· Xylem sap → Acidic.

· $\Psi_w = \Psi_s + \Psi_p + \Psi_m + \Psi_g$

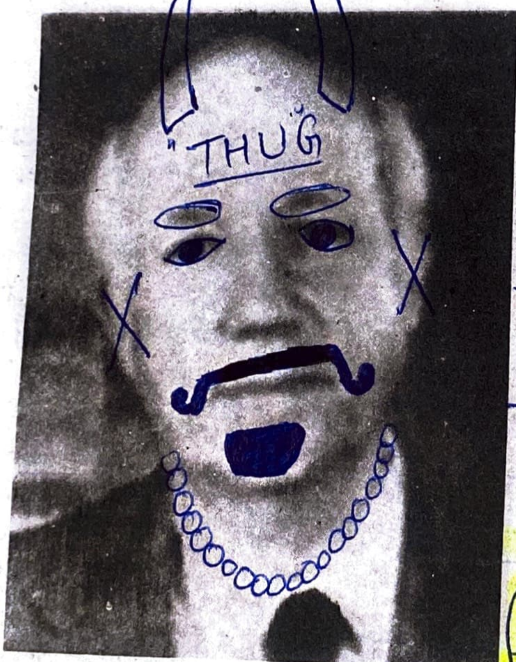
· Root pressure not developed in plant having ectomycorrhiza.

| A | B |
| --- | --- |
| 1g Glu | 1g starch |

B → A
(starch insoluble)

· Outer layer of potato
↓
periderm. (suberised)

· DPD = $-\Psi_w$




Melvin Calvin

MELVIN CALVIN born in Minnesota in April, 1911, received Ph.D. in Chemistry from the University of Minnesota. He se[rved] as Professor of Chemistry at the University of Califor[nia] Berkeley.

Just after world war II, when the world was under sh[ock] after the Hiroshima-Nagasaki bombings, and seeing the effects of radio-activity, Calvin and co-workers put ra[dio-] activity to beneficial use. He along with J.A. Bassham stud[ied] reactions in green plants forming sugar and other substan[ces] from raw materials like carbon dioxide, water and miner[als] by labelling the carbon dioxide with $C^{14}$. Calvin proposed th[at] plants change light energy to chemical energy by transferr[ing] an electron in an organised array of pigment molecules a[nd] other substances. The mapping of the pathway of carb[on] assimilation in photosynthesis earned him Nobel Prize in 19[61].

The principles of photosynthesis as established by Cal[vin] are, at present, being used in studies on renewable resou[rces] for energy and materials and basic studies in solar ener[gy] research.

?

Types of Membrane :-
① Impermeable → Ex- suberised, cutinised CW.
② Permeable → Ex: cellulosic CW
③ Semipermeable → Allow passage of solvent molecules through them & prevent movt. of solute particles.
Ex- egg membrane, parchment membrane, collodion membrane, copper ferricyanide membrane etc.
④ Selectively/differentially permeable → Normally semi permeable but allow selective passage of solutes
eg:- plasmalemma, tonoplast.

# Chapter 11

# Transport in Plants



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.**

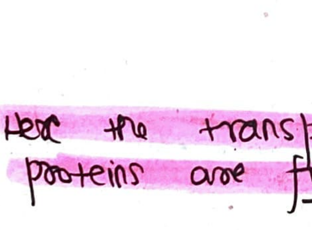
An important aspect that needs to be considered is the direction of transport. In rooted plants, transport in xylem (of water and minerals) is essentially unidirectional, from roots to the stems. Organic and mineral nutrients however, undergo multidirectional transport. Organic compounds synthesised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

• Diffusing particles create pressure called diffusion pressure. DP ∝ no. of particles. Particles from higher DP to lower DP.

## 11.1 MEANS OF TRANSPORT

### 11.1.1 Diffusion

• Direction of diffusion of one substance is independent of movt. of another substance.




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

Here the transport proteins are fixed.

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

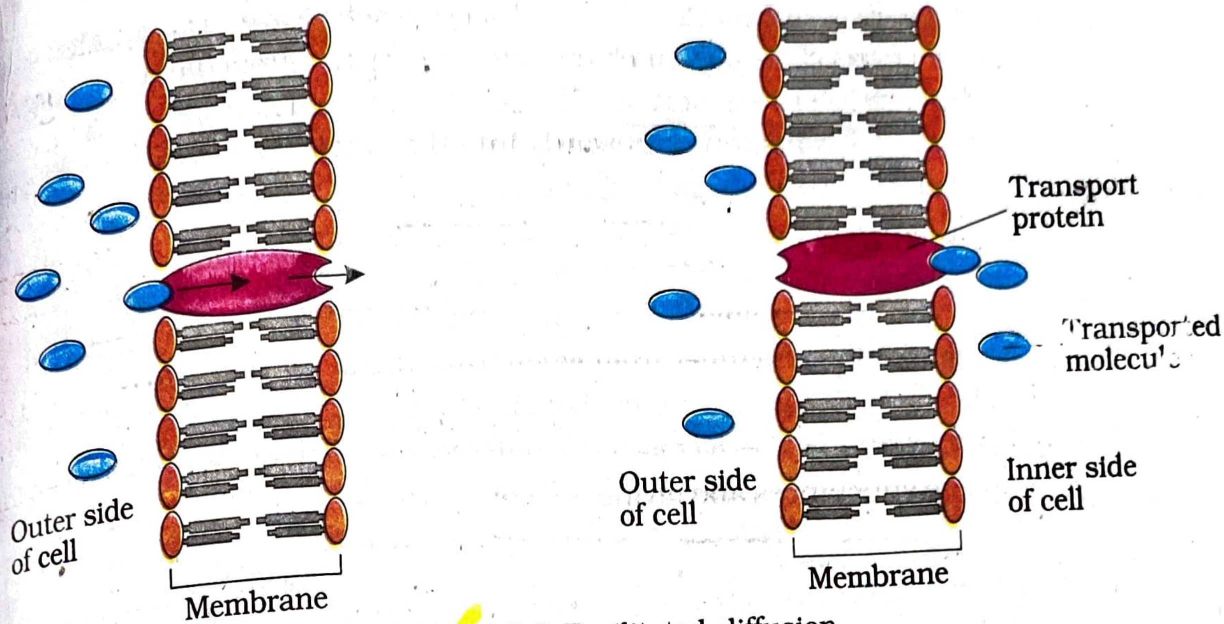



**Figure 11.1** Facilitated diffusion

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 large 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

