TRANSPORT IN PLANTS

- A plant cell has three physiological compartments – cell wall, protoplast and vacuole. Two membranes separate these compartments tonoplast around central vacuole and plasmolemma around protoplast and is attached to cell wall. Both membranes are selectively permeable. Central vacuole contains an osmotically active fluid called sap. Plant cell forms a living continuum called simpleast with the help of plasmodesmata which functions as cytoplasmic bridges between adjacent cells. A non-living continuum called apoplast also occurs in plants. It is formed of adjacent cell walls and intercellular spaces.

WATER POTENTIAL

- Chemical potential is free energy of one mole of a substance in system under constant temperature and pressure. All reactions and processes involve a decrease in chemical potential. Chemical potential of water is called water potential (Ψ_w) .
- The term water potential was first used by Slatyer and Jaylor (1960).
- Its value for pure water is taken as zero ($\Psi_w = 0$).
- $\Psi_w = \Psi_m + \Psi_s + \Psi_p$,
  Where Ψ_w is water potential.
  Ψ_m is matric potential.
  Ψ_s is solute potential.
  Ψ_p is pressure potential.

MATRIC POTENTIAL

- Matric potential (Ψ_m) expresses the adsorption affinity of water to colloidal substances and surfaces in plant cells.
- In herbaceous plants, the matric potential is almost negligible and it is therefore ignored. Thus $\Psi_w = \Psi_s + \Psi_p$

SOLUTE POTENTIAL OR OSMOTIC POTENTIAL

- It is the decrease in chemical potential of water due to occurrence of solute particles in it.
- The potential osmotic pressure which can develop in a system due to entry of water into it, is termed osmotic potential.
- Solute potential in a solution depends upon the total number of solute particles.
- Solute potential = - (Osmotic pressure) = - C.R.T

- Solute potential in the leaves of most temperate region crops, ranges from -20 to -10 bars. In leaves of xerophytes this value may be even less than -100 bars. Solute potential in leaf cell sap is more negative during the day and less negative at night.

PRESSURE POTENTIAL

- When a cell absorbs water the cell wall exerts pressure – wall pressure (wp). Hydrostatic pressure develops in the vacuole which is known as turgor pressure (TP) or pressure potential (Ψ_p). Ψ_p is equal and opposite to wp. It is usually positive. In plasmolysed cells it is zero and negative in xylem elements during rapid transpiration. In leaves +3 to +5 bars during a summer afternoon and is about +15 bars at night.
- At zero turgor $\Psi_p = 0$, the $\Psi_w = \Psi_s$. At full turgor Ψ_p and Ψ_a are equal but with opposite signs hence $\Psi_w = 0$. Mature cells show intermediate state between zero turgor and full turgor.

DIFFUSION

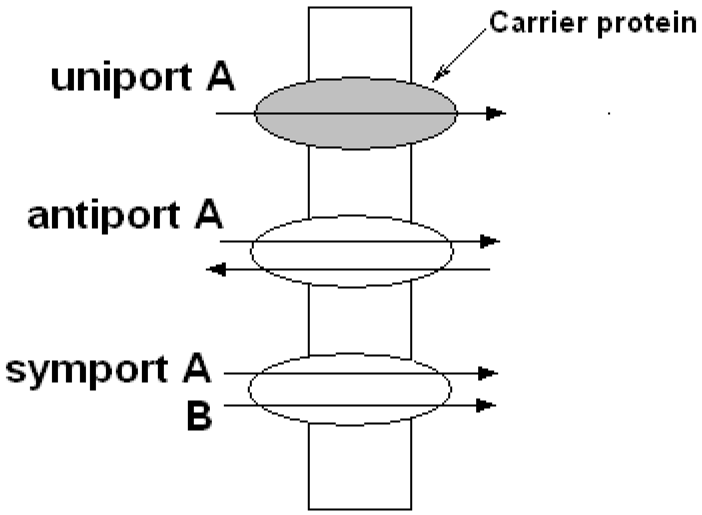
- Diffusion is the movement of particles of gases, liquids and solids from the region of higher concentration to lower concentration.
- Diffusion is due to random kinetic motion of particles. Different substances present in the same medium perform independent diffusion as per their own partial pressure or individual diffusion pressure
- Diffusion pressure is the pressure exerted by the tendency of particle of a substance to diffuse from area of its higher concentration to the region of its lower concentration.
- The diffusion pressure is directly proportional to the concentration or the number of diffusing particles in the system i.e. greater the concentration of diffusing particles, their diffusion pressure will also be greater and vice-versa.
- Diffusion will be more rapid when density of the diffusing substances and liquid as compared to solids. It also depends upon temperature, density of medium and diffusion pressure gradient.
- Diffusion will continue till a state of equilibrium is reached, osmosis is a type of diffusion. Transpiration, exchange of gases and a part of solute absorption are due to diffusion.

