

CHAPTER 10

CELL CYCLE AND CELL DIVISION

10.1 Cell Cycle

10.2 M Phase

10.3 Significance of Mitosis

10.4 Meiosis

10.5 Significance of Meiosis

Are you aware that all organisms, even the largest, start their life from a single cell? You may wonder how a single cell then goes on to form such large organisms. Growth and reproduction are characteristics of cells, indeed of all living organisms. All cells reproduce by dividing into two, with each parental cell giving rise to two daughter cells each time they divide. These newly formed daughter cells can themselves grow and divide, giving rise to a new cell population that is formed by the growth and division of a single parental cell and its progeny. In other words, such cycles of growth and division allow a single cell to form a structure consisting of millions of cells.

10.1 CELL CYCLE

Cell division is a very important process in all living organisms. During the division of a cell, DNA replication and cell growth also take place. All these processes, i.e., cell division, DNA replication, and cell growth, hence, have to take place in a coordinated way to ensure correct division and formation of progeny cells containing intact genomes. The sequence of events by which a cell duplicates its genome, synthesises the other constituents of the cell and eventually divides into two daughter cells is termed **cell cycle**. Although cell growth (in terms of cytoplasmic increase) is a continuous process, DNA synthesis occurs only during one specific stage in the cell cycle. The replicated chromosomes (DNA) are then distributed to daughter nuclei by a complex series of events during cell division. These events are themselves under genetic control.

10.1.1 Phases of Cell Cycle

A typical eukaryotic cell cycle is illustrated by human cells in culture. These cells divide once in approximately every 24 hours (Figure 10.1). However, this duration of cell cycle can vary from organism to organism and also from cell type to cell type. Yeast for example, can progress through the cell cycle in only about 90 minutes.

The cell cycle is divided into two basic phases:

- **Interphase**
- **M Phase (Mitosis phase)**

The M Phase represents the phase when the actual cell division or mitosis occurs and the interphase represents the phase between two successive M phases. It is significant to note that in the 24 hour average duration of cell cycle of a human cell, cell division proper lasts for only about an hour. The interphase lasts more than 95% of the duration of cell cycle.

The M Phase starts with the nuclear division, corresponding to the separation of daughter chromosomes (**karyokinesis**) and usually ends with division of cytoplasm (**cytokinesis**). The interphase, though called the resting phase, is the time during which the cell is preparing for division by undergoing both cell growth and DNA replication in an orderly manner. The interphase is divided into three further phases:

- **G₁ phase (Gap 1)**
- **S phase (Synthesis)**
- **G₂ phase (Gap 2)**

G₁ phase corresponds to the interval between mitosis and initiation of DNA replication. During G₁ phase the cell is metabolically active and continuously grows but does not replicate its DNA. S or **synthesis** phase marks the period during which DNA synthesis or replication takes place. During this time the amount of DNA per cell doubles. If the initial amount of DNA is denoted as 2C then it increases to 4C. However, there is no increase in the chromosome number; if the cell had diploid or 2n number of chromosomes at G₁, even after S phase the number of chromosomes remains the same, i.e., 2n.

In animal cells, during the S phase, DNA replication begins in the nucleus, and the centriole duplicates in the cytoplasm. During the G₂ phase, proteins are synthesised in preparation for mitosis while cell growth continues.

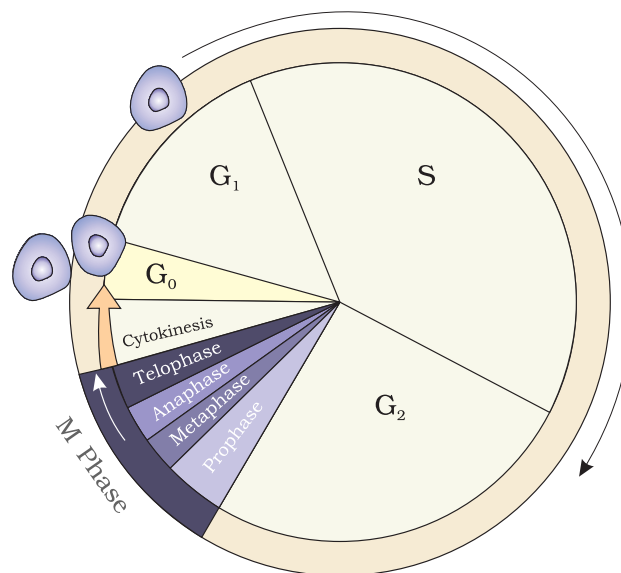


Figure 10.1 A diagrammatic view of cell cycle indicating formation of two cells from one cell

How do plants and animals continue to grow all their lives? Do all cells in a plant divide all the time? Do you think all cells continue to divide in all plants and animals? Can you tell the name and the location of tissues having cells that divide all their life in higher plants? Do animals have similar meristematic tissues?

You have studied mitosis in onion root tip cells. It has 14 chromosomes in each cell. Can you tell how many chromosomes will the cell have at G_1 phase, after S phase, and after M phase? Also, what will be the DNA content of the cells at G_1 , after S and at G_2 , if the content after M phase is $2C$?

Some cells in the adult animals do not appear to exhibit division (e.g., heart cells) and many other cells divide only occasionally, as needed to replace cells that have been lost because of injury or cell death. These cells that do not divide further exit G_1 phase to enter an inactive stage called **quiescent stage (G_0)** of the cell cycle. Cells in this stage remain metabolically active but no longer proliferate unless called on to do so depending on the requirement of the organism.

In animals, mitotic cell division is only seen in the diploid somatic cells. Against this, the plants can show mitotic divisions in both haploid and diploid cells. From your recollection of examples of alternation of generations in plants (Chapter 3) identify plant species and stages at which mitosis is seen in haploid cells.

10.2 M PHASE

This is the most dramatic period of the cell cycle, involving a major reorganisation of virtually all components of the cell. Since the number of chromosomes in the parent and progeny cells is the same, it is also called as **equational division**. Though for convenience mitosis has been divided into four stages of nuclear division, it is very essential to understand that cell division is a progressive process and very clear-cut lines cannot be drawn between various stages. Mitosis is divided into the following four stages:

- **Prophase**
- **Metaphase**
- **Anaphase**
- **Telophase**

10.2.1 Prophase

Prophase which is the first stage of mitosis follows the S and G_2 phases of interphase. In the S and G_2 phases the new DNA molecules formed are not distinct but intertwined. Prophase is marked by the initiation of condensation of chromosomal material. The chromosomal material becomes untangled during the process of chromatin condensation (Figure 10.2 a). The centriole, which had undergone duplication during S phase of interphase, now begins to move towards opposite poles of the cell. The completion of prophase can thus be marked by the following characteristic events:

- Chromosomal material condenses to form compact mitotic chromosomes. Chromosomes are seen to be composed of two chromatids attached together at the centromere.
- Initiation of the assembly of mitotic spindle, the microtubules, the proteinaceous components of the cell cytoplasm help in the process.

Cells at the end of prophase, when viewed under the microscope, do not show golgi complexes, endoplasmic reticulum, nucleolus and the nuclear envelope.

10.2.2 Metaphase

The complete disintegration of the nuclear envelope marks the start of the second phase of mitosis, hence the chromosomes are spread through the cytoplasm of the cell. By this stage, condensation of chromosomes is completed and they can be observed clearly under the microscope. This then, is the stage at which morphology of chromosomes is most easily studied. At this stage, metaphase chromosome is made up of two sister chromatids, which are held together by the centromere (Figure 10.2 b). Small disc-shaped structures at the surface of the centromeres are called kinetochores. These structures serve as the sites of attachment of spindle fibres (formed by the spindle fibres) to the chromosomes that are moved into position at the centre of the cell. Hence, the metaphase is characterised by all the chromosomes coming to lie at the equator with one chromatid of each chromosome connected by its kinetochore to spindle fibres from one pole and its sister chromatid connected by its kinetochore to spindle fibres from the opposite pole (Figure 10.2 b). The plane of alignment of the chromosomes at metaphase is referred to as the **metaphase plate**. The key features of metaphase are:

- Spindle fibres attach to kinetochores of chromosomes.
- Chromosomes are moved to spindle equator and get aligned along metaphase plate through spindle fibres to both poles.

