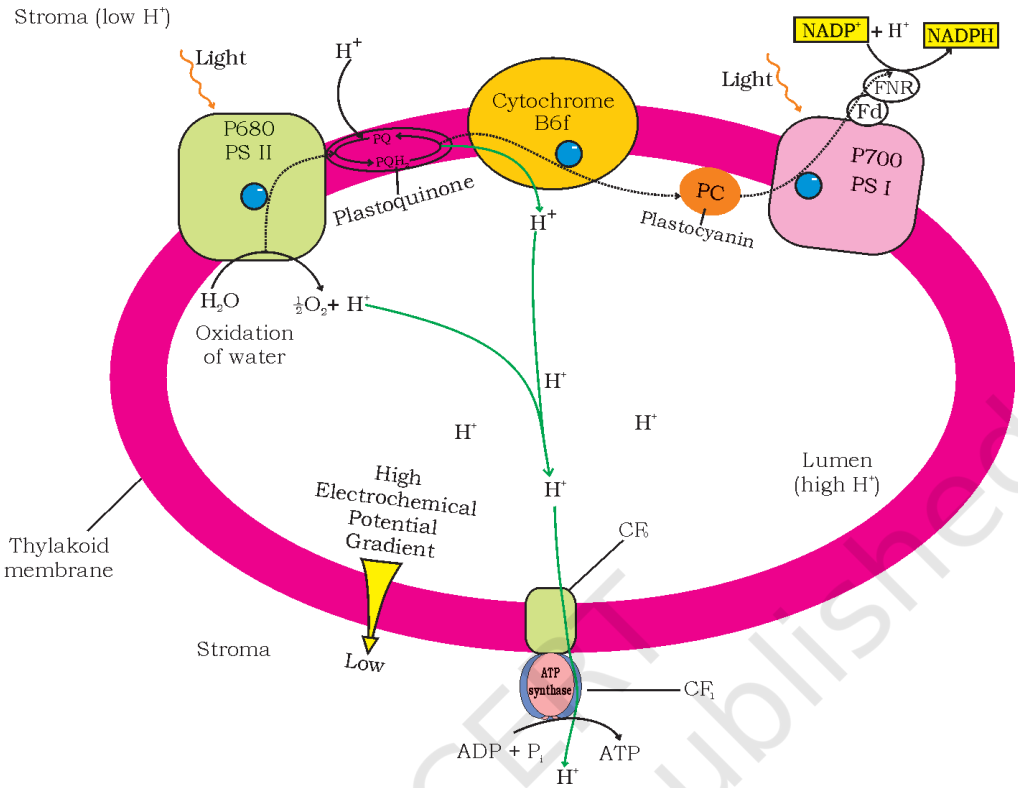


Figure 13.7 ATP synthesis through chemiosmosis

(b) As electrons move through the photosystems, protons are transported across the membrane. This happens because the primary accepter of electron which is located towards the outer side of the membrane transfers its electron not to an electron carrier but to an H carrier. Hence, this molecule removes a proton from the stroma while transporting an electron. When this molecule passes on its electron to the electron carrier on the inner side of the membrane, the proton is released into the inner side or the lumen side of the membrane.

(c) The NADP reductase enzyme is located on the stroma side of the membrane. Along with electrons that come from the acceptor of electrons of PS I, protons are necessary for the reduction of $NADP^+$ to NADPH+ H^+. These protons are also removed from the stroma.

Hence, within the chloroplast, protons in the stroma decrease in number, while in the lumen there is accumulation of protons. This creates a proton gradient across the thylakoid membrane as well as a measurable decrease in pH in the lumen.

Why are we so interested in the proton gradient? This gradient is important because it is the breakdown of this gradient that leads to the synthesis of ATP. The gradient is broken down due to the movement of protons across the membrane to the stroma through the transmembrane

channel of the CF_0 of the ATP synthase. The ATP synthase enzyme consists of two parts: one called the CF_0 is embedded in the thylakoid membrane and forms a transmembrane channel that carries out facilitated diffusion of protons across the membrane. The other portion is called CF_1 and protrudes on the outer surface of the thylakoid membrane on the side that faces the stroma. The break down of the gradient provides enough energy to cause a conformational change in the CF_1 particle of the ATP synthase, which makes the enzyme synthesise several molecules of energy-packed ATP.

Chemiosmosis requires a membrane, a proton pump, a proton gradient and ATP synthase. Energy is used to pump protons across a membrane, to create a gradient or a high concentration of protons within the thylakoid lumen. ATP synthase has a channel that allows diffusion of protons back across the membrane; this releases enough energy to activate ATP synthase enzyme that catalyses the formation of ATP.

Along with the NADPH produced by the movement of electrons, the ATP will be used immediately in the biosynthetic reaction taking place in the stroma, responsible for fixing CO_2, and synthesis of sugars.

13.7 WHERE ARE THE ATP AND NADPH USED?

We learnt that the products of light reaction are ATP, NADPH and O_2. Of these O_2 diffuses out of the chloroplast while ATP and NADPH are used to drive the processes leading to the synthesis of food, more accurately, sugars. This is the **biosynthetic phase** of photosynthesis. This process does not directly depend on the presence of light but is dependent on the products of the light reaction, i.e., ATP and NADPH, besides CO_2 and H_2O. You may wonder how this could be verified; it is simple: immediately after light becomes unavailable, the biosynthetic process continues for some time, and then stops. If then, light is made available, the synthesis starts again.

*Can we, hence, say that calling the biosynthetic phase as the **dark reaction** is a misnomer? Discuss this amongst yourselves.*

Let us now see how the ATP and NADPH are used in the biosynthetic phase. We saw earlier that CO_2 is combined with H_2O to produce $(CH_2O)_n$ or sugars. It was of interest to scientists to find out how this reaction proceeded, or rather what was the first product formed when CO_2 is taken into a reaction or fixed. Just after world war II, among the several efforts to put radioisotopes to beneficial use, the work of Melvin Calvin is exemplary. The use of radioactive ^{14}C by him in algal photosynthesis studies led to the discovery that the first CO_2 fixation product was a 3-carbon organic acid. He also contributed to working out the complete biosynthetic pathway; hence it was called **Calvin cycle** after him. The first product identified was **3-phosphoglyceric** acid or in short **PGA**. *How many carbon atoms does it have?*

Scientists also tried to know whether all plants have PGA as the first product of CO_2 fixation, or whether any other product was formed in other plants. Experiments conducted over a wide range of plants led to the discovery of another group of plants, where the first stable product of CO_2 fixation was again an organic acid, but one which had 4 carbon atoms in it. This acid was identified to be **oxaloacetic acid** or OAA. Since then CO_2 assimilation during photosynthesis was said to be of two main types: those plants in which the first product of CO_2 fixation is a C_3 acid (PGA), i.e., the **C_3 pathway,** and those in which the first product was a C_4 acid (OAA), i.e., the **C_4 pathway**. These two groups of plants showed other associated characteristics that we will discuss later.

13.7.1 The Primary Acceptor of CO_2

Let us now ask ourselves a question that was asked by the scientists who were struggling to understand the 'dark reaction'. *How many carbon atoms would a molecule have which after accepting (fixing) CO_2, would have 3 carbons (of PGA)?*

The studies very unexpectedly showed that the acceptor molecule was a 5-carbon ketose sugar – ribulose bisphosphate (RuBP). *Did any of you think of this possibility?* Do not worry; the scientists also took a long time and conducted many experiments to reach this conclusion. They also believed that since the first product was a C_3 acid, the primary acceptor would be a 2-carbon compound; they spent many years trying to identify a 2-carbon compound before they discovered the 5-carbon RuBP.

13.7.2 The Calvin Cycle

Calvin and his co-workers then worked out the whole pathway and showed that the pathway operated in a cyclic manner; the RuBP was regenerated. Let us now see how the Calvin pathway operates and where the sugar is synthesised. Let us at the outset understand very clearly that the Calvin pathway occurs in **all photosynthetic plants**; it does not matter whether they have C_3 or C_4 (or any other) pathways (Figure 13.8).

For ease of understanding, the Calvin cycle can be described under three stages: carboxylation, reduction and regeneration.

1. **Carboxylation** – Carboxylation is the fixation of CO_2 into a stable organic intermediate. Carboxylation is the most crucial step of the Calvin cycle where CO_2 is utilised for the carboxylation of RuBP. This reaction is catalysed by the enzyme RuBP carboxylase which results in the formation of two molecules of 3-PGA. Since this enzyme also has an oxygenation activity it would be more correct to call it RuBP carboxylase-oxygenase or **RuBisCO**.

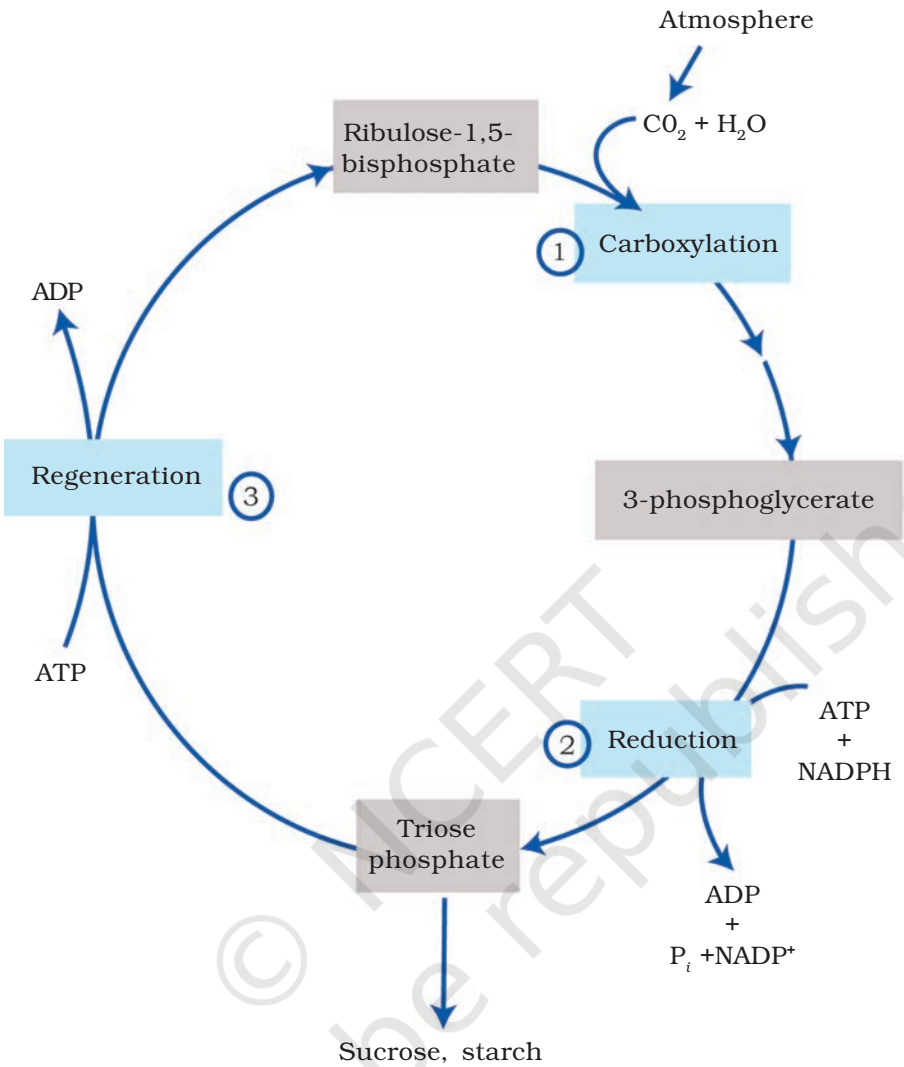


Figure 13.8 The Calvin cycle proceeds in three stages : (1) carboxylation, during which CO_2 combines with ribulose-1,5-bisphosphate; (2) reduction, during which carbohydrate is formed at the expense of the photochemically made ATP and NADPH; and (3) regeneration during which the CO_2 acceptor ribulose-1,5-bisphosphate is formed again so that the cycle continues

2. **Reduction** – These are a series of reactions that lead to the formation of glucose. The steps involve utilisation of 2 molecules of ATP for phosphorylation and two of NADPH for reduction per CO_2 molecule fixed. The fixation of six molecules of CO_2 and 6 turns of the cycle are required for the formation of one molecule of glucose from the pathway.

3. **Regeneration** – Regeneration of the CO_2 acceptor molecule RuBP is crucial if the cycle is to continue uninterrupted. The regeneration steps require one ATP for phosphorylation to form RuBP.

Hence for every CO_2 molecule entering the Calvin cycle, 3 molecules of ATP and 2 of NADPH are required. It is probably to meet this difference in number of ATP and NADPH used in the dark reaction that the cyclic phosphorylation takes place.

To make one molecule of glucose 6 turns of the cycle are required. *Work out how many ATP and NADPH molecules will be required to make one molecule of glucose through the Calvin pathway.*

It might help you to understand all of this if we look at what goes in and what comes out of the Calvin cycle.

In	Out
Six CO_2	One glucose
18 ATP	18 ADP
12 NADPH	12 NADP

13.8 The C_4 Pathway

Plants that are adapted to dry tropical regions have the C_4 pathway mentioned earlier. Though these plants have the C_4 oxaloacetic acid as the first CO_2 fixation product they use the C_3 pathway or the Calvin cycle as the main biosynthetic pathway. Then, in what way are they different from C_3 plants? This is a question that you may reasonably ask.

C_4 plants are special: They have a special type of leaf anatomy, they tolerate higher temperatures, they show a response to high light intensities, they lack a process called photorespiration and have greater productivity of biomass. Let us understand these one by one.

Study vertical sections of leaves, one of a C_3 plant and the other of a C_4 plant. *Do you notice the differences? Do both have the same types of mesophylls? Do they have similar cells around the vascular bundle sheath?*

The particularly large cells around the vascular bundles of the C_4 plants are called **bundle sheath cells**, and the leaves which have such anatomy are said to have **'Kranz' anatomy**. 'Kranz' means 'wreath' and is a reflection of the arrangement of cells. The bundle sheath cells may form **several layers** around the vascular bundles; they are characterised by having a large number of chloroplasts, thick walls impervious to gaseous exchange and no intercellular spaces. You may like to cut a section of the leaves of C_4 plants – maize or sorghum – to observe the Kranz anatomy and the distribution of mesophyll cells.

It would be interesting for you to collect leaves of diverse species of plants around you and cut vertical sections of the leaves. Observe under the microscope – look for the bundle sheath around the vascular bundles. The presence of the bundle sheath would help you identify the C_4 plants.

Now study the pathway shown in Figure 13.9. This pathway that has been named the Hatch and Slack Pathway, is again a cyclic process. Let us study the pathway by listing the steps.

The primary CO_2 acceptor is a 3-carbon molecule **phosphoenol pyruvate (PEP)** and is present in the mesophyll cells. The enzyme responsible for this fixation is **PEP carboxylase** or PEPcase. It is important to register that the mesophyll cells lack RuBisCO enzyme. The C_4 acid OAA is formed in the mesophyll cells.

It then forms other 4-carbon compounds like malic acid or aspartic acid in the mesophyll cells itself, which are transported to the bundle sheath cells. In the bundle sheath cells these C_4 acids are broken down to release CO_2 and a 3-carbon molecule.

The 3-carbon molecule is transported back to the mesophyll where it is converted to PEP again, thus, completing the cycle.

The CO_2 released in the bundle sheath cells enters the C_3 or the Calvin pathway, a pathway common to all plants. The bundle sheath cells are

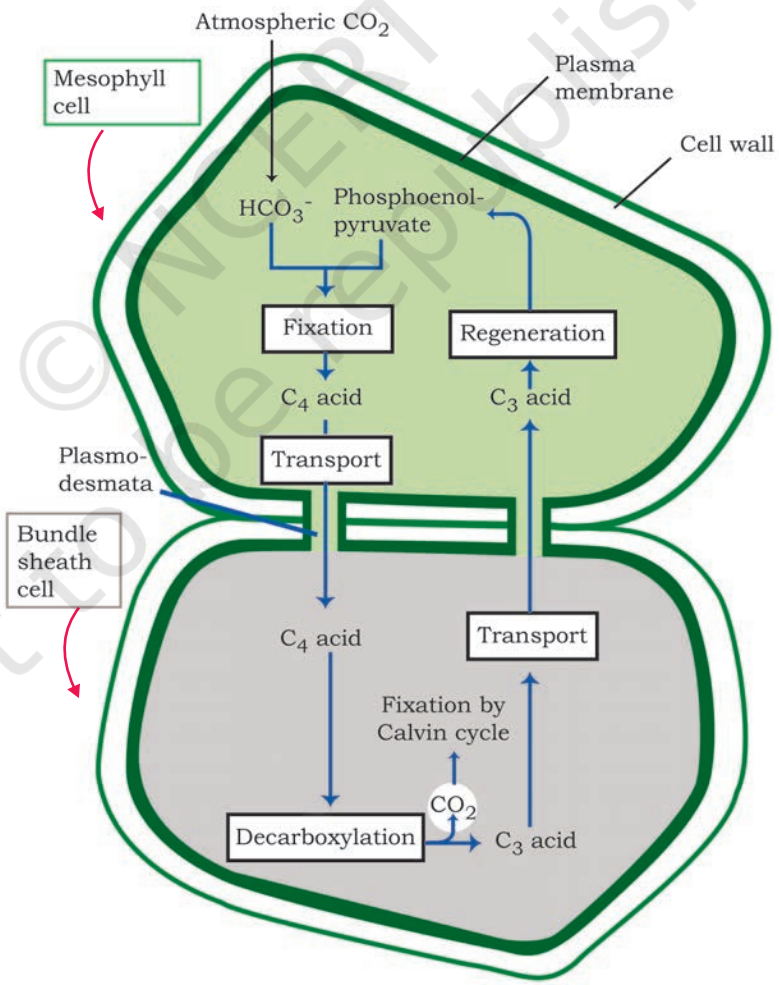


Figure 13.9 Diagrammatic representation of the Hatch and Slack Pathway

rich in an enzyme Ribulose bisphosphate carboxylase-oxygenase **(RuBisCO)**, but lack PEPcase. Thus, the basic pathway that results in the formation of the sugars, the Calvin pathway, is common to the C_3 and C_4 plants.

Did you note that the Calvin pathway occurs in all the mesophyll cells of the C_3 plants? In the C_4 plants it does not take place in the mesophyll cells but does so only in the bundle sheath cells.

13.9 PHOTORESPIRATION

Let us try and understand one more process that creates an important difference between C_3 and C_4 plants – **Photorespiration**. To understand photorespiration we have to know a little bit more about the first step of the Calvin pathway – the first CO_2 fixation step. This is the reaction where RuBP combines with CO_2 to form 2 molecules of 3PGA, that is catalysed by RuBisCO.

$$RuBP + CO_2 \xrightarrow{RuBisCo} 2 \times 3PGA$$

RuBisCO that is the most abundant enzyme in the world (Do you wonder why?) is characterised by the fact that its active site can bind to both CO_2 and O_2 – hence the name. *Can you think how this could be possible?* RuBisCO has a much greater affinity for CO_2 when the CO_2: O_2 is nearly equal than for O_2. Imagine what would happen if this were not so! This binding is competitive. It is the relative concentration of O_2 and CO_2 that determines which of the two will bind to the enzyme.

In C_3 plants some O_2 does bind to RuBisCO, and hence CO_2 fixation is decreased. Here the RuBP instead of being converted to 2 molecules of PGA binds with O_2 to form one molecule of phosphoglycerate and phosphoglycolate (2 Carbon) in a pathway called photorespiration. In the photorespiratory pathway, there is neither synthesis of sugars, nor of ATP. Rather it results in the release of CO_2 with the utilisation of ATP. In the photorespiratory pathway there is no synthesis of ATP or NADPH. The biological function of photorespiration is not known yet.

In C_4 plants photorespiration does not occur. This is because they have a mechanism that increases the concentration of CO_2 at the enzyme site. This takes place when the C_4 acid from the mesophyll is broken down in the bundle sheath cells to release CO_2 – this results in increasing the intracellular concentration of CO_2. In turn, this ensures that the RuBisCO functions as a carboxylase minimising the oxygenase activity.

Now that you know that the C_4 plants lack photorespiration, you probably can understand why productivity and yields are better in these plants. In addition these plants show tolerance to higher temperatures.

Based on the above discussion can you compare plants showing the C_3 and the C_4 pathway? Use the table format given and fill in the information.

TABLE 13.1 Fill in the Columns 2 and 3 in this table to highlight the differences between C_3 and C_4 Plants

Characteristics	C_3 Plants	C_4 Plants	Choose from
Cell type in which the Calvin cycle takes place			Mesophyll/Bundle sheath/both
Cell type in which the initial carboxylation reaction occurs			Mesophyll/Bundle sheath /both
How many cell types does the leaf have that fix CO_2.			Two: Bundle sheath and mesophyll One: Mesophyll Three: Bundle sheath, palisade, spongy mesophyll
Which is the primary CO_2 acceptor			RuBP/PEP/PGA
Number of carbons in the primary CO_2 acceptor			5 / 4 / 3
Which is the primary CO_2 fixation product			PGA/OAA/RuBP/PEP
No. of carbons in the primary CO_2 fixation product			3 / 4 / 5
Does the plant have RuBisCO?			Yes/No/Not always
Does the plant have PEP Case?			Yes/No/Not always
Which cells in the plant have Rubisco?			Mesophyll/Bundle sheath/none
CO_2 fixation rate under high light conditions			Low/ high/ medium
Whether photorespiration is present at low light intensities			High/negligible/sometimes
Whether photorespiration is present at high light intensities			High/negligible/sometimes
Whether photorespiration would be present at low CO_2 concentrations			High/negligible/sometimes
Whether photorespiration would be present at high CO_2 concentrations			High/negligible/sometimes
Temperature optimum			30-40 C/20-25C/above 40 C
Examples			Cut vertical sections of leaves of different plants and observe under the microscope for Kranz anatomy and list them in the appropriate columns.

13.10 FACTORS AFFECTING PHOTOSYNTHESIS

An understanding of the factors that affect photosynthesis is necessary. The rate of photosynthesis is very important in determining the yield of plants including crop plants. Photosynthesis is under the influence of several factors, both internal (plant) and external. The plant factors include the number, size, age and orientation of leaves, mesophyll cells and chloroplasts, internal CO_2 concentration and the amount of chlorophyll. The plant or internal factors are dependent on the genetic predisposition and the growth of the plant.

The external factors would include the availability of sunlight, temperature, CO_2 concentration and water. As a plant photosynthesises, all these factors will simultaneously affect its rate. Hence, though several factors interact and simultaneously affect photosynthesis or CO_2 fixation, usually one factor is the major cause or is the one that limits the rate. Hence, at any point the rate will be determined by the factor available at sub-optimal levels.

When several factors affect any [bio] chemical process, Blackman's (1905) **Law of Limiting Factors** comes into effect. This states the following:

If a chemical process is affected by more than one factor, then its rate will be determined by the factor which is nearest to its minimal value: it is the factor which directly affects the process if its quantity is changed.

For example, despite the presence of a green leaf and optimal light and CO_2 conditions, the plant may not photosynthesise if the temperature is very low. This leaf, if given the optimal temperature, will start photosynthesising.

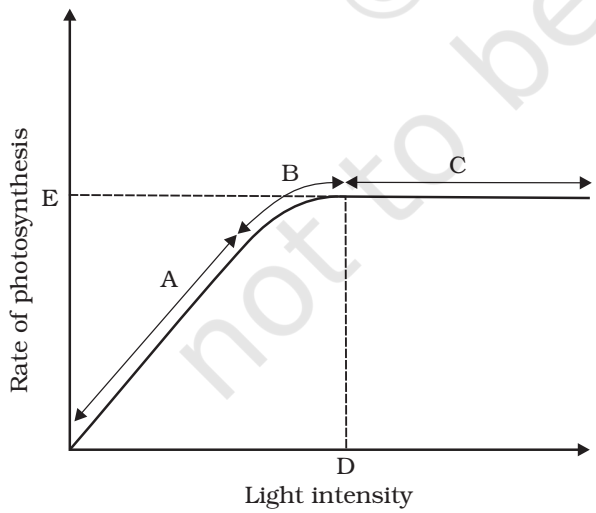


Figure 13.10 Graph of light intensity on the rate of photosynthesis

13.10.1 Light

We need to distinguish between light quality, light intensity and the duration of exposure to light, while discussing light as a factor that affects photosynthesis. There is a linear relationship between incident light and CO_2 fixation rates at low light intensities. At higher light intensities, gradually the rate does not show further increase as other factors become limiting (Figure 13.10). What is interesting to note is that light saturation occurs at 10 per cent of the full sunlight. Hence, except for plants in shade or in dense forests, light is rarely a limiting factor in nature. Increase in

incident light beyond a point causes the breakdown of chlorophyll and a decrease in photosynthesis.

13.10.2 Carbon dioxide Concentration

Carbon dioxide is the major limiting factor for photosynthesis. The concentration of CO_2 is very low in the atmosphere (between 0.03 and 0.04 per cent). Increase in concentration upto 0.05 per cent can cause an increase in CO_2 fixation rates; beyond this the levels can become damaging over longer periods.

The C_3 and C_4 plants respond differently to CO_2 concentrations. At low light conditions neither group responds to high CO_2 conditions. At high light intensities, both C_3 and C_4 plants show increase in the rates of photosynthesis. What is important to note is that the C_4 plants show saturation at about 360 $\mu l L^{-1}$ while C_3 responds to increased CO_2 concentration and saturation is seen only beyond 450 $\mu l L^{-1}$. Thus, current availability of CO_2 levels is limiting to the C_3 plants.

The fact that C_3 plants respond to higher CO_2 concentration by showing increased rates of photosynthesis leading to higher productivity has been used for some greenhouse crops such as tomatoes and bell pepper. They are allowed to grow in carbon dioxide enriched atmosphere that leads to higher yields.

13.10.3 Temperature

The dark reactions being enzymatic are temperature controlled. Though the light reactions are also temperature sensitive they are affected to a much lesser extent. The C_4 plants respond to higher temperatures and show higher rate of photosynthesis while C_3 plants have a much lower temperature optimum.

The temperature optimum for photosynthesis of different plants also depends on the habitat that they are adapted to. Tropical plants have a higher temperature optimum than the plants adapted to temperate climates.

13.10.4 Water

Even though water is one of the reactants in the light reaction, the effect of water as a factor is more through its effect on the plant, rather than directly on photosynthesis. Water stress causes the stomata to close hence reducing the CO_2 availability. Besides, water stress also makes leaves wilt, thus, reducing the surface area of the leaves and their metabolic activity as well.

SUMMARY

Green plants make their own food by photosynthesis. During this process carbon dioxide from the atmosphere is taken in by leaves through stomata and used for making carbohydrates, principally glucose and starch. Photosynthesis takes place only in the green parts of the plants, mainly the leaves. Within the leaves, the mesophyll cells have a large number of chloroplasts that are responsible for CO_2 fixation. Within the chloroplasts, the membranes are sites for the light reaction, while the chemosynthetic pathway occurs in the stroma. Photosynthesis has two stages: the light reaction and the carbon fixing reactions. In the light reaction the light energy is absorbed by the pigments present in the antenna, and funnelled to special chlorophyll *a* molecules called reaction centre chlorophylls. There are two photosystems, PS I and PS II. PS I has a 700 nm absorbing chlorophyll *a* P700 molecule at its reaction centre, while PS II has a P680 reaction centre that absorbs red light at 680 nm. After absorbing light, electrons are excited and transferred through PS II and PS I and finally to NAD forming NADH. During this process a proton gradient is created across the membrane of the thylakoid. The breakdown of the protons gradient due to movement through the F_0 part of the ATPase enzyme releases enough energy for synthesis of ATP. Splitting of water molecules is associated with PS II resulting in the release of O_2, protons and transfer of electrons to PS II.

In the carbon fixation cycle, CO_2 is added by the enzyme, RuBisCO, to a 5-carbon compound RuBP that is converted to 2 molecules of 3-carbon PGA. This is then converted to sugar by the Calvin cycle, and the RuBP is regenerated. During this process ATP and NADPH synthesised in the light reaction are utilised. RuBisCO also catalyses a wasteful oxygenation reaction in C_3 plants: photorespiration.

Some tropical plants show a special type of photosynthesis called C_4 pathway. In these plants the first product of CO_2 fixation that takes place in the mesophyll, is a 4-carbon compound. In the bundle sheath cells the Calvin pathway is carried out for the synthesis of carbohydrates.

EXERCISES

1. By looking at a plant externally can you tell whether a plant is C_3 or C_4? Why and how?
2. By looking at which internal structure of a plant can you tell whether a plant is C_3 or C_4? Explain.
3. Even though a very few cells in a C_4 plant carry out the biosynthetic – Calvin pathway, yet they are highly productive. Can you discuss why?

4. RuBisCO is an enzyme that acts both as a carboxylase and oxygenase. Why do you think RuBisCO carries out more carboxylation in C_4 plants?
5. Suppose there were plants that had a high concentration of Chlorophyll *b*, but lacked chlorophyll *a*, would it carry out photosynthesis? Then why do plants have chlorophyll *b* and other accessory pigments?
6. Why is the colour of a leaf kept in the dark frequently yellow, or pale green? Which pigment do you think is more stable?
7. Look at leaves of the same plant on the shady side and compare it with the leaves on the sunny side. Or, compare the potted plants kept in the sunlight with those in the shade. Which of them has leaves that are darker green ? Why?
8. Figure 13.10 shows the effect of light on the rate of photosynthesis. Based on the graph, answer the following questions:

   (a) At which point/s (A, B or C) in the curve is light a limiting factor?
   (b) What could be the limiting factor/s in region A?
   (c) What do C and D represent on the curve?
9. Give comparison between the following:

   (a) C_3 and C_4 pathways
   (b) Cyclic and non-cyclic photophosphorylation
   (c) Anatomy of leaf in C_3 and C_4 plants

Chapter 14
Respiration in Plants

All of us breathe to live, but why is breathing so essential to life? What happens when we breathe? Also, do all living organisms, including plants and microbes, breathe? If so, how?

All living organisms need energy for carrying out daily life activities, be it absorption, transport, movement, reproduction or even breathing. Where does all this energy come from? We know we eat food for energy – but how is this energy taken from food? How is this energy utilised? Do all foods give the same amount of energy? Do plants 'eat'? Where do plants get their energy from? And micro-organisms – for their energy requirements, do they eat 'food'?

You may wonder at the several questions raised above – they may seem to be very disconnected. But in reality, the process of breathing is very much connected to the process of release of energy from food. Let us try and understand how this happens.

All the energy required for 'life' processes is obtained by oxidation of some macromolecules that we call 'food'. Only green plants and cyanobacteria can prepare their own food; by the process of photosynthesis they trap light energy and convert it into chemical energy that is stored in the bonds of carbohydrates like glucose, sucrose and starch. We must remember that in green plants too, not all cells, tissues and organs photosynthesise; only cells containing chloroplasts, that are most often located in the superficial layers, carry out photosynthesis. Hence, even in green plants all other organs, tissues and cells that are non-green, need food for oxidation. Hence, food has to be translocated to all non-green parts. Animals are heterotrophic, i.e., they obtain food from plants

directly (herbivores) or indirectly (carnivores). Saprophytes like fungi are dependent on dead and decaying matter. What is important to recognise is that ultimately all the food that is respired for life processes comes from photosynthesis. This chapter deals with **cellular respiration** or the mechanism of breakdown of food materials within the cell to release energy, and the trapping of this energy for synthesis of ATP.

Photosynthesis, of course, takes place within the chloroplasts (in the eukaryotes), whereas the breakdown of complex molecules to yield energy takes place in the cytoplasm and in the mitochondria (also only in eukaryotes). The breaking of the C-C bonds of complex compounds through oxidation within the cells, leading to release of considerable amount of energy is called **respiration**. The compounds that are oxidised during this process are known as **respiratory substrates.** Usually carbohydrates are oxidised to release energy, but proteins, fats and even organic acids can be used as respiratory substances in some plants, under certain conditions. During oxidation within a cell, all the energy contained in respiratory substrates is not released free into the cell, or in a single step. It is released in a series of slow step-wise reactions controlled by enzymes, and it is trapped as chemical energy in the form of ATP. Hence, it is important to understand that the energy released by oxidation in respiration is not (or rather cannot be) used directly but is used to synthesise ATP, which is broken down whenever (and wherever) energy needs to be utilised. Hence, ATP acts as the energy currency of the cell. This energy trapped in ATP is utilised in various energy-requiring processes of the organisms, and the carbon skeleton produced during respiration is used as precursors for biosynthesis of other molecules in the cell.

14.1 DO PLANTS BREATHE?

Well, the answer to this question is not quite so direct. Yes, plants require O_2 for respiration to occur and they also give out CO_2. Hence, plants have systems in place that ensure the availability of O_2. Plants, unlike animals, have no specialised organs for gaseous exchange but they have stomata and lenticels for this purpose. There are several reasons why plants can get along without respiratory organs. First, each plant part takes care of its own gas-exchange needs. There is very little transport of gases from one plant part to another. Second, plants do not present great demands for gas exchange. Roots, stems and leaves respire at rates far lower than animals do. Only during photosynthesis are large volumes of gases exchanged and, each leaf is well adapted to take care of its own needs during these periods. When cells photosynthesise, availability of O_2 is not a problem in these cells since O_2 is released within the cell. Third, the

distance that gases must diffuse even in large, bulky plants is not great. Each living cell in a plant is located quite close to the surface of the plant. 'This is true for leaves', you may ask, 'but what about thick, woody stems and roots?' In stems, the 'living' cells are organised in thin layers inside and beneath the bark. They also have openings called lenticels. The cells in the interior are dead and provide only mechanical support. Thus, most cells of a plant have at least a part of their surface in contact with air. This is also facilitated by the loose packing of parenchyma cells in leaves, stems and roots, which provide an interconnected network of air spaces.

The complete combustion of glucose, which produces CO_2 and H_2O as end products, yields energy most of which is given out as heat.

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

If this energy is to be useful to the cell, it should be able to utilise it to synthesise other molecules that the cell requires. The strategy that the plant cell uses is to catabolise the glucose molecule in such a way that not all the liberated energy goes out as heat. The key is to oxidise glucose not in one step but in several small steps enabling some steps to be just large enough such that the energy released can be coupled to ATP synthesis. How this is done is, essentially, the story of respiration.

During the process of respiration, oxygen is utilised, and carbon dioxide, water and energy are released as products. The combustion reaction requires oxygen. But some cells live where oxygen may or may not be available. *Can you think of such situations (and organisms) where O_2 is not available?* There are sufficient reasons to believe that the first cells on this planet lived in an atmosphere that lacked oxygen. Even among present-day living organisms, we know of several that are adapted to anaerobic conditions. Some of these organisms are facultative anaerobes, while in others the requirement for anaerobic condition is obligate. In any case, all living organisms retain the enzymatic machinery to partially oxidise glucose without the help of oxygen. This breakdown of glucose to pyruvic acid is called **glycolysis.**

14.2 GLYCOLYSIS

The term glycolysis has originated from the Greek words, *glycos* for sugar, and *lysis* for splitting. The scheme of glycolysis was given by Gustav Embden, Otto Meyerhof, and J. Parnas, and is often referred to as the EMP pathway. In anaerobic organisms, it is the only process in respiration. Glycolysis occurs in the cytoplasm of the cell and is present in all living organisms. In this process, glucose undergoes partial oxidation to form two molecules of pyruvic acid. In plants, this glucose is derived from sucrose, which is the end product of photosynthesis, or from storage

carbohydrates. Sucrose is converted into glucose and fructose by the enzyme, invertase, and these two monosaccharides readily enter the glycolytic pathway. Glucose and fructose are phosphorylated to give rise to glucose-6-phosphate by the activity of the enzyme hexokinase. This phosphorylated form of glucose then isomerises to produce fructose-6-phosphate. Subsequent steps of metabolism of glucose and fructose are same. The various steps of glycolysis are depicted in Figure 14.1. In glycolysis, a chain of ten reactions, under the control of different enzymes, takes place to produce pyruvate from glucose. While studying the steps of glycolysis, please note the steps at which utilisation or synthesis of ATP or (in this case) NADH + H^+ take place.

ATP is utilised at two steps: first in the conversion of glucose into glucose 6-phosphate and second in the conversion of fructose 6-phosphate to fructose 1, 6-bisphosphate.

The fructose 1, 6-bisphosphate is split into dihydroxyacetone phosphate and 3-phosphoglyceraldehyde (PGAL). We find that there is one step where NADH + H^+ is formed from NAD^+; this is when 3-phosphoglyceraldehyde (PGAL) is converted to 1, 3-bisphosphoglycerate (BPGA). Two redox-equivalents are removed (in the form of two hydrogen atoms) from PGAL and transferred to a molecule of NAD^+. PGAL is oxidised and with inorganic phosphate to get converted into BPGA. The conversion of BPGA to 3-phosphoglyceric acid (PGA), is also an energy yielding process; this energy is trapped by the formation of ATP. Another ATP is synthesised during the conversion of PEP to pyruvic acid. ***Can you then calculate how many ATP molecules are directly synthesised in this pathway from one glucose molecule?***

Pyruvic acid is then the key product of glycolysis. What is the metabolic fate of pyruvate? This depends on the cellular need.

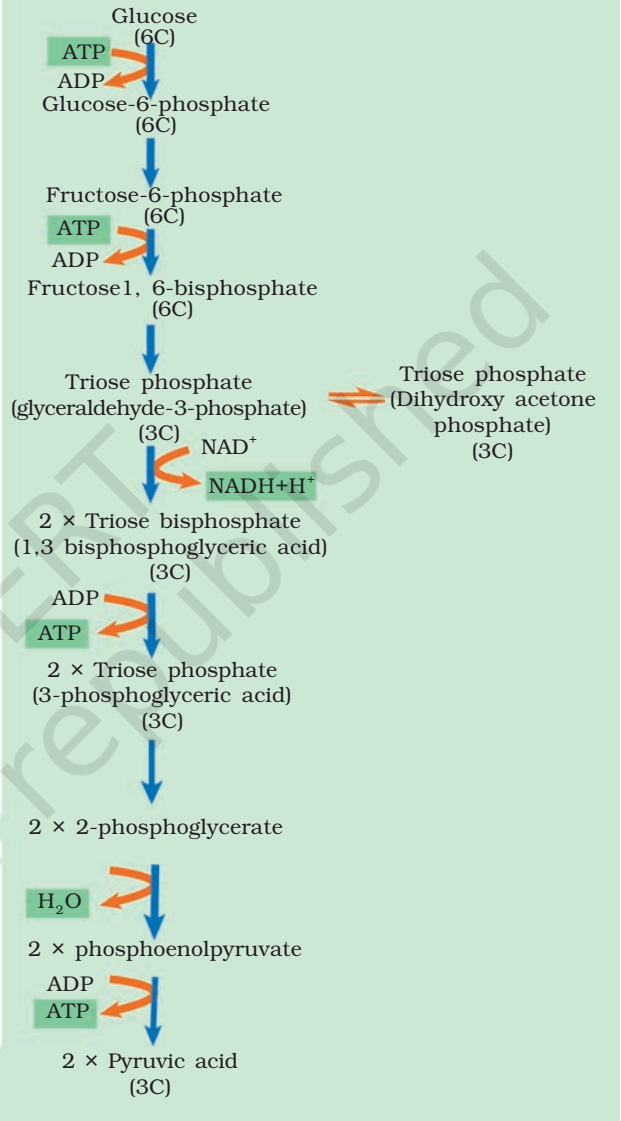


Figure 14.1 Steps of glycolysis

There are three major ways in which different cells handle pyruvic acid produced by glycolysis. These are lactic acid fermentation, alcoholic fermentation and aerobic respiration. Fermentation takes place under anaerobic conditions in many prokaryotes and unicellular eukaryotes. For the complete oxidation of glucose to CO_2 and H_2O, however, organisms adopt Krebs' cycle which is also called as aerobic respiration. This requires O_2 supply.

14.3 FERMENTATION

In fermentation, say by yeast, the incomplete oxidation of glucose is achieved under anaerobic conditions by sets of reactions where pyruvic acid is converted to CO_2 and ethanol. The enzymes, pyruvic acid decarboxylase and alcohol dehydrogenase catalyse these reactions. Other organisms like some bacteria produce lactic acid from pyruvic acid. The steps involved are shown in Figure 14.2. In animal cells also, like muscles during exercise, when oxygen is inadequate for cellular respiration pyruvic acid is reduced to lactic acid by lactate dehydrogenase. The reducing agent is $NADH+H^+$ which is reoxidised to NAD^+ in both the processes.

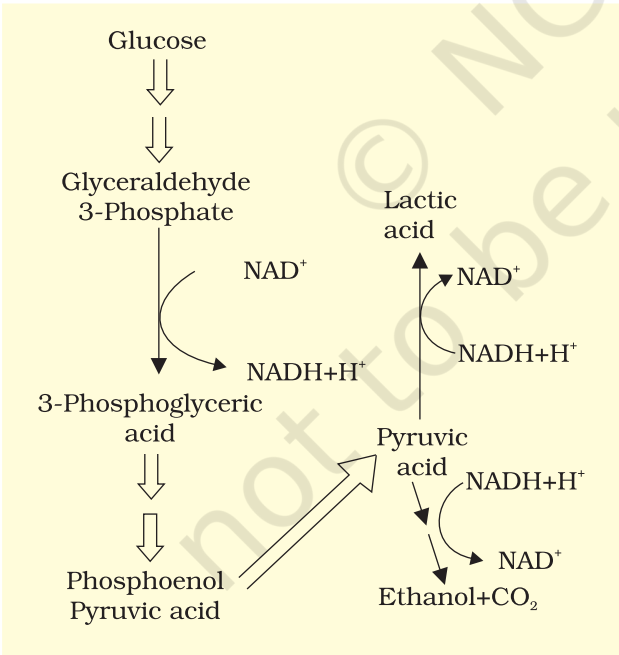


Figure 14.2 Major pathways of anaerobic respiration

In both lactic acid and alcohol fermentation not much energy is released; less than seven per cent of the energy in glucose is released and not all of it is trapped as high energy bonds of ATP. Also, the processes are hazardous – either acid or alcohol is produced. What is the net ATPs that is synthesised (calculate how many ATP are synthesised and deduct the number of ATP utilised during glycolysis) when one molecule of glucose is fermented to alcohol or lactic acid? Yeasts poison themselves to death when the concentration of alcohol reaches about 13 per cent. ***What then would be the maximum concentration of alcohol in beverages that are naturally fermented?*** How do you think alcoholic beverages of alcohol content greater than this concentration are obtained?