INDEPENDENT DIFFUSION

- A system may have two or more types of diffusing particles.
- Each diffusing particle exerts its own diffusion pressure called partial pressure. Each particle according to its partial pressure.
- Tendency of different substances to diffuse according to their own partial pressure or concentration is known as independent diffusion.

FACILITATED DIFFUSION

- A gradient must already be present for diffusion to occur. The diffusion rate depends on the size of the substances; smaller substances diffuse faster
- The diffusion of any substance across a membrane also depends on its solubility in liquids. Substances soluble in lipids diffuse through the membrane faster. Substances that have a hydrophilic moiety, find it difficult to pass through the membrane; their movement has to be facilitated.
- Membrane proteins provide sites at which such molecules cross the membrane. They do not set up a concentration gradient; a concentration gradients to diffuse even if facilitated by the proteins. This process is called facilitated diffusion
- In facilitated diffusion, special proteins help to move substances across membranes without expenditure of ATP energy. Facilitated diffusion cannot cause net transport of molecules from a low to a high concentration this would require input of energy.
- Transport rate reaches maximum when all of the protein transporters are being used.
- Facilitated diffusion is very specific, it allows cell to select substances for uptake. It is sensitive to inhibitors which react with protein side chains.
- The proteins form channels in the membrane for molecules to pass through some channels are always open; others can be controlled. Some are large, allowing a variety of molecules to cross,
- The porins are proteins that form huge pores in the outer membranes of the plastids, mitochondria and some bacteria allowing molecules up to the size of small protein to pass through.



PASSIVE SYMPORTS AND ANTIPORTS

- Two major types of transport proteins are known viz, carrier proteins and channel proteins. Carrier proteins bind the particular solute to be transported and deliver the same to the outer side of the membrane. Channel proteins allow diffusion of the solutes of appropriate sizes.
- Some carrier proteins allow transport only if two types of molecules move together. This is called cotransport. It is of two types.
- In symport method of cotransport, both molecules cross the membrane in the same direction at the same time.
- In antiport method of cotransport, both molecules move in opposite direction. When a molecule move across a membrane independent of other molecule, the process is called uniport.

FACTORS INFLUENCING DIFFUSION

- Rate of diffusion depends upon a number of factors. They are temperature, density of diffusing substance, density of medium, diffusion pressure and distance through which diffusion has to occur.
- Temperature – Increase in temperature increases the rate of diffusion. It is due to increase in kinetic energy of the diffusing particles.
- Density of substance – Heavier particles will diffuse at a slower rate as compared to lighter particles. Diffusion rate is inversely related to square root of relative density of the diffusing substance.
- As the density of gases is lower as compared to liquid, they diffuse more rapidly than liquids. Liquids similarly diffuse more rapidly than solids.

- Amongst gases, the lighter ones will show higher rate of diffusion. For example hydrogen diffuses faster as compared to oxygen.
- Density of medium – Diffusion is quicker, if the medium has lower density. It decreases with increase in density of the medium.
- Concentration or diffusion pressure – Rate of diffusion is proportional to the concentration or diffusion pressure of the substance. It is faster, if the difference in concentration or diffusion pressure is higher.
- Distance – Net diffusion will be high if the distance through which diffusion has to occur is small. It will be low if the distance is large.

IMPORTANCE OF DIFFUSION

- Diffusion keeps the cell walls of the internal plant tissues moist.
- Gaseous exchange during the process of photosynthesis and respiration takes place with the help of diffusion.
- The process of diffusion is involved in the respiration of water vapour.
- Aroma of flowers is due to diffusion of volatile aromatic compounds to attract pollinating animals.
- During passive salt uptake, the ions are absorbed by the process of diffusion.
- Diffusion helps in trans-location of food materials.

