**water and nutrients in plant**

**Water potential**

*The concept of water potential*

All living things, including plants, require a continuous input of free energy to maintain and repair their highly organised structures, as well as to grow and reproduce. Chemical potential is a quantitative expression of the free energy associated with a substance. The chemical potential of the water represents the free energy associated with water. Water flows without energy input from regions of higher chemical potential to ones of lower chemical potential. The concept of water potential was introduced in 1960 by R.O. Slatyer and S.A. Taylor, as a measure of the free energy of water per unit volume (J m-3). These units are equivalent to pressure units such as the pascal, which is the common measurement unit for water potential.

The major factors influencing the water potential in plants are *concentration, pressure and gravity*. Water potential is symbolized by Ψw (the Greek letter psi), and the water potential of solutions may be dissected into individual components, usually written as the following sum:

Ψw = Ψs + Ψp + Ψg

The terms Ψs and Ψp and Ψg denote the effects of solutes, pressure, and gravity, respectively, on the free energy of water. The reference state most often used to define water potential is pure water at ambient temperature and standard atmospheric pressure.

The term Ψs, called the **solute potential** or the **osmotic potential**, represents the effect of dissolved solutes on water potential. Solutes reduce the free energy of water by diluting the water. It’s value is negative or maximum zero. The minus sign indicates that dissolved solutes reduce the water potential of a solution relative to the reference state of pure water. Osmosis can be easily demonstrated using a device known as osmometer. The increase in the volume of the solution will continue until the hydrostatic pressure developed in the tube of the osmometer is sufficient to balance the force driving the water into the solution. This force, measured in units of pressure, is known as osmotic pressure. It is convention to define osmotic potential as the negative of the osmotic pressure, since they are equal but opposite forces.

The term Ψp is the **hydrostatic pressure** of the solution. Positive pressures raise the water potential; negative pressures reduce it. The positive hydrostatic pressure within cells is the turgor pressure. Negative hydrostatic pressure (**tension**) develops in the xylem and in the walls between cells. Gravity causes water to move downward unless the force of gravity is opposed by an equal and opposite force. The term Ψg depends on the height (h) of the water above the reference state water. The gravitational component (Ψg) of the water potential Water and nutrients in plant

is generally omitted in considerations of water transport in the cell level. Thus in these cases the equation can be simplified as follows:

Ψw = Ψs + Ψp

**Absorption by roots**

*Water in the soil*

The water content and the rate of water movement in soils depend to a large extent on soil type and soil structure. Like the water potential of the plant cells, the water potential of soils may be dissected into three components: the osmotic potential, the hydrostatic pressure and the gravitational potential. The osmotic potential (Ψs) of soil water is generally negligible. The second component of soil water potential is hydrostatic pressure (Ψp). For wet soils, Ψp is very close to zero. As soil dries out Ψp decreases and can become quite negative. As the water content of the soil decreases, the water recedes into the interstices between soil particles, forming air-water surfaces whose curvature represents the balance between the tendency to minimize the surface area of the air-water interface and the attraction of the water for the soil particles. Water under a curved surface develops a negative pressure (like in leaf mesophyll). As soil dries out, water is first removed from the largest

*Water absorption by roots*

Intimate contact between the surface of root and the soil is essential for effective water absorption. **Root hairs** are filamentous outgrowths of root epidermal cells that greatly increase the surface area of the root, thus providing greater capacity for absorption of ions and water from the soil (**Figure 1.6**). Water enters the root most readily near the root tip. The intimate contact between the soil and the root surface is easily ruptured when the soil is disturbed. It is for this reason that newly transplanted seedlings and plants need to be protected from water loss for the first few days after transplantation.

**Figure 1.6** Root hairs intimate contact with soil particles and greatly amplify the surface area used for water absorption by the plant (*source: Taiz L., Zeiger E., 2010*)

From the epidermis to the endodermis of the root, **there are three pathways through which water can flow: the apoplast, the symplast and** **the transmembrane pathway** (**Figure 1.7**).

1. The apoplast is the continuous system of cell walls and intercellular air spaces. In this pathway water moves without crossing any membranes as it travels across the root cortex.

2. The symplast consists of the entire network of cell cytoplasm interconnected by plasmodesmata. In this pathway, water travels across the root cortex via the plasmodesmata.

3. The transmembrane pathway is the route by which water enters a cell on one side, exits the cell on the other side, enters the next in the series, and so on. In this pathway, water crosses the plasma membrane of each cell in its path twice.