10.2.3 Anaphase

At the onset of anaphase, each chromosome arranged at the metaphase plate is split simultaneously and the two daughter chromatids, now referred to as chromosomes of the future daughter nuclei, begin their migration towards the two opposite poles. As each chromosome moves away from the equatorial plate, the centromere of each chromosome is towards the pole and hence at the leading edge, with the arms of the chromosome trailing behind (Figure 10.2 c). Thus, anaphase stage is characterised by

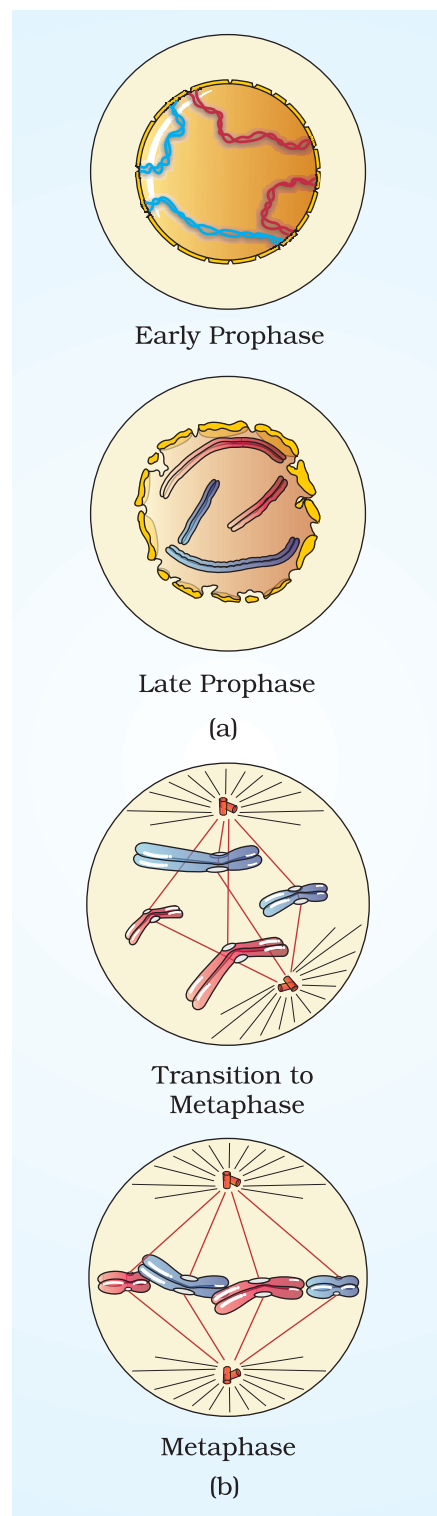


Figure 10.2 a and b : A diagrammatic view of stages in mitosis

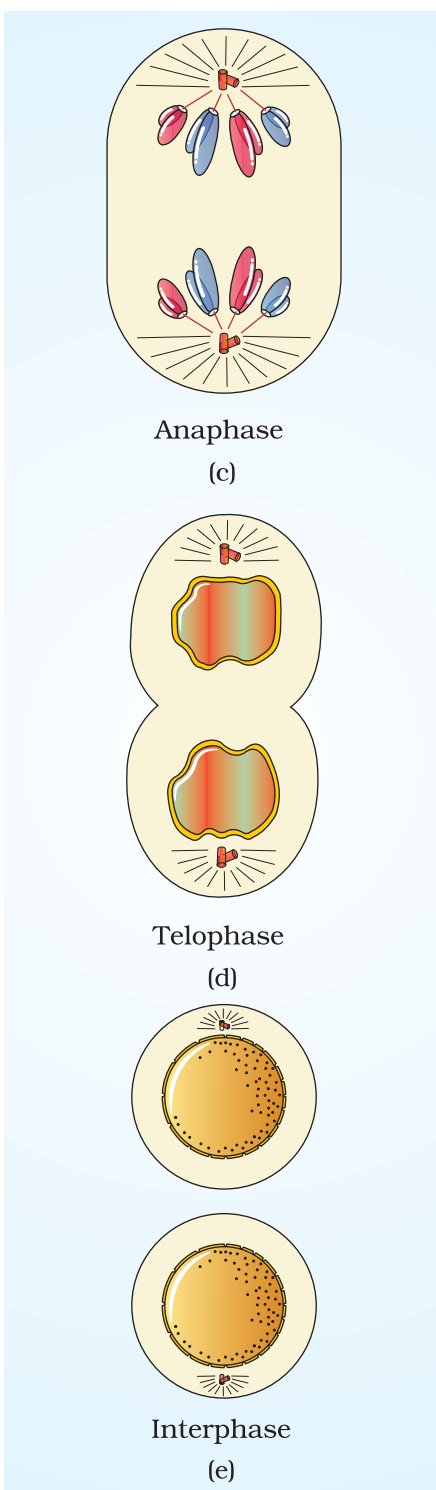


Figure 10.2 c to e : A diagrammatic view of stages in Mitosis

the following key events:

- Centromeres split and chromatids separate.
- Chromatids move to opposite poles.

10.2.4 Telophase

At the beginning of the final stage of mitosis, i.e., telophase, the chromosomes that have reached their respective poles decondense and lose their individuality. The individual chromosomes can no longer be seen and chromatin material tends to collect in a mass in the two poles (Figure 10.2 d). This is the stage which shows the following key events:

- Chromosomes cluster at opposite spindle poles and their identity is lost as discrete elements.
- Nuclear envelope assembles around the chromosome clusters.
- Nucleolus, golgi complex and ER reform.

10.2.5 Cytokinesis

Mitosis accomplishes not only the segregation of duplicated chromosomes into daughter nuclei (karyokinesis), but the cell itself is divided into two daughter cells by a separate process called cytokinesis at the end of which cell division is complete (Figure 10.2 e). In an animal cell, this is achieved by the appearance of a furrow in the plasma membrane. The furrow gradually deepens and ultimately joins in the centre dividing the cell cytoplasm into two. Plant cells however, are enclosed by a relatively inextensible cell wall, therefore they undergo cytokinesis by a different mechanism. In plant cells, wall formation starts in the centre of the cell and grows outward to meet the existing lateral walls. The formation of the new cell wall begins with the formation of a simple precursor, called the **cell-plate** that represents the middle lamella between the walls of two adjacent cells. At the time of cytoplasmic division, organelles like mitochondria and plastids get distributed between the two daughter cells. In some organisms karyokinesis is not followed by cytokinesis as a result of which multinucleate condition arises leading to the formation of syncytium (e.g., liquid endosperm in coconut).

10.3 Significance of Mitosis

Mitosis or the equational division is usually restricted to the diploid cells only. However, in some lower plants and in some social insects haploid cells also divide by mitosis. It is very essential to understand the significance of this division in the life of an organism. Are you aware of some examples where you have studied about haploid and diploid insects?

Mitosis usually results in the production of diploid daughter cells with identical genetic complement. The growth of multicellular organisms is due to mitosis. Cell growth results in disturbing the ratio between the nucleus and the cytoplasm. It therefore becomes essential for the cell to divide to restore the nucleo-cytoplasmic ratio. A very significant contribution of mitosis is cell repair. The cells of the upper layer of the epidermis, cells of the lining of the gut, and blood cells are being constantly replaced. Mitotic divisions in the meristematic tissues – the apical and the lateral cambium, result in a continuous growth of plants throughout their life.