OSMOSIS

- It is the movement of water or solvent from a solution having its higher concentration to solution having its lower concentration separated by a semi permeable membrane
- Osmosis is influenced by temperature and pressure. A positive pressure applied over an osmotically active solution will reduce the entry of water into it. A pressure applied over external solution will enhance the passage of water into the internal solution. A perfect semi permeable membrane is essential for osmosis. However, osmosis cannot continue indefinitely. It stops after some time when the difference in chemical potential is counter balanced by hydrostatic pressure or pressure developed due to flow of water in confined solution.
- Reverse osmosis – It is expulsion of pure water from a solution through semi permeable membrane under the influence of external pressure higher than O.P. of water. Reverse osmosis is used in removing slats from saline water as well as extra-purification of water.

- Endosmosis – Osmotic entry of water into a cell or system as when placed in pure water or hypotonic solution is called endosmosis.
- Exosmosis – Osmotic withdrawal of water from a cell or system as when placed in hypertonic solution is called exosmosis.
- Isotonic solution – It is solution that has the osmotic concentration lower than that of another solution.
- Hypertonic solution – A solution having osmotic concentration greater than that of another solution.
- Semipermeable membrane – It is a membrane which allows the passage of solvent across it but prevents the passage of solutes. Example, animal bladder, parchment paper. Egg membrane.
- Permeable membrane – It membrane which allows the passage of both solute and solvent across it. Example, cell wall.
- Selective or differentially permeable membrane
  It is a membrane which is normally semi-permeable but allows selective semi-permeable but allows selective transport of certain solutes.

IMPORTANCE OF OSMOSIS

- Osmosis is responsible for absorption of water by roots.
- Osmosis is responsible for turgidity of plant organs.
- Osmosis is responsible for cell to cell movement of water.
- It is responsible for opening and closing of stomata.
- It is responsible for resistance of plant to drought, frost, etc.

OSMOTIC PRESSURE (O.P)

- It is maximum pressure which can develop in a system due to osmotic entry of water into it under ideal conditions.
- Osmotic pressure is also defined as the pressure required to completely stop the entry of water into an osmotically active solution across a semi-permeable membrane.
- It is measured in atmosphere, bars or pascals.
- Osmotic pressure is numerically equal to osmotic or solute potential but osmotic potential has negative sign where as osmotic pressure has a positive sign.
- Instrument used for measuring osmotic pressure is called osmometer.

FACTORS INFLUENCEING OSMOTIC PRESSURE

- Concentration of solute particles – Osmotic pressure is influenced by the ratio of solute and the solvent particles. More are the solute particles more would be osmotic pressure.
- Temperature – The osmotic pressure of solution increases with increase in temperature

PLASMOLYSIS

- The shrinkage of protoplast from cell wall due to exosmosis caused by hypertonic solution is called plasmolysis.
- Permanent plasmolysis causes death plasmolysis has here stages –

(i) Limiting: Cell size becomes minimum but cytoplasm does not withdraw from cell wall.
(ii) Incipient: Cytoplasm withdraws from the edges.
(iii) Evident: Cytoplasm withdrawn from cell wall except from one or more points.

- Limiting plasmolysis is used for measuring osmotic potential of plant materials. The common materials used for demonstrating plasmolysis are spirogyra.

IMPORTANCE OF PLASMOLYSIS

- Plasmolysis is the characteristic feature of living plant cells. All living plant cells plasmolyse when kept in a hypertonic solution.
- Pickles, meat and fish are preserved by salting. Jams and jellies are persevered by sweetening of sugars. Salting and sweetening create hypertonic solution in which the fungi and bacteria get killed by plasmolysis.
- Salting kills the weeds of tennis lawn by inducing plasmolysis in their cells.
- Plants are not allowed to grow in the cracks of the walls by the method of salting.

DEPLASMOYSIS

- Swelling of shrunken protoplast so as to come in contact with cell wall due to endosmosis caused by hypotonic solution is known as deplasmolysis.
- It can occur only immediately after plasmolysis otherwise the cell protoplast becomes permanently damaged.
- Turgid – It is a condition of being fully distended due to exosmosis.