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**Transport through the xylem**

Vascular tissues include the xylem and phloem, which conduct water and nutrients between the various organs. In leaves, the larger veins subdivide into smaller veins such that no photosynthetic leaf cell is more than a few cells removed from a small vein ending. Xylem tissue is responsible for the transport of water and dissolved minerals from the root to the stem to aerial organs. Phloem, on the other hand, is responsible primarily for the translocation of organic materials from sites of synthesis to storage sites or sites of metabolic demand.

Transpiration speeds up the movement of xylem sap, but it seems unlikely that this is an essential requirement. Transpiration involves the evaporation of water, it can assume a significant role in the cooling of leaves. However, the main evolutionary function of stomata is to ensure an adequate supply of carbon dioxide for photosynthesis

**The xylem consists of two types of tracheary elements**

There are two main types of **tracheary elements** in the xylem: tracheids and vessel elements. Vessel elements are found in angiosperms. Tracheids are present in both angiosperms and gymnosperms. Both tracheids and vessel elements dead cells with thick, lignified cell walls, which form hollow tubes through which water can flow with relatively little resistance. **Tracheids** are elongated, spindle-shaped cells that are arranged in overlapping vertical files. **Vessel elements** tend to be shorter and wider than tracheids and have perforated end walls that form a perforation plate at each end of the cell.

**Water moves through the xylem by pressure-driven bulk flow**

Pressure-driven bulk flow of water is responsible for long-distance transport of water in the xylem. It is independent of solute concentration gradient, as long as viscosity changes are negligible.

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**The cohesion-tension theory explains water transport in the** **xylem**

In theory, the pressure gradients needed to move water through the xylem could result from the generation of positive pressures at the base of the plant or negative pressures at the top of the plant. However, root pressure is typically less than 0.1 MPa and disappears when the transpiration rate is high or when soils are dry, so it is clearly inadequate to move water up a tall tree. Instead, the water at the top of a tree develops a large tension (negative hydrostatic pressure), and this tension pulls water through the xylem (**Figure 1.8**). This mechanism, first proposed toward the end of the nineteenth century, is called the cohesion-tension theory of sap ascent because it requires the cohesive properties of water to sustain large tensions in the xylem water column. The theory is generally credited to H.H. Dixon, who gave the first detailed account of it in 1914.

**Figure 1.8** The driving force for water movement through plants originates in leaves The negative pressure that causes water to move up through the xylem develops at the surface of the cell walls in the leaf. As water evaporates from mesophyll cells within the leaf, the surface of the remaining water is drawn into the interstices of the cell wall, where it forms curved air interfaces. Because of the high surface tension of water, the curvature of these interfaces induces a tension, or negative pressure, in water. The cohesion-tension theory explains how the substantial movement of water through plants occur without the direct expenditure of metabolic energy.

**Transpiration**

Water movement is determined by differences in water potential. It can be assumed that the driving force for transpiration is the difference in water potential between the substomatal air space and the external atmosphere. However, because the problem is now concerned with the diffusion of water vapour rather than liquid water, it will be more convenient to think in terms of vapour systems. We can say that when a gas phase has reached equilibrium and is saturated with water vapour, the system will have achieved its **saturation vapour pressure**. The vapour pressure over a solution at atmospheric pressure is influenced by solute concentration and mainly by temperature. In principle we can assume that the substomatal air space of leaf is normally saturated or very nearly saturated with water vapour. On the other hand, the atmosphere that surrounds the leaf is usually unsaturated and may often have a very low water content. This difference in water vapour pressure between the internal air spaces of the leaf and the surrounding air is the driving force of transpiration.

On its way from the leaf to the atmosphere, water is pulled from the xylem into the cell walls of the mesophyll, where it evaporates into the air spaces of the leaf. The water vapor than exits the leaf through the stomatal pore.

The movement of liquid water through the living tissues of the leaf is controlled by gradients in water potential. However, transport in the vapor phase is by diffusion, so the final part of the transpiration stream is controlled by the concentration gradient of water vapor. Almost all of the water lost from leaves is lost by diffusion of water vapour through the tiny stomatal pores. The stomatal transpiration accounts for 90 to 95% of water loss from leaves. The remaining 5 to 10% is accounted for by cuticular transpiration. In most herbaceous species, stomata are present in both the upper and lower surfaces of the leaf, usually more abundant on the lower surface. In many tree species, stomata are located only on the lower surface of the leaf.