10.4 MEIOSIS

The production of offspring by sexual reproduction includes the fusion of two gametes, each with a complete haploid set of chromosomes. Gametes are formed from specialised diploid cells. This specialised kind of cell division that reduces the chromosome number by half results in the production of haploid daughter cells. This kind of division is called **meiosis**. Meiosis ensures the production of haploid phase in the life cycle of sexually reproducing organisms whereas fertilisation restores the diploid phase. We come across meiosis during gametogenesis in plants and animals. This leads to the formation of haploid gametes. The key features of meiosis are as follows:

- Meiosis involves two sequential cycles of nuclear and cell division called **meiosis I** and **meiosis II** but only a single cycle of DNA replication.
- Meiosis I is initiated after the parental chromosomes have replicated to produce identical sister chromatids at the S phase.
- Meiosis involves pairing of homologous chromosomes and recombination between them.
- Four haploid cells are formed at the end of meiosis II.

Meiotic events can be grouped under the following phases:

Meiosis I	Meiosis II
Prophase I	Prophase II
Metaphase I	Metaphase II
Anaphase I	Anaphase II
Telophase I	Telophase II

10.4.1 Meiosis I

Prophase I: Prophase of the first meiotic division is typically longer and more complex when compared to prophase of mitosis. It has been further subdivided into the following five phases based on chromosomal behaviour, i.e., Leptotene, Zygotene, Pachytene, Diplotene and Diakinesis.

During **leptotene** stage the chromosomes become gradually visible under the light microscope. The compaction of chromosomes continues throughout leptotene. This is followed by the second stage of prophase I called **zygotene**. During this stage chromosomes start pairing together and this process of association is called synapsis. Such paired chromosomes are called homologous chromosomes. Electron micrographs of this stage indicate that chromosome synapsis is accompanied by the formation of complex structure called **synaptonemal complex**. The complex formed by a pair of synapsed homologous chromosomes is called a **bivalent** or a tetrad. However, these are more clearly visible at the next stage. The first two stages of prophase I are relatively short-lived compared to the next stage that is **pachytene**. During this stage bivalent chromosomes now clearly appears as tetrads. This stage is characterised by the appearance of recombination nodules, the sites at which crossing over occurs between non-sister chromatids of the homologous chromosomes. Crossing over is the exchange of genetic material between two homologous chromosomes. Crossing over is also an enzyme-mediated process and the enzyme involved is called recombinase. Crossing over leads to recombination of genetic material on the two chromosomes. Recombination between homologous chromosomes is completed by the end of pachytene, leaving the chromosomes linked at the sites of crossing over.

The beginning of **diplotene** is recognised by the dissolution of the synaptonemal complex and the tendency of the recombined homologous chromosomes of the bivalents to separate from each other except at the sites of crossovers. These X-shaped structures, are called **chiasmata**. In oocytes of some vertebrates, diplotene can last for months or years.

The final stage of meiotic prophase I is **diakinesis**. This is marked by terminalisation of chiasmata. During this phase the chromosomes are fully condensed and the meiotic spindle is assembled to prepare the homologous chromosomes for separation. By the end of diakinesis, the nucleolus disappears and the nuclear envelope also breaks down. Diakinesis represents transition to metaphase.

Metaphase I: The bivalent chromosomes align on the equatorial plate (Figure 10.3). The microtubules from the opposite poles of the spindle attach to the pair of homologous chromosomes.

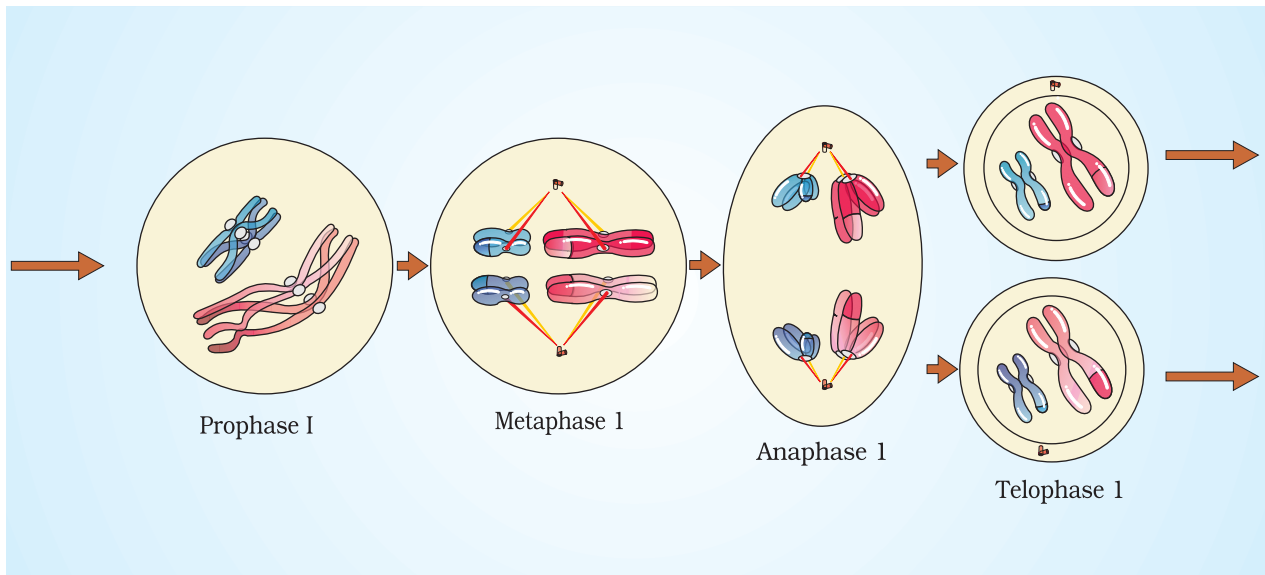


Figure 10.3 Stages of Meiosis I

Anaphase I: The homologous chromosomes separate, while sister chromatids remain associated at their centromeres (Figure 10.3).

Telophase I: The nuclear membrane and nucleolus reappear, cytokinesis follows and this is called as dyad of cells (Figure 10.3). Although in many cases the chromosomes do undergo some dispersion, they do not reach the extremely extended state of the interphase nucleus. The stage between the two meiotic divisions is called interkinesis and is generally short lived. Interkinesis is followed by prophase II, a much simpler prophase than prophase I.

10.4.2 Meiosis II

Prophase II: Meiosis II is initiated immediately after cytokinesis, usually before the chromosomes have fully elongated. In contrast to meiosis I, meiosis II resembles a normal mitosis. The nuclear membrane disappears by the end of prophase II (Figure 10.4). The chromosomes again become compact.

Metaphase II: At this stage the chromosomes align at the equator and the microtubules from opposite poles of the spindle get attached to the kinetochores (Figure 10.4) of sister chromatids.

Anaphase II: It begins with the simultaneous splitting of the centromere of each chromosome (which was holding the sister chromatids together), allowing them to move toward opposite poles of the cell (Figure 10.4).

