UNIT 12 MINERAL NUTRITION

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12.1 INTRODUCTION

Three basic needs of human beings are food, clothing and shelter. For all these, we directly or indirectly depend upon plants. Late (Prof.) P. Maheswari once said, "We are all guests of plants on this earth." What an apt remark on our dependence on plants! Modern living, in addition requires many industrial products, the raw materials for many of these again come from plants. Therefore, successful cultivation of plants, on which we depend so much, is of prime importance.

Like man and animals, plants too need wholesome nutrition for healthy growth and development. While man and animals are mobile and can gather their food from wherever it is available, plants are stationary and manufacture their own food from simple inorganic nutrients, relying mostly on what they get from their immediate environment. For successful production of a healthy crop, an in-depth knowledge of their nutritional requirements is a must. Our attempt in this unit will be to find out what these requirements are, how plants obtain them from the environment and how they are transported to all parts of the plant body.

Objectives

After studying this unit you should be able to :

- list the essential macro and micronutrients that a plant must absorb in order to live and grow,
- describe the role of the essential elements in plants,
- list the factors that influence the uptake of ions by the root from soil,
- explain how these elements are taken in selectively by root cells from the soil and transported to different parts of the plant body,
- list a few deficiency symptoms of specific nutrients in a plant and name the chemicals that are applied to correct the deficiency.

Study Guide

The understanding of Section 12.4 of this unit requires knowledge of membrane transport processes. You may revise Sections 7.4, 7.5, 8.2, 8.3 and 8.4 of LSE-01 Block II. Section 12.5 on the role of essential nutrients is lengthy but it makes easy reading. To save time jot down the important information in the first reading itself.

12.2 NUTRIENT ELEMENTS OF PLANTS

Let us first find out the chemical composition of plants and see which element nature has selected to support their healthy growth. Only then we will be able to know the nutritional requirement of plants.

As you know a major part of plant tissue is comprised of water. This we can demonstrate by taking a known amount of plant tissue and drying it for a few hours in an oven at a temperature of 65-80°C. If we condense and analyse the vapours coming out from the plant tissue we will find that it is nothing but water. In fact, about 85-90 per cent of the tissue is composed of water. The part of the tissue which is left behind is called the **dry matter** and typically it is about 10-15 per cent of the original weight. The dry matter consists mainly of organic compounds. About 90% of the dry matter consists of plant cell walls, primarily cellulose and related carbohydrates. This can be eliminated in the form of gases on combustion at 600°C. The residue now left is the ash which varies in different plant tissue from about 1 per cent to 0.15 per cent of the dry weight. Interestingly, a careful analysis of the ash shows that it contains almost all of the chemical elements present in the soil surrounding the plant.

Now, the question is whether all the elements found in the ash are essential for the plant in order to lead a healthy life? How do we distinguish the essential elements from the non-essential ones?

12.2.1 Criteria of Essentiality

Arnon and Stout (University of California, USA), as early as 1939, suggested certain criteria that an element must fulfil in order to be classified as essential. These criteria are listed below.

1) An element is essential if in its absence the plant cannot complete its life cycle and form viable seeds.
2) An element is essential if it forms a part of any molecule or a constituent of the plant that in itself is essential for the plant. For example, nitrogen in protein, magnesium in chlorophyll and iron in cytochromes.
3) The element must act directly inside the plant, and not enhance or suppress the availability of some other element.

Although the first two criteria mentioned above are sufficient to judge if an element is essential, the third criterion can eliminate doubtful candidates from the list. For example, the plant *Astragalus* is a selenium accumulator. When grown in seleniferous soils the element shows growth promoting effect. However, experiments have shown that this property is due to the ability of selenate ion to inhibit the absorption of phosphate, which otherwise is absorbed by the plant in toxic amounts. From a practical point of view, an element is considered essential if plants show deficiency symptoms when they are raised without that element in the medium even if the plants are able to form viable seeds. You may note that rigorous exclusion of elements, specially trace elements is very difficult as they can come from seeds themselves, from dust in air, or as contaminants of major salts.

The following couplet will help you to remember the mineral requirement of plants.

See Hopkins Cafe managed By Mine Cousin Mo Very Clean Naturally Cool.

(C H O P K I N S Ca Fe Mg B Mn Cu Zn Mo Va Cl Na Co)

You will notice that the couplet includes iodine. Actually plants do not need iodine, while animals do, as you know the lack of which causes goiter.

Table 12.1 shows the list of sixteen elements that fulfil the criteria of essentiality stated above, their approximate adequate concentration and approximate number of atoms required with molybdenum (Mo) serving as the reference point. Look at the difference! The requirement of hydrogen atoms is about 60 million times the number of Mo atoms. It is because H is an essential part of thousands of chemical compounds with which the plant is made of, whereas Mo is required only in one or two enzyme mediated reactions.

It has been shown that Na^+ as micronutrient is required by certain desert species, such as *Atriplex vesicaria* and some species that assimilate CO_2 in photosynthesis by C_4 pathway or crassulacean acid metabolism. Deficiency of Na^+ is manifested by severe chlorosis in leaves and necrosis in leaf margin and tips.

Scientists have added a few more elements to the list of sixteen though they have found them essential only for certain group of plants. These are, sodium (Na), cobalt (Co), silicon (Si), nickel (Ni) and even chromium (Cr), tin (Sn) and fluorine (F). Some specific organisms may require other elements. For example, certain algae apparently also require the elements vanadium (Va), silicon (Si) or iodine (I), while some ferns utilise aluminium (Al) and some local weeds absorb and accumulate selenium (Se) in high amounts. Fig. 12.1 shows the effect of nutrient deficiency on the growth of barley seedlings.

Table 12.1 : The essential elements required by higher plants**

Element	Chemical Symbol	Form available to plants	Concentration in dry matter (%)	Relative no. of atoms compared of Molybdenum
1. Hydrogen	H	H_2O	6.0	60,000,000
2. Carbon	C	CO_2	45	35,000,000
3. Oxygen	O	O_2, H_2O, CO_2	45	30,000,000
4. Nitrogen	N	$*NO_3^-, NH_4^+$	1.5	1,000,000
5. Potassium	K	K^+	1.0	250,000
6. Calcium	Ca	Ca^{2+}	0.5	125,000
7. Magnesium	Mg	Mg^{2+}	0.2	80,000
8. Phosphorus	P	$*H_2PO_4^-, HPO_4^{2-}$	0.2	60,000
9. Sulphur	S	SO_4^{2-}	0.1	30,000
10. Chlorine	Cl	Cl^-	0.010	3,000
11. Iron	Fe	$Fe^{3+}, *Fe^{2+}$	0.010	2,000
12. Boron	B	H_3BO_3	0.002	2,000
13. Manganese	Mn	Mn^{2+}	0.005	1,000
14. Zinc	Zn	Zn^{2+}	0.002	300
15. Copper	Cu	$Cu^+, *Cu^{2+}$	0.0006	100
16. Molybdenum	Mo	MoO_4^{2-}	0.00001	1

* More common form.

** Modified after P.R. Stout (1961), Proceedings of the Ninth Annual California Fertiliser Conference.

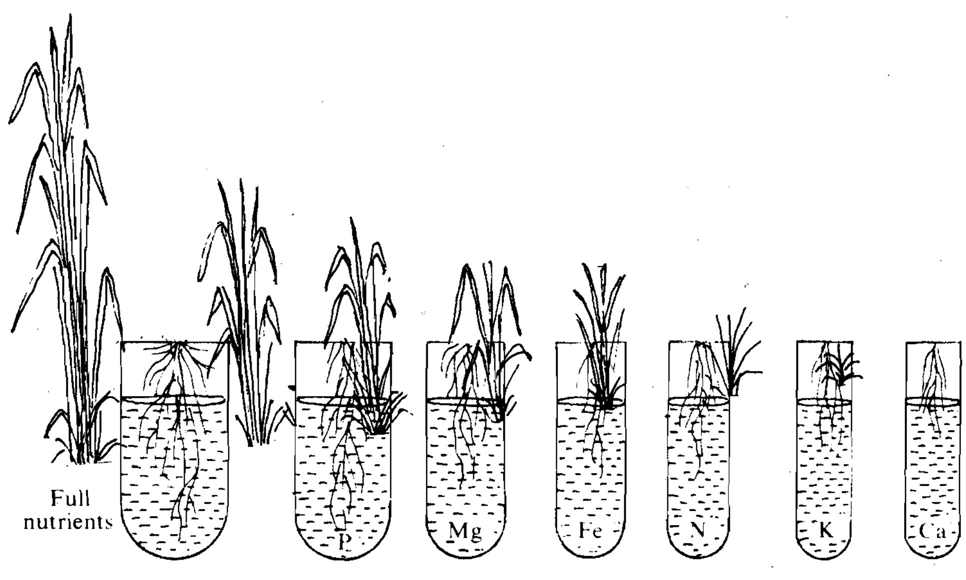

Fig. 12.1 : Effect of nutrient deficiency on growth of barley plants in water culture.

You will have opportunity to learn more about the eseential elements towards the end of the unit.

12.2.2 Classification of Elements

The conventional system of classification is based on the concentration of element g^{-1} dry matter found in the plant. Those which are found in concentration of 1000 μg or more are called **macronutrients** and those found in less than 100 $\mu g\ g^{-1}$ dry matter are designated as **micronutrients**. Thus, the first nine elements listed in Table 12.1 are macronutrients and the rest seven are micronutrients.

This classification though useful in some respects, is arbitrary and in many cases the difference between the contents of the two groups is not much. To give an example, the Fe and Mn contents of plant tissues very often are as high as the content of S or Mg. Hence, scientists are trying to evolve a more satisfactory classification based on physiological and biochemical parameters.

12.2.3 Functions of Essential Elements

Essential elements in plants serve the following three functions:

1) **Osmotic Function :** Plant cells generally contain mineral ions 10 to 1000 times higher in concentration than the surrounding soil. That is why water enters the cells by osmosis and builds up turgor. You know that turgor maintains the shape and size of non-rigid plant parts such as leaves. Potassium is a key ion in this respect. Changes in its concentration in guard cells affect turgor and thus result in opening and closing of stomata. Turgor is also essential for the growth of plant cells.

2) **Structural Function** : The elements nitrogen, phosphorus and sulphur absorbed from the soil are essential components of amino acids and nucleotides. The other two elements that are constituents of important compounds are Mg^{2+} and Ca^{2+}. While Mg^{2+} is part of chlorophyll molecule and Ca^{2+} is an integral part of the middle lamella and is thought to be essential for maintaining structural characteristic of cell walls. It also maintains the permeability of plasma membrane. In its absence cells begin to leak out. In recent years a new regulatory role that Ca^{2+} plays in the cell is beginning to be appreciated. It plays the role of a second messenger.

3) **Biochemical Function** : Elements Mg, Mn, K, Ca and Fe are cofactors for many enzymatic reactions. Fe is carrier of electrons in electron transfer chain. Phosphorus plays a great role in cell chemistry. Phosphorylated sugars are essential for photosynthesis and respiratory metabolism, and phosphorus in the form of phosphate is essential for the formation of the high-energy bonds of ATP.