DIFFUSION PRESSURE DEFICIENT (DPD)

- The term diffusion pressure and diffusion pressure deficient were coined by B.S.Meyer in 1938.
- When solute particles are added to it, the diffusion pressure of the solution gets lowered. The amount by which diffusion pressure of solution is lower than that of its pure solvent is known as diffusion pressure deficit.

IMIBITION

- Imbibition is the phenomenon of adsorption of water or any other liquid by the solid particles of substance without forming a solution.
- Imbibition is plant cells refers to the adsorption of water by hydrophilic – protoplasmic and cell wall constituents.
- I f a dry piece of wood is placed in water; it swells and increases in volume. Similarly, if dry gum or pieces of agar-agar are placed in water, they swell and their volume increases. These are the examples in plant systems are adsorption of after by cell wall, swelling and rupture of seed coats during germination, etc.
- The solid particles which imbibe water or any other liquid are called imbibate.
- During imbibitions, the water molecules get tightly adsorbed and becomes immobilized. They lose most of their kinetic energy in the form of heat. It is called heat of wetting.
- The swelling imbibant also develops a pressure called imbibant pressure.

CONDITIONS NECESSARY FOR IMBIBITION

- A water potential gradient should occur between imbibant and liquid imbibed.
- There should be some force of attraction between imbibant and imbibed liquid for imbibitions to occur.
- Adsorption is the property of colloids and hence the materials which have high proportion of colloids, are good imbibants. It is for this reason, the wood (plant material) is good imbibants, because it contains proteins, cellulose and starch as colloidal substances.

FACTORS INFLUENCING IMBIBITION

- Looseness of imbibant shows more imbibitions while compactness less.
- Imbibition rises with rise in temperature.
- It decreases with rise in pressure.

- It also decreases with electrolytes.
- Imbibition either decreases or increases depending upon the charge of imbibant.

IMPORTANCE OF IMBIBITION

- Imbibition plays an important role in absorbing and retaining water.
- Absorption of water by young cell is mostly through imbibitions.
- Water is absorbed by the germinating seeds through imbibitions.
- Breaking of the seed in germinating seeds is due to greater imbibitional swelling of the seed kernel as compared to seed covering.
- A seedling is able to come out of soil due to development of imbibitions pressure.
- Jamming of wooden frames during rains is caused by swelling of wood due to imbibitions.
- It was used in breaking the rocks and stones.
- Fruits of many plants come in develop matric potential in addition to their osmotic potential in order to maintain inflow of water even under conditions of water scarcity.
- Imbibition is dominant in the initial stage of water absorption by roots.
- Since the imbibition is not dependent on metabolic activity of cell, it can occur under anaerobic conditions.
- The water moves into ovules which are ripening into seeds by the process of imbibitions.

ABSORPTION OF WATER

- Aerial parts of plants can absorb only a small quantity of water from atmosphere when it is saturated.
- Most of the water absorption occurs from soil through roots. For this, the roots must be metabolically active, respiring aerobically and continuously growing.
- Roots are usually restricted to that area of soil which lies well above the water table.
- Water table is the depth at which the earth’s crust is saturated with water.
- Usually water absorption occurs in plant through roots, but sometimes through shoots also.
- The zone of rapid absorption is characterized by the presence of root hairs. Root hairs help in absorption of water from soil by increasing the surface area

of root. Maximum absorption of water occurs through root hair zone. Some amount of water absorption occurs by zone of elongation but no absorption takes place at root cap and meristematic zone.

- A root hair is the unicellular tubular prolongation of the outer wall of the epiblema.
- It is generally delicate and short lived.
- The cell wall of root hair is composed of two distinct layers
- The outer layer, which is composed of pectic substances, helps to adhere soil particles. The inner layer is made up of cellulose.
- The cell wall is permeable both source and solvent molecules. It surrounds plasma membrane and a thin layer of cytoplasm.
- For long distance, plants have developed a mass or bulk flow system which operates through development of pressure difference between source and sink.
- In mass or bulk flow all the substances dissolved or suspended in solution travel at the same pace. Long distance bulk movement of substances that occurs through conducting or vascular tissues, xylem and phloem.
- Xylem translocation is mainly from roots to aerial parts. It passes water with mineral salts, some organic nitrogen and hormones.
- Phloem translocates organic substances and inorganic solutes first from leaves to all other parts of the plant and storage organs.
- Storage translocates organic nutrients to those parts which require the same as newly formed leaves and fruits.
- Translocation operates due to positive hydrostatic pressure gradient as in phloem or a negative hydrostatic pressure gradient as in xylem.
- Water absorption takes place by two methods – passive absorption and active absorption.