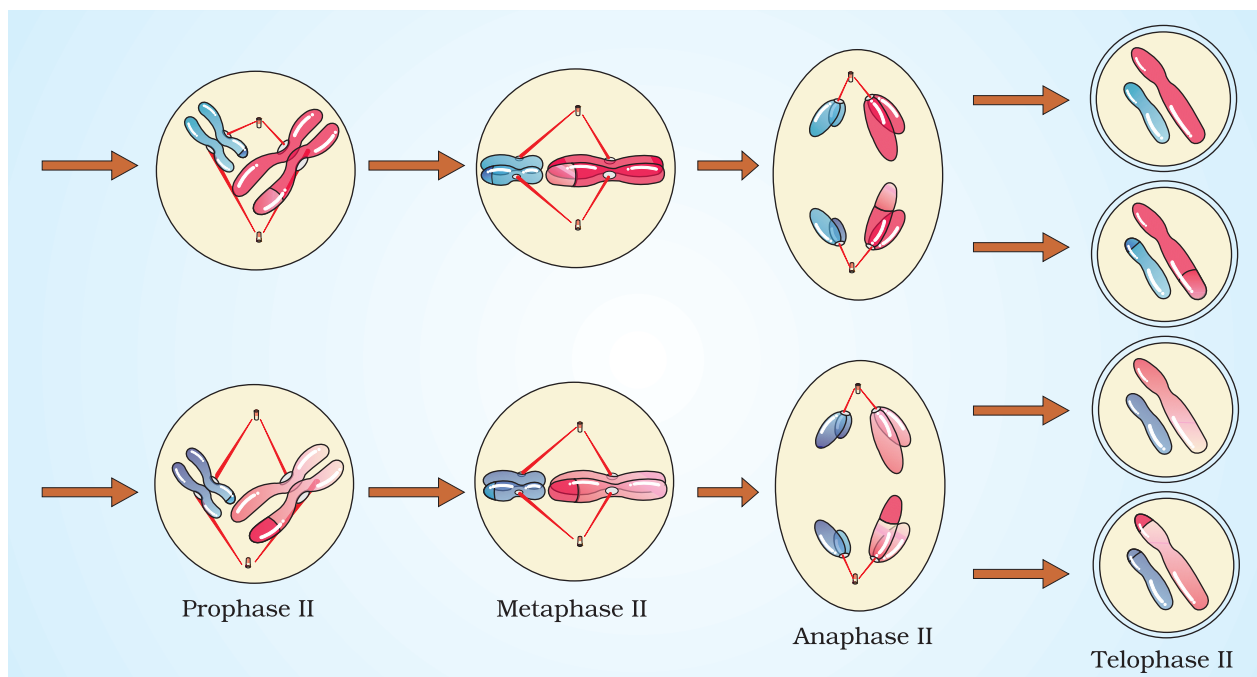


Figure 10.4 Stages of Meiosis II

Telophase II: Meiosis ends with telophase II, in which the two groups of chromosomes once again get enclosed by a nuclear envelope; cytokinesis follows resulting in the formation of tetrad of cells i.e., four haploid daughter cells (Figure 10.4).

10.5 SIGNIFICANCE OF MEIOSIS

Meiosis is the mechanism by which conservation of specific chromosome number of each species is achieved across generations in sexually reproducing organisms, even though the process, per se, paradoxically, results in reduction of chromosome number by half. It also increases the genetic variability in the population of organisms from one generation to the next. Variations are very important for the process of evolution.

SUMMARY

According to the cell theory, cells arise from preexisting cells. The process by which this occurs is called cell division. Any sexually reproducing organism starts its life cycle from a single-celled zygote. Cell division does not stop with the formation of the mature organism but continues throughout its life cycle.

The stages through which a cell passes from one division to the next is called the cell cycle. Cell cycle is divided into two phases called (i) Interphase – a period of preparation for cell division, and (ii) Mitosis (M phase) – the actual period of cell division. Interphase is further subdivided into G_1 , S and G_2 . G_1 phase is the period when the cell grows and carries out normal metabolism. Most of the organelle duplication also occurs during this phase. S phase marks the phase of DNA replication and chromosome duplication. G_2 phase is the period of cytoplasmic growth. Mitosis is also divided into four stages namely prophase, metaphase, anaphase and telophase. Chromosome condensation occurs during prophase. Simultaneously, the centrioles move to the opposite poles. The nuclear envelope and the nucleolus disappear and the spindle fibres start appearing. Metaphase is marked by the alignment of chromosomes at the equatorial plate. During anaphase the centromeres divide and the chromatids start moving towards the two opposite poles. Once the chromatids reach the two poles, the chromosomal elongation starts, nucleolus and the nuclear membrane reappear. This stage is called the telophase. Nuclear division is then followed by the cytoplasmic division and is called cytokinesis. Mitosis thus, is the equational division in which the chromosome number of the parent is conserved in the daughter cell.

In contrast to mitosis, meiosis occurs in the diploid cells, which are destined to form gametes. It is called the reduction division since it reduces the chromosome number by half while making the gametes. In sexual reproduction when the two gametes fuse the chromosome number is restored to the value in the parent. Meiosis is divided into two phases – meiosis I and meiosis II. In the first meiotic division the homologous chromosomes pair to form bivalents, and undergo crossing over. Meiosis I has a long prophase, which is divided further into five phases. These are leptotene, zygotene, pachytene, diplotene and diakinesis. During metaphase I the bivalents arrange on the equatorial plate. This is followed by anaphase I in which homologous chromosomes move to the opposite poles with both their chromatids. Each pole receives half the chromosome number of the parent cell. In telophase I, the nuclear membrane and nucleolus reappear. Meiosis II is similar to mitosis. During anaphase II the sister chromatids separate. Thus at the end of meiosis four haploid cells are formed.

EXERCISES

1. What is the average cell cycle span for a mammalian cell?
2. Distinguish cytokinesis from karyokinesis.
3. Describe the events taking place during interphase.
4. What is G_0 (quiescent phase) of cell cycle?

5. Why is mitosis called equational division?
6. Name the stage of cell cycle at which one of the following events occur:
 - (i) Chromosomes are moved to spindle equator.
 - (ii) Centromere splits and chromatids separate.
 - (iii) Pairing between homologous chromosomes takes place.
 - (iv) Crossing over between homologous chromosomes takes place.
7. Describe the following:
 - (a) synapsis (b) bivalent (c) chiasmataDraw a diagram to illustrate your answer.
8. How does cytokinesis in plant cells differ from that in animal cells?
9. Find examples where the four daughter cells from meiosis are equal in size and where they are found unequal in size.
10. Distinguish anaphase of mitosis from anaphase I of meiosis.
11. List the main differences between mitosis and meiosis.
12. What is the significance of meiosis?
13. Discuss with your teacher about
 - (i) haploid insects and lower plants where cell-division occurs, and
 - (ii) some haploid cells in higher plants where cell-division does not occur.
14. Can there be mitosis without DNA replication in 'S' phase?
15. Can there be DNA replication without cell division?
16. Analyse the events during every stage of cell cycle and notice how the following two parameters change
 - (i) number of chromosomes (N) per cell
 - (ii) amount of DNA content (C) per cell



UNIT 4

PLANT PHYSIOLOGY

Chapter 11
Transport in Plants

Chapter 12
Mineral Nutrition

Chapter 13
Photosynthesis in Higher
Plants

Chapter 14
Respiration in Plants

Chapter 15
Plant Growth and
Development

The description of structure and variation of living organisms over a period of time, ended up as two, apparently irreconcilable perspectives on biology. The two perspectives essentially rested on two levels of organisation of life forms and phenomena. One described at organismic and above level of organisation while the second described at cellular and molecular level of organisation. The first resulted in ecology and related disciplines. The second resulted in physiology and biochemistry. Description of physiological processes, in flowering plants as an example, is what is given in the chapters in this unit. The processes of mineral nutrition of plants, photosynthesis, transport, respiration and ultimately plant growth and development are described in molecular terms but in the context of cellular activities and even at organism level. Wherever appropriate, the relation of the physiological processes to environment is also discussed.



Melvin Calvin

MELVIN CALVIN born in Minnesota in April, 1911, received his Ph.D. in Chemistry from the University of Minnesota. He served as Professor of Chemistry at the University of California, Berkeley.

Just after world war II, when the world was under shock after the Hiroshima-Nagasaki bombings, and seeing the ill-effects of radio-activity, Calvin and co-workers put radio-activity to beneficial use. He along with J.A. Bassham studied reactions in green plants forming sugar and other substances from raw materials like carbon dioxide, water and minerals by labelling the carbon dioxide with C^{14} . Calvin proposed that plants change light energy to chemical energy by transferring an electron in an organised array of pigment molecules and other substances. The mapping of the pathway of carbon assimilation in photosynthesis earned him Nobel Prize in 1961.

The principles of photosynthesis as established by Calvin are, at present, being used in studies on renewable resource for energy and materials and basic studies in solar energy research.