SAQ 1

a) Which of the following statements are true? Write T for true and F for false in the given boxes.

   i) The matter which is left after drying the plant tissue is called ash. ☐

   ii) Plants contain more calcium than phosphorus. ☐

   iii) The elements that are found in concentration of 1000 μg are called micronutrients. ☐

   iv) The element sodium plays a key role in maintaining the turgor of plant cells. ☐

b) Fill in the blanks with appropriate words.

   i) The key element that performs osmotic function in plants is ....

   ii) .... maintains the permeability of plasma membrane.

   iii) Mg^{2+} is part of .... molecule.

   iv) .... is carrier of electrons in electron transfer chain.

12.3 NUTRIENT ABSORPTION

Except for carbon, oxygen and hydrogen which are provided by CO_2 and water, all the other elements essential for plants are provided by the soil. Hence, hereafter, in this unit on 'Mineral Nutrition' we will confine our discussion to those elements which are acquired from the soil by the plants.

Hydroponics
Plants can be grown without soil in a solution of mineral salts of required composition. This technique of growing plants is called hydroponics, soil-less culture or solution culture.

12.3.1 Nutrients and the Soil

Early experiments on mineral uptake were performed by Hoagland, Stout and Arnon in 1923. They showed that minerals were taken up from the soil primarily in ionic form. The rate of uptake of different ions by roots varied and one ion influenced the

$Micelle\text{-}Mg^{2+} + 2H^+$
$\rightarrow Micelle\text{-}H^+ + Mg^{2+}$
(In soil solution)

$CO_2 + H_2O \rightleftharpoons H_2CO_3$
$H_2CO_3 \rightleftharpoons H^+ + HCO_3^-$
(From respiration)

uptake of other ions. As soil is the medium for the storage and exchange of mineral ions, its properties, ion exchange capacity, pH and the presence of different cations and anions affect the availability of ions to the plant. In other words, the presence of a certain mineral ions in abundance in the soil cannot ensure its availability to the plant because ions may adhere to clay or precipitate out of the solution as insoluble salts. The soil with high water holding capacity generally has high mineral holding capacity as well. The fine particles of clay and humus possess a relatively large surface to volume ratio and are negatively charged. Hence, they have higher ion-binding capacity than the soil composed of coarse particles. Fig. 12.2 shows the colloidal clay crystals (micelles) with innumerable negative surface charges. The cations are loosely bound to negative charges by ionic bond and are capable of exchanging rapidly and reversibly with those in the soil solution. H^+ ions have greater affinity for charged soil particles than Ca^{2+}, Mg^{2+} or K^+ ions. Therefore, these cations are released in soil water by H^+ ions and made available for uptake by roots. The acidity of soil also increases due to respiration because CO_2 released reacts with soil water to form carbonic acid.

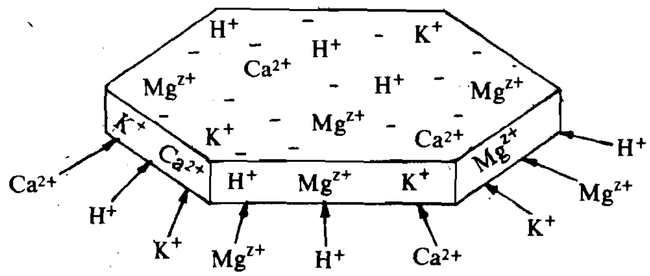

Fig. 12.2 : Diagrammatic representation of the outside surfaces of a clay micelle. Note many negative surface charges and the various cations surrounding them.

The ion exchange capacity of mineral ions is affected by the pH of soil which in turn affects the availability of different ions to the plant as shown in the graph below (Fig. 12.3).

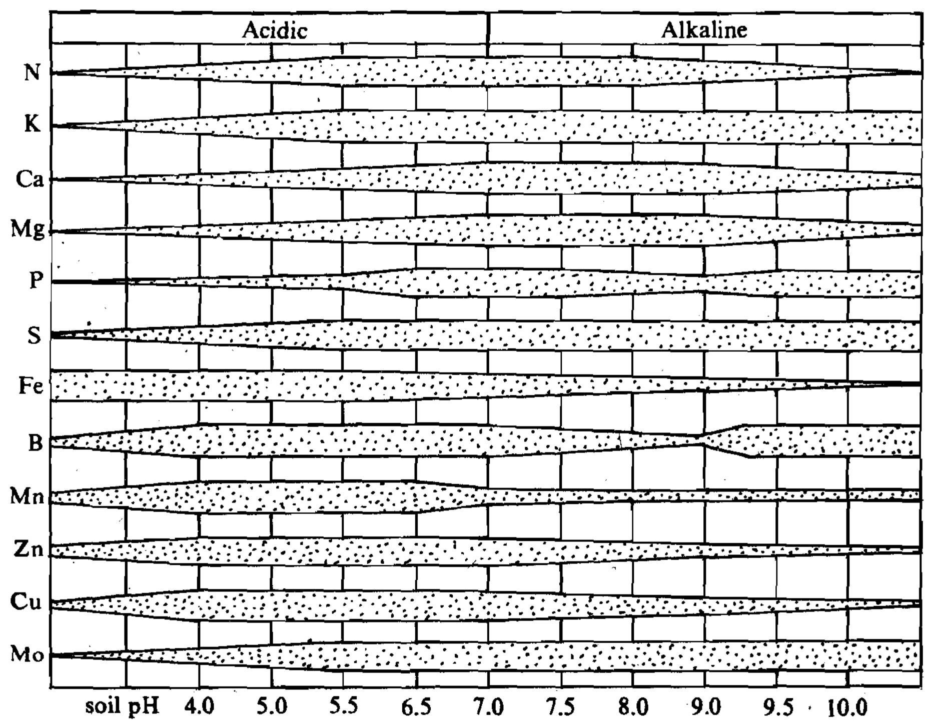

Fig. 12.3 : The effect of soil pH on the availability of different ions to the plant. The wider the bar greater the availability.

12.3.2 Uptake of Mineral Ions

Let us now see, what happens to ıne solute concentration in the root cells when plants are raised for a few days in a nutrient solution of known concentration. Data from a typical experiment are given in Table 12.2. Two plants, maize and beans are selected for comparison.

Table 12.2 : Changes in the ion concentration of the external nutrient solution and in the root sap of maize and bean expressed in mM. The data are recorded after 4 days

Ion	After 4 days				
		External Concentration		Concentration in the root sap	
	Initial Concentration	Maize	Bean	Maize	Bean
Potassium	2.00	0.14	0.67	160	84
Nitrate	2.00	0.13	0.07	38	35
Calcium	1.00	0.94	0.59	3	10
Sulphate	0.67	0.61	0.81	14	6
Sodium	0.32	0.51	0.58	0.6	6
Phosphate	0.25	0.06	0.09	6	12

A careful study of the above table shows the following:

i) The concentration of potassium, phosphate and nitrate declined significantly in the bathing medium within four days.

ii) The concentration of sodium and sulphate, however, increased indicating that water was absorbed faster than either of the two ions, or possibly they leach out.

iii) The rate of uptake especially of potassium and calcium, differed between the two plant species, maize and bean.

iv) The ion concentration (particularly of K^+, NO_3^- and SO_4^{2-}) in the root was considerably higher than in the nutrient solution used for the experiment.

These results show certain characteristics of nutrient uptake.

1) **Selectivity** : Certain mineral elements are taken up preferentially while others are discriminated against or nearly excluded.

2) **Accumulation** : The concentration of mineral elements can be much higher in the plant sap than in external solution. This means the uptake is against concentration gradient.

3) **Genotype** : Plant species differ genetically in nutrient uptake characteristics.

You know that chemically Na^+ resembles K^+ very closely but the rate of absorption of K^+ is not influenced by similar concentration of Na^+ ions in the medium. The process of K^+ absorption is, therefore, selective and uninfluenced by a related ion. Similarly, several other monovalent and less related divalent ions also have no effect on K^+ uptake. Likewise, absorption of Cl^- is unaffected by related halides, fluoride and iodide, as well as other anions like NO_3^-, $H_2PO_4^-$ or SO_4^{2-}. However, interestingly, Ca^{2+} is an absolute requirement for this selectivity. For example, in the absence of Ca^{2+}, K^+ absorption is inhibited by Na^+

Even though the ion uptake mechanism is highly specific, yet it can often by 'fooled' by similar ions. For example, it has been seen that absorption of K^+ can be competitively inhibited by rubidium (Rb^+). Similarly, competitive inhibition of Cl^- by Br^-, of Ca^{2+}; Sr^{2+} by Mg^{2+}, and sulphate by selenate (SeO_4^{2-}) has also been observed.

The selectivity and the rate of uptake of the nutrients and metabolites are influenced by temperature, O_2, poisons, carbohydrate content of the tissues and light. Such effects are similar to enzyme-mediated reactions and indicate that proteins are involved in solute uptake. You will learn about transport proteins and mechanism of ion uptake in a later section.

12.3.3 Movement of Nutrients into the Roots

In the previous unit we told you about the two main routes — apoplast and symplast — by which water and dissolved solutes are conducted across the root interior into xylem vessels and tracheids. The cell wall spaces and intercellular spaces in the root's epidermis and cortex are virtually continuous with the external soil solution.

As shown in the Fig. 11.9 of the previous unit ions can move up into the root hair as well as epidermal cells. An ion that is absorbed by an epidermal cell and moving

Many fungi grow in soil in close association or even into the roots in symbiosis called mycorrhizae. The fungal hyphae have superior mineral absorptive ability and supply plant with more nitrogen, phosphorus and potassium. Plants in return provide food to the fungi.

towards the xylem in the symplast must cross the epidermis, several cortical cells, the endodermis and the pericycle. The movement would involve transport directly through each of the two primary walls, middle lamella and plasma membranes between the cytosol of adjacent cells. Alternatively, the solute could move through plasmodesmata without crossing the plasma membrane or diffusing through cell walls.

The nutrient movement along the apoplasm is prevented at root endodermal cells because these cells are lined with Casparian strips. Therefore, the water and dissolved substances must enter the cell and pass through them via the symplastic route. Thus all minerals must pass through the cytoplasm in order to reach the xylem.

With this background we are now ready to trace the path of a solute (or nutrient) entering the root from the surrounding soil solution.

Free Space

You have learnt that the primary cell wall of the plant cell consists of mainly cellulose microfibrils which are embedded in an amorphous matrix of two polysaccharides, hemicelluloses and pectic substances. Hemicelluloses are made of sugars other than glucose (e.g. xyloglucans) while pectic substances are partly made from polygalacturonic acids. These acids have weak carboxylic acid groups ($-COOH$) that ionize and give rise to negative charges ($-COO^-$) on which hydrogen ions are loosely held. When positively charged ions such as K^+, Mg^{2+}, Ca^{2+} pass through the plant cell wall they displace hydrogen ions of the carboxyl groups and are held there by the weak inter-ionic attractive forces. The negative charges of the COO^- group cell wall are termed cation adsorption sites or cation exchange sites or Donnan Free Space. A cation such as Ca^{2+} with a relatively high adsorptive capacity will displace ions with a lesser adsorptive affinity (e.g. K^+).