What then is the process by which organisms can carry out complete oxidation of glucose and extract the energy stored to

synthesise a larger number of ATP molecules needed for cellular metabolism? In eukaryotes these steps take place within the mitochondria and this requires O_2. **Aerobic respiration** is the process that leads to a complete oxidation of organic substances in the presence of oxygen, and releases CO_2, water and a large amount of energy present in the substrate. This type of respiration is most common in higher organisms. We will look at these processes in the next section.

14.4 AEROBIC RESPIRATION

For aerobic respiration to take place within the mitochondria, the final product of glycolysis, pyruvate is transported from the cytoplasm into the mitochondria. The crucial events in aerobic respiration are:

- The complete oxidation of pyruvate by the stepwise removal of all the hydrogen atoms, leaving three molecules of CO_2.
- The passing on of the electrons removed as part of the hydrogen atoms to molecular O_2 with simultaneous synthesis of ATP.

What is interesting to note is that the first process takes place in the matrix of the mitochondria while the second process is located on the inner membrane of the mitochondria.

Pyruvate, which is formed by the glycolytic catabolism of carbohydrates in the cytosol, after it enters mitochondrial matrix undergoes oxidative decarboxylation by a complex set of reactions catalysed by pyruvic dehydrogenase. The reactions catalysed by pyruvic dehydrogenase require the participation of several coenzymes, including NAD^+ and Coenzyme A.

$$\text{Pyruvic acid} + \text{CoA} + \text{NAD}^+ \xrightarrow[\text{Pyruvate dehydrogenase}]{\text{Mg}^{2+}} \text{Acetyl CoA} + \text{CO}_2 + \text{NADH} + \text{H}^+$$

During this process, two molecules of NADH are produced from the metabolism of two molecules of pyruvic acid (produced from one glucose molecule during glycolysis).

The acetyl CoA then enters a cyclic pathway, tricarboxylic acid cycle, more commonly called as Krebs' cycle after the scientist Hans Krebs who first elucidated it.

14.4.1 Tricarboxylic Acid Cycle

The TCA cycle starts with the condensation of acetyl group with oxaloacetic acid (OAA) and water to yield citric acid (Figure 14.3). The reaction is catalysed by the enzyme citrate synthase and a molecule of CoA is released. Citrate is then isomerised to isocitrate. It is followed by two successive steps of decarboxylation, leading to the formation of α-ketoglutaric acid

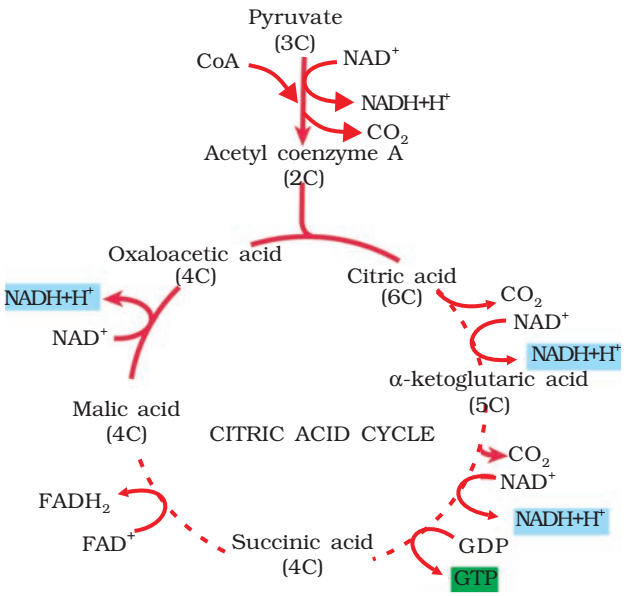


Figure 14.3 The Citric acid cycle

and then succinyl-CoA. In the remaining steps of citric acid cycle, succinyl-CoA is oxidised to OAA allowing the cycle to continue. During the conversion of succinyl-CoA to succinic acid a molecule of GTP is synthesised. This is a substrate level phosphorylation. In a coupled reaction GTP is converted to GDP with the simultaneous synthesis of ATP from ADP. Also there are three points in the cycle where NAD^+ is reduced to $NADH + H^+$ and one point where FAD^+ is reduced to $FADH_2$. The continued oxidation of acetyl CoA via the TCA cycle requires the continued replenishment of oxaloacetic acid, the first member of the cycle. In addition it also requires regeneration of NAD^+ and FAD^+ from NADH and $FADH_2$ respectively. The summary equation for this phase of respiration may be written as follows:

$$\text{Pyruvic acid} + 4NAD^+ + FAD^+ + 2H_2O + ADP + Pi \xrightarrow{\text{Mitochondrial Matrix}} 3CO_2 + 4NADH + 4H^+ + FADH_2 + ATP$$

We have till now seen that glucose has been broken down to release CO_2 and eight molecules of $NADH + H^+$; two of $FADH_2$ have been synthesised besides just two molecules of ATP in TCA cycle. You may be wondering why we have been discussing respiration at all – neither O_2 has come into the picture nor the promised large number of ATP has yet been synthesised. Also what is the role of the $NADH + H^+$ and $FADH_2$ that is synthesised? Let us now understand the role of O_2 in respiration and how ATP is synthesised.

14.4.2 Electron Transport System (ETS) and Oxidative Phosphorylation

The following steps in the respiratory process are to release and utilise the energy stored in $NADH+H^+$ and $FADH_2$. This is accomplished when they are oxidised through the electron transport system and the electrons are passed on to O_2 resulting in the formation of H_2O. The metabolic pathway through which the electron passes from one carrier to another, is called the ***electron transport system*** (ETS) (Figure 14.4) and it is present in the inner mitochondrial membrane. Electrons from NADH

produced in the mitochondrial matrix during citric acid cycle are oxidised by an NADH dehydrogenase (complex I), and electrons are then transferred to ubiquinone located within the inner membrane. Ubiquinone also receives reducing equivalents via $FADH_2$ (complex II) that is generated during oxidation of succinate in the citric acid cycle. The reduced ubiquinone (ubiquinol) is then oxidised with the transfer of electrons to cytochrome *c* via cytochrome bc_1 complex (complex III). Cytochrome *c* is a small protein attached to the outer surface of the inner membrane and acts as a mobile carrier for transfer of electrons between complex III and IV. Complex IV refers to cytochrome *c* oxidase complex containing cytochromes *a* and a_3, and two copper centres.

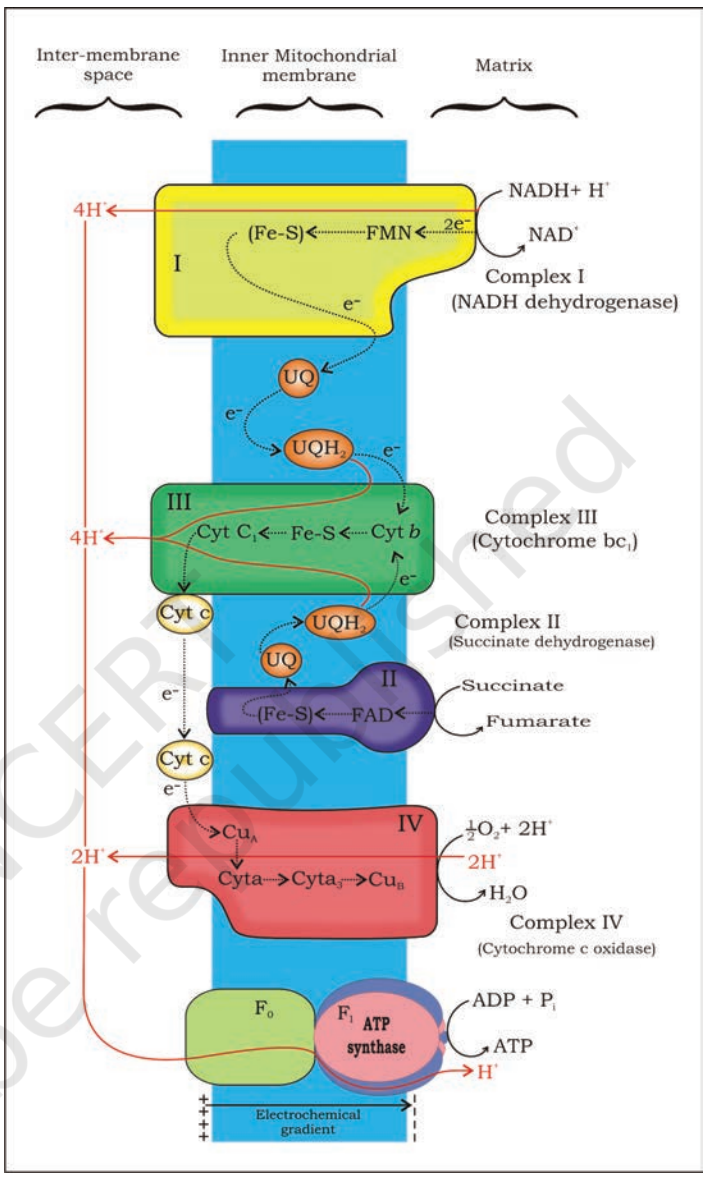


Figure 14.4 Electron Transport System (ETS)

When the electrons pass from one carrier to another via complex I to IV in the electron transport chain, they are coupled to ATP synthase (complex V) for the production of ATP from ADP and inorganic phosphate. The number of ATP molecules synthesised depends on the nature of the electron donor. Oxidation of one molecule of NADH gives rise to 3 molecules of ATP, while that of one molecule of $FADH_2$ produces 2 molecules of ATP. Although the aerobic process of respiration takes place only in the presence of oxygen, the role of oxygen is limited to the terminal stage of the process. Yet, the presence of oxygen is vital, since it drives the whole process by removing hydrogen from the system. Oxygen acts as the final hydrogen acceptor. Unlike photophosphorylation where it is the light energy that is utilised for the production of proton gradient required for phosphorylation, in respiration it is the energy of oxidation-reduction utilised for the same process. It is for this reason that the process is called oxidative phosphorylation.

You have already studied about the mechanism of membrane-linked ATP synthesis as explained by chemiosmotic hypothesis in the earlier chapter. As mentioned earlier, the energy released during the electron

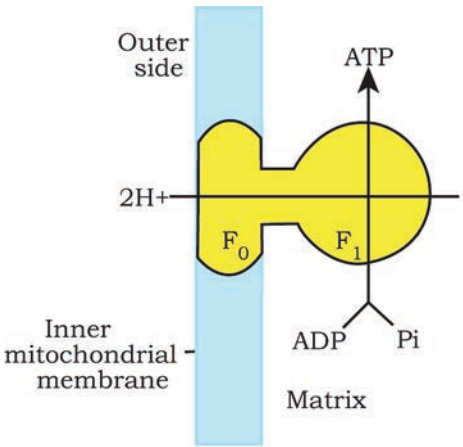


Figure 14.5 Diagramatic presentation of ATP synthesis in mitochondria

transport system is utilised in synthesising ATP with the help of ATP synthase (complex V). This complex consists of two major components, F_1 and F_0 (Figure 14.5). The F_1 headpiece is a peripheral membrane protein complex and contains the site for synthesis of ATP from ADP and inorganic phosphate. F_0 is an integral membrane protein complex that forms the channel through which protons cross the inner membrane. The passage of protons through the channel is coupled to the catalytic site of the F_1 component for the production of ATP. For each ATP produced, $2H^+$ passes through F_0 from the intermembrane space to the matrix down the electrochemical proton gradient.

14.5 The Respiratory Balance Sheet

It is possible to make calculations of the net gain of ATP for every glucose molecule oxidised; but in reality this can remain only a theoretical exercise. These calculations can be made only on certain assumptions that:

- There is a sequential, orderly pathway functioning, with one substrate forming the next and with glycolysis, TCA cycle and ETS pathway following one after another.
- The NADH synthesised in glycolysis is transferred into the mitochondria and undergoes oxidative phosphorylation.
- None of the intermediates in the pathway are utilised to synthesise any other compound.
- Only glucose is being respired – no other alternative substrates are entering in the pathway at any of the intermediary stages.

But this kind of assumptions are not really valid in a living system; all pathways work simultaneously and do not take place one after another; substrates enter the pathways and are withdrawn from it as and when necessary; ATP is utilised as and when needed; enzymatic rates are controlled by multiple means. Yet, it is useful to do this exercise to appreciate the beauty and efficiency of the living system in extraction and storing energy. Hence, there can be a net gain of 38 ATP molecules during aerobic respiration of one molecule of glucose.

Now let us compare fermentation and aerobic respiration:

- Fermentation accounts for only a partial breakdown of glucose whereas in aerobic respiration it is completely degraded to CO_2 and H_2O.
- In fermentation there is a net gain of only two molecules of ATP for each molecule of glucose degraded to pyruvic acid whereas many more molecules of ATP are generated under aerobic conditions.
- NADH is oxidised to NAD^+ rather slowly in fermentation, however the reaction is very vigorous in case of aerobic respiration.

14.6 AMPHIBOLIC PATHWAY

Glucose is the favoured substrate for respiration. All carbohydrates are usually first converted into glucose before they are used for respiration. Other substrates can also be respired, as has been mentioned earlier, but then they do not enter the respiratory pathway at the first step. See Figure 14.6 to see the points of entry of different substrates in the respiratory pathway. Fats would need to be broken down into glycerol and fatty acids first. If fatty acids were to be respired they would first be degraded to acetyl CoA and enter the pathway. Glycerol would enter the pathway after being converted to PGAL. The proteins would be degraded by proteases and the individual amino acids (after deamination) depending on their structure would enter the pathway at some stage within the Krebs' cycle or even as pyruvate or acetyl CoA.

Since respiration involves breakdown of substrates, the respiratory process has traditionally been considered a catabolic process and the respiratory pathway as a catabolic pathway. But is this understanding correct? We have discussed above, at which points in the respiratory pathway different substrates would enter if they were to be respired and used to derive energy. What is important to recognise is that it is these very compounds that would be withdrawn from the respiratory pathway for the synthesis of the said substrates. Hence, fatty acids would be broken down to acetyl CoA before entering the respiratory pathway when it is used as a substrate. But when the organism needs to synthesise fatty acids, acetyl CoA would be withdrawn from the respiratory pathway for it. Hence, the respiratory pathway comes into the picture both during breakdown and synthesis of fatty acids. Similarly, during breakdown and synthesis of protein too, respiratory intermediates form the link. Breaking down processes within the living organism is catabolism, and synthesis is anabolism. Because the respiratory pathway is involved in both anabolism and catabolism, it would hence be better to consider the respiratory pathway as an **amphibolic pathway** rather than as a catabolic one.

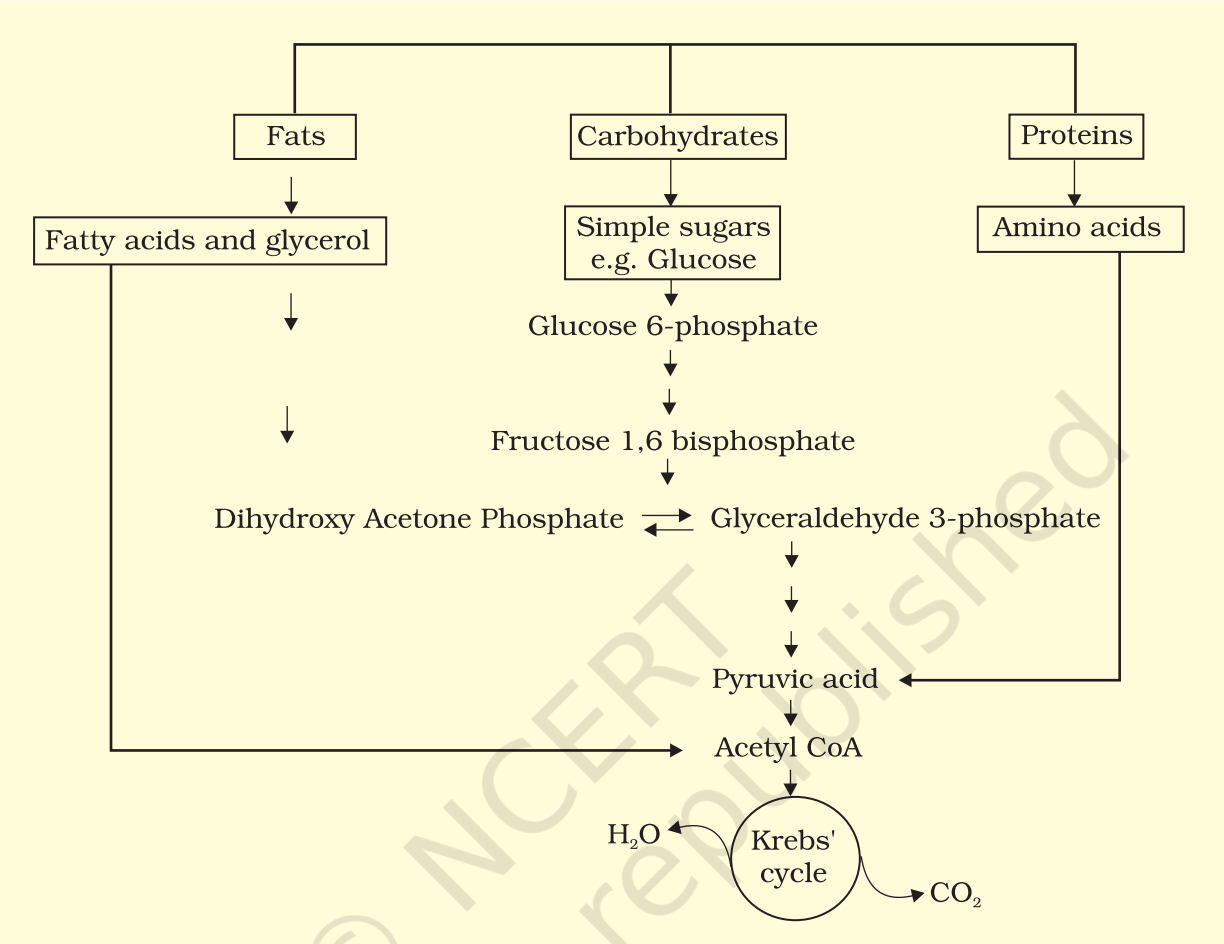


Figure 14.6 Interrelationship among metabolic pathways showing respiration mediated breakdown of different organic molecules to CO_2 and H_20

14.7 Respiratory Quotient

Let us now look at another aspect of respiration. As you know, during aerobic respiration, O_2 is consumed and CO_2 is released. The ratio of the volume of CO_2 evolved to the volume of O_2 consumed in respiration is called the **respiratory quotient** (RQ) or respiratory ratio.

$$RQ = \frac{\text{volume of } CO_2 \text{ evolved}}{\text{volume of } O_2 \text{ consumed}}$$

The respiratory quotient depends upon the type of respiratory substrate used during respiration.

When carbohydrates are used as substrate and are completely oxidised, the RQ will be 1, because equal amounts of CO_2 and O_2 are evolved and consumed, respectively, as shown in the equation below :

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

$$RQ = \frac{6CO_2}{6O_2} = 1.0$$

When fats are used in respiration, the RQ is less than 1. Calculations for a fatty acid, tripalmitin, if used as a substrate is shown:

$$2(C_{51}H_{98}O_6) + 145O_2 \longrightarrow 102CO_2 + 98H_2O + \text{energy}$$

Tripalmitin

$$RQ = \frac{102CO_2}{145O_2} = 0.7$$

When proteins are respiratory substrates the ratio would be about 0.9.

What is important to recognise is that in living organisms respiratory substrates are often more than one; pure proteins or fats are never used as respiratory substrates.

SUMMARY

Plants unlike animals have no special systems for breathing or gaseous exchange. Stomata and lenticels allow gaseous exchange by diffusion. Almost all living cells in a plant have their surfaces exposed to air.

The breaking of C-C bonds of complex organic molecules by oxidation cells leading to the release of a lot of energy is called cellular respiration. Glucose is the favoured substrate for respiration. Fats and proteins can also be broken down to yield energy. The initial stage of cellular respiration takes place in the cytoplasm. Each glucose molecule is broken through a series of enzyme catalysed reactions into two molecules of pyruvic acid. This process is called glycolysis. The fate of the pyruvate depends on the availability of oxygen and the organism. Under anaerobic conditions either lactic acid fermentation or alcohol fermentation occurs. Fermentation takes place under anaerobic conditions in many prokaryotes, unicellular eukaryotes and in germinating seeds. In eukaryotic organisms aerobic respiration occurs in the presence of oxygen. Pyruvic acid is transported into the mitochondria where it is converted into acetyl CoA with the release of CO_2. Acetyl CoA then enters the tricarboxylic acid pathway or Krebs' cycle operating in the matrix of the mitochondria. NADH + H^+ and $FADH_2$ are generated in the Krebs' cycle. The energy in these molecules as well as that in the NADH + H^+ synthesised during glycolysis are used to synthesise ATP. This is accomplished through a

system of electron carriers called electron transport system (ETS) located on the inner membrane of the mitochondria. The electrons, as they move through the system, release enough energy that are trapped to synthesise ATP. This is called oxidative phosphorylation. In this process O_2 is the ultimate acceptor of electrons and it gets reduced to water.

The respiratory pathway is an amphibolic pathway as it involves both anabolism and catabolism. The respiratory quotient depends upon the type of respiratory substance used during respiration.

EXERCISES

1. Differentiate between
   (a) Respiration and Combustion
   (b) Glycolysis and Krebs' cycle
   (c) Aerobic respiration and Fermentation
2. What are respiratory substrates? Name the most common respiratory substrate.
3. Give the schematic representation of glycolysis?
4. What are the main steps in aerobic respiration? Where does it take place?
5. Give the schematic representation of an overall view of Krebs' cycle.
6. Explain ETS.
7. Distinguish between the following:
   (a) Aerobic respiration and Anaerobic respiration
   (b) Glycolysis and Fermentation
   (c) Glycolysis and Citric acid Cycle
8. What are the assumptions made during the calculation of net gain of ATP?
9. Discuss "The respiratory pathway is an amphibolic pathway."
10. Define RQ. What is its value for fats?
11. What is oxidative phosphorylation?
12. What is the significance of step-wise release of energy in respiration?

Chapter 15

Plant Growth and Development

You have already studied the organisation of a flowering plant in Chapter 5. Have you ever thought about where and how the structures like roots, stems, leaves, flowers, fruits and seeds arise and that too in an orderly sequence? You are, by now, aware of the terms seed, seedling, plantlet, mature plant. You have also seen that trees continue to increase in height or girth over a period of time. However, the leaves, flowers and fruits of the same tree not only have limited dimensions but also appear and fall periodically and some time repeatedly. Why does vegetative phase precede flowering in a plant? All plant organs are made up of a variety of tissues; is there any relationship between the structure of a cell, a tissue, an organ and the function they perform? Can the structure and the function of these be altered? All cells of a plant are descendents of the zygote. The question is, then, why and how do they have different structural and functional attributes? Development is the sum of two processes: growth and differentiation. To begin with, it is essential and sufficient to know that the development of a mature plant from a zygote (fertilised egg) follow a precise and highly ordered succession of events. During this process a complex body organisation is formed that produces roots, leaves, branches, flowers, fruits, and seeds, and eventually they die (Figure 15.1). The first step in the process of plant growth is seed germination. The seed germinates when favourable conditions for growth exist in the environment. In absence of such favourable conditions the seeds do not germinate and goes into a period of suspended growth or rest. Once favourable conditions return, the seeds resume metabolic activities and growth takes place.

In this chapter, you shall also study some of the factors which govern and control these developmental processes. These factors are both intrinsic (internal) and extrinsic (external) to the plant.

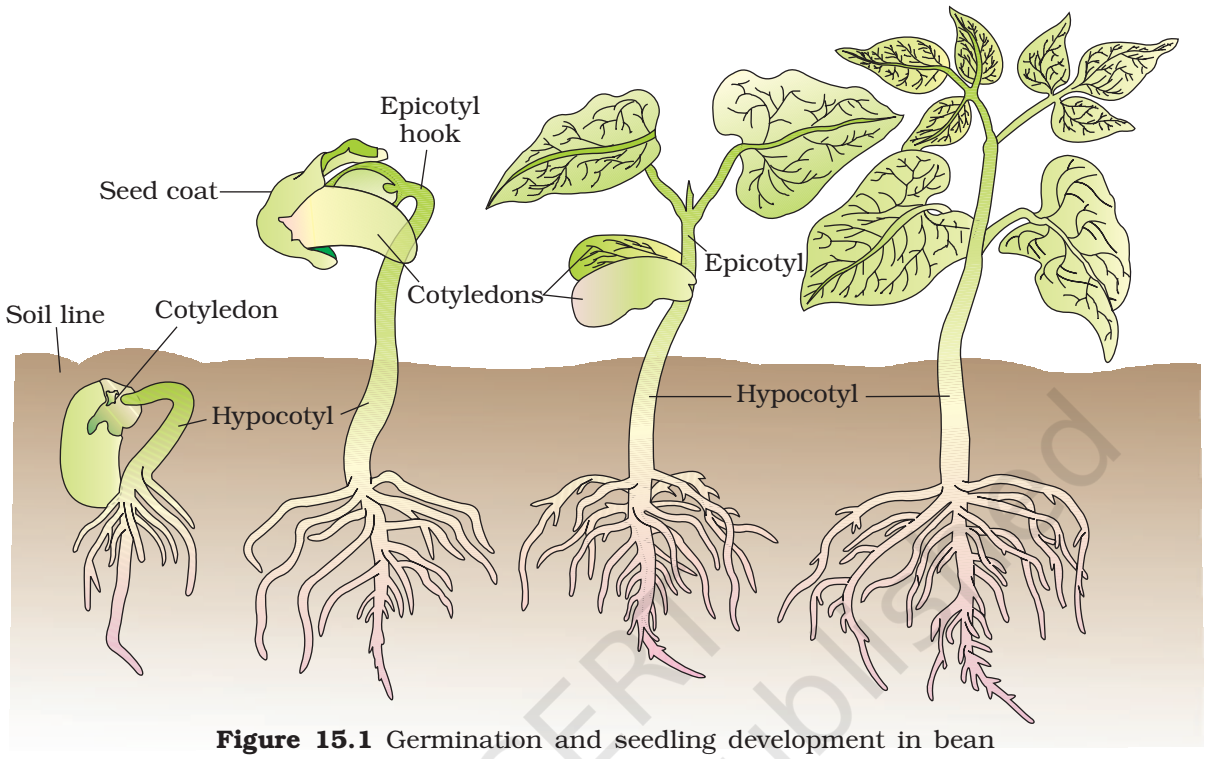


Figure 15.1 Germination and seedling development in bean

15.1 GROWTH

Growth is regarded as one of the most fundamental and conspicuous characteristics of a living being. What is growth? Growth can be defined as an irreversible permanent increase in size of an organ or its parts or even of an individual cell. Generally, growth is accompanied by metabolic processes (both anabolic and catabolic), that occur at the expense of energy. Therefore, for example, expansion of a leaf is growth. How would you describe the swelling of piece of wood when placed in water?

15.1.1 Plant Growth Generally is Indeterminate

Plant growth is unique because plants retain the capacity for unlimited growth throughout their life. This ability of the plants is due to the presence of meristems at certain locations in their body. The cells of such meristems have the capacity to divide and self-perpetuate. The product, however, soon loses the capacity to divide and such cells make up the plant body. This form of growth wherein new cells are always being added to the plant body by the activity of the meristem is called the open form of growth. What would happen if the meristem ceases to divide? Does this ever happen?

In Chapter 6, you have studied about the root apical meristem and the shoot apical meristem. You know that they are responsible for the

primary growth of the plants and principally contribute to the elongation of the plants along their axis. You also know that in dicotyledonous plants and gymnosperms, the lateral meristems, vascular cambium and cork-cambium appear later in life. These are the meristems that cause the increase in the girth of the organs in which they are active. This is known as secondary growth of the plant (see Figure 15.2).

15.1.2 Growth is Measurable

Growth, at a cellular level, is principally a consequence of increase in the amount of protoplasm. Since increase in protoplasm is difficult to measure directly, one generally measures some quantity which is more or less proportional to it. Growth is, therefore, measured by a variety of parameters some of which are: increase in fresh weight, dry weight, length, area, volume and cell number. You may find it amazing to know that one single maize root apical mersitem can give rise to more than 17,500 new cells per hour, whereas cells in a watermelon may increase in size by upto 3,50,000 times. In the former, growth is expressed as increase in cell number; the latter expresses growth as increase in size of the cell. While the growth of a pollen tube is measured in terms of its length, an increase in surface area denotes the growth in a dorsiventral leaf.

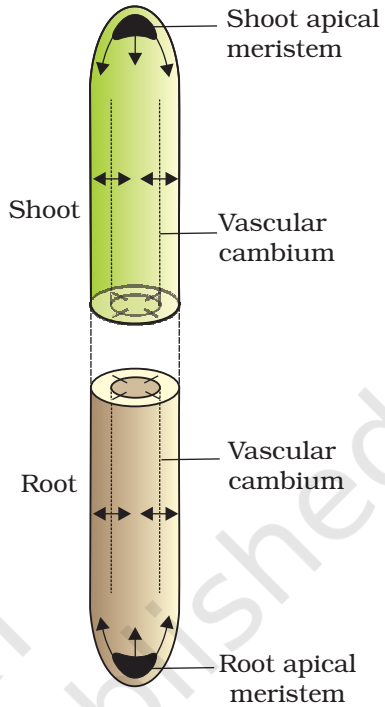


Figure 15.2 Diagrammatic representation of locations of root apical meristem, shoot aplical meristem and vascular cambium. Arrows exhibit the direction of growth of cells and organ

15.1.3 Phases of Growth

The period of growth is generally divided into three phases, namely, meristematic, elongation and maturation (Figure 15.3). Let us understand this by looking at the root tips. The constantly dividing cells, both at the root apex and the shoot apex, represent the meristematic phase of growth. The cells in this region are rich in protoplasm, possess large conspicuous nuclei. Their cell walls are primary in nature, thin and cellulosic with abundant plasmodesmatal connections. The cells proximal (just next, away from the tip) to the

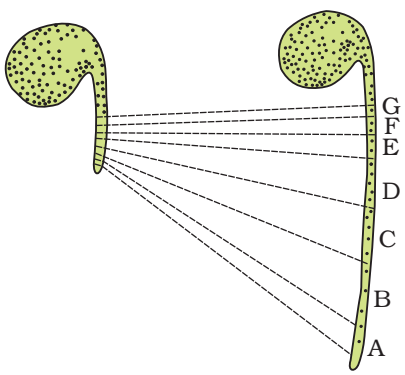


Figure 15.3 Detection of zones of elongation by the parallel line technique. Zones A, B, C, D immediately behind the apex have elongated most.

meristematic zone represent the phase of elongation. Increased vacuolation, cell enlargement and new cell wall deposition are the characteristics of the cells in this phase. Further away from the apex, i.e., more proximal to the phase of elongation, lies the portion of axis which is undergoing the phase of maturation. The cells of this zone, attain their maximal size in terms of wall thickening and protoplasmic modifications. Most of the tissues and cell types you have studied in Chapter 6 represent this phase.

15.1.4 Growth Rates

The increased growth per unit time is termed as growth rate. Thus, rate of growth can be expressed mathematically. An organism, or a part of the organism can produce more cells in a variety of ways.

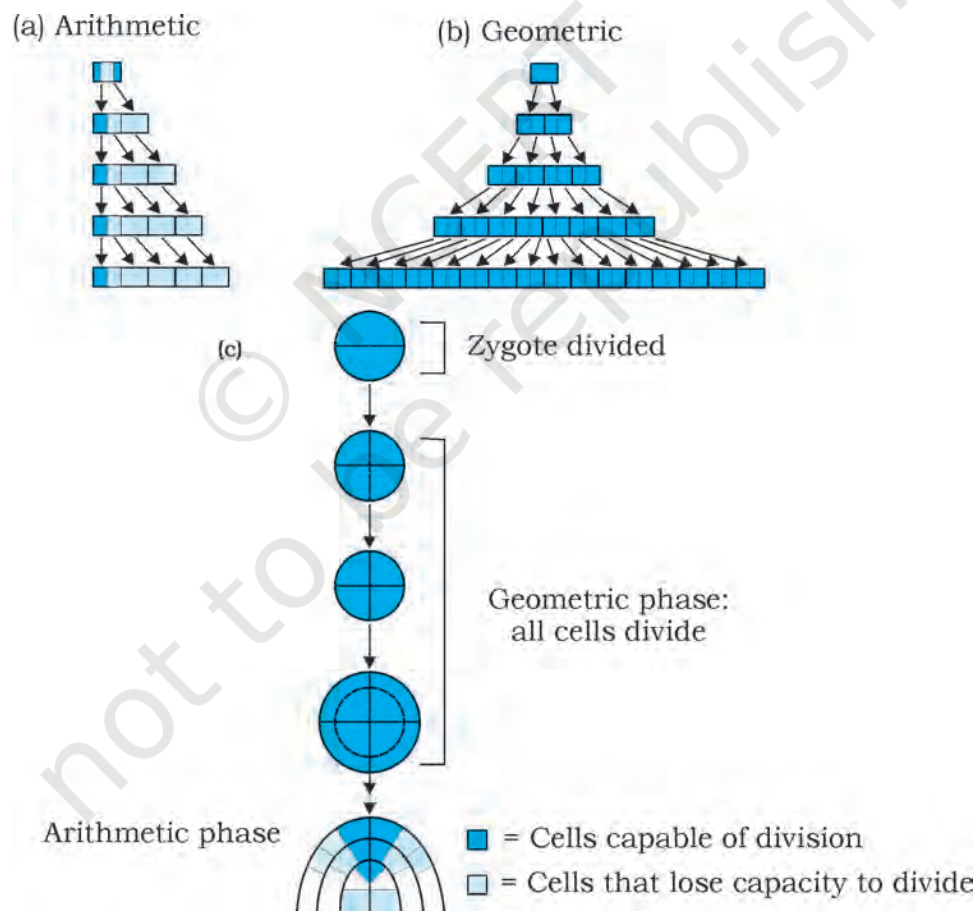


Figure 15.4 Diagrammatic representation of : (a) Arithmetic (b) Geometric growth and (c) Stages during embryo development showing geometric and arithematic phases

The growth rate shows an increase that may be arithmetic or geometrical (Figure 15.4).

In arithmetic growth, following mitotic cell division, only one daughter cell continues to divide while the other differentiates and matures. The simplest expression of arithmetic growth is exemplified by a root elongating at a constant rate. Look at Figure 15.5. On plotting the length of the organ against time, a linear curve is obtained. Mathematically, it is expressed as

$L_t = L_0 + rt$

L_t = length at time 't'

L_0 = length at time 'zero'

r = growth rate / elongation per unit time.

Let us now see what happens in geometrical growth. In most systems, the initial growth is slow (lag phase), and it increases rapidly thereafter – at an exponential rate (log or exponential phase). Here, both the progeny cells following mitotic cell division retain the ability to divide and continue to do so. However, with limited nutrient supply, the growth slows down leading to a stationary phase. If we plot the parameter of growth against time, we get a typical sigmoid or S-curve (Figure 15.6). A sigmoid curve is a characteristic of living organism growing in a natural environment. It is typical for all cells, tissues and organs of a plant. *Can you think of more similar examples? What kind of a curve can you expect in a tree showing seasonal activities?*

The exponential growth can be expressed as

$W_1 = W_0 e^{rt}$

W_1 = final size (weight, height, number etc.)

W_0 = initial size at the beginning of the period

r = growth rate

t = time of growth

e = base of natural logarithms

Here, r is the relative growth rate and is also the measure of the ability of the plant to produce new plant material, referred to as efficiency index. Hence, the final size of W_1 depends on the initial size, W_0.

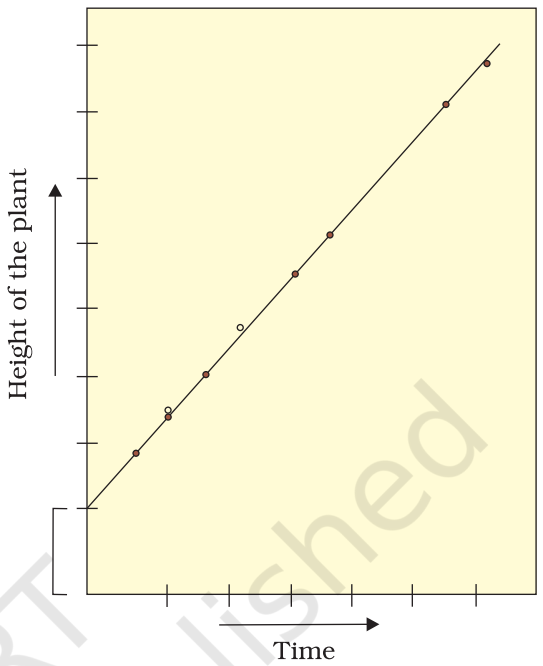


Figure 15.5 Constant linear growth, a plot of length L against time t

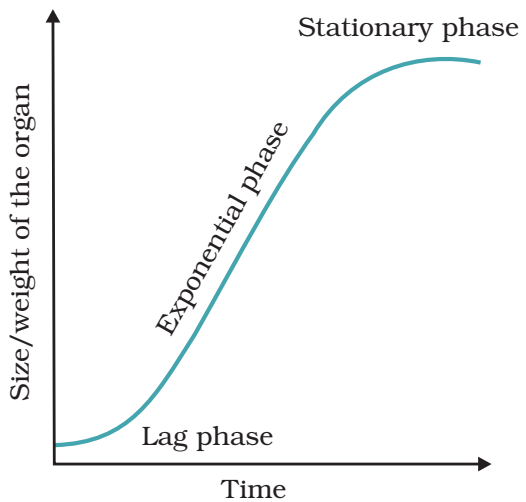


Figure 15.6 An idealised sigmoid growth curve typical of cells in culture, and many higher plants and plant organs

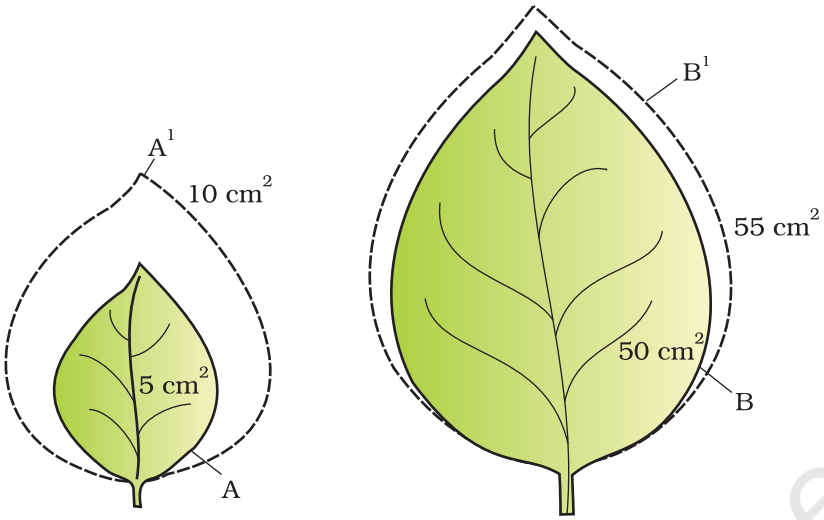


Figure 15.7 Diagrammatic comparison of absolute and relative growth rates. Both leaves A and B have increased their area by 5 cm^2 in a given time to produce A^1, B^1 leaves.

Quantitative comparisons between the growth of living system can also be made in two ways : (i) measurement and the comparison of total growth per unit time is called the absolute growth rate. (ii) The growth of the given system per unit time expressed on a common basis, e.g., per unit initial parameter is called the relative growth rate. In Figure 15.7 two leaves, A and B, are drawn that are of different sizes but shows absolute increase in area in the given time to give leaves, A^1 and B^1. However, one of them shows much higher relative growth rate. Which one and why?

15.1.5 Conditions for Growth

Why do you not try to write down what you think are necessary conditions for growth? This list may have water, oxygen and nutrients as very essential elements for growth. The plant cells grow in size by cell enlargement which in turn requires water. Turgidity of cells helps in extension growth. Thus, plant growth and further development is intimately linked to the water status of the plant. Water also provides the medium for enzymatic activities needed for growth. Oxygen helps in releasing metabolic energy essential for growth activities. Nutrients (macro and micro essential elements) are required by plants for the synthesis of protoplasm and act as source of energy.

In addition, every plant organism has an optimum temperature range best suited for its growth. Any deviation from this range could be detrimental to its survival. Environmental signals such as light and gravity also affect certain phases/stages of growth.

15.2 DIFFERENTIATION, DEDIFFERENTIATION AND REDIFFERENTIATION

The cells derived from root apical and shoot-apical meristems and cambium differentiate and mature to perform specific functions. This act leading to maturation is termed as **differentiation**. During differentiation, cells undergo few to major structural changes both in their cell walls and protoplasm. For example, to form a tracheary element, the cells would lose their protoplasm. They also develop a very strong, elastic, lignocellulosic secondary cell walls, to carry water to long distances even under extreme tension. Try to correlate the various anatomical features you encounter in plants to the functions they perform.

Plants show another interesting phenomenon. The living differentiated cells, that by now have lost the capacity to divide can regain the capacity of division under certain conditions. This phenomenon is termed as **dedifferentiation**. For example, formation of meristems – interfascicular cambium and cork cambium from fully differentiated parenchyma cells. While doing so, such meristems/tissues are able to divide and produce cells that once again lose the capacity to divide but mature to perform specific functions, i.e., get **redifferentiated**. List some of the tissues in a woody dicotyledenous plant that are the products of redifferentiation. How would you describe a tumour? What would you call the parenchyma cells that are made to divide under controlled laboratory conditions during plant tissue culture?

Recall, in Section 15.1.1, we have mentioned that the growth in plants is open, i.e., it can be indeterminate or determinate. Now, we may say that even differentiation in plants is open, because cells/tissues arising out of the same meristem have different structures at maturity. The final structure at maturity of a cell/tissue is also determined by the location of the cell within. For example, cells positioned away from root apical meristems differentiate as root-cap cells, while those pushed to the periphery mature as epidermis. Can you add a few more examples of open differentiation correlating the position of a cell to its position in an organ?

15.3 DEVELOPMENT

Development is a term that includes all changes that an organism goes through during its life cycle from germination of the seed to senescence. Diagrammatic representation of the sequence of processes which constitute the development of a cell of a higher plant is given in Figure 15.8. It is also applicable to tissues/organs.