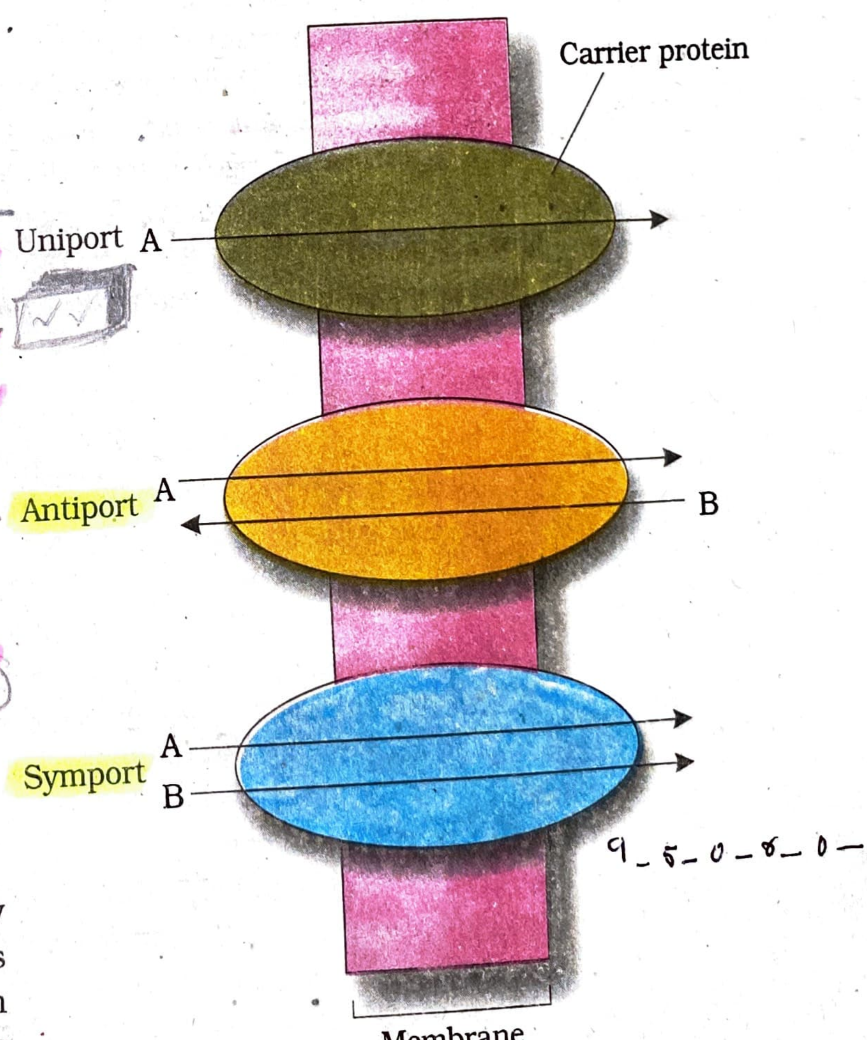



**Figure 11.2** Facilitated diffusion

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

### 11.1.3 Active Transport

· It's faster than passive transport & uses mobile carrier proteins.

Active transport uses energy to transport and pump molecules against a concentration gradient. Active transport is carried out by specific 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 characterstics 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** ($\Psi_w$) is a concept fundamental to understanding water movement. **Solute potential** ($\Psi_s$) and **pressure potential** ($\Psi_p$) 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 $\Psi$ 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 molecules and the concentration (free energy) 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 $\Psi_s$. $\Psi_s$ is always negative. The more the solute molecules, the lower (more negative) is the $\Psi_s$. For a solution at atmospheric pressure (water potential) $\Psi_w$ = (solute potential) $\Psi_s$.

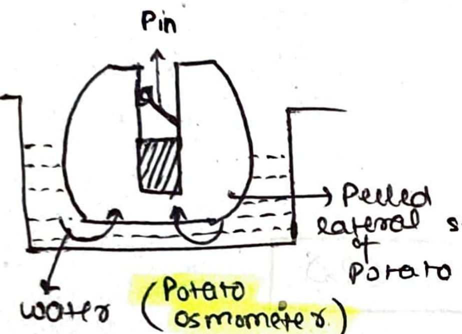
If a pressure greater than atmospheric pressure is applied to pure water or a solution, its water potential increases. It is equivalent to pumping water from one place to another. Can you think of any system in our body where pressure is built up? Pressure can build up in a plant system when water enters 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 usua positive, though in plants negative potential or tension in the water colu in the xylem plays a major role in water transport up a stem. Pressu potential is denoted as $\Psi_p$.

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

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

## 11.2.2 Osmosis




$\Psi_s$ → osmotic potential

· Factors affecting OP :-
① Conc. of solute particles
② Ionization of solute particles
③ Temperature.
④ Hydration of solute particles.

· Osmotic potential is present whether the solution occurs in confined system or an open system, whereas osmotic pressure develops only in confined system.

The plant cell is surrounded by a cell membrane and a cell wall. The ce wall is freely permeable to water and substances in solution hence is n a barrier to movement. In plants the cells usually contain a large centr vacuole, whose contents, the vacuolar sap, contribute to the solu potential of the cell. In plant cells, the cell membrane and the membra of the vacuole, the tonoplast together are important determinants movement of molecules in or out of the cell.

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

You may have made a potato osmometer in your earlier classes stag in school. If the tuber is placed in water, the water enters the cavity in th potato tuber containing a concentrated solution of sugar due to osmosis.

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

(a) *Solution of which chamber has a lower water potential?* B
(b) *Solution of which chamber has a lower solute potential?* B
(c) *In which direction will osmosis occur?* A → B
(d) *Which solution has a higher solute potential?* A
(e) *At equilibrium which chamber wil have lower water potential?* Same
(f) *If one chamber has a Ψ of – 200 kPa, and the other – 1000 kPa, whic is the chamber that has the highe Ψ?* (–1000)
(g) What will be the direction of th movement of water when two solutions with $\Psi_w$ = 0.2 MPa and $\Psi_w$ = 0.1 MPa are separated by a selectively permeable membrane? (0.2) → 0.1

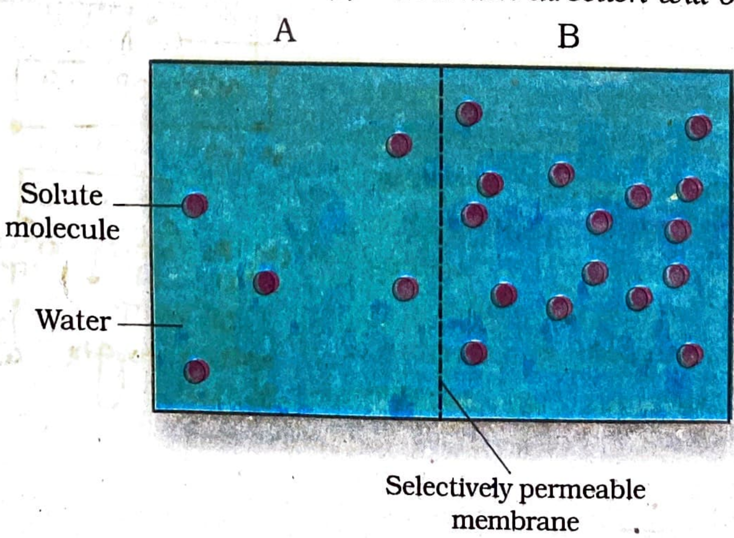



**Figure 11.3**

Let us discuss another experiment where a solution of sucrose in water taken in a funnel is separated from pure water in a beaker by a selectively 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.

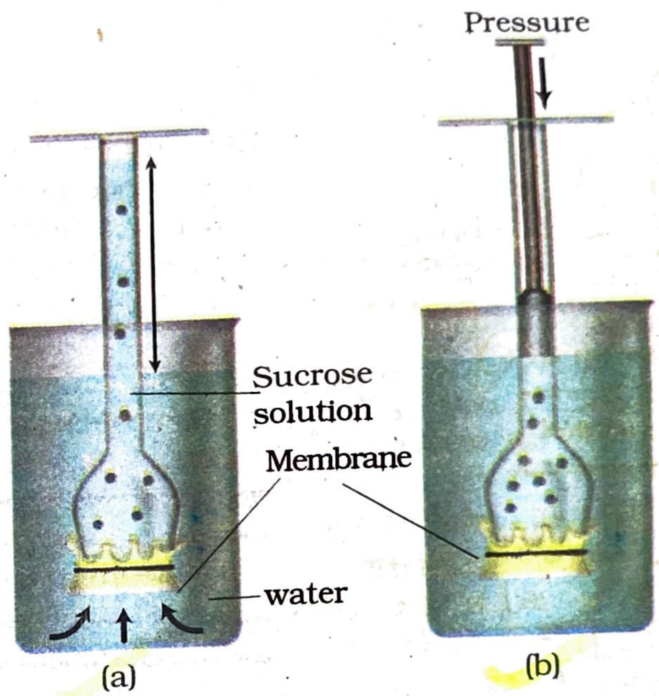



**Figure 11.4** A demonstration of osmosis. A thistle funnel is filled with sucrose solution and kept inverted in a beaker containing water. (a) Water will diffuse across the membrane (as shown by arrows) to raise the level of the solution in the funnel (b) Pressure can be applied as shown to stop the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