*The driving force for transpiration is the difference in water vapour concentration*

Transpiration from the leaf depends on two major factors: (1) the **difference in water vapor concentration** between the leaf air spaces and the external bulk air and (2) the **diffusional resistance** of this pathway. Air space volume is about 10% in corn leaves, 30% in barley, and 40% in tobacco leaves. In contrast to the volume of the air space, the internal surface area from which water evaporates may be from 7 to 30 times the external leaf area. The air space in the leaf is close to water potential equilibrium with the cell wall surfaces from which liquid water is evaporating. The concentration of water vapor changes at various points along the transpiration pathway from the cell wall surface to the bulk air outside the leaf.

The second important factor governing water loss from the leaf is the diffusional resistance of the transpiration pathway, which consists of two varying components:

1. The resistance associated with diffusion through the stomatal pore, the **leaf stomatal resistance**.

2. The resistance due to the layer of unstirred air next to the leaf surface through which water vapor must diffuse to reach the turbulent air of the atmosphere. This second resistance is called the leaf boundary layer resistance.

Some species are able to change the orientation of their leaves and thereby influence their transpiration rates. Many grass leaves roll up as they experience water deficits, in this way increasing their boundary layer resistance.

*Stomatal control couples leaf transpiration to leaf photosynthesis*

Because the cuticle covering the leaf is nearly impermeable to water, most leaf transpiration results from the diffusion of water vapor through the stomatal pore. The microscopic stomatal pores provide a low-resistance pathway for diffusional movement of gases across the epidermis and cuticle. Changes in stomatal resistance are important for the regulation of water loss by the plant and for controlling the rate of carbon dioxide uptake necessary for sustained CO2 fixation during photosynthesis. At night, when there is no photosynthesis and thus no demand for CO2 inside the leaf, stomatal apertures are kept small or closed, preventing unnecessary loss of water. Leaf can regulate its stomatal resistance by opening and closing of the stomatal pore. This biological control is exerted by a pair of specialized epidermal cells, the **guard cells**, which surround the stomatal pore.

*The cell walls of guard cells have specialized features*

Guard cells are found in leaves of all vascular plants. In grasses, guard cells have a characteristic dumpbell shape, with bulbous ends (**Figure 1.9**). These guard cells are always flanked by a pair of differentiated epidermal cells called **subsidiary cells**, which help the guard cells control the stomatal pores. In dicots and nongrass monocots, guard cells have an elliptical contour (often called “kidney-shaped”) with the pore at their center. Subsidiary cells are often absent, the guard cells are surrounded by ordinary epidermal cells. A distinctive feature of guard cells is the specialized structure of their walls. The alignment of cellulose microfibrils, which reinforce all plant cell walls and are an important determinant of cell shape, play an essential role in the opening and closing of the stomatal pore.

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**Figure 1.9** The radial alignment of the cellulose microfibrils in guard cells and epidermal cells of (A) a kidney-shaped stoma and (B) a grasslike stoma (*source: Taiz L., Zeiger E., 2010*)

*An increase in guard cell turgor pressure opens the stomata*

Guard cells function as multisensory hydraulic valves. Environmental factors such as light intensity and quality, temperature, leaf water status, and intracellular CO2 concentrations are sensed by guard cells, and these signals are integrated into well-defined stomatal responses. The early aspects of this process are ion uptake and other metabolic changes in the guard cells. The decrease of osmotic potential (Ψs) resulting from ion uptake and from biosynthesis of organic molecules in the guard cells. Water relations in guard cells follow the same rules as in other cells. As Ψs decreases, the water potential decreases, and water consequently moves into the guard cells. As water enters the cell, turgor pressure increases. Because of the elastic properties of their walls, guard cells can reversible increase their volume by 40 to 100%, depending on the species. Such changes in cell volume lead to opening or closing of the stomatal pore. Subsidiary cells appear to play an important role in allowing stomata to open quickly and to achieve large apertures.

*The transpiration ratio measures the relationship between water loss and carbon gain*

The effectiveness of plants in moderating water loss while allowing sufficient CO2 uptake for photosynthesis can be assessed by a parameter called the **transpiration ratio**. This value is defined as the amount of water transpired by the plant divided by the amount of carbon dioxide assimilated by photosynthesis. For plants in which the first stable product of carbon fixation is a 3-carbon compound (C3 plants), as many as 400 molecules of water are lost every molecule of CO2 fixed by photosynthesis, giving a transpiration ratio of 400. Plants in which a 4-carbon compound is the first stable product of photosynthesis (C4 plants), generally transpire less water per molecule of CO2 fixed than C3 plants do. A typical transpiration ratio for C4 plants is about 150. Plants with crassulacean acid metabolism (CAM) photosynthesis the transpiration ratio is low, values of about

### ESSENTIAL MINERAL ELEMENTS

In fact, all elements found in a plant are not essential for its growth and life cycle. An essential element is known without which the plant cannot complete its life cycle. It is clear physiological role to play. For finding out whether an elements is essential or not for a plant, the plant is raised in complete absence of that particular elements under controlled culture conditions. If the plant grows normally, the elements are non-essential and if it does not grow normally, it means that the element is truly essential.

The important criteria for essential elements are as follows-

1. These elements are absolutely necessary for supporting normal growth and reproduction of plant.
2. These elements are always specific and cannot be replaced by only other elements. 3- These elements is directly involved in the metabolism of the plant.

It has since long been known that carbon, hydrogen and oxygen are essential elements for the plant. In the middle of last century water culture and sand culture experiments has established

that the elements nitrogen phosphorus, potassium, magnesium, calcium and iron were indispensable for the plants. In the absence of any one of these elements the growth of shoots or roots are stunted.

The essential elements are classified into two broad categories called (i) Macronutrients and (ii) Micronutrients.

The macronutrients are carbon, hydrogen, oxygen nitrogen, phosphorus, sulphur, potassium, calcium, magnesium are generally present in plant tissues in concentrations of 1 to 10mg per gram of dry matter.

The micronutrients or trace elements are manganese, copper, molybednum, zinc, boron and chlorine, recently some other such elements have also been discovered, e.g. cobalt, vanadium and nickel.

The microelements are required in very low quantity. i.e., about 0.1 mg per gram of dry matter.

#### Role of Essential Elements

The most important role of the elements is to participate in various metabolic activities such as regulation of permeability of cell membranes; some elements are required for maintenance of osmotic pressure of cell sap. While others take part in an electron transport system.

### MACRONUTRIENTS

#### 3.4.1- Carbon, Hydrogen and Oxygen

These are not minerals in origin but are discussed here because they enter into the composition of practically all organic compounds present in the plant and accounts for a major part of the dry weight. The significance of water (H2O) can be felt when it is said that water is the liquid of life. The source for carbon and oxygen is atmosphere and for hydrogen it is water.

#### 3.4.2-Nitrogen

**Functions of Nitrogen:** The sources of nitrogen are soil and atmosphere. About 78% of nitrogen is found is atmospheric air but this is of no use to plants in its free state. This enters in the plants through stomata along with other gases and comes out in the same state unused. The plants can take nitrogen from the soil in the form of nitrates, nitrites and ammonium salts. The chief sources of nitrate are sodium nitrate, potassium nitrate, ammonium nitrate and calcium nitrate. Besides, there are certain highly specialized organism called nitrogen fixers, such as bacteria and cyanobacteria. They fix atmospheric nitrogen into the soil in the form of nitrites (No2) and Nitrates (No3).

**Nitrogen deficiency symptoms:** Nitrogen deficiency causes yellowing of older leaves (Chlorosis). The plant growth is stunted as protein content, cell division and cell enlargement are decreased. It also causes dormancy of lateral buds, late flowering, purple coloration and wrinkling of cereal grains.

#### 3.4.3-Sulphur

**Functions of Sulphur:** Sulphur is the constituent of amino acids, vitamin B, coenzyme A and volatile oils. It is absorbed from the soil as sulphate iron. Through the different amino acids it participates in protein synthesis. Sulphur affects an increase in nodule formation in root of leguminous plants.

**Sulphur deficiency symptoms:** Sulphur deficiency causes yellowing (i.e. chlorosis) of leaves younger leaves are affected first trips and margins of leaves roll inward a hard woody stem due to development of sclerenchyma. Sulphur starvation results in shortage of protein.

#### Phosphorus

**Functions of Phosphorus:** Phosphorus is absorbed by the plant from the soil in the form of phosphate ions. It is one of the most important element for the plants.

Phosphorus is vital structural component of the nucleic acids nucleoprotein, phytin, phospholipids, sugar phosphates, ATP, NADP and numerous phosphorylated compounds. It is an essential element participating in the skeleton of Plasma membrane.

**Phosphorus deficiency symptoms:** Phosphorus deficiency causes decrease in the rate of protein synthesis. It causes premature leaf fall and purple anthocyanin pigmentation. The leaves become dark blue green in colour and brown necrotic areas are developed on leaves and petioles. The growth of root and shoot is extremely restricted. Flowering is delayed.

#### Calcium

**Functions of Calcium:** This element is always found in green plants. The middle lamella of the cell wall consists of calcium pectate. Only because of these elements the permeability of the protoplasm is maintained calcium affects the hydration of colloids. Calcium is believed to be important in regulating metabolic activities as it activates certain enzymes.

**Calcium deficiency symptoms:** Calcium deficiency causes disintegration of growing meristematic regions of root, stem and leaves. Chlorosis generally occurs along the margins of younger leaves. It also causes malformation of the younger leaves.

#### Potassium

**Functions of Potassium:** Potassium is the only monovalent cation essential for plant growth. This element is usually found in the growing regions of the plant. It is one of the constituents of protoplasm. Potassium is essential for the formation of sugar and starch and also for their translocation throughout the plant. It is also needed in cell division, reduction of nitrate, development of chlorophyll, stomata movements etc.

**Potassium deficiency symptoms**: Potassium deficiency inhibits synthesis of proteins, which results in the accumulation of organic nitrogenous compounds in the plant cells Carbohydrate metabolism is checked. The rate of respiration increases. Mottled chlorosis of leaves occurs Necrotic areas are developed at the tips and margins of leaves.

#### Magnesium

**Functions of Magnesium:** It is a constituent of chlorophyll and therefore essential for the formation of this pigment. Magnesium activates enzymes is respiration and photosynthesis. It plays an important role in synthesis of ATP from ADP and inorganic phosphates.

**Magnesium deficiency symptoms:** Magnesium deficiency causes interveinal chlorosis of the leaves. stem becomes yellowish green, often hard and woody. Deficiency symptoms develop on the older leaves and proceed systematically towards the younger leaves.

#### Iron

**Functions of Iron:** Iron is normally absorbed in the ferrous, form though it can be absorbed in the ferric form as well. It plays an important role in the formation of chlorophyll, constitution of the chlorophyll. It plays the role of catalyst. Iron in found in ferrodoxin, FRS, flavoprotein and the iron porphyrin protein, which include cytochromes peroxidases and catalases. It therefore plays an important role in respiratory mechanism.

**Iron deficiency symptoms:** Iron deficiency causes rapid chlorosis of the leaves which is generally interveinal chlorosis may produce a mottled pattern of the leaf may show complete bleaching, or often become necrotic.

### MICRONUTRIENTS

#### Manganese

**Functions of Manganese:** Manganese activates many enzymes which are involved in photosynthesis, respiration and nitrogen metabolism. It also plays some role in the synthesis of chlorophyll and in the transfer of electron from H2O to photo-oxidized chlorophyll in photosynthesis (Homann, 1967)

**Manganese deficiency symptoms:** Manganese deficiency causes chlorosis which is distinct from that of iron deficiency. The leaf takes mottled appearance. The chloroplast loss chlorophyll and starch grains and become yellow green in colour. Dead tissue spots are found scattered over the leaf.

#### Copper

**Functions of copper deficiency:** The element is required is very small quantity. It is very toxic when present is larger quantity. It acts as catalyst in oxidation reduction reactions, since it is a constituent of certain oxidising and reducing agents. Copper helps in formation of starch. It is required for the overall metabolism in plants.

**Copper Deficiency symptoms:** Copper deficiency causes necrosis of the tips of young leaves. Both vegetative and reproductive growths are reduced. In crops, the younger leaves wither and

show marginal chlorosis of the tips. Grain formation is more severely restricted than vegetative growth.

#### Zinc

**Functions of Zinc:** Zinc helps in the formation of chloroplasts. It functions as activator of certain enzymes. e.g. carbonic anahydrase, alcohol dehydrogenase, hexose kinase etc. Zinc in required in synthesis of auxins.

**Zinc deficiency symptoms:** Zinc deficiency causes reduced stem growth due to decreased synthesis of auxin. It causes chlorosis of older leaves which starts from tips and margin. The absence of zinc also suppresses seed formation and causes malformation in fruiting trees.

#### Boron

**Functions of Boron:** Boron differs from the other micronutrients in that there is no evidence to suggest its connection with the enzyme systems and it also differs in that it is absorbed as an onion, i.e. borate and tetraborate, rather than a cation, like the other metallic nutrients.

It is necessary for translocation of sugars and involved in the reproduction and germination of pollens. It is concerned with water reactions in cells and regulates the intake of water into the cell. It also affects flowering and fruiting, cell division, metabolism, active salt absorption, photosynthesis etc.

**Boron deficiency symptoms:** Boron deficiency causes death of the shoot tip. Flowers formation is suppressed, root growth is stunted and shoot apices die. Fruit become of small size and root nodules in leguminous plants are not formed and leaves become coppery in texture.