Table 12.3 : Comparative Dimensions in (nm)

Cortical cell wall of maize	100-200
Pores of cell wall	>5.0
Sucrose	1.0
Hydrated ions	
K^+	0.66
Ca^{2+}	0.82

The cellulose microfibrils are not very tightly packed; as a result they leave small pores between them. The pores are large enough to allow free movement of water and dissolved substances. The diameter of these pores is in the range of 5.0 nm whereas, the dimensions of hydrated ions such as K^+ and Ca^{2+} are smaller (Table 12.3). So, the pores do not restrict the movement of ions. Water and dissolved nutrient molecules, ions and metabolites of the size of glucose, sucrose, and amino acids diffuse readily across primary cell walls.

The intercellular spaces, the negatively charged regions (Donnan Free Space) in the amorphous matrix and the pores in the cellulose microfibrils are readily accessible to water and dissolved ions. The fraction of the volume of the plant tissue readily accessible to diffusion of an external solute dissolved in water is termed 'Free space'. The free space in the root is bound by the plasma membrane of the epidermal and cortical cells and the Casparian strip of the endodermis.

Any substance which can easily pass through the free space then reaches the external surface of the protoplasm. Here, it encounters the plasma membrane which is an effective barrier to its movement further inward. Nevertheless, the plasma membrane does not act like a passive barrier, it has the ability to allow the passage of some substances into the cell interior while selectively inhibiting the passage of certain others. In the following section, we will discuss the transport of nutrients across the plasma membrane. You can check your progress by trying the SAQ given below.

SAQ 2

a) Tick mark the correct alternative from the words given in each parenthesis.

   i) The clay micelles have (negative/positive) charge.

   ii) Cytoplasmic strands connecting the adjacent cells are (plasmodesmata/ Casparian strip).

   iii) The iron exchange capacity is affected by (temperature/pH) of the soil.

   iv) The apoplastic pathway is broken at the (Casparian strip/plasmodesmata) of the endodermal cells.

   v) The fixed negative charges formed by the weakly acidic carboxyl groups of polygalacturonic acids form (cation exchange sites/anion exchange sites).

   vi) K^+ absorption can be competitively inhibited by (Sodium/Rubidium).

12.4 TRANSPORT OF IONS

In this section, we will study transport of solutes particularly inorganic ions across plasma membrane, their entry into xylem elements and long distance transport from root to shoot. In Units 7 and 8 on membrane transport processes (Cell Biology course), you had learnt that the transport of solutes across the membrane can take place by simple diffusion, facilitated diffusion and active transport (Fig. 12.4).

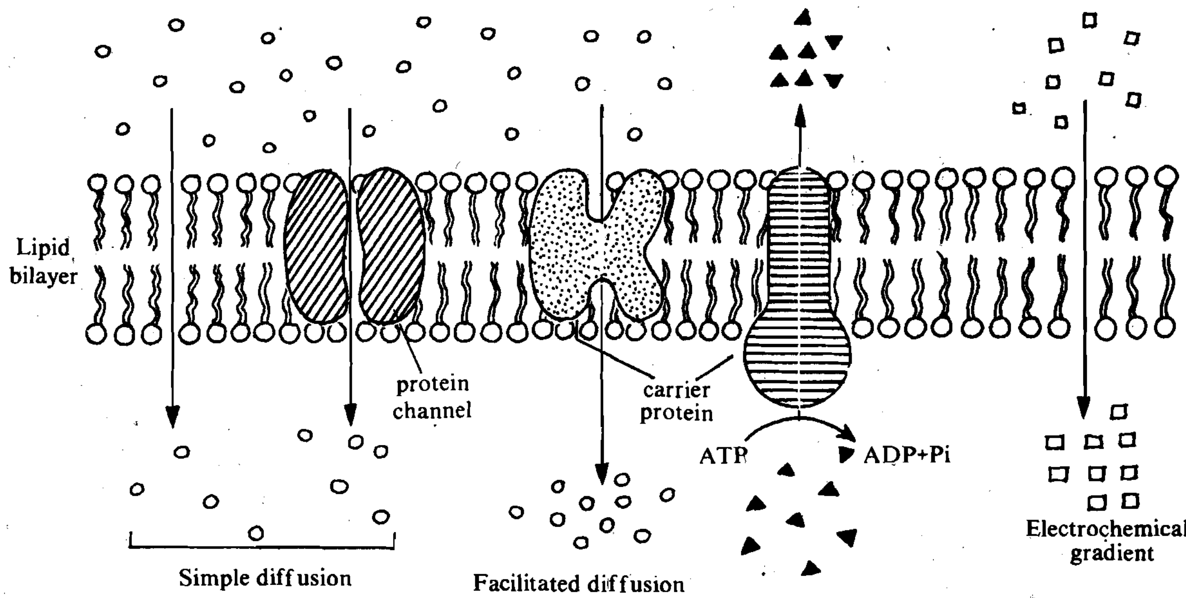

Fig. 12.4 : Passive and active transport mechanisms of mineral ions and other molecules across the plasma membrane.

12.4.1 Ion Transport Across the Plasma Membrane

As we have mentioned earlier ions must cross plasma membrane either before Casparian strip or at the Casparian strip in order to move further. The transport can take place by passive as well as active processes.

Diffusion

Simple diffusion can be a mechanism of transport of ions across plant cell membrane. Let us imagine a lipid bilayer without the various proteins in it (Fig. 12.5). Such a

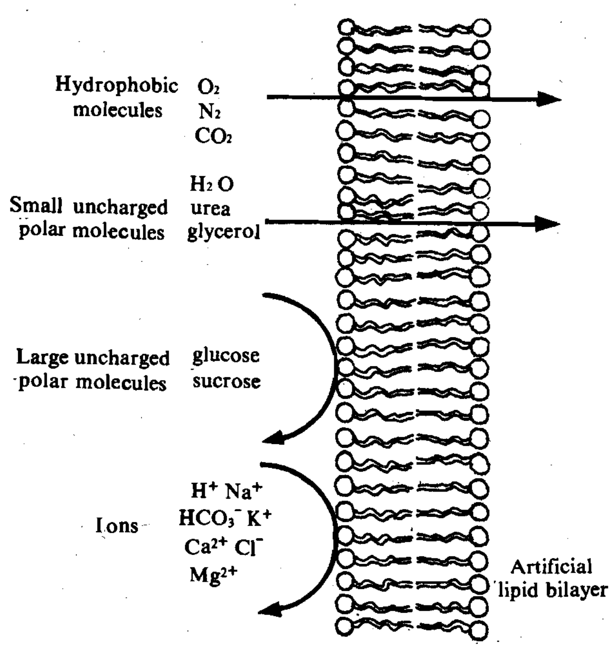

Fig. 12.5 : The relative permeability of an artificial lipid bilayer to different class of molecules.

membrane can be made in the laboratory. Given enough time, molecules can diffuse across the lipid bilayer down its concentration gradient by virtue of their own kinetic energy. However, the rate at which a molecule diffuses across such a lipid bilayer depends on the size of the molecule and its relative solubility in the lipid. Non-ionic hydrophilic substances are generally taken up as inverse function of their size, whereas hydrophobic substances are transported as a function of their lipid solubility. Small non-polar and hydrophobic molecules like O_2 and N_2 readily dissolve in lipid and therefore, rapidly diffuse across the bilayer. Ethanol (46 dalton) carbon dioxide (44 dalton) and urea (60 dalton) cross the bilayer rapidly while bigger molecules like glycerol (92 dalton) less rapidly and glucose (180 dalton) hardly at all. Water molecule (18 dalton) even though is relatively insoluble in lipids diffuses very rapidly across a lipid bilayer. On the contrary, lipid bilayers are impermeable to charged molecules (ions), even if they are very small. Because the charge and large hydration shell around prevent them from entering the hydrocarbon phase of the bilayer. As a result, lipid bilayers are 10^9 times more permeable to water than to even such small ions as Na^+ or K^+ (Fig. 12.6).

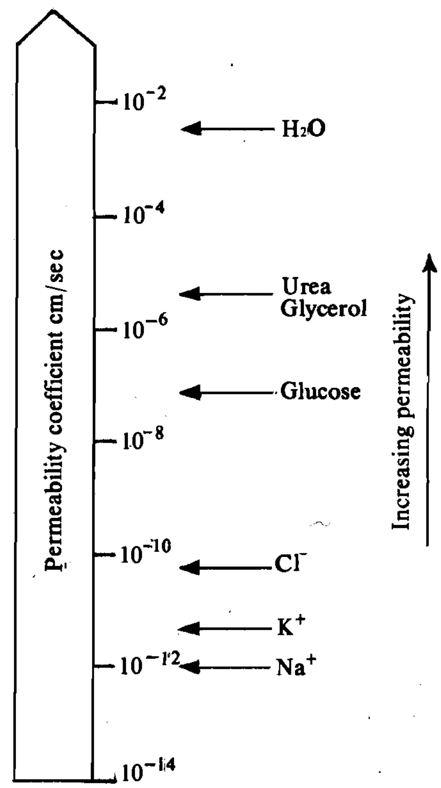

Fig. 12.6 : Permeability coefficients cm sec^{-1} for the passage of various molecules through artificial lipid bilayers.

K^+ is more permeable than most ions. Its permeability coefficient is arbitrarily set at 1.0 and is taken as standard. The permeability of other ions is compared with K^+

The ability of the lipid bilayer to discriminate between low and high molecular weight hydrophilic materials, permitting the former to diffuse across but not the latter is due to the presence of pores in the bilayer. These pores are formed randomly as a result of thermal movement of acyl phospholipid chains. They are called 'statistical pores'. Since these pores are only transient, they cannot be viewed even under the electron microscope.

The driving force for diffusion is a concentration gradient and obeys Fick's law; which states that the rate of movement of a substance is directly proportional to the concentration gradient. Simple diffusion thus shows a linear relationship between the concentration of solute and its rate of transport across the membrane.

12.4.2 Transport with the Help of Membrane Protein

Even though, the lipid bilayers do not permit the entry of polar molecules such as ions, sugars, amino acids, nucleotides and cell metabolities, these molecules enter the cell through i) aqueous protein channels (pores), ii) carrier proteins that rotate and move across the membrane and iii) transmembrane proteins that transport solute by undergoing changes in shape, (Fig. 12.7).

Studies on plants cell membrane suggest that inorganic ions can permeate through aqueous protein channels called permeases. The permeases are ion specific because the permeability of different ions varies. Most membranes are more permeable to K^+ than to other ions.

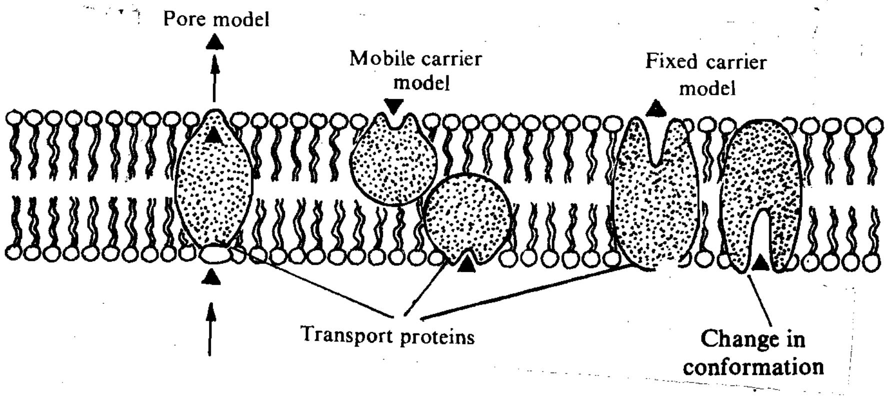

Fig. 12.7 : Three different possible modes of transport of ions and other molecules across the plasma membrane.

We had mentioned in Section 12.3.1 that ion uptake though specific can be fooled by similar ions. It seems probable that certain proteins transport more than one ion at the same site and so the ions compete with each other. For example, K^+, Cs^+, Rb^+ are apparently transported at the same site and Na^+ and Li^+ both are transported at the other site. But ions transported at different sites do not compete with each other; for instance K^+ does not compete with Na^+.

Ion transport in plants also takes place through ionophores. As you know ionophores are small polypeptides and proteins that shield the charge of ions from hydrophobic environment of the membrane. Ionophores have been isolated from bacteria and fungi. When they are added to the artificial lipid bilayer, they increase the rate of diffusion of specific ions by as much as one million fold!

There is much indirect evidence for mobile carrier proteins in plant membranes. So far only sucrose carrier is identified.

Driving Force

Let us now find out what is the driving force involved in protein mediated transport. Many membrane transport proteins allow specific solutes to move across the lipid bilayer. If the transported molecule is uncharged, then the difference in its concentration on the two sides of the membrane, that is its concentration gradient — determines the direction of transport. However, if the solute to be transported carries a net charge, then both its concentration gradient and the total electrical gradient across the membrane influence its transport. For instance, an ion will move across a membrane if there is sufficient electrical gradient across the membrane even if the concentration gradient does not favour such a movement. In other words, the direction of movement is decided by which of the two forces is steepest. The two gradients together constitute the electrochemical gradient. The gradient can develop in part due to the selective permeability of the membrane. So the related diffusion of cations may be more than anions or vice versa. For example, K^+ diffuses out more rapidly due to differences in electrical gradient than Cl^- in the immediate exterior and hence excess of Cl^- in the cell gives it a negative charge.

In fact, all plasma membranes have electric potentials (transmembrane potential) across them with inside of the cell more negative compared to the outside. This is due to active transport of ions particularly H^+ ions out of the cell. This potential difference allows the entry of positively charged ions into the cell but opposes the entry of negatively charged ions.

The relationship of electrical potential inside of a cell to the distribution of charged ions inside and outside of a cell is given by Nernst equation. You have already learnt this equation in Cell Biology course (Unit 7, Section 7.4). It is possible to measure transmembrane potential by a very fine glass microelectrode (μm in diameter). In plants the difference in potential of cell vacuole and cellular exterior is measured by inserting a narrow tipped fine ions-selective micro electrode through the cell wall and

When different concentrations of freely diffusing ions are separated by a membrane, a voltage gradient develops across the membrane. This is called transmembrane potential.

plasmalemma into the vacuole (Fig. 12.8). The other larger reference electrode is placed in the solution bathing the tissue. Such measurements show potential difference ranging between 50 to 200 millivolts (mv), the interior of cell being more negative.

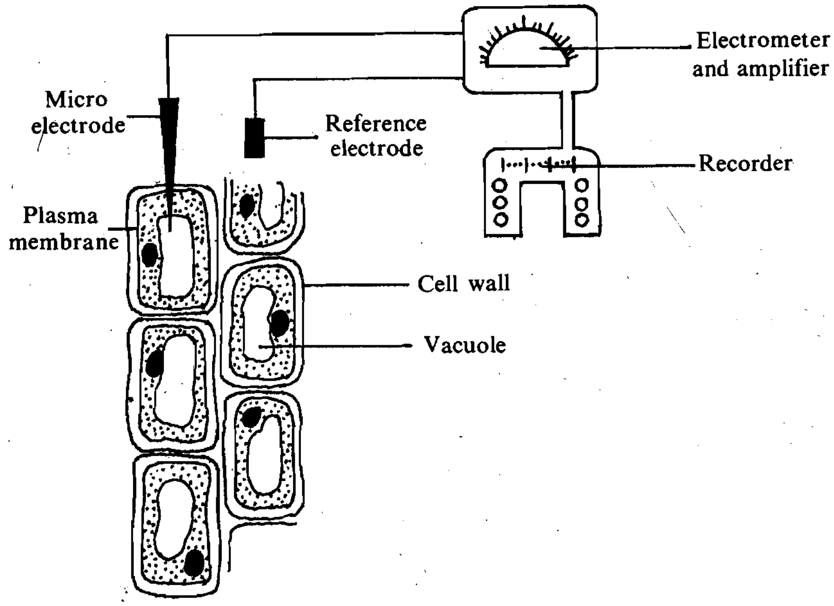

Fig. 12.8 : Equipment used to measure the transmembrane potential of plant cells (see text for details).

Active Transport

We have mentioned above that transmembrane potential develops due to active transport of ions (H^+) outside the cell. Since this transport takes place against a concentration gradient it utilises energy of hydrolysis of ATP. The proton motive force generated by proton pumping provides the driving force for the transport of solutes including cations, anions, amino acids and sugars. Electrical potential and pH measurements of intact plant cells have suggested that proton pumps are localised on the plasma membrane.

A dalton is a unit of mass equivalent of 1/12 of the mass of ^{12}C. Thus the mass of ^{12}C is 12 dalton. Dalton can be converted to grams by multiplying with 1.66×10^{-24} grams.

The plant plasma membrane ATPase is a transmembrane protein composed of a single polypeptide chain of 100 KD. The most possible coupling mechanism between ATP hydrolysis and proton transport is shown in Fig. 12.9. The enzyme exists in two conformations differing in catalytic and transport properties. In conformation I, the transport site faces the cytoplasm and has high affinity for protons. In conformation II, the transport site is externally oriented and has low affinity for protons. The enzyme is forced to alternate between these two conformations and to bind and release the transported proton because neither conformation can affect the complete catalytic cycle. In conformation I, the enzyme acts as a kinase; after binding a proton it catalyses the formation of phosphorylated intermediate. In the new state (conformation II) it acts as a phosphatase and after releasing the proton it returns to its original state, conformation I. Thus, when steady state is reached, a proton

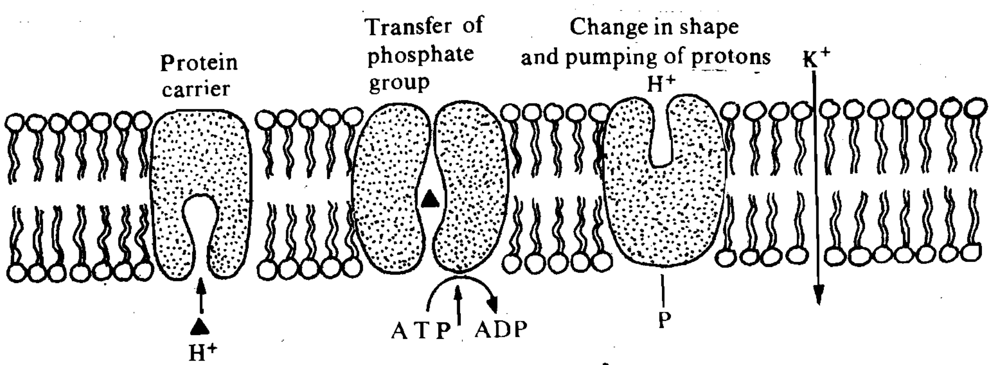

Fig. 12.9 : Simplified picture of active transport. Transport of proton across the membrane is coupled with transport of other cations in opposite direction. The transport protein receives an energy boost from ATPase and thereby undergoes changes in its shape that are necessary to the transport process.

gradient is developed, the concentration of protons being more on the outside of the membrane (i.e. around the cell wall region) and less in the cytoplasm. This leads to the generation of **proton motive force.** The net result of the proton pump is that the pH of the medium outside the plasma membrane becomes more acidic and the cytoplasm more alkaline.

An enzyme that promotes hydrolysis of ATP in the presence of K^+ has also been isolated from plants. It is suggested that enzyme binds K^+ ion at specific site and changes conformation on binding ATP. After hydrolysis of ATP it returns to its original conformation and the ion is released to the other side of the membrane. A working model depicting the active transport in plant cell with H^+ translocating ATPase located in plasma membrane and tonoplast is shown in Fig. 12.9.

A study on the rate of uptake of K^+ using radioactive isotope shows that uptake resembles an enzyme-substrate reaction curve and carriers involved behave like specialised membrane-bound enzymes. At higher concentration the carrier site for ions gets saturated, hence the uptake does not increase further with increase in concentration of ions in the solution. The binding sites of the carrier can also be inhibited by competitive inhibitors.

Transmembrane potential thus generated by proton pumping provides the driving force for the subsequent movement of cations, anions, amino acids and sugars by specific carrier or ion channels. Movement of sucrose into and out of phloem cells occurs along with H^+ (symport) through a permease. In roots hydrogen is frequently exchanged for K^+, (Fig 12.10). Various ions and metabolites also accumulate in plant cell vacuole via ion channels and proton antiports present in tonoplast Fig. 12.10.