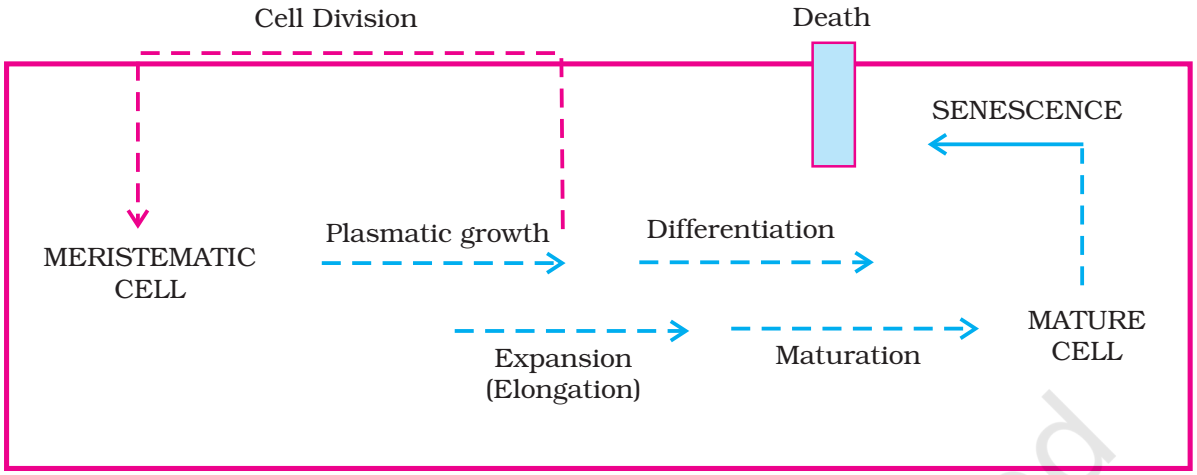


Figure 15.8 Sequence of the developmental process in a plant cell

Plants follow different pathways in response to environment or phases of life to form different kinds of structures. This ability is called **plasticity,** e.g., heterophylly in cotton, coriander and larkspur. In such plants, the leaves of the juvenile plant are different in shape from those in mature plants. On the other hand, difference in shapes of leaves produced in air and those produced in water in buttercup also represent the heterophyllous development due to environment (Figure 15.9). This phenomenon of heterophylly is an example of plasticity.

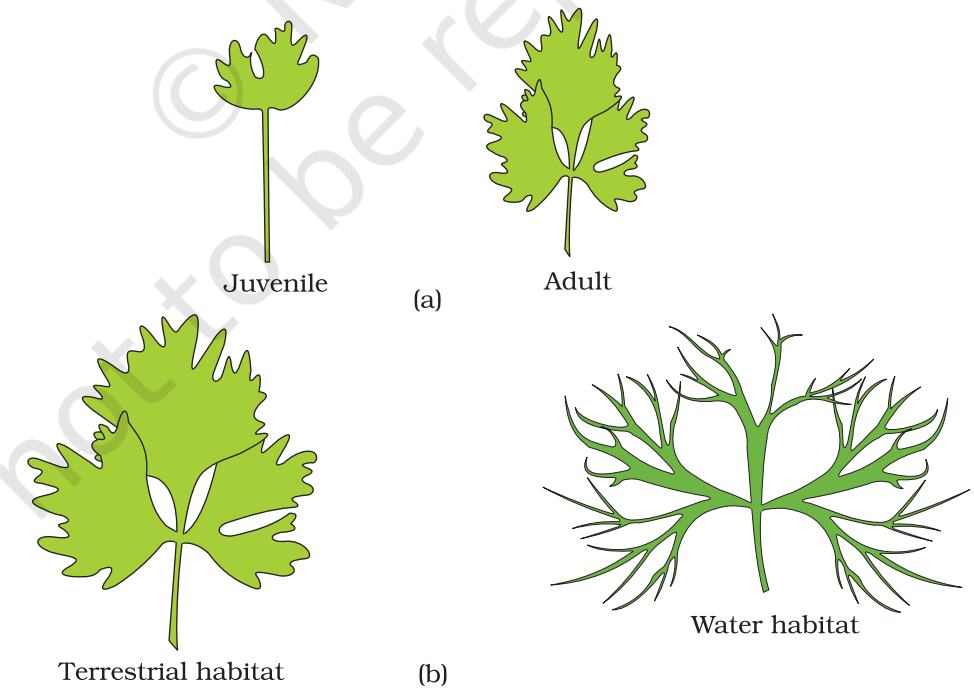


Figure 15.9 Heterophylly in (a) larkspur and (b) buttercup

Thus, growth, differentiation and development are very closely related events in the life of a plant. Broadly, development is considered as the sum of growth and differentiation. Development in plants (i.e., both growth and differentiation) is under the control of intrinsic and extrinsic factors. The former includes both intracellular (genetic) or intercellular factors (chemicals such as plant growth regulators) while the latter includes light, temperature, water, oxygen, nutrition, etc.

15.4 PLANT GROWTH REGULATORS

15.4.1 Characteristics

The plant growth regulators (PGRs) are small, simple molecules of diverse chemical composition. They could be indole compounds (indole-3-acetic acid, IAA); adenine derivatives (N^6-furfurylamino purine, kinetin), derivatives of carotenoids (abscisic acid, ABA); terpenes (gibberellic acid, GA_3) or gases (ethylene, C_2H_4). Plant growth regulators are variously described as plant growth substances, plant hormones or phytohormones in literature.

The PGRs can be broadly divided into two groups based on their functions in a living plant body. One group of PGRs are involved in growth promoting activities, such as cell division, cell enlargement, pattern formation, tropic growth, flowering, fruiting and seed formation. These are also called plant growth promoters, e.g., auxins, gibberellins and cytokinins. The PGRs of the other group play an important role in plant responses to wounds and stresses of biotic and abiotic origin. They are also involved in various growth inhibiting activities such as dormancy and abscission. The PGR abscisic acid belongs to this group. The gaseous PGR, ethylene, could fit either of the groups, but it is largely an inhibitor of growth activities.

15.4.2 The Discovery of Plant Growth Regulators

Interestingly, the discovery of each of the five major groups of PGRs have been accidental. All this started with the observation of Charles Darwin and his son Francis Darwin when they observed that the coleoptiles of canary grass responded to unilateral illumination by growing towards the light source (phototropism). After a series of experiments, it was concluded that the tip of coleoptile was the site of transmittable influence that caused the bending of the entire coleoptile (Figure 15.10). Auxin was isolated by F.W. Went from tips of coleoptiles of oat seedlings.

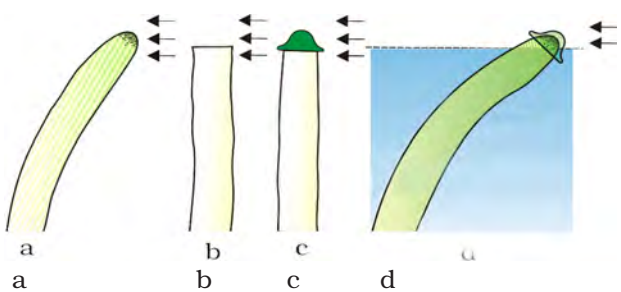


Figure 15.10 Experiment used to demonstrate that tip of the coleoptile is the source of auxin. Arrows indicate direction of light

The 'bakanae' (foolish seedling) disease of rice seedlings, was caused by a fungal pathogen *Gibberella fujikuroi*. E. Kurosawa (1926) reported the appearance of symptoms of the disease in rice seedlings when they were treated with sterile filtrates of the fungus. The active substances were later identified as gibberellic acid.

F. Skoog and his co-workers observed that from the internodal segments of tobacco stems the callus (a mass of undifferentiated cells) proliferated only if, in addition to auxins the nutrients medium was supplemented with one of the following: extracts of vascular tissues, yeast extract, coconut milk or DNA. Skoog and Miller, later identified and crystallised the cytokinesis promoting active substance that they termed kinetin.

During mid-1960s, three independent researches reported the purification and chemical characterisation of three different kinds of inhibitors: inhibitor-B, abscission II and dormin. Later all the three were proved to be chemically identical. It was named abscisic acid (ABA).

Cousins confirmed the release of a volatile substance from ripened oranges that hastened the ripening of stored unripened bananas. Later this volatile substance was identified as ethylene, a gaseous PGR.

Let us study some of the physiological effects of these five categories of PGRs in the next section.

15.4.3 Physiological Effects of Plant Growth Regulators

15.4.3.1 Auxins

Auxins (from Greek 'auxein' : to grow) was first isolated from human urine. The term 'auxin' is applied to the indole-3-acetic acid (IAA), and to other natural and synthetic compounds having certain growth regulating properties. They are generally produced by the growing apices of the stems and roots, from where they migrate to the regions of their action. Auxins like IAA and indole butyric acid (IBA) have been isolated from plants. NAA (naphthalene acetic acid) and 2, 4-D (2, 4-dichlorophenoxyacetic) are synthetic auxins. All these auxins have been used extensively in agricultural and horticultural practices.

They help to initiate rooting in stem cuttings, an application widely used for plant propagation. Auxins promote flowering e.g. in pineapples. They help to prevent fruit and leaf drop at early stages but promote the abscission of older mature leaves and fruits.

In most higher plants, the growing apical bud inhibits the growth of the lateral (axillary) buds, a phenomenon called **apical dominance**. Removal of shoot tips (decapitation) usually results in the growth of lateral buds (Figure 15.11). It is widely applied in tea plantations, hedge-making. Can you explain why?

Auxins also induce parthenocarpy, e.g., in tomatoes. They are widely used as herbicides. 2, 4-D, widely used to kill dicotyledonous weeds, does not affect mature monocotyledonous plants. It is used to prepare weed-free lawns by gardeners. Auxin also controls xylem differentiation and helps in cell division.

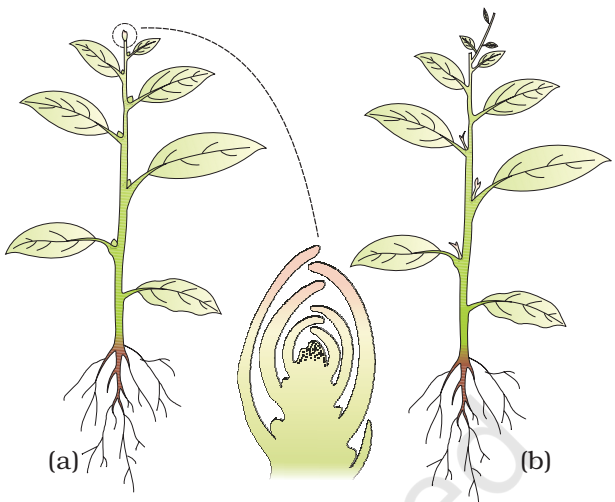


Figure 15.11 Apical dominance in plants : (a) A plant with apical bud intact (b) A plant with apical bud removed Note the growth of lateral buds into branches after decapitation.

15.4.3.2 *Gibberellins*

Gibberellins are another kind of promotory PGR. There are more than 100 gibberellins reported from widely different organisms such as fungi and higher plants. They are denoted as GA_1, GA_2, GA_3 and so on. However, Gibberellic acid (GA_3) was one of the first gibberellins to be discovered and remains the most intensively studied form. All GAs are acidic. They produce a wide range of physiological responses in the plants. Their ability to cause an increase in length of axis is used to increase the length of grapes stalks. Gibberellins, cause fruits like apple to elongate and improve its shape. They also delay senescence. Thus, the fruits can be left on the tree longer so as to extend the market period. GA_3 is used to speed up the malting process in brewing industry.

Sugarcane stores carbohydrate as sugar in their stems. Spraying sugarcane crop with gibberellins increases the length of the stem, thus increasing the yield by as much as 20 tonnes per acre.

Spraying juvenile conifers with GAs hastens the maturity period, thus leading to early seed production. Gibberellins also promotes bolting (internode elongation just prior to flowering) in beet, cabbages and many plants with rosette habit.

15.4.3.3 *Cytokinins*

Cytokinins have specific effects on cytokinesis, and were discovered as kinetin (a modified form of adenine, a purine) from the autoclaved herring sperm DNA. Kinetin does not occur naturally in plants. Search for natural substances with cytokinin-like activities led to the isolation of zeatin from corn-kernels and coconut milk. Since the discovery of zeatin, several naturally occurring cytokinins, and some synthetic compounds with cell division promoting activity, have been identified. Natural cytokinins are synthesised in regions where rapid cell division occurs, for example, root apices, developing shoot buds, young fruits etc. It helps to produce new

leaves, chloroplasts in leaves, lateral shoot growth and adventitious shoot formation. Cytokinins help overcome the apical dominance. They promote nutrient mobilisation which helps in the delay of leaf senescence.

15.4.3.4 Ethylene

Ethylene is a simple gaseous PGR. It is synthesised in large amounts by tissues undergoing senescence and ripening fruits. Influences of ethylene on plants include horizontal growth of seedlings, swelling of the axis and apical hook formation in dicot seedlings. Ethylene promotes senescence and abscission of plant organs especially of leaves and flowers. Ethylene is highly effective in fruit ripening. It enhances the respiration rate during ripening of the fruits. This rise in rate of respiration is called respiratory climactic.

Ethylene breaks seed and bud dormancy, initiates germination in peanut seeds, sprouting of potato tubers. Ethylene promotes rapid internode/petiole elongation in deep water rice plants. It helps leaves/upper parts of the shoot to remain above water. Ethylene also promotes root growth and root hair formation, thus helping the plants to increase their absorption surface.

Ethylene is used to initiate flowering and for synchronising fruit-set in pineapples. It also induces flowering in mango. Since ethylene regulates so many physiological processes, it is one of the most widely used PGR in agriculture. The most widely used compound as source of ethylene is ethephon. Ethephon in an aqueous solution is readily absorbed and transported within the plant and releases ethylene slowly. Ethephon hastens fruit ripening in tomatoes and apples and accelerates abscission in flowers and fruits (thinning of cotton, cherry, walnut). It promotes female flowers in cucumbers thereby increasing the yield.

15.4.3.5 Abscisic acid

As mentioned earlier, abscisic acid **(ABA)** was discovered for its role in regulating abscission and dormancy. But like other PGRs, it also has other wide ranging effects on plant growth and development. It acts as a general plant growth inhibitor and an inhibitor of plant metabolism. ABA inhibits seed germination. ABA stimulates the closure of stomata in the epidermis and increases the tolerance of plants to various kinds of stresses. Therefore, it is also called the stress hormone. ABA plays an important role in seed development, maturation and dormancy. By inducing dormancy, ABA helps seeds to withstand desiccation and other factors unfavourable for growth. In most situations, ABA acts as an antagonist to GAs.

We may summarise that for any and every phase of growth, differentiation and development of plants, one or the other PGR has some role to play. Such roles could be complimentary or antagonistic. These could be individualistic or synergistic.

Similarly, there are a number of events in the life of a plant where more than one PGR interact to affect that event, e.g., dormancy in seeds/ buds, abscission, senescence, apical dominance, etc.

Remember, the role of PGR is of only one kind of intrinsic control. Along with genomic control and extrinsic factors, they play an important role in plant growth and development. Many of the extrinsic factors such as temperature and light, control plant growth and development via PGR. Some of such events could be: vernalisation, flowering, dormancy, seed germination, plant movements, etc.

We shall discuss briefly the role of light and temperature (both of them, the extrinsic factors) on initiation of flowering.

15.5 PHOTOPERIODISM

It has been observed that some plants require a periodic exposure to light to induce flowering. It is also seen that such plants are able to measure the duration of exposure to light. For example, some plants require the exposure to light for a period exceeding a well defined critical duration, while others must be exposed to light for a period less than this critical duration before the flowering is initiated in them. The former group of plants are called **long day plants** while the latter ones are termed **short day plants**. The critical duration is different for different plants. There are many plants, however, where there is no such correlation between exposure to light duration and induction of flowering response; such plants are called **day-neutral plants** (Figure 15.12). It is now also

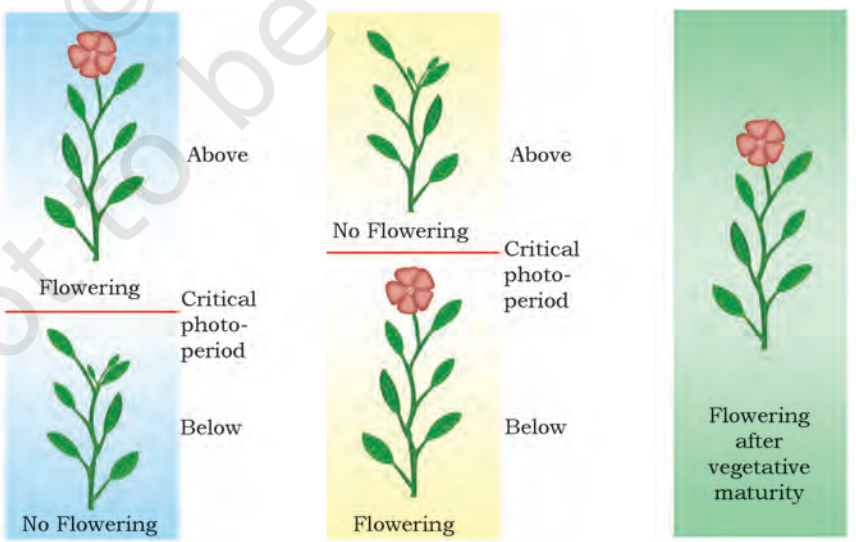


Figure 15.12 Photoperiodism : Long day, short day and day neutral plants

known that not only the duration of light period but that the duration of dark period is also of equal importance. Hence, it can be said that flowering in certain plants depends not only on a combination of light and dark exposures but also their relative durations. This response of plants to periods of day/night is termed **photoperiodism**. It is also interesting to note that while shoot apices modify themselves into flowering apices prior to flowering, they (i.e., shoot apices of plants) by themselves cannot percieve photoperiods. The site of perception of light/dark duration are the leaves. It has been hypothesised that there is a hormonal substance(s) that is responsible for flowering. This hormonal substance migrates from leaves to shoot apices for inducing flowering only when the plants are exposed to the necessary inductive photoperiod.

15.6 VERNALISATION

There are plants for which flowering is either quantitatively or qualitatively dependent on exposure to low temperature. This phenomenon is termed **vernalisation**. It prevents precocious reproductive development late in the growing season, and enables the plant to have sufficient time to reach maturity. Vernalisation refers specially to the promotion of flowering by a period of low temperature. Some important food plants, wheat, barley, rye have two kinds of varieties: winter and spring varieties. The 'spring' variety are normally planted in the spring and come to flower and produce grain before the end of the growing season. Winter varieties, however, if planted in spring would normally fail to flower or produce mature grain within a span of a flowering season. Hence, they are planted in autumn. They germinate, and over winter come out as small seedlings, resume growth in the spring, and are harvested usually around mid-summer.

Another example of vernalisation is seen in biennial plants. Biennials are monocarpic plants that normally flower and die in the second season. Sugarbeet, cabbages, carrots are some of the common biennials. Subjecting the growing of a biennial plant to a cold treatment stimulates a subsequent photoperiodic flowering response.

15.7 SEED DORMANCY

There are certain seeds which fail to germinate even when external conditions are favourable. Such seeds are understood to be undergoing a period of dormancy which is controlled not by external environment but are under endogenous control or conditions within the seed itself. Impermeable and hard seed coat; presence of chemical inhibitors such as abscissic acids, phenolic acids, para-ascorbic acid; and immature

embryos are some of the reasons which causes seed dormancy. This dormancy however can be overcome through natural means and various other man-made measures. For example, the seed coat barrier in some seeds can be broken by mechanical abrasions using knives, sandpaper, etc. or vigorous shaking. In nature, these abrasions are caused by microbial action, and passage through digestive tract of animals. Effect of inhibitory substances can be removed by subjecting the seeds to chilling conditions or by application of certain chemicals like gibberellic acid and nitrates. Changing the environmental conditions, such as light and temperature are other methods to overcome seed dormancy.

SUMMARY

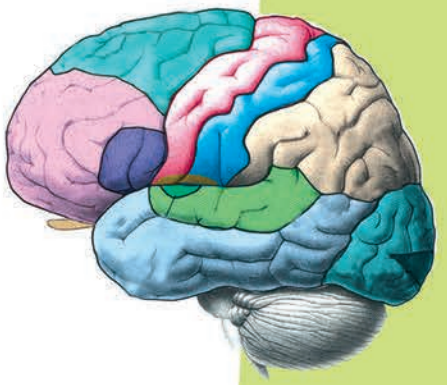
Growth is one of the most conspicuous events in any living organism. It is an irreversible increase expressed in parameters such as size, area, length, height, volume, cell number etc. It conspicuously involves increased protoplasmic material. In plants, meristems are the sites of growth. Root and shoot apical meristems sometimes alongwith intercalary meristem, contribute to the elongation growth of plant axes. Growth is indeterminate in higher plants. Following cell division in root and shoot apical meristem cells, the growth could be arithmetic or geometrical. Growth may not be and generally is not sustained at a high rate throughout the life of cell/tissue/organ/organism. One can define three principle phases of growth – the lag, the log and the senescent phase. When a cell loses the capacity to divide, it leads to differentiation. Differentiation results in development of structures that is commensurate with the function the cells finally has to perform. General principles for differentiation for cell, tissues and organs are similar. A differentiated cell may dedifferentiate and then redifferentiate. Since differentiation in plants is open, the development could also be flexible, i.e., the development is the sum of growth and differentiation. Plant exhibit plasticity in development.

Plant growth and development are under the control of both intrinsic and extrinsic factors. Intercellular intrinsic factors are the chemical substances, called plant growth regulators (PGR). There are diverse groups of PGRs in plants, principally belonging to five groups: auxins, gibberellins, cytokinins, abscisic acid and ethylene. These PGRs are synthesised in various parts of the plant; they control different differentiation and developmental events. Any PGR has diverse physiological effects on plants. Diverse PGRs also manifest similar effects. PGRs may act synergistically or antagonistically. Plant growth and development is also affected by light, temperature, nutrition, oxygen status, gravity and such external factors.

Flowering in some plants is induced only when exposed to certain duration of photoperiod. Depending on the nature of photoperiod requirements, the plants are called short day plants, long day plants and day-neutral plants. Certain plants also need to be exposed to low temperature so as to hasten flowering later in life. This treatement is known as vernalisation.

EXERCISES

1. Define growth, differentiation, development, dedifferentiation, redifferentiation, determinate growth, meristem and growth rate.
2. Why is not any one parameter good enough to demonstrate growth throughout the life of a flowering plant?
3. Describe briefly:
   (a) Arithmetic growth
   (b) Geometric growth
   (c) Sigmoid growth curve
   (d) Absolute and relative growth rates
4. List five main groups of natural plant growth regulators. Write a note on discovery, physiological functions and agricultural/horticultural applications of any one of them.
5. What do you understand by photoperiodism and vernalisation? Describe their significance.
6. Why is abscisic acid also known as stress hormone?
7. 'Both growth and differentiation in higher plants are *open*'. Comment.
8. 'Both a short day plant and a long day plant can produce can flower simultaneously in a given place'. Explain.
9. Which one of the plant growth regulators would you use if you are asked to:
   (a) induce rooting in a twig
   (b) quickly ripen a fruit
   (c) delay leaf senescence
   (d) induce growth in axillary buds
   (e) 'bolt' a rosette plant
   (f) induce immediate stomatal closure in leaves.
10. Would a defoliated plant respond to photoperiodic cycle? Why?
11. What would be expected to happen if:
    (a) GA_3 is applied to rice seedlings
    (b) dividing cells stop differentiating
    (c) a rotten fruit gets mixed with unripe fruits
    (d) you forget to add cytokinin to the culture medium.



UNIT 5

HUMAN PHYSIOLOGY

The reductionist approach to study of life forms resulted in increasing use of physico-chemical concepts and techniques. Majority of these studies employed either surviving tissue model or straightaway cell-free systems. An explosion of knowledge resulted in molecular biology. Molecular physiology became almost synonymous with biochemistry and biophysics. However, it is now being increasingly realised that neither a purely organismic approach nor a purely reductionistic molecular approach would reveal the truth about biological processes or living phenomena. Systems biology makes us believe that all living phenomena are emergent properties due to interaction among components of the system under study. Regulatory network of molecules, supra molecular assemblies, cells, tissues, organisms and indeed, populations and communities, each create emergent properties. In the chapters under this unit, major human physiological processes like digestion, exchange of gases, blood circulation, locomotion and movement are described in cellular and molecular terms. The last two chapters point to the coordination and regulation of body events at the organismic level.

Alfonso Corti
(1822 – 1888)

ALFONSO CORTI, Italian anatomist, was born in 1822. Corti began his scientific career studying the cardiovascular systems of reptiles. Later, he turned his attention to the mammalian auditory system. In 1851, he published a paper describing a structure located on the basilar membrane of the cochlea containing hair cells that convert sound vibrations into nerve impulses, the organ of Corti. He died in the year 1888.

Chapter 16
Digestion and Absorption

Food is one of the basic requirements of all living organisms. The major components of our food are carbohydrates, proteins and fats. Vitamins and minerals are also required in small quantities. Food provides energy and organic materials for growth and repair of tissues. The water we take in, plays an important role in metabolic processes and also prevents dehydration of the body. Biomacromolecules in food cannot be utilised by our body in their original form. They have to be broken down and converted into simple substances in the digestive system. This process of conversion of complex food substances to simple absorbable forms is called **digestion** and is carried out by our digestive system by mechanical and biochemical methods. General organisation of the human digestive system is shown in Figure 16.1.

16.1 Digestive System

The human digestive system consists of the alimentary canal and the associated glands.

16.1.1 Alimentary Canal

The alimentary canal begins with an anterior opening – the mouth, and it opens out posteriorly through the anus. The mouth leads to the buccal cavity or oral cavity. The oral cavity has a number of teeth and a muscular tongue. Each tooth is embedded in a socket of jaw bone (Figure16.2). This type of attachment is called **thecodont**. Majority of mammals including human being forms two sets of teeth during their life, a set of temporary milk or deciduous teeth replaced by a set of permanent or adult teeth. This type of dentition is called **diphyodont**. An adult human

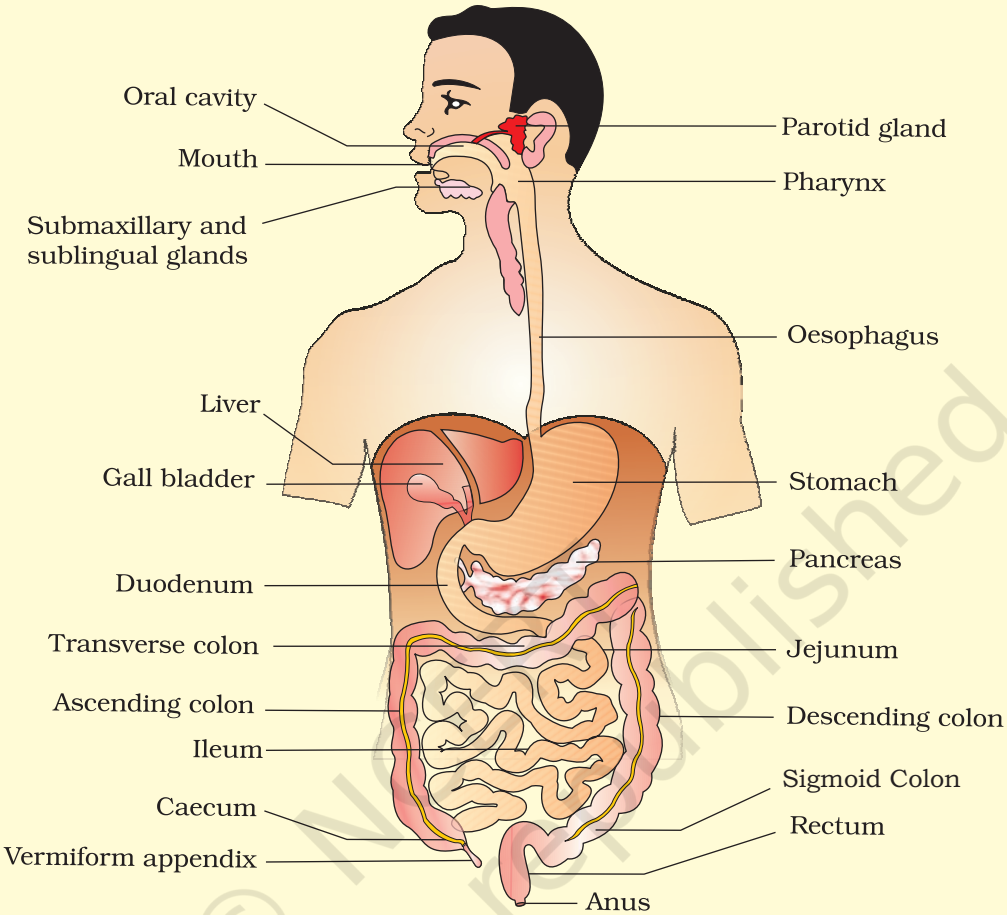


Figure 16.1 The human digestive system

has 32 permanent teeth which are of four different types (Heterodont dentition), namely, incisors (I), canine (C), premolars (PM) and molars (M). Arrangement of teeth in each half of the upper and lower jaw in the order I, C, PM, M is represented by a dental formula which in human is $\frac{2123}{2123}$. The hard chewing surface of the teeth, made up of enamel, helps in the mastication of food. The tongue is a freely movable muscular organ attached to the floor of the oral cavity by the frenulum. The upper surface of the tongue has small projections called papillae, some of which bear taste buds.

The oral cavity leads into a short pharynx which serves as a common passage for food and air. The oesophagus and the trachea (wind pipe) open into the pharynx. A cartilaginous flap called epiglottis prevents the entry of food into the glottis – opening of the wind pipe – during swallowing. The oesophagus is a thin, long tube which extends posteriorly passing through the neck, thorax and diaphragm and leads to a 'J' shaped bag

like structure called stomach. A muscular sphincter (gastro-oesophageal) regulates the opening of oesophagus into the stomach. The stomach, located in the upper left portion of the abdominal cavity, has four major parts – a **cardiac** portion into which the oesophagus opens, a **fundic** region, **body** (main central region) and a **pyloric** portion which opens into the first part of small intestine (Figure 16.3). Small intestine is distinguishable into three regions, a 'C' shaped duodenum, a long coiled middle portion jejunum and a highly coiled ileum. The opening of the stomach into the duodenum is guarded by the pyloric sphincter. Ileum opens into the large intestine. It consists of caecum, colon and rectum. Caecum is a small blind sac which hosts some symbiotic micro-organisms. A narrow finger-like tubular projection, the vermiform appendix which is a vestigial organ, arises from the caecum. The caecum opens into the colon. The colon is divided into four parts – an ascending, a transverse, descending part and a sigmoid colon. The descending part opens into the rectum which opens out through the anus.

The wall of alimentary canal from oesophagus to rectum possesses four layers (Figure 16.4) namely serosa, muscularis, sub-mucosa and mucosa. Serosa is the outermost layer and is made up of a thin mesothelium (epithelium of visceral organs) with some connective tissues. Muscularis is formed by smooth muscles usually arranged into an inner circular and an outer longitudinal layer. An oblique muscle layer may be present in some regions. The sub-mucosal layer is formed of loose connective tissues containing nerves, blood and lymph vessels. In duodenum, glands are also present in sub-mucosa. The innermost layer lining the lumen of the alimentary canal is the mucosa. This layer forms irregular folds (rugae) in the stomach and small finger-like foldings called **villi** in the small intestine (Figure 16.5). The cells lining the villi produce numerous microscopic

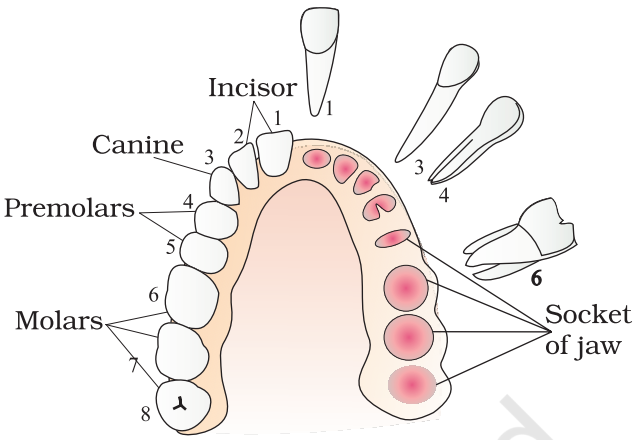


Figure 16.2 Arrangement of different types of teeth in the jaws on one side and the sockets on the other side

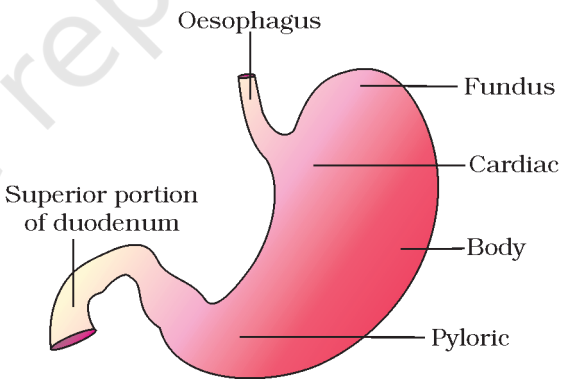


Figure 16.3 Anatomical regions of human stomach

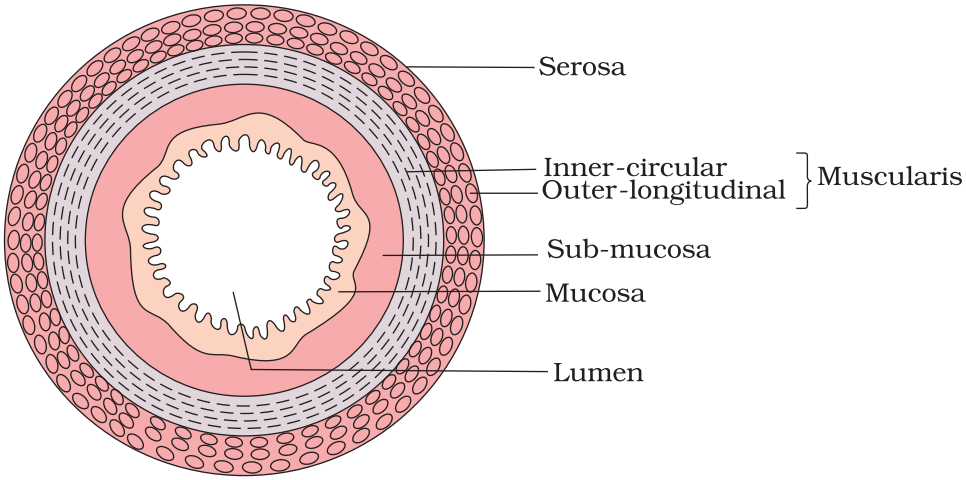


Figure 16.4 Diagrammatic representation of transverse section of gut

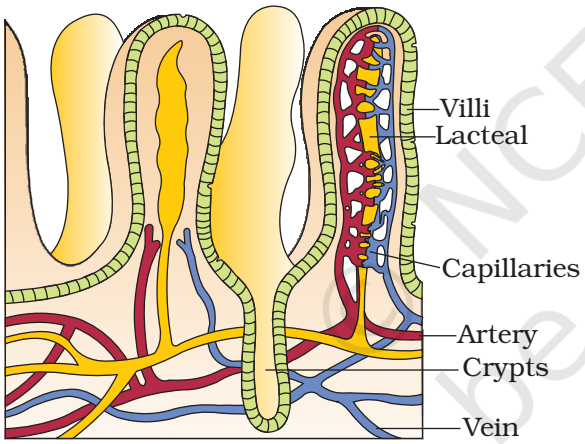


Figure 16.5 A section of small intestinal mucosa showing villi

projections called microvilli giving a brush border appearance. These modifications increase the surface area enormously. Villi are supplied with a network of capillaries and a large lymph vessel called the lacteal. Mucosal epithelium has goblet cells which secrete mucus that help in lubrication. Mucosa also forms glands in the stomach (gastric glands) and crypts in between the bases of villi in the intestine (crypts of Lieberkuhn). All the four layers show modifications in different parts of the alimentary canal.

16.1.2 Digestive Glands

The digestive glands associated with the alimentary canal include the salivary glands, the liver and the pancreas.

Saliva is mainly produced by three pairs of salivary glands, the parotids (cheek), the sub-maxillary/sub-mandibular (lower jaw) and the sub- linguals (below the tongue). These glands situated just outside the buccal cavity secrete salivary juice into the buccal cavity.

Liver is the largest gland of the body weighing about 1.2 to 1.5 kg in an adult human. It is situated in the abdominal cavity, just below the diaphragm and has two lobes. The hepatic lobules are the structural and functional units of liver containing hepatic cells arranged in the form of cords. Each lobule is covered by a thin connective tissue sheath called the Glisson's capsule. The bile secreted by the hepatic cells passes through the hepatic ducts and is stored and concentrated in a thin muscular sac called the gall bladder. The duct of gall bladder (cystic duct) along with

the hepatic duct from the liver forms the common bile duct (Figure 16.6). The bile duct and the pancreatic duct open together into the duodenum as the common hepato-pancreatic duct which is guarded by a sphincter called the sphincter of Oddi.

The pancreas is a compound (both exocrine and endocrine) elongated organ situated between the limbs of the 'C' shaped duodenum. The exocrine portion secretes an alkaline pancreatic juice containing enzymes and the endocrine portion secretes hormones, insulin and glucagon.

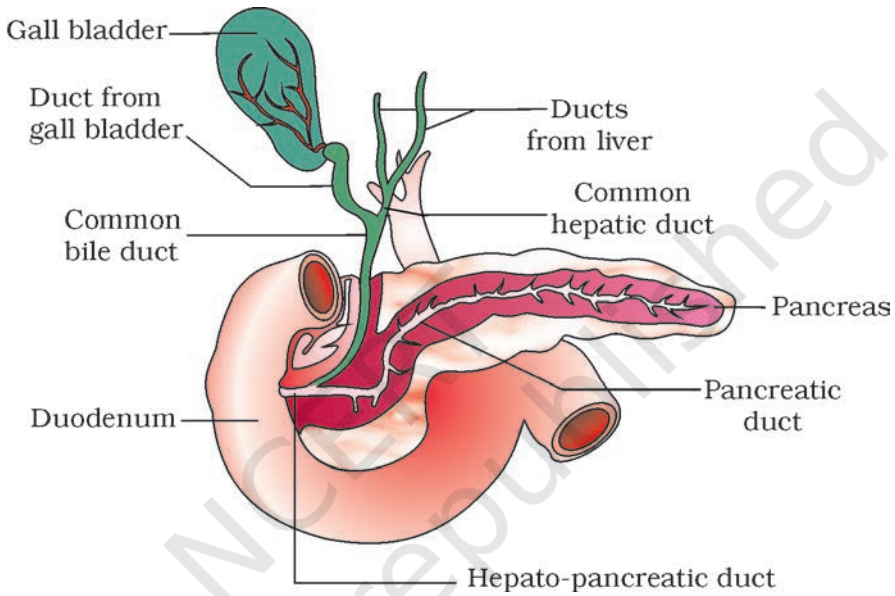


Figure 16.6 The duct systems of liver, gall bladder and pancreas

16.2 DIGESTION OF FOOD

The process of digestion is accomplished by mechanical and chemical processes.

The buccal cavity performs two major functions, mastication of food and facilitation of swallowing. The teeth and the tongue with the help of saliva masticate and mix up the food thoroughly. Mucus in saliva helps in lubricating and adhering the masticated food particles into a **bolus**. The bolus is then conveyed into the pharynx and then into the oesophagus by swallowing or **deglutition**. The bolus further passes down through the oesophagus by successive waves of muscular contractions called peristalsis. The gastro-oesophageal sphincter controls the passage of food into the stomach.The saliva secreted into the oral cavity contains electrolytes (Na^+, K^+, Cl^-, HCO_3^-) and enzymes, salivary amylase and lysozyme. The chemical process of digestion is initiated in the oral cavity by the hydrolytic action of the carbohydrate splitting enzyme, the salivary

amylase. About 30 per cent of starch is hydrolysed here by this enzyme (optimum pH 6.8) into a disaccharide – maltose. Lysozyme present in saliva acts as an antibacterial agent that prevents infections.

$$\text{Starch} \xrightarrow[\text{pH 6.8}]{\text{Salivary Amylase}} \text{Maltose}$$

The mucosa of stomach has gastric glands. Gastric glands have three major types of cells namely -

(i) mucus neck cells which secrete mucus;
(ii) peptic or chief cells which secrete the proenzyme pepsinogen; and
(iii) parietal or oxyntic cells which secrete HCl and intrinsic factor (factor essential for absorption of vitamin B_{12}).

The stomach stores the food for 4-5 hours. The food mixes thoroughly with the acidic gastric juice of the stomach by the churning movements of its muscular wall and is called the **chyme**. The proenzyme pepsinogen, on exposure to hydrochloric acid gets converted into the active enzyme pepsin, the proteolytic enzyme of the stomach. Pepsin converts proteins into proteoses and peptones (peptides). The mucus and bicarbonates present in the gastric juice play an important role in lubrication and protection of the mucosal epithelium from excoriation by the highly concentrated hydrochloric acid. HCl provides the acidic pH (pH 1.8) optimal for pepsins. Rennin is a proteolytic enzyme found in gastric juice of infants which helps in the digestion of milk proteins. Small amounts of lipases are also secreted by gastric glands.

Various types of movements are generated by the muscularis layer of the small intestine. These movements help in a thorough mixing up of the food with various secretions in the intestine and thereby facilitate digestion. The bile, pancreatic juice and the intestinal juice are the secretions released into the small intestine. Pancreatic juice and bile are released through the hepato-pancreatic duct. The pancreatic juice contains inactive enzymes – trypsinogen, chymotrypsinogen, procarboxypeptidases, amylases, lipases and nucleases. Trypsinogen is activated by an enzyme, enterokinase, secreted by the intestinal mucosa into active trypsin, which in turn activates the other enzymes in the pancreatic juice. The bile released into the duodenum contains bile pigments (bilirubin and bili-verdin), bile salts, cholesterol and phospholipids but no enzymes. Bile helps in emulsification of fats, i.e., breaking down of the fats into very small micelles. Bile also activates lipases.