PASSIVE WATER ABSORPTION

- It is the common method of water absorption (96% of the total). The driving force for passive water absorption develops in the aerial parts through transpiration.
- Transpiration produces negative pressure or tension in xylem channels. The rate of water absorption closely follows the rate of transpiration. Root hair cells function as tiny osmotic systems as they have a, D.P.D of 3-8 bars while D.P.D of soil water is 0.1-0.3 bars. Root hair cells absorb water from soil which causes a decrease in their D.P.D as compared to adjacent cortical cells. As a

result cortical cells absorb water from root hair cells. They in turn lose water to inner cortical cells absorb water from root hair cells. They in turn lose water to inner cortical cells, the latter to endodermal pericycle and xylem parenchyma cells. Xylem channels have the maximum D.P.D or lower water potential Therefore, water passes into them. In this way water travels from soil to xylem along the gradient of D.P.D / suction pressure.

ACTIVE WATER ABSORPTION

- The force for this type of water absorption resides in the root. Active water absorption requires energy.
- The energy is used for

(i) Direct absorption and pumping activity of cells
(ii) Maintenance of bioelectric potential in the root cells.
(iii) Maintenance of high salt content in xylem channels.

- Active water absorption is manifested by root pressure. Root pressure is a positive pressure that is found in the sap contained in xylem channels of the root in certain plants and in certain seasons probably due to active water absorption. It shows a diurnal rhythm being maximum in early morning. Root pressure is exhibited by the exudation of sap if the stem is cur. Pressure can be measured by means of manometer.

FACTORS AFFECTING WATER ABSORPTION

- External or environmental factors.

(i) Available soil water: It is optimum at field capacity. Water absorption decreases above it. It begins to decline and stop of PWP.
(ii) DPD of soil water: Normal DPD of soil water is 0.1 – 0.3 atm. Above 1 atm, the rate of water absorption begins to decline. Near 4at,. Water absorption falls below requirement. Halophytes are exceptional.
(iii) Soil air: Oxygen content of soil air is generally less than that of atmosphere while carbon dioxide content is higher. Rate of water absorption begins to decline below 15% oxygen and 1% carbon dioxide.
(iv) Transpiration: It creates a force for passive absorption of water. When transpiration is very high, the rate of water absorption declines due to development of root-soil resistance and concentration of root.
(v) Soil temperature: optimum soil temperature for water absorption is 15-25^{O} C. A higher or lower temperature can reduce water absorption.

- Internal or plant factors

(i) Extent of root system: The amount of water absorption is directly dependent on the extensiveness of the root system, especially the number of rootlets and their root hairs.

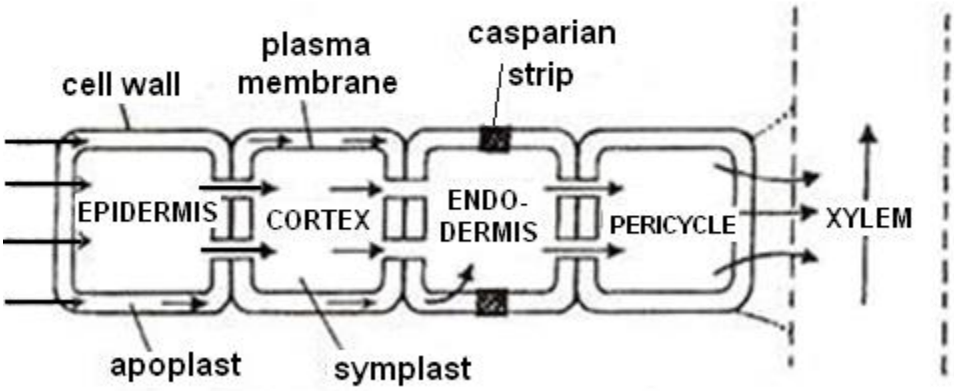
(ii) Growth and metabolism of root: Root hairs have a short life span. Continued water absorption depends upon growth of root branches and formation of new root hairs.

(iii) Depth of root system: Deeper roots are less efficient than the upper ones.