### 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

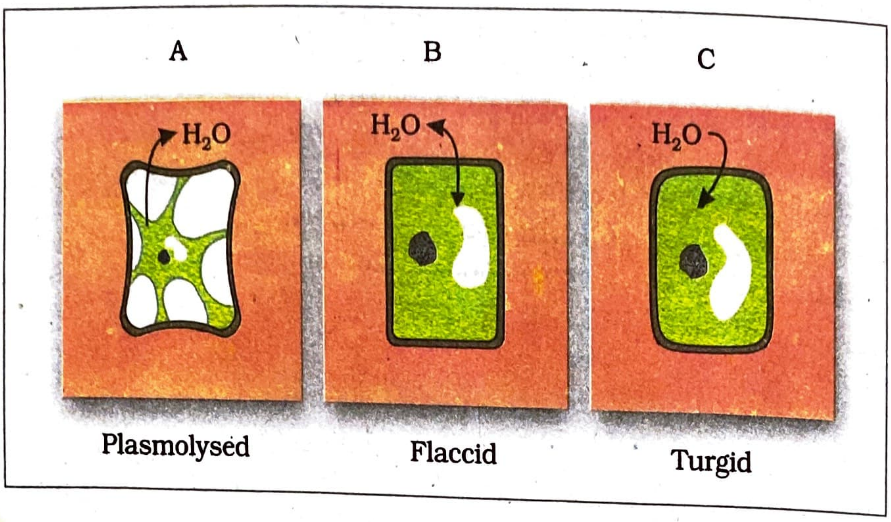



**Figure 11.5** Plant cell plasmolysis

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 $\Psi_p$. 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 $\Psi_p$ 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 increase in volume. The classical

· phycocolloids are best plant imbibants.

iples of imbibition are absorption of water by seeds and dry wood. ressure that is produced by the swelling of wood had been used by storic man to split rocks and boulders. If it were not for the pressure to imbibition, seedlings would not have been able to emerge out of oil into the open; they probably would not have been able to establish! mbibition is also diffusion since water movement is along a entration gradient; the seeds and other such materials have almost no r hence they absorb water easily. Water potential gradient between bsorbent and the liquid imbibed is essential for imbibition. In addition, ny substance to imbibe any liquid, affinity between the adsorbant and liquid is also a pre-requisite.

## .3 LONG DISTANCE TRANSPORT OF WATER

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

Long distance transport of substances within a plant cannot be by ffusion alone. Diffusion is a slow process. It can account for only short stance movement of molecules. For example, the movement of a molecule cross a typical plant cell (about 50 µm) takes approximately 2.5 s. *At this ate, can you calculate how many years it would take for the movement f molecules over a distance of 1 m within a plant by diffusion alone?* 0.57 days. ≈ 14 hours

In large and complex organisms, often substances have to be moved o long distances. Sometimes the sites of production or absorption and ites of storage are too far from each other; diffusion or active transport vould not suffice. Special long distance transport systems become necessary so as to move substances across long distances and at a much aster 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 vas[cular] tissues of plants is called **translocation.**

Do you remember studying cross sections of roots, stems and le[aves] of higher plants and studying the vascular system? The higher pl[ants] have highly specialised vascular tissues – xylem and phloem. Xyle[m is] associated with translocation of mainly water, mineral salts, some org[anic] nitrogen and hormones, from roots to the aerial parts of the plants. [The] phloem translocates a variety of organic and inorganic solutes, ma[inly] 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 plan[ts;] obviously that is why we apply water to the soil and not on the leave[s.] The responsibility of absorption of water and minerals is more specifica[lly] the function of the root hairs that are present in millions at the tips of t[he] roots. Root hairs are thin-walled slender extensions of root epiderm[al] 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 roo[t] 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

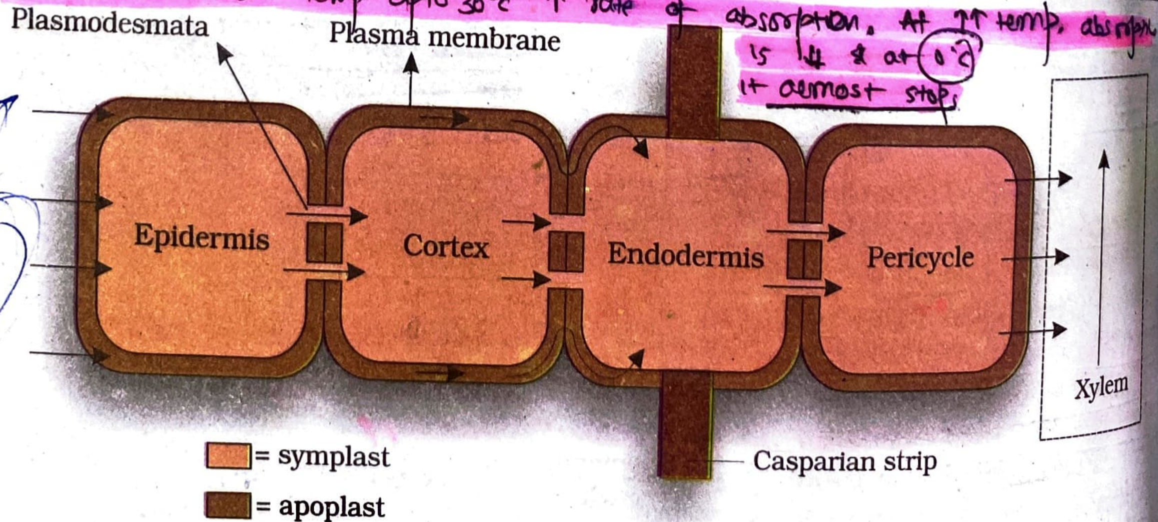



**Figure 11.6** Pathway of water movement in the root

embrane. This movement is dependent on the gradient. The apoplast oes not provide any barrier to water movement and water movement is rough mass flow. As water evaporates into the intercellular spaces or e atmosphere, tension develop in the continuous stream of water in the poplast, hence mass flow of water occurs due to the adhesive and cohesive roperties of water.

The **symplastic** system is the system of interconnected protoplasts. eighbouring cells are connected through cytoplasmic strands that xtend through **plasmodesmata.** During symplastic movement, the water avels through the cells – their cytoplasm; intercellular movement is rough the plasmodesmata. Water has to enter the cells through the ell membrane, hence the movement is relatively slower. Movement is again own a potential gradient. Symplastic movement may be aided by ytoplasmic streaming. You may have observed cytoplasmic streaming n cells of the *Hydrilla* leaf; the movement of chloroplast due to streaming s easily visible.

Most of the water flow in the roots occurs via the apoplast since the ortical cells are loosely packed, and hence offer no resistance to water novement. However, the inner boundary of the cortex, the **endodermis**, s impervious to water because of a band of suberised matrix called the **asparian 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.

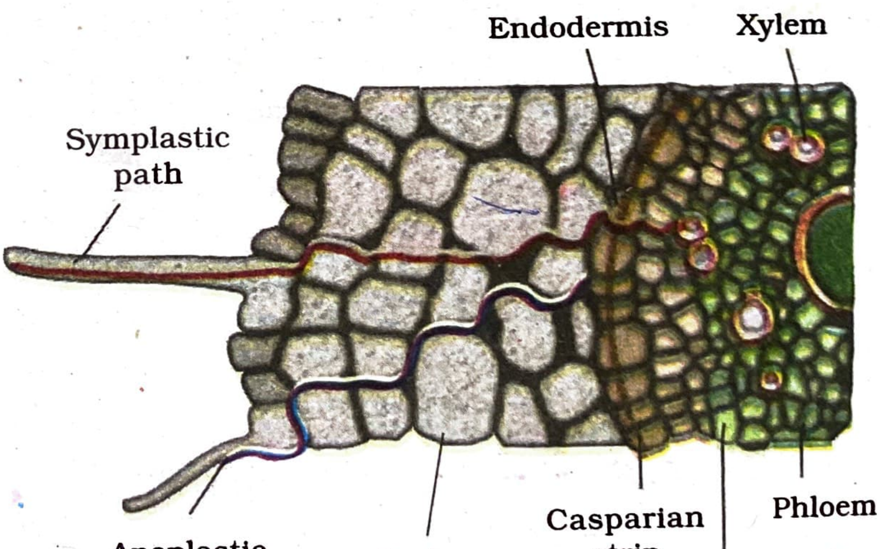



**Figure 11.7** Symplastic and apoplastic pathways of water and ion absorption and movement in roots

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 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 upward flow of water through the xylem in plants can achieve fairly high tes, up to 15 metres per hour. How is this movement accomplished? A ng standing question is, whether water is 'pushed' or 'pulled' through e plant. Most researchers agree that water is mainly 'pulled' through e plant, and that the driving force for this process is transpiration from e leaves. This is referred to as the **cohesion-tension-transpiration ull model** of water transport. But, what generates this transpirational pull?

Water is transient in plants. Less than 1 per cent of the water reaching he leaves is used in photosynthesis and plant growth. Most of it is lost hrough the **stomata** in the leaves. This water loss is known as **ranspiration**.