The intestinal mucosal epithelium has **goblet cells** which secrete mucus. The secretions of the brush border cells of the mucosa alongwith the secretions of the goblet cells constitute the intestinal juice or **succus entericus**. This juice contains a variety of enzymes like disaccharidases (e.g., maltase), dipeptidases, lipases, nucleosidases, etc. The mucus alongwith the bicarbonates from the pancreas protects the intestinal mucosa from acid as well as provide an alkaline medium (pH 7.8) for enzymatic activities. Sub-mucosal glands (Brunner's glands) also help in this.

Proteins, proteoses and peptones (partially hydrolysed proteins) in the chyme reaching the intestine are acted upon by the proteolytic enzymes of pancreatic juice as given below:

$$\left.\begin{matrix}\text{Proteins}\\ \text{Peptones}\\ \text{Proteoses}\end{matrix}\right\} \xrightarrow[\text{Carboxypeptidase}]{\text{Trypsin/Chymotrypsin}} \text{Dipeptides}$$

Carbohydrates in the chyme are hydrolysed by pancreatic amylase into disaccharides.

$$\text{Polysaccharides (starch)} \xrightarrow{\text{Amylase}} \text{Disaccharides}$$

Fats are broken down by lipases with the help of bile into di-and monoglycerides.

$$\text{Fats} \xrightarrow{\text{Lipases}} \text{Diglycerides} \longrightarrow \text{Monoglycerides}$$

Nucleases in the pancreatic juice acts on nucleic acids to form nucleotides and nucleosides

$$\text{Nucleic acids} \xrightarrow{\text{Nucleases}} \text{Nucleotides} \longrightarrow \text{Nucleosides}$$

The enzymes in the succus entericus act on the end products of the above reactions to form the respective simple absorbable forms. These final steps in digestion occur very close to the mucosal epithelial cells of the intestine.

$$\text{Dipeptides} \xrightarrow{\text{Dipeptidases}} \text{Amino acids}$$

$$\text{Maltose} \xrightarrow{\text{Maltase}} \text{Glucose + Glucose}$$

$$\text{Lactose} \xrightarrow{\text{Lactase}} \text{Glucose + Galactose}$$

$$\text{Sucrose} \xrightarrow{\text{Sucrase}} \text{Glucose + Fructose}$$

$$\text{Nucleotides} \xrightarrow{\text{Nucleotidases}} \text{Nucleosides} \xrightarrow{\text{Nucleosidases}} \text{Sugars + Bases}$$

$$\text{Di and Monoglycerides} \xrightarrow{\text{Lipases}} \text{Fatty acids + Glycerol}$$

The breakdown of biomacromolecules mentioned above occurs in the duodenum region of the small intestine. The simple substances thus formed are absorbed in the jejunum and ileum regions of the small intestine. The undigested and unabsorbed substances are passed on to the large intestine.

No significant digestive activity occurs in the large intestine. The functions of large intestine are:

(i) absorption of some water, minerals and certain drugs;
(ii) secretion of mucus which helps in adhering the waste (undigested) particles together and lubricating it for an easy passage.

The undigested, unabsorbed substances called faeces enters into the caecum of the large intestine through ileo-caecal valve, which prevents the back flow of the faecal matter. It is temporarily stored in the rectum till defaecation.

The activities of the gastro-intestinal tract are under neural and hormonal control for proper coordination of different parts. The sight, smell and/or the presence of food in the oral cavity can stimulate the secretion of saliva. Gastric and intestinal secretions are also, similarly, stimulated by neural signals. The muscular activities of different parts of the alimentary canal can also be moderated by neural mechanisms, both local and through CNS. Hormonal control of the secretion of digestive juices is carried out by local hormones produced by the gastric and intestinal mucosa.

CALORIFIC VALUE OF PROTEIN, CARBOHYDRATE AND FAT
(Boxed item – Not for evaluation)

The energy requirements of animals, and the energy content of food, are expressed in terms of measure of heat energy because heat is the ultimate form of all energies. This is often measured to as calorie (cal) or joule (J), which is the amount of heat energy required to raise the temperature of 1 g of water by 1 °C. Since this value is tiny amount of energy, physiologists commonly use kilocalorie (kcal) or kilo joule (kJ). One kilo calorie is the amount of energy required to raise the temperature of 1 kg of water by 1 °C. Nutritionists, traditionally refer to kcal as the Calorie or Joule (always capitalised). The amount of heat liberated from complete combustion of 1 g food in a bomb calorimeter (a closed metal chamber filled with O_2) is its gross calorific or gross energy value. The actual amount of energy combustion of 1 g of food is the physiologic value of food. Gross calorific values of carbohydrates, proteins and fats are 4.1 kcal/g, 5.65 kcal/g and 9.45 kcal/g, respectively, whereas their physiologic values are 4.0 kcal/g, 4.0 kcal/g and 9.0 kcal/g, respectively.

16.3 ABSORPTION OF DIGESTED PRODUCTS

Absorption is the process by which the end products of digestion pass through the intestinal mucosa into the blood or lymph. It is carried out by passive, active or facilitated transport mechanisms. Small amounts of monosaccharides like glucose, amino acids and some electrolytes like chloride ions are generally absorbed by simple diffusion. The passage of these substances into the blood depends upon the concentration gradients. However, some substances like glucose and amino acids are absorbed with the help of carrier proteins. This mechanism is called the facilitated transport.

Transport of water depends upon the osmotic gradient. Active transport occurs against the concentration gradient and hence requires energy. Various nutrients like amino acids, monosaccharides like glucose, electrolytes like Na^+ are absorbed into the blood by this mechanism.

Fatty acids and glycerol being insoluble, cannot be absorbed into the

blood. They are first incorporated into small droplets called micelles which move into the intestinal mucosa. They are re-formed into very small protein coated fat globules called the chylomicrons which are transported into the lymph vessels (lacteals) in the villi. These lymph vessels ultimately release the absorbed substances into the blood stream.

Absorption of substances takes place in different parts of the alimentary canal, like mouth, stomach, small intestine and large intestine. However, maximum absorption occurs in the small intestine. A summary of absorption (sites of absorption and substances absorbed) is given in Table 16.1.

TABLE 16.1 The Summary of Absorption in Different Parts of Digestive System

Mouth	Stomach	Small Intestine	Large Intestine
Certain drugs coming in contact with the mucosa of mouth and lower side of the tongue are absorbed into the blood capillaries lining them.	Absorption of water, simple sugars, and alcohol etc. takes place.	Principal organ for absorption of nutrients. The digestion is completed here and the final products of digestion such as glucose, fructose, fatty acids, glycerol and amino acids are absorbed through the mucosa into the blood stream and lymph.	Absorption of water, some minerals and drugs takes place.

The absorbed substances finally reach the tissues which utilise them for their activities. This process is called assimilation.

The digestive wastes, solidified into coherent faeces in the rectum initiate a neural reflex causing an urge or desire for its removal. The egestion of faeces to the outside through the anal opening (defaecation) is a voluntary process and is carried out by a mass peristaltic movement.

16.4 DISORDERS OF DIGESTIVE SYSTEM

The inflammation of the intestinal tract is the most common ailment due to bacterial or viral infections. The infections are also caused by the parasites of the intestine like tapeworm, roundworm, threadworm, hookworm, pin worm, etc.

Jaundice: The liver is affected, skin and eyes turn yellow due to the deposit of bile pigments.

Vomiting: It is the ejection of stomach contents through the mouth. This reflex action is controlled by the vomit centre in the medulla. A feeling of nausea precedes vomiting.

Diarrhoea: The abnormal frequency of bowel movement and increased liquidity of the faecal discharge is known as diarrhoea. It reduces the absorption of food.

Constipation: In constipation, the faeces are retained within the colon as the bowel movements occur irregularly.

Indigestion: In this condition, the food is not properly digested leading to a feeling of fullness. The causes of indigestion are inadequate enzyme secretion, anxiety, food poisoning, over eating, and spicy food.

PEM

Dietary deficiencies of proteins and total food calories are widespread in many underdeveloped countries of South and South-east Asia, South America, and West and Central Africa. **Protein-energy malnutrition (PEM)** may affect large sections of the population during drought, famine and political turmoil. This happened in Bangladesh during the liberation war and in Ethiopia during the severe drought in mid-eighties. PEM affects infants and children to produce Marasmus and Kwashiorkar.

Marasmus is produced by a simultaneous deficiency of proteins and calories. It is found in infants less than a year in age, if mother's milk is replaced too early by other foods which are poor in both proteins and caloric value. This often happens if the mother has second pregnancy or childbirth when the older infant is still too young. In Marasmus, protein deficiency impairs growth and replacement of tissue proteins; extreme emaciation of the body and thinning of limbs results, the skin becomes dry, thin and wrinkled. Growth rate and body weight decline considerably. Even growth and development of brain and mental faculties are impaired.

Kwashiorkar is produced by protein deficiency unaccompanied by calorie deficiency. It results from the replacement of mother's milk by a high calorie-low protein diet in a child more than one year in age. Like marasmus, kwashiorkor shows wasting of muscles, thinning of limbs, failure of growth and brain development. But unlike marasmus, some fat is still left under the skin; moreover, extensive oedema and swelling of body parts are seen.

SUMMARY

The digestive system of humans consists of an alimentary canal and associated digestive glands. The alimentary canal consists of the mouth, buccal cavity, pharynx, oesophagus, stomach, small intestine, large intestine, rectum and the anus. The accessory digestive glands include the salivary glands, the liver (with gall bladder) and the pancreas. Inside the mouth the teeth masticates the food, the tongue tastes the food and manipulates it for proper mastication by mixing with the saliva. Saliva contains a starch digestive enzyme, salivary amylase that digests the starch and converts it into maltose (disaccharide). The food then passes into the pharynx and enters the oesophagus in the form of bolus, which is further carried down through the oesophagus by peristalsis into the stomach. In stomach mainly protein digestion takes place. Absorption of simple sugars, alcohol and medicines also takes place in the stomach.

The chyme (food) enters into the duodenum portion of the small intestine and is acted on by the pancreatic juice, bile and finally by the enzymes in the succus entericus, so that the digestion of carbohydrates, proteins and fats is completed. The food then enters into the jejunum and ileum portions of the small intestine. Carbohydrates are digested and converted into monosaccharides like glucose. Proteins are finally broken down into amino acids. The fats are converted to fatty acids and glycerol.

The digested end products are absorbed into the body through the epithelial lining of the intestinal villi. The undigested food (faeces) enters into the caecum of the large intestine through ileo-caecal valve, which prevents the back flow of the faecal matter. Most of the water is absorbed in the large intestine. The undigested food becomes semi-solid in nature and then enters into the rectum, anal canal and is finally egested out through the anus.

EXERCISES

1. Choose the correct answer among the following :
   (a) Gastric juice contains
      (i) pepsin, lipase and rennin
      (ii) trypsin, lipase and rennin
      (iii) trypsin, pepsin and lipase
      (iv) trypsin, pepsin and renin
   (b) Succus entericus is the name given to
      (i) a junction between ileum and large intestine
      (ii) intestinal juice
      (iii) swelling in the gut
      (iv) appendix
2. Match column I with column II

Column I	**Column II**
(a) Bilirubin and biliverdin	(i) Parotid
(b) Hydrolysis of starch	(ii) Bile
(c) Digestion of fat	(iii) Lipases
(d) Salivary gland	(iv) Amylases

3. Answer briefly:
   (a) Why are villi present in the intestine and not in the stomach?
   (b) How does pepsinogen change into its active form?
   (c) What are the basic layers of the wall of alimentary canal?
   (d) How does bile help in the digestion of fats?
4. State the role of pancreatic juice in digestion of proteins.
5. Describe the process of digestion of protein in stomach.
6. Give the dental formula of human beings.
7. Bile juice contains no digestive enzymes, yet it is important for digestion. Why?
8. Describe the digestive role of chymotrypsin. Which two other digestive enzymes of the same category are secreted by its source gland?
9. How are polysaccharides and disaccharides digested?
10. What would happen if HCl were not secreted in the stomach?
11. How does butter in your food get digested and absorbed in the body?
12. Discuss the main steps in the digestion of proteins as the food passes through different parts of the alimentary canal.
13. Explain the term thecodont and diphyodont.
14. Name different types of teeth and their number in an adult human.
15. What are the functions of liver?

Chapter 17

Breathing and Exchange of Gases

As you have read earlier, oxygen (O_2) is utilised by the organisms to indirectly break down simple molecules like glucose, amino acids, fatty acids, etc., to derive energy to perform various activities. Carbon dioxide (CO_2) which is harmful is also released during the above catabolic reactions. It is, therefore, evident that O_2 has to be continuously provided to the cells and CO_2 produced by the cells have to be released out. This process of exchange of O_2 from the atmosphere with CO_2 produced by the cells is called **breathing,** commonly known as **respiration**. Place your hands on your chest; you can feel the chest moving up and down. You know that it is due to breathing. How do we breathe? The respiratory organs and the mechanism of breathing are described in the following sections of this chapter.

17.1 Respiratory Organs

Mechanisms of breathing vary among different groups of animals depending mainly on their habitats and levels of organisation. Lower invertebrates like sponges, coelenterates, flatworms, etc., exchange O_2 with CO_2 by simple diffusion over their entire body surface. Earthworms use their moist cuticle and insects have a network of tubes (tracheal tubes) to transport atmospheric air within the body. Special vascularised structures called **gills** (branchial respiration) are used by most of the aquatic arthropods and molluscs whereas vascularised bags called **lungs** (pulmonary respiration) are used by the terrestrial forms for the exchange of gases. Among vertebrates, fishes use gills whereas amphibians, reptiles, birds and mammals respire through lungs. Amphibians like frogs can respire through their moist skin (cutaneous respiration) also.

17.1.1 Human Respiratory System

We have a pair of external nostrils opening out above the upper lips. It leads to a nasal chamber through the nasal passage. The nasal chamber opens into the **pharynx**, a portion of which is the common passage for food and air. The pharynx opens through the larynx region into the **trachea**. Larynx is a cartilaginous box which helps in sound production and hence called the **sound box**. During swallowing glottis can be covered by a thin elastic cartilaginous flap called epiglottis to prevent the entry of food into the larynx. Trachea is a straight tube extending up to the mid-thoracic cavity, which divides at the level of 5th thoracic vertebra into a right and left primary **bronchi**. Each bronchi undergoes repeated divisions to form the secondary and tertiary bronchi and bronchioles ending up in very thin terminal **bronchioles**. The tracheae, primary, secondary and tertiary bronchi, and initial bronchioles are supported by incomplete cartilaginous rings. Each terminal bronchiole gives rise to a number of very thin, irregular-walled and vascularised bag-like structures called **alveoli**. The branching network of bronchi, bronchioles and alveoli comprise the lungs (Figure 17.1). We have two lungs which are covered by a double layered pleura, with pleural fluid between them. It reduces friction on the lung-surface. The outer pleural membrane is in close contact with the thoracic

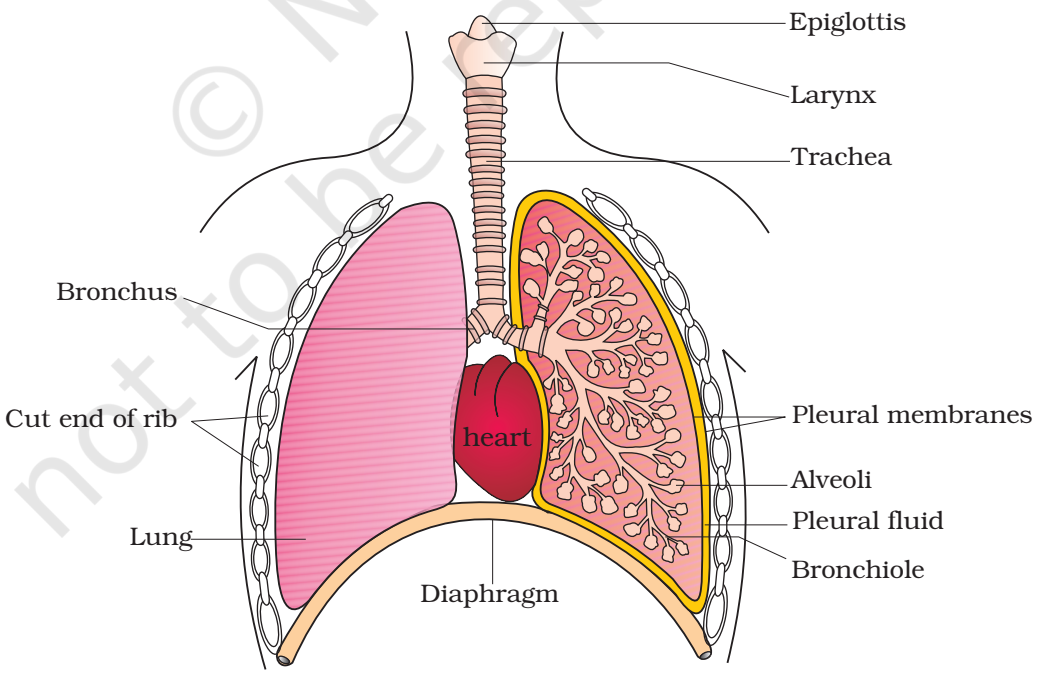


Figure 17.1 Diagrammatic view of human respiratory system (sectional view of the left lung is also shown)

lining whereas the inner pleural membrane is in contact with the lung surface. The part starting with the external nostrils up to the terminal bronchioles constitute the conducting part whereas the alveoli and their ducts form the respiratory or exchange part of the respiratory system. The conducting part transports the atmospheric air to the alveoli, clears it from foreign particles, humidifies and also brings the air to body temperature. Exchange part is the site of actual diffusion of O_2 and CO_2 between blood and atmospheric air.

The lungs are situated in the thoracic chamber which is anatomically an air-tight chamber. The thoracic chamber is formed dorsally by the vertebral column, ventrally by the sternum, laterally by the ribs and on the lower side by the dome-shaped diaphragm. The anatomical setup of lungs in thorax is such that any change in the volume of the thoracic cavity will be reflected in the lung (pulmonary) cavity. Such an arrangement is essential for breathing, as we cannot directly alter the pulmonary volume.

Respiration involves the following steps:

(i) Breathing or pulmonary ventilation by which atmospheric air is drawn in and CO_2 rich alveolar air is released out.

(ii) Diffusion of gases (O_2 and CO_2) across alveolar membrane.

(iii) Transport of gases by the blood.

(iv) Diffusion of O_2 and CO_2 between blood and tissues.

(v) Utilisation of O_2 by the cells for catabolic reactions and resultant release of CO_2 (cellular respiration as dealt in the Chapter 14).

17.2 Mechanism of Breathing

Breathing involves two stages : **inspiration** during which atmospheric air is drawn in and **expiration** by which the alveolar air is released out. The movement of air into and out of the lungs is carried out by creating a pressure gradient between the lungs and the atmosphere. Inspiration can occur if the pressure within the lungs (intra-pulmonary pressure) is less than the atmospheric pressure, i.e., there is a negative pressure in the lungs with respect to atmospheric pressure. Similarly, expiration takes place when the intra-pulmonary pressure is higher than the atmospheric pressure. The diaphragm and a specialised set of muscles – external and internal intercostals between the ribs, help in generation of such gradients. Inspiration is initiated by the contraction of diaphragm which increases the volume of thoracic chamber in the antero-posterior axis. The contraction of external inter-costal muscles lifts up the ribs and the

sternum causing an increase in the volume of the thoracic chamber in the dorso-ventral axis. The overall increase in the thoracic volume causes a similar increase in pulmonary volume. An increase in pulmonary volume decreases the intra-pulmonary pressure to less than the atmospheric pressure which forces the air from outside to move into the lungs, i.e., inspiration (Figure 17.2a). Relaxation of the diaphragm and the inter-costal muscles returns the diaphragm and sternum to their normal positions and reduce the thoracic volume and thereby the pulmonary volume. This leads to an increase in intra-pulmonary pressure to slightly above the atmospheric pressure causing the expulsion of air from the lungs, i.e., expiration (Figure 17.2b). We have the ability to increase the strength of inspiration and expiration with the help of additional muscles in the abdomen. On an average, a healthy human breathes 12-16 times/minute. The volume of air involved in breathing movements can be estimated by using a spirometer which helps in clinical assessment of pulmonary functions.

17.2.1 Respiratory Volumes and Capacities

Tidal Volume (TV): Volume of air inspired or expired during a normal respiration. It is approx. 500 mL., i.e., a healthy man can inspire or expire approximately 6000 to 8000 mL of air per minute.

Inspiratory Reserve Volume (IRV): Additional volume of air, a person can inspire by a forcible inspiration. This averages 2500 mL to 3000 mL.

Expiratory Reserve Volume (ERV): Additional volume of air, a person can expire by a forcible expiration. This averages 1000 mL to 1100 mL.

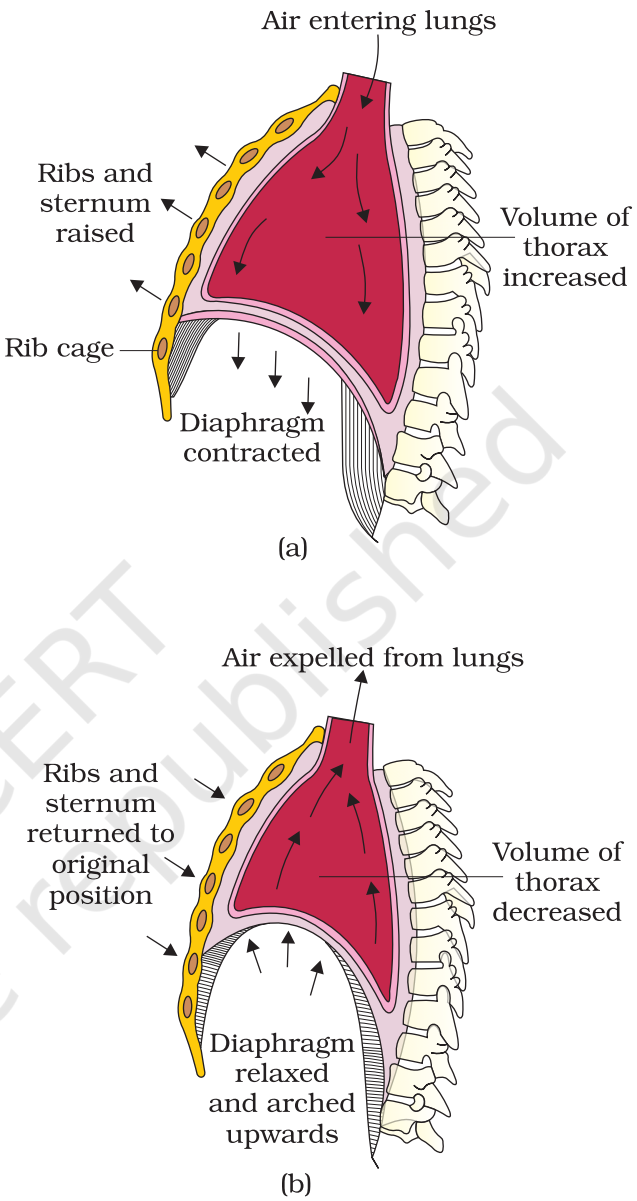


Figure 17.2 Mechanism of breathing showing : (a) inspiration (b) expiration

Residual Volume (RV): Volume of air remaining in the lungs even after a forcible expiration. This averages 1100 mL to 1200 mL.

By adding up a few respiratory volumes described above, one can derive various pulmonary capacities, which can be used in clinical diagnosis.

Inspiratory Capacity (IC): Total volume of air a person can inspire after a normal expiration. This includes tidal volume and inspiratory reserve volume (TV+IRV).

Expiratory Capacity (EC): Total volume of air a person can expire after a normal inspiration. This includes tidal volume and expiratory reserve volume (TV+ERV).

Functional Residual Capacity (FRC): Volume of air that will remain in the lungs after a normal expiration. This includes ERV+RV.

Vital Capacity (VC): The maximum volume of air a person can breathe in after a forced expiration. This includes ERV, TV and IRV or the maximum volume of air a person can breathe out after a forced inspiration.

Total Lung Capacity: Total volume of air accommodated in the lungs at the end of a forced inspiration. This includes RV, ERV, TV and IRV or vital capacity + residual volume.

17.3 EXCHANGE OF GASES

Alveoli are the primary sites of exchange of gases. Exchange of gases also occur between blood and tissues. O_2 and CO_2 are exchanged in these sites by simple diffusion mainly based on pressure/concentration gradient. Solubility of the gases as well as the thickness of the membranes involved in diffusion are also some important factors that can affect the rate of diffusion.

Pressure contributed by an individual gas in a mixture of gases is called partial pressure and is represented as pO_2 for oxygen and pCO_2 for carbon dioxide. Partial pressures of these two gases in the atmospheric air and the two sites of diffusion are given in Table 17.1 and in Figure 17.3. The data given in the table clearly indicates a concentration gradient for oxygen from alveoli to blood and blood to tissues. Similarly,

TABLE 17.1 Partial Pressures (in mm Hg) of Oxygen and Carbon dioxide at Different Parts Involved in Diffusion in Comparison to those in Atmosphere

Respiratory Gas	Atmospheric Air	Alveoli	Blood (Deoxygenated)	Blood (Oxygenated)	Tissues
O_2	159	104	40	95	40
CO_2	0.3	40	45	40	45

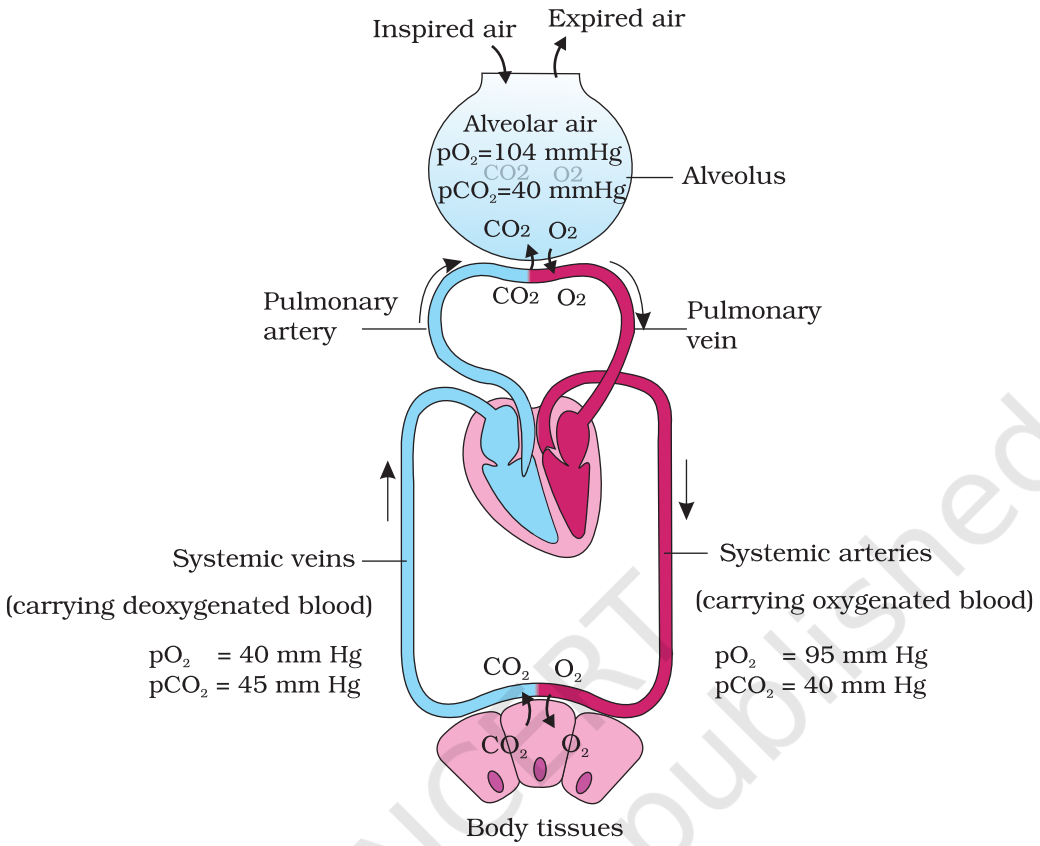


Figure 17.3 Diagrammatic representation of exchange of gases at the alveolus and the body tissues with blood and transport of oxygen and carbon dioxide

a gradient is present for CO_2 in the opposite direction, i.e., from tissues to blood and blood to alveoli. As the solubility of CO_2 is 20-25 times higher than that of O_2, the amount of CO_2 that can diffuse through the diffusion membrane per unit difference in partial pressure is much higher compared to that of O_2. The diffusion membrane is made up of three major layers (Figure 17.4) namely, the thin squamous epithelium of alveoli, the endothelium of alveolar capillaries and the basement substance in between them. However, its total thickness is much less than a millimetre. Therefore, all the factors in our body are favourable for diffusion of O_2 from alveoli to tissues and that of CO_2 from tissues to alveoli.

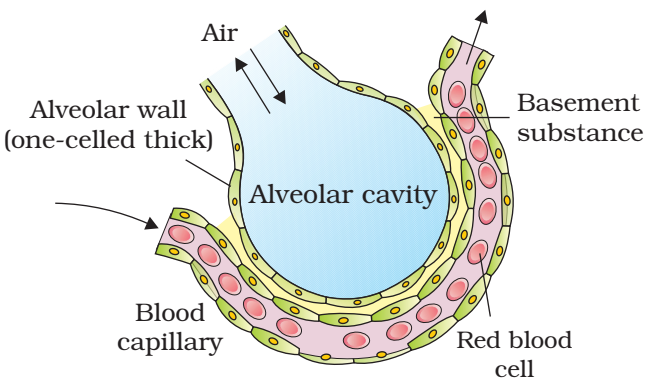


Figure 17.4 A Diagram of a section of an alveolus with a pulmonary capillary.

17.4 TRANSPORT OF GASES

Blood is the medium of transport for O_2 and CO_2. About 97 per cent of O_2 is transported by RBCs in the blood. The remaining 3 per cent of O_2 is carried in a dissolved state through the plasma. Nearly 20-25 per cent of CO_2 is transported by RBCs whereas 70 per cent of it is carried as bicarbonate. About 7 per cent of CO_2 is carried in a dissolved state through plasma.

17.4.1 Transport of Oxygen

Haemoglobin is a red coloured iron containing pigment present in the RBCs. O_2 can bind with haemoglobin in a reversible manner to form **oxyhaemoglobin**. Each haemoglobin molecule can carry a maximum of four molecules of O_2. Binding of oxygen with haemoglobin is primarily related to partial pressure of O_2. Partial pressure of CO_2, hydrogen ion concentration and temperature are the other factors which can interfere with this binding. A sigmoid curve is obtained when percentage saturation of haemoglobin with O_2 is plotted against the pO_2. This curve is called the Oxygen dissociation curve (Figure 17.5) and is highly useful in studying the effect of factors like pCO_2, H^+ concentration, etc., on binding of O_2 with haemoglobin. In the alveoli, where there is high pO_2, low pCO_2, lesser H^+ concentration and lower temperature, the factors are all favourable for the formation of oxyhaemoglobin, whereas in the tissues, where low pO_2, high pCO_2, high H^+ concentration and higher temperature exist, the conditions are favourable for dissociation of oxygen from the oxyhaemoglobin. This clearly indicates that O_2 gets bound to haemoglobin in the lung surface and gets dissociated at the tissues. Every 100 ml of oxygenated blood can deliver around 5 ml of O_2 to the tissues under normal physiological conditions.

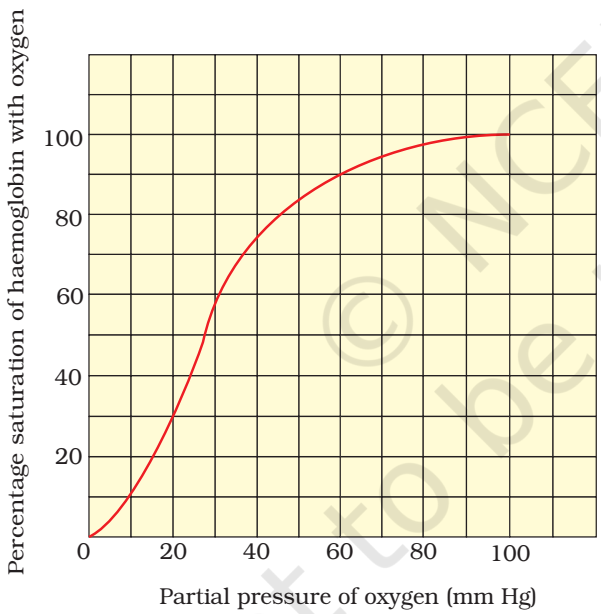


Figure 17.5 Oxygen dissociation curve

17.4.2 Transport of Carbon dioxide

CO_2 is carried by haemoglobin as **carbamino-haemoglobin** (about 20-25 per cent). This binding is related to the partial pressure of CO_2. pO_2 is a major factor which could affect this binding. When pCO_2 is high and pO_2 is low as in the tissues, more binding of carbon dioxide occurs whereas, when the pCO_2 is low and pO_2 is high as in the alveoli, dissociation

of CO_2 from carbamino-haemoglobin takes place, i.e., CO_2 which is bound to haemoglobin from the tissues is delivered at the alveoli. RBCs contain a very high concentration of the enzyme, carbonic anhydrase and minute quantities of the same is present in the plasma too. This enzyme facilitates the following reaction in both directions.

$$CO_2 + H_2O \xleftrightarrow{\text{Carbonic anhydrase}} H_2CO_3 \xleftrightarrow{\text{Carbonic anhydrase}} HCO_3^- + H^+$$

At the tissue site where partial pressure of CO_2 is high due to catabolism, CO_2 diffuses into blood (RBCs and plasma) and forms HCO_3^- and H^+. At the alveolar site where pCO_2 is low, the reaction proceeds in the opposite direction leading to the formation of CO_2 and H_2O. Thus, CO_2 trapped as bicarbonate at the tissue level and transported to the alveoli is released out as CO_2 (Figure 17.4). Every 100 ml of deoxygenated blood delivers approximately 4 ml of CO_2 to the alveoli.

17.5 REGULATION OF RESPIRATION

Human beings have a significant ability to maintain and moderate the respiratory rhythm to suit the demands of the body tissues. This is done by the neural system. A specialised centre present in the medulla region of the brain called respiratory rhythm centre is primarily responsible for this regulation. Another centre present in the pons region of the brain called pneumotaxic centre can moderate the functions of the respiratory rhythm centre. Neural signal from this centre can reduce the duration of inspiration and thereby alter the respiratory rate. A chemosensitive area is situated adjacent to the rhythm centre which is highly sensitive to CO_2 and hydrogen ions. Increase in these substances can activate this centre, which in turn can signal the rhythm centre to make necessary adjustments in the respiratory process by which these substances can be eliminated. Receptors associated with aortic arch and carotid artery also can recognise changes in CO_2 and H^+ concentration and send necessary signals to the rhythm centre for remedial actions. The role of oxygen in the regulation of respiratory rhythm is quite insignificant.

17.6 DISORDERS OF RESPIRATORY SYSTEM

Asthma is a difficulty in breathing causing wheezing due to inflammation of bronchi and bronchioles.

Emphysema is a chronic disorder in which alveolar walls are damaged due to which respiratory surface is decreased. One of the major causes of this is cigarette smoking.

Occupational Respiratory Disorders: In certain industries, especially those involving grinding or stone-breaking, so much dust is produced that the defense mechanism of the body cannot fully cope with the situation. Long exposure can give rise to inflammation leading to fibrosis (proliferation of fibrous tissues) and thus causing serious lung damage. Workers in such industries should wear protective masks.

SUMMARY

Cells utilise oxygen for metabolism and produce energy along with substances like carbon dioxide which is harmful. Animals have evolved different mechanisms for the transport of oxygen to the cells and for the removal of carbon dioxide from there. We have a well developed respiratory system comprising two lungs and associated air passages to perform this function.

The first step in respiration is breathing by which atmospheric air is taken in (inspiration) and the alveolar air is released out (expiration). Exchange of O_2 and CO_2 between deoxygenated blood and alveoli, transport of these gases throughout the body by blood, exchange of O_2 and CO_2 between the oxygenated blood and tissues and utilisation of O_2 by the cells (cellular respiration) are the other steps involved.

Inspiration and expiration are carried out by creating pressure gradients between the atmosphere and the alveoli with the help of specialised muscles – intercostals and diaphragm. Volumes of air involved in these activities can be estimated with the help of spirometer and are of clinical significance.

Exchange of O_2 and CO_2 at the alveoli and tissues occur by diffusion. Rate of diffusion is dependent on the partial pressure gradients of O_2 (pO_2) and CO_2 (pCO_2), their solubility as well as the thickness of the diffusion surface. These factors in our body facilitate diffusion of O_2 from the alveoli to the deoxygenated blood as well as from the oxygenated blood to the tissues. The factors are favourable for the diffusion of CO_2 in the opposite direction, i.e., from tissues to alveoli.

Oxygen is transported mainly as oxyhaemoglobin. In the alveoli where pO_2 is higher, O_2 gets bound to haemoglobin which is easily dissociated at the tissues where pO_2 is low and pCO_2 and H^+ concentration are high. Nearly 70 per cent of carbon dioxide is transported as bicarbonate (HCO_3^-) with the help of the enzyme carbonic anhydrase. 20-25 per cent of carbon dioxide is carried by haemoglobin as carbamino-haemoglobin. In the tissues where pCO_2 is high, it gets bound to blood whereas in the alveoli where pCO_2 is low and pO_2 is high, it gets removed from the blood.

Respiratory rhythm is maintained by the respiratory centre in the medulla region of brain. A pneumotaxic centre in the pons region of the brain and a chemosensitive area in the medulla can alter respiratory mechanism.

EXERCISES

1. Define vital capacity. What is its significance?
2. State the volume of air remaining in the lungs after a normal breathing.
3. Diffusion of gases occurs in the alveolar region only and not in the other parts of respiratory system. Why?
4. What are the major transport mechanisms for CO_2? Explain.
5. What will be the pO_2 and pCO_2 in the atmospheric air compared to those in the alveolar air ?
   (i) pO_2 lesser, pCO_2 higher
   (ii) pO_2 higher, pCO_2 lesser
   (iii) pO_2 higher, pCO_2 higher
   (iv) pO_2 lesser, pCO_2 lesser
6. Explain the process of inspiration under normal conditions.
7. How is respiration regulated?
8. What is the effect of pCO_2 on oxygen transport?
9. What happens to the respiratory process in a man going up a hill?
10. What is the site of gaseous exchange in an insect?
11. Define oxygen dissociation curve. Can you suggest any reason for its sigmoidal pattern?
12. Have you heard about hypoxia? Try to gather information about it, and discuss with your friends.
13. Distinguish between
    (a) IRV and ERV
    (b) Inspiratory capacity and Expiratory capacity.
    (c) Vital capacity and Total lung capacity.
14. What is Tidal volume? Find out the Tidal volume (approximate value) for a healthy human in an hour.

Chapter 18
Body Fluids and Circulation

You have learnt that all living cells have to be provided with nutrients, O_2 and other essential substances. Also, the waste or harmful substances produced, have to be removed continuously for healthy functioning of tissues. It is therefore, essential to have efficient mechanisms for the movement of these substances to the cells and from the cells. Different groups of animals have evolved different methods for this transport. Simple organisms like sponges and coelenterates circulate water from their surroundings through their body cavities to facilitate the cells to exchange these substances. More complex organisms use special fluids within their bodies to transport such materials. **Blood** is the most commonly used body fluid by most of the higher organisms including humans for this purpose. Another body fluid, **lymph,** also helps in the transport of certain substances. In this chapter, you will learn about the composition and properties of blood and lymph (tissue fluid) and the mechanism of circulation of blood is also explained herein.

18.1 Blood

Blood is a special connective tissue consisting of a fluid matrix, plasma, and formed elements.

18.1.1 Plasma

Plasma is a straw coloured, viscous fluid constituting nearly 55 per cent of the blood. 90-92 per cent of plasma is water and proteins contribute 6-8 per cent of it. Fibrinogen, globulins and albumins are the major proteins.

Fibrinogens are needed for clotting or coagulation of blood. Globulins primarily are involved in defense mechanisms of the body and the albumins help in osmotic balance. Plasma also contains small amounts of minerals like Na^+, Ca^{++}, Mg^{++}, HCO_3^-, Cl^-, etc. Glucose, amino acids, lipids, etc., are also present in the plasma as they are always in transit in the body. Factors for coagulation or clotting of blood are also present in the plasma in an inactive form. Plasma without the clotting factors is called serum.

18.1.2 Formed Elements

Erythrocytes, leucocytes and platelets are collectively called formed elements (Figure 18.1) and they constitute nearly 45 per cent of the blood.

Erythrocytes or red blood cells (RBC) are the most abundant of all the cells in blood. A healthy adult man has, on an average, 5 millions to 5.5 millions of RBCs mm^{-3} of blood. RBCs are formed in the red bone marrow in the adults. RBCs are devoid of nucleus in most of the mammals and are biconcave in shape. They have a red coloured, iron containing complex protein called haemoglobin, hence the colour and name of these cells. A healthy individual has 12-16 gms of haemoglobin in every 100 ml of blood. These molecules play a significant role in transport of respiratory gases. RBCs have an average life span of 120 days after which they are destroyed in the spleen (graveyard of RBCs).

Leucocytes are also known as white blood cells (WBC) as they are colourless due to the lack of haemoglobin. They are nucleated and are relatively lesser in number which averages 6000-8000 mm^{-3} of blood. Leucocytes are generally short lived. We have two main categories of WBCs – granulocytes and agranulocytes. Neutrophils, eosinophils and basophils are different types of granulocytes, while lymphocytes and monocytes are the agranulocytes. Neutrophils are the most abundant cells (60-65 per cent) of the total WBCs and basophils are the least (0.5-1 per cent) among them. Neutrophils and monocytes (6-8 per cent) are phagocytic cells which destroy foreign organisms entering the body. Basophils secrete histamine, serotonin, heparin, etc., and are involved in inflammatory reactions. Eosinophils (2-3 per cent) resist infections and are also

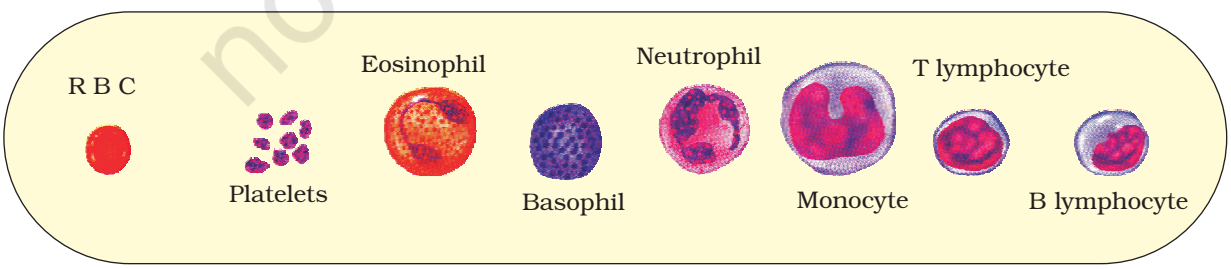


Figure 18.1 Diagrammatic representation of formed elements in blood

associated with allergic reactions. Lymphocytes (20-25 per cent) are of two major types – 'B' and 'T' forms. Both B and T lymphocytes are responsible for immune responses of the body.