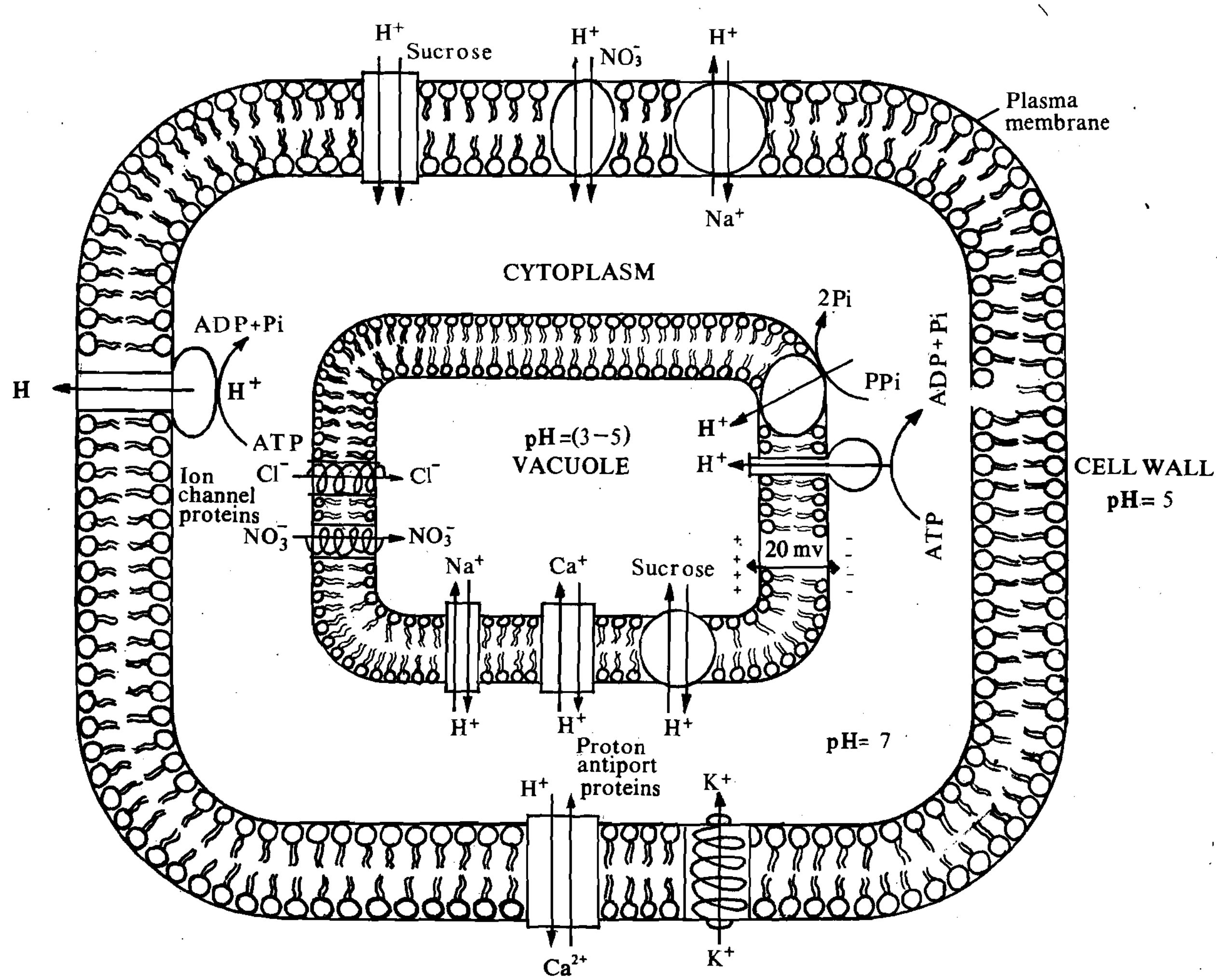

Fig. 12.10 : The transport of ions across cell and vacuole membranes. Note the two types of proton pumps — ATPase and unique pyrophosphate-hydrolysing proton pump. The pH of vacuole falls because of transport of protons inside the vacuole.

The proton pumping activity of the enzyme directly controls intracellular pH, nutrient uptake, turgor, cell growth, loading of nutrients into root xylem, loading of leaf phloem with organic nutrients, turgor changes responsible for stomata and pulvini movements, regulation of cell elongation and cell wall synthesis, early response to hormones especially IAA and many other functions. Thus, proton pumps have a central role in plant physiology and are considered as master enzymes. The proton pump has now been isolated and characterised biochemically.

12.4.3 Radial Movement of Ions into the Roots

Fig. 12.11 shows schematic drawing of the radial movement of ions by symplastic and apoplastic routes. As nutrients move along the cell wall and intercellular spaces of the epidermal and cortical cells, some nutrients are absorbed by these cells and enter

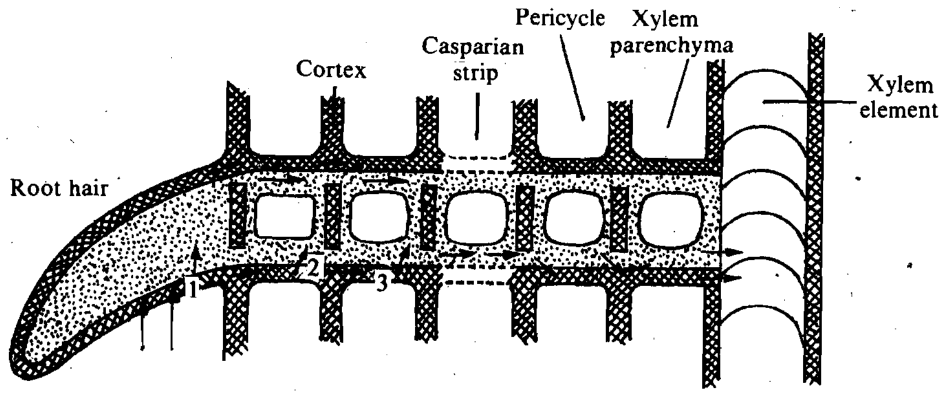

Fig. 12.11 : Schematic drawing showing the apoplast and symplast in cross-section of a root. The heavily stippled dark regions constitute the apoplast while the lightly stippled regions constitute the symplast. The vacuole is not part of either system. The Casparian strip creates a discontinuity in the apoplast. Therefore, all ions absorbed by root hairs must cross the plasma membrane of a cell (1, 2 or 3) exterior to the Casparian strip, thereby entering the symplast.

symplastic pathway in cytoplasm through plasmodesmata. Rest of the ions are screened by the membranes of endodermal cells which control the rates of absorption and type of solute absorbed. Some of these solutes are transported into the vacuole, where they contribute greatly to the negative osmotic potential of root facilitating water uptake, turgor pressure and growth of roots through soil.

The preferential use of apoplastic or symplastic pathway by different ions is not clearly known. Experiments with radioisotopes of ^{86}Rb and ^{36}Cl on the water plant *Vallisneria* show that these ions take only symplastic pathway probably through plasmodesmata. So far, it has been technically difficult to ascertain the role of plasmodesmata, however, their presence in regions where transport is active indirectly indicates that ions move through them in symplastic routes.

Studies using radioisotopes of ^{45}Ca in barley seedlings show that it is preferentially transported along apoplastic pathway and its concentration in the cytoplasm remains minimum because it can precipitate both organic and inorganic phosphates within the cells. Mg^{2+} also moves slowly through apoplastic pathway.

Regardless of the pathway, the radial movement through symplasm brings the mineral elements and other solutes to the stele where they are released into the xylem. This transfer is an energy requiring process in which xylem parenchyma plays an important role. The mechanism is more or less similar to that described above for loading of nutrients into the cells and involves carrier proteins.

12.4.4 Long Distance Transport

Once in the xylem vessels, the transport of the mineral elements from the root to the shoot is driven by the gradient of hydrostatic pressure (root pressure) and by the gradient of water potential. The gradient of water potential between roots and shoots is usually quite steep during the day when the stomata are open. It follows the pattern: atmosphere << leaf cells << xylem sap < root cells < external solution (soil). Transport in xylem vessels is mainly unidirectional. An increase in the transpiration rate enhances both the uptake and the translocation of mineral elements in the xylem.

The lateral transport of ions from root xylem to leaves probably takes place via xylem transfer cells (Fig. 12.12) which have two special features:

i) the cell wall of these cells facing xylem is elaborately corrugated for providing large surface area for absorption; and

ii) the cells contain many mitochondria that are located close to the corrugated wall in order to supply ATP for the active transport that takes place across these walls.

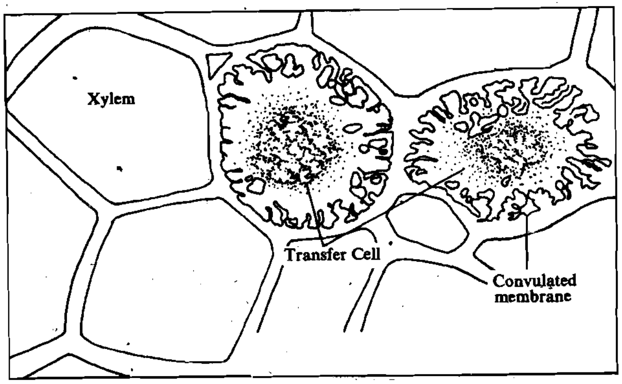

Fig. 12.12 : Xylem transfer cells.

The transfer cells are also present at places where large quantities of ions or organic solutes are moved into and out of conducting cells or storage tissue. You will learn more about transfer cells in Unit 14 on phloem transport.

Mineral elements which are phloem mobile can be retranslocated from the shoot to the root via phloem, though the main transported compound in the phloem is sucrose and other organic compounds. The transport in phloem is bidirectional. The direction of transport is determined by the nutritional requirements of various plant organs or tissues.

SAQ 3

a) In the following statements fill in the blank spaces with appropriate words.

   i) The driving force for diffusion is ....

   ii) The proton pump in plant is an ATP hydrolysing enzyme called ....

   iii) When proton pump works, protons are transported from .... to .... of the cell.

b) In the following statements tick mark the correct word given in the parenthesis.

   i) Most membranes are permeable to (K^+/Na^+).

   ii) When ionophores are added to the artificial lipid bilayer the permeability of the membrane (decreases/increases).

   iii) Transport of the proton across the membrane develops an electric potential gradient which is (negative/positive) outside of the cell.

   iv) The net result of the operation of the proton pump is that the pH of the medium outside the plasma membrane becomes (acidic/alkaline).

   v) An element which is preferentially translocated by the apoplastic pathway is (potassium/calcium).

12.5 ROLE OF ESSENTIAL ELEMENTS

11.5.1 Macronutrients

Nitrogen (N)

In the atmosphere nitrogen (N) is present as gas (N_2) to the extent of 79% by volume. However, plants with a few exceptions cannot use it. From the soil only a very small portion of nitrogen is available to plants. The available forms in soil are NO_3^- and NH_4^+ ions. Because of the numerous factors which affect nitrogen turnover in the soil, the concentration of N dissolved in the soil solution can change considerably over short periods. This is particularly true of NO_3^-. Usually the NO_3^- content in the soil solution is of major importance in plant nitrogen nutrition.

Nitrogen is an indispensable elementary constituent of important organic compounds like amino acids, proteins and nucleic acids. Dry plant material contain about 2 to 4% N. In green plant parts, protein nitrogen is by far the largest N fraction and accounts for 80 to 85% of the total nitrogen. In vegetative parts, the proteins are mainly enzyme proteins, whereas in seeds and grains, special storage protein make up the major protein fraction. Nitrogen is also an essential constituent of various coenzymes.

Although nitrate ion is preferred, plants can absorb NH_4^+ as well. Crops mainly take up NO_3^- even when NH_4^+ fertilisers are applied because of the rapid microbial oxidation of NH_4^+ to NO_3^- in the soil. The rate of uptake of NO_3^- is generally very high as plants require large amounts of Nitrogen. An important difference between uptake of NO_3^- and NH_4^+ ion is in their sensitivity to pH. NH_4^+ uptake takes place best in a neutral medium and it is depressed as the pH falls. The converse is true for NO_3^- absorption; a more rapid uptake occurs at low pH values. Gaseous ammonia may also be absorbed by the upper plant parts via the stomata.

Within the plant, nitrate is to be reduced to ammonia before it is incorporated into amino acids and proteins. In Unit 15, you will learn about metabolism of nitrogen.

The form in which translocation occurs depends on the nitrogen source and metabolism in the root. Nearly all the NH_4^+ ions absorbed are assimilated in the root tissue and translocated as amino acids. Nitrate can be translocated as such to shoots and leaves but this depends on the nitrate reduction potential of the roots.

When the supply of nitrogen from the root is inadequate, nitrogen from older leaves is mobilised to feed the younger plant organs. For this reason plants suffering from N-deficiency first show deficiency symptoms in older leaves.

Nitrogen deficiency is characterised by a poor growth rate. The leaves are small and the older ones often fall off prematurely. Shoot growth is affected and in particular branching is restricted. Leaves deficient in nitrogen show chlorosis which is generally rather evenly distributed over the whole leaf. Necrosis of leaves occurs when deficiency is severe. Deficiency symptoms of Fe, Ca, S are also characterised by yellowish and pale leaves similar to nitrogen deficiency. In these deficiencies, however, the symptoms occur first in the younger leaves. Nitrogen deficiency in cereals is characterised by poor tillering, the reduction in the number of ears per unit area and also the number of grains per ear.

Of all the nutrient amendments made to soils, nitrogen fertiliser application by far has been the most effective in increasing crop production. High yielding crop cultivars in particular respond to N-fertilisers. High physiological efficiency of nitrogen usage in cereal crop is achieved when a large proportion of the nitrogen taken up is used in grain formation.

The most common N-fertilisers are given in the Table 12.4.

Table 12.4 : Nitrogen Fertilisers

N-Fertiliser	Formula	% N
Ammonium sulphate	$(NH_4)_2SO_4$	21
Ammonium chloride	NH_4Cl	26
Ammonium nitrate	NH_4NO_3	35
Potassium nitrate	KNO_3	14
Urea	$CO(NH_2)_2$	46
Calcium cynamide	$CaCN_2$	21
Anhydrous ammonia	NH_3	82

Nitrogen fertilisers supply NO_3^- and NH_4^+ to the soil. Between the two, NH_4^+ is partially adsorbed on soil colloids and its uptake rate is usually, therefore, lower than that of NO_3^- under field conditions. For this reason most crops do not respond as quickly to NH_4^+ fertilisers as to NO_3^- application.

In paddy soils, nitrogen is lost as a result of denitrification. These soils should not, therefore, receive NO_3^- containing fertilisers. Hence urea and NH_4^+ fertilisers are recommended. The main drawback of anhydrous ammonia is the special equipment required for its transport and application.

Phosphorus (P)

In soil, phosphorus occurs almost exclusively in the form of orthophosphate. Substantial amount of P is associated with the soil organic matter. The major P-containing ions in soil solutions are HPO_4^{2-} and H_2PO_4.

Roots are capable of absorbing phosphate from solution low in phosphate content. The phosphate content of roots and xylem sap is about 100-1000 fold higher than that of the soil solution. This shows that phosphate is absorbed by plants against a very steep concentration gradient. Phosphate is highly mobile in the plant and can be translocated in upward or downward direction.

The inorganic form of phosphate found in plants are orthophosphate and to a minor extent, pyrophosphate. The organic form of phosphates are compounds in which the orthophosphate is esterified with hydroxyl groups of sugars and alcohols or bound through a pyrophosphate bond to another phosphate group. You know that phosphorylated sugars and alcohols are the major intermediary compounds of metabolism. Phosphate is also present in phospholipids. The nucleotide phosphates — ATP, UTP, GTP, CTP supply energy to various endergonic processes including active ion uptake and the synthesis of various organic compounds.

Another important phosphorus containing compound is phytin which is mainly found in seeds. It is Ca or Mg salt of phytic acid and is formed during seed formation. Phytic acid is the hexaphosphoric ester of inositol. Immediately after pollination there is an increase in P transport towards the developing seeds. Phosphorus in the phytin of seeds is regarded as a P reserve. During seed germination phytin is mobilised and converted into other phosphate forms that are needed in the metabolism of young plants.

Inositol is a sugar (hexose) alcohol.

Plants suffering from P deficiency are retarded in growth. In cereals tillering is reduced. Generally, the symptoms of P deficiency appear in the older leaves which become darkish green in colour. The stems of many annual plant species suffering from P deficiency develop reddish colour due to enhanced formation of anthocyanin pigments.

Potassium (K)

The main source of K^+ for plants comes from withering of K containing minerals. Potassium released by withering dissolves in the soil solution. It can then be taken up by plants or adsorbed onto soil colloids.

In plants, K^+ is an important cation. It is taken up by the plant at high rates through K^+ channels present in the membranes.

The concentration of K^+ in the cytoplasm is about 100 mM which is 5-10 times higher than K^+ concentration in the vacuole. The phloem sap is rich in K^+. It is the most abundant cation present in phloem with the concentration approaching that in the cytoplasm. As the solutes of the phloem sap can be translocated both upwards and downwards in the plant, K^+ movement is bidirectional.

Potassium is necessary for meristematic growth. It is involved in controlling water status of plants and maintains cell turgor. There is less water loss from plants supplied with K^+ due to a reduction in transpiration rate. As you know K^+ plays an important role in opening and closing of stomata. Plants inadequately supplied with K^+ have impaired stomatal activity. It is also involved in the translocation of photosynthates. The main biochemical function of K^+ is the activation of various enzymes.

Potassium deficiency does not immediately result in visible symptoms. At first there is only a reduction in growth rate. Chlorosis and necrosis appear later. These symptoms generally apppear on the margins and tips of older leaves. Plants suffering from K^+ deficiency show a decrease in turgor. They easily become flaccid under water stress. Resistance to drought is, therefore, poor. Inadequate soil K^+ levels can be corrected by the use of K^+ fertilisers. The most widely used and cheapest potash fertilisers is potassium chloride (KCl) which is known commercially as muriate of potash.

Sulphur (S)

Sulphur is present in the soil in inorganic and organic forms. In most soils organically bound S is the major S reservoir. The inorganic forms of S in soil consists mainly of SO_4^{2-}. In arid regions, soil mav accumulate high amounts of sulphur salts such as $CaSO_4$, $MgSO_4$ and Na_2SO_4. Under humid conditions however, SO_4^{2-} is present either in soil solution or is adsorbed on soil colloids.

The organic S of the soil is made available to plants by microbial activity. In this process of mineralisation H_2S is formed which under aerobic conditions readily undergoes autooxidation and forms SO_4^{2-}. In anaerobic media, however, H_2S is oxidised to elemental S by chemotrophic sulphur bacteria such as *Beggiatoa*, and *Thiothrix*. Further oxidation of S results in the formation of H_2SO_4. As a result increase in soil acidity can occur.

Many plant species contain a small amount of volatile S compounds. These are mainly di- or polysulphides. In onions these compounds are responsible for the lachrymatory (tear producing) effect. The main component of garlic oil is diallyl-disulphide.

Plants mainly absorb S in the form of SO_4^{2-}. It is mainly translocated in an upward (acropetal) direction. Downward (basipetal) movement of S is relatively poor. There is now a considerable evidence to show that plants can utilise sulphur dioxide also.

The most important sulphur containing compounds are cysteine, methionine, lipoic acid, coenzyme A, biotin, thiamin and ferredoxin (an electron carrier, a type of non-heme iron-sulphur protein). Sulphur forms disulphide bridges in polypeptides.

In field crops sulphur deficiency and nitrogen deficiency are sometimes difficult to distinguish. In plants suffering from S deficiency the rate of plant growth is reduced. Generally, the growth of the shoots is more affected than root. In contrast to N deficiency, chlorotic symptoms occur first in the younger, the most recently formed leaves.

Although the content of S in crops is similar to P content, S application does not play an important role as P fertilisation. This is because SO_4^{2-} is not strongly bound to soil particles as phosphate and is thus more available to plants. In addition, substantial amounts of S can come from the atmosphere or from fertilisers which contain S along with other major nutrients being applied e.g. ammonium sulphate or potassium sulphate. The most important sulphur containing fertilisers are gypsum, super-phosphate, ammonium sulphate and potassium sulphate.

Calcium (Ca)

Soils differ very widely in their Ca content. Plant species may be classified into calcicoles and calcifuges. The calcicoles are those growing on calcareous soils where as the calcifuge species grow on acidic soils poor in Ca.

Generally, Ca^{2+} concentration of the soil solution is about 10 times higher than that of K^+ but the uptake rate of Ca^{2+} is usually lower than that of K^+. This low Ca^{2+} uptake is because Ca^{2+} can be absorbed only by young root tips in which the cell walls of the endodermis are still not suberised. The uptake of Ca^{2+} can also be competitively depressed by K^+ and NH_4^+ which are rapidly taken up by roots. Calcium is translocated in an upward direction in the xylem with the transpiration stream. It is translocated only in very small concentrations in the phloem. Once Ca is deposited in older leaves it cannot be mobilised to the growing tips.

In the absence of Ca^{2+}, growth rate is reduced and after a few days the root tips become brown and gradually die. Ca^{2+} is required for cell elongation and cell division. It is essential for the stabilisation of newly synthesised membranes. In the absence of Ca^{2+}, membrane permeability increases to such an extent that inorganic and organic constituents can diffuse out of the cell causing considerable damage to the cells. In whole plants, this disorder occurs first in the meristematic tissue such as root tips, growing points of the upper plant parts and storage organs.

Most of the Ca^{2+} present in plant tissues is located in the apoplast and in the vacuoles. The Ca^{2+} concentration of the cytoplasm is low. The maintenance of low cytoplasmic Ca^{2+} is of vital importance for the plant cell because the evidence shows that Ca^{2+} may inhibit various cytoplasmic enzymes, and also precipitate as Ca-phosphate. The maintenance of low Ca^{2+} is achieved by pumping Ca^{2+} out of the cytoplasm into the apoplast or into the vacuole.

In the cytoplasm, the function of Ca^{2+} is related to calmodulin, which is involved in the activation of many enzymes by allosteric induction. Calcium is present in plant tissues as free Ca^{2+} adsorbed to indiffusible ions such as carboxylic, phosphoric and phenolic hydroxyl groups. It is also present as Ca oxalates, carbonates and phosphates. These compounds often occur as deposits in cell vacuoles. Calcium in the cell wall is associated with the free carboxylic groups of pectins.

Calcium deficiency is characterised by a reduction in growth of meristematic tissues. The deficiency can be first observed in the growing tips and young leaves. They become deformed and chlorotic. At a more advanced stage necrosis occurs at the leaf margins. The affected tissue becomes soft due to a dissolution of the cell walls. Brown coloured substances accumulate in intracellular spaces and also in the vascular tissue where they can affect the transport mechanism. In apple the disease is called 'bitter pit' because the surface of the apple is pitted with small brown necrotic spots. In tomato the disease is known as 'blossom end rot' and is characterised by a cellular breakdown at the distal end of fruit.

Magnesium (Mg)

Magnesium like Ca^{2+} is present in fairly high concentrations in the soil solution. Generally the concentration in soil solution is higher than that of K^+ but the rate of uptake of Mg^{2+} is much lower than the uptake rate of K^+; Mg^{2+} is very mobile in the phloem and can be translocated from older to younger leaves or to the apex.