You have studied transpiration in an earlier class by enclosing a healthy plant in polythene bag and observing the droplets of water formed inside the bag. You could also study water loss from a leaf using cobalt chloride paper, which turns colour on absorbing water.

## 11.4 TRANSPIRATION

Transpiration is the evaporative loss of water by plants. It occurs mainly through **stomata** (sing. : stoma). Besides the loss of water vapour in transpiration, exchange of oxygen and carbon dioxide in the leaf also occurs through these stomata. Normally stomata are open in the day time and close during the night. The immediate cause of the opening or closing of stomata is a change in the turgidity of the **guard cells**. The inner wall of each guard cell, towards the pore or **stomatal aperture,** is thick and elastic. When turgidity increases within the two guard cells flanking each stomatal aperture or pore, the thin outer walls bulge out and force the inner walls into a crescent shape. The opening of the stoma is also aided due to the orientation of the microfibrils in the cell walls of the guard cells. Cellulose microfibrils are oriented radially rather than longitudinally making it easier for the stoma to open. When the guard cells lose turgor, due to water loss (or water stress) the elastic inner walls regain their original shape, the guard cells become flaccid and the stoma closes.

Usually the lower surface of a dorsiventral (often dicotyledonous) leaf has a greater number of stomata while in an isobilateral (often monocotyledonous) leaf they are about equal on both surfaces.

Transpiration is affected by several external factors: temperature, light, humidity, wind speed. Plant factors that affect transpiration include number and distribution of stomata, per cent of open stomata, water status of the plant, canopy structure etc.

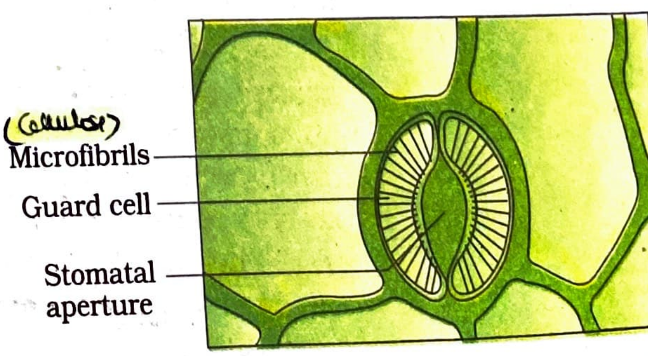



**Figure 11.8** A stomatal aperture with guard cells

The transpiration driven ascent of xylem sap depends mainly on the following physical properties of water:

- **Cohesion** – mutual attraction between water molecules.
- **Adhesion** – attraction of water molecules to polar surfaces (s... as the surface of tracheary elements).
- **Surface Tension** – water molecules are attracted to each othe... the liquid phase more than to water in the gas phase.

These properties give water high **tensile strength**, i.e., an abilit... resist a pulling force, and high **capillarity**, i.e., the ability to rise in t... tubes. In plants capillarity is aided by the small diameter of the trache... elements – the **tracheids** and **vessel elements**.

The process of photosynthesis requires water. The system of xyle... vessels from the root to the leaf vein can supply the needed water. B... what force does a plant use to move water molecules into the le... parenchyma cells where they are needed? As water evaporates throu... the stomata, since the thin film of water over the cells is continuous, results in pulling of water, molecule by molecule, into the leaf from t... xylem. Also, because of lower concentration of water vapour in th... atmosphere as compared to the substomatal cavity and intercellul... spaces, water diffuses into the surrounding air. This creates a 'pu... (Figure 11.9).

Measurements reveal that the forces generated by transpiration ca... create pressures sufficient to lift a xylem sized column of water over 13... metres high.

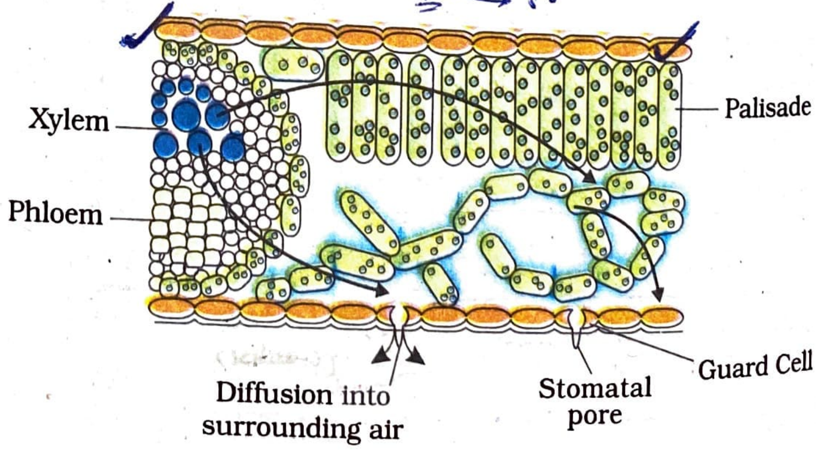



**Figure 11.9** Water movement in the leaf. Evaporation from the leaf sets up a pressure gradient between the outside air and the air spaces of the leaf. The gradient is transmitted into the photosynthetic cells and on the water-filled xylem in the leaf vein.

### .1 Transpiration and Photosynthesis – a Compromise

piration has more than one purpose; it
- creates transpiration pull for absorption and transport of plants
- supplies water for photosynthesis
- transports minerals from the soil to all parts of the plant
- cools leaf surfaces, sometimes 10 to 15 degrees, by evaporative cooling
- maintains the shape and structure of the plants by keeping cells turgid

n actively photosynthesising plant has an insatiable need for water. osynthesis is limited by available water which can be swiftly depleted anspiration. The humidity of rainforests is largely due to this vast ng of water from root to leaf to atmosphere and back to the soil. he evolution of the $C_4$ photosynthetic system is probably one of the egies for maximising the availability of $CO_2$ while minimising water $C_4$ plants are twice as efficient as $C_3$ plants in terms of fixing carbon ide (making sugar). However, a $C_4$ plant loses only half as much water $C_3$ plant for the same amount of $CO_2$ fixed.

Transpiration and photosynthesis occurs simultaneously.

## 5 UPTAKE AND TRANSPORT OF MINERAL NUTRIENTS

ts obtain their carbon and most of their oxygen from $CO_2$ in the osphere. However, their remaining nutritional requirements are ined from water and minerals in the soil.

### 5.1 Uptake of Mineral Ions

ike water, all minerals cannot be passively absorbed by the roots. factors account for this: (i) minerals are present in the soil as charged ticles (ions) which cannot move across cell membranes and (ii) the centration of minerals in the soil is usually lower than the concentration inerals in the root. Therefore, most minerals must enter the root by **ve absorption** into the cytoplasm of epidermal cells. This needs energy he form of ATP. The active uptake of ions is partly responsible for the ter potential gradient in roots, and therefore for the uptake of water by nosis. Some ions also move into the epidermal cells passively.

Ions are absorbed from the soil by both passive and active transport. ecific proteins in the membranes of root hair cells actively pump ions m the soil into the cytoplasms of the epidermal cells. Like all cells, the dodermal cells have many transport proteins embedded in their plasma embrane; they let some solutes cross the membrane, but not others. ansport proteins of *endodermal cells are control points, where a plant* *justs the quantity and types of solutes that reach the xylem.* Note at the root endodermis because of the layer of suberin has the ability to tively transport ions in one direction only.

### 11.5.2 Translocation of Mineral Ions

After the ions have reached xylem through active or passive upt combination of the two, their further transport up the stem to al the plant is through the transpiration stream.

The chief sinks for the mineral elements are the growing regio plant, such as the apical and lateral meristems, young leaves, de flowers, fruits and seeds, and the storage organs. Unloading of ions occurs at the fine vein endings through diffusion and active by these cells.

Mineral ions are frequently remobilised, particularly fro senescing parts. Older dying leaves export much of their mineral to younger leaves. Similarly, before leaf fall in decidous plants, r are removed to other parts. Elements most readily mobili phosphorus, sulphur, nitrogen and potassium. Some elements structural components like calcium are not remobilised.