CHAPTER 11

TRANSPORT IN PLANTS

- 11.1 *Means of Transport*
- 11.2 *Plant-Water Relations*
- 11.3 *Long Distance Transport of Water*
- 11.4 *Transpiration*
- 11.5 *Uptake and Transport of Mineral Nutrients*
- 11.6 *Phloem Transport: Flow from Source to Sink*

Have you ever wondered how water reaches the top of tall trees, or for that matter how and why substances move from one cell to the other, whether all substances move in a similar way, in the same direction and whether metabolic energy is required for moving substances. Plants need to move molecules over very long distances, much more than animals do; they also do not have a circulatory system in place. Water taken up by the roots has to reach all parts of the plant, up to the very tip of the growing stem. The photosynthates or food synthesised by the leaves have also to be moved to all parts including the root tips embedded deep inside the soil. Movement across short distances, say within the cell, across the membranes and from cell to cell within the tissue has also to take place. To understand some of the transport processes that take place in plants, one would have to recollect one's basic knowledge about the structure of the cell and the anatomy of the plant body. We also need to revisit our understanding of diffusion, besides gaining some knowledge about chemical potential and ions.

When we talk of the movement of substances we need first to define what kind of movement we are talking about, and also what substances we are looking at. In a flowering plant the substances that would need to be transported are water, mineral nutrients, organic nutrients and plant growth regulators. Over small distances substances move by diffusion and by cytoplasmic streaming supplemented by active transport. Transport over longer distances proceeds through the vascular system (the xylem and the phloem) and is called **translocation**.

An important aspect that needs to be considered is the direction of transport. In rooted plants, transport in xylem (of water and minerals) is essentially unidirectional, from roots to the stems. Organic and mineral nutrients however, undergo multidirectional transport. Organic

compounds synthesised in the photosynthetic leaves are exported to all other parts of the plant including storage organs. From the storage organs they are later re-exported. The mineral nutrients are taken up by the roots and transported upwards into the stem, leaves and the growing regions. When any plant part undergoes senescence, nutrients may be withdrawn from such regions and moved to the growing parts. Hormones or plant growth regulators and other chemical stimuli are also transported, though in very small amounts, sometimes in a strictly polarised or unidirectional manner from where they are synthesised to other parts. Hence, in a flowering plant there is a complex traffic of compounds (but probably very orderly) moving in different directions, each organ receiving some substances and giving out some others.

11.1 MEANS OF TRANSPORT

11.1.1 Diffusion

Movement by **diffusion** is passive, and may be from one part of the cell to the other, or from cell to cell, or over short distances, say, from the inter-cellular spaces of the leaf to the outside. No energy expenditure takes place. In diffusion, molecules move in a random fashion, the net result being substances moving from regions of higher concentration to regions of lower concentration. Diffusion is a slow process and is not dependent on a 'living system'. Diffusion is obvious in gases and liquids, but diffusion *in solids* rather than *of solids* is more likely. Diffusion is very important to plants since it is the only means for gaseous movement within the plant body.

Diffusion rates are affected by the gradient of concentration, the permeability of the membrane separating them, temperature and pressure.

11.1.2 Facilitated Diffusion

As pointed out earlier, a gradient must already be present for diffusion to occur. The diffusion rate depends on the size of the substances; obviously smaller substances diffuse faster. The diffusion of any substance across a membrane also depends on its solubility in lipids, the major constituent of the membrane. Substances soluble in lipids diffuse through the membrane faster. Substances that have a hydrophilic moiety, find it difficult to pass through the membrane; their movement has to be facilitated. Membrane proteins provide sites at which such molecules cross the membrane. They do not set up a concentration gradient: a concentration gradient must already be present for molecules to diffuse even if facilitated by the proteins. This process is called **facilitated diffusion**.

In facilitated diffusion special proteins help move substances across membranes without expenditure of ATP energy. Facilitated diffusion cannot cause net transport of molecules from a low to a high concentration – this would require input of energy. Transport rate reaches a maximum when all of the protein transporters are being used (saturation). Facilitated

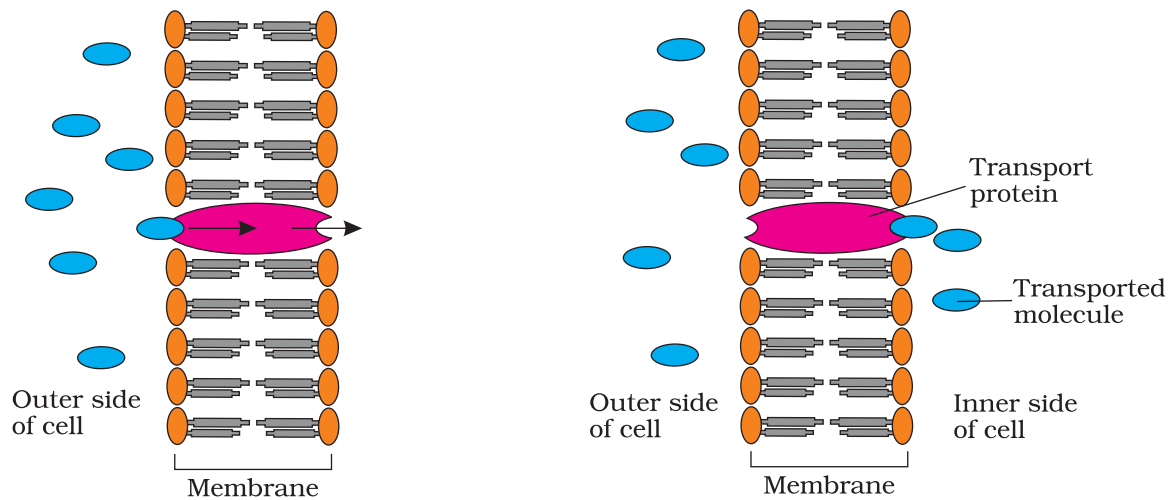


Figure 11.1 Facilitated diffusion

diffusion is very specific: it allows cell to select substances for uptake. It is sensitive to inhibitors which react with protein side chains.

The proteins form channels in the membrane for molecules to pass through. Some channels are always open; others can be controlled. Some are large, allowing a variety of molecules to cross. The **porins** are proteins that form huge pores in the outer membranes of the plastids, mitochondria and some bacteria allowing molecules up to the size of small proteins to pass through.

Figure 11.1 shows an extracellular molecule bound to the transport protein; the transport protein then rotates and releases the molecule inside the cell, e.g., water channels – made up of eight different types of **aquaporins**.

11.1.2.1 *Passive symports and antiports*

Some carrier or transport proteins allow diffusion only if two types of molecules move together. In a **symport**, both molecules cross the membrane in the same direction; in an **antiport**, they move in opposite directions (Figure 11.2). When a

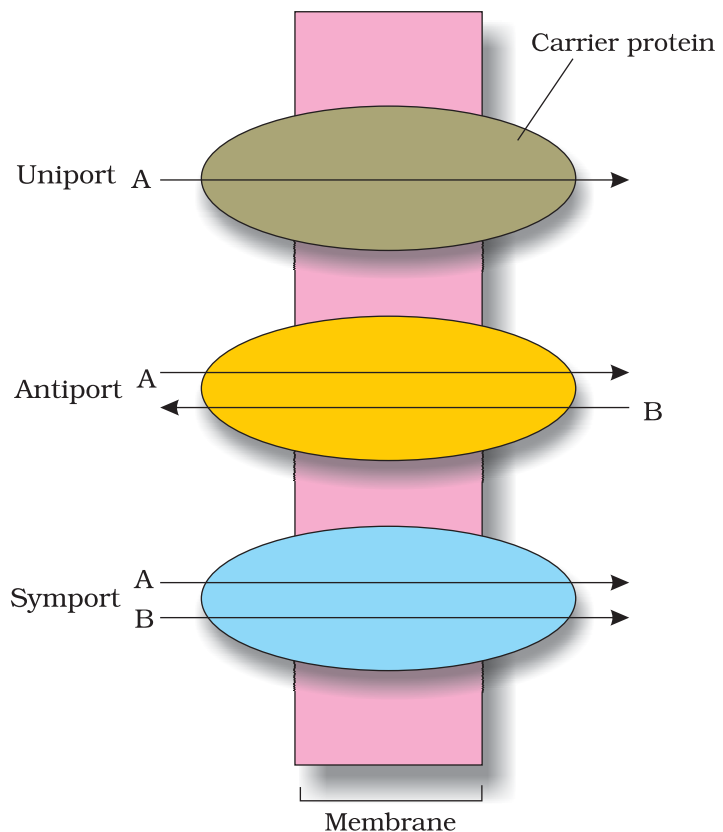


Figure 11.2 Facilitated diffusion

molecule moves across a membrane independent of other molecules, the process is called **uniport**.