Platelets also called **thrombocytes**, are cell fragments produced from megakaryocytes (special cells in the bone marrow). Blood normally contains 1,500,00-3,500,00 platelets mm^{-3}. Platelets can release a variety of substances most of which are involved in the coagulation or clotting of blood. A reduction in their number can lead to clotting disorders which will lead to excessive loss of blood from the body.

18.1.3 Blood Groups

As you know, blood of human beings differ in certain aspects though it appears to be similar. Various types of grouping of blood has been done. Two such groupings – the ABO and Rh – are widely used all over the world.

18.1.3.1 ABO grouping

ABO grouping is based on the presence or absence of two surface antigens (chemicals that can induce immune response) on the RBCs namely A and B. Similarly, the plasma of different individuals contain two natural antibodies (proteins produced in response to antigens). The distribution of antigens and antibodies in the four groups of blood, **A, B, AB** and **O** are given in Table 18.1. You probably know that during blood transfusion, any blood cannot be used; the blood of a donor has to be carefully matched with the blood of a recipient before any blood transfusion to avoid severe problems of clumping (destruction of RBC). The donor's compatibility is also shown in the Table 18.1.

TABLE 18.1 Blood Groups and Donor Compatibility

Blood Group	Antigens on RBCs	Antibodies in Plasma	Donor's Group
A	A	anti-B	A, O
B	B	anti-A	B, O
AB	A, B	nil	AB, A, B, O
O	nil	anti-A, B	O

From the above mentioned table it is evident that group 'O' blood can be donated to persons with any other blood group and hence 'O' group individuals are called 'universal donors'. Persons with 'AB' group can accept blood from persons with AB as well as the other groups of blood. Therefore, such persons are called 'universal recipients'.

18.1.3.2 Rh grouping

Another antigen, the Rh antigen similar to one present in Rhesus monkeys (hence Rh), is also observed on the surface of RBCs of majority (nearly 80 per cent) of humans. Such individuals are called **Rh positive** (Rh+ve) and those in whom this antigen is absent are called **Rh negative** (Rh-ve). An Rh-ve person, if exposed to Rh+ve blood, will form specific antibodies against the Rh antigens. Therefore, Rh group should also be matched before transfusions. A special case of Rh incompatibility (mismatching) has been observed between the Rh-ve blood of a pregnant mother with Rh+ve blood of the foetus. Rh antigens of the foetus do not get exposed to the Rh-ve blood of the mother in the first pregnancy as the two bloods are well separated by the placenta. However, during the delivery of the first child, there is a possibility of exposure of the maternal blood to small amounts of the Rh+ve blood from the foetus. In such cases, the mother starts preparing antibodies against Rh antigen in her blood. In case of her subsequent pregnancies, the Rh antibodies from the mother (Rh-ve) can leak into the blood of the foetus (Rh+ve) and destroy the foetal RBCs. This could be fatal to the foetus or could cause severe anaemia and jaundice to the baby. This condition is called *erythroblastosis foetalis*. This can be avoided by administering anti-Rh antibodies to the mother immediately after the delivery of the first child.

18.1.4 Coagulation of Blood

You know that when you cut your finger or hurt yourself, your wound does not continue to bleed for a long time; usually the blood stops flowing after sometime. *Do you know why?* Blood exhibits coagulation or clotting in response to an injury or trauma. This is a mechanism to prevent excessive loss of blood from the body. You would have observed a dark reddish brown scum formed at the site of a cut or an injury over a period of time. It is a clot or coagulam formed mainly of a network of threads called fibrins in which dead and damaged formed elements of blood are trapped. Fibrins are formed by the conversion of inactive fibrinogens in the plasma by the enzyme thrombin. Thrombins, in turn are formed from another inactive substance present in the plasma called prothrombin. An enzyme complex, thrombokinase, is required for the above reaction. This complex is formed by a series of linked enzymic reactions (cascade process) involving a number of factors present in the plasma in an inactive state. An injury or a trauma stimulates the platelets in the blood to release certain factors which activate the mechanism of coagulation. Certain factors released by the tissues at the site of injury also can initiate coagulation. Calcium ions play a very important role in clotting.

18.2 LYMPH (TISSUE FLUID)

As the blood passes through the capillaries in tissues, some water along with many small water soluble substances move out into the spaces between the cells of tissues leaving the larger proteins and most of the formed elements in the blood vessels. This fluid released out is called the interstitial fluid or tissue fluid. It has the same mineral distribution as that in plasma. Exchange of nutrients, gases, etc., between the blood and the cells always occur through this fluid. An elaborate network of vessels called the lymphatic system collects this fluid and drains it back to the major veins. The fluid present in the lymphatic system is called the lymph. Lymph is a colourless fluid containing specialised lymphocytes which are responsible for the immune responses of the body. Lymph is also an important carrier for nutrients, hormones, etc. Fats are absorbed through lymph in the lacteals present in the intestinal villi.

18.3 CIRCULATORY PATHWAYS

The circulatory patterns are of two types – open or closed. **Open circulatory system** is present in arthropods and molluscs in which blood pumped by the heart passes through large vessels into open spaces or body cavities called sinuses. Annelids and chordates have a **closed circulatory system** in which the blood pumped by the heart is always circulated through a closed network of blood vessels. This pattern is considered to be more advantageous as the flow of fluid can be more precisely regulated.

All vertebrates possess a muscular chambered heart. Fishes have a 2-chambered heart with an atrium and a ventricle. Amphibians and the reptiles (except crocodiles) have a 3-chambered heart with two atria and a single ventricle, whereas crocodiles, birds and mammals possess a 4-chambered heart with two atria and two ventricles. In fishes the heart pumps out deoxygenated blood which is oxygenated by the gills and supplied to the body parts from where deoxygenated blood is returned to the heart (single circulation). In amphibians and reptiles, the left atrium receives oxygenated blood from the gills/lungs/skin and the right atrium gets the deoxygenated blood from other body parts. However, they get mixed up in the single ventricle which pumps out mixed blood (incomplete double circulation). In birds and mammals, oxygenated and deoxygenated blood received by the left and right atria respectively passes on to the ventricles of the same sides. The ventricles pump it out without any mixing up, i.e., two separate circulatory pathways are present in these organisms, hence, these animals have double circulation. Let us study the human circulatory system.

18.3.1 Human Circulatory System

Human circulatory system, also called the blood vascular system consists of a muscular chambered heart, a network of closed branching blood vessels and blood, the fluid which is circulated.

Heart, the mesodermally derived organ, is situated in the thoracic cavity, in between the two lungs, slightly tilted to the left. It has the size of a clenched fist. It is protected by a double walled membranous bag, **pericardium,** enclosing the pericardial fluid. Our heart has four chambers, two relatively small upper chambers called **atria** and two larger lower chambers called **ventricles**. A thin, muscular wall called the inter-atrial septum separates the right and the left atria, whereas a thick-walled, the inter-ventricular septum, separates the left and the right ventricles (Figure 18.2). The atrium and the ventricle of the same side are also separated by a thick fibrous tissue called the atrio-ventricular septum. However, each of these septa are provided with an opening through which the two chambers of the same side are connected. The opening between the right atrium and the right ventricle is guarded by a valve formed of three muscular flaps or cusps, the tricuspid valve, whereas a bicuspid or mitral valve guards the opening between the left atrium and the left ventricle. The openings of the right and the left ventricles into the

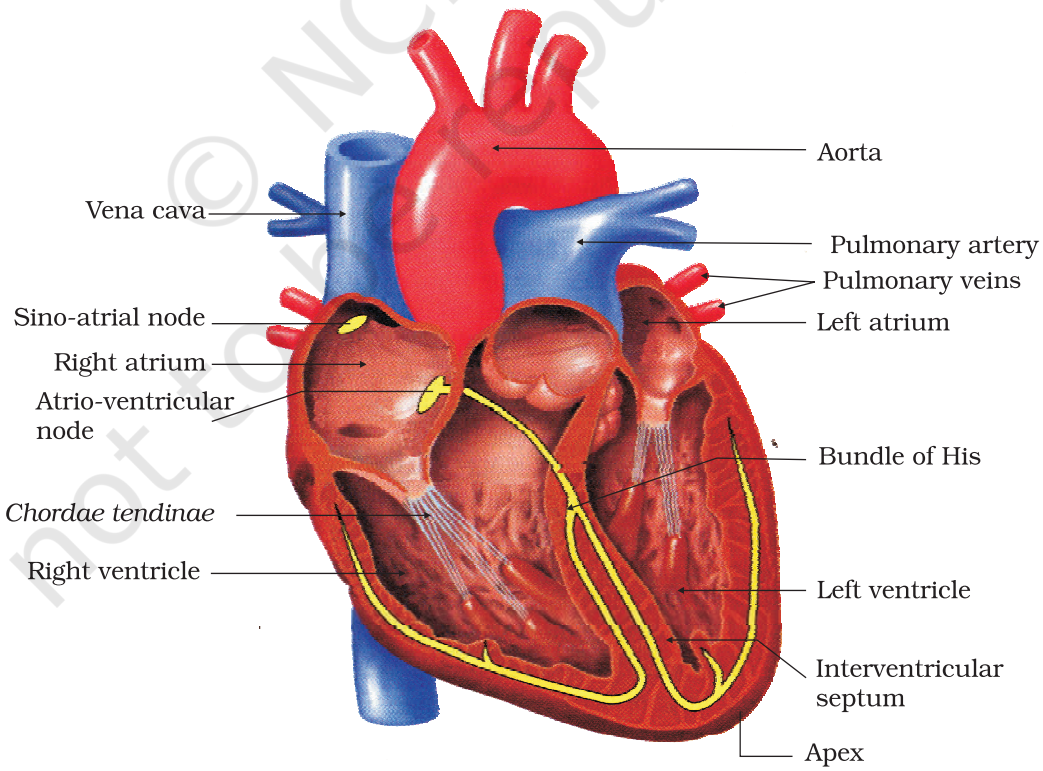


Figure 18.2 Section of a human heart

pulmonary artery and the aorta respectively are provided with the semilunar valves. The valves in the heart allows the flow of blood only in one direction, i.e., from the atria to the ventricles and from the ventricles to the pulmonary artery or aorta. These valves prevent any backward flow.

The entire heart is made of cardiac muscles. The walls of ventricles are much thicker than that of the atria. A specialised cardiac musculature called the nodal tissue is also distributed in the heart (Figure 18.2). A patch of this tissue is present in the right upper corner of the right atrium called the **sino-atrial node** (SAN). Another mass of this tissue is seen in the lower left corner of the right atrium close to the atrio-ventricular septum called the **atrio-ventricular node** (AVN). A bundle of nodal fibres, atrio-ventricular bundle (AV bundle) continues from the AVN which passes through the atrio-ventricular septa to emerge on the top of the inter-ventricular septum and immediately divides into a right and left bundle. These branches give rise to minute fibres throughout the ventricular musculature of the respective sides and are called purkinje fibres. The nodal musculature has the ability to generate action potentials without any external stimuli, i.e., it is autoexcitable. However, the number of action potentials that could be generated in a minute vary at different parts of the nodal system. The SAN can generate the maximum number of action potentials, i.e., 70-75 min^{-1}, and is responsible for initiating and maintaining the rhythmic contractile activity of the heart. Therefore, it is called the pacemaker. Our heart normally beats 70-75 times in a minute (average 72 beats min^{-1}).

18.3.2 Cardiac Cycle

How does the heart function? Let us take a look. To begin with, all the four chambers of heart are in a relaxed state, i.e., they are in joint diastole. As the tricuspid and bicuspid valves are open, blood from the pulmonary veins and vena cava flows into the left and the right ventricle respectively through the left and right atria. The semilunar valves are closed at this stage. The SAN now generates an action potential which stimulates both the atria to undergo a simultaneous contraction – the atrial systole. This increases the flow of blood into the ventricles by about 30 per cent. The action potential is conducted to the ventricular side by the AVN and AV bundle from where the bundle of His transmits it through the entire ventricular musculature. This causes the ventricular muscles to contract, (ventricular systole), the atria undergoes relaxation (diastole), coinciding with the ventricular systole. Ventricular systole increases the ventricular pressure causing the closure of tricuspid and

bicuspid valves due to attempted backflow of blood into the atria. As the ventricular pressure increases further, the semilunar valves guarding the pulmonary artery (right side) and the aorta (left side) are forced open, allowing the blood in the ventricles to flow through these vessels into the circulatory pathways. The ventricles now relax (ventricular diastole) and the ventricular pressure falls causing the closure of semilunar valves which prevents the backflow of blood into the ventricles. As the ventricular pressure declines further, the tricuspid and bicuspid valves are pushed open by the pressure in the atria exerted by the blood which was being emptied into them by the veins. The blood now once again moves freely to the ventricles. The ventricles and atria are now again in a relaxed (joint diastole) state, as earlier. Soon the SAN generates a new action potential and the events described above are repeated in that sequence and the process continues.

This sequential event in the heart which is cyclically repeated is called the cardiac cycle and it consists of systole and diastole of both the atria and ventricles. As mentioned earlier, the heart beats 72 times per minute, i.e., that many cardiac cycles are performed per minute. From this it could be deduced that the duration of a cardiac cycle is 0.8 seconds. During a cardiac cycle, each ventricle pumps out approximately 70 mL of blood which is called the stroke volume. The stroke volume multiplied by the heart rate (no. of beats per min.) gives the cardiac output. Therefore, the cardiac output can be defined as the volume of blood pumped out by each ventricle per minute and averages 5000 mL or 5 litres in a healthy individual. The body has the ability to alter the stroke volume as well as the heart rate and thereby the cardiac output. For example, the cardiac output of an athlete will be much higher than that of an ordinary man.

During each cardiac cycle two prominent sounds are produced which can be easily heard through a stethoscope. The first heart sound (lub) is associated with the closure of the tricuspid and bicuspid valves whereas the second heart sound (dub) is associated with the closure of the semilunar valves. These sounds are of clinical diagnostic significance.

18.3.3 Electrocardiograph (ECG)

You are probably familiar with this scene from a typical hospital television show: A patient is hooked up to a monitoring machine that shows voltage traces on a screen and makes the sound "... pip... pip... pip..... peeeeeeeeeeeeeeeeeeeeee" as the patient goes into cardiac arrest. This type of machine (electro-cardiograph) is used to obtain an electrocardiogram (ECG). ECG is a graphical representation of the electrical activity of the heart during a cardiac cycle. To obtain a standard ECG (as shown in the

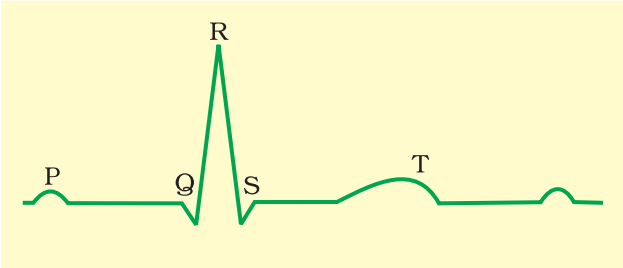


Figure 18.3 Diagrammatic presentation of a standard ECG

Figure 18.3), a patient is connected to the machine with three electrical leads (one to each wrist and to the left ankle) that continuously monitor the heart activity. For a detailed evaluation of the heart's function, multiple leads are attached to the chest region. Here, we will talk only about a standard ECG.

Each peak in the ECG is identified with a letter from P to T that corresponds to a specific electrical activity of the heart.

The P-wave represents the electrical **excitation (or depolarisation) of the atria**, which leads to the contraction of both the atria.

The QRS complex represents the **depolarisation of the ventricles**, which initiates the ventricular contraction. The contraction starts shortly after Q and marks the beginning of the systole.

The T-wave represents the return of the ventricles from excited to normal state (**repolarisation**). The end of the T-wave marks the end of systole.

Obviously, by counting the number of QRS complexes that occur in a given time period, one can determine the heart beat rate of an individual. Since the ECGs obtained from different individuals have roughly the same shape for a given lead configuration, any deviation from this shape indicates a possible abnormality or disease. Hence, it is of a great clinical significance.

18.4 Double Circulation

The blood flows strictly by a fixed route through **Blood Vessels**—the arteries and veins. Basically, each artery and vein consists of three layers: an inner lining of squamous endothelium, the **tunica intima**, a middle layer of smooth muscle and elastic fibres, the tunica media, and an external layer of fibrous connective tissue with collagen fibres, the **tunica externa**. The tunica media is comparatively thin in the veins (Figure 18.4).

As mentioned earlier, the blood pumped by the right ventricle enters the pulmonary artery, whereas the left ventricle pumps blood into the aorta. The deoxygenated blood pumped into the pulmonary artery is passed on to the lungs from where the oxygenated blood is carried by the pulmonary veins into the left atrium. This pathway constitutes the pulmonary circulation. The oxygenated blood entering the aorta is carried by a network of arteries, arterioles and capillaries to the tissues from where the deoxygenated blood is collected by a system of venules, veins and vena cava and emptied into the right atrium. This is the systemic circulation (Figure 18.4). The systemic circulation provides nutrients, O_2 and other essential substances to the tissues and takes CO_2 and other harmful substances away for elimination. A unique vascular connection exists between the digestive tract and liver called

hepatic portal system. The hepatic portal vein carries blood from intestine to the liver before it is delivered to the systemic circulation. A special coronary system of blood vessels is present in our body exclusively for the circulation of blood to and from the cardiac musculature.

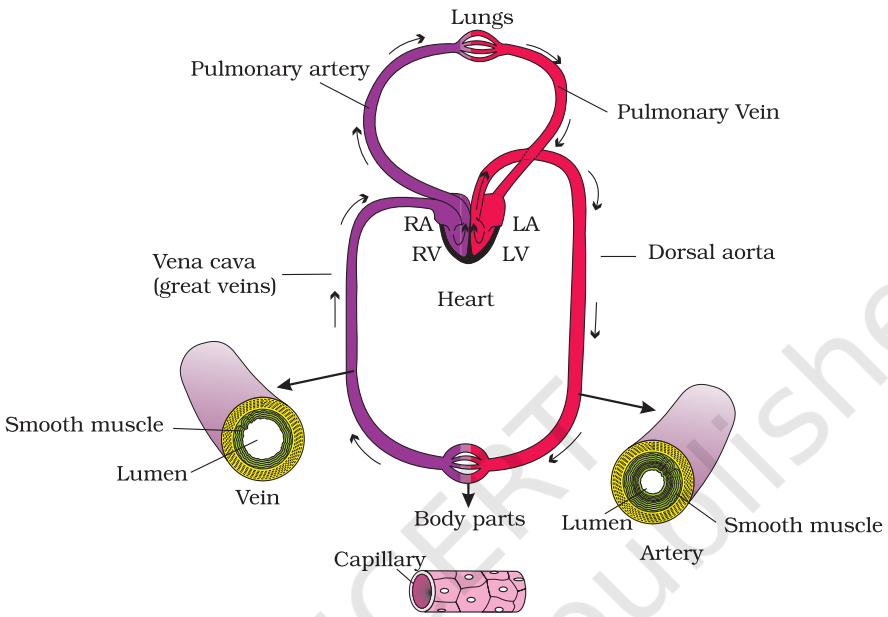


Figure 18.4 Schematic plan of blood circulation in human

18.5 REGULATION OF CARDIAC ACTIVITY

Normal activities of the heart are regulated intrinsically, i.e., auto regulated by specialised muscles (nodal tissue), hence the heart is called myogenic. A special neural centre in the medulla oblangata can moderate the cardiac function through autonomic nervous system (ANS). Neural signals through the sympathetic nerves (part of ANS) can increase the rate of heart beat, the strength of ventricular contraction and thereby the cardiac output. On the other hand, parasympathetic neural signals (another component of ANS) decrease the rate of heart beat, speed of conduction of action potential and thereby the cardiac output. Adrenal medullary hormones can also increase the cardiac output.

18.6 DISORDERS OF CIRCULATORY SYSTEM

High Blood Pressure (Hypertension): Hypertension is the term for blood pressure that is higher than normal (120/80). In this measurement 120 mm Hg (millimetres of mercury pressure) is the systolic, or pumping, pressure and 80 mm Hg is the diastolic, or resting, pressure. If repeated checks of blood pressure of an individual is 140/90 (140 over 90) or

higher, it shows hypertension. High blood pressure leads to heart diseases and also affects vital organs like brain and kidney.

Coronary Artery Disease (CAD): Coronary Artery Disease, often referred to as **atherosclerosis**, affects the vessels that supply blood to the heart muscle. It is caused by deposits of calcium, fat, cholesterol and fibrous tissues, which makes the lumen of arteries narrower.

Angina: It is also called 'angina pectoris'. A symptom of acute chest pain appears when no enough oxygen is reaching the heart muscle. Angina can occur in men and women of any age but it is more common among the middle-aged and elderly. It occurs due to conditions that affect the blood flow.

Heart Failure: Heart failure means the state of heart when it is not pumping blood effectively enough to meet the needs of the body. It is sometimes called congestive heart failure because congestion of the lungs is one of the main symptoms of this disease. Heart failure is not the same as cardiac arrest (when the heart stops beating) or a heart attack (when the heart muscle is suddenly damaged by an inadequate blood supply).

SUMMARY

Vertebrates circulate blood, a fluid connective tissue, in their body, to transport essential substances to the cells and to carry waste substances from there. Another fluid, lymph (tissue fluid) is also used for the transport of certain substances.

Blood comprises of a fluid matrix, plasma and formed elements. Red blood cells (RBCs, erythrocytes), white blood cells (WBCs, leucocytes) and platelets (thrombocytes) constitute the formed elements. Blood of humans are grouped into A, B, AB and O systems based on the presence or absence of two surface antigens, A, B on the RBCs. Another blood grouping is also done based on the presence or absence of another antigen called Rhesus factor (Rh) on the surface of RBCs. The spaces between cells in the tissues contain a fluid derived from blood called tissue fluid. This fluid called lymph is almost similar to blood except for the protein content and the formed elements.

All vertebrates and a few invertebrates have a closed circulatory system. Our circulatory system consists of a muscular pumping organ, heart, a network of vessels and a fluid, blood. Heart has two atria and two ventricles. Cardiac musculature is auto-excitable. Sino-atrial node (SAN) generates the maximum number of action protentials per minute (70-75/min) and therefore, it sets the pace of the activities of the heart. Hence it is called the Pacemaker. The action potential causes the atria and then the ventricles to undergo contraction (systole) followed by their relaxation (diastole). The systole forces the blood to move from the atria to the ventricles and to the pulmonary artery and the aorta. The cardiac cycle is formed by sequential events in the heart which is cyclically repeated and is called the cardiac cycle. A healthy person shows 72 such cycles per minute. About 70 mL of blood is pumped out by each ventricle during a cardiac cycle and it is called the stroke or beat volume. Volume of blood pumped out by each ventricle of heart per minute is called the cardiac output and it is equal to the product of stroke volume and heart rate (approx 5 litres). The electrical activity of the heart can be recorded from

the body surface by using electrocardiograph and the recording is called electrocardiogram (ECG) which is of clinical importance.

We have a complete double circulation, i.e., two circulatory pathways, namely, pulmonary and systemic are present. The pulmonary circulation starts by the pumping of deoxygenated blood by the right ventricle which is carried to the lungs where it is oxygenated and returned to the left atrium. The systemic circulation starts with the pumping of oxygenated blood by the left ventricle to the aorta which is carried to all the body tissues and the deoxygenated blood from there is collected by the veins and returned to the right atrium. Though the heart is autoexcitable, its functions can be moderated by neural and hormonal mechanisms.

EXERCISES

1. Name the components of the formed elements in the blood and mention one major function of each of them.
2. What is the importance of plasma proteins?
3. Match Column I with Column II :

Column I	**Column II**
(a) Eosinophils	(i) Coagulation
(b) RBC	(ii) Universal Recipient
(c) AB Group	(iii) Resist Infections
(d) Platelets	(iv) Contraction of Heart
(e) Systole	(v) Gas transport

4. Why do we consider blood as a connective tissue?
5. What is the difference between lymph and blood?
6. What is meant by double circulation? What is its significance?
7. Write the differences between :
   (a) Blood and Lymph
   (b) Open and Closed system of circulation
   (c) Systole and Diastole
   (d) P-wave and T-wave
8. Describe the evolutionary change in the pattern of heart among the vertebrates.
9. Why do we call our heart myogenic?
10. Sino-atrial node is called the pacemaker of our heart. Why?
11. What is the significance of atrio-ventricular node and atrio-ventricular bundle in the functioning of heart?
12. Define a cardiac cycle and the cardiac output.
13. Explain heart sounds.
14. Draw a standard ECG and explain the different segments in it.

Chapter 19

Excretory Products and their Elimination

Animals accumulate ammonia, urea, uric acid, carbon dioxide, water and ions like Na^+, K^+, Cl^-, phosphate, sulphate, etc., either by metabolic activities or by other means like excess ingestion. These substances have to be removed totally or partially. In this chapter, you will learn the mechanisms of elimination of these substances with special emphasis on common nitrogenous wastes. Ammonia, urea and uric acid are the major forms of nitrogenous wastes excreted by the animals. Ammonia is the most toxic form and requires large amount of water for its elimination, whereas uric acid, being the least toxic, can be removed with a minimum loss of water.

The process of excreting ammonia is *Ammonotelism*. Many bony fishes, aquatic amphibians and aquatic insects are ***ammonotelic*** in nature. Ammonia, as it is readily soluble, is generally excreted by diffusion across body surfaces or through gill surfaces (in fish) as ammonium ions. Kidneys do not play any significant role in its removal. Terrestrial adaptation necessitated the production of lesser toxic nitrogenous wastes like urea and uric acid for conservation of water. Mammals, many terrestrial amphibians and marine fishes mainly excrete urea and are called ***ureotelic*** animals. Ammonia produced by metabolism is converted into urea in the liver of these animals and released into the blood which is filtered and excreted out by the kidneys. Some amount of urea may be retained in the kidney matrix of some of these animals to maintain a desired osmolarity. Reptiles, birds, land snails and insects excrete nitrogenous wastes as uric acid in the form of pellet or paste with a minimum loss of water and are called ***uricotelic*** animals.

A survey of animal kingdom presents a variety of excretory structures. In most of the invertebrates, these structures are simple tubular forms whereas vertebrates have complex tubular organs called kidneys. Some of these structures are mentioned here. Protonephridia or flame cells are the excretory structures in Platyhelminthes (Flatworms, e.g., *Planaria*), rotifers, some annelids and the cephalochordate – *Amphioxus*. Protonephridia are primarily concerned with ionic and fluid volume regulation, i.e., osmoregulation. Nephridia are the tubular excretory structures of earthworms and other annelids. Nephridia help to remove nitrogenous wastes and maintain a fluid and ionic balance. Malpighian tubules are the excretory structures of most of the insects including cockroaches. Malpighian tubules help in the removal of nitrogenous wastes and osmoregulation. Antennal glands or green glands perform the excretory function in crustaceans like prawns.

19.1 HUMAN EXCRETORY SYSTEM

In humans, the excretory system consists of a pair of kidneys, one pair of ureters, a urinary bladder and a urethra (Figure 19.1). Kidneys are reddish brown, bean shaped structures situated between the levels of last thoracic and third lumbar vertebra close to the dorsal inner wall of the abdominal cavity. Each kidney of an adult human measures 10-12 cm in length, 5-7 cm in width, 2-3 cm in thickness with an average weight of 120-170 g. Towards the centre of the inner concave surface of the kidney is a notch called hilum through which ureter, blood vessels and nerves enter. Inner to the hilum is a broad funnel shaped space called the renal pelvis with projections called calyces. The outer layer of kidney is a tough capsule. Inside the kidney, there are two zones, an outer *cortex* and an inner *medulla*. The medulla is divided into a few conical masses (medullary pyramids) projecting into the calyces (sing.: calyx). The cortex extends in between the

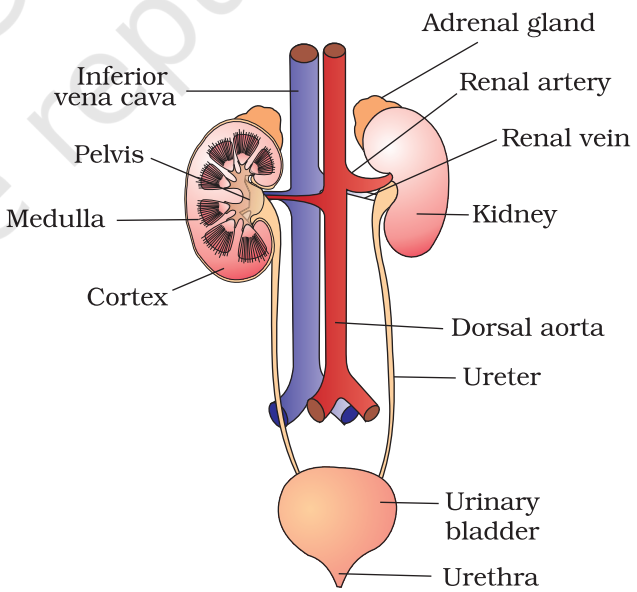


Figure 19.1 Human Urinary system

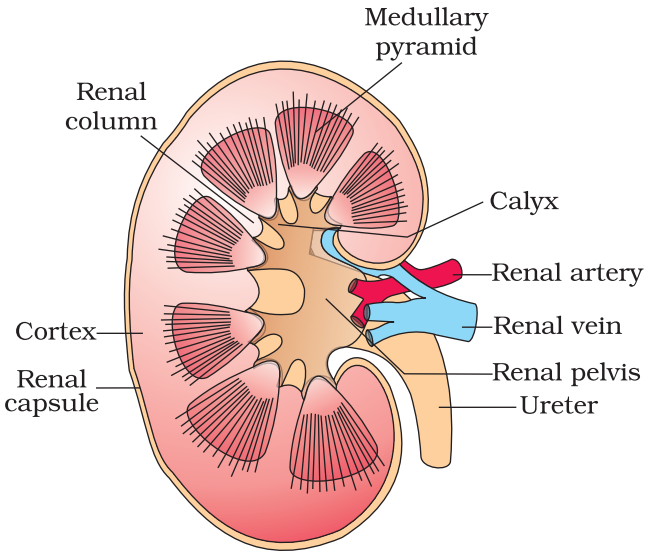


Figure 19.2 Longitudinal section (Diagrammatic) of Kidney

medullary pyramids as renal columns called **Columns of Bertini** (Figure 19.2).

Each kidney has nearly one million complex tubular structures called **nephrons** (Figure 19.3), which are the functional units. Each nephron has two parts – the glomerulus and the renal tubule. Glomerulus is a tuft of capillaries formed by the afferent arteriole – a fine branch of renal artery. Blood from the glomerulus is carried away by an efferent arteriole.

The renal tubule begins with a double walled cup-like structure called **Bowman's capsule**, which encloses the glomerulus. Glomerulus alongwith Bowman's capsule, is called the malpighian body or renal corpuscle (Figure 19.4). The tubule continues further to form a highly coiled network – **proximal convoluted tubule**

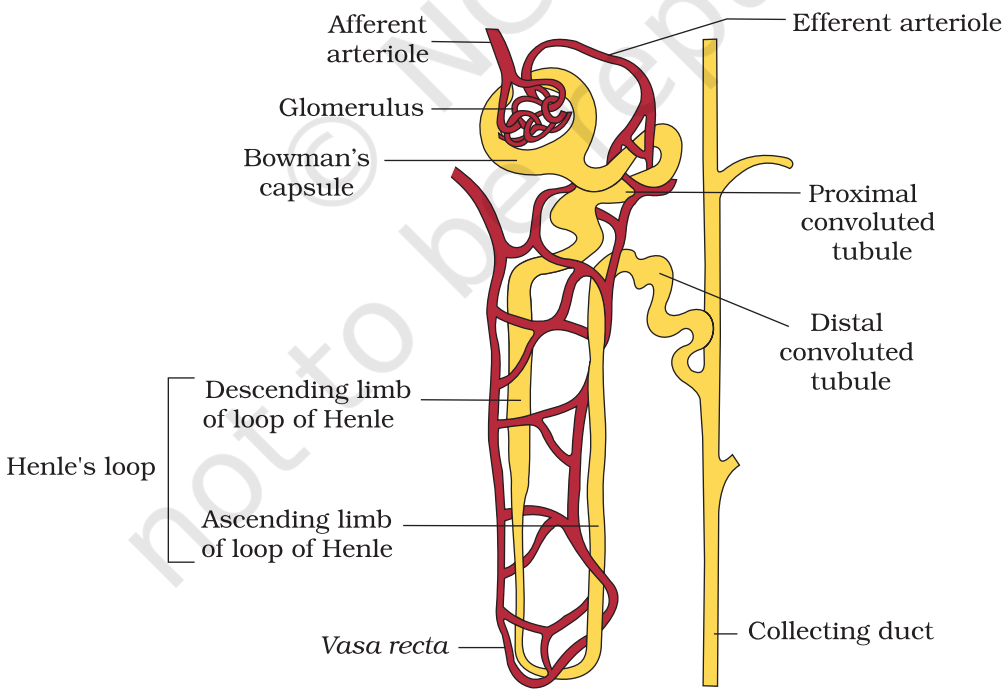


Figure 19.3 A diagrammatic representation of a nephron showing blood vessels, duct and tubule

(PCT). A hairpin shaped **Henle's loop** is the next part of the tubule which has a descending and an ascending limb. The ascending limb continues as another highly coiled tubular region called **distal convoluted tubule** (DCT). The DCTs of many nephrons open into a straight tube called *collecting duct*, many of which converge and open into the renal pelvis through medullary pyramids in the calyces.

The Malpighian corpuscle, PCT and DCT of the nephron are situated in the cortical region of the kidney whereas the loop of Henle dips into the medulla. In majority of nephrons, the loop of Henle is too short and extends only very little into the medulla. Such nephrons are called cortical nephrons. In some of the nephrons, the loop of Henle is very long and runs deep into the medulla. These nephrons are called juxta medullary nephrons.

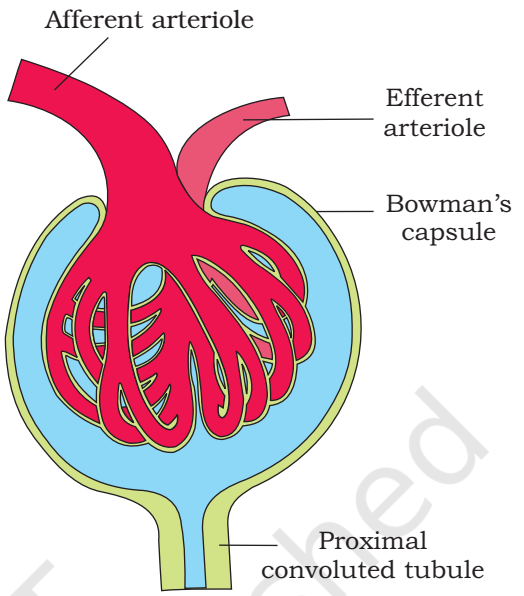


Figure 19.4 Malpighian body (renal corpuscle)

The efferent arteriole emerging from the glomerulus forms a fine capillary network around the renal tubule called the peritubular capillaries. A minute vessel of this network runs parallel to the Henle's loop forming a 'U' shaped *vasa recta*. *Vasa recta* is absent or highly reduced in cortical nephrons.

19.2 URINE FORMATION

Urine formation involves three main processes namely, glomerular filtration, reabsorption and secretion, that takes place in different parts of the nephron.

The first step in urine formation is the filtration of blood, which is carried out by the glomerulus and is called **glomerular filtration**. On an average, 1100-1200 ml of blood is filtered by the kidneys per minute which constitute roughly 1/5th of the blood pumped out by each ventricle of the heart in a minute. The glomerular capillary blood pressure causes filtration of blood through 3 layers, i.e., the endothelium of glomerular blood vessels, the epithelium of Bowman's capsule and a basement membrane between these two layers. The epithelial cells of Bowman's capsule called podocytes are arranged in an intricate manner so as to leave some minute spaces called filtration slits or slit pores. Blood is filtered so finely through these membranes, that almost all the constituents of the plasma except the proteins pass onto the lumen of the Bowman's capsule. Therefore, it is considered as a process of **ultra filtration.**

The amount of the filtrate formed by the kidneys per minute is called **glomerular filtration rate** (GFR). GFR in a healthy individual is approximately 125 ml/minute, i.e., 180 litres per day !

The kidneys have built-in mechanisms for the regulation of glomerular filtration rate. One such efficient mechanism is carried out by juxta glomerular apparatus (JGA). JGA is a special sensitive region formed by cellular modifications in the distal convoluted tubule and the afferent arteriole at the location of their contact. A fall in GFR can activate the JG cells to release renin which can stimulate the glomerular blood flow and thereby the GFR back to normal.

A comparison of the volume of the filtrate formed per day (180 litres per day) with that of the urine released (1.5 litres), suggest that nearly 99 per cent of the filtrate has to be reabsorbed by the renal tubules. This process is called **reabsorption**. The tubular epithelial cells in different segments of nephron perform this either by active or passive mechanisms. For example, substances like glucose, amino acids, Na^+, etc., in the filtrate are reabsorbed actively whereas the nitrogenous wastes are absorbed by passive transport. Reabsorption of water also occurs passively in the initial segments of the nephron (Figure 19.5).

During urine formation, the tubular cells secrete substances like H^+, K^+ and ammonia into the filtrate. Tubular secretion is also an important step in urine formation as it helps in the maintenance of ionic and acid base balance of body fluids.

19.3 Function of the Tubules

Proximal Convoluted Tubule (PCT): PCT is lined by simple cuboidal brush border epithelium which increases the surface area for reabsorption. Nearly all of the essential nutrients, and 70-80 per cent of electrolytes and water are reabsorbed by this segment. PCT also helps to maintain the pH and ionic balance of the body fluids by selective secretion of hydrogen ions, ammonia and potassium ions into the filtrate and by absorption of HCO_3^- from it.

Henle's Loop: Reabsorption is minimum in its ascending limb. However, this region plays a significant role in the maintenance of high osmolarity of medullary interstitial fluid. The descending limb of loop of Henle is permeable to water but almost impermeable to electrolytes. This concentrates the filtrate as it moves down. The ascending limb is impermeable to water but allows transport of electrolytes actively or passively. Therefore, as the concentrated filtrate pass upward, it gets diluted due to the passage of electrolytes to the medullary fluid.

Distal Convoluted Tubule (DCT): Conditional reabsorption of Na^+ and water takes place in this segment. DCT is also capable of reabsorption of HCO_3^- and selective secretion of hydrogen and potassium ions and NH_3 to maintain the pH and sodium-potassium balance in blood.

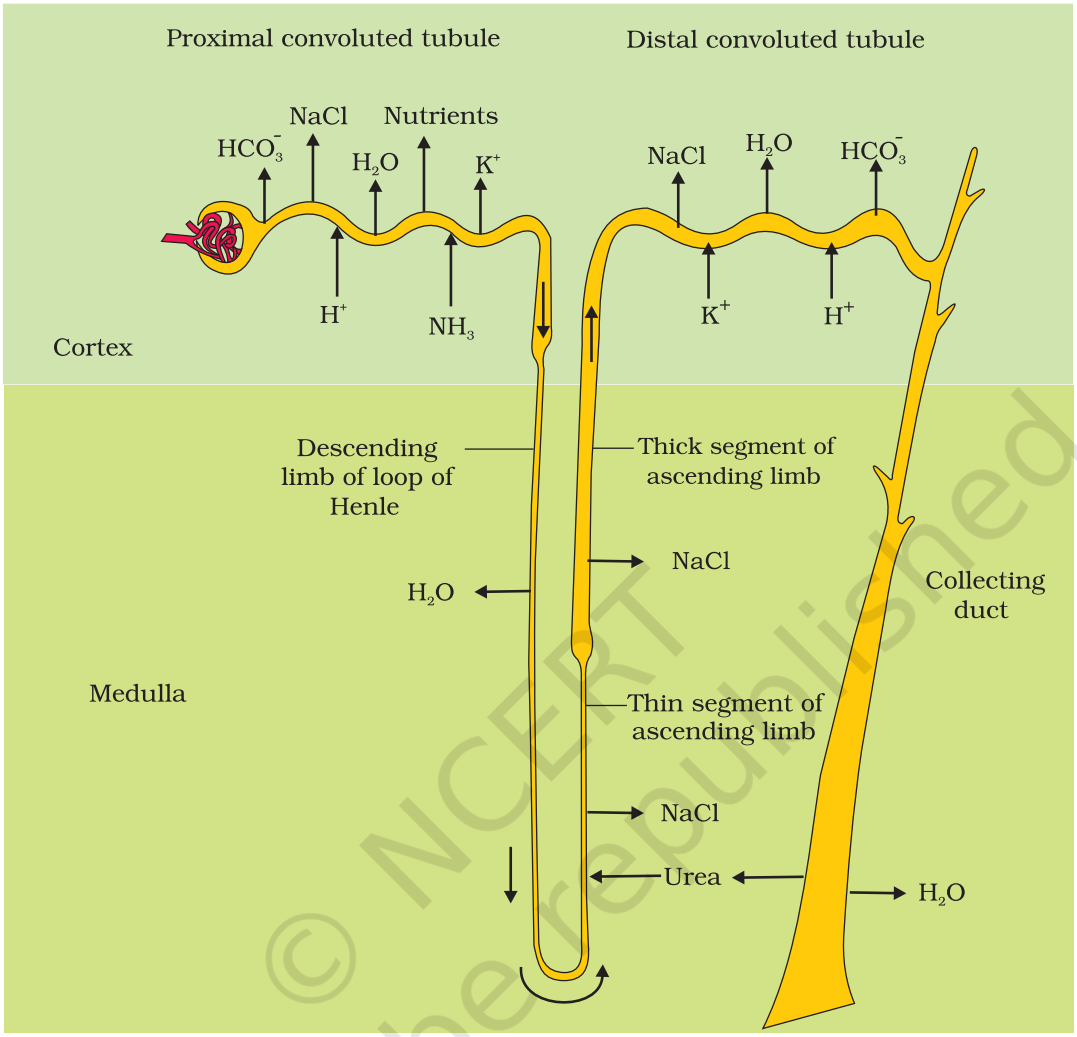


Figure 19.5 Reabsorption and secretion of major substances at different parts of the nephron (Arrows indicate direction of movement of materials.)