#### Molybdenum

**Functions of Molybdenum**: The main role of molybdenum in plants has been found in the nitrogen metabolism. It acts as an activator for the enzyme nitrate reductase. It also helps in formation of proteins. This is absorbed by plant from soil in the form of molybdenum ion (Mo2). **Molybdenum deficiency symptoms**

Molybdenum deficiency causes chlorotic interveinal mottling of the older leaves. This may cause nitrogen deficiency, as it is component of enzymes involved in nitrogen metabolism. It also inhibits the flower formation.

#### 3.5.6 Chlorine

##### Functions of chlorine

Chlorine helps in determining solute concentration and anion cation balance in cells. It is required for cell division in roots and leaves. Chloride ions are essential in the transfer of electrons from H20 to photo oxidised chlorophyll in photosynthesis.

**Chlorine deficiency symptoms:** The deficiency of chlorine in plants causes wilting of leaves.

### ABSORPTION OF MINERAL SALT

Besides water, the plant absorbs from the environment consideration quantities of mineral salts, gases and various other salts. All these are absorbed in the form of aqueous solutions. The mineral salts are absorbed from the external solution by the roots.

In [plants](https://en.wikipedia.org/wiki/Plant) **mineral absorption**, also called **mineral uptake**. In plants, the entrance portal for mineral uptake is usually through the [roots](https://en.wikipedia.org/wiki/Root). (Roots, 2005) Some mineral [ions](https://en.wikipedia.org/wiki/Ion) diffuse in- between the [cells.](https://en.wikipedia.org/wiki/Cell_(biology)) In contrast to water, some minerals are actively taken up by plant.

Most of the elements required by the plants are absorbed by them from the soil. The clay particles of the soil are present in the form of colloids. The micelles of colloidal clay are usually negatively charged. These charges are balanced by the binding of positively charged ions (cations) which are taken up from the soil solution. In acidic soil H+ and in alkalins soil ca2++ are the principal cations associated with the clay particles. In the acidic soil the particles may also take up and binds potassium, ammonium and other cations. This reversible binding of cations, a property possessed by clay particles is known as cation exchange. The soil also contains the anions like Cl-, So4-, HCO3-, H2PO4-, No3-, and OH-. Most anions except the phosphate ions leach out of soil rapidly.

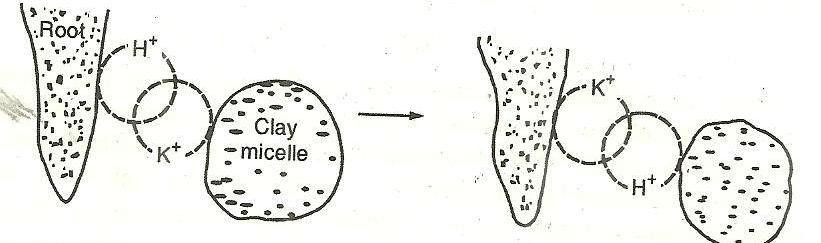
**Passive Absorption:** In most cases, the movement of mineral ions into the root occurs by diffusion. Molecules or ions diffused from a region of their higher concentration to a region of their lower concentration. As these substances diffuse they exert a pressure. The movement of mineral ions into root cells as a result of diffusion is called passive absorbtion.

1. **Mass flow theory (Bulk Flow):** According to this theory ions are taken up by the roots along with mass flow of water under the influence of transpiration. Russel and Barber (1960) also supported this theory but raised a question whether the effect of transpiration is direct or indirect. Lopushimsky (1964) worked in this problem and studied the uptake of radioactive p32 and Ca45, they found that an increase in the hydrostatic pressure (comparable to transpiration pull) increases ion uptake. So transpiration effect on salt absorption is direct. However, both mass flow theory and direct influence of transpiration have been challenged in view of recent research. Both of these fail to explain salt accumulation against osmotic gradient.
2. **Ion exchange:** In ionic exchange mechanism anions or cations from within the cells are exchanged for anions or cations of equivalent charge of the external solution in which the tissue is immersed.

The phenomenon has been experimentally confirmed in excised barley roots in which radioactive K+ ions exchange place with the non-radioactive K+ ions. A similar exchange mechanism operates between soil solution and clay micelles. The ions get accumulated against a concentration gradient without the participation of metabolic energy because cations and anions

of the external medium get exchanged with H+ and OH- ions, which always remain absorbed on the surface of the membrane. H+ and OH- are readily available from water.