(iv) Resistance: Water absorbed by root hairs travels to root interior and from there it rises upwardly. The rate of this transfer is inversely related to degree of internal resistance.

PATHWAYS OF WATER MOVEMENTS IN ROOTS

- There are two pathways of water passage from root hairs to xylem inside the root, apoplast and symplast.
- In apoplast pathway water passes from root hairs to xylem through the walls of intervening cells without crossing any membrane or cytoplasm.
- It provides least resistance to movement of water.
- It is interrupted by the presence of impermeable lignosuberin casparin strips in the walls of endodermal cells.
- In symplast pathway water passes from cell to cell through their protoplasm facing plasmalemma (cell membrane) at least at one place. It is also called transmemebrane pathway.
- It does not enter cell vacuoles
- The cytoplasm of adjacent cells are connected through bridge call palsmodesmata.
- Symplastic movement is aided by cytoplasmic streaming of individual cells.
- It is, however, slower than apoplastic movements.
- In mycorrhizal association large number of fungal hyphae extend to sufficient distance into the soil and have a large surface area.
- These hyphae are specialized to absorb both water and minerals and provide them.



Pathways of water movement inside the root

ASCENT OF SAP (TRANSLOCATION OF WATER)

- The passage of absorbed water from root to the aerial parts of the plant is known as ascent of sap.
- It occurs the lumen of tracheary elements or vessels and tracheids with the rate of about 75cm/min
- Many theories have been put forward to explain the upward movement of water, the important ones are:
  - Root pressure theory
  - Transpiration pull or cohesion – tension theory.
  - Vital force theories.

ROOT PRESSURE THEORY

- Root pressure theory was proposed by Priestly (1916)
- Root pressure is defined as a pressure developing in the tracheary element of xylem due to metabolic activities of roots.
- The pressure is caused due to diffusion pressure gradient and is maintained by the activity of living cells.
- The root pressure is therefore, referred to as an active process, which is confirmed by the following:
  - The pressure is not observed if the roots are placed in hypertonic or isotonic solutions.
  - Oxygen supply and some poisons also effect the root pressure without affecting semi permeability of protoplasm.
  - Living roots are essential for it to occur.
- It is believed that root pressure is largely responsible for ascent of sap in herbaceous plants.

- The pressure develops more in certain seasons which favours optimum metabolic activity and reduce transpiration.
- The magnitude of root pressure is about 2 bars.

PHYSICAL FORCE THEORIES

- As sap can rise upwards even in the absence of living cells, physical phenomena were thought to operate in the ascent of sap. Example, capillarity, imbibitions.
- Capillary force theory: The theory was put forward by Bohm (1863). According to this theory, xylem channels functions as fine capillary tubes wherein water rises up automatically due to force of surface tension. Water is attracted to walls of the capillary tubes due to phenomenon of adhesion. As the water passes up the wall of capillary tube, the cohesive force existing amongst the water molecules causes pulling of water in the form of a thin column. Capillary rise will continue till the force of surface tension is counter-balanced by the downward pull of gravity.
- The force of capillary is small. It can raise water to a maximum height on one metre in a tube having a diameter of 30μm found in xylem vessels. Capillary cannot be useful in gymnosperms which are devoid of vessels. They possess tracheids which have closed ends.
- Atmospheric pressure theory: According to this theory, the ascent of sap is due to the atmospheric pressure. During active transpiration, a vacuum is created in the tissue. As a result, the water is forced below.
- According to Boehm's concept, upward movement of water is due to the joint force of capillarity and atmospheric pressure. However the atmospheric pressure theory was criticized as this pressure can raise water upto the height of about 30 feet. Hence it could not be operative in tall parts.
- Imbibition theory: This theory was proposed by Sachs (1878). According to this theory, the upward movement of water in stem is due to the force of imbibitions. This theory was rejected as large quantity of water moves through the lumen of xylem which can be checked by artificially blocking the lumen by gelatin or oil.
- Transpirational pull or cohesion-tension theory : This theory was originally proposed by Dixon and Jolly in 1894 and further improved by Dixon in 1914. This theory is based on the following features.
- Cohesive and adhesive properties of water molecules to form an unbroken continuous water column in the xylem.

- Transpirational pull or tension exerted by this water column
- Cohesion force: Water molecules are healed together by strong cohesion force which is due to hydrogen bonds amongst them. