UNIT 11 PLANT WATER RELATIONS

Structure

11.1 INTRODUCTION

At one time it was thought that man would be able to colonise the moon and other planets. However, even before man landed on moon his hope was shattered. The reason, neither there was the atmosphere containing gases which sustain us on the earth nor was there any water which is essential for life. Life originated in water of the oceans and water remains a key molecule in maintaining life on earth.

The intimate relationship between water and plant is apparent from the greenery in areas where water is abundant and barren deserts in areas where it is in extreme deficit. Among the environmental factors — light, temperature, water and soil, it is the water that limits plant growth in virtually all environments.

The quantity of water absorbed by plant is enormous and is far greater than taken by animals of the same weight. This is because the loss of water by plants through transpiration is enormous. A major challenge before plant physiologists is to find ways to decrease water losses and increase the efficiency of water use by the plants.

Plants can move water to great heights in trees. Even the tallest tree *Sequoia sempervirens* (113.1m, and still growing) found in California faces no problem in moving water to its top leaves. This was puzzling for the scientists. They tried to find out the forces that move water to such great heights.

We have the following questions before us with regard to water relations of plants:

i) What is the force that drives the flow and direction of water in plants? ii) What are the forces that drive water to great heights in trees? iii) What are the factors that control the opening and closure of stomatal aperture? and iv) Why do plants transpire so much water in an apparently wasteful way?

In this unit we will try to find answer to these questions.

Objectives

- describe early experiments on water movement through vascular plants,
- explain the cohesion-tension theory of water movement in plants,
- draw and explain radial movement of water from soil to roots and long distance transport from xylem to leaves,
- describe the factors that affect water potential and explain their significance in the transport of water in soil-plant-atmosphere system.
- explain how differences in water potential, $\Delta\psi_w$, affect the direction of water movement,
- calculate ψ_π, ψ_p, $\Delta\psi_w$, water flux and resistance using mathematical expression;

- discuss various resistances that impede water flow in plant and explain their significance to the plant,
- describe the factors that affect water absorption and water loss,
- relate the structure and properties of stomata to their function,
- explain how changes in turgor bring about opening and closure of stomata,
- explain the causes that alter the relative turgor in the guard cells, and
- list factors that control movement of stomatal aperture.

11.2 PLANT WATER

Role of Water in Plants

You know that water is the main constituent of plant cells. It performs the following major functions.

i) Water as a Solvent

Water is a very good solvent. It easily dissolves electrolytes and small molecules such as glucose and amino acids. As you know life evolved as a result of chemical reactions that occurred in aqueous medium of the oceans and even today we know that all reactions in a cell occur in aqueous medium.

ii) Water as a Chemical Reactant

Water participates in many biochemical reactions. It is involved in photosynthesis, the most important process of life. The photochemical splitting of water evolves oxygen, and the hydrogen atoms are denotated to CO_2 for making glucose. During catabolism, carbohydrates, fats and proteins require water for hydrolyses. In the course of your study, you will come across many other biochemical reactions which also involve water.

iii) Water Provides Turgidity to the Cells

Plants maintain their shape due to turgidity which is brought about by the hydrostatic pressure of water in the cells. If water moves out, the cells become flaccid (Fig. 11.1). Hydrostatic pressure is also necessary for the enlargement of cells and as a consequence growth results.

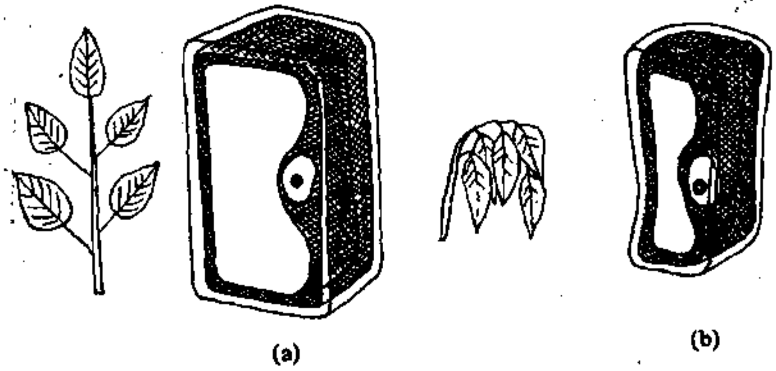


Fig. 11.1 : Cells of a normal (a) and a wilted plant (b). In fully turgid plant the central vacuole of each cell is filled with water and the protoplasm is pushed towards the cell wall, stretching it tight, while in the wilted plant the cell walls may partially deflate after the vacuole shrinks.

How much Water is Present in Plants?

The amount of water in plants varies among different species depending upon their structure. Aquatic plants such as *Chlamydomonas, Spirogyra, Chara,* red algae and others contain 97-98% of their weight as water. This is true also of *Azolla, Eichhornia* and other fresh water plants. However, among terrestrial plants, whether they are crops such as wheat, rice, maize, or trees such as sheesham, mango, neem and others, the amount of water varies in different plant parts. It would be as high as 95% or more in young roots and as low as 30-40% in wood of a tree trunk. Young leaves often contain 85-90% water whereas mature leaves contain 60-80%. This means that the amount of water changes during the growth of the plant as well as during the growth of an organ such as leaf and seed.

Relation of Water Content to Functions

If an aquatic plant appearing turgid is removed from water and left in the open, it quickly wilts. The water content of the leaves may change hardly by 3 to 5 per cent but the plant looks functionless. This is also true for young leaves of wheat which have 90-95% water, they wilt if water content drops by 3-4 per cent. However, an older leaf has only 80-85% water but is fully turgid. Thus, water content cannot be the basis of judging the activity of leaves. Therefore, it is necessary to have an expression for plant water status which could be related to plant function. We will discuss this in one of the sections later.

11.3 EARLY HISTORY OF ASCENT OF SAP

It is a familiar fact that water runs downhill. But plants can raise water upwards from soil by roots to great heights of trees. This was one of the puzzles of early plant physiologists. They tried to know what the forces are that drive water upwards. They considered two possibilities : i) water is either pushed up by the driving forces that might develop at the bottom (roots) or ii) it is pulled up by the forces created at the top (leaf) of the plant.

Even 400 years ago, it was recognised that it is the xylem conduits and not the phloem that translocate water in plants. It was Italian anatomist, Marcello Malpighi who in 1679 demonstrated that if a ring of phloem was removed from the stem the path of water was unaffected. Water moves through dead xylem cells was shown by Edward Strasburger in 1883 who sawed an oak tree and placed it in a bucket of water containing picric acid or $CuSO_4$. Though the chemical killed the bark and other living cells the movement of water was uninterrupted. Experiments have also been done using coloured or radioactive water. The water is observed to move into the root system and upward through xylem. Now, we know that xylem vessels form an intricate plumbing network whose supply lines extend to all parts of the plant.

Water has a great tensile strength
Theoretical calculations, from heats of evaporation and surface tension, indicate a tensile strength for water of several thousand atmospheres. Experimental values, however, are somewhat lower, ranging from 25 to 300 atmospheres. In one illustrative experiment the British investigator H.M. Budgett wrung two polished steel plates together with a film of water between them. Tensions of up to 60 kilograms per square centimeter was required to pull the plates apart.

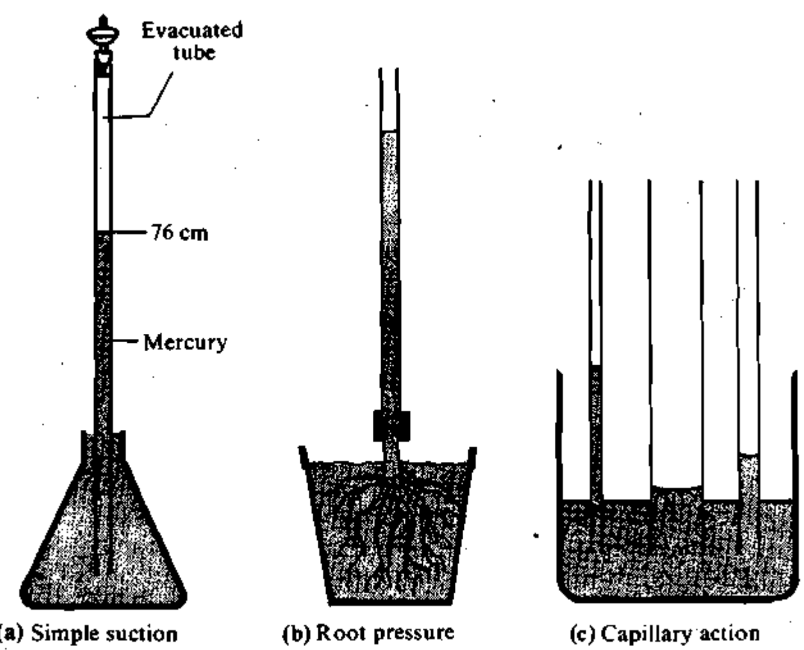


Fig. 11.2 : Experiments on water movement through vascular plants. a) Simple suction — mercury is raised 76 cm up in an evacuated tube by atmospheric pressure. b) Root pressure — a glass tube is fitted on the cut stem of a potted plant. The soil is kept well watered. Root pressure forces water to exude out from the cut stem and up the tube. The water column may rise up to a height of 14 m or more. c) Capillary action — water rises in the capillary tube due to high surface tension of water. The greater the surface tension greater the rise in the capillary.

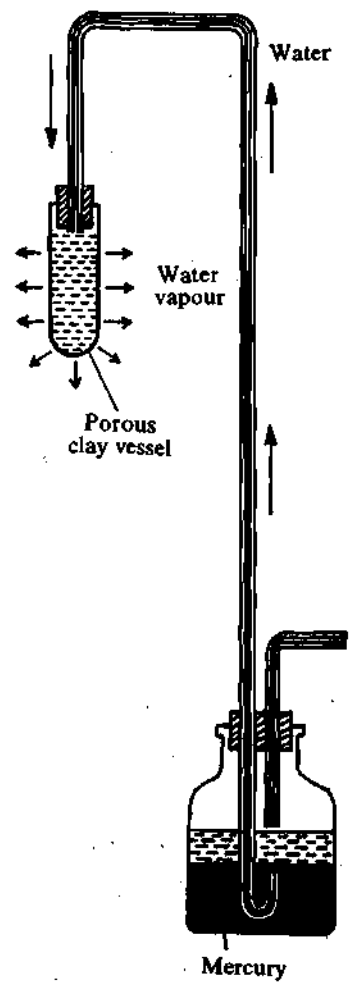


Fig. 11.3 : Demonstration of the principle of water movement up the plant stem by a physical model. Evaporation of water from the porous clay pot exerts more pulling force than simple suction. It can pull mercury behind it to a height of more than 100 cm.

For investigating which of the forces were responsible for the upward movement of water, initially forces such as atmospheric pressure, capillary action and root pressure were considered (Fig. 11.2 a, b and c). But none of these forces could account for the movement of water beyond a height of 100 cm. It was an Irish Botanist Josef Bohm (1883) who demonstrated by a simple experiment that if water were to be evaporated from a closed system like a porous pot connected to a set up as shown in Fig. 11.3, mercury could be lifted to a height of more than 100 cm, considerably

Guttation
Under certain environmental conditions root pressure forces water through special water pores around the edge of the leaves or at the tip. This is known as **guttation**.

higher than 76 cm to which it can be pulled by a vacuum. Irish Botanist H.H. Dixon and his collaborator J. Joly repeated the same experiment using a transpiring pine leaf instead of a porous pot and got the same results. A similar experiment shown in Fig. 11.4 illustrates the rise of water in plants. Dixon and Joly (1895) then proposed the now famous **cohesion theory of ascent of sap.**

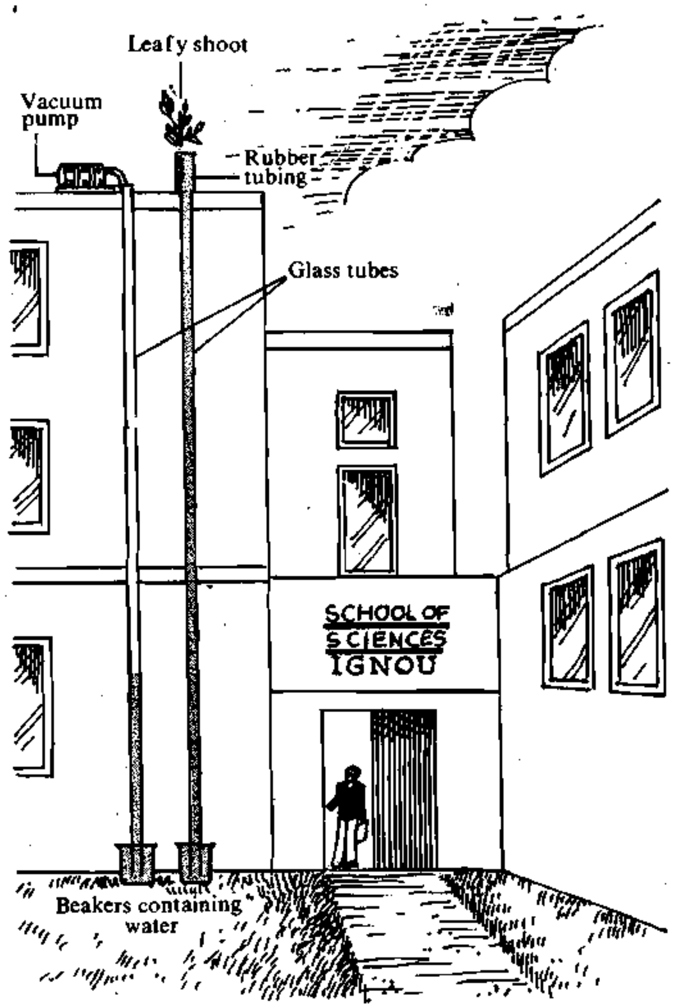


Fig. 11.4 : Experiment to show the cohesion-tension theory of water movement in the plant. Two long slender tubes dipped in water from below are extended up to the height of the building. A vacuum pump fails to suction the water to this height while a tiny leafy shoot succeeds. A short piece of rubber tubing is used to connect the cut tip of a leafy shoot to a slender glass tubing (14m length and 0.5 mm in diameter) which is dipped in a beaker containing water and dye. The entire system is made continuous water filled air proof system.

You are aware that plants lose water through stomatal openings by the process of transpiration. Dixon's theory suggests that water can be continuously pulled upward due to the transpiration pull. As the water molecules vacate transpiration sites (the mesophyll cells of leaf lining stomata) due to evaporation, other water molecules are pulled to fill their places. This results in the creation of a negative hydrostatic pressure downward extending from leaves to the xylem vessels and finally to the roots. In other words, a state of water tension is created inside the xylem conduits. The water molecules do not snap away from each other due to tension in the xylem, instead they travel as a continuous column due to their cohesive property. Cohesion is a phenomenon by which water molecules cling tightly to one another by hydrogen bonds (Fig. 11.5) and resist being pulled apart. If water is indeed moving through an upward pull, it would be expected to recede in the xylem, if its continuum is broken by cutting a branch above the ground level. The state of water in xylem is more or less analogous to a stretched rubber band. Suppose if we cut a stretched rubber band at some point, it would immediately recede in both direction from the point where it is cut. A similar receding occurs in xylem vessels and water pulls away from the cut point. The pulling force of water column or tension in the xylem can be measured by a Scholander pressure bomb (Fig. 11.6) by forcing the xylem sap back to the original point by applying pressure.

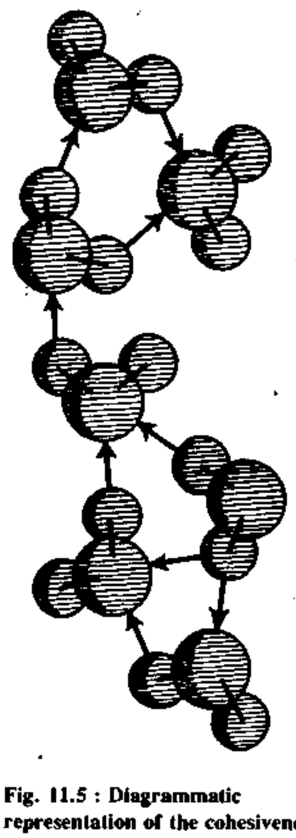


Fig. 11.5 : Diagrammatic representation of the cohesiveness of water molecules due to hydrogen bonds. Water molecules cling together due to electrostatic attraction between the partial negative charge on the oxygen atom of one water molecule and the partial positive charge on the hydrogen atom of an adjacent water molecule.

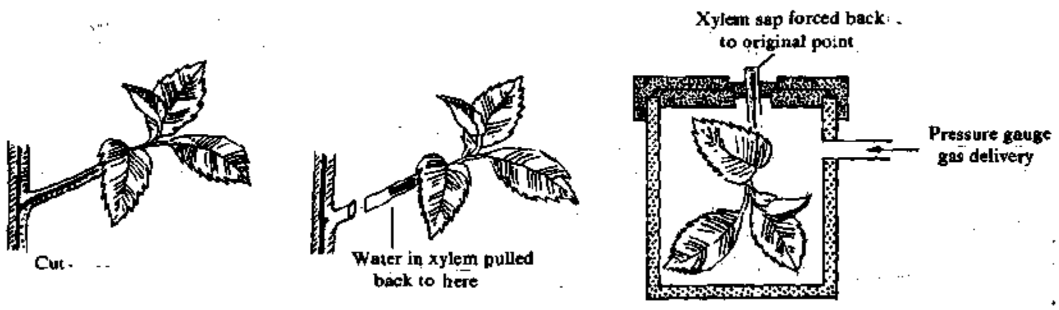


Fig. 11.6 : Demonstration of tension in xylem sap. When a twig is cut the tension in xylem pulls the sap away from the cut point. The pressure applied in Scholander Pressure Bomb forces xylem sap back to the cut point.

It is important to point out here that the dead cells of the xylem are greatly strengthened with cellulose fibrils encrusted with lignin. Such strengthening of walls can be compared with reinforced concrete and thus the xylem cells are strong enough not to collapse when water is pulled through them.

Studies on the movement of water at various times of the day also suggest that the "motor" for ascent of sap lies in the leaves of the tree. The velocity of sap flow in the wood was also measured by inserting a heating element into the xylem. After a time interval the distance covered by the heated xylem sap was measured by a thermocouple. The velocities as high as 75-100 cm/hr were recorded (Fig. 11.7).

Although, the cohesion theory of water was proposed about a century ago yet it holds good even today. However, it explains only the long distance transport of water through dead xylem tissue. Many questions — such as what the factors are that affect water absorption from soil, how does water move from cell to cell and in tissues other than xylem and what are the driving forces that determine the direction of water movement — remain to be answered.

In the following sections we explain to you the concept of water potential which can tell us not only the water status, but also the direction and rate of movement of water in a plant.

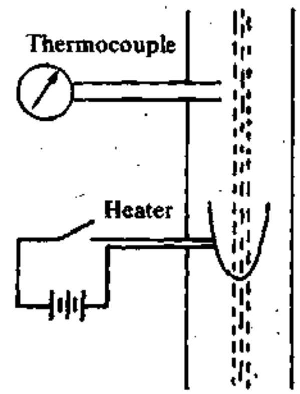


Fig. 11.7 : Measurement of velocity of xylem sap. A small heating element can be inserted at a point in the trunk upto the xylem. After a time interval the upward movement of the sap can be detected by a thermocouple.

11.4 THE PATHWAY OF TRANSPORT OF WATER

Plants absorb water from the soil by roots, mainly near the root-hair zone in the region of maturation (Fig. 11.8). The radial movement of water is shown in

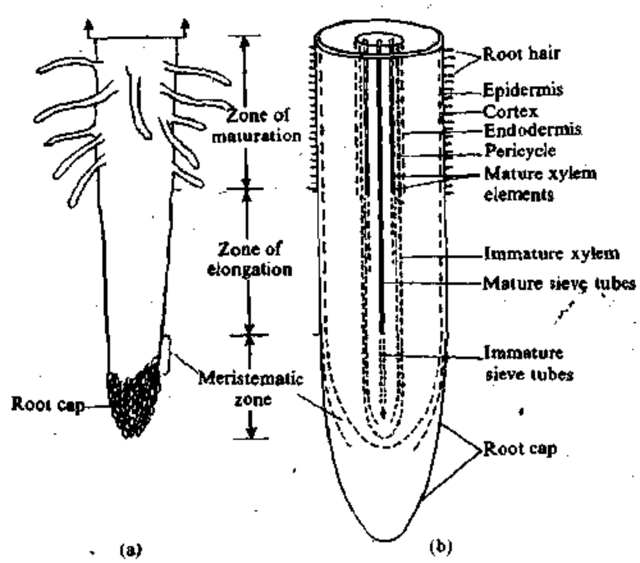


Fig. 11.8 : a) General morphology of root tip showing root cap, meristematic zone, zone of elongation and zone of maturation with root hair. b) position of various tissues including xylem and phloem.

Fig. 11.9a. At most stages of its journey water molecules have the option of moving either through protoplast or through cell walls. Water may first enter the epidermal cells of the root by crossing plasma membrane and then move along through the cytoplasm of the cortical cells, the endodermis, the pericycle and finally into the xylem vessels and/or tracheids. The movement of water through cell to cell occurs probably via plasmodesmata — the protoplasmic bridges between the cells. This transport route is termed **symplastic pathway** (Fig. 11.9b). Since cells are joined via intercellular connections, the entire living portion of the plant forms a continuous single entity and is called **symplasm**.

The other route for the transport of water is through cell walls, intercellular spaces and non-living cells of the xylem (Fig. 11.9b). This is called **apoplastic pathway** and the non-living portion of plants is called **apoplasm**. The cell wall is composed of hydrophilic substances like cellulose, hemicellulose, pectin, lignin and hydrophilic proteins, and carbohydrates, polymers of gums and mucilages. The molecules of these substances retain a lot of water and let it permeate easily without any resistance, when the supply of water is in plenty. When water moves through the cell walls of epidermis and the cortex, its movement is restricted at the highly packed endodermal cells, because the radial and transverse cell walls but not the tangential walls of these cells are lined with suberin a hydrophobic substance in the form of strip called Casparian strip (Fig. 11.9c).