The process of ionic exchange has been explained by two theories 1 the contact exchange theory and 2-carbonic acid exchange theory. According to the contact exchange theory an ion may be absorbed by the plant root without being first dissolved in the soil solution. An ion absorbed electrostatically to a solid particle such as a plant root or clay micelle, is not held too tightly, but oscillates within a certain small volume of space. An exchange of ions takes place when the oscillation volume of one ion overlaps to oscillation volume of another ion. The soil solution, however, plays an important part in the carbonic acid theory in the it provides the medium for the exchange of ions between the roots and the clay micelles. Carbon dioxide released in respiration combines with water to form carbonic acid in the soil solution. Carbonic acid dissociates into (H+) and (HCO-) ions. A cation absorbed to the clay surface may be exchanged with H+ of the soil solution. This cation them may diffuse to the root surface in exchange for H+. The cation them may diffuse to the root surface in exchange for H+. The cation may also be absorbed as ion pairs with bicarbonate. Thus ion exchange mechanism would allow for greater absorption of ions from the external medium than could normally be accepted for by the free diffusion.



**Fig.3.1 Figure explaining cation exchange theory (Contact exchange theory)**

1. **Donnan equilibrium:** This theory explains the passive accumulation of ions that are non- diffusible, which may be present on one side of the membrane (Donnan, 1927). Unlike diffusible ions, the membrane is not permeable to non-diffusible ions. Such ions are called fixed ions. They may be anions or cations. In which there are no fixed ions, there are equal number of anions and cations on both sides of the membrane at equilibrium. But in Donnan equilibrium, in order to balance the charge of the fixed ions (anions) more ions of the order charge (cations) would be required.

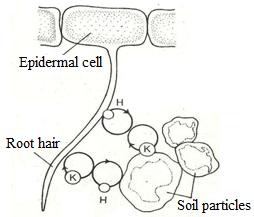
For example there is a membrane that separates a cell from the external medium and allows exchange of some ions and not others. To the inner side of this membrane there are anions, which are fixed and non diffusible and therefore the membrane becomes impermeable to these anions. In such a situation for equilibrium to be reached additional cations are needed to balance the negative charges of the anions that are structurally formed to the inner side of the above membrane.

According to the theory, Donnan equilibrium is attained if the product of anions and cations in the internal solution becomes equal to the product of anions and cations in the external solution, depicted by the equation as follows:

Cations inside, Ci+ Anions outside, Ao-

Cations outside Co+ Anions inside, Ai-

For example, a membrane which is permeable to Mg+ and CI- ions and to X- ions present inside the cell. Here, membrane has 6X- fixed ions on the inner side. CI- ions make across the membrane by diffusion along the concentration gradient. The concentration of anions on the inner side is now more than that of cations. In order to balance electrochemical equilibrium within the cell sap, Mg++ ions move across the membrane against the concentration gradient. Similarly, if these are fixed cations the anions shall move against the concentration gradient to bring about equilibrium.



**Fig.3.2 Contact exchange theory**

##### Objection to Passive Absorption Concept

Certain strong objections have been raised against passive absorption concept of salt uptake. A few of them are:

1. In actual process, the rate of absorption of minerals is too rapid to be explained by passive absorption.
2. No theory of passive absorption adequately explains absorption and accumulation of salts or ions against the osmotic gradients (or against the laws of diffusion). However, cases of extra accumulation of K+ ions within the cells (like 1000 times as against the surrounding medium) are now frequently known in *Nitella translucens*, *Chara australis* and *Hydrodictyon africanum* (Hober, 1945 and Raven, 1967).
3. It has been experimentally demonstrated that there is a close relationship between salt uptake and metabolic activities. This may be supported by the following examples:
   1. A quantitative relationship has been found between anion absorption and respiration.
   2. A close relationship between salt accumulation and respiration is found in all cases. Hopkins (1956) observed that salt accumulation is slowed, and even prevented completely, with the decrease in the oxygen content of the nutrient medium.
   3. The active phase of salt absorption is inhibited by the absence of oxygen, i.e. oxygen is required during salt uptake.
   4. There is a close relationship between metabolic activites and ability to absorb and accumulate solutes.
   5. The metabolic inhibitors influence the salt absorption Lundegadh (1955) reported that salt uptake is inhibited by oxidiase inhibitors azides, carbon monoxides and cyanides (all metabolic inhibitors)
   6. Salt uptake has been found to stimulate and increase the rate of respiration. This increased respiration has been termed as *salt induced respiration.*
   7. Factors like pH, light, oxygen tension and growth affect the salt absorption suggesting that there is some essential role of metabolic activities in salt uptake.

**Active Absorption:** According to active absorption concept of salt uptake, it is believed that this process is supported by metabolic energy, thus the absorption of ions, involving use of metabolic energy is called active absorption. There have been modification from time to time to discuss the nature of participation of metabolic energy and that is why several theories have been proposed.