11.1.3 Active Transport

Active transport uses energy to pump molecules against a concentration gradient. Active transport is carried out by membrane-proteins. Hence different proteins in the membrane play a major role in both active as well as passive transport. Pumps are proteins that use energy to carry substances across the cell membrane. These pumps can transport substances from a low concentration to a high concentration ('uphill' transport). Transport rate reaches a maximum when all the protein transporters are being used or are saturated. Like enzymes the carrier protein is very specific in what it carries across the membrane. These proteins are sensitive to inhibitors that react with protein side chains.

11.1.4 Comparison of Different Transport Processes

Table 11.1 gives a comparison of the different transport mechanisms. Proteins in the membrane are responsible for facilitated diffusion and active transport and hence show common characteristics of being highly selective; they are liable to saturate, respond to inhibitors and are under hormonal regulation. But diffusion whether facilitated or not – take place only along a gradient and do not use energy.

TABLE 11.1 Comparison of Different Transport Mechanisms

Property	Simple Diffusion	Facilitated Transport	Active Transport
Requires special membrane proteins	No	Yes	Yes
Highly selective	No	Yes	Yes
Transport saturates	No	Yes	Yes
Uphill transport	No	No	Yes
Requires ATP energy	No	No	Yes

11.2 PLANT-WATER RELATIONS

Water is essential for all physiological activities of the plant and plays a very important role in all living organisms. It provides the medium in which most substances are dissolved. The protoplasm of the cells is nothing but water in which different molecules are dissolved and (several particles) suspended. A watermelon has over 92 per cent water; most herbaceous plants have only about 10 to 15 per cent of its fresh weight as dry matter. Of course, distribution of water within a plant varies – woody parts have relatively very little water, while soft parts mostly contain

water. A seed may appear dry but it still has water – otherwise it would not be alive and respiring!

Terrestrial plants take up huge amount water daily but most of it is lost to the air through evaporation from the leaves, i.e., **transpiration**. A mature corn plant absorbs almost three litres of water in a day, while a mustard plant absorbs water equal to its own weight in about 5 hours. Because of this high demand for water, it is not surprising that water is often the limiting factor for plant growth and productivity in both agricultural and natural environments.

11.2.1 Water Potential

To comprehend plant-water relations, an understanding of certain standard terms is necessary. **Water potential (Ψ_w)** is a concept fundamental to understanding water movement. **Solute potential (Ψ_s)** and **pressure potential (Ψ_p)** are the two main components that determine water potential.

Water molecules possess kinetic energy. In liquid and gaseous form they are in random motion that is both rapid and constant. The greater the concentration of water in a system, the greater is its kinetic energy or 'water potential'. Hence, it is obvious that pure water will have the greatest water potential. If two systems containing water are in contact, random movement of water molecules will result in net movement of water molecules from the system with higher energy to the one with lower energy. Thus water will move from the system containing water at higher water potential to the one having low water potential. This process of movement of substances down a gradient of free energy is called diffusion. Water potential is denoted by the Greek symbol Psi or Ψ and is expressed in pressure units such as pascals (Pa). By convention, the water potential of pure water at standard temperatures, which is not under any pressure, is taken to be zero.

If some solute is dissolved in pure water, the solution has fewer free water and the concentration of water decreases, reducing its water potential. Hence, all solutions have a lower water potential than pure water; the magnitude of this lowering due to dissolution of a solute is called **solute potential** or Ψ_s . Ψ_s is always negative. The more the solute molecules, the lower (more negative) is the Ψ_s . For a solution at atmospheric pressure (water potential) $\Psi_w = (\text{solute potential}) \Psi_s$.

If a pressure greater than atmospheric pressure is applied to pure water or a solution, its water potential increases. It is equivalent to pumping water from one place to another. Can you think of any system in our body where pressure is built up? Pressure can build up in a plant system when water enters a plant cell due to diffusion causing a pressure built up against the cell wall, it makes the cell **turgid** (see section 11.2.2);

this increases the **pressure potential**. Pressure potential is usually positive, though in plants negative potential or tension in the water column in the xylem plays a major role in water transport up a stem. Pressure potential is denoted as Ψ_p .

Water potential of a cell is affected by both solute and pressure potential. The relationship between them is as follows:

$$\Psi_w = \Psi_s + \Psi_p$$

11.2.2 Osmosis

The plant cell is surrounded by a cell membrane and a cell wall. The cell wall is freely permeable to water and substances in solution hence is not a barrier to movement. In plants the cells usually contain a large central vacuole, whose contents, the vacuolar sap, contribute to the solute potential of the cell. In plant cells, the cell membrane and the membrane of the vacuole, the tonoplast together are important determinants of movement of molecules in or out of the cell.

Osmosis is the term used to refer specifically to the diffusion of water across a differentially- or semi-permeable membrane. Osmosis occurs spontaneously in response to a driving force. The net direction and rate of osmosis depends on both the **pressure gradient** and **concentration gradient**. Water will move from its region of higher chemical potential (or concentration) to its region of lower chemical potential until equilibrium is reached. At equilibrium the two chambers should have the same water potential.

You may have made a potato osmometer at some earlier stage in school. If the tuber is placed in water, the cavity in the potato tuber containing a concentrated solution of sugar collects water due to osmosis.

Study Figure 11.3 in which the two chambers, A and B, containing solutions are separated by a semi-permeable membrane.

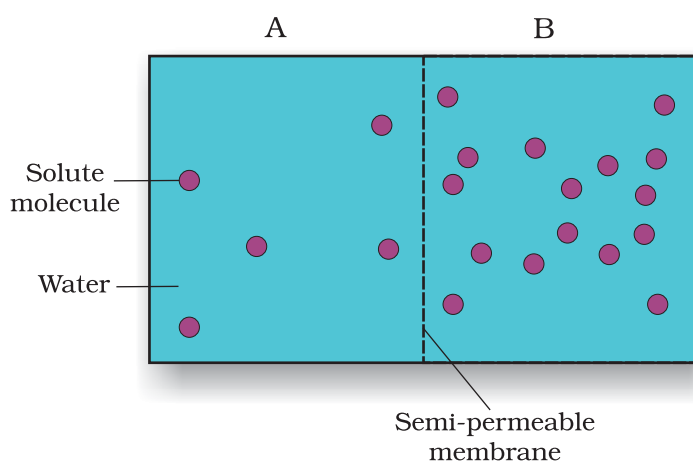


Figure 11.3

- Solution of which chamber has a lower water potential?
- Solution of which chamber has a lower solute potential?
- In which direction will osmosis occur?
- Which solution has a higher solute potential?
- At equilibrium which chamber will have lower water potential?
- If one chamber has a Ψ of -2000 kPa, and the other -1000 kPa, which is the chamber that has the higher Ψ ?

Let us discuss another experiment where a solution of sucrose in water taken in a funnel is separated from pure water in a beaker through a semi-permeable membrane (Figure 11.4). You can get this kind of a membrane in an egg. Remove the yolk and albumin through a small hole at one end of the egg, and place the shell in dilute solution of hydrochloric acid for a few hours. The egg shell dissolves leaving the membrane intact. Water will move into the funnel, resulting in rise in the level of the solution in the funnel. This will continue till the equilibrium is reached. In case sucrose does diffuse out through the membrane, will this equilibrium be ever reached?

External pressure can be applied from the upper part of the funnel such that no water diffuses into the funnel through the membrane. This pressure required to prevent water from diffusing is in fact, the osmotic pressure and this is the function of the solute concentration; more the solute concentration, greater will be the pressure required to prevent water from diffusing in. Numerically osmotic pressure is equivalent to the osmotic potential, but the sign is opposite. Osmotic pressure is the positive pressure applied, while osmotic potential is negative.

11.2.3 Plasmolysis

The behaviour of the plant cells (or tissues) with regard to water movement depends on the surrounding solution. If the external solution balances the osmotic pressure of the cytoplasm, it is said to be **isotonic**. If the external solution is more dilute than the cytoplasm, it is **hypotonic** and if the external solution is more concentrated, it is **hypertonic**. Cells swell in hypotonic solutions and shrink in hypertonic ones.

Plasmolysis occurs when water moves out of the cell and the cell membrane of a plant cell shrinks away from its cell wall. This occurs when

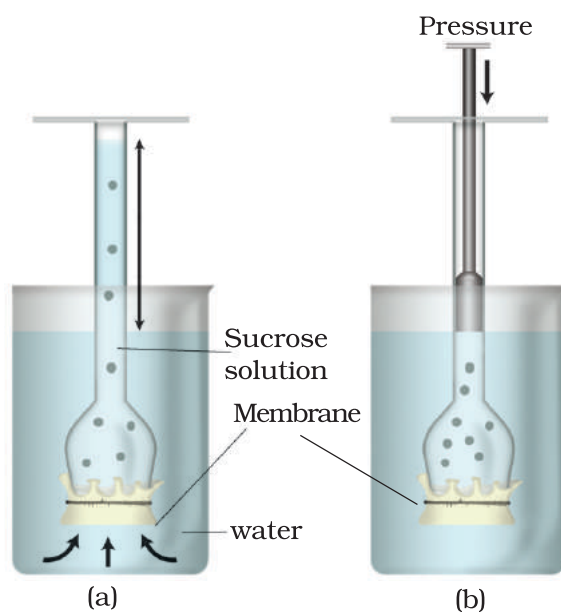


Figure 11.4 A demonstration of osmosis. A thistle funnel is filled with sucrose solution and kept inverted in a beaker containing water. (a) Water will diffuse across the membrane (as shown by arrows) to raise the level of the solution in the funnel (b) Pressure can be applied as shown to stop the water movement into the funnel

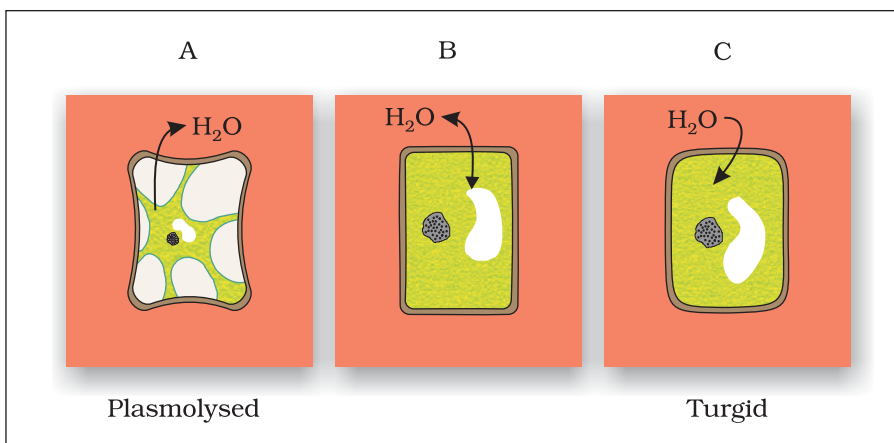


Figure 11.5 Plant cell plasmolysis

the cell (or tissue) is placed in a solution that is hypertonic (has more solutes) to the protoplasm. Water moves out; it is first lost from the cytoplasm and then from the vacuole. The water when drawn out of the cell through diffusion into the extracellular (outside cell) fluid causes the protoplast to shrink away from the walls. The cell is said to be plasmolysed. The movement of water occurred across the membrane moving from an area of high water potential (i.e., the cell) to an area of lower water potential outside the cell (Figure 11.5).

What occupies the space between the cell wall and the shrunken protoplast in the plasmolysed cell?

When the cell (or tissue) is placed in an **isotonic** solution, there is no net flow of water towards the inside or outside. If the external solution balances the osmotic pressure of the cytoplasm it is said to be isotonic. When water flows into the cell and out of the cell and are in equilibrium, the cells are said to be **flaccid**.

The process of plasmolysis is usually reversible. When the cells are placed in a **hypotonic** solution (higher water potential or dilute solution as compared to the cytoplasm), water diffuses into the cell causing the cytoplasm to build up a pressure against the wall, that is called **turgor pressure**. The pressure exerted by the protoplasts due to entry of water against the rigid walls is called pressure potential Ψ_p . Because of the rigidity of the cell wall, the cell does not rupture. This turgor pressure is ultimately responsible for enlargement and extension growth of cells.

What would be the Ψ_p of a flaccid cell? Which organisms other than plants possess cell wall?

11.2.4 Imbibition

Imbibition is a special type of diffusion when water is absorbed by solids – colloids – causing them to enormously increase in volume. The classical

examples of imbibition are absorption of water by seeds and dry wood. The pressure that is produced by the swelling of wood had been used by prehistoric man to split rocks and boulders. If it were not for the pressure due to imbibition, seedlings would not have been able to emerge out of the soil into the open; they probably would not have been able to establish!

Imbibition is also diffusion since water movement is along a concentration gradient; the seeds and other such materials have almost no water hence they absorb water easily. Water potential gradient between the absorbent and the liquid imbibed is essential for imbibition. In addition, for any substance to imbibe any liquid, affinity between the adsorbant and the liquid is also a pre-requisite.

11.3 LONG DISTANCE TRANSPORT OF WATER

At some earlier stage you might have carried out an experiment where you had placed a twig bearing white flowers in coloured water and had watched it turn colour. On examining the cut end of the twig after a few hours you had noted the region through which the coloured water moved. That experiment very easily demonstrates that the path of water movement is through the vascular bundles, more specifically, the xylem. Now we have to go further and try and understand the mechanism of movement of water and other substances up a plant.

Long distance transport of substances within a plant cannot be by diffusion alone. Diffusion is a slow process. It can account for only short distance movement of molecules. For example, the movement of a molecule across a typical plant cell (about 50 μm) takes approximately 2.5 s. *At this rate, can you calculate how many years it would take for the movement of molecules over a distance of 1 m within a plant by diffusion alone?*

In large and complex organisms, often substances have to be moved across very large distances. Sometimes the sites of production or absorption and sites of storage are too far from each other; diffusion or active transport would not suffice. Special long distance transport systems become necessary so as to move substances across long distances and at a much faster rate. Water and minerals, and food are generally moved by a **mass** or **bulk flow** system. Mass flow is the movement of substances in bulk or *en masse* from one point to another as a result of pressure differences between the two points. It is a characteristic of mass flow that substances, whether in solution or in suspension, are swept along at the same pace, as in a flowing river. This is unlike diffusion where different substances move independently depending on their concentration gradients. Bulk flow can be achieved either through a positive hydrostatic pressure gradient (e.g., a garden hose) or a negative hydrostatic pressure gradient (e.g., suction through a straw).

The bulk movement of substances through the conducting or vascular tissues of plants is called **translocation**.

Do you remember studying cross sections of roots, stems and leaves of higher plants and studying the vascular system? The higher plants have highly specialised vascular tissues – xylem and phloem. Xylem is associated with translocation of mainly water, mineral salts, some organic nitrogen and hormones, from roots to the aerial parts of the plants. The phloem translocates a variety of organic and inorganic solutes, mainly from the leaves to other parts of the plants.