An analysis of the xylem exudates shows that though som nitrogen travels as inorganic ions, much of it is carried in the form as amino acids and related compounds. Similarly, small a of P and S are carried as organic compounds. In addition, small of exchange of materials does take place between xylem and Hence, it is not that we can clearly make a distinction and say cate that xylem transports only inorganic nutrients while phloem tra only organic materials, as was traditionally believed.

## 11.6 Phloem Transport: Flow from Source to Sink

Food, primarily sucrose, is transported by the vascular tissue from a source to a sink. Usually the source is understood to part of the plant which synthesises the food, i.e., the leaf, and s part that needs or stores the food. But, the source and sink reversed depending on the season, or the plant's needs. Sugar in roots may be mobilised to become a source of food in the early when the buds of trees, act as sink; they need energy for grow development of the photosynthetic apparatus. Since the sour relationship is variable, the direction of movement in the phloe be upwards or downwards, i.e., **bi-directional**. This contras that of the xylem where the movement is always **unidirection** upwards. Hence, unlike onc-way flow of water in transpiratio in phloem sap can be transported in any required direction s as there is a source of sugar and a sink able to use, store or r the sugar.

Phloem sap is mainly water and sucrose, but other sugars, hor and amino acids are also transported or **translocated** through p

### 11.6.1 The Pressure Flow or Mass Flow Hypothesis

The accepted mechanism used for the translocation of sugars from source to sink is called the pressure flow hypothesis. (see Figure 11.10). As glucose is prepared at the source (by photosynthesis) it is converted to sucrose (a dissacharide). The sugar is then moved in the form of sucrose into the companion cells and then into the living phloem sieve tube cells by active transport. This process of loading at the source produces a hypertonic condition in the phloem. Water in the adjacent xylem moves into the phloem by osmosis. As osmotic pressure builds up the phloem sap will move to areas of lower pressure. At the sink osmotic pressure must be reduced. Again active transport is necessary to move the sucrose out of the phloem sap and into the cells which will use the sugar – converting it into energy, starch, or cellulose. As sugars are removed, the osmotic pressure decreases and water moves out of the phloem.

To summarise, the movement of sugars in the phloem begins at the source, where sugars are loaded (actively transported) into a sieve tube. Loading of the phloem sets up a water potential gradient that facilitates the mass movement in the phloem.

Phloem tissue is composed of sieve tube cells, which form long columns with holes in their end walls called sieve plates. Cytoplasmic strands pass through the holes in the sieve plates, so forming continuous filaments. As hydrostatic pressure in the sieve tube of phloem increases, pressure flow begins, and the sap moves through the phloem. Meanwhile, at the sink, incoming sugars are actively transported out of the phloem and removed

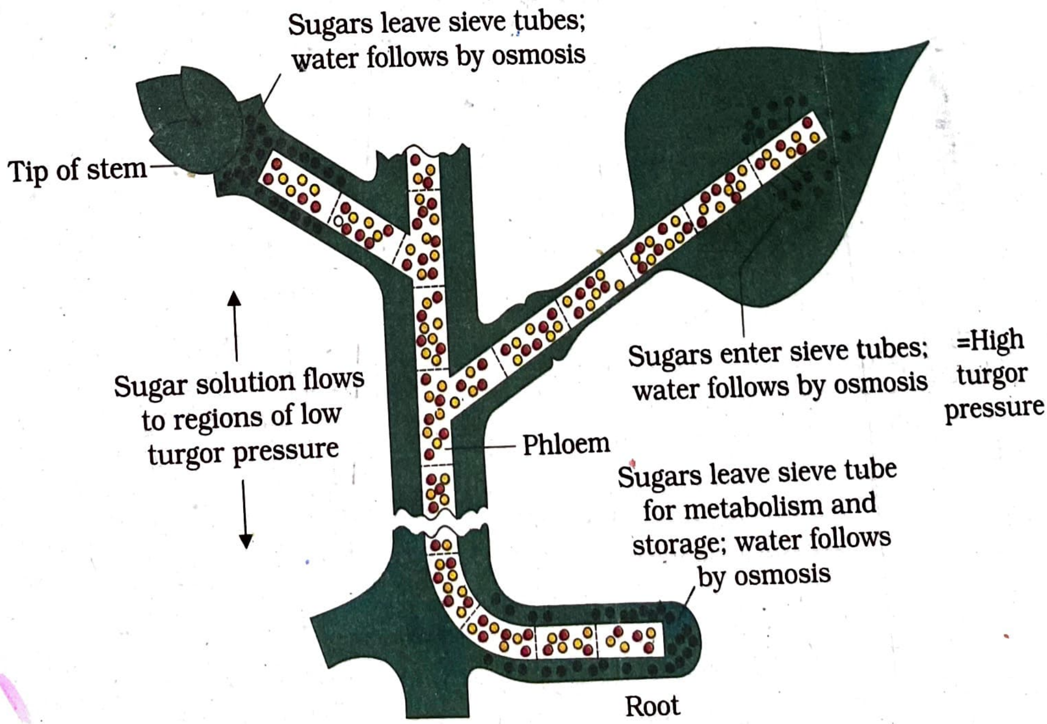



**Figure 11.10** Diagrammatic presentation of mechanism of translocation

as complex carbohydrates. The loss of solute produces a high water potential in the phloem, and water passes out, returning eventually to xylem.

A simple experiment, called girdling, was used to identify the tissues through which food is transported. On the trunk of a tree a ring of bark up to a depth of the phloem layer, can be carefully removed. In the absence of downward movement of food the portion of the bark above the ring on the stem becomes swollen after a few weeks. This simple experiment shows that phloem is the tissue responsible for translocation of food; and that transport takes place in one direction, i.e., towards the roots. This experiment can be performed by you easily.

## SUMMARY

Plants obtain a variety of inorganic elements (ions) and salts from their surroundings especially from water and soil. The movement of these nutrients from environment into the plant as well as from one plant cell to another plant cell essentially involves movement across a cell membrane. Transport across cell membrane can be through diffusion, facilitated transport or active transport. Water and minerals absorbed by roots are transported by xylem and the organic material synthesised in the leaves is transported to other parts of plant through phloem.

Passive transport (diffusion, osmosis) and active transport are the two modes of nutrient transport across cell membranes in living organisms. In passive transport, nutrients move across the membrane by diffusion, without any use of energy as it is always down the concentration gradient and hence entropy driven. This diffusion of substances depends on their size, solubility in water or organic solvents. Osmosis is the special type of diffusion of water across a selectively permeable membrane which depends on pressure gradient and concentration gradient. In active transport, energy in the form of ATP is utilised to pump molecules against a concentration gradient across membranes. Water potential is the potential energy of water molecules which helps in the movement of water. It is determined by solute potential and pressure potential. The osmotic behaviour of cells depends on the surrounding solution. If the surrounding solution of the cell is hypertonic, it gets plasmolysed. The absorption of water by seeds and drywood takes place by a special type of diffusion called imbibition.

In higher plants, there is a vascular system comprising of xylem and phloem, responsible for translocation. Water minerals and food cannot be moved within the body of a plant by diffusion alone. They are therefore, transported by a mass flow system – movement of substance in bulk from one point to another as a result of pressure differences between the two points.

Water absorbed by root hairs moves into the root tissue by two distinct pathways, i.e., apoplast and symplast. Various ions, and water from soil can be transported upto a small height in stems by root pressure. Transpiration pull model is the most acceptable to explain the transport of water. Transpiration is

The study of source, mode of absorption, distribution & metabolism of various inorganic minerals by plants is called Mineral Nutrition.

Aeroponics: technique of soil-less culture in which roots of plants are suspended in oxygenated mist of nutrients.

Sand culture: sand used as rooting medium & nutrient soln is added. It's better than solution cultures in providing solid medium & natural aeration.
Drawback - (i) sand being alkaline has to be treated with acid
(ii) temp. change in sand are fast
(iii) frequent watering..

Stem nodules are found in Sesbania & 
Cobalt occurs mostly in hydathodes.
Phytotron → when plant is grown in controlled conditions of temp. light, pH etc in enclosed green house for studying interactions b/w plants & environment.

# CHAPTER 12

Phytoremediation → Efforts are made to mine metals from soil by plants so that soil can be recovered.

# MINERAL NUTRITION

Etiolation → growth in absence of light. pale yellow coloring, sparse leaves, weak elongated stems.



The basic needs of all living organisms are essentially the same. They require macromolecules, such as carbohydrates, proteins and fats, and water and minerals for their growth and development.