Mg is constituent of chlorophyll molecule. It is a cofactor in almost all phosphorylation reactions. Mg^{2+} forms a bridge between the pyrophosphate structure of ATP or ADP and the enzyme molecule. The activation of ATPase by Mg^{2+} is brought about by this bridge formation. Another key function of Mg^{2+} is in the activation of ribulose bisphosphate carboxylase. Light triggers the import of Mg^{2+} into the stroma of the chloroplast in exchange of H^+ thus providing optimum conditions for the carboxylase reaction. Mg deficiency inhibits protein synthesis.

Mg is mobile in the plant and deficiency always begins in the older and then moves to the younger leaves. Interveinal yellowing or chlorosis occurs and in extreme cases the areas become necrotic.

Mg application is recommended for all crops growing on soils with less than 25 ppm exchangeable Mg. The major Mg fertilisers are, magnesium limestone (Mg CO_3 — 5 to 20% MgO) ground burnt magnesium lime (Mg oxide — 10 to 33% MgO), kiesernite ($MgSO_4.H_2O$ — 27% MgO), Epsom salt ($MgSO_4.7H_2O$ — 16% MgO) and Magnesite ($MgCO_3$ — 45% MgO).

SAQ 4

1) In the following sentences choose the right alternate word given in the parenthesis.
   i) The form of nitrogen preferred by plant is (NH_4^+/NO_3^-).
   ii) Largest fraction of N present in plant is in the form of (proteins/nucleic acids).
   iii) In soil (NO_3^-/NH_4^+) is converted by microbial action into (NO_3^-/NH_4^+).
   iv) Uptake of NH_4^+ is best in neutral medium. It (decreases/increases) as pH falls.
   v) In plants (NH_4^+/NO_3^-) is converted into (NH_4^+/NO_3^-) before it is incorporated into proteins.
   vi) The symptoms of nitrogen deficiency first appear in (older/younger) leaves.
   vii) Generally the concentration of (Ca^{2+}/K^+) is higher in soil but uptake rate of (Ca^{2+}/K^+) is higher.
   viii) Calcium is mainly translocated through (xylem/phloem). It (can/cannot) be mobilised from older leaves.
   ix) The rate of uptake of (Mg^{2+}/K^+) is lower than (Mg^2/K^+).
   x) Deficiency of phosphorus would affect (carbohydrate/protein) metabolism.
   xi) The colour of stem of some annuals becomes red due to the formation of anthocyanin pigment. This is due to the deficiency of (phosphorus/sulphur).
   xii) Phosphorus is highly (mobile/immobile) in plants.
   xiii) The most mobile nutrient in plants is (K/P).
   xiv) K deficiency results in loss of (membrane permeability/turgor).

b) List four important compounds of plant containing sulphur.

....

....

....

c) Match the content of column 1 corresponding with those of column 2.

Column 1	Column 2
i) Magnesium	a) deficiency affects cell division and cell elongation.
ii) Calcium	b) cofactor in all phosphorylation reactions.
iii) Sulphur	c) component of coenzyme A.

12.5.2 Micronutrients

Iron (Fe)

Iron is present in all soils. Soluble Fe in soil is extremely low in comparison with its total content. Soluble inorganic forms are Fe^{3+}, $Fe(OH)^{2+}$ (hydroxoferric ion), $Fe(OH)_2^+$ (dihydroxoferric ion) and Fe^{2+}.

When soils are waterlogged, a reduction of Fe^{3+} to Fe^{2+} occurs which is accompanied by an increase in solubility. Anaerobic bacteria which use Fe oxides as electron acceptors in respiration, bring about this reduction. This process is of particular interest in paddy soils where it can lead to high Fe^{2+} concentrations. Such high concentrations often produce toxic effects in rice plants.

Fe must be reduced before it can be taken up by the roots. Iron in the free spaces of roots may be present in the ionic form or as chelate. The reduction of Fe^{3+} chelate destabilises the complex and the resulting Fe^{2+} can be absorbed. The rate of Fe reduction is pH dependent and is higher at low pH.

The uptake of iron is competitively inhibited by other cations, like Mn^{2+}, Cu^{2+}, Ca^{2+}, Mg^{2+}, K^+ and Zn^{2+}. Iron is not readily mobile between the various plant parts. Green plants lacking Fe become chlorotic in the younger plant parts, whilst older parts remain green. Younger parts are, therefore, dependent on a continuous supply through the xylem. The major form in which Fe in translocated in the xylem is considered to be as ferric citrate.

The well-known function of Fe is in enzyme systems in which heme forms the prosthetic group. Here, Fe plays a somewhat similar role to Mg in the chlorophyll molecule. The heme enzyme system include catalase, peroxidase, cytochrome oxidase and the various cytochromes. Another important compound containing Fe is the non-heme iron protein 'ferredoxin' which is an iron sulfur protein. It is an electron carrier, in photosynthetic light reactions.

The deficiency of Fe and Mg are more or less similar as both are characterised by a failure of chlorophyll production. Iron deficiency, however, unlike Mg deficiency, always begins in the younger leaves, the darker green veins contrasting markedly against a lighter green or yellow background. The youngest leaves may often be completely white and totally devoid of chlorophyll. In the leaves of cereals the deficiency is shown by alternate yellow and green stripes along the length of the leaf.

Iron toxicity is particularly a problem in flooded rice soils, since within a few weeks of flooding it may increase 500-1000 folds. Iron toxicity in rice is known as 'Bronzing'. In this disorder the leaves are first covered by tiny brown spots which develop into a uniform brown colour. This frequently occurs in rice leaves containing excessively high Fe concentrations.

In the treatment of Fe chlorosis, the addition of inorganic Fe salts to the soil is mostly without effect for the Fe is rapidly made insoluble as oxides. Foliar treatment with ferrous salts is also not satisfactory. Iron chelates are more effective and can be used as fertilisers applied to the soil or as a foliar spary.

Manganese (Mn)

Mn^{2+} and Mn oxides in which Mn is present in trivalent or tetravalent forms are the important soil fractions. In soil solutions, divalent Mn is the most important form.

Mn^{2+} resembles Mg^{2+} in its biochemical functions. Both ions bridge ATP with the enzyme complex. Decarboxylases and dehydrogenases of the TCA cycle are also activated by Mn^{2+}. Nevertheless, Mn^{2+} is not specific for these enzymes and can be substituted by Mg^{2+}. The most well documented role of Mn in green plants is in the Hill reaction of photosynthesis where a manganese protein catalyses water splitting and O_2 evolution.

Mn deficiency causes disorganisation of the lamellar system of chloroplasts. Mn deficiency symptoms resemble Mg deficiency, as in both cases interveinal chlorosis occurs in the leaves. In contrast to Mg deficiency, however, Mn deficiency symptoms are first visible in the younger leaves whereas in Mg deficiency older leaves are first affected. Organic soils high in pH are particularly low in available Mn and it is in crops growing on these soils Mn deficiency often occurs. Application of Mn salts to the soil, e.g. $MnSO_4$, usually does not alleviate the deficiency because the applied Mn^{2+} is rapidly oxidised. Spraying 1 to 5 kg $MnSO_4$/ha is the best way of removing the deficiency in most crops. Of the organic Mn carriers, Mn-EDTA gives the best response.

Zinc (Zn)

In its function in some enzyme systems, Zn^{2+} resembles Mn^{2+} in that it brings about substrate binding and conformational changes in enzymes. A number of enzymes are thus activated in more or less the same way by Mn^{2+}, Mg^{2+}, or Zn^{2+}.

Zn is actively involved in the N metabolism of the plant. In Zn deficient plants, protein synthesis and protein levels are markedly lowered, and amino acids and amides accumulate. Zn deficiency affects protein metabolism through the inactivation of RNA polymerase. It affects structural integrity of ribosomes, and enhances RNA degradation by increasing RNase activity. Zn is also required for the synthesis of indole acetic acid from tryptophan.

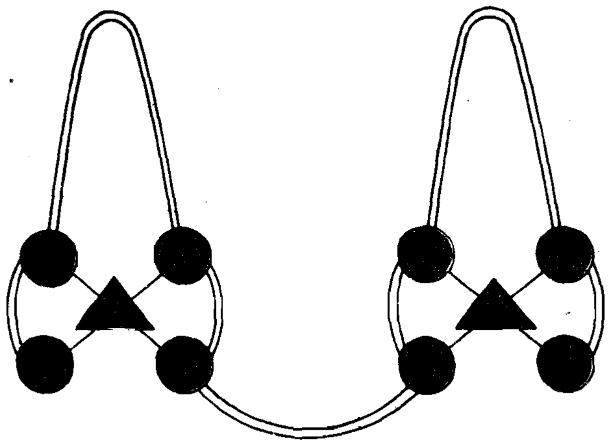

Fig. 12.13: The zinc in each finger is bound to four amino acids: two cysteines and two histidines, holding the finger in the proper shape for DNA binding. These four key amino acids are found in the same places in each finger.

Plants suffering from Zn-deficiency often show chlorosis in the interveinal areas of the leaves. They become pale green, yellow or even white. In fruit trees leaf development is adversely affected. Unevenly distributed clusters or rosettes of small stiff leaves are formed at the ends of the young shoots. Frequently, the shoots die off and the leaves fall prematurely. In apple trees the disease is known as 'rosette' or 'little leaf'.

Zn toxicity may occur in areas of Zn ore deposits. Some plant species are, however, Zn tolerant and are able to withstand high soil Zn levels.

Recently a very special role that Zinc plays in gene activation has been discovered. There are proteins which act as transcription factors. These are folded in the form of fingers with zinc liganded at the bottom of each finger. Interestingly, as soon as the fingers touch the DNA the gene is turned on.

Zinc deficiency is one of the commonest micronutrient deficiencies and it is becoming increasingly important in areas of high yield agriculture. Plant species and even cultivars vary considerably in the susceptibility to Zn deficiency.

Zn-deficiency can be alleviated either by spraying or by soil application of Zn fertilisers. $ZnSO_4$ is the most commonly used fertiliser because of its high solubility. On acid sandy soils it is preferable to spray the crop because $ZnSO_4$ is very easily leached from soil.

Copper (Cu)

Copper occurs in the soil almost exclusively in its divalent form. Copper is absorbed by the plant only in very small quantities. Zn inhibits the uptake of Cu and vice versa. It is not definitely known whether Cu is taken up as Cu^{2+} or as copper chelate. Copper is not readily mobile in the plant although it can be translocated from older to younger leaves.

Copper has a number of attributes which control its biochemical behaviour. Cu bound to protein participates in redox reactions which are mostly dependent on the valency change. ($Cu^{2+} + e^{-} \longrightarrow Cu^{+}$).

The most important copper containing proteins are plastocyanin, superoxide dismutase, amine oxidases, ascorbic acid oxidase and lactase. Cytochrome oxidase, the terminal oxidase in the mitochondrial transport chain is one of the most well studied of the Cu containing enzymes. As in the case of Fe, high concentration of Cu is found in chloroplasts. There is also a specific requirement of Cu in symbiotic N_2-fixation. In the absence of Cu, nodule development and N_2-fixation are depressed.