Collecting Duct: This long duct extends from the cortex of the kidney to the inner parts of the medulla. Large amounts of water could be reabsorbed from this region to produce a concentrated urine. This segment allows passage of small amounts of urea into the medullary interstitium to keep up the osmolarity. It also plays a role in the maintenance of pH and ionic balance of blood by the selective secretion of H^+ and K^+ ions (Figure 19.5).

19.4 MECHANISM OF CONCENTRATION OF THE FILTRATE

Mammals have the ability to produce a concentrated urine. The Henle's loop and *vasa recta* play a significant role in this. The flow of filtrate in the two limbs of Henle's loop is in opposite directions and thus forms a counter current. The flow of blood through the two limbs of *vasa recta* is

also in a counter current pattern. The proximity between the Henle's loop and *vasa recta*, as well as the counter current in them help in maintaining an increasing osmolarity towards the inner medullary interstitium, i.e., from 300 mOsmolL^{-1} in the cortex to about 1200 mOsmolL^{-1} in the inner medulla. This gradient is mainly caused by NaCl and urea. NaCl is transported by the ascending limb of Henle's loop which is exchanged with the descending limb of *vasa recta*. NaCl is returned to the interstitium by the ascending portion of *vasa recta*. Similarly, small amounts of urea enter the thin segment of the ascending limb of Henle's loop which is transported back to the interstitium by the collecting tubule. The above described transport of substances facilitated by the special arrangement of Henle's loop and *vasa recta* is called the **counter current mechanism** (Figure. 19.6). This mechanism helps to maintain a concentration gradient

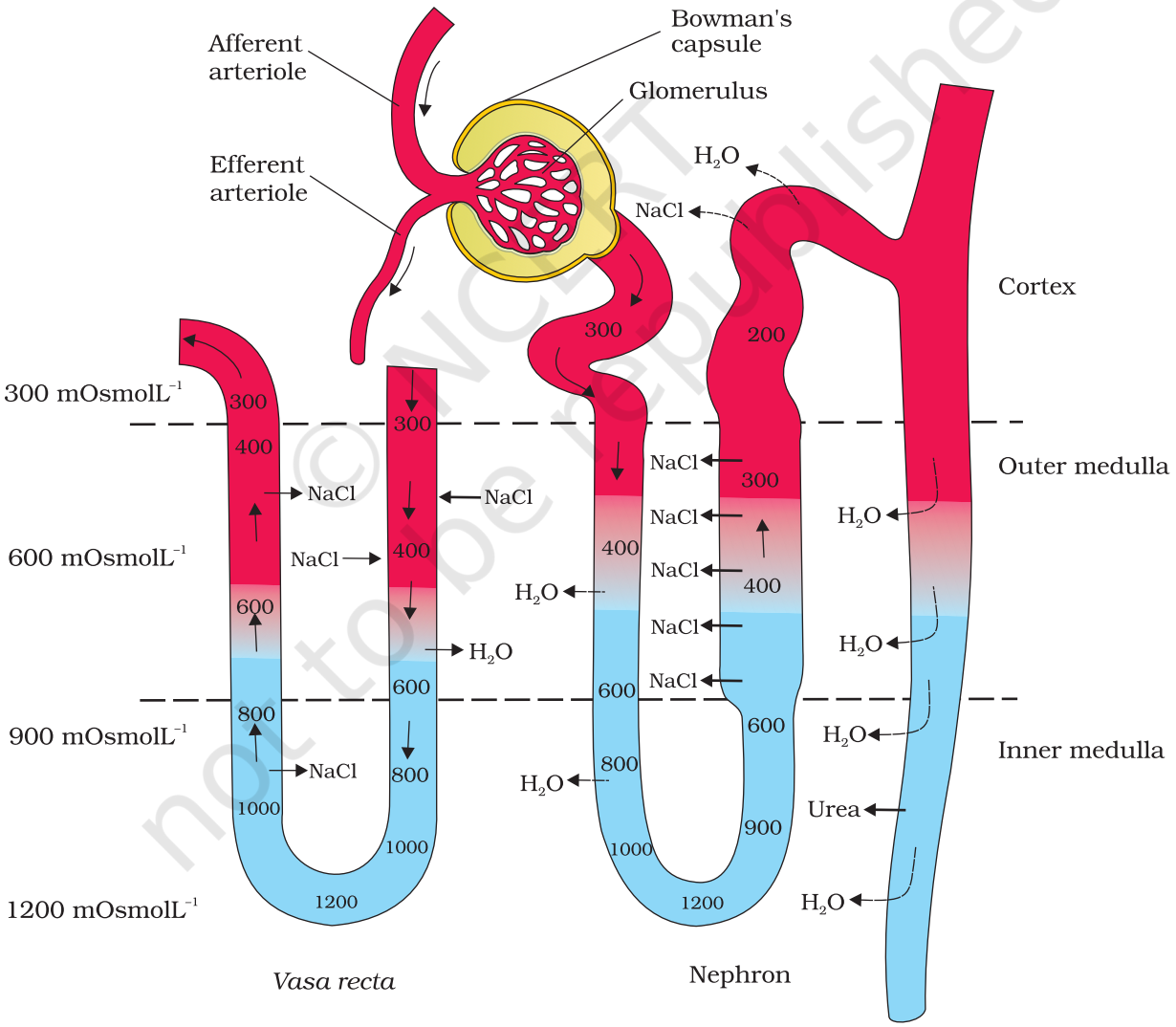


Figure 19.6 Diagrammatic representation of a nephron and *vasa recta* showing counter current mechanisms

in the medullary interstitium. Presence of such interstitial gradient helps in an easy passage of water from the collecting tubule thereby concentrating the filtrate (urine). Human kidneys can produce urine nearly four times concentrated than the initial filtrate formed.

19.5 REGULATION OF KIDNEY FUNCTION

The functioning of the kidneys is efficiently monitored and regulated by hormonal feedback mechanisms involving the hypothalamus, JGA and to a certain extent, the heart.

Osmoreceptors in the body are activated by changes in blood volume, body fluid volume and ionic concentration. An excessive loss of fluid from the body can activate these receptors which stimulate the hypothalamus to release antidiuretic hormone (ADH) or vasopressin from the neurohypophysis. ADH facilitates water reabsorption from latter parts of the tubule, thereby preventing diuresis. An increase in body fluid volume can switch off the osmoreceptors and suppress the ADH release to complete the feedback. ADH can also affect the kidney function by its constrictory effects on blood vessels. This causes an increase in blood pressure. An increase in blood pressure can increase the glomerular blood flow and thereby the GFR.

The JGA plays a complex regulatory role. A fall in glomerular blood flow/glomerular blood pressure/GFR can activate the JG cells to release **renin** which converts angiotensinogen in blood to angiotensin I and further to angiotensin II. Angiotensin II, being a powerful vasoconstrictor, increases the glomerular blood pressure and thereby GFR. Angiotensin II also activates the adrenal cortex to release Aldosterone. Aldosterone causes reabsorption of Na^+ and water from the distal parts of the tubule. This also leads to an increase in blood pressure and GFR. This complex mechanism is generally known as the **Renin-Angiotensin** mechanism.

An increase in blood flow to the atria of the heart can cause the release of **Atrial Natriuretic Factor** (ANF). ANF can cause vasodilation (dilation of blood vessels) and thereby decrease the blood pressure. ANF mechanism, therefore, acts as a check on the renin-angiotensin mechanism.

19.6 MICTURITION

Urine formed by the nephrons is ultimately carried to the urinary bladder where it is stored till a voluntary signal is given by the central nervous system (CNS). This signal is initiated by the stretching of the urinary bladder as it gets filled with urine. In response, the stretch receptors on the walls of the bladder send signals to the CNS. The CNS passes on motor messages

to initiate the contraction of smooth muscles of the bladder and simultaneous relaxation of the urethral sphincter causing the release of urine. The process of release of urine is called micturition and the neural mechanisms causing it is called the micturition reflex. An adult human excretes, on an average, 1 to 1.5 litres of urine per day. The urine formed is a light yellow coloured watery fluid which is slightly acidic (pH-6.0) and has a characterestic odour. On an average, 25-30 gm of urea is excreted out per day. Various conditions can affect the characteristics of urine. Analysis of urine helps in clinical diagnosis of many metabolic discorders as well as malfunctioning of the kidney. For example, presence of glucose (Glycosuria) and ketone bodies (Ketonuria) in urine are indicative of diabetes mellitus.

19.7 Role of other Organs in Excretion

Other than the kidneys, lungs, liver and skin also help in the elimination of excretory wastes.

Our lungs remove large amounts of CO_2 (approximately 200mL/ minute) and also significant quantities of water every day. Liver, the largest gland in our body, secretes bile-containing substances like bilirubin, biliverdin, cholesterol, degraded steroid hormones, vitamins and drugs. Most of these substances ultimately pass out alongwith digestive wastes.

The sweat and sebaceous glands in the skin can eliminate certain substances through their secretions. Sweat produced by the sweat glands is a watery fluid containing NaCl, small amounts of urea, lactic acid, etc. Though the primary function of sweat is to facilitate a cooling effect on the body surface, it also helps in the removal of some of the wastes mentioned above. Sebaceous glands eliminate certain substances like sterols, hydrocarbons and waxes through sebum. This secretion provides a protective oily covering for the skin. Do you know that small amounts of nitrogenous wastes could be eliminated through saliva too?

19.8 Disorders of the Excretory System

Malfunctioning of kidneys can lead to accumulation of urea in blood, a condition called **uremia**, which is highly harmful and may lead to kidney failure. In such patients, urea can be removed by a process called **hemodialysis**. During the process of haemodialysis, the blood drained from a convenient artery is pumped into a dialysing unit called **artificial kidney**. Blood drained from a convenient artery is pumped into a dialysing unit after adding an anticoagulant like heparin. The unit contains a coiled cellophane tube surrounded by a fluid (dialysing fluid) having the same

composition as that of plasma except the nitrogenous wastes. The porous cellophane membrance of the tube allows the passage of molecules based on concentration gradient. As nitrogenous wastes are absent in the dialysing fluid, these substances freely move out, thereby clearing the blood. The cleared blood is pumped back to the body through a vein after adding anti-heparin to it. This method is a boon for thousands of uremic patients all over the world.

Kidney transplantation is the ultimate method in the correction of acute **renal failures** (kidney failure). A functioning kidney is used in transplantation from a donor, preferably a close relative, to minimise its chances of rejection by the immune system of the host. Modern clinical procedures have increased the success rate of such a complicated technique.

Renal calculi: Stone or insoluble mass of crystallised salts (oxalates, etc.) formed within the kidney.

Glomerulonephritis: Inflammation of glomeruli of kidney.

SUMMARY

Many nitrogen containing substances, ions, CO_2, water, etc., that accumulate in the body have to be eliminated. Nature of nitrogenous wastes formed and their excretion vary among animals, mainly depending on the habitat (availability of water). Ammonia, urea and uric acid are the major nitrogenous wastes excreted.

Protonephridia, nephridia, malpighian tubules, green glands and the kidneys are the common excretory organs in animals. They not only eliminate nitrogenous wastes but also help in the maintenance of ionic and acid-base balance of body fluids.

In humans, the excretory system consists of one pair of kidneys, a pair of ureters, a urinary bladder and a urethra. Each kidney has over a million tubular structures called nephrons. Nephron is the functional unit of kidney and has two portions – glomerulus and renal tubule. Glomerulus is a tuft of capillaries formed from afferent arterioles, fine branches of renal artery. The renal tubule starts with a double walled Bowman's capsule and is further differentiated into a proximal convoluted tubule (PCT), Henle's loop (HL) and distal convoluted tubule (DCT). The DCTs of many nephrons join to a common collecting duct many of which ultimately open into the renal pelvis through the medullary pyramids. The Bowman's capsule encloses the glomerulus to form Malpighian or renal corpuscle.

Urine formation involves three main processes, i.e., filtration, reabsorption and secretion. Filtration is a non-selective process performed by the glomerulus using the glomerular capillary blood pressure. About 1200 ml of blood is filtered by the glomerulus per minute to form 125 ml of filtrate in the Bowman's capsule per

minute (GFR). JGA, a specialised portion of the nephrons, plays a significant role in the regulation of GFR. Nearly 99 per cent reabsorption of the filtrate takes place through different parts of the nephrons. PCT is the major site of reabsorption and selective secretion. HL primarily helps to maintain osmolar gradient (300 $mOsmolL^{-1}$ -1200 $mOsmolL^{-1}$) within the kidney interstitium. DCT and collecting duct allow extensive reabsorption of water and certain electrolytes, which help in osmoregulation: H^+, K^+ and NH_3 could be secreted into the filtrate by the tubules to maintain the ionic balance and pH of body fluids.

A counter current mechanism operates between the two limbs of the loop of Henle and those of *vasa recta* (capillary parallel to Henle's loop). The filtrate gets concentrated as it moves down the descending limb but is diluted by the ascending limb. Electrolytes and urea are retained in the interstitium by this arrangement. DCT and collecting duct concentrate the filtrate about four times, i.e., from 300 $mOsmolL^{-1}$ to 1200 $mOsmolL^{-1}$, an excellent mechanism of conservation of water. Urine is stored in the urinary bladder till a voluntary signal from CNS carries out its release through urethra, i.e., micturition. Skin, lungs and liver also assist in excretion.

EXERCISES

1. Define Glomerular Filtration Rate (GFR)
2. Explain the autoregulatory mechanism of GFR.
3. Indicate whether the following statements are true or false :
   (a) Micturition is carried out by a reflex.
   (b) ADH helps in water elimination, making the urine hypotonic.
   (c) Protein-free fluid is filtered from blood plasma into the Bowman's capsule.
   (d) Henle's loop plays an important role in concentrating the urine.
   (e) Glucose is actively reabsorbed in the proximal convoluted tubule.
4. Give a brief account of the counter current mechanism.
5. Describe the role of liver, lungs and skin in excretion.
6. Explain micturition.
7. Match the items of column I with those of column II :

Column I	**Column II**
(a) Ammonotelism	(i) Birds
(b) Bowman's capsule	(ii) Water reabsorption
(c) Micturition	(iii) Bony fish
(d) Uricotelism	(iv) Urinary bladder
(d) ADH	(v) Renal tubule

8. What is meant by the term osmoregulation?
9. Terrestrial animals are generally either ureotelic or uricotelic, not ammonotelic, why ?
10. What is the significance of juxta glomerular apparatus (JGA) in kidney function?
11. Name the following:
    (a) A chordate animal having flame cells as excretory structures
    (b) Cortical portions projecting between the medullary pyramids in the human kidney
    (c) A loop of capillary running parallel to the Henle's loop.
12. Fill in the gaps :
    (a) Ascending limb of Henle's loop is _____ to water whereas the descending limb is _____ to it.
    (b) Reabsorption of water from distal parts of the tubules is facilitated by hormone _____.
    (c) Dialysis fluid contain all the constituents as in plasma except _____.
    (d) A healthy adult human excretes (on an average) _____ gm of urea/day.

Chapter 20

Locomotion and Movement

Movement is one of the significant features of living beings. Animals and plants exhibit a wide range of movements. Streaming of protoplasm in the unicellular organisms like *Amoeba* is a simple form of movement. Movement of cilia, flagella and tentacles are shown by many organisms. Human beings can move limbs, jaws, eyelids, tongue, etc. Some of the movements result in a change of place or location. Such voluntary movements are called **locomotion**. Walking, running, climbing, flying, swimming are all some forms of locomotory movements. Locomotory structures need not be different from those affecting other types of movements. For example, in *Paramoecium*, cilia helps in the movement of food through cytopharynx and in locomotion as well. *Hydra* can use its tentacles for capturing its prey and also use them for locomotion. We use limbs for changes in body postures and locomotion as well. The above observations suggest that movements and locomotion cannot be studied separately. The two may be linked by stating that all locomotions are movements but all movements are not locomotions.

Methods of locomotion performed by animals vary with their habitats and the demand of the situation. However, locomotion is generally for search of food, shelter, mate, suitable breeding grounds, favourable climatic conditions or to escape from enemies/predators.

20.1 Types of Movement

Cells of the human body exhibit three main types of movements, namely, amoeboid, ciliary and muscular.

Some specialised cells in our body like macrophages and leucocytes in blood exhibit amoeboid movement. It is effected by pseudopodia formed by the streaming of protoplasm (as in *Amoeba*). Cytoskeletal elements like microfilaments are also involved in amoeboid movement.

Ciliary movement occurs in most of our internal tubular organs which are lined by ciliated epithelium. The coordinated movements of cilia in the trachea help us in removing dust particles and some of the foreign substances inhaled alongwith the atmospheric air. Passage of ova through the female reproductive tract is also facilitated by the ciliary movement.

Movement of our limbs, jaws, tongue, etc, require muscular movement. The contractile property of muscles are effectively used for locomotion and other movements by human beings and majority of multicellular organisms. Locomotion requires a perfect coordinated activity of muscular, skeletal and neural systems. In this chapter, you will learn about the types of muscles, their structure, mechanism of their contraction and important aspects of the skeletal system.

20.2 MUSCLE

You have studied in Chapter 8 that the cilia and flagella are the outgrowths of the cell membrane. **Flagellar movement** helps in the swimming of spermatozoa, maintenance of water current in the canal system of sponges and in locomotion of Protozoans like *Euglena.* Muscle is a specialised tissue of mesodermal origin. About 40-50 per cent of the body weight of a human adult is contributed by muscles. They have special properties like excitability, contractility, extensibility and elasticity. Muscles have been classified using different criteria, namely location, appearance and nature of regulation of their activities. Based on their location, three types of muscles are identified : (i) Skeletal (ii) Visceral and (iii) Cardiac.

Skeletal muscles are closely associated with the skeletal components of the body. They have a striped appearance under the microscope and hence are called **striated muscles**. As their activities are under the voluntary control of the nervous system, they are known as voluntary muscles too. They are primarily involved in locomotory actions and changes of body postures.

Visceral muscles are located in the inner walls of hollow visceral organs of the body like the alimentary canal, reproductive tract, etc. They do not exhibit any striation and are smooth in appearance. Hence, they are called **smooth muscles (nonstriated muscle)**. Their activities are not under the voluntary control of the nervous system and are therefore known as involuntary muscles. They assist, for example, in the transportation of food through the digestive tract and gametes through the genital tract.

As the name suggests, **Cardiac muscles** are the muscles of heart. Many cardiac muscle cells assemble in a branching pattern to form a cardiac muscle. Based on appearance, cardiac muscles are striated. They are involuntary in nature as the nervous system does not control their activities directly.

Let us examine a skeletal muscle in detail to understand the structure and mechanism of contraction. Each organised skeletal muscle in our body is made of a number of **muscle bundles** or **fascicles** held together by a common collagenous connective tissue layer called **fascia**. Each muscle bundle contains a number of muscle fibres (Figure 20.1). Each

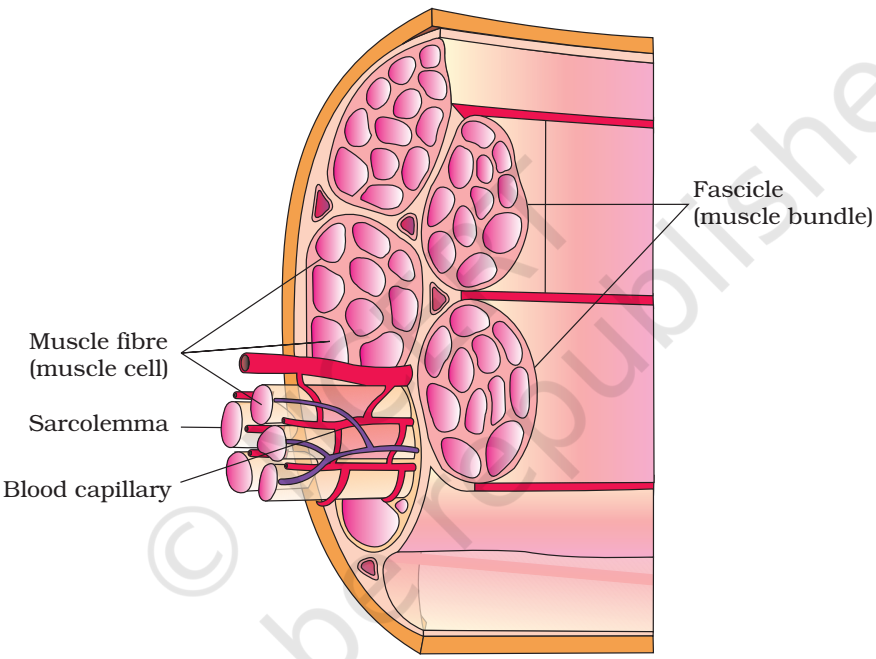


Figure 20.1 Diagrammatic cross sectional view of a muscle showing muscle bundles and muscle fibres

muscle fibre is lined by the plasma membrane called sarcolemma enclosing the sarcoplasm. Muscle fibre is a syncitium as the sarcoplasm contains many nuclei. The endoplasmic reticulum, i.e., sarcoplasmic reticulum of the muscle fibres is the store house of calcium ions. A characteristic feature of the muscle fibre is the presence of a large number of parallelly arranged filaments in the sarcoplasm called myofilaments or **myofibrils**. Each myofibril has alternate dark and light bands on it. A detailed study of the myofibril has established that the striated appearance is due to the distribution pattern of two important proteins – **Actin** and **Myosin**. The light bands contain actin and is called I-band or Isotropic band, whereas the dark band called 'A' or Anisotropic band contains

myosin. Both the proteins are arranged as rod-like structures, parallel to each other and also to the longitudinal axis of the myofibrils. Actin filaments are thinner as compared to the myosin filaments, hence are commonly called thin and thick filaments respectively. In the centre of each 'I' band is an elastic fibre called 'Z' line which bisects it. The thin filaments are firmly attached to the 'Z' line. The thick filaments in the 'A' band are also held together in the middle of this band by a thin fibrous membrane called 'M' line. The 'A' and 'I' bands are arranged alternately throughout the length of the myofibrils. The portion of the myofibril between two successive 'Z' lines is considered as the functional unit of contraction and is called a sarcomere (Figure 20.2). In a resting state, the edges of thin filaments on either side of the thick filaments partially overlap the free ends of the thick filaments leaving the central part of the thick filaments. This central part of thick filament, not overlapped by thin filaments is called the 'H' zone.

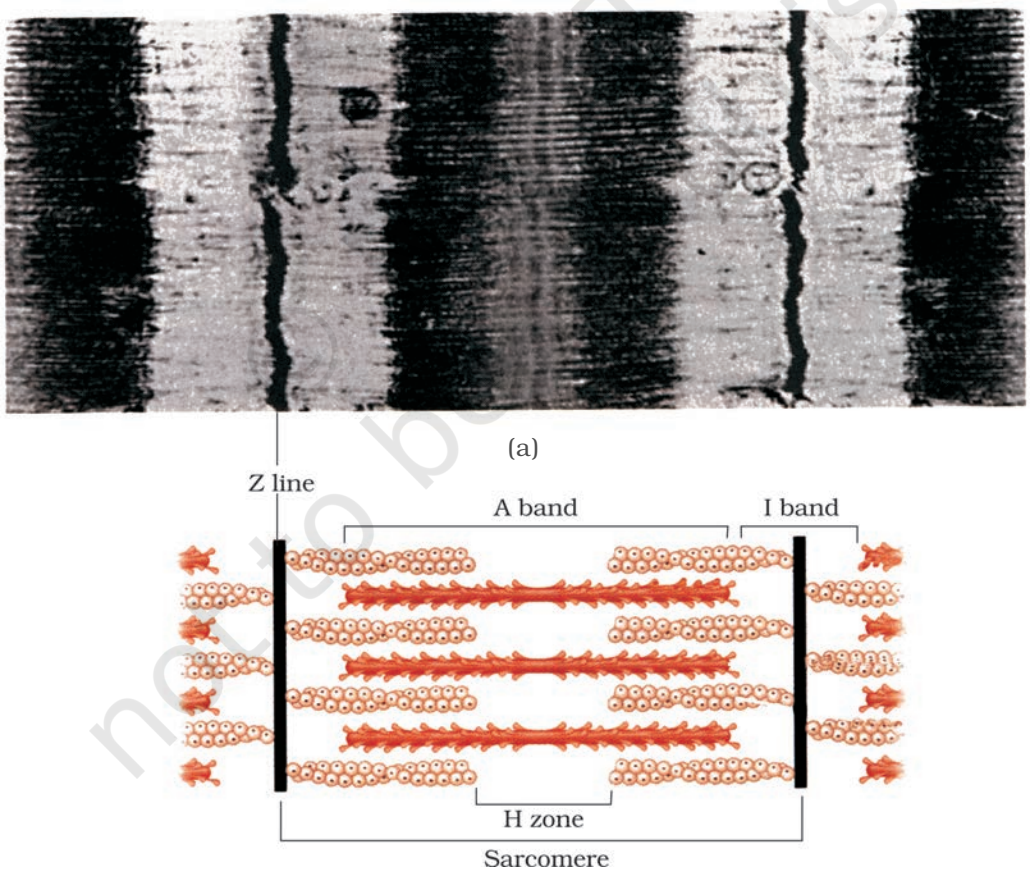


Figure 20.2 Diagrammatic representation of (a) anatomy of a muscle fibre showing a sarcomere (b) a sarcomere

20.2.1 Structure of Contractile Proteins

Each actin (thin) filament is made of two 'F' (filamentous) actins helically wound to each other. Each 'F' actin is a polymer of monomeric 'G' (Globular) actins. Two filaments of another protein, tropomyosin also run close to the 'F' actins throughout its length. A complex protein Troponin is distributed at regular intervals on the tropomyosin. In the resting state a subunit of troponin masks the active binding sites for myosin on the actin filaments (Figure 20.3a).

Each myosin (thick) filament is also a polymerised protein. Many monomeric proteins called Meromyosins (Figure 20.3b) constitute one thick filament. Each meromyosin has two important parts, a globular head with a short arm and a tail, the former being called the heavy meromyosin (HMM) and the latter, the light meromyosin (LMM). The HMM component, i.e.; the head and short arm projects outwards at regular distance and angle from each other from the surface of a polymerised myosin filament and is known as cross arm. The globular head is an active ATPase enzyme and has binding sites for ATP and active sites for actin.

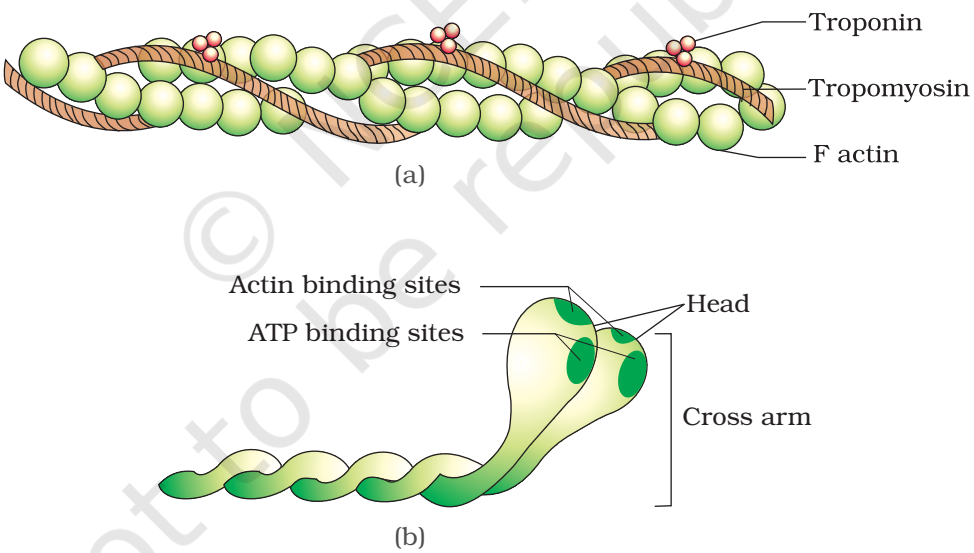


Figure 20.3 (a) An actin (thin) filament (b) Myosin monomer (Meromyosin)

20.2.2 Mechanism of Muscle Contraction

Mechanism of muscle contraction is best explained by the sliding filament theory which states that contraction of a muscle fibre takes place by the sliding of the thin filaments over the thick filaments.

Muscle contraction is initiated by a signal sent by the central nervous system (CNS) via a motor neuron. A motor neuron alongwith the muscle fibres connected to it constitute a motor unit. The junction between a motor neuron and the sarcolemma of the muscle fibre is called the neuromuscular junction or motor-end plate. A neural signal reaching this junction releases a neurotransmitter (Acetyl choline) which generates an action potential in the sarcolemma. This spreads through the muscle fibre and causes the release of calcium ions into the sarcoplasm. Increase in Ca^{++} level leads to the binding of calcium with a subunit of troponin on actin filaments and thereby remove the masking of active sites for myosin. Utilising the energy from ATP hydrolysis, the myosin head now binds to the exposed active sites on actin to form a cross bridge (Figure 20.4). This

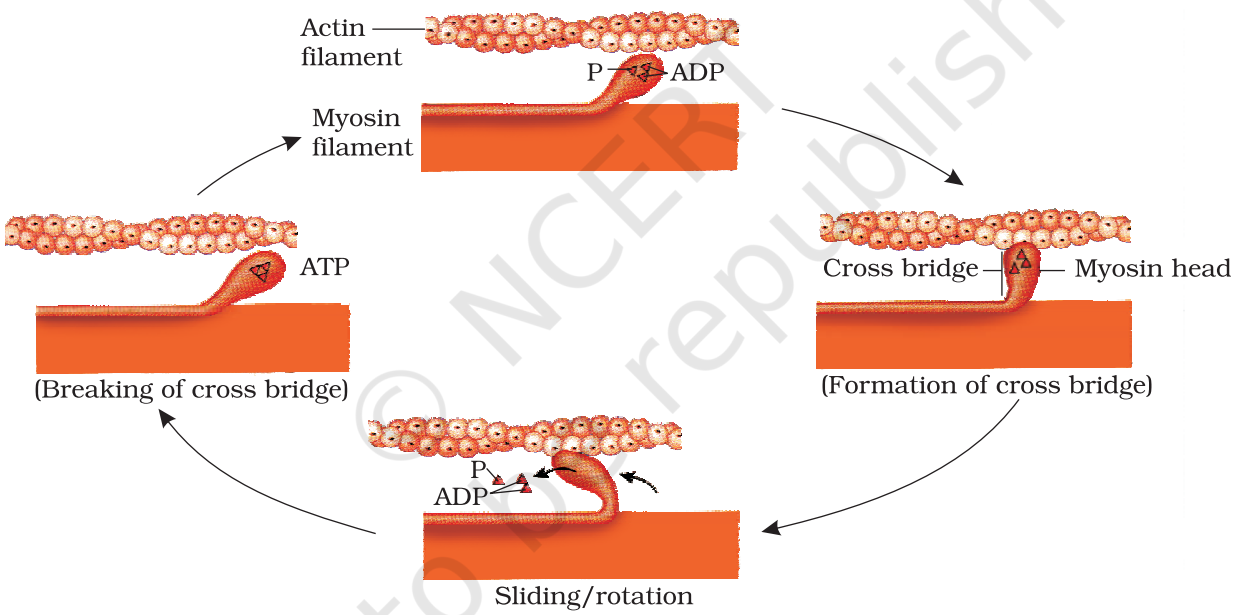


Figure 20.4 Stages in cross bridge formation, rotation of head and breaking of cross bridge

pulls the attached actin filaments towards the centre of 'A' band. The 'Z' line attached to these actins are also pulled inwards thereby causing a shortening of the sarcomere, i.e., contraction. It is clear from the above steps, that during shortening of the muscle, i.e., contraction, the 'I' bands get reduced, whereas the 'A' bands retain the length (Figure 20.5). The myosin, releasing the ADP and P_i goes back to its relaxed state. A new ATP binds and the cross-bridge is broken (Figure 20.4). The ATP is again hydrolysed by the myosin head and the cycle of cross bridge formation

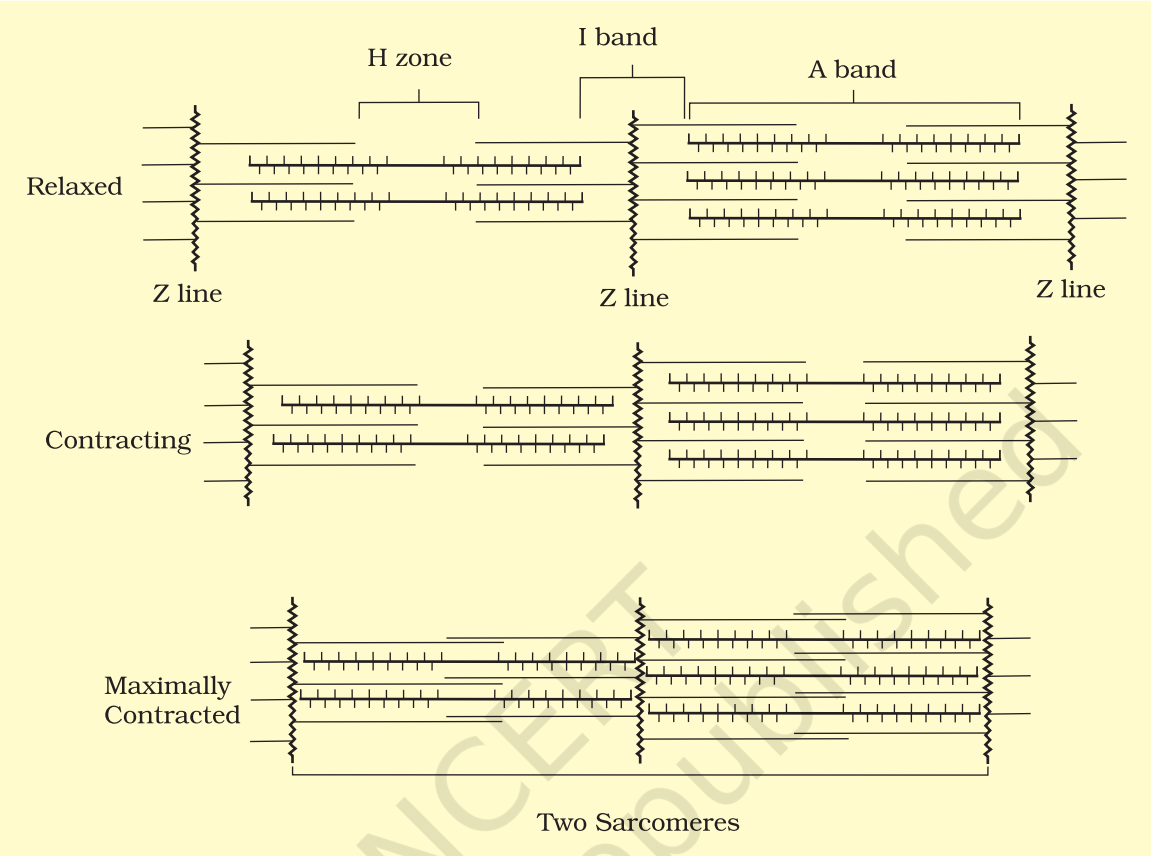


Figure 20.5 Sliding-filament theory of muscle contraction (movement of the thin filaments and the relative size of the I band and H zones)

and breakage is repeated causing further sliding. The process continues till the Ca^{++} ions are pumped back to the sarcoplasmic cisternae resulting in the masking of actin filaments. This causes the return of 'Z' lines back to their original position, i.e., relaxation. The reaction time of the fibres can vary in different muscles. Repeated activation of the muscles can lead to the accumulation of lactic acid due to anaerobic breakdown of glycogen in them, causing fatigue. Muscle contains a red coloured oxygen storing pigment called myoglobin. Myoglobin content is high in some of the muscles which gives a reddish appearance. Such muscles are called the Red fibres. These muscles also contain plenty of mitochondria which can utilise the large amount of oxygen stored in them for ATP production. These muscles, therefore, can also be called aerobic muscles. On the other hand, some of the muscles possess very less quantity of myoglobin and therefore, appear pale or whitish. These are the White fibres. Number of mitochondria are also few in them, but the amount of sarcoplasmic reticulum is high. They depend on anaerobic process for energy.

20.3 SKELETAL SYSTEM

Skeletal system consists of a framework of bones and a few cartilages. This system has a significant role in movement shown by the body. Imagine chewing food without jaw bones and walking around without the limb bones. Bone and cartilage are specialised connective tissues. The former has a very hard matrix due to calcium salts in it and the latter has slightly pliable matrix due to chondroitin salts. In human beings, this system is made up of 206 bones and a few cartilages. It is grouped into two principal divisions – the axial and the appendicular skeleton.

Axial skeleton comprises 80 bones distributed along the main axis of the body. The skull, vertebral column, sternum and ribs constitute axial skeleton. The **skull** (Figure 20.6) is composed of two sets of bones –

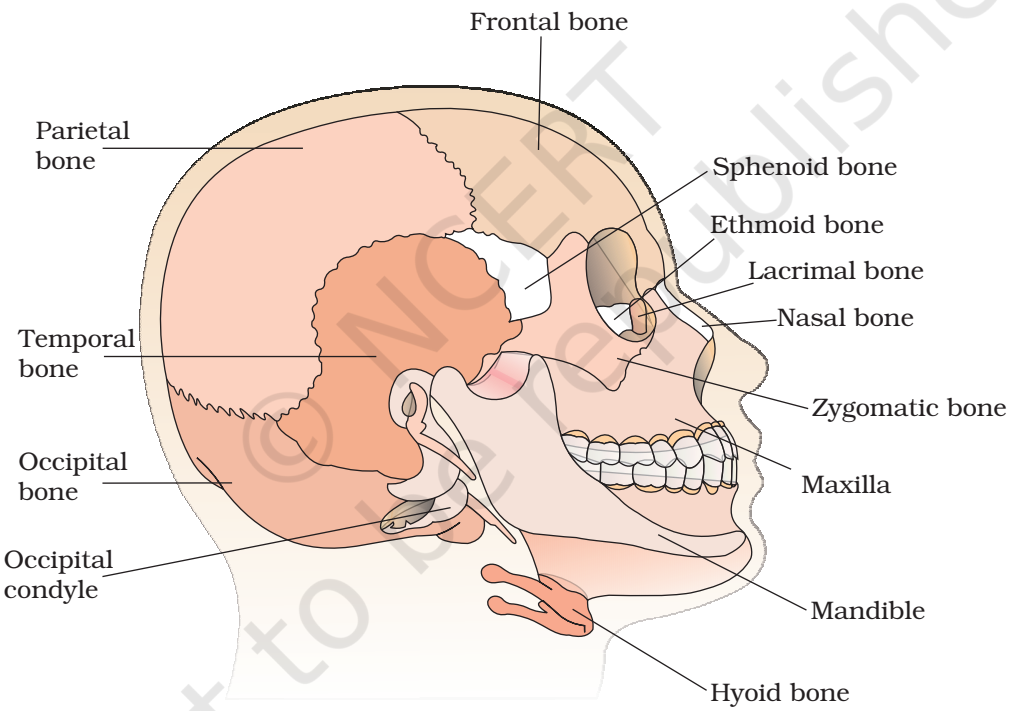


Figure 20.6 Diagrammatic view of human skull

cranial and facial, that totals to 22 bones. Cranial bones are 8 in number. They form the hard protective outer covering, cranium for the brain. The facial region is made up of 14 skeletal elements which form the front part of the skull. A single U-shaped bone called hyoid is present at the base of the buccal cavity and it is also included in the skull. Each middle ear contains three tiny bones – Malleus, Incus and Stapes, collectively called **Ear Ossicles**. The skull region articulates with the superior region of the

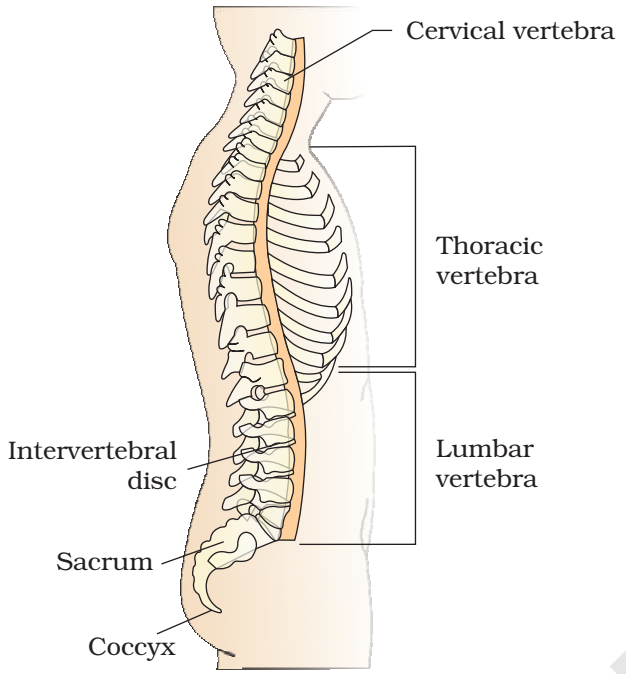


Figure 20.7 Vertebral column (right lateral view)

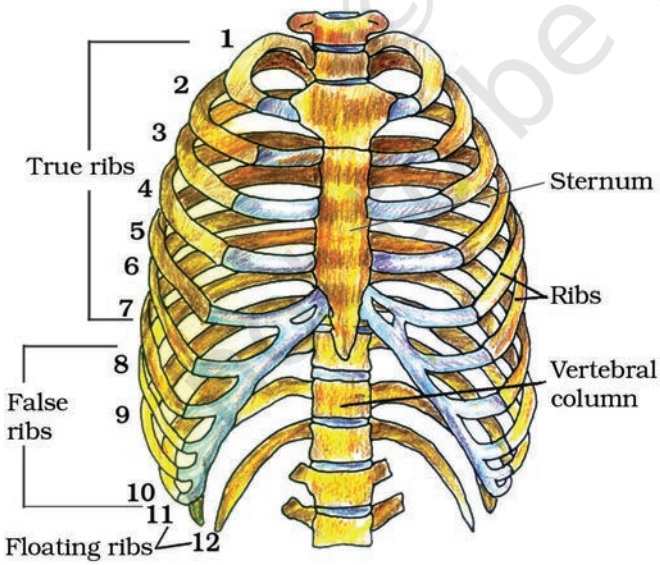


Figure 20.8 Ribs and rib cage

vertebral column with the help of two occipital condyles (dicondylic skull).