This chapter focusses mainly on inorganic plant nutrition, wherein you will study the methods to identify elements essential to growth and development of plants and the criteria for establishing the essentiality. You will also study the role of the essential elements, their major deficiency symptoms and the mechanism of absorption of these essential elements. The chapter also introduces you briefly to the significance and the mechanism of biological nitrogen fixation.

## 12.1 Methods to Study the Mineral Requirements of Plants

In 1860, Julius von Sachs, a prominent German botanist, demonstrated, for the first time, that plants could be grown to maturity in a defined nutrient solution in complete absence of soil. This technique of growing plants in a nutrient solution is known as **hydroponics**. Since then, a number of improvised methods have been employed to try and determine the mineral nutrients essential for plants. The essence of all these methods involves the culture of plants in a soil-free, defined mineral solution. These methods require purified water and mineral nutrient salts. *Can you explain why is this so essential?*

After a series of experiments in which the roots of the plants were immersed in nutrient solutions and wherein an element was added / substituted / removed or given in varied concentration, a mineral solution suitable for the plant growth was obtained. By this method, essential elements were identified and their deficiency symptoms discovered. Hydroponics has been successfully employed as a technique for the commercial production of vegetables such as tomato, seedless cucumber and lettuce. It must be emphasised that the nutrient solutions must be adequately aerated to obtain the optimum growth. What would happen if solutions were poorly aerated? Diagrammatic views of the hydroponic technique is given in Figures 12.1 and 12.2.

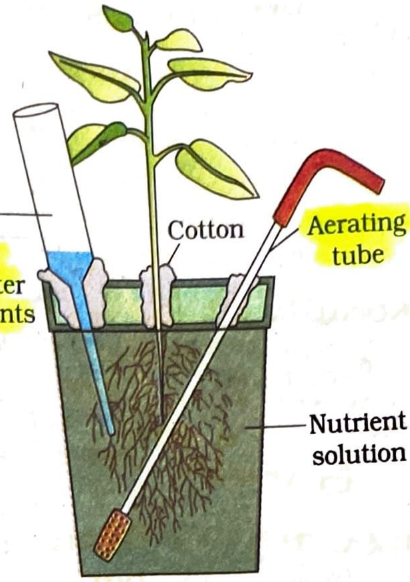



**Figure 12.1** Diagram of a typical set-up for nutrient solution culture

## 12.2 Essential Mineral Elements

Most of the minerals present in soil can enter plants through roots. In fact, more than sixty elements of the 105 discovered so far are found in different plants. Some plant species accumulate selenium, some others gold, while some plants growing near nuclear test sites take up radioactive strontium. There are techniques that are able to detect the minerals even at a very low concentration ($10^{-8}$ g/ mL). The question is, whether all the diverse mineral elements present in a plant, for example, gold and selenium as mentioned above, are really necessary for plants? How do we decide what is essential for plants and what is not?

### 12.2.1 Criteria for Essentiality

The criteria for essentiality of an element are given below:

(a) The element must be absolutely necessary for supporting normal growth and reproduction. In the absence of the element the plants do not complete their life cycle or set the seeds.

(b) The requirement of the element must be specific and not replaceable by another element. In other words, deficiency of any one element cannot be met by supplying some other element.

(c) The element must be directly involved in the metabolism of the plant.

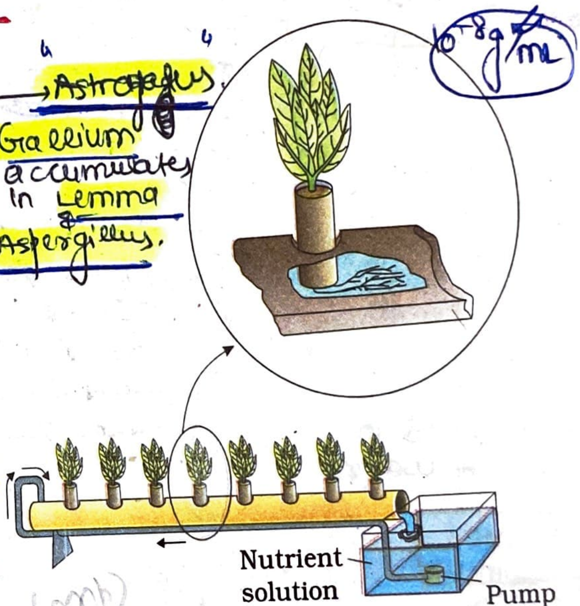



**Figure 12.2** Hydroponic plant production. Plants are grown in a tube or trough placed on a slight incline. A pump circulates a nutrient solution from a reservoir to the elevated end of the tube. The solution flows down the tube and returns to the reservoir due to gravity. Inset shows a plant whose roots are continuously bathed in aerated nutrient solution. The arrows indicates the direction of the flow.

Based upon the above criteria only a few elements have been found to be absolutely essential for plant growth and metabolism. These elements are further divided into two broad categories based on their quantitative requirements.

(i) Macronutrients, and

(ii) Micronutrients

**Macronutrients** are generally present in plant tissues in large amounts (in excess of 10 mmole $Kg^{-1}$ of dry matter). The macronutrients include carbon, hydrogen, oxygen, nitrogen, phosphorous, sulphur, potassium, calcium and magnesium. Of these, carbon, hydrogen and oxygen are mainly obtained from $CO_2$ and $H_2O$, while the others are absorbed from the soil as mineral nutrition.

**Micronutrients** or trace elements, are needed in very small amounts (less than 10 mmole $Kg^{-1}$ of dry matter). These include iron, manganese, copper, molybdenum, zinc, boron, chlorine and nickel.

In addition to the 17 essential elements named above, there are some beneficial elements such as sodium, silicon, cobalt and selenium. They are required by higher plants.

Essential elements can also be grouped into four broad categories on the basis of their diverse functions. These categories are:

(i) Essential elements as components of biomolecules and hence structural elements of cells (e.g., carbon, hydrogen, oxygen and nitrogen).

(ii) Essential elements that are components of energy-related chemical compounds in plants (e.g., magnesium in chlorophyll and phosphorous in ATP).

(iii) Essential elements that activate or inhibit enzymes, for example $Mg^{2+}$ is an activator for both ribulose bisphosphate carboxylase-oxygenase and phosphoenol pyruvate carboxylase, both of which are critical enzymes in photosynthetic carbon fixation; $Zn^{2+}$ is an activator of alcohol dehydrogenase and Mo of nitrogenase during nitrogen metabolism. *Can you name a few more elements that fall in this category?* For this, you will need to recollect some of the biochemical pathways you have studied earlier.

(iv) Some essential elements can alter the osmotic potential of a cell. Potassium plays an important role in the opening and closing of stomata. You may recall the role of minerals as solutes in determining the water potential of a cell.

### 12.2.2 Role of Macro- and Micro-nutrients

Essential elements perform several functions. They participate in various metabolic processes in the plant cells such as permeability of cell membrane, maintenance of osmotic concentration of cell sap, electron-transport systems, buffering action, enzymatic activity and act as major constituents of macromolecules and co-enzymes.

Various forms and functions of essential nutrient elements are given below.

**Nitrogen:** This is the essential nutrient element required by plants in the greatest amount. It is absorbed mainly as $NO_3^-$ though some are also taken up as $NO_2^-$ or $NH_4^+$. Nitrogen is required by all parts of a plant, particularly the meristematic tissues and the metabolically active cells. Nitrogen is one of the major constituents of proteins, nucleic acids, vitamins and hormones.

**Phosphorus:** Phosphorus is absorbed by the plants from soil in the form of phosphate ions (either as $H_2PO_4^-$ or $HPO_4^{2-}$). Phosphorus is a constituent of cell membranes, certain proteins, all nucleic acids and nucleotides, and is required for all phosphorylation reactions.

**Potassium:** It is absorbed as potassium ion ($K^+$). In plants, this is required in more abundant quantities in the meristematic tissues, buds, leaves and root tips. Potassium helps to maintain an anion-cation balance in cells and is involved in protein synthesis, opening and closing of stomata, activation of enzymes and in the maintenance of the turgidity of cells.