11.3.1 How do Plants Absorb Water?

We know that the roots absorb most of the water that goes into plants; obviously that is why we apply water to the soil and not on the leaves. The responsibility of absorption of water and minerals is more specifically the function of the root hairs that are present in millions at the tips of the roots. Root hairs are thin-walled slender extensions of root epidermal cells that greatly increase the surface area for absorption. Water is absorbed along with mineral solutes, by the root hairs, purely by diffusion. Once water is absorbed by the root hairs, it can move deeper into root layers by two distinct pathways:

- apoplast pathway
- symplast pathway

The **apoplast** is the system of adjacent cell walls that is continuous throughout the plant, except at the **casparian** strips of the endodermis in the roots (Figure 11.6). The apoplastic movement of water occurs exclusively through the intercellular spaces and the walls of the cells. Movement through the apoplast does not involve crossing the cell

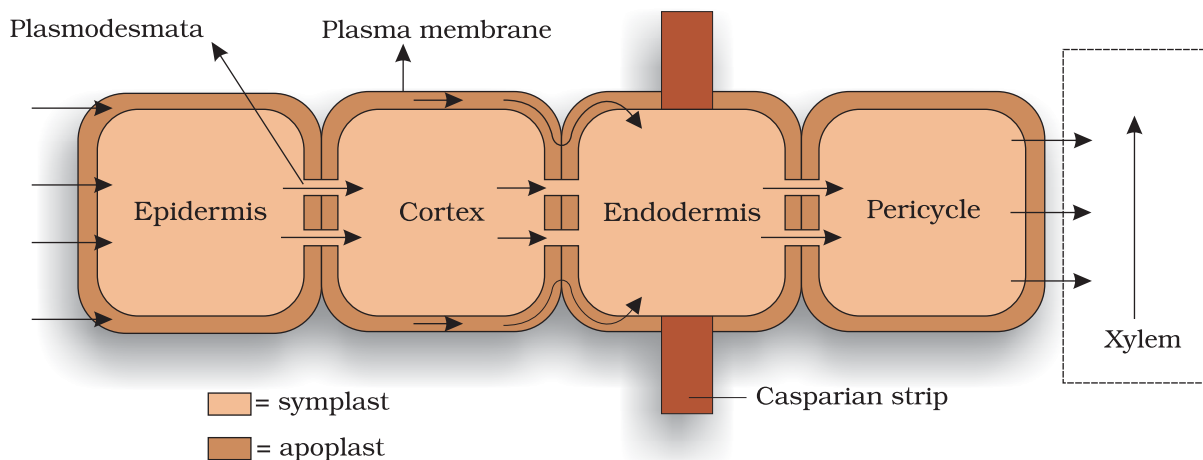


Figure 11.6 Pathway of water movement in the root

membrane. This movement is dependent on the gradient. The apoplast does not provide any barrier to water movement and water movement is through mass flow. As water evaporates into the intercellular spaces or the atmosphere, tension develops in the continuous stream of water in the apoplast, hence mass flow of water occurs due to the adhesive and cohesive properties of water.

The **symplastic** system is the system of interconnected protoplasts. Neighbouring cells are connected through cytoplasmic strands that extend through **plasmodesmata**. During symplastic movement, the water travels through the cells – their cytoplasm; intercellular movement is through the plasmodesmata. Water has to enter the cells through the cell membrane, hence the movement is relatively slower. Movement is again down a potential gradient. Symplastic movement may be aided by cytoplasmic streaming. You may have observed cytoplasmic streaming in cells of the *Hydrilla* leaf; the movement of chloroplast due to streaming is easily visible.

Most of the water flow in the roots occurs via the apoplast since the cortical cells are loosely packed, and hence offer no resistance to water movement. However, the inner boundary of the cortex, the **endodermis**, is impervious to water because of a band of suberised matrix called the **casparian strip**. Water molecules are unable to penetrate the layer, so they are directed to wall regions that are not suberised, into the cells proper through the membranes. The water then moves through the symplast and again crosses a membrane to reach the cells of the xylem. The movement of water through the root layers is ultimately symplastic in the endodermis. This is the only way water and other solutes can enter the vascular cylinder.

Once inside the xylem, water is again free to move between cells as well as through them. In young roots, water enters directly into the xylem vessels and/or tracheids. These are non-living conduits and so are parts of the apoplast. The path of water and mineral ions into the root vascular system is summarised in Figure 11.7.

Some plants have additional structures associated with them that help in water (and mineral) absorption. A **mycorrhiza** is a symbiotic association of a fungus with a root system. The fungal

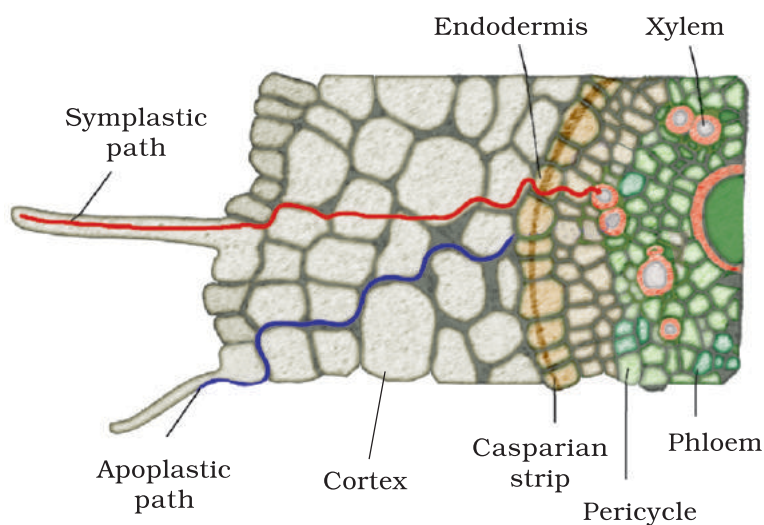


Figure 11.7 Symplastic and apoplastic pathways of water and ion absorption and movement in roots

filaments form a network around the young root or they penetrate the root cells. The hyphae have a very large surface area that absorb mineral ions and water from the soil from a much larger volume of soil that perhaps a root cannot do. The fungus provides minerals and water to the roots, in turn the roots provide sugars and N-containing compounds to the mycorrhizae. Some plants have an obligate association with the mycorrhizae. For example, *Pinus* seeds cannot germinate and establish without the presence of mycorrhizae.

11.3.2 Water Movement up a Plant

We looked at how plants absorb water from the soil, and move it into the vascular tissues. We now have to try and understand how this water is transported to various parts of the plant. Is the water movement active, or is it still passive? Since the water has to be moved up a stem against gravity, what provides the energy for this?

11.3.2.1 Root Pressure

As various ions from the soil are actively transported into the vascular tissues of the roots, water follows (its potential gradient) and increases the **pressure** inside the xylem. This positive pressure is called **root pressure**, and can be responsible for pushing up water to small heights in the stem. How can we see that root pressure exists? Choose a small soft-stemmed plant and on a day, when there is plenty of atmospheric moisture, cut the stem horizontally near the base with a sharp blade, early in the morning. You will soon see drops of solution ooze out of the cut stem; this comes out due to the positive root pressure. If you fix a rubber tube to the cut stem as a sleeve you can actually collect and measure the rate of exudation, and also determine the composition of the exudates. Effects of root pressure is also observable at night and early morning when evaporation is low, and excess water collects in the form of droplets around special openings of veins near the tip of grass blades, and leaves of many herbaceous parts. Such water loss in its liquid phase is known as **guttation**.

Root pressure can, at best, only provide a modest push in the overall process of water transport. They obviously do not play a major role in water movement up tall trees. The greatest contribution of root pressure may be to re-establish the continuous chains of water molecules in the xylem which often break under the enormous tensions created by transpiration. Root pressure does not account for the majority of water transport; most plants meet their need by transpiratory pull.

11.3.2.2 Transpiration pull

Despite the absence of a heart or a circulatory system in plants, the flow of water upward through the xylem in plants can achieve fairly high rates,