Our **vertebral column** (Figure 20.7) is formed by 26 serially arranged units called vertebrae and is dorsally placed. It extends from the base of the skull and constitutes the main framework of the trunk. Each vertebra has a central hollow portion (neural canal) through which the spinal cord passes. First vertebra is the atlas and it articulates with the occipital condyles. The vertebral column is differentiated into cervical (7), thoracic (12), lumbar (5), sacral (1-fused) and coccygeal (1-fused) regions starting from the skull. The number of cervical vertebrae are seven in almost all mammals including human beings. The vertebral column protects the spinal cord, supports the head and serves as the point of attachment for the ribs and musculature of the back. **Sternum** is a flat bone on the ventral midline of thorax.

There are 12 pairs of **ribs.** Each rib is a thin flat bone connected dorsally to the vertebral column and ventrally to the sternum. It has two articulation surfaces on its dorsal end and is hence called bicephalic. First seven pairs of ribs are called true ribs. Dorsally, they are attached to the thoracic vertebrae and ventrally connected to the sternum with the help of hyaline cartilage. The 8^{th}, 9^{th} and 10^{th} pairs of ribs do not articulate directly with the sternum but join the seventh rib with the help of hyaline cartilage. These are called vertebrochondral (false) ribs. Last 2 pairs (11^{th} and 12^{th}) of ribs are not connected ventrally and are therefore, called floating ribs. Thoracic vertebrae, ribs and sternum together form the rib cage (Figure 20.8).

The bones of the limbs alongwith their girdles constitute the **appendicular skeleton.** Each **limb** is made of 30 bones. The bones of the hand (fore limb) are humerus, radius and

ulna, carpals (wrist bones – 8 in number), metacarpals (palm bones – 5 in number) and phalanges (digits – 14 in number) (Figure 20.9). Femur (thigh bone – the longest bone), tibia and fibula, tarsals (ankle bones – 7 in number), metatarsals (5 in number) and phalanges (digits – 14 in number) are the bones of the legs (hind limb) (Figure 20.10). A cup shaped bone called patella cover the knee ventrally (knee cap).

Pectoral and **Pelvic girdle** bones help in the articulation of the upper and the lower limbs respectively with the axial skeleton. Each girdle is formed of two halves. Each half of pectoral girdle consists of a clavicle and a scapula (Figure 20.9). Scapula is a large triangular flat bone situated in the dorsal part of the thorax between the second and the seventh ribs. The dorsal, flat, triangular body of scapula has a slightly elevated ridge called the spine which projects as a flat, expanded process called the acromion. The clavicle articulates with this. Below the acromion is a depression called the glenoid cavity which articulates with the head of the humerus to form the shoulder joint. Each clavicle is a long slender bone with two curvatures. This bone is commonly called the collar bone.

Pelvic girdle consists of two coxal bones (Figure 20.10). Each coxal bone is formed by the fusion of three bones – ilium, ischium and pubis. At the point of fusion of the above bones is a cavity called acetabulum to which the thigh bone articulates. The two halves of the pelvic girdle meet ventrally to form the pubic symphysis containing fibrous cartilage.

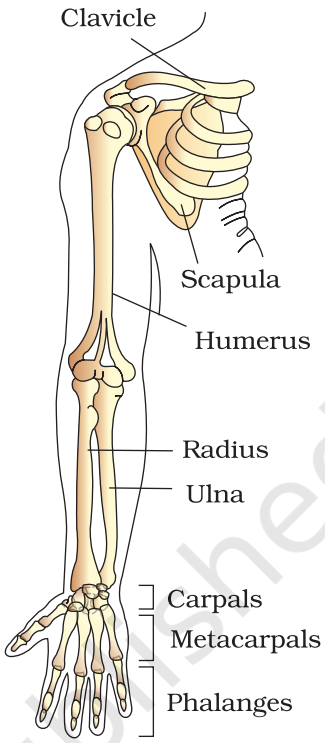


Figure 20.9 Right pectoral girdle and upper arm. (frontal view)

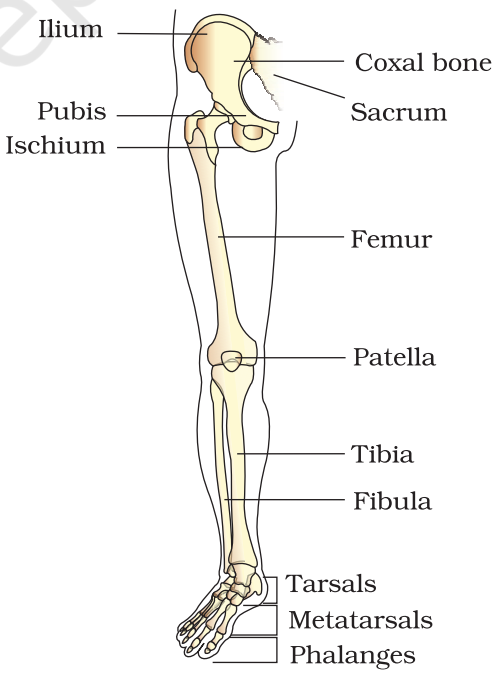


Figure 20.10 Right pelvic girdle and lower limb bones (frontal view)

20.4 JOINTS

Joints are essential for all types of movements involving the bony parts of the body. Locomotory movements are no exception to

this. Joints are points of contact between bones, or between bones and cartilages. Force generated by the muscles is used to carry out movement through joints, where the joint acts as a fulcrum. The movability at these joints vary depending on different factors. Joints have been classified into three major structural forms, namely, fibrous, cartilaginous and synovial.

Fibrous joints do not allow any movement. This type of joint is shown by the flat skull bones which fuse end-to-end with the help of dense fibrous connective tissues in the form of sutures, to form the cranium.

In **cartilaginous joints,** the bones involved are joined together with the help of cartilages. The joint between the adjacent vertebrae in the vertebral column is of this pattern and it permits limited movements.

Synovial joints are characterised by the presence of a fluid filled synovial cavity between the articulating surfaces of the two bones. Such an arragement allows considerable movement. These joints help in locomotion and many other movements. Ball and socket joint (between humerus and pectoral girdle), hinge joint (knee joint), pivot joint (between atlas and axis), gliding joint (between the carpals) and saddle joint (between carpal and metacarpal of thumb) are some examples.

20.5 Disorders of Muscular and Skeletal System

Myasthenia gravis: Auto immune disorder affecting neuromuscular junction leading to fatigue, weakening and paralysis of skeletal muscle.

Muscular dystrophy: Progressive degeneration of skeletal muscle mostly due to genetic disorder.

Tetany: Rapid spasms (wild contractions) in muscle due to low Ca^{++} in body fluid.

Arthritis: Inflammation of joints.

Osteoporosis: Age-related disorder characterised by decreased bone mass and increased chances of fractures. Decreased levels of estrogen is a common cause.

Gout: Inflammation of joints due to accumulation of uric acid crystals.

Summary

Movement is an essential feature of all living beings. Protoplasmic streaming, ciliary movements, movements of fins, limbs, wings, etc., are some forms exhibited by animals. A voluntary movement which causes the animal to change its place, is

called locomotion. Animals move generally in search of food, shelter, mate, breeding ground, better climate or to protect themselves.

The cells of the human body exhibit amoeboid, ciliary and muscular movements. Locomotion and many other movements require coordinated muscular activities. Three types of muscles are present in our body. Skeletal muscles are attached to skeletal elements. They appear striated and are voluntary in nature. Visceral muscles, present in the inner walls of visceral organs are nonstriated and involuntary. Cardiac muscles are the muscles of the heart. They are striated, branched and involuntary. Muscles possess excitability, contractility, extensibility and elasticity.

Muscle fibre is the anatomical unit of muscle. Each muscle fibre has many parallelly arranged myofibrils. Each myofibril contains many serially arranged units called sarcomere which are the functional units. Each sarcomere has a central 'A' band made of thick myosin filaments, and two half 'I' bands made of thin actin filaments on either side of it marked by 'Z' lines. Actin and myosin are polymerised proteins with contractility. The active sites for myosin on resting actin filament are masked by a protein-troponin. Myosin head contains ATPase and has ATP binding sites and active sites for actin. A motor neuron carries signal to the muscle fibre which generates an action potential in it. This causes the release of Ca^{++} from sarcoplasmic reticulum. Ca^{++} activates actin which binds to the myosin head to form a cross bridge. These cross bridges pull the actin filaments causing them to slide over the myosin filaments and thereby causing contraction. Ca^{++} are then returned to sarcoplasmic reticulum which inactivate the actin. Cross bridges are broken and the muscles relax.

Repeated stimulation of muscles leads to fatigue. Muscles are classified as Red and White fibres based primarily on the amount of red coloured myoglobin pigment in them.

Bones and cartilages constitute our skeletal system. The skeletal system is divisible into axial and appendicular. Skull, vertebral column, ribs and sternum constitute the axial skeleton. Limb bones and girdles form the appendicular skeleton. Three types of joints are formed between bones or between bone and cartilage – fibrous, cartilaginous and synovial. Synovial joints allow considerable movements and therefore, play a significant role in locomotion.

EXERCISES

1. Draw the diagram of a sarcomere of skeletal muscle showing different regions.
2. Define sliding filament theory of muscle contraction.
3. Describe the important steps in muscle contraction.

4. Write true or false. If false change the statement so that it is true.
   (a) Actin is present in thin filament
   (b) H-zone of striated muscle fibre represents both thick and thin filaments.
   (c) Human skeleton has 206 bones.
   (d) There are 11 pairs of ribs in man.
   (e) Sternum is present on the ventral side of the body.
5. Write the difference between :
   (a) Actin and Myosin
   (b) Red and White muscles
   (c) Pectoral and Pelvic girdle
6. Match Column I with Column II :

Column I	**Column II**
(a) Smooth muscle	(i) Myoglobin
(b) Tropomyosin	(ii) Thin filament
(c) Red muscle	(iii) Sutures
(d) Skull	(iv) Involuntary

7. What are the different types of movements exhibited by the cells of human body?
8. How do you distinguish between a skeletal muscle and a cardiac muscle?
9. Name the type of joint between the following:-
   (a) atlas/axis
   (b) carpal/metacarpal of thumb
   (c) between phalanges
   (d) femur/acetabulum
   (e) between cranial bones
   (f) between pubic bones in the pelvic girdle
10. Fill in the blank spaces:
    (a) All mammals (except a few) have _____ cervical vertebra.
    (b) The number of phalanges in each limb of human is _____
    (c) Thin filament of myofibril contains 2 'F' actins and two other proteins namely _____ and _____.
    (d) In a muscle fibre Ca^{++} is stored in _____
    (e) _____ and _____ pairs of ribs are called floating ribs.
    (f) The human cranium is made of _____ bones.

Chapter 21
Neural Control and Coordination

As you know, the functions of the organs/organ systems in our body must be coordinated to maintain homeostasis. **Coordination** is the process through which two or more organs interact and complement the functions of one another. For example, when we do physical exercises, the energy demand is increased for maintaining an increased muscular activity. The supply of oxygen is also increased. The increased supply of oxygen necessitates an increase in the rate of respiration, heart beat and increased blood flow via blood vessels. When physical exercise is stopped, the activities of nerves, lungs, heart and kidney gradually return to their normal conditions. Thus, the functions of muscles, lungs, heart, blood vessels, kidney and other organs are coordinated while performing physical exercises. In our body the neural system and the endocrine system jointly coordinate and integrate all the activities of the organs so that they function in a synchronised fashion.

The neural system provides an organised network of point-to-point connections for a quick coordination. The endocrine system provides chemical integration through hormones. In this chapter, you will learn about the neural system of human, mechanisms of neural coordination like transmission of nerve impulse, impulse conduction across a synapse and the physiology of reflex action.

21.1 NEURAL SYSTEM

The neural system of all animals is composed of highly specialised cells called **neurons** which can detect, receive and transmit different kinds of stimuli.

The neural organisation is very simple in lower invertebrates. For example, in *Hydra* it is composed of a network of neurons. The neural system is better organised in insects, where a brain is present along with a number of ganglia and neural tissues. The vertebrates have a more developed neural system.

21.2 HUMAN NEURAL SYSTEM

The human neural system is divided into two parts :

(i) the **central neural system** (CNS)

(ii) the **peripheral neural system** (PNS)

The CNS includes the **brain** and the **spinal cord** and is the site of information processing and control. The PNS comprises of all the nerves of the body associated with the CNS (brain and spinal cord). The nerve fibres of the PNS are of two types :

(a) **afferent fibres**

(b) **efferent fibres**

The afferent nerve fibres transmit impulses from tissues/organs to the CNS and the efferent fibres transmit regulatory impulses from the CNS to the concerned peripheral tissues/organs.

The PNS is divided into two divisions called **somatic neural system** and **autonomic neural system**. The somatic neural system relays impulses from the CNS to skeletal muscles while the autonomic neural system transmits impulses from the CNS to the involuntary organs and smooth muscles of the body. The autonomic neural system is further classified into **sympathetic neural system** and **parasympathetic neural system**.

Visceral nervous system is the part of the peripheral nervous system that comprises the whole complex of nerves, fibres, ganglia, and plexuses by which impulses travel from the central nervous system to the viscera and from the viscera to the central nervous system.

21.3 NEURON AS STRUCTURAL AND FUNCTIONAL UNIT OF NEURAL SYSTEM

A neuron is a microscopic structure composed of three major parts, namely, **cell body**, **dendrites** and **axon** (Figure 21.1). The cell body contains cytoplasm with typical cell organelles and certain granular bodies called **Nissl's granules**. Short fibres which branch repeatedly and project out of the cell body also

contain Nissl's granules and are called dendrites. These fibres transmit impulses towards the cell body. The axon is a long fibre, the distal end of which is branched. Each branch terminates as a bulb-like structure called **synaptic knob** which possess synaptic vesicles containing chemicals called **neurotransmitters**. The axons transmit nerve impulses away from the cell body to a synapse or to a neuro-muscular junction. Based on the number of axon and dendrites, the neurons are divided into three types, i.e., **multipolar** (with one axon and two or more dendrites; found in the cerebral cortex), **bipolar** (with one axon and one dendrite, found in the retina of eye) and **unipolar** (cell body with one axon only; found usually in the embryonic stage). There are two types of axons, namely, **myelinated** and **non-myelinated**. The myelinated nerve fibres are enveloped with **Schwann cells,** which form a myelin sheath around the axon. The gaps between two adjacent myelin sheaths are called **nodes of Ranvier**. Myelinated nerve fibres are found in spinal and cranial nerves. Unmyelinated nerve fibre is enclosed by a Schwann cell that does not form a myelin sheath around the axon, and is commonly found in autonomous and the somatic neural systems.

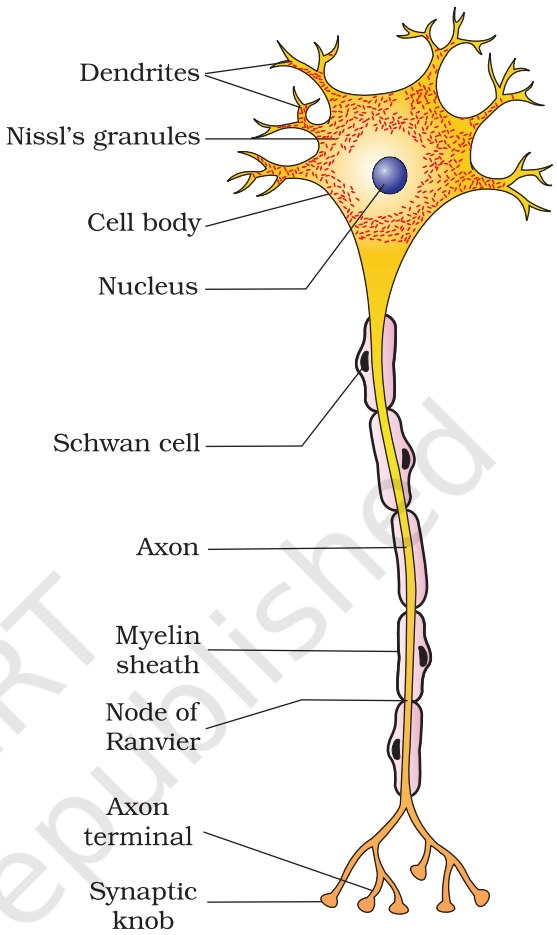


Figure 21.1 Structure of a neuron

21.3.1 Generation and Conduction of Nerve Impulse

Neurons are excitable cells because their membranes are in a polarised state. *Do you know why the membrane of a neuron is polarised?* Different types of ion channels are present on the neural membrane. These ion channels are selectively permeable to different ions. When a neuron is not conducting any impulse, i.e., resting, the axonal membrane is comparatively more permeable to potassium ions (K^+) and nearly impermeable to sodium ions (Na^+). Similarly, the membrane is impermeable to negatively charged proteins present in the axoplasm. Consequently, the axoplasm inside the axon contains high concentration of K^+ and negatively charged proteins and low concentration of Na^+. In contrast, the fluid outside the axon contains a low concentration of K^+, a high concentration of Na^+ and thus form a concentration gradient. These ionic gradients across the resting membrane are maintained by the active transport of ions by the sodium-potassium pump which transports 3 Na^+ outwards for 2 K^+ into the cell. As a result, the outer surface of the axonal membrane possesses a positive charge while its inner surface

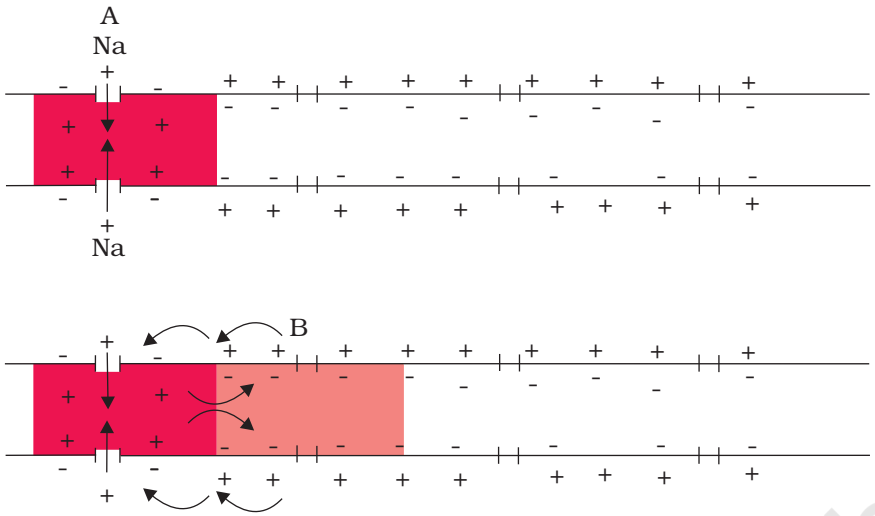


Figure 21.2 Diagrammatic representation of impulse conduction through an axon (at points A and B)

becomes negatively charged and therefore is polarised. The electrical potential difference across the resting plasma membrane is called as the **resting potential**.

You might be curious to know about the mechanisms of generation of nerve impulse and its conduction along an axon. When a stimulus is applied at a site (Figure 21.2 e.g., point A) on the polarised membrane, the membrane at the site A becomes freely permeable to Na^+. This leads to a rapid influx of Na^+ followed by the reversal of the polarity at that site, i.e., the outer surface of the membrane becomes negatively charged and the inner side becomes positively charged. The polarity of the membrane at the site A is thus reversed and hence depolarised. The electrical potential difference across the plasma membrane at the site A is called the **action potential**, which is in fact termed as a **nerve impulse**. At sites immediately ahead, the axon (e.g., site B) membrane has a positive charge on the outer surface and a negative charge on its inner surface. As a result, a current flows on the inner surface from site A to site B. On the outer surface current flows from site B to site A (Figure 21.2) to complete the circuit of current flow. Hence, the polarity at the site is reversed, and an action potential is generated at site B. Thus, the **impulse** (action potential) generated at site A arrives at site B. The sequence is repeated along the length of the axon and consequently the impulse is conducted. The rise in the stimulus-induced permeability to Na^+ is extremely short-lived. It is quickly followed by a rise in permeability to K^+. Within a fraction of a second, K^+ diffuses outside the membrane and restores the resting potential of the membrane at the site of excitation and the fibre becomes once more responsive to further stimulation.

21.3.2 Transmission of Impulses

A nerve impulse is transmitted from one neuron to another through junctions called synapses. A **synapse** is formed by the membranes of a pre-synaptic neuron and a post-synaptic neuron, which may or may not be separated by a gap called **synaptic cleft**. There are two types of synapses, namely, electrical synapses and chemical synapses. At electrical synapses, the membranes of pre- and post-synaptic neurons are in very close proximity. Electrical current can flow directly from one neuron into the other across these synapses. Transmission of an impulse across electrical synapses is very similar to impulse conduction along a single axon. Impulse transmission across an electrical synapse is always faster than that across a chemical synapse. Electrical synapses are rare in our system.

At a chemical synapse, the membranes of the pre- and post-synaptic neurons are separated by a fluid-filled space called synaptic cleft (Figure 21.3). *Do you know how the pre-synaptic neuron transmits an impulse (action potential) across the synaptic cleft to the post-synaptic neuron*? Chemicals called neurotransmitters are involved in the transmission of impulses at these synapses. The axon terminals contain vesicles filled with these neurotransmitters. When an impulse (action potential) arrives at the axon terminal, it stimulates the movement of the synaptic vesicles towards the membrane where they fuse with the plasma

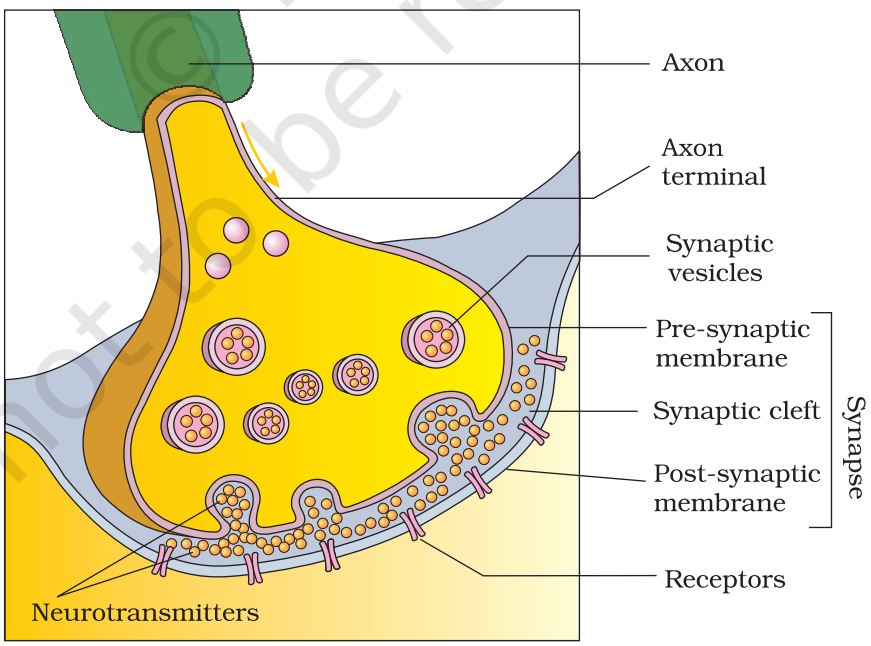


Figure 21.3 Diagram showing axon terminal and synapse

membrane and release their neurotransmitters in the synaptic cleft. The released neurotransmitters bind to their specific **receptors**, present on the post-synaptic membrane. This binding opens ion channels allowing the entry of ions which can generate a new potential in the post-synaptic neuron. The new potential developed may be either excitatory or inhibitory.

21.4 CENTRAL NEURAL SYSTEM

The brain is the central information processing organ of our body, and acts as the 'command and control system'. It controls the voluntary movements, balance of the body, functioning of vital involuntary organs (e.g., lungs, heart, kidneys, etc.), thermoregulation, hunger and thirst, circadian (24-hour) rhythms of our body, activities of several endocrine glands and human behaviour. It is also the site for processing of vision, hearing, speech, memory, intelligence, emotions and thoughts.

The human brain is well protected by the skull. Inside the skull, the brain is covered by **cranial meninges** consisting of an outer layer called **dura mater**, a very thin middle layer called **arachnoid** and an inner layer (which is in contact with the brain tissue) called **pia mater**. The brain can be divided into three major parts: (i) **forebrain**, (ii) **midbrain**, and (iii) **hindbrain** (Figure 21.4).

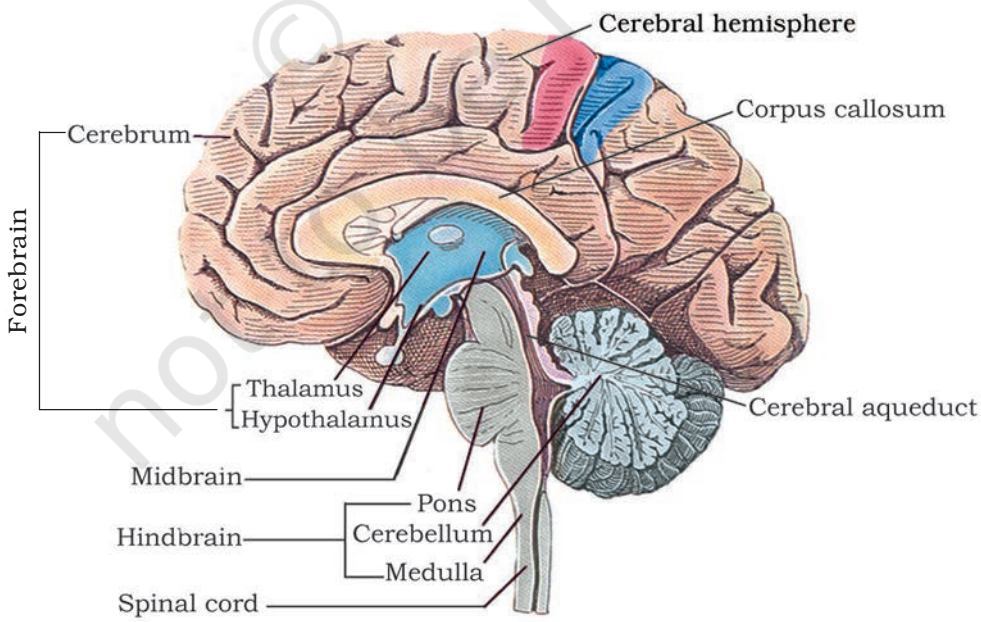


Figure 21.4 Diagram showing sagital section of the human brain

21.4.1 Forebrain

The forebrain consists of **cerebrum**, **thalamus** and **hypothalamus** (Figure 21.4). Cerebrum forms the major part of the human brain. A deep cleft divides the cerebrum longitudinally into two halves, which are termed as the left and right **cerebral hemispheres**. The hemispheres are connected by a tract of nerve fibres called **corpus callosum**. The layer of cells which covers the cerebral hemisphere is called cerebral cortex and is thrown into prominent folds. The cerebral cortex is referred to as the grey matter due to its greyish appearance. The neuron cell bodies are concentrated here giving the colour. The cerebral cortex contains motor areas, sensory areas and large regions that are neither clearly sensory nor motor in function. These regions called as the **association areas** are responsible for complex functions like intersensory associations, memory and communication. Fibres of the tracts are covered with the myelin sheath, which constitute the inner part of cerebral hemisphere. They give an opaque white appearance to the layer and, hence, is called the white matter. The cerebrum wraps around a structure called thalamus, which is a major coordinating centre for sensory and motor signaling. Another very important part of the brain called **hypothalamus** lies at the base of the thalamus. The hypothalamus contains a number of centres which control body temperature, urge for eating and drinking. It also contains several groups of neurosecretory cells, which secrete hormones called hypothalamic hormones. The inner parts of cerebral hemispheres and a group of associated deep structures like amygdala, hippocampus, etc., form a complex structure called the limbic lobe or limbic system. Along with the hypothalamus, it is involved in the regulation of sexual behaviour, expression of emotional reactions (e.g., excitement, pleasure, rage and fear), and motivation.

21.4.2 Midbrain

The midbrain is located between the thalamus/hypothalamus of the forebrain and pons of the hindbrain. A canal called the **cerebral aqueduct** passess through the midbrain. The dorsal portion of the midbrain consists mainly of four round swellings (lobes) called **corpora quadrigemina**. Midbrain and hindbrain form the brain stem.

21.4.3 Hindbrain

The hindbrain comprises **pons**, **cerebellum** and **medulla** (also called the medulla oblongata). Pons consists of fibre tracts that interconnect different regions of the brain. Cerebellum has very convoluted surface in order to provide the additional space for many more neurons. The medulla of the brain is connected to the spinal cord. The medulla contains centres which control respiration, cardiovascular reflexes and gastric secretions. Brain stem forms the connections between the brain and spinal cord. Three major regions make up the brain stem; mid brain, pons and medulla oblongata.

21.5 REFLEX ACTION AND REFLEX ARC

You must have experienced a sudden withdrawal of a body part which comes in contact with objects that are extremely hot, cold pointed or animals that are scary or poisonous. The entire process of response to a peripheral nervous stimulation, that occurs involuntarily, i.e., without conscious effort or thought and requires the involvment of a part of the central nervous system is called a **reflex action**. The reflex pathway comprises at least one afferent neuron (receptor) and one efferent (effector or excitor) neuron appropriately arranged in a series (Figure 21.5). The afferent neuron receives signal from a sensory organ and transmits the impulse via a dorsal nerve root into the CNS (at the level of spinal cord). The efferent nueuron then carries signals from CNS to the effector. The stimulus and response thus forms a reflex arc as shown below in the knee jerk reflex. You should carefully study Figure 21.5 to understand the mechanism of a knee jerk reflex.

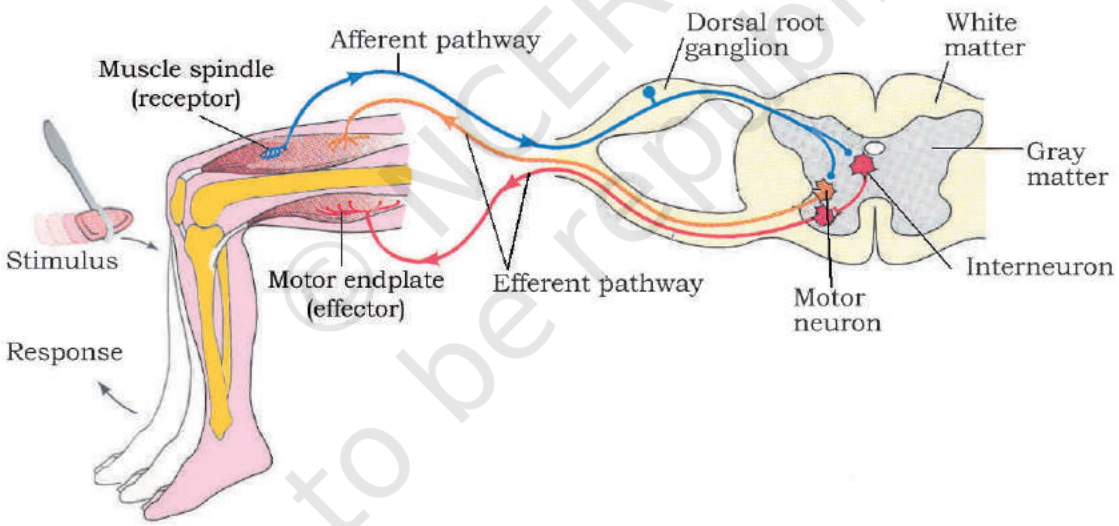


Figure 21.5 Diagrammatic presentation of reflex action (showing knee jerk reflex)

21.6 SENSORY RECEPTION AND PROCESSING

Have you ever thought how do you feel the climatic changes in the environment? How do you see an object and its colour? How do you hear a sound? The sensory organs detect all types of changes in the environment and send appropriate signals to the CNS, where all the inputs are processed and analysed. Signals are then sent to different parts/ centres of the brain. This is how you can sense changes in the environment.

Sense Organs

We smell things by our nose, taste by tongue, hear by ear and see objects by eyes.

The **nose** contains mucus-coated receptors which are specialised for receiving the sense of smell and called **olfactory receptors.** These are made up of olfactory epithelium that consists of three kinds of cells. The neurons of the olfactory epithelium extend from the outside environment directly into a pair of broad bean-sized organs, called **olfactory bulb**, which are extensions of the brain's limbic system.

Both nose and **tongue** detect dissolved chemicals. The chemical senses of gustation (taste) and olfactory (smell) are functionally similar and interrelated. The tongue detects tastes through **taste buds**, containing **gustatory receptors**. With each taste of food or sip of drink, the brain integrates the differential input from the taste buds and a complex flavour is perceived.

In the following sections, you will be introduced to the structure and functioning of the eye (sensory organ for vision) and the ear (sensory organ for hearing).

21.6.1 Eye

Our paired eyes are located in sockets of the skull called **orbits**. A brief account of structure and functions of the human eye is given in the following sections.

21.6.1.1 Parts of an eye

The adult human eye ball is nearly a spherical structure. The wall of the eye ball is composed of three layers (Figure 21.6). The external layer is composed of a dense connective tissue and is called the **sclera**. The anterior portion of this layer is called the **cornea**. The middle layer, **choroid**, contains many blood vessels and looks bluish in colour. The choroid layer is thin over the posterior two-thirds of the eye ball, but it becomes thick in the anterior part to form the **ciliary body**. The ciliary body

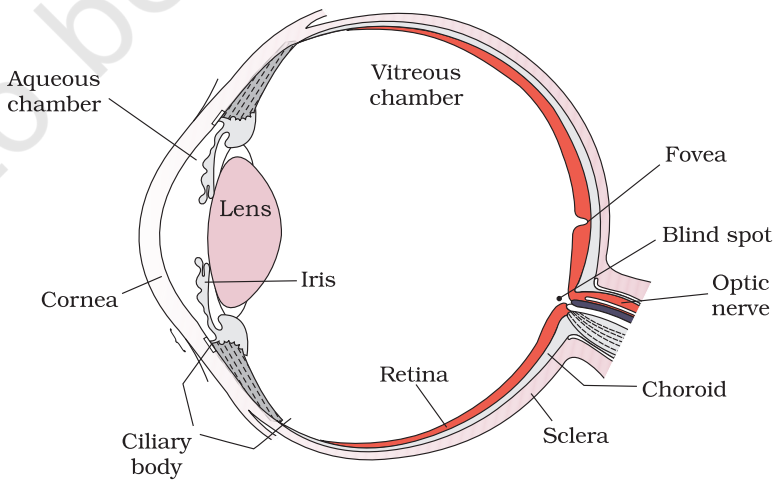


Figure 21.6 Diagram showing parts of an eye

itself continues forward to form a pigmented and opaque structure called the **iris** which is the visible coloured portion of the eye. The eye ball contains a transparent crystalline **lens** which is held in place by ligaments attached to the ciliary body. In front of the lens, the aperture surrounded by the iris is called the **pupil**. The diameter of the pupil is regulated by the muscle fibres of iris.

The inner layer is the **retina** and it contains three layers of neural cells – from inside to outside – ganglion cells, bipolar cells and photoreceptor cells. There are two types of photoreceptor cells, namely, **rods** and **cones**. These cells contain the light-sensitive proteins called the photopigments. The daylight (photopic) vision and colour vision are functions of cones and the twilight (scotopic) vision is the function of the rods. The rods contain a purplish-red protein called the rhodopsin or visual purple, which contains a derivative of Vitamin A. In the human eye, there are three types of cones which possess their own characteristic photopigments that respond to red, green and blue lights. The sensations of different colours are produced by various combinations of these cones and their photopigments. When these cones are stimulated equally, a sensation of white light is produced.

The **optic nerves** leave the eye and the retinal blood vessels enter it at a point medial to and slightly above the posterior pole of the eye ball. Photoreceptor cells are not present in that region and hence it is called the **blind spot**. At the posterior pole of the eye lateral to the blind spot, there is a yellowish pigmented spot called macula lutea with a central pit called the **fovea**. The fovea is a thinned-out portion of the retina where only the cones are densely packed. It is the point where the visual acuity (resolution) is the greatest.

The space between the cornea and the lens is called the **aqueous chamber** and contains a thin watery fluid called aqueous humor. The space between the lens and the retina is called the **vitreous chamber** and is filled with a transparent gel called vitreous humor.

21.6.1.2 Mechanism of Vision

The light rays in visible wavelength focussed on the retina through the cornea and lens generate potentials (impulses) in rods and cones. As mentioned earlier, the photosensitive compounds (photopigments) in the human eyes is composed of **opsin** (a protein) and **retinal** (an aldehyde of vitamin A). Light induces dissociation of the retinal from opsin resulting in changes in the structure of the opsin. This causes membrane permeability changes. As a result, potential differences are generated in the photoreceptor cells. This produces a signal that generates action potentials in the ganglion cells through the bipolar cells. These action potentials (impulses) are transmitted by the optic nerves to the **visual**

cortex area of the brain, where the neural impulses are analysed and the image formed on the retina is recognised based on earlier memory and experience.

21.6.2 The Ear

The ears perform two sensory functions, hearing and maintenance of body balance. Anatomically, the ear can be divided into three major sections called the **outer ear**, the **middle ear** and the **inner ear** (Figure 21.7). The outer ear consists of the **pinna** and **external auditory meatus** (canal). The pinna collects the vibrations in the air which produce sound. The external auditory meatus leads inwards and extends up to the **tympanic membrane** (the **ear drum**). There are very fine hairs and wax-secreting glands in the skin of the pinna and the meatus. The tympanic membrane is composed of connective tissues covered with skin outside and with mucus membrane inside.

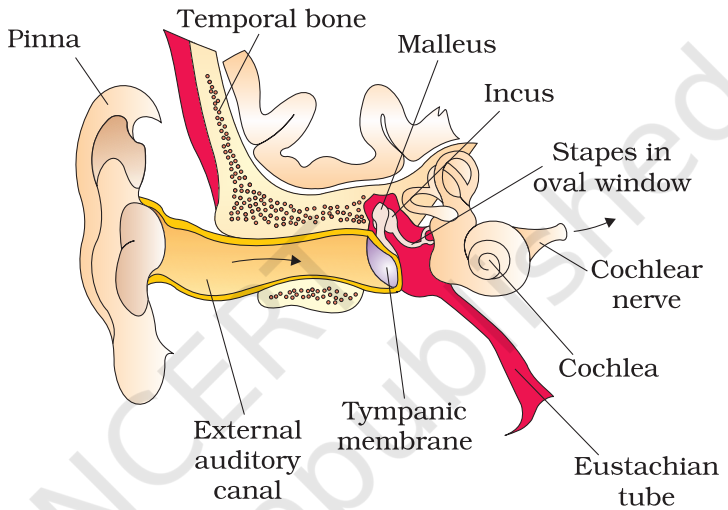


Figure 21.7 Diagrammatic view of ear

The middle ear contains three ossicles called **malleus**, **incus** and **stapes** which are attached to one another in a chain-like fashion. The malleus is attached to the tympanic membrane and the stapes is attached to the **oval window** of the cochlea. The ear ossicles increase the efficiency of transmission of sound waves to the inner ear. An **Eustachian tube** connects the middle ear cavity with the pharynx. The Eustachian tube helps in equalising the pressures on either sides of the ear drum.

The fluid-filled inner ear called **labyrinth** consists of two parts, the bony and the membranous labyrinths. The bony labyrinth is a series of channels. Inside these channels lies the membranous labyrinth, which is surrounded by a fluid called perilymph. The membranous labyrinth is filled with a fluid called endolymph. The coiled portion of the labyrinth is called **cochlea**. The membranes constituting cochlea, the reissner's and basilar, divide the surounding perilymph filled bony labyrinth into an upper scala vestibuli and a lower scala tympani (Figure 21.8). The space

within cochlea called scala media is filled with endolymph. At the base of the cochlea, the scala vestibuli ends at the oval window, while the scala tympani terminates at the round window which opens to the middle ear.

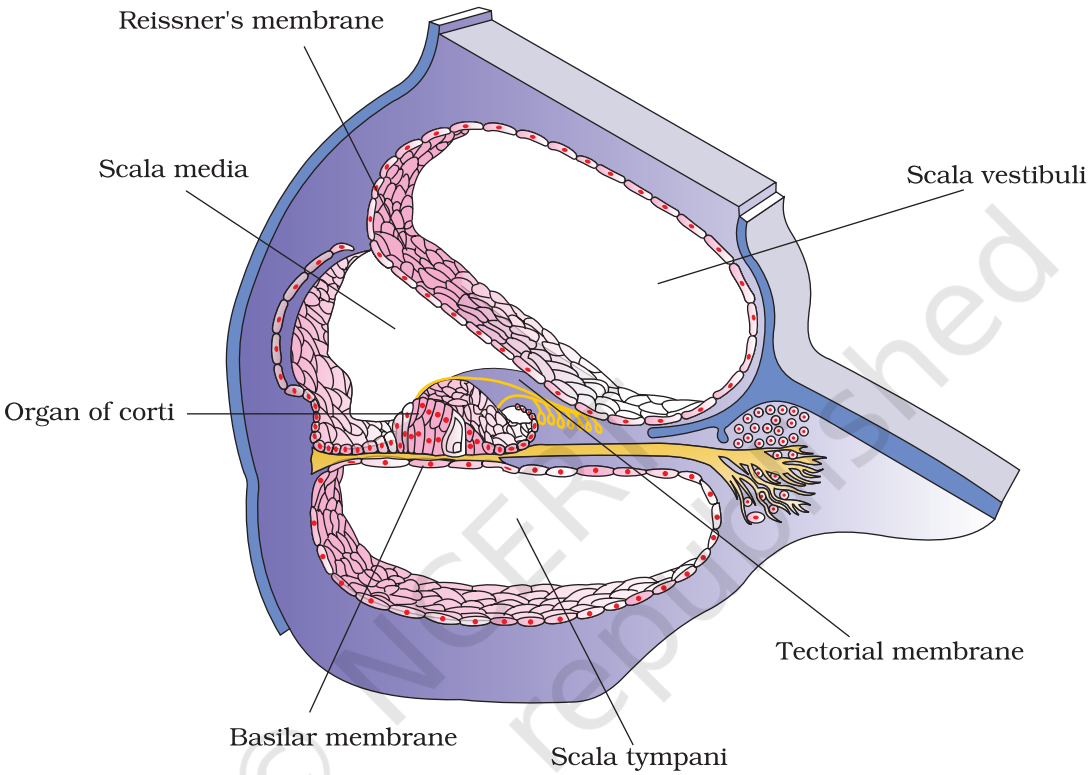


Figure 21.8 Diagrammatic representation of the sectional view of cochlea

The **organ of corti** is a structure located on the basilar membrane which contains **hair cells** that act as auditory receptors. The hair cells are present in rows on the internal side of the organ of corti. The basal end of the hair cell is in close contact with the afferent nerve fibres. A large number of processes called stereo cilia are projected from the apical part of each hair cell. Above the rows of the hair cells is a thin elastic membrane called **tectorial membrane**.