Chemically suberin is like cutin and lignin of cuticle which are impermeable to water. Therefore, water crosses membranes in order to enter endodermal cells and joins the symplastic route. Some water may enter cells at any point prior to endodermis and

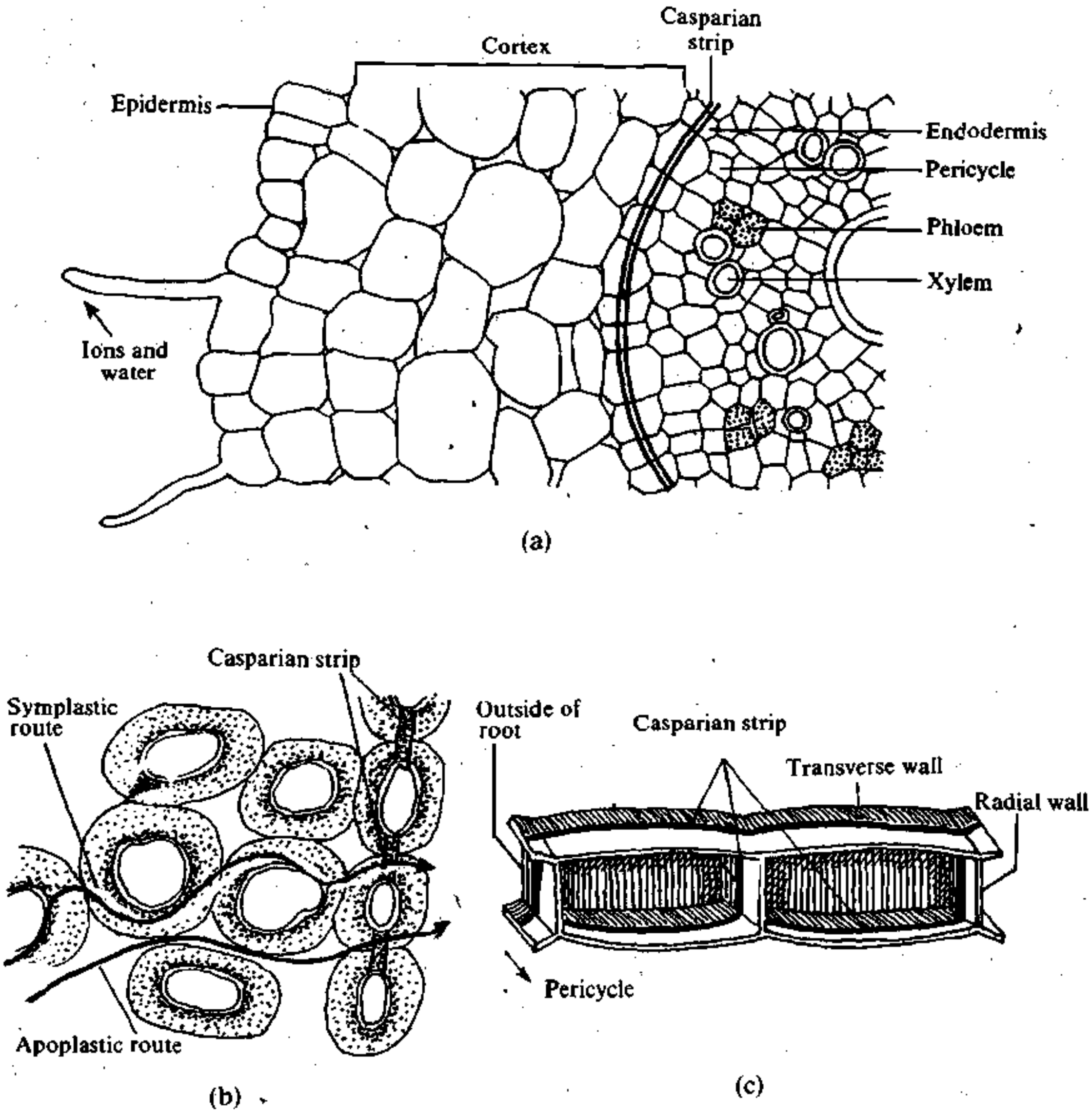


Fig. 11.9 : a) Cross-section of a root showing radial movement of water from root to xylem. b) symplastic and apoplastic routes. c) Casparian strips.

join the symplastic pathway. Once the water reaches xylem conduits it spontaneously moves upwards through xylem of root, shoot, petiole and finally in the tracheid of leaf vein and mesophyll cells (Fig. 11.10). Most of the water evaporates from the mesophyll cells that line the stomatal cavity and diffuses out to the air through stomatal pore.

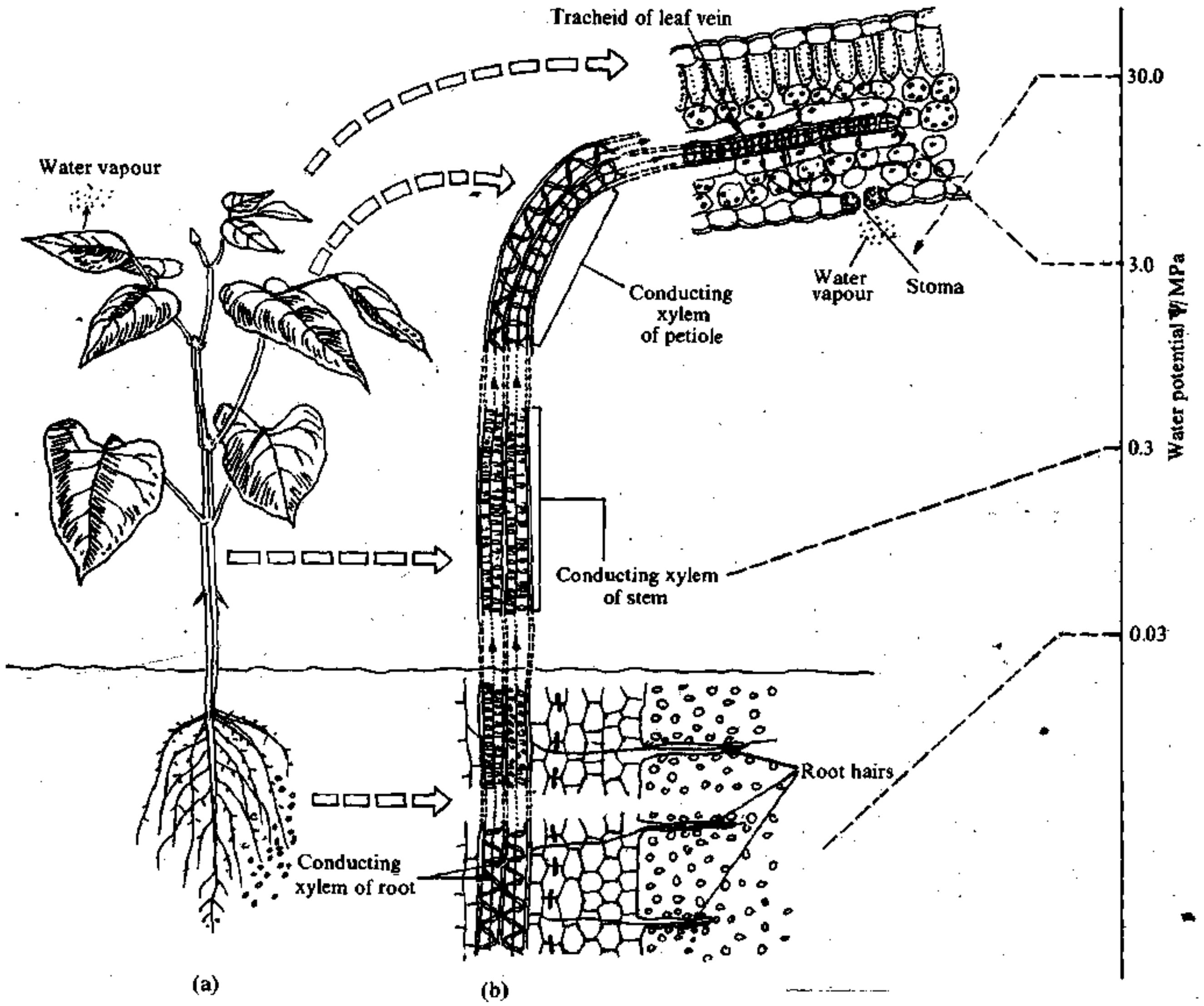


Fig. 11.10 : The pathway of water movement in a plant : a) whole plant. b) movement through xylem. The scale shows water potential at different points in the plant.

SAQ 1

a) Which of the following statements are true :

i) A plant (without roots) would not translocate a dye solution if first placed in picric acid solution for about one hour. ☐

ii) If a rapidly transpiring plant is cut off just above the ground, water will ooze out of xylem vessels. ☐

iii) Removing all the leaves from a plant will probably reduce flow of water up the stem. ☐

iv) A soap solution injected in the xylem of a tree-trunk could prevent water from reaching at the top. ☐

Hint : Soap solution reduces the surface tension of water.

11.5 SOME BASIC PHYSICAL CONCEPTS

The main idea of this section is to explain the concept of chemical potential of water or water potential and the effect of various factors that change its value in plant cell and its immediate environment. The flow of water depends upon the gradient of water potential in soil-plant-atmospheric system. The understanding of this section requires some knowledge of certain basic physical concepts such as diffusion, osmosis, imbibition, and chemical potential. We will explain them briefly. (You need to revise Section 7.3 of Cell Biology Course before reading this section.)

Diffusion

Diffusion is a spontaneous process that leads to net movement of a substance from a region of higher concentration to a region of lower concentration. It can also be defined as the net movement of molecules from region of **high free energy** to a region of **low free energy**.

The principle of diffusion is of importance in plants because several of the transport processes such as uptake of water and minerals, intake of CO_2 and release of O_2 by leaf cells, loss of water due to transpiration depend in part on diffusion.

Osmosis

Osmosis is a special case of diffusion. Here, the movement of water (solvent) takes place from a region of higher concentration to a region of lower concentration, if the two are separated by a semi-permeable membrane.

Osmotic Pressure

It is the pressure necessary to prevent the flow of water or a pure solvent to a solution (osmosis) when the two are separated by a semi-permeable membrane. Osmotic pressure is given by the following equation

$$\pi = CRT \qquad \text{... (11.1)}$$

π = osmotic pressure in bars

C = concentration of solution in mol/l

R = gas constant litre bar $mol^{-1}K^{-1}$
Its value is 0.08 litre bar $mol^{-1}K^{-1}$

T = absolute temperature in Kelvin

Vapour Pressure
It is the pressure exerted by vapour over a liquid where it is in equilibrium with itself.