##### Active absorption of solutes or theory of salt accumulation

According to this theory Hoagland (1923) suggested that absorption of solutes takes place against higher concentration of salts. The cells near the tips of roots also have the capacity of accumulating ions (Hoagland and Broyer 1936). If the initial salt content of the root cells is low and if other conditions are favorable, the concentration of ions in the absorbing cells may greatly be increased than that present in soil solution. This involves an expenditure of energy. This energy in supplied by the respiratory activity of the absorbing cells. The rate of accumulation is often influenced therefore by the previous metabolic status of the absorbing cells.

The phenomenon of salt accumulation seems confined largely to cells which have the capacity for cells division and growth, Meristematic cells and cells in the early stages of enlargement are particularly active in absorbing ions. As cells lose their capacity for growth they also lose their capacity of mineral salt accumulation. As already referred earlier that accumulation of salt requires expenditure of energy which is supplied by respiratory activity of cells.

Hoagland and Broyer (1936) found that if excised roots (young roots) are immersed in dilute solutions of mineral salts through which N2 is bubbled little or no accumulation of salts occurs in the root cells. If on the other hand O2 is bubbled through the solution, a rapid accumulation of salts within root cells takes place. Lack of O2 checks aerobic respiration and prevents absorption of ions. The accumulation of ions of root cells and their retention within these cells in a free condition requires an expenditure of energy which is supplied by the process of respiration.

Salt accumulation is also affected by the rate of photosynthesis because on this process depends the supply of carbohydrates which are the respiratory substrates for efficient respiration. So any factor which reduces photosynthesis, also reduces salt accumulation.

The fact that salt accumulation by root cells is dependent on respiration, suggests that temperature may have also marked effect on salt accumulation process.

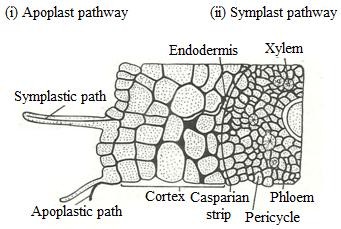
1. **Carrier concept:** Ions, which are accumulated in cells, may move into the inner space against concentration and for this movement additional energy is required. This additional energy is derived directly or indirectly through metabolism. This theory of active absorption has been supported by various evidences which show that active ion uptake is carried our by carrier mechanism for both influx and efflux of ions.

Unlike ion channels, the carrier proteins do not have pores. The membrane does not allow the ions to pass through as it is. The activated ions combine with carrier proteins and form ion- carrier complex, which is capable of moving across the membrane. The complex moves across the membrane and reaches the inner surface. Here, the complex breaks and release ions into the cytoplasm of the cell. Carriers are specific, and combine with particular types of ion.

1. **Ion Movement into the Root:** Mineral nutrients absorbed by the root are carried to the xylem. This absorption takes place by two pathways. They are (i) Apoplast pathway and (ii) Symplast pathway.
2. **Apoplastic pathway-** This pathway essentially involves diffusion and mass flow of water from cell to cell through spaces between cell wall polysaccharides.

The ions that enter the cell wall of epidermis move across cell wall of cortex, cytoplasm of endodermis cell wall of pericycle and finally accumulate in xylem vessels.

1. **Symplast pathway-** In this pathway, ions that enter the cytoplasm of epidermis move across the cytoplasm, cortex, endodermis and pericycle through plasmodesmata, and finally reach to xylem vessels.



**Fig.3.3 Apoplastic and symplastic pathways of ion absorption**

**Table-1 Differences between Passive Absorption and Active Absorption**

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| **S.No.** | **Passive Absorption** | **Active Absorption** |
| 1 | This processes physical driving force,  which is non-metabolic | Here the driving force is energy derived  form metrabollic processes. |
| 2 | This type of absorption of ions and molecules is sponataneous and proceeds  towards equilibrium | This type of absorption is not spontaneous and does not proceed  towards equipbrium |
| 3 | Such absorption of a substance occurs across a protoplasmic membrane from its higher to lower chemical potential. | The active absorption of a substance occurs across a protoplasmic membrane from its lower to higher chemical potential i.e. against concentration  gradient. |
| 4 | In passive absorption the energy yielding metabolic processes are not involved. | When energy yielding metabolic processes are weakened, active transport  system is also checked. |
| 5 | The passive transport takes place through  the protoplasmic layer in between the cell wall and the vacuole. | The active transport takes place across the  protoplasmic membrane (i.e. plasma membrane, tonoplast, etc.) |