Cu deficiency symptoms appear first in the younger leaves. In cereals, the deficiency appears first on the leaf tips. The plants develop a bushy habit with white twisted tips accompanied by a reduction in panicle formation. Copper chelates can be used either as foliar spray or as soil dressing to overcome the deficiency.

Molybdenum (Mo)

Mo is absorbed as molybdate (MoO_4^{2-}) ion by plants. Its uptake can be competitively reduced by SO_4^{2-}. The requirement of plants for Mo is very low. Mo is an essential component of two major enzymes, nitrogenase and nitrate reductase. The functional mechanism of both enzymes probably depends on valency changes of Mo.

The most important function of Mo in plant metabolism is in N assimilation. Mo deficiency resembles N-deficiency. Older leaves becoming chlorotic first, but in contrast to N-deficiency, necrotic symptoms rapidly appear at the leaf margins because of nitrate accumulation. In Cruciferae, in extreme deficiency of Mo, leaf laminae are not formed and only the mid rib is formed. The leaf thus appears like a whip and for this reason the deficiency is called 'Whip tail'.

Boron (B)

It is absorbed by the plants as the undissociated boric acid. Though it has convincingly been shown that B is an essential element for higher plants, its functional role is not well understood. Unlike other plant nutrients B is not known to be a component of any enzyme.

Abnormal or retarded growth of the apical growing points is the first deficiency symptom. The youngest leaves are malformed, wrinkled or are often thicker and of darkish blue-green in colour. The leaves and the stem become brittle indicating a disturbance in transpiration. As the deficiency progresses the terminal growing point dies and flower and fruit formation is restricted or inhibited. Boron is known to have a role in germination of pollen and formation of pollen tubes. Thus plants growing on boron deficient soils show a disturbance in pollen germination and impairment of in fruit formation. In some plant species, the affected growth of pollen leads to parthenogenesis. The most well-known B deficiency symptoms are 'crown' and 'heart rot' in sugarbeet.

Boron deficiency is more pronounced in a wide range of crops under wide climatic conditions than deficiencies of any other micronutrient. The most well-known B fertiliser is borax ($Na_2B_4O_4.10H_2O$). Borated super phosphates are also available. Boric acid (H_3BO_3) is frequently applied as leaf spray particularly when the soil is potentially capable of fixing high amounts of boron.

Chlorine (Cl)

The role of Cl^- in plant is not clearly understood. Cl^- is required in Hill reaction, the water splitting reaction of photosystem II about which you will learn in Unit 13. In the presence of Cl^-, both the evolution of O_2 and photophosphorylation are enhanced. Cl^- may also influence photosynthesis indirectly via its effect on stomatal regulation of the guard cells.

Wilting of leaves at the margin is a deficiency symptom of chloride. Cl^- deficiency is noticed only rarely. The presence of Cl^- in the atmosphere and in the rain water is more than enough to meet the demand of the crops. In fact, its presence in excess in plants is a more serious problem. Crops growing on salt affected soils often show symptoms of Cl^- toxicity. These are burning of leaf tips or margins, bronzing, premature yellowing and abscission of leaves.

Silicon (Si)

Plant species may be divided into Si accumulators and non-accumulators. The accumulators include paddy rice (*Oryza ativa*), horse tails (*Equisetum arvense*) and members of the Pineceae, all of which contain 10-15% SiO_2 in the dry matter. Other cereals, sugarcane and a number of dicots with 1 to 3% SiO_2 are also included in this category. The non-accumulators are most of the dicots including the legumes with less than 0.5% SiO_2.

Necrosis of older leaves and wilting associated with higher rates of transpiration are the typical deficiency symptoms. There is little biochemical evidence to justify Si as an essential element for higher plants, however, it shows a number of well established beneficial effects on plant growth. In plants well supplied with Si, cuticular water loss is lowered because of the epidermal accumulation of silica. In cereals, the presence of silicon is important for keeping the leaves erect and decreasing susceptibility to logging. In rice, a significant relationship is observed between the Si content of the straw and the yield of rice. Silicon especially promotes the formation of reproductive organ in rice. The important silica fertilisers are soluble silicates, sinter phosphates and Ca silicate slags.

Cobalt (Co)

The Co concentration in the dry matter of plants grown in soil normally lies around 0.02 to 0.5 ppm. In soils the content varies from 1 to 40 ppm. Cobalt is not readily mobile in the plant.

Co is essential for symbiotic N_2-fixation. Increasing the supply of Co increases rhizobial growth, N_2-fixation and the formation of leghaemoglobin in nodules. Co is essential component of vitamin cyanocobalamin.

SAQ 5

a) List three molecules that contain heme iron in their prosthetic group.

....

....

b) i) Protein containing Mn ion catalyse .... during photosynthesis.

ii) Zinc deficiency enhances the degradation of .... and inactivates enzyme ....

iii) Zinc is required for the synthesis of hormone ....

iv) In cell, copper ions play a role in .... reaction by undergoing valancy change.

v) Enzyme nitrogenase and nitrate reductase contain ....

vi) .... is an essential element but it is not known to be a component of any plant chemical.

vii) In some plants boron deficiency leads to fruit formation by ....

viii) Chlorine is required in .... reaction of photosynthesis.

ix) Excess of chlorine result in .... leaf tips or margins, ... and premature yellowing and abscission of leaves.

x) .... and .... are essential for symbiotic nitrogen fixation.

xi) Iron deficiency is corrected by fertiliser application foliar spray of ....

c) List three important compounds containing copper.

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12.6 SUMMARY

In this unit you have learnt that :

- On an average mineral elements account for about 1.5 per cent of fresh weight of plant. Not all the elements detected may be essential for a plant. Essential elements are necessary for the completion of the plant's life-cycle.
- Besides, C, H, and O that make the backbone of organic molecules, N, P, K, Ca, S and Mg are required by plants in a relatively large amounts and are referred to as macronutrients, whereas Fe, Cu, Mn, Zn, Cl, B and Mo are required in lesser amounts and are referred to as micronutrients.
- Mineral elements perform structural, osmotic and biochemical functions in plants.
- Plants obtain carbon, hydrogen and oxygen from CO_2 and water Other elements are absorbed by roots from the soil in ionic form.
- The uptake of ions by roots from the soil is influenced by ion exchange capacity of the soil, pH and the presence of different cations and anions.
- Minerals move rapidly towards root interior either through intercellular spaces in root epidermis and cortex or across the selectively permeable membrane of the epidermis or cortex and join symplasm. All minerals must cross cell membrane and pass through cytoplasm, if they are to reach the xylem vessels which carry them upward alongwith water and transports them throughout the plant body.
- Ions are transported across plasma membrane with the help of proteins in the lipid bilayer. Some of the proteins such as permeases form ion channels and others function as carriers. The driving force involved in the transport is a concentration gradient or electrochemical gradient. The movement of ions against electrochemical gradient is an active transport process and requires energy in the form of ATP. Electrochemical gradient is also maintained by proton pumps which operate constantly and generate transmembrane potential across the membrane and facilitate transport of cations, anions, amino acids and sugars.
- Long distance transport of ions from root to shoot is driven by the gradient of hydrostatic pressure and water potential.
- Nitrate and ammonia are two nitrogen sources of plants. Between the two, NO_3^- is the preferred source and is absorbed at low pH. Nitrate may be translocated as such or many get reduced to nitrite in the roots before translocation. The deficiency symptom — chlorosis appears first in older leaves and plants show poor growth rates.
- Phosphorus is absorbed by plants against steep concentration gradient. It is highly mobile. Its deficiency manifests by the formation of anthocyanin pigments and by the older leaves becoming darkish green.
- Potassium is required in large amounts because it maintains turgidity of cells. In its deficiency plants resistance to drought is poor.
- Sulphur is an important constituent of several compounds in plants. Its deficiency results in poor growth rates.
- Calcium is required for cell elongation and cell division. In its deficiency the permeability of membranes increases and thus causes damage to cells.
- Mg and Mn are cofactors in phosphorylation reaction. Mg is part of chlorophyll. Mn and Cl are necessary for an important reaction in photosynthesis.
- Iron, copper and Mo are constituents of proteins that take part in redox reactions. Iron and Mg both are necessary for chlorophyll synthesis, zinc for protein synthesis and Cobalt for N_2-fixation.

12.7 TERMINAL QUESTIONS

1) In what form the following elements are available to the plant from soil.
   i) Nitrogen
   ii) Phosphorus

iii) Boron
iv) Molybdenum

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2) a) The uptake of minerals is very specific. Explain the mechanism that ensures this specificity.

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b) How is the uptake of ions in some cases fooled by similar ones?

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3) List the three factors that influence the uptake of ions by the roots from soil.

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4) Why can't potassium and sodium ions cross the artificial lipid bilayer?

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5) While studying uptake of K^+ by plant membrane it was observed that uptake was affected by chemicals that inhibit respiration. What inference can be drawn from this observation.

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12.8 ANSWERS

Self-assessment Questions

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

b) i) Potassium
ii) Calcium
iii) Chlorophyll
iv) Iron

2) i) Negative
ii) Plasmodesmata
iii) pH
iv) Casparian strip
v) Cation exchange sites
vi) Rubidium

3) a) i) Concentration gradient
ii) ATPase
iii) Cytoplasm, Outside

b) i) K^+
ii) Increases
iii) Positive
iv) Acidic
v) Calcium

4) a) i) NO_3^-
ii) protein
iii) NH_4^+, NO_3^-
iv) decreases
v) NO_3^-, NH_4^+
vi) older
vii) Ca^{2+}, K^+
viii) xylem, cannot
ix) Mg, K^+
x) carbohydrate
xi) phosphorus
xii) mobile
xiii) K^+
xiv) turgor

b) Ferredoxin, cysteine, methionine, coenzyme A, biotin, thiamine

c) i) b, ii) a, iii) c,

5) Any three of the following

a) cytochrome oxidase, catalase, peroxidase, cytochrome f and cytochrome c.

b) i) water splitting
ii) RNA, RNA polymerase
iii) indole acetic acid
iv) oxidation — reduction reaction.
v) molybdenum
vi) boron
vii) parthenogenesis
viii) water splitting
ix) burning of, bronzing
x) Mo and Co
xi) iron chelates

c) plastocyanin, cytochrome oxidase, lactase, ascorbic acid oxidase, superoxide dismutase.

Terminal Questions

1) i) NO_3^-, NH_4^+, ii) $H_2PO_4^-$, HPO_4^{2-}, iii) H_3BO_3, iv) SO_4^{2-}

2) a) The specificity of transport of certain ions is due to carrier proteins which behave more like enzymes and the transport is similar to enzyme mediated reactions. The carrier protein has a specific site for binding an ion that is to be transported.

b) Uptake is fooled when two or more than two ions can bind at the same site of carrier protein.

3) i) Ion exchange capacity of soil
ii) pH
iii) Presence of different cations and anions.

4) Although both K^+ and Na^+ ions are small in size but the charge and hydration shell around them prevents them from entering the hydrophobic hydrocarbon phase of the lipid bilayer.

5) Inhibition of K^+ uptake by respiratory inhibitors shows that K^+ transport is linked to, and dependent on ATP produced from respiration.