The inner ear also contains a complex system called **vestibular apparatus**, located above the cochlea. The vestibular apparatus is composed of three **semi-circular canals** and the **otolith** (macula is the sensory part of saccule and utricle). Each semi-circular canal lies in a different plane at right angles to each other. The membranous canals are suspended in the perilymph of the bony canals. The base of canals is

swollen and is called ampulla, which contains a projecting ridge called **crista ampullaris** which has hair cells. The saccule and utricle contain a projecting ridge called **macula**. The crista and macula are the specific receptors of the vestibular apparatus responsible for maintenance of balance of the body and posture.

20.6.2.1 *Mechanism of Hearing*

How does ear convert sound waves into neural impulses, which are sensed and processed by the brain enabling us to recognise a sound ? The external ear receives sound waves and directs them to the ear drum. The ear drum vibrates in response to the sound waves and these vibrations are transmitted through the ear ossicles (malleus, incus and stapes) to the oval window. The vibrations are passed through the oval window on to the fluid of the cochlea, where they generate waves in the lymphs. The waves in the lymphs induce a ripple in the basilar membrane. These movements of the basilar membrane bend the hair cells, pressing them against the tectorial membrane. As a result, nerve impulses are generated in the associated afferent neurons. These impulses are transmitted by the afferent fibres via auditory nerves to the auditory cortex of the brain, where the impulses are analysed and the sound is recognised.

SUMMARY

The neural system coordinates and integrates functions as well as metabolic and homeostatic activities of all the organs. Neurons, the functional units of neural system are excitable cells due to a differential concentration gradient of ions across the membrane. The electrical potential difference across the resting neural membrane is called the 'resting potential'. The nerve impulse is conducted along the axon membrane in the form of a wave of depolarisation and repolarisation. A synapse is formed by the membranes of a pre-synaptic neuron and a post-synaptic neuron which may or may not be separated by a gap called synaptic cleft. Chemicals involved in the transmission of impulses at chemical synapses are called neurotransmitters.

Human neural system consists of two parts : (i) central neural system (CNS) and (ii) the peripheral neural system. The CNS consists of the brain and spiral cord. The brain can be divided into three major parts : (i) forebrain, (ii) midbrain and (iii) hindbrain. The forebrain consists of cerebrum, thalamus and hypothalamus. The cerebrum is longitudinally divided into two halves that are connected by the corpus callosum. A very important part of the forebrain called hypothalamus controls the body temperature, eating and drinking. Inner parts

of cerebral hemispheres and a group of associated deep structures form a complex structure called limbic system which is concerned with olfaction, autonomic responses, regulation of sexual behaviour, expression of emotional reactions, and motivation. The midbrain receives and integrates visual, tactile and auditory inputs. The hindbrain comprises pons, cerebellum and medulla. The cerebellum integrates information received from the semicircular canals of the ear and the auditory system. The medulla contains centres, which control respiration, cardiovascular reflexes, and gastric secretions. Pons consist of fibre tracts that interconnect different regions of the brain. The entire process of involuntary response to a peripheral nervous stimulation is called reflex action.

Information regarding changes in the environment is received by the CNS through the sensory organs which are processed and analysed. Signals are then sent for necessary adjustments. The wall of the human eye ball is composed of three layers. The external layer is composed of cornea and sclera. Inside sclera is the middle layer, which is called the choroid. Retina, the innermost layer, contains two types of photoreceptor cells, namely rods and cones. The daylight (photopic) vision and colour vision are functions of cones and twilight (scotopic) vision is the function of the rods. The light enters through cornea, the lens and the images of objects are formed on the retina.

The ear can be divided into the outer ear, the middle ear and the inner ear. The middle ear contains three ossicles called malleus, incus and stapes. The fluid filled inner ear is called the labyrinth, and the coiled portion of the labyrinth is called cochlea. The organ of corti is a structure which contains hair cells that act as auditory receptors and is located on the basilar membrane. The vibrations produced in the ear drum are transmitted through the ear ossicles and oval window to the fluid-filled inner ear. Nerve impulses are generated and transmitted by the afferent fibres to the auditory cortex of the brain. The inner ear also contains a complex system located above the cochlea called vestibular apparatus. It is influenced by gravity and movements, and helps us in maintaining balance of the body and posture.

EXERCISES

1. Briefly describe the structure of the following:
   (a) Brain (b) Eye (c) Ear
2. Compare the following:
   (a) Central neural system (CNS) and Peripheral neural system (PNS)
   (b) Resting potential and action potential
   (c) Choroid and retina
3. Explain the following processes:
   (a) Polarisation of the membrane of a nerve fibre
   (b) Depolarisation of the membrane of a nerve fibre
   (c) Conduction of a nerve impulse along a nerve fibre
   (d) Transmission of a nerve impulse across a chemical synapse
4. Draw labelled diagrams of the following:
   (a) Neuron (b) Brain (c) Eye (d) Ear
5. Write short notes on the following:
   (a) Neural coordination (b) Forebrain (c) Midbrain
   (d) Hindbrain (e) Retina (f) Ear ossicles
   (g) Cochlea (h) Organ of Corti (i) Synapse
6. Give a brief account of:
   (a) Mechanism of synaptic transmission
   (b) Mechanism of vision
   (c) Mechanism of hearing
7. Answer briefly:
   (a) How do you perceive the colour of an object?
   (b) Which part of our body helps us in maintaining the body balance?
   (c) How does the eye regulate the amount of light that falls on the retina.
8. Explain the following:
   (a) Role of Na^+ in the generation of action potential.
   (b) Mechanism of generation of light-induced impulse in the retina.
   (c) Mechanism through which a sound produces a nerve impulse in the inner ear.
9. Differentiate between:
   (a) Myelinated and non-myelinated axons
   (b) Dendrites and axons
   (c) Rods and cones
   (d) Thalamus and Hypothalamus
   (e) Cerebrum and Cerebellum

10. Answer the following:
    (a) Which part of the ear determines the pitch of a sound?
    (b) Which part of the human brain is the most developed?
    (c) Which part of our central neural system acts as a master clock?
11. The region of the vertebrate eye, where the optic nerve passes out of the retina, is called the
    (a) fovea
    (b) iris
    (c) blind spot
    (d) optic chaisma
12. Distinguish between:
    (a) afferent neurons and efferent neurons
    (b) impulse conduction in a myelinated nerve fibre and unmyelinated nerve fibre
    (c) aqueous humor and vitreous humor
    (d) blind spot and yellow spot
    (f) cranial nerves and spinal nerves.

Chapter 22
Chemical Coordination and Integration

You have already learnt that the neural system provides a point-to-point rapid coordination among organs. The neural coordination is fast but short-lived. As the nerve fibres do not innervate all cells of the body and the cellular functions need to be continuously regulated; a special kind of coordination and integration has to be provided. This function is carried out by hormones. The neural system and the endocrine system jointly coordinate and regulate the physiological functions in the body.

22.1 Endocrine Glands and Hormones

Endocrine glands lack ducts and are hence, called ductless glands. Their secretions are called hormones. The classical definition of hormone as a chemical produced by endocrine glands and released into the blood and transported to a distantly located target organ has current scientific definition as follows: **Hormones are non-nutrient chemicals which act as intercellular messengers and are produced in trace amounts**. The new definition covers a number of new molecules in addition to the hormones secreted by the organised endocrine glands. Invertebrates possess very simple endocrine systems with few hormones whereas a large number of chemicals act as hormones and provide coordination in the vertebrates. The human endocrine system is described here.

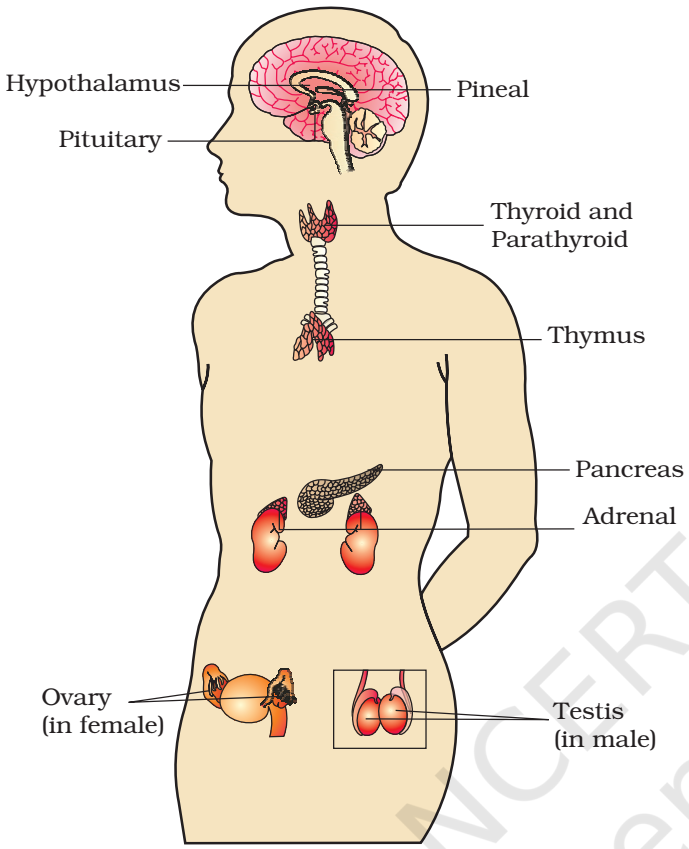


Figure 22.1 Location of endocrine glands

22.2 HUMAN ENDOCRINE SYSTEM

The endocrine glands and hormone producing diffused tissues/cells located in different parts of our body constitute the endocrine system. Pituitary, pineal, thyroid, adrenal, pancreas, parathyroid, thymus and gonads (testis in males and ovary in females) are the organised endocrine bodies in our body (Figure 22.1). In addition to these, some other organs, e.g., gastrointestinal tract, liver, kidney, heart also produce hormones. A brief account of the structure and functions of all major endocrine glands and hypothalamus of the human body is given in the following sections.

22.2.1 The Hypothalamus

As you know, the hypothalamus is the basal part of diencephalon, forebrain (Figure 22.1) and it regulates a wide spectrum of body functions. It contains several groups of neurosecretory cells called nuclei which produce hormones. These hormones regulate the synthesis and secretion of pituitary hormones. However, the hormones produced by hypothalamus are of two types, the releasing hormones (which stimulate secretion of pituitary hormones) and the inhibiting hormones (which inhibit secretions of pituitary hormones). For example a hypothalamic hormone called Gonadotrophin releasing hormone (GnRH) stimulates the pituitary synthesis and release of gonadotrophins. On the other hand, somatostatin from the hypothalamus inhibits the release of growth hormone from the pituitary. These hormones originating in the hypothalamic neurons, pass through axons and are released from their nerve endings. These hormones reach the pituitary gland through a portal circulatory system and regulate the functions of the anterior pituitary. The posterior pituitary is under the direct neural regulation of the hypothalamus (Figure 22.2).

22.2.2 The Pituitary Gland

The pituitary gland is located in a bony cavity called sella tursica and is attached to hypothalamus by a stalk (Figure 22.2). It is divided anatomically into an **adenohypophysis** and a **neurohypophysis**. Adenohypophysis consists of two portions, pars distalis and pars intermedia. The pars distalis region of pituitary, commonly called anterior pituitary, produces **growth hormone** (GH), **prolactin** (PRL), **thyroid stimulating hormone** (TSH), **adrenocorticotrophic hormone** (ACTH), **luteinizing hormone** (LH) and **follicle stimulating hormone** (FSH). Pars intermedia secretes only one hormone called **melanocyte stimulating hormone** (MSH). However, in humans, the pars intermedia is almost merged with pars distalis. Neurohypophysis (pars nervosa) also known as posterior pituitary, stores and releases two hormones called **oxytocin** and **vasopressin,** which are actually synthesised by the hypothalamus and are transported axonally to neurohypophysis.

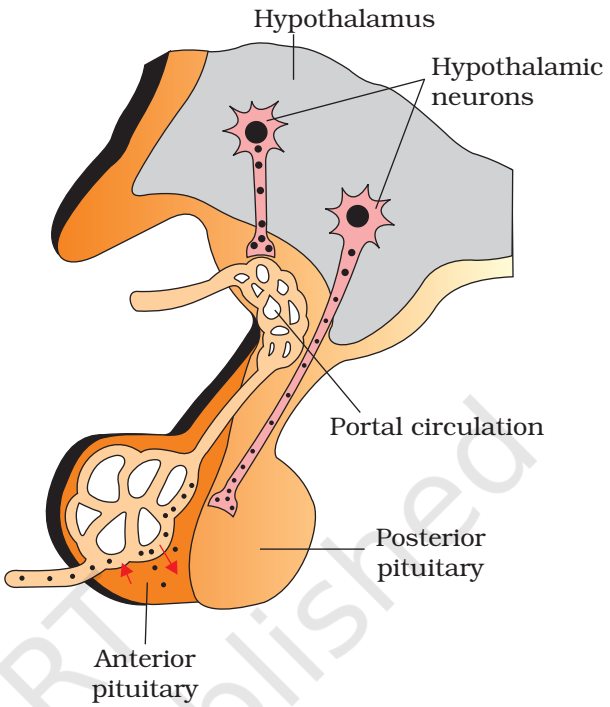


Figure 22.2 Diagrammatic representation of pituitary and its relationship with hypothalamus

Over-secretion of GH stimulates abnormal growth of the body leading to gigantism and low secretion of GH results in stunted growth resulting in pituitary dwarfism. Excess secretion of growth hormone in adults especially in middle age can result in severe disfigurement (especially of the face) called **Acromegaly**, which may lead to serious complications, and premature death if unchecked. The disease is hard to diagnose in the early stages and often goes undetected for many years, until changes in external features become noticeable. Prolactin regulates the growth of the mammary glands and formation of milk in them. TSH stimulates the synthesis and secretion of thyroid hormones from the thyroid gland. ACTH stimulates the synthesis and secretion of steroid hormones called **glucocorticoids** from the adrenal cortex. LH and FSH stimulate gonadal activity and hence are called **gonadotrophins**. In males, LH stimulates the synthesis and secretion of hormones called **androgens** from testis. In males, FSH and androgens regulate spermatogenesis. In females, LH induces ovulation of fully mature follicles (graafian follicles) and maintains the corpus luteum, formed from the remnants of the graafian follicles

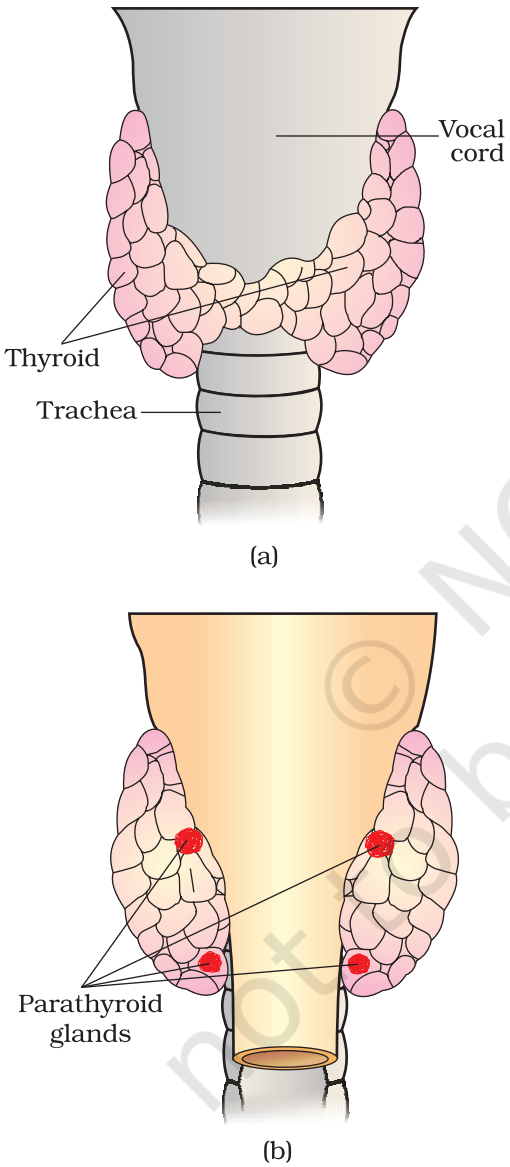


Figure 22.3 Diagrammatic view of the position of Thyroid and Parathyroid
(a) Ventral side
(b) Dorsal side

after ovulation. FSH stimulates growth and development of the ovarian follicles in females. MSH acts on the melanocytes (melanin containing cells) and regulates pigmentation of the skin. Oxytocin acts on the smooth muscles of our body and stimulates their contraction. In females, it stimulates a vigorous contraction of uterus at the time of child birth, and milk ejection from the mammary gland. Vasopressin acts mainly at the kidney and stimulates resorption of water and electrolytes by the distal tubules and thereby reduces loss of water through urine (diuresis). Hence, it is also called as **anti-diuretic hormone** (ADH).

An impairment affecting synthesis or release of ADH results in a diminished ability of the kidney to conserve water leading to water loss and dehydration. This condition is known as **Diabetes Insipidus**.

22.2.3 The Pineal Gland

The pineal gland is located on the dorsal side of forebrain. Pineal secretes a hormone called **melatonin**. Melatonin plays a very important role in the regulation of a 24-hour (diurnal) rhythm of our body. For example, it helps in maintaining the normal rhythms of sleep-wake cycle, body temperature. In addition, melatonin also influences metabolism, pigmentation, the menstrual cycle as well as our defense capability.

22.2.4 Thyroid Gland

The thyroid gland is composed of two lobes which are located on either side of the trachea (Figure 22.3). Both the lobes are interconnected with a thin flap of connective tissue called isthmus. The thyroid gland is composed of **follicles** and **stromal tissues**. Each thyroid follicle is composed of follicular cells, enclosing a cavity. These follicular cells synthesise two hormones, **tetraiodothyronine** or **thyroxine** (T_4) and **triiodothyronine** (T_3). Iodine is essential for the normal rate of hormone synthesis in the thyroid. Deficiency of iodine in our diet results in **hypothyroidism** and enlargement of the thyroid gland, commonly called **goitre**. Hypothyroidism during pregnancy causes defective development and maturation of the growing

baby leading to stunted growth (cretinism), mental retardation, low intelligence quotient, abnormal skin, deaf-mutism, etc. In adult women, hypothyroidism may cause menstrual cycle to become irregular. Due to cancer of the thyroid gland or due to development of nodules of the thyroid glands, the rate of synthesis and secretion of the thyroid hormones is increased to abnormal high levels leading to a condition called **hyperthyroidism** which adversely affects the body physiology.

Exopthalmic goitre is a form of hyperthyroidism, characterised by enlargement of the thyroid gland, protrusion of the eyeballs, increased basal metabolic rate, and weight loss, also called **Graves' disease.**

Thyroid hormones play an important role in the regulation of the basal metabolic rate. These hormones also support the process of red blood cell formation. Thyroid hormones control the metabolism of carbohydrates, proteins and fats. Maintenance of water and electrolyte balance is also influenced by thyroid hormones. Thyroid gland also secretes a protein hormone called thyrocalcitonin (TCT) which regulates the blood calcium levels.

22.2.5 Parathyroid Gland

In humans, four parathyroid glands are present on the back side of the thyroid gland, one pair each in the two lobes of the thyroid gland (Figure 22.3b). The parathyroid glands secrete a peptide hormone called **parathyroid hormone** (PTH). The secretion of PTH is regulated by the circulating levels of calcium ions.

Parathyroid hormone (PTH) increases the Ca^{2+} levels in the blood. PTH acts on bones and stimulates the process of bone resorption (dissolution/ demineralisation). PTH also stimulates reabsorption of Ca^{2+} by the renal tubules and increases Ca^{2+} absorption from the digested food. It is, thus, clear that PTH is a hypercalcemic hormone, i.e., it increases the blood Ca^{2+} levels. Along with TCT, it plays a significant role in calcium balance in the body.

22.2.6 Thymus

The thymus gland is a lobular structure located between lungs behind sternum on the ventral side of aorta. The thymus plays a major role in the development of the immune system. This gland secretes the peptide hormones called **thymosins**. Thymosins play a major role in the differentiation of **T-lymphocytes**, which provide **cell-mediated immunity**. In addition, thymosins also promote production of antibodies to provide **humoral immunity**. Thymus is degenerated in old individuals resulting in a decreased production of thymosins. As a result, the immune responses of old persons become weak.

22.2.7 Adrenal Gland

Our body has one pair of adrenal glands, one at the anterior part of each kidney (Figure 22.4 a). The gland is composed of two types of tissues. The centrally located tissue is called the **adrenal medulla**, and outside this lies the **adrenal cortex** (Figure 22.4 b).

Underproduction of hormones by the adrenal cortex alters carbohydrate metabolism causing acute weakness and fatigue leading to a disease called **Addison's disease**.

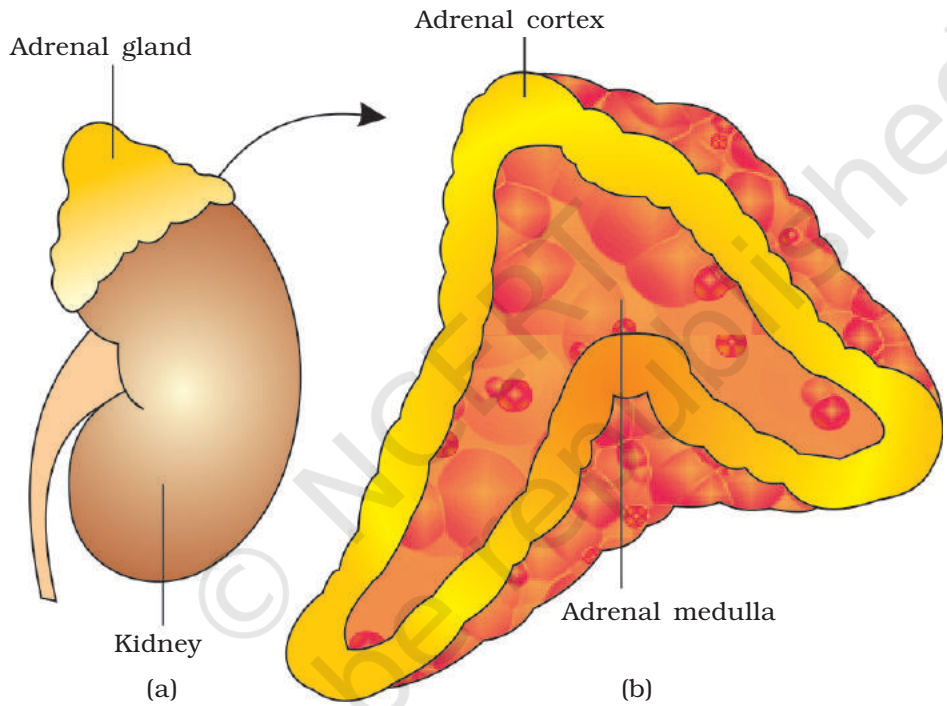


Figure 22.4 Diagrammatic representation of : (a) Adrenal gland above kidney (b) Section showing two parts of adrenal gland

The adrenal medulla secretes two hormones called **adrenaline** or **epinephrine** and **noradrenaline** or **norepinephrine**. These are commonly called as **catecholamines**. Adrenaline and noradrenaline are rapidly secreted in response to stress of any kind and during emergency situations and are called **emergency hormones** or **hormones of Fight or Flight**. These hormones increase alertness, pupilary dilation, piloerection (raising of hairs), sweating etc. Both the hormones increase the heart beat, the strength of heart contraction and the rate of respiration. Catecholamines also stimulate the breakdown of glycogen resulting in

an increased concentration of glucose in blood. In addition, they also stimulate the breakdown of lipids and proteins.

The adrenal cortex can be divided into three layers, called **zona reticularis** (inner layer), **zona fasciculata** (middle layer) and **zona glomerulosa** (outer layer). The adrenal cortex secretes many hormones, commonly called as **corticoids**. The corticoids, which are involved in carbohydrate metabolism are called glucocorticoids. In our body, cortisol is the main glucocorticoid. Corticoids, which regulate the balance of water and electrolytes in our body are called mineralocorticoids. Aldosterone is the main mineralocorticoid in our body.

Glucocorticoids stimulate gluconeogenesis, lipolysis and proteolysis; and inhibit cellular uptake and utilisation of amino acids. Cortisol is also involved in maintaining the cardio-vascular system as well as the kidney functions. Glucocorticoids, particularly cortisol, produces anti-inflammatory reactions and suppresses the immune response. Cortisol stimulates the RBC production. Aldosterone acts mainly at the renal tubules and stimulates the reabsorption of Na^+ and water and excretion of K^+ and phosphate ions. Thus, aldosterone helps in the maintenance of electrolytes, body fluid volume, osmotic pressure and blood pressure. Small amounts of androgenic steroids are also secreted by the adrenal cortex which play a role in the growth of axial hair, pubic hair and facial hair during puberty.

22.2.8 Pancreas

Pancreas is a composite gland (Figure 22.1) which acts as both exocrine and endocrine gland. The endocrine pancreas consists of 'Islets of Langerhans'. There are about 1 to 2 million Islets of Langerhans in a normal human pancreas representing only 1 to 2 per cent of the pancreatic tissue. The two main types of cells in the Islet of Langerhans are called **α-cells** and **β-cells**. The α-cells secrete a hormone called **glucagon**, while the β-cells secrete **insulin**.

Glucagon is a peptide hormone, and plays an important role in maintaining the normal blood glucose levels. Glucagon acts mainly on the liver cells (hepatocytes) and stimulates glycogenolysis resulting in an increased blood sugar (**hyperglycemia**). In addition, this hormone stimulates the process of gluconeogenesis which also contributes to hyperglycemia. Glucagon reduces the cellular glucose uptake and utilisation. Thus, glucagon is a **hyperglycemic hormone**.

Insulin is a peptide hormone, which plays a major role in the regulation of glucose homeostasis. Insulin acts mainly on hepatocytes and adipocytes (cells of adipose tissue), and enhances cellular glucose

uptake and utilisation. As a result, there is a rapid movement of glucose from blood to hepatocytes and adipocytes resulting in decreased blood glucose levels (**hypoglycemia**). Insulin also stimulates conversion of glucose to glycogen (**glycogenesis**) in the target cells. The glucose homeostasis in blood is thus maintained jointly by the two – insulin and glucagons.

Prolonged hyperglycemia leads to a complex disorder called **diabetes mellitus** which is associated with loss of glucose through urine and formation of harmful compounds known as ketone bodies. Diabetic patients are successfully treated with insulin therapy.

22.2.9 Testis

A pair of testis is present in the scrotal sac (outside abdomen) of male individuals (Figure 22.1). Testis performs dual functions as a primary sex organ as well as an endocrine gland. Testis is composed of **seminiferous tubules** and **stromal or interstitial tissue.** The **Leydig cells** or **interstitial cells**, which are present in the intertubular spaces produce a group of hormones called **androgens** mainly **testosterone.**

Androgens regulate the development, maturation and functions of the male accessory sex organs like epididymis, vas deferens, seminal vesicles, prostate gland, urethra etc. These hormones stimulate muscular growth, growth of facial and axillary hair, aggressiveness, low pitch of voice etc. Androgens play a major stimulatory role in the process of spermatogenesis (formation of spermatozoa). Androgens act on the central neural system and influence the male sexual behaviour (libido). These hormones produce anabolic (synthetic) effects on protein and carbohydrate metabolism.

22.2.10 Ovary

Females have a pair of ovaries located in the abdomen (Figure 22.1). Ovary is the primary female sex organ which produces one ovum during each menstrual cycle. In addition, ovary also produces two groups of steroid hormones called **estrogen** and **progesterone**. Ovary is composed of ovarian follicles and stromal tissues. The estrogen is synthesised and secreted mainly by the growing ovarian follicles. After ovulation, the ruptured follicle is converted to a structure called **corpus luteum**, which secretes mainly **progesterone**.

Estrogens produce wide ranging actions such as stimulation of growth and activities of female secondary sex organs, development of growing

ovarian follicles, appearance of female secondary sex characters (e.g., high pitch of voice, etc.), mammary gland development. Estrogens also regulate female sexual behaviour.

Progesterone supports pregnancy. Progesterone also acts on the mammary glands and stimulates the formation of alveoli (sac-like structures which store milk) and milk secretion.

22.3 HORMONES OF HEART, KIDNEY AND GASTROINTESTINAL TRACT

Now you know about the endocrine glands and their hormones. However, as mentioned earlier, hormones are also secreted by some tissues which are not endocrine glands. For example, the atrial wall of our heart secretes a very important peptide hormone called **atrial natriuretic factor** (ANF), which decreases blood pressure. When blood pressure is increased, ANF is secreted which causes dilation of the blood vessels. This reduces the blood pressure.

The juxtaglomerular cells of kidney produce a peptide hormone called **erythropoietin** which stimulates erythropoiesis (formation of RBC).

Endocrine cells present in different parts of the gastro-intestinal tract secrete four major peptide hormones, namely **gastrin**, **secretin**, **cholecystokinin** (CCK) and **gastric inhibitory peptide** (GIP). Gastrin acts on the gastric glands and stimulates the secretion of hydrochloric acid and pepsinogen. Secretin acts on the exocrine pancreas and stimulates secretion of water and bicarbonate ions. CCK acts on both pancreas and gall bladder and stimulates the secretion of pancreatic enzymes and bile juice, respectively. GIP inhibits gastric secretion and motility. Several other non-endocrine tissues secrete hormones called **growth factors.** These factors are essential for the normal growth of tissues and their repairing/regeneration.

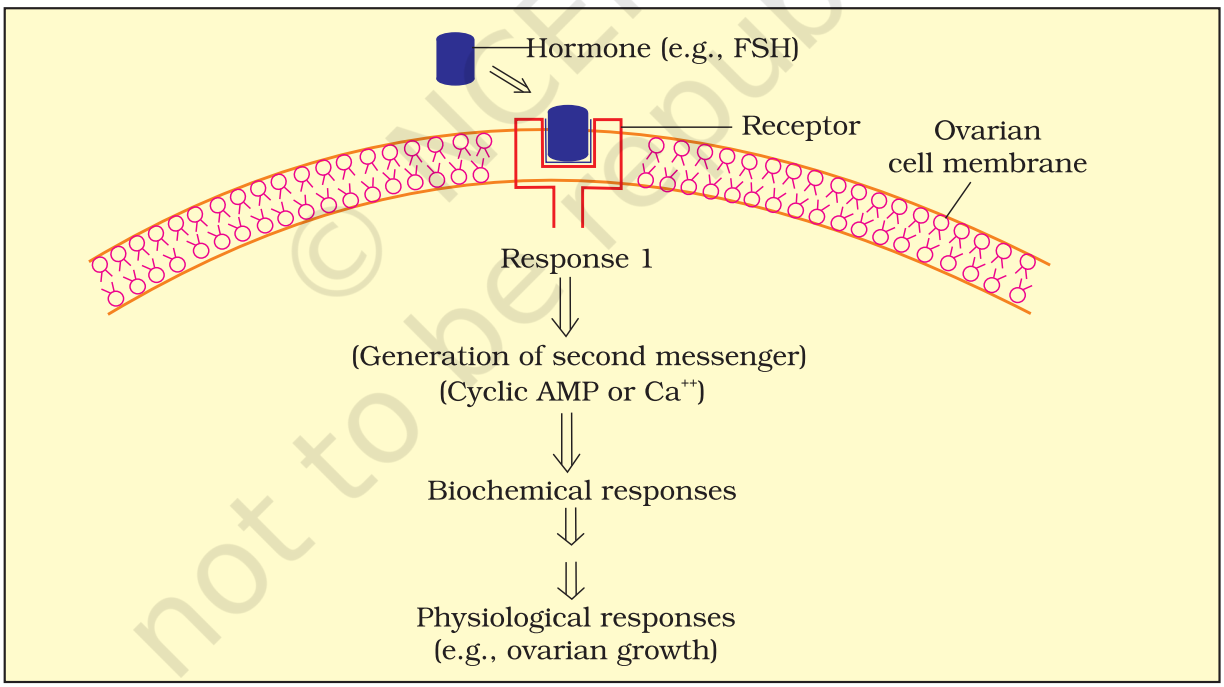
22.4 MECHANISM OF HORMONE ACTION

Hormones produce their effects on target tissues by binding to specific proteins called **hormone receptors** located in the target tissues only. Hormone receptors present on the cell membrane of the target cells are called membrane-bound receptors and the receptors present inside the target cell are called intracellular receptors, mostly nuclear receptors (present in the nucleus). Binding of a hormone to its receptor leads to the formation of a **hormone-receptor complex** (Figure 22.5 a, b). Each receptor is specific to one hormone only and hence receptors are specific. Hormone-Receptor complex formation leads to certain biochemical changes in the target tissue. Target tissue metabolism and hence

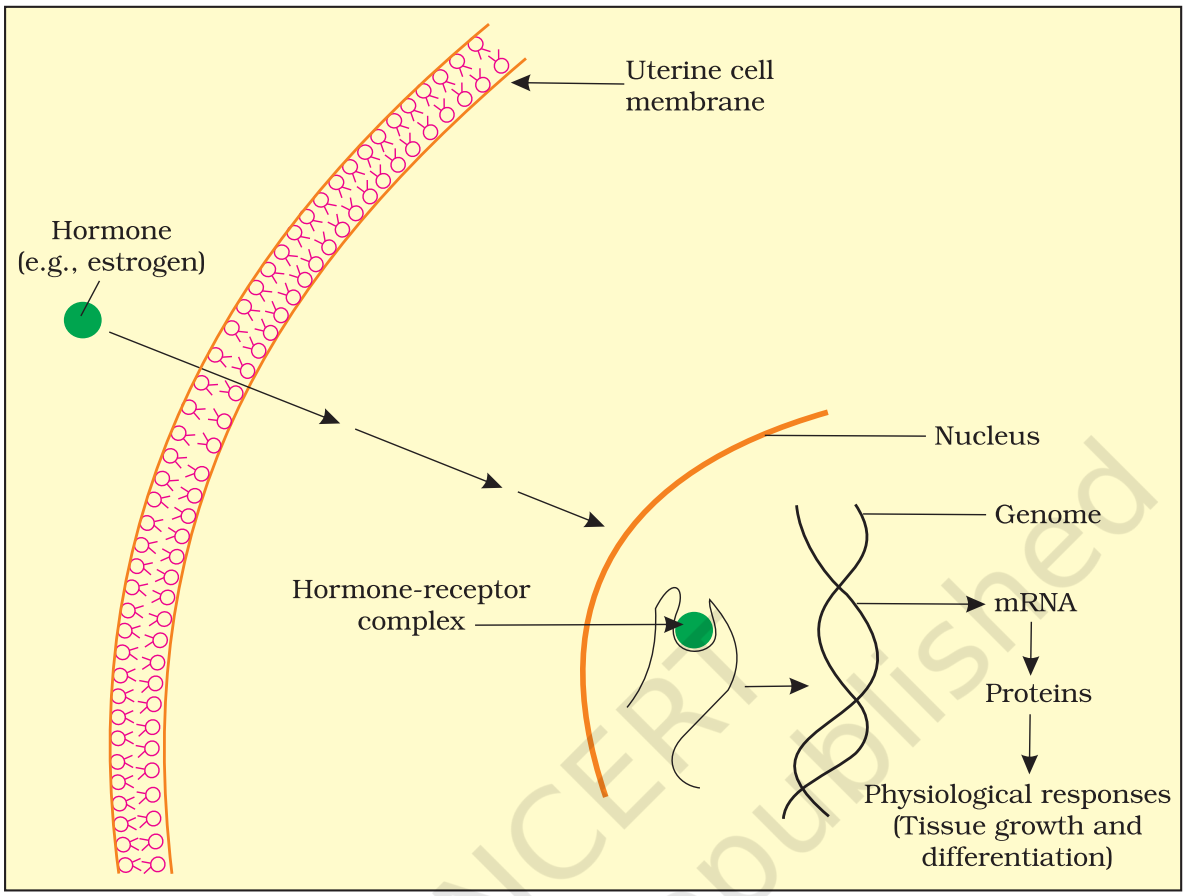
physiological functions are regulated by hormones. On the basis of their chemical nature, hormones can be divided into groups :

(i) **peptide, polypeptide, protein hormones** (e.g., insulin, glucagon, pituitary hormones, hypothalamic hormones, etc.)
(ii) **steroids** (e.g., cortisol, testosterone, estradiol and progesterone)
(iii) **iodothyronines** (thyroid hormones)
(iv) **amino-acid derivatives** (e.g., epinephrine).

Hormones which interact with membrane-bound receptors normally do not enter the target cell, but generate second messengers (e.g., cyclic AMP, IP_3, Ca^{++} etc) which in turn regulate cellular metabolism (Figure 22.5a). Hormones which interact with intracellular receptors (e.g., steroid hormones, iodothyronines, etc.) mostly regulate gene expression or chromosome function by the interaction of hormone-receptor complex with the genome. Cumulative biochemical actions result in physiological and developmental effects (Figure 22.5b).



(a)



(b)

Figure 22.5 Diagramatic representation of the mechanism of hormone action : (a) Protein hormone (b) Steroid hormone

SUMMARY

There are special chemicals which act as hormones and provide chemical coordination, integration and regulation in the human body. These hormones regulate metabolism, growth and development of our organs, the endocrine glands or certain cells. The endocrine system is composed of hypothalamus, pituitary and pineal, thyroid, adrenal, pancreas, parathyroid, thymus and gonads (testis and ovary). In addition to these, some other organs, e.g., gastrointestinal tract, kidney, heart etc., also produce hormones. The pituitary gland is divided into three major parts, which are called as pars distalis, pars intermedia and pars nervosa. Pars distalis produces six trophic hormones. Pars intermedia secretes

only one hormone, while pars nervosa (neurohypophysis) secretes two hormones. The pituitary hormones regulate the growth and development of somatic tissues and activities of peripheral endocrine glands. Pineal gland secretes melatonin, which plays a very important role in the regulation of 24-hour (diurnal) rhythms of our body (e.g., rhythms of sleep and state of being awake, body temperature, etc.). The thyroid gland hormones play an important role in the regulation of the basal metabolic rate, development and maturation of the central neural system, erythropoiesis, metabolism of carbohydrates, proteins and fats, menstrual cycle. Another thyroid hormone, i.e., thyrocalcitonin regulates calcium levels in our blood by decreasing it. The parathyroid glands secrete parathyroid hormone (PTH) which increases the blood Ca^{2+} levels and plays a major role in calcium homeostasis. The thymus gland secretes thymosins which play a major role in the differentiation of T-lymphocytes, which provide cell-mediated immunity. In addition, thymosins also increase the production of antibodies to provide humoral immunity. The adrenal gland is composed of the centrally located adrenal medulla and the outer adrenal cortex. The adrenal medulla secretes epinephrine and norepinephrine. These hormones increase alertness, pupilary dilation, piloerection, sweating, heart beat, strength of heart contraction, rate of respiration, glycogenolysis, lipolysis, proteolysis. The adrenal cortex secretes glucocorticoids and mineralocorticoids. Glucocorticoids stimulate gluconeogenesis, lipolysis, proteolysis, erythropoiesis, cardio-vascular system, blood pressure, and glomerular filtration rate and inhibit inflammatory reactions by suppressing the immune response. Mineralocorticoids regulate water and electrolyte contents of the body. The endocrine pancreas secretes glucagon and insulin. Glucagon stimulates glycogenolysis and gluconeogenesis resulting in hyperglycemia. Insulin stimulates cellular glucose uptake and utilisation, and glycogenesis resulting in hypoglycemia. Insulin deficiency and/or insulin resistance result in a disease called diabetes mellitus.

The testis secretes androgens, which stimulate the development, maturation and functions of the male accessory sex organs, appearance of the male secondary sex characters, spermatogenesis, male sexual behaviour, anabolic pathways and erythropoiesis. The ovary secretes estrogen and progesterone. Estrogen stimulates growth and development of female accessory sex organs and secondary sex characters. Progesterone plays a major role in the maintenance of pregnancy as well as in mammary gland development and lactation. The atrial wall of the heart produces atrial natriuretic factor which decreases the blood pressure. Kidney produces erythropoietin which stimulates erythropoiesis. The gastrointestinal tract secretes gastrin, secretin, cholecystokinin and gastric inhibitory peptide. These hormones regulate the secretion of digestive juices and help in digestion.

EXERCISES

1. Define the following:
   (a) Exocrine gland
   (b) Endocrine gland
   (c) Hormone
2. Diagrammatically indicate the location of the various endocrine glands in our body.
3. List the hormones secreted by the following:
   (a) Hypothalamus (b) Pituitary (c) Thyroid (d) Parathyroid
   (e) Adrenal (f) Pancreas (g) Testis (h) Ovary
   (i) Thymus (j) Atrium (k) Kidney (l) G-I Tract
4. Fill in the blanks:

Hormones	**Target gland**
(a) Hypothalamic hormones	_____
(b) Thyrotrophin (TSH)	_____
(c) Corticotrophin (ACTH)	_____
(d) Gonadotrophins (LH, FSH)	_____
(e) Melanotrophin (MSH)	_____

5. Write short notes on the functions of the following hormones:
   (a) Parathyroid hormone (PTH) (b) Thyroid hormones
   (c) Thymosins (d) Androgens
   (e) Estrogens (f) Insulin and Glucagon
6. Give example(s) of:
   (a) Hyperglycemic hormone and hypoglycemic hormone
   (b) Hypercalcemic hormone
   (c) Gonadotrophic hormones
   (d) Progestational hormone
   (e) Blood pressure lowering hormone
   (f) Androgens and estrogens
7. Which hormonal deficiency is responsible for the following:
   (a) Diabetes mellitus (b) Goitre (c) Cretinism
8. Briefly mention the mechanism of action of FSH.
9. Match the following:

Column I	**Column II**
(a) T_4	(i) Hypothalamus
(b) PTH	(ii) Thyroid
(c) GnRH	(iii) Pituitary
(d) LH	(iv) Parathyroid

Note

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