**Calcium:** Plant absorbs calcium from the soil in the form of calcium ions ($Ca^{2+}$). Calcium is required by meristematic and differentiating tissues. During cell division it is used in the synthesis of cell wall, particularly as calcium pectate in the middle lamella. It is also needed during the formation of mitotic spindle. It accumulates in older leaves. It is involved in the normal functioning of the cell membranes. It activates certain enzymes and plays an important role in regulating metabolic activities.

**Magnesium:** It is absorbed by plants in the form of divalent $Mg^{2+}$. It activates the enzymes of respiration, photosynthesis and are involved in the synthesis of DNA and RNA. Magnesium is a constituent of the ring structure of chlorophyll and helps to maintain the ribosome structure.

**Sulphur:** Plants obtain sulphur in the form of sulphate ($SO_4^{2-}$). Sulphur is present in two amino acids – cysteine and methionine and is the main constituent of several coenzymes, vitamins (thiamine, biotin, Coenzyme A) and ferredoxin.

**Iron:** Plants obtain iron in the form of ferric ions ($Fe^{3+}$). It is required in larger amounts in comparison to other micronutrients. It is an important constituent of proteins involved in the transfer of electrons like ferredoxin and cytochromes. It is reversibly oxidised from $Fe^{2+}$ to $Fe^{3+}$ during electron transfer. It activates catalase enzyme, and is essential for the formation of chlorophyll.

**Manganese:** It is absorbed in the form of manganous ions ($Mn^{2+}$). It activates many enzymes involved in photosynthesis, respiration and nitrogen metabolism. The best defined function of manganese is in the splitting of water to liberate oxygen during photosynthesis.

**Zinc:** Plants obtain zinc as $Zn^{2+}$ ions. It activates various enzymes, especially carboxylases. It is also needed in the synthesis of auxin.

**Copper:** It is absorbed as cupric ions ($Cu^{2+}$). It is essential for the overall metabolism in plants. Like iron, it is associated with certain enzymes involved in redox reactions and is reversibly oxidised from $Cu^{+}$ to $Cu^{2+}$.

**Boron :** It is absorbed as $BO_3^{3-}$ or $B_4O_7^{2-}$. Boron is required for uptake and utilisation of $Ca^{2+}$, membrane functioning, pollen germination, cell elongation, cell differentiation and carbohydrate translocation.

**Molybdenum:** Plants obtain it in the form of molybdate ions ($MoO_2^{2+}$). It is a component of several enzymes, including nitrogenase and nitrate reductase both of which participate in nitrogen metabolism.

**Chlorine:** It is absorbed in the form of chloride anion ($Cl^{-}$). Along with $Na^{+}$ and $K^{+}$, it helps in determining the solute concentration and the anion-cation balance in cells. It is essential for the water-splitting reaction in photosynthesis, a reaction that leads to oxygen evolution.

### 12.2.3 Deficiency Symptoms of Essential Elements

Whenever the supply of an essential element becomes limited, plant growth is retarded. The concentration of the essential element below which plant growth is retarded is termed as **critical concentration.** The element is said to be deficient when present below the critical concentration.

Since each element has one or more specific structural or functional role in plants, in the absence of any particular element, plants show certain morphological changes. These morphological changes are indicative of certain element deficiencies and are called deficiency symptoms. The deficiency symptoms vary from element to element and they disappear when the deficient mineral nutrient is provided to the plant. However, if deprivation continues, it may eventually lead to the death of the plant. The parts of the plants that show the deficiency symptoms also depend on the mobility of the element in the plant. For elements that are actively mobilised within the plants and exported to young developing tissues, the deficiency symptoms tend to appear first in the older tissues. For example, the deficiency symptoms of nitrogen, potassium and magnesium are visible first in the senescent leaves. In the older leaves, biomolecules containing these elements are broken down, making these elements available for mobilising to younger leaves.

The deficiency symptoms tend to appear first in the young tissues whenever the elements are relatively immobile and are not transported out of the mature organs, for example, element like sulphur and m are a part of the structural component of the cell and hence are sily released. This aspect of mineral nutrition of plants is of a great cance and importance to agriculture and horticulture.

e kind of deficiency symptoms shown in plants include chlorosis, sis, stunted plant growth, premature fall of leaves and buds, and tion of cell division. Chlorosis is the loss of chlorophyll leading to ving in leaves. This symptom is caused by the deficiency of elements Mg, S, Fe, Mn, Zn and Mo. Likewise, necrosis, or death of tissue, cularly leaf tissue, is due to the deficiency of Ca, Mg, Cu, K. Lack or evel of N, K, S, Mo causes an inhibition of cell division. Some elements N, S, Mo delay flowering if their concentration in plants is low.

ou can see from the above that the deficiency of any element can e multiple symptoms and that the same symptoms may be caused he deficiency of one of several different elements. Hence, to identify deficient element, one has to study all the symptoms developed in all various parts of the plant and compare them with the available ndard tables. We must also be aware that different plants also respond erently to the deficiency of the same element.

### .2.4 Toxicity of Micronutrients

e requirement of micronutrients is always in low amounts while their oderate decrease causes the deficiency symptoms and a moderate increase uses toxicity. In other words, there is a narrow range of concentration at hich the elements are optimum. Any mineral ion concentration in tissues at reduces the dry weight of tissues by about 10 per cent is considered xic. Such critical concentrations vary widely among different icronutrients. The toxicity symptoms are difficult to identify. Toxicity levels r any element also vary for different plants. Many a times, excess of an lement may inhibit the uptake of another element. For example, the rominent symptom of manganese toxicity is the appearance of brown pots surrounded by chlorotic veins. It is important to know that nanganese competes with iron and magnesium for uptake and with nagnesium for binding with enzymes. Manganese also inhibit calcium ranslocation in shoot apex. Therefore, excess of manganese may, in fact, nduce deficiencies of iron, magnesium and calcium. Thus, what appears as symptoms of manganese toxicity may actually be the deficiency symptoms of iron, magnesium and calcium. Can this knowledge be of some importance to a farmer? a gardener? or even for you in your kitchen-garden?

## 12.3 Mechanism of Absorption of Elements

Much of the studies on mechanism of absorption of elements by plants has been carried out in isolated cells, tissues or organs. These studies revealed that the process of absorption can be demarcated into two main phases. In the first phase, an initial rapid uptake of ions into the 'free space' or 'outer space' of cells – the apoplast, is passive. In the second phase of uptake, the ions are taken in slowly into the 'inner space' – the symplast of the cells. The passive movement of ions into the apoplast usually occurs through ion-channels, the trans-membrane proteins that function as selective pores. On the other hand, the entry or exit of ions to and from the symplast requires the expenditure of metabolic energy, which is an **active** process. The movement of ions is usually called **flux**; the inward movement into the cells is influx and the outward movement, efflux. You have read the aspects of mineral nutrient uptake and translocation in plants in Chapter 11.

## 12.4 Translocation of Solutes

Mineral salts are translocated through xylem along with the ascending stream of water, which is pulled up through the plant by transpirational pull. Analysis of xylem sap shows the presence of mineral salts in it. Use of radioisotopes of mineral elements also substantiate the view that they are transported through the xylem. You have already discussed the movement of water in xylem in Chapter 11.

## 12.5 Soil as Reservoir of Essential Elements

Majority of the nutrients that are essential for the growth and development of plants become available to the roots due to weathering and breakdown of rocks. These processes enrich the soil with dissolved ions and inorganic salts. Since they are derived from the rock minerals, their role in plant nutrition is referred to as mineral nutrition. Soil consists of a wide variety of substances. Soil not only supplies minerals but also harbours nitrogen-fixing bacteria, other microbes, holds water, supplies air to the roots and acts as a matrix that stabilises the plant. Since deficiency of essential minerals affect the crop-yield, there is often a need for supplying them through fertilisers. Both macro-nutrients (N, P, K, S, etc.) and micro-nutrients (Cu, Zn, Fe, Mn, etc.) form components of fertilisers and are applied as per need.

## 12.6 Metabolism of Nitrogen

### 12.6.1 Nitrogen Cycle

Apart from carbon, hydrogen and oxygen, nitrogen is the most prevalent element in living organisms. Nitrogen is a constituent of amino acids, proteins, hormones, chlorophylls and many of the vitamins. Plants compete with microbes for the limited nitrogen that available in soil. Thus, nitrogen is limiting nutrient for both natural and agricultural eco-systems.

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

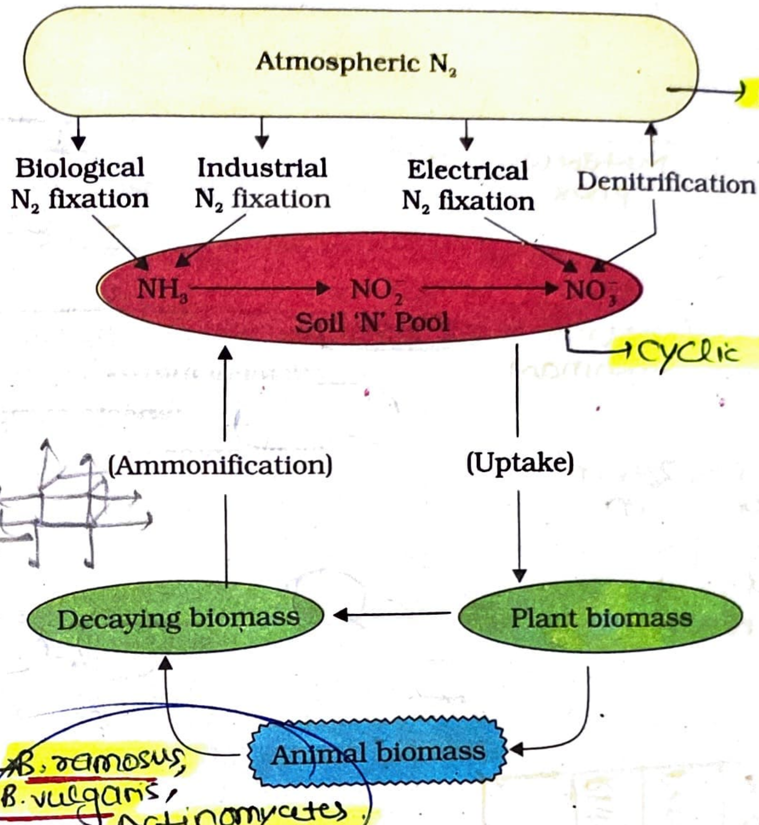



**Figure 12.3** The nitrogen cycle showing relationship between the three main nitrogen pools – atmospheric soil, and biomass

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

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

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

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

## 12.6.2 Biological Nitrogen Fixation

Very few living organisms can utilise the nitrogen in the form $N_2$, available abundantly in the air. Only certain prokaryotic species are capable of fixing nitrogen. Reduction of nitrogen to ammonia by living organisms is called **biological nitrogen fixation.** The enzyme, nitrogenase which is capable of nitrogen reduction is present exclusively in prokaryotes. Such microbes are called $N_2$- fixers.

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

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

**Symbiotic biological nitrogen fixation**

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

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

**Nodule Formation**

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

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

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

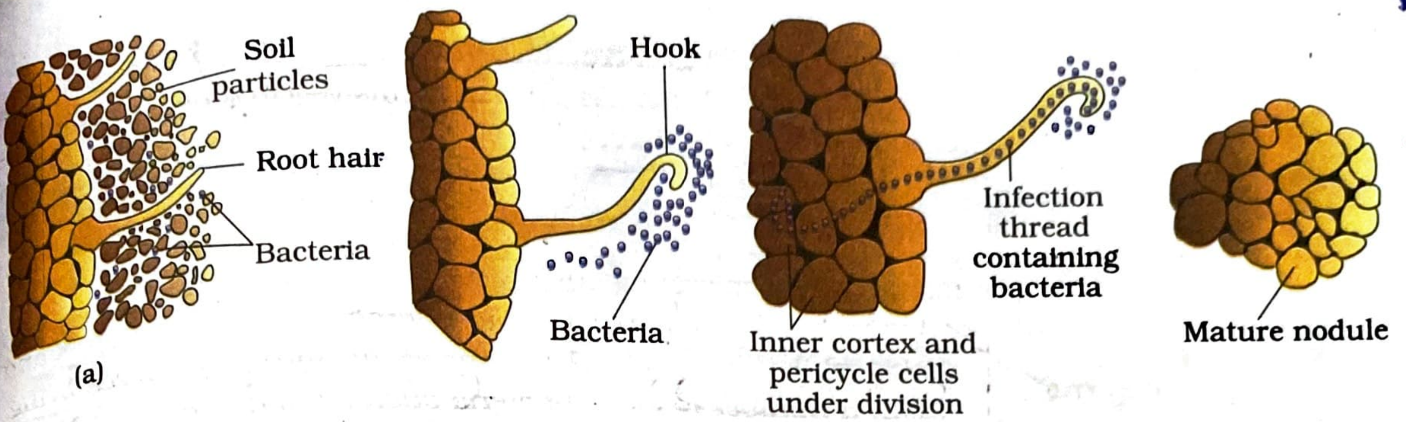



**Figure 12.4** Development of root nodules in soyabean : (a) *Rhizobium* bacteria contact a susceptible root hair, divide near it, (b) Successful infection of the root hair causes it to curl, (c) Infected thread carries the bacteria to the inner cortex. The bacteria get modified into rod-shaped bacteroids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

The reaction is as follows:

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

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

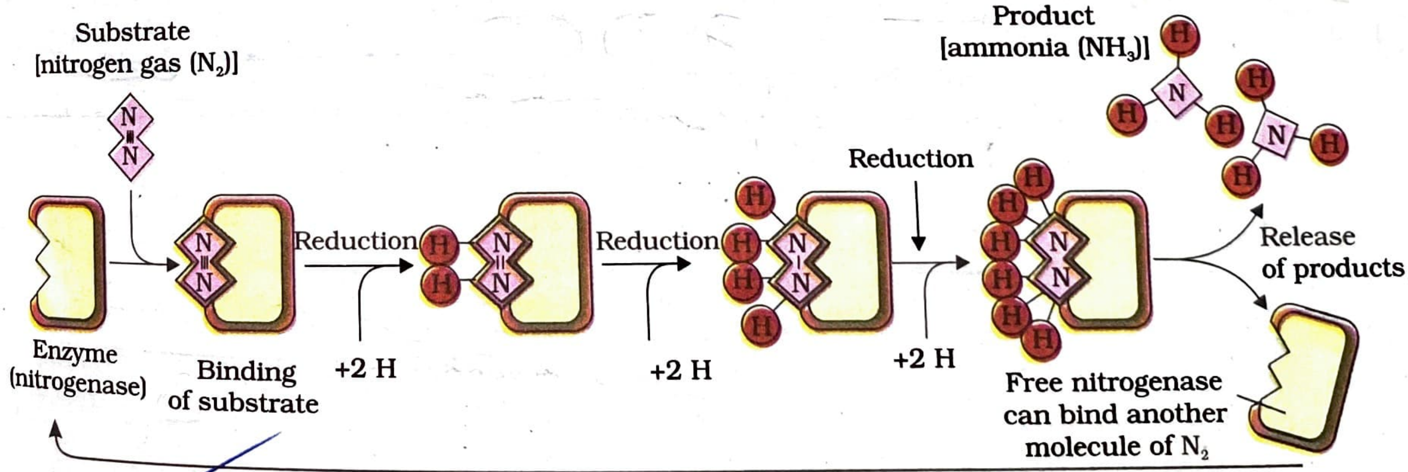



**Figure 12.5** Steps of conversion of atmospheric nitrogen to ammonia by nitrogenase enzyme complex found in nitrogen-fixing bacteria

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

**Fate of ammonia:** At physiological pH, the ammonia is protonated to form $NH_4^+$ (ammonium) ion. While most of the plants can assimilate nitrate as well as ammonium ions, the latter is quite toxic to plants and hence canno accumulate in them. Let us now see how the $NH_4^+$ is used to synthesis amino acids in plants. There are two main ways in which this can take place:

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

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

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

$$\underset{\text{Amino-donor}}{R_1-\overset{H}{\underset{NH_3^+}{C}}-COO^-} + \underset{\text{Amino-acceptor}}{R_2-\underset{O}{\overset{\|}{C}}-COO^-} \rightleftharpoons R_1-\underset{O}{\overset{\|}{C}}-COO^- + R_2-\overset{H}{\underset{NH_3^+}{C}}-COO^-$$

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

## SUMMARY

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