The osmotic pressure of a molar solution (i.e. one mole/litre) is thus

$$= \frac{1\ \text{mol}}{\text{litre}} \times \frac{0.08\ \text{litre bar}}{\text{mol K}} \times 273\ \text{K}$$

$$= 21.84\ \text{bars} \qquad (T = 273\ K)$$

Imbibition

It is the process of absorption of water to the nearly dry surface such as seeds and wood. There is liberation of substantial amount of heat during the process.

Gradient

It is the difference between concentration or pressure or any other parameter indicative of energy between two specified points. The direction of flow is always from higher energy towards lower energy.

Chemical Potential

The chemical potential of a substance in a system is a measure of its free energy, i.e. energy available to do work. Here the system refers to thermodynamic concept wherein studies are of system rather than individuals or bodies. Thus when we study the properties of a solution in the container, we are studying a system wherein each individual component interacts internally. For example, suppose we have pure water in a system be it in a beaker or soil, all the molecules of water can do work, so their free energy is maximum. When a small amount of sugar is added a few molecules of water get associated with each molecule of sugar, the free energy of water decreases. Hence, the free energy of pure water is always maximum. Addition of any solute lowers the free energy or chemical potential of water.

The chemical potential of water in a solution is related to its vapour pressure and is given by the following equation.

$$\mu_w - \mu w^\circ = RT \ln \frac{e}{e^o}$$

$$\Delta\mu = RT \ln \frac{e}{e^o} \qquad \ldots (11.2)$$

μ_w = chemical potential of water in question (joules/mole)

μw° = chemical potential of pure water under STP

$\Delta\mu$ = change in free energy

R = gas constant

T = absolute temperature

e = vapour pressure of water in question

e^o = vapour pressure of pure water

Note that

Relative humidity $= \frac{e}{e^o} \times 100$

If e is also pure water then $\ln \frac{e}{e^o}$ is zero and $\Delta\mu$ becomes zero. So the chemical potential of pure water is set to zero. If e is less than that of pure water then $\ln \frac{e}{e^o}$ will be negative number, therefore, $\Delta\mu$ will be less than zero – a negative number.

Water Potential

It is the difference between chemical potential of water at any point in a system and that of pure water at STP. By convention the chemical potential of water is referred to as water potential and is denoted by ψ_w (ψ—pronounced as psi).

ψ_w is expressed in pressure units. It is the free energy per unit volume of water (joules per cm^3).

$$\psi_w = \frac{\Delta\mu}{\bar{\upsilon}}$$

$\bar{\upsilon}$ = partial molal volume

If water potential of the source (the region supplying the water) is higher than the water potential of the sink (the receiving region), then there is a spontaneous transfer of water from source to sink ($\psi_{source} > \psi_{sink}$).

Partial molal volume (J) of a solution is the change in volume of a solution when one mole of a substance is added to it.

By convention the water potential of pure water is taken as zero. Therefore, water potentials other than that of pure water will generally be negative. Thus lower potential means a more negative value, and higher potential a less negative value.

Water potential in plants is affected by the solute, hydrostatic pressure and matric forces. In order to predict the movement of water inside or outside a cell we must consider the effect of the above three factors.

Effect of Solute

Let us take pure water in two chambers A and B separated by a semi-permeable membrane (Fig. 11.11 a). The water potential of both the chambers is zero. Addition of solute in chamber A (Fig. 11.11b) would reduce the free energy of water and the water potential will fall below zero. Consequently, water will move from B to A (Fig. 11.11c). The effect of dissolved solutes on water potential (ψ_w) is called osmotic potential (ψ_π). It can be estimated numerically if we know the osmotic pressure of the solution. The two are related as

$$\pi = -\pi \qquad \ldots (11.3)$$

For example, if π of a solution is 5 bars then ψ_π would be −5 bar.

Water potential is expressed in pressure units. Energy per unit volume of water is expressed in joules per cm^3. This is equivalent to dynes per cm^2. 10^6 dynes = 1 bar. The present unit used for pressure is pascal (Pa). It is a pressure equal to the force of one Newton acting uniformly over one square meter.

1 bar = 10^5 Pa
10^3 Pa = 1 KPa (1 kilo pascal)
10^3 KPa = 1 MPa (mega Pascal)

Effect of Pressure

Let us now see the effect of pressure on water potential. As Fig. 11.11d illustrates, when pressure is applied the flow of water begins from chamber A to chamber B through a semi-permeable membrane. This means that pressure increases the free energy of water and thus raises the potential of pure water above zero. The effect of pressure on water potential is called pressure potential and is designated as ψ_p. The level of water in B rises due to increase in water potential of A (Fig. 11.11e).

What would happen if pressure is applied on the chamber containing solutes? Now the ψ_w will be affected by both solute and pressure. The solute would lower the water potential and pressure will raise the water potential. So the flow of water from B to A would start decreasing. An equilibrium condition will reach when ψ_p will be equal but opposite in magnitude to ψ_π and there will no net flow of water in the two chambers (Fig. 11.11e). This can be represented by the following equation:

$$\psi_{w(B)} = (\psi_\pi + \psi_p)_B \qquad \ldots (11.4)$$

Let us suppose if ψ_p is equal and opposite to ψ_π. Then

$$\psi_{wA} = (\psi_{\pi A} + \psi_{\pi B})$$

$$= 0$$

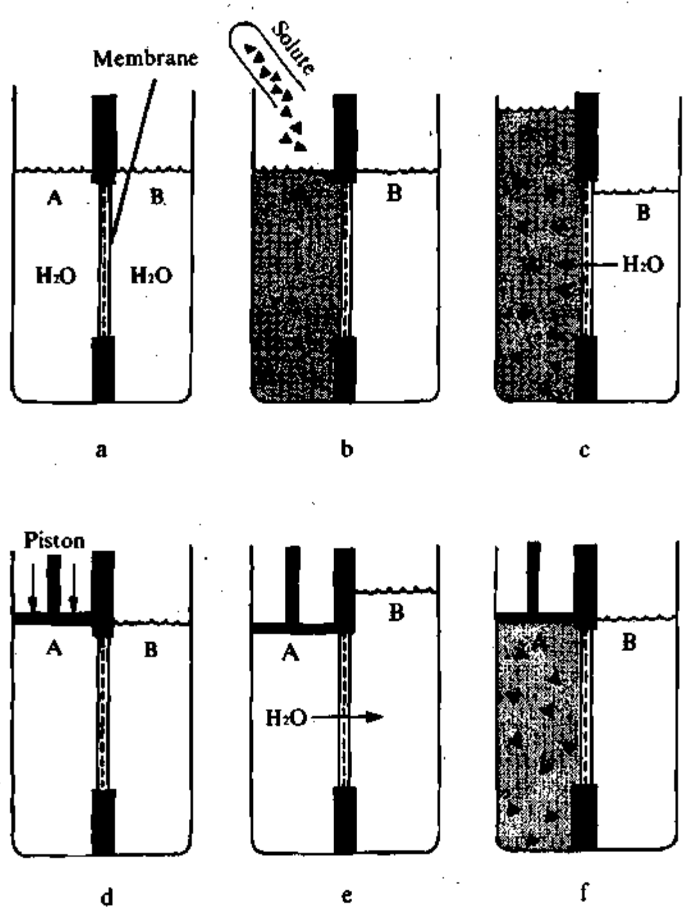


Fig. 11.11 : Experiment to show the effect of solute and pressure on water potential, see text for details.

Effect of Matric Pressure

Water can get absorbed to the wettable surface of solids such as soil, wood, seeds and cellular constituents. A force operates between solid-liquid interface and is called matric suction or matric pressure. The absorption process is accompanied by heat loss and results in decrease in free energy of water. In other words, the effect of matric forces on water potential is called matric potential (ψ_m). Its value will be negative.

In a well watered soil ψ_m is not very significant, however, when the soil is near drying ψ_m determines water potential of the soil.

So we find that the ψ_m is composed of the following main component forces:

$$\psi_w = \psi_\pi + \psi_p + \psi_m + \psi_{\ldots} \qquad \ldots (11.5)$$

$\psi_{\ldots}$ = any other forces that may influence ψ_w.

11.6 RESISTANCES TO WATER MOVEMENT AND WATER FLUX

We have explained earlier that if water potential drops from source to sink ($\psi_{source} > \psi_{sink}$) than there will be spontaneous flow of water. But we do not know the rate of this transfer i.e. flux.

Recall from Section 7.2 of the Unit 7, Cell Biology Course, the rate of diffusion dc/dt is flux. The flux for water flow is denoted by J_w which is volume of water flow through unit surface area per unit time. Water in plants flows from cell to cell and also through cell walls.

When water moves from cell to cell the flow is the function of water permeability of the membrane. The flux of water is given by

$$J_w = L_p \Delta\psi_w \quad \ldots (11.6)$$

L_p = permeability coefficient of limiting membranes

$\Delta\psi_w$ = difference in water potential at two points

From equation (11.4) we know that

$$\psi_w = (\psi_\pi + \psi_p)$$

$$\Delta\psi_w = (\Delta\psi_\pi + \Delta\psi_p)$$

substituting the value of $\Delta\psi_w$ in above equation

$$J_w = L_p (\Delta\psi_\pi + \Delta\psi_p) \quad \ldots (11.7)$$

Thus, the inward or outward rate of flow or water from cell to cell and tissues can be calculated from the above expression.

Let us now consider the flow of water in the plant through intercellular spaces (apoplasm) where the limiting membranes are absent. Then the flux is given by

$$J_w = H_c \Delta\psi_w$$

H_c = hydraulic conductance

Because $H_c = \frac{1}{R}$

R = Hydraulic resistance to flow of water

$$J_w = \frac{\Delta\psi_w}{R} \quad \ldots (11.8)$$

The water flux is directly proportional to $\Delta\psi$ and inversely proportional to hydraulic resistance (R). In other words, higher the $\Delta\psi_w$ more will be flux but high R will decrease the flux.

In plants water will move through the pathway which offers least resistance. Between the two routes — cell walls and cell to cell, the membranes of the cells exert more resistance (because of low permeability) than the cell walls. Therefore, water can flow relatively easily through cell walls. Water will not experience the resistance of plasma membrane when it moves from cell to cell via plasmodesmata. The xylem conduits which are not obstructed by cell membranes have least resistance and the rate of flow of water is very high. The ratio of R in xylem, cell walls and cell membranes is in the order of 0·3 : 1 : 50. This explains why xylem is the pathway for long distance transport as has been observed experimentally. The resistance in xylem varies inversely with the diameter of xylem elements. The smaller the diameter of xylem greater will be the resistance.

Hydrostatic pressure is the pressure exerted by or on a liquid above or below atmospheric pressure.

In soil, pressure potential is insignificant and osmotic potential is zero because there are no membranes (solute and water move together). Hence, the driving force $\Delta\psi_w$ in soil is determined by the matric pressure.

$$\Delta\psi_{w(soil)} = -\Delta\psi_{m(soil)}$$

The hydraulic resistance varies from soil to soil. The fine soil particles with small space between them offer more resistance than coarse particles with large spaces. When ψ_w of soil falls R increases and then the plant take up less water.

Also, in the cell walls the driving force is determined by $\Delta\psi_m$. In those leaf cells which are losing water rapidly, matric forces become significant and consequently ψ_w of leaf decreases. So water moves from the wetter cells. Thus a continuous gradient develops which operates along the cell walls throughout the plants. Of course, it will break at points where cell walls are impregnated with hydrophobic substance for example — Casparian strip.

SAQ 2

a) List the three factors that determine the value of ψ_w in plant.

....

....

....

b) The water potential in a cup (ψ_c) containing salt solution will be

$\psi_c > \psi_w$

$\psi_c > \psi_w$

$\psi_c = \psi_w$

....

....

....

c) What will be the water potential of a plasmolysed cell if its osmotic pressure is 7.9 MPa.

....

....

d) Fill in the blank spaces in the following statements with appropriate words:

i) At full turgor ψ_w of a cell will be ....

ii) The net flow of water movement in a system will stop when ψ_p will be equal and .... to ψ_π.

iii) Greater matric suction will .... the water potential in a system.

11.7 GRADIENTS OF WATER POTENTIAL

The absorption of water by a plant involves the water relations of an individual cell, a group of cells and finally of the whole plant. Therefore, we will consider water relations at different levels of organisation. We have already discussed the long distance transport of water.

Movement of Water in a Single Cell

Isolated cells, single celled organisms and root hairs absorb water directly from their surrounding media. Let us consider an ideal parenchymatous cell. The vacuole occupies 90% of the cell and contains cell sap which is a dilute solution of salt and other small molecules. Due to osmotic potential the cell sap has a lower water potential than pure water. When such a cell is placed in pure water a gradient develops due to the difference in water potential. This results in the movement of water inside the cell (Fig. 11.12). However, in no time the concentration of sap also decreases which lowers the osmotic potential of the sap. Thus, the difference between the potential of pure water and cell sap gets reduced. This lowers the force by which water enters the cell. We can represent the relationship with the following equation:

$$\psi_w \text{ (outside the cell)} = (\psi_\pi + \psi_P)_r \text{ inside the cell}$$

where, ψ_w is total water potential of the system, ψ_π is the osmotic or solute potential and ψ_p is pressure potential due to cell wall pressure or turgor pressure. At full turgor pressure the sum of ψ_p and ψ_π is zero. Hence ψ_w is zero.

The driving force F that causes water to move can be represented by the following equation:

$$F = \text{gradient } (\psi_c - \psi_e)$$

where ψ_c is the total water potential of the cell including that of the cell sap and ψ_e is the total water potential of the external medium. If the latter is pure water then its value will be zero. In that case the driving force will be equal to ψ_c. However, as the water will move into the cell ψ_c will be regulated by ψ_π and ψ_p. In this relationship the elasticity of the cell wall would also play an important role. The volume of the cell would increase upto a certain limit with the dilution of the cell sap and this will increase the total osmotic potential. This in turn would influence the force developed due to the gradient between the cell and the medium.

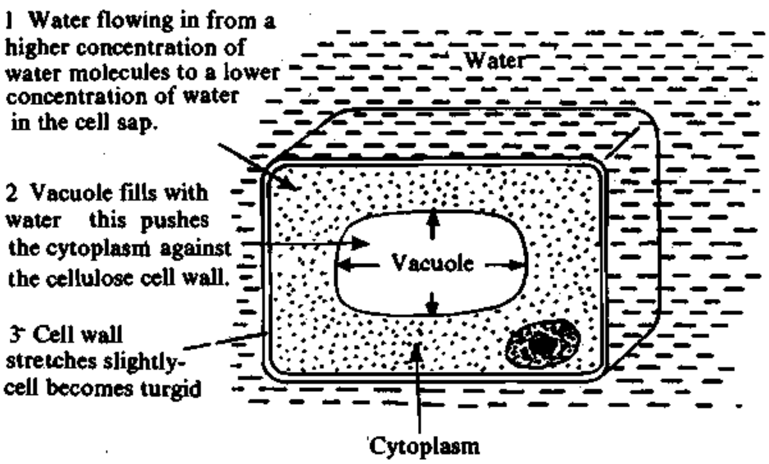


Fig. 11.12 : A single cell surrounded by water.

In the cells of root, leaf and other parts of plant, the external medium is the water in the cell walls and intercellular spaces (apoplast) which is under atmospheric pressure and has very low osmotic potential. But the matric forces exerted by the cell walls are higher, therefore, the water potential in apoplasm is determined by matric forces exerted in cell wall.

Water Relations of a Tissue

In higher plants no cell exists in isolation from others. Even a root hair which is projected outside into the surrounding medium is attached with other cells on all the remaining sides. In a transverse section, it would appear to be surrounded on the three sides by other cells. Thus, the water relations of a root hair are governed on one side by the surrounding medium and on the other by other cells. Let us just consider two cells A and B joined with each other through a common cell wall. If these two cells individually have the same total water potential, then there will not be any net exchange of water between them. This can be shown as follows:

The total water potential of cell A (ψ_{wA}) will be equal to the sum of its osmotic potential and pressure potential ($\psi_{\pi A} + \psi_{pA}$). Let us say that for the cells A and B these values are

$$\psi_{wA} = (\psi_{\pi A} + \psi_{pA})$$
$$\psi_{wB} + (\psi_{\pi B} + \psi_{pB})$$

In a cell the matric forces are much less. Here the ψ_w is lowered because of ψ_π. If the ψ_w in the vacuole is lower than ψ_w in apoplast, then water flows inwards.

Now, the driving force (F) will be the difference in the water potential of two cells.

$$F = (\psi_{wA} - \psi_{wB})$$

If ψ_{wA} is equal to ψ_{wB} the gradient will be zero and so will be the F. Therefore, no net exchange of water will take place between the cells A and B. However, we must realise that the same value of ψ_{wA} and ψ_{wB} does not necessarily mean that the two cells should have the same osmotic potential and the same turgor pressure or wall pressure.

On the other hand, if the total water potential of cell B is lower than that of cell A, a driving force will develop which would cause influx of water into cell B till the two cells attain the same water potential. Now, this example can be extended to a larger number of cells which are connected with each other in tissue. If there are 20 cells beginning from 1 to 20 they will attain an equilibrium amongst themselves, depending on their total water potential in the same way as discussed for the two cells attached to each other. Under such conditions a situation may come when water absorption and movement will come to a standstill.

Water Relations of a Whole Plant

Let us now consider the water relations of a plant considering leaves, stem and roots, that provide a continuum for water in soil-plant-atmosphere system. The total water potential in the atmosphere could be very low, depending upon the temperature and humidity. Table 11.1 shows an approximate magnitude of water potential in the soil-plant-atmosphere-system.

Table 11.1 : Approximate magnitudes of water potential in the soil-plant-atmosphere system

Component	Water Potential (Bar)
Soil	−0.1 to −20.0
Leaf	−5.0 to −50.0
Atmosphere	−100 to −2000

It is clear from the data in Table 11.1 that the difference in total water potential in the soil-plant-atmosphere system would generate a driving force for water movement from the soil through the plant to atmosphere. If this continuum is broken, the driving force would automatically disappear.

SAQ 3

a) In a plant water moves from an organ A to an organ B bacause

i) $\psi_{wA} < \psi_{wB}$

ii) $\psi_{wA} > \psi_{wB}$

iii) $\psi_{wA} = \psi_{wB}$

b) Calculate the value of $\Delta\psi_w$ if water potential of xylem is −0.5 MPa at the base of the tree trunk and −1.5 MPa at the top.

....

....

....

....

c) Water potential in a tree in three tissues A, B, and C was found to be −0.4, −3.1 and −0.09 MPa. What would be the direction of movement of water.

....

....

d) A raisin swells in water because

i) $\psi_{w\ raisin} > \psi_w$ or

ii) $\psi_w > \psi_{w\ raisin}$

11.8 WATER ABSORPTION

Water status of a plant is determined by two major factors: i) water absorption and ii) water loss. We deal with water absorption in this section and water loss in the following section.

Water absorption is regulated by soil factors, rate of transpiration and size and distribution of roots. The soil factors that regulate water absorption are: i) soil water content, ii) difference in water potential between soil and root, iii) concentration of soil solution, iv) soil temperature and v) aeration of the soil.

Soil Characteristics

The physical properties of soil govern water-holding capacity and the water availability to the plant. The fine soil particles of clay have much more water-holding capacity than silt and sand. Addition of humus increases the water-holding capacity of soil. Water moves through pores present in soil. The pores form because individual soil particles aggregate to form large particles of varying sizes called micelles. The pores are spaces left between micelles. The size of pores can be small (micropores) or large (macropores) depending upon the soil type. The pores get filled with water.

A soil freshly wet with irrigation or rain water cannot retain all the water. Much of the water percolates through macropores due to gravity. This water has been termed as **gravitational water**. The remaining water that is held tightly by hydrogen bonds to the soil particles against gravitational forces is called **capillary water**. This water is available to the roots. Part of the capillary water that is held very tightly and is not available to the root is termed **hygroscopic water**.

The water content of a soil is expressed as

$$\% \text{ of soil water} = \frac{FW - DW}{DW} \times 100$$

FW = Field weight of wet soil

DW = Dry weight (obtained by heating soil to 60°C)

Two terms field capacity (FC) and permanent wilting percentage (PWP) are often used to describe the water status (capillary water) of the soil.

Field Capacity (FC)

It is the capacity of a field to hold the amount of water against gravitational forces. It is expressed as the percentage of the dry weight of the soil. Field capacity represents the upper limit of water availability and its value differs from soil to soil. The capacity of clay soil on an average is about 40-45%, silt 20% and sand 5-10%.

Permanent Wilting Percentage (PWP)

It is the percentage of moisture in the soil at which a plant wilts and does not recover unless water is added to the soil. PWP for clay is about 26%, for silt 10% and for sand 3-5%. It must be noted that PWP is used to express property of a soil not any feature of the plant.

However, the moisture content at which any plant shows permanent wilting need not be the same for all plants even in the same soil. This happens because some plants are prone to wilting at fairly reasonable water content of soil while others wilt only when the moisture content is very much reduced.

The water status of a plant in terms of FC and PWP is significant only if the soil properties are known. This is because the soil determines the availability of water. However, it is desirable as well as easier to express soil water status in terms of water potential so that soils become uniform with respect to water.

Soil Temperature

Soil temperature is known to influence water absorption and ultimately transpiration to a considerable extent. In many plants water absorption is reduced sharply below 10°C. Water absorption also slows down above 25°C. In most instances, temperatures above 40°C in the rhizosphere does not support water absorption and plant may show signs of wilting. The following are the reasons suggested for the reduced absorption of water at low temperature: i) decreased root growth, ii) increased viscosity of water, iii) increased resistance of water into roots due to decreased permeability (increased hydraulic resistance) of cell membranes and iv) decreased metabolic activity of root cells.

Soil Aeration and Flooding

It is not unusual to observe some plants wilting while they stand in water. The following are the possible reasons of flood injury.

i) Poor availability of O_2 and accumulation of high concentration of CO_2 around roots.

ii) Changes in the pattern of ion uptake resulting in the accumulation of some ions to toxic levels.

iii) Accumulation of toxic substances in the root and/or around them.

Poor availability of oxygen affects respiratory activity of roots, thus lowering the ATP supply. In the following units you will learn that ATP is required for the active uptake of ions. Low uptake lowers the osmotic potential of roots cells and hence water cannot enter because $\Delta\psi_w$ between root cells and soil is not sustained. Increased concentration of CO_2 affects the permeability of membranes and thus affects water uptake adversely.

Among toxic substances are the metabolites produced as a result of anaerobic respiration. These could be alcohol or aldehyde and even ethylene. Plants usually become chlorotic under waterlogged conditions. This is apparently due to reduction in translocation of iron from roots to the top of the plant.

Root

Root system is directly related to the absorption of water and its growth under field conditions is very much influenced by soil. In dryland agriculture, particularly root structure has apparently greater significance. The rates of water absorption into roots of different plants differ in their stage of growth. Highest rates of water entry are associated with root hair and unsuberised roots and lowest with suberised woody root.

Water Absorption and Transpiration

The rate of water absorption is controlled by the rate of transpiration. A high water potential in the atmosphere would reduce water loss from the plant and consequently slow down water absorption. But it does not follow from this that water will be continuously absorbed if the water potential of the atmosphere is very low and soil is near drying. When the equilibrium in the soil-plant-atmosphere system is disturbed either due to soil or atmosphere, the plant can respond appropriately and can control water absorption or water loses. We discuss below some of these aspects.

Let us first see the relationship of water absorption and transpiration in a well watered plant (Fig. 11.13). By and large all plants show a diurnal behaviour in their rates of transpiration. There is a rapid increase in transpiration during the morning hours and a peak is reached in the early afternoon. Then a decline begins and a minimum is reached during the night.

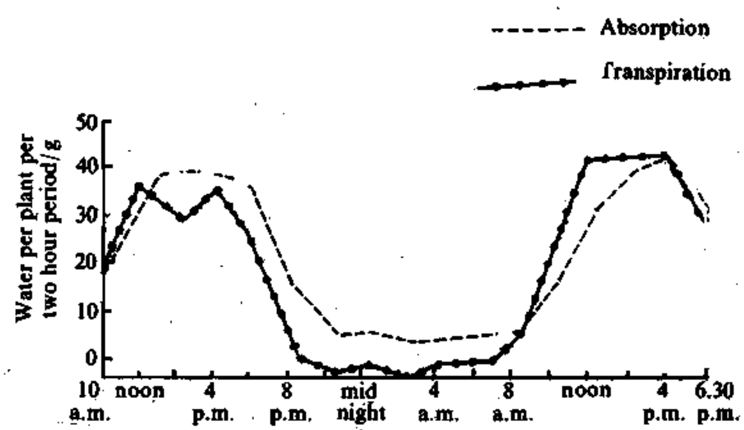


Fig. 11.13 : Diurnal variations in rates of transpiration and absorption of water by a plant.

You may note in the graph that water absorption keeps pace with losses due to transpiration except around noon when it lags behind. Why is it so? You have learnt that the resistance to the movement of water across the roots is generally higher than in the leaves because in roots water moves through symplasm. In roots it faces high resistance of the membranes of cortical cell and that is why there is an absorption lag. This idea is supported by an experiment where water absorption was recorded after removing the roots of a plant. As shown in the graph (Fig. 11.14) the absorption lag is reduced greatly.

Let us now see what happens to water loss if soil is not moist. Ralph O. Slater (1967), a plant physiologist at Australian National University, Canberra, studied the relationship between water potential of soil ($\psi_{w\,soil}$), root ($\psi_{w\,root}$) and leaf ($\psi_{w\,leaf}$) of a plant where water supply was withheld for five days. The graph (Fig. 11.15) shows diurnal changes in leaf potential, water stress around the noon time and recovery of lag in absorption at night. The water potential of the soil decreased almost linearly

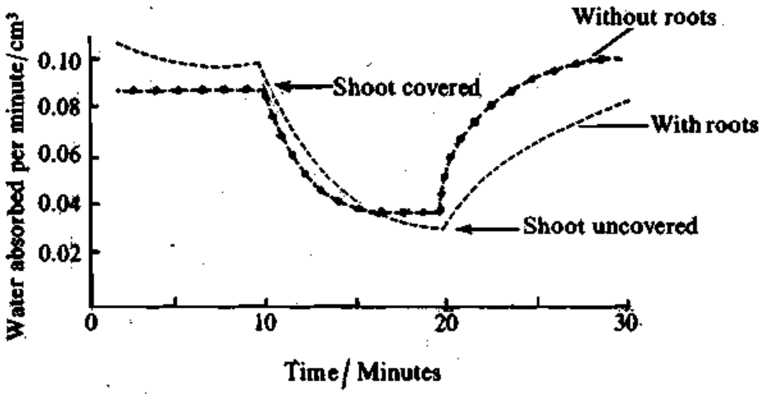


Fig. 11.14 : Comparison of rate of water absorption in rooted and rootless plant. When transpiration is high (shoot uncovered), the rate of water absorption in a rooted plant is less than rootless plant.

after second day. It must be pointed out that when plants are under water stress, water tends to move out of the cells that are not situated in the main pathway of transport of water. This causes reduction in turgor, i.e. cell volume. In fact, it was demonstrated a century ago by Josef Friedrich that there are daily fluctuations in the diameter of tree trunk, shrinkage in the morning and recovery in the diameter by night.

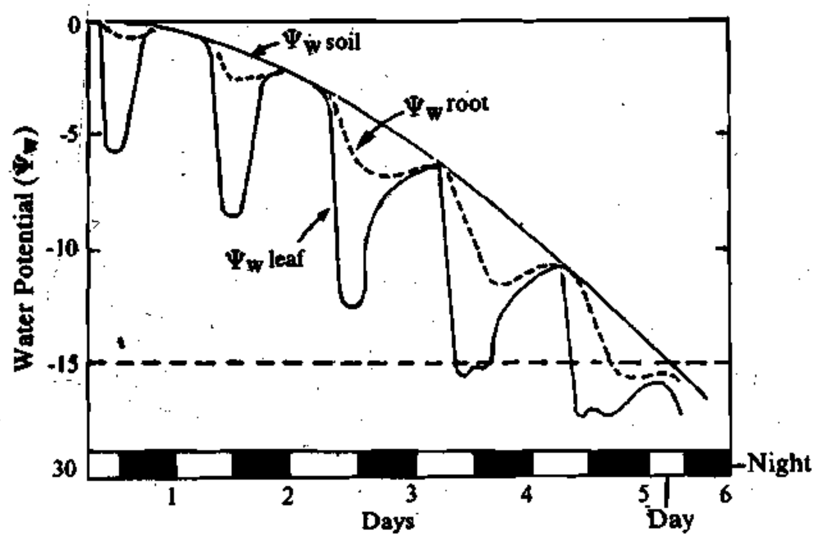


Fig. 11.15 : Diagram showing probable changes in leaf water potential ($\psi_{w\,leaf}$) and root water potential ($\psi_{w\,root}$) of a transpiring plant rooted in soil allowed to dry from a water potential near zero to a water potential ($\psi_{w\,soil}$) at which wilting occurs.

SAQ 4

Which among the following suggestions are desirable for growing healthy plants. Put a tick mark for the correct ones.

i) Excess use of fertilisers. ☐

ii) Saturation of plants, particularly growing in pot, with water. ☐

iii) High humidity area for water-sensitive plant, ☐

iv) Use of very cold water in warm season. ☐

v) Use of lukewarm water in cold season. ☐

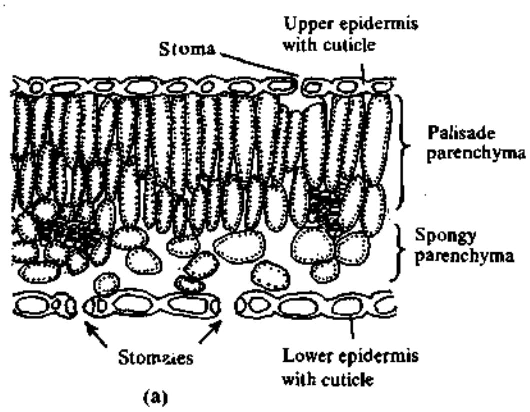
11.9 WATER LOSS

Plants lose about 98% of water to the atmosphere by transpiration. Often water loss by transpiration exceeds gain by absorption and results in negative water balance within the plant. Small and moderate deficit that occur due to high temperature during the day are compensated during the night but prolonged deficit causes irreversible damages and threatens the plant's survival.

Transpiration is essentially evaporation of water from the aerial portion of the plant. However, evaporation of water from open surface meets less resistance while evaporation of water from leaves faces considerable resistance. Transpiration occurs mainly through stomata of the leaves. This is called **stomatal transpiration**. About 5% of the water is lost from the leaf through the cuticle. This is called **cuticular transpiration**. In woody plants there are lenticels opening within the bark that function in gas exchange. The water loss through these cells is called **lenticular transpiration**.

11.9.1 Stomata

The cross-section of a leaf shown in Fig. 11.16a shows the position of a typical stoma (plural stomata) which however, differs from species to species, with respect to the size of the pore, structure and size of the guard cells and depth and size of the stomatal cavity. As indicated in the diagram b, water evaporates from wet mesophyll cell walls that border intercellular spaces, the vapours then diffuse out through sub-stomatal cavity and stomatal pores to the air outside the leaf. The water potential gradient develops in the sub-stomatal cavity, stomatal pore, boundary layer and the atmosphere. During transpiration the sub-stomatal cavity has relatively much higher water potential as compared to the atmosphere, therefore, the water vapours move out. This is turn lowers the water potential of the sub-stomatal cavity. Consequently, the cells surrounding the sub-stomatal cavity evaporate water through their cell walls. Depending upon the water potential of the environment, the water potential of the sub-stomatal cavity and the surrounding cells is lowered. This gradient eventually acts as a 'pull' on the water column which maintains continuity through the vascular bundles of the leaf. The intercellular spaces also play an important role in this respect because they are in continuity with the sub-stomatal cavity and cause a gradient quickly.



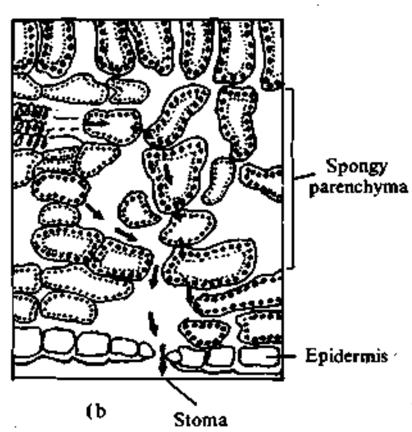


Fig. 11.16 : a) Cross-section of a leaf showing the relationship of stoma with other leaf tissues. b) Stoma enlarged to show the path of water vapours from leaf to atmosphere.

When water evaporates through leaves it experiences considerable amount of resistance (Fig. 11.17) which can be grouped into the following two categories: a) leaf resistance (internal resistance), and b) air boundary resistance (external resistance).

The components of leaf resistance are cuticle, mesophyll cells, intercellular spaces of the leaf and stomata. The cuticular resistance is maximum followed by stomatal resistance and air boundary layer resistance. The pathway of movement of water vapours is analogous to the electric current moving in circuit, the greater the resistance, the smaller the flow of water and vice versa.

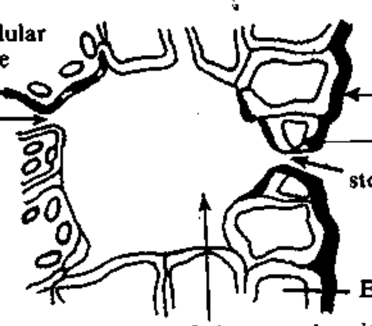


Fig. 11.17 : Schematic cross-section of a leaf showing different resistances.

The cuticle forms outermost surface of the leaf and offers resistance to the evaporation of water vapour and entry of carbon dioxide necessary for photosynthesis. Stomata perform the following main functions:

i) They allow entry of CO_2 necessary for photosynthesis,

ii) They control water loss through transpiration and thus protect the plant from desiccation,

iii) At higher temperature (above 35°C) they promote transpiration which serves to cool the leaves.

Stomatal resistance is most important because gas exchange between leaves and external atmosphere takes place entirely through stomatal pores. Stomatal resistance depends mainly on the size and shape of the stomatal cavity and size of stomatal aperture. Can you tell which pore size, small or large would exert greater resistance? Of course, smaller the pore greater would be the resistance for the outward movement of water vapour. On an average a standard pore measures about 20 μm in length and about 11 μm wide at its widest point when fully open.

Water loss from the leaf also depends on the number of stomata per leaf. One of the aims of agricultural scientists is to find ways of minimising the water loss from the plants so as to increase the efficiency of water use. One way is through a study of the number of stomata per leaf. Some investigations have been carried out keeping the following questions in view:

i) What is the distribution of stomata and how is it related to water loss and carbon dioxide intake?

ii) How can water loss be reduced without seriously impairing carbon dioxide intake?

iii) Is it possible to evolve varieties which possess characteristics associated with low evaporation of water?

There are two parameters normally used for expressing the distribution of stomata.

a) **Stomatal frequency** : The number of stomata per unit area.

b) **Stomatal index** : The ratio of number of stomata to the total number of cells per unit area.

Plants differ in their stomatal frequency. In monocots the upper and lower surfaces usually have the same frequency but in dicots the lower surface usually has a higher frequency than the upper surface. However, the frequency of stomata can change with the position of leaves on the plant.

Studies have been carried out to see if any relationship exists between i) stomatal frequency or stomatal index and transpiration and ii) stomatal opening or stomatal index and photosynthesis. Using two barley lines which were high and low in stomatal frequency Misken and coworkers (1972) found that stomatal resistance and transpiration rates differed significantly between lines but photosynthetic rates were the same. The lines having low stomatal frequency had higher stomatal resistance, transpired less water than lines having more stomata. A decrease of 25% in stomatal frequency reduced transpiration rates by about 25%. However, the photosynthetic rate was unaffected by decrease in stomatal frequency. These studies suggested that it should be possible to alter transpiration without altering photosynthesis by selecting varieties with fewer stomata in barley or other crops.

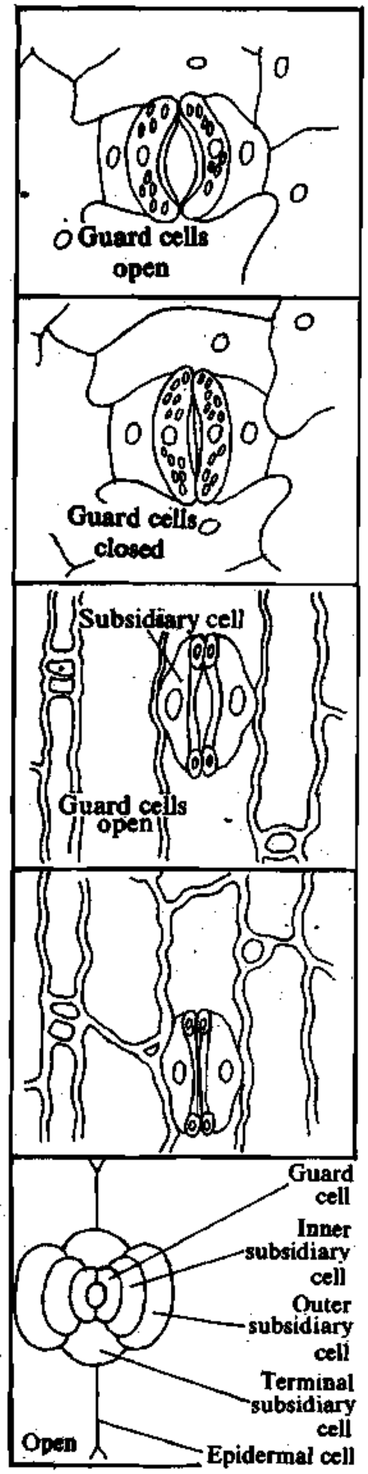


Fig. 11.18 : Surface view of an open a) and a closed b) stomatal aperture in a leaf of a dicotyledon c) and d) of monocotyledon e) guard cells surrounded by subsidiary cells.

Let us first have a close look at the stomatal aperture. Fig. 11.18 illustrates an open (a) and a closed (b) stoma in surface view. As you may know each stomatal pore is surrounded by a pair of guard cells. In closed stoma guard cells appear like two joined kidney beans. In monocots guard cells are dumbell shaped and are arranged in pairs in contact at the bulbous ends (Fig. 11.18c). In some species the epidermal cell adjoining the guard cells are specialised and are called subsidiary cells (Fig. 11.18d). It is important to mention here that guard cells contain chloroplasts and mitochondria and can synthesise starch while no other epidermal cells contain chloroplasts.

11.9.2 The Mechanism of Stomatal Opening

It has been known for over a century that stomata open because of reversible turgor changes in the guard cells. Stomata open when turgor in the guard cells is high and close when it is low. It is clear that the turgor would increase only if the solute content of guard cells would be higher than the neighbouring epidermal cells. Falling of solute content would decrease turgor.

How do the two guard cells on swelling form an aperture? The cell wall of guard cells is peculiar because the cellulose microfibrils which constitute the major strictural feature of plant cell are arranged radially extending from the centre towards the periphery (Fig. 11.19).

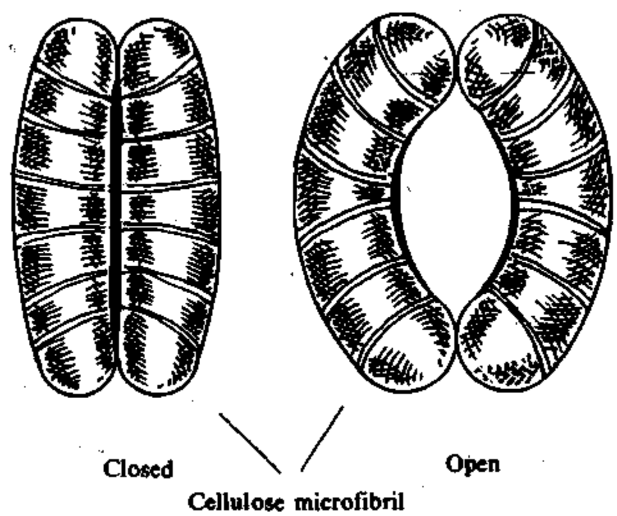


Fig. 11.19 : Diagrammatic representation of arrangement of cellulose microfibrils (lines) in guard cells

This arrangement restricts the expansion of cell wall in transverse direction. Since the inner wall (towards the pore) is thickened and is less elastic than the outer wall, the uneven longitudinal expansion causes the cells to arch away from each other forming a pore in the centre.

Before we discuss the mechanism of control of stomata, it is important to bear in mind the following observations made in this regard.

i) Normally, stomata are open in the day and are closed at night. However, a drop in supply of water leads to the day time closure of stomata.

ii) Stomata open when the internal concentration of CO_2 drops and close when the internal concentration of CO_2 is maximum.

iii) Dark CO_2 fixation (CAM plants, refer to Unit 13) occurs in the guard cells.

iv) In guard cells there is a change of pH in light (day) and dark (night) which is associated with the interconversion of starch and sugar.

v) Opening and closing of stomata are related to the osmotic potential of the guard cells and the permeability of membranes.

vi) At the time of opening of stomata, there is an inflow of potassium ions into the guard cells but when the stomata close, the guard cells lose their acquired potassium to the surrounding cells.

vii) Inhibitors of cyclic phosphorylation can also close stomata.

viii) Blue light also brings about changes in stomatal movement — serving to open stomata.

ix) Abscisic acid — a plant hormone, at a very low concentration can lead to the closure of stomata.

There are two ways in which the relative turgor of guard cells may be altered. i) a decrease in osmotic potential or ii) a decrease in pressure potential. In both instances the water potential of guard cells will fall and hence water from neighbouring cells would move in. Alternatively, guard cells may face mechanical pressure from the subsidiary cells if they face a sudden change in their turgor.

There is overwhelming evidence that the osmotic potential of the guard cells decreases due to the migration of K^+ ions from the surrounding cells into the guard cells (Fig. 11.20). It is also observed that the uptake of K^+ requires ATP which may be generated by degradation of starch through respiratory metabolism and photophosphorylation. ATP is utilised to pump out protons out of the guard cells by a membrane bound ATPase (refer to section 8.4 LSE-01). The supply of protons is maintained by malic acid which is synthesised from stored starch. Due to the active pumping of protons, an electrochemical gradient develops across guard cell membrane. Now the ions can move passively into the guard cells. In some species Cl^- ions or other anions move along with K^+ in and out of the guard cells. Thus, there is a decrease in osmotic potential due to accumulation of K^+, Cl^- and/or potassium salt of organic acid mostly malate. Consequently, water enters guard cells and builds up turgor. Reverse events would bring about closure of stomata.

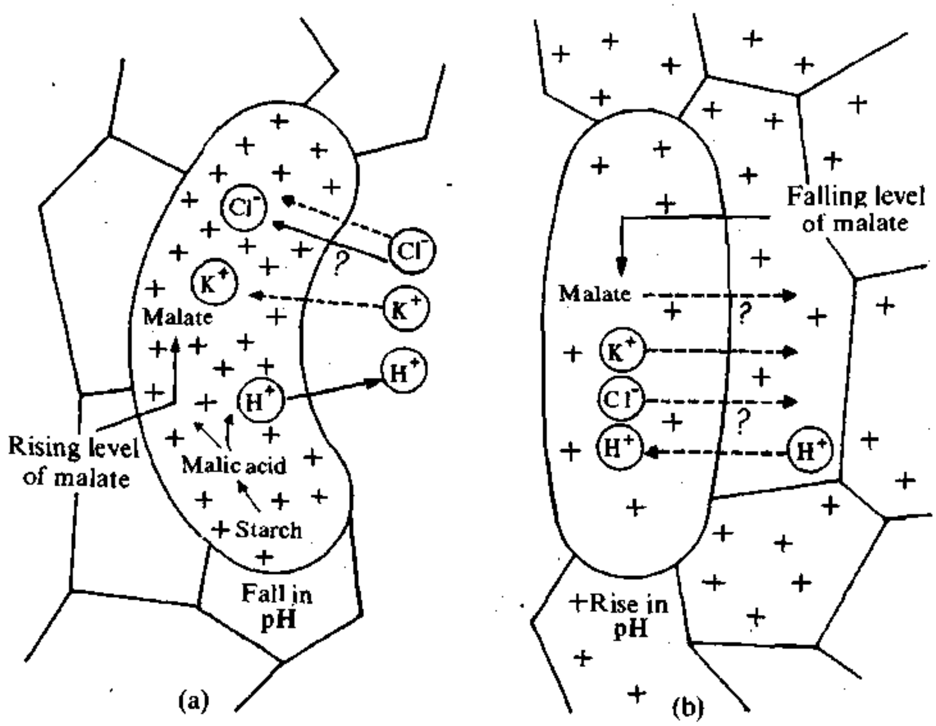


Fig. 11.20 : Changes in the turgor of guard cells by the movement of K^+ and other ions. Solid lines indicate active transport, broken line passive fluxes and ? mark uncertainty. Upward arrow indicates rising level of malate (a) and downward arrow falling level (b).

11.10 FACTORS CONTROLLING STOMATAL APERTURE

'Khul Ja Sim Sim' the two rocks slide and the gates to a great treasure open. With these magic words "Ali Baba and Chalis Chor" could open the door. Let us now find out what is 'Khul Ja Sim Sim' for moving the guard cells of the stomata, so that CO_2 can enter the stomata and make food for organisms of the earth. You have learnt that more than one factor can trigger the change in the turgor of the guard cells and bring about stomatal movements and control the size of stomatal aperture. The main controlling factors are:

i) light,
ii) the level of CO_2, and
iii) high temperature.

To understand better you can imagine the factors as hands that can open and close stomata by moving the turgor operated valve — the guard cells (Fig. 11.21). The stomata open when the level of CO_2 falls due to its rapid utilisation in photosynthesis during the day. However, it is not known how guard cells sense the low level of CO_2. The highest rates of photosynthesis are obtained when the conditions for light and temperature are optimum and plants are well watered. But if the water potential in the leaf falls under low level of CO_2, then conserving water becomes more urgent than food production for the plant and the stomata close. In other words, the water status of plant overrides the control by CO_2.

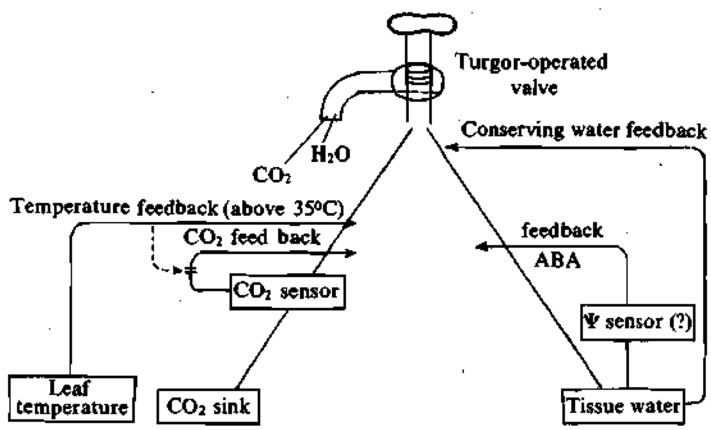


Fig. 11.21 : A simplified model showing the effect of various factors on stomatal aperture.

The rate of photosynthesis increases with increase of temperature but above 35°C cooling of the plant becomes necessary. Therefore, irrespective of CO_2 concentration stomata open widely above 35°C provided that there is no shortage of water. Here again the temperature overrides the control by CO_2 concentration. This makes sense because high temperatures are deleterious to the health of the leaves, and evaporation of water through transpiration can lower the temperature of leaves.

Before we close this unit, it is important to point out that the water loss by a plant due to transpiration is very high usually in the range of 0.1 to 2.5 g $dm^{-2}h^{-1}$ during day time. However, it plays no major role in growth and development of plant so far is known. We have mentioned above that it cools the plant at high temperatures. Perhaps, the transpiration stream facilitates the availability of mineral ions to all parts of the plant. Soil contains minerals in very dilute concentration but in cells they get accumulated in much higher concentration due to active transport aided by their rapid availability in the transpiration stream.

You have learnt that the external application of plant hormone abscisic acid (ABA) to leaves causes stomata to close. During water stress, increase in the level of ABA of the leaves has also been observed. Therefore, it is quite likely that ABA is an internal control for the regulation of water content. Phenyl mercuric acetate — a fungicide has been used as foliar spray in low concentration (10^{-4}M). It brings about partial closure of stomata for about two weeks without visible damaging effects to the plant. Other chemicals such as colourless plastics, silicon oils and low-viscosity waxes are also used as foliar spray. These chemicals form on leaves a film permeable to CO_2 and O_2 but not to H_2O. Water-saving strategy by reducing transpiration though seems quite promising, yet it is a big challenge for plant physiologists.

SAQ 5

a) List the features of guard cells essential for opening the stomata.

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11.11 SUMMARY

- Water is the key molecule for the maintenance of life on the earth. About 85 to 90% of a plant is made up of water. The quantities of water used by plants are enormous.
- Water is a good solvent and reactant in the cell. For plants water is also crucial because the hydrostatic pressure of water provides turgidity to the cells, so that the soft stem parts are able to stand erect.
- Water moves up into the trees due to negative hydrostatic pressure created in xylem by the transpiring leaves. The continuity of water column in the xylem is maintained because of cohesive property of water.
- In plant tissue water molecules move through two routes — apoplasm and symplasm. Apoplast transport is through non-living portion of the plant and symplast is through cell to cell via plasmodesmata.
- Water status in a plant is expressed by water potential (ψ_w). The rate of flow and the direction of movement depend upon the gradient of water potential between the two points. Water tends to move from a region of high water potential to a region of low water potential.
- Water potential is affected by solute concentration, pressure and absorptive or matric forces. Addition of solute lowers the water potential while increased pressure on water causes a rise in water potential. Absorptive forces between solid-liquid interfaces lower the water potential. Water potential is computed as the algebraic sum of component forces: osmotic potential (due to solute), pressure potential (due to hydrostatic pressure, matric or suction potential (due to adhesive forces).
- In a cell both solute concentration and turgor pressure can have offsetting effect on water potential. The combined effect of the two in cells can build up the gradient and determine the rate of flow and direction of water movement.
- The gradient of water potential — the driving force for water movement in soil is due to differences in matric potential. This gradient also occurs along the cell walls.
- Water movement within the dead xylem cells occurs along the gradient of hydrostatic pressure.
- There is resistance to water flow in the soil and in the plant. Water takes up the path of least resistance. Membranes of cells exert greatest resistance while xylem offers least resistance.
- Water status of a plant depends upon water absorption and water loss due to transpiration. Soil characteristics, soil temperature, aeration, flooding and structure of roots are the factors which affect water absorption.
- The rate of water movement in plant is determined by the rate of transpiration in a well watered plant. Temperature, wind velocity, humidity of the air, light intensity and degree of stomatal opening affect the rate of transpiration. However, ultimate limit to transpiration is the supply of water from soil.

- Among stomatal, cuticular and lenticular transpiration, stomatal transpiration accounts for major water loss. Evaporation of water faces considerable resistance from the leaf — cuticle, mesophyll cell, intercellular spaces, stomata and air boundary layer of the leaf.
- Stomata control water loss through transpiration, allow gas exchange and control temperature of the leaf. Some efforts have been made to reduce water loss through stomata without affecting CO_2 intake.
- Stomatal aperture is controlled by the changes in the turgor of guard cells. The turgor in turn is affected by the metabolism and the movement of K^+ and other ions into and out of the guard cells. A proton pump powered by ATPase operates in the plasma membrane of the guard cell and the K^+ uptake is a passive uptake.
- Stomatal aperture is controlled by the level of CO_2, light and high temperature. However, if conserving water or saving plants from deleterious effects of high temperature becomes more urgent than food production then these factors override the system.

11.12 TERMINAL QUESTIONS

1) Why do animals need less water than plants?

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2) What would happen if a twig of a potted plant is cut into two pieces and joined with tygon tubing in such a way that it leaves an air gap between the cut ends? Will water continue to move?

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3) A plant cell with an osmotic potential of -7.6 bars and pressure potential of 3 bars is placed in a slide with a drop of pure water, in which direction the water will flow? What is the ψ_π, ψ_p and ψ_w of the cell and water initially and after equilibrium?

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4) Draw the structure of stomata and explain how stomatal aperture opens by the increase in the turgor of the guard cells.

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11.13 ANSWERS

Self-assessment Questions

1) i) F, ii) F, iii) T, iv) T

2) a) Osmotic potential (ψ_π), pressure potential (ψ_p) and matric potential (ψ_m)

   b) $\psi_c = \psi_w$. The ψ_c of salt solution in a cup will be zero because there are no membranes present. Therefore, its water potential is equal to pure water.

   c) -7.9 MPa.
   We know that $\pi = -\psi_\pi$. Therefore, the osmotic potential will be -7.9 MPa. Since $\psi_p = 0$, therefore, $\psi_{wc} = \psi_\pi$

   d) i) zero ii) opposite iii) lower

3) a) ii

   b) $$\begin{aligned} \triangle\psi_w &= \psi_{w\ Base} - \psi_{w\ top} \\ &= -0.5 - (-15) \\ &= -0.5 + 1.5 \\ &= 1\ \text{MPa} \end{aligned}$$

   c) A = -0.4 MPa, B = -3.1 MPa, C = 0.09 MPa
   $\psi_w = 0.09 > -0.4 > -3.1$
   the flow of water will be from C $\rightarrow$ A $\rightarrow$ B

   d) ii)

4) iii) and iv) are the right suggestions

5) a) i) A thickened cell wall, facing the pore,
   ii) presence of chloroplasts,
   iii) supply of ATP,
   iv) a proton pump in the membrane,
   v) the capacity to generate higher turgor pressure than adjacent cells.

   b) i) F, ii) T, iii) T, iv) F.

Terminal Questions

1) In animals a great deal of water is recycled through the body in the form of blood plasma and other fluids in vertebrates. In plants more than 90% of the water absorbed by leaves is lost into the air as water vapour through the process of transpiration.

2) The plant will absorb water but the upper part of the plant will wilt. This is because the air column between the two stem pieces does not provide a continuum. In plants the movement of water takes place only in liquid phase which can stand enormous pressure without breaking the liquid column.

3) Water will flow into the cell until the water potential of cell and water drop is equal.

The following are initial and final (equilibrium potentials

	Initial		Equilibrium	
	water drop	cell	water drop	cell
ψ_π	0	-7.9	0	-7.9
ψ_p	0	$+3$	0	$+7.9$
ψ_w	0	-4.9	0	0

4) Please see text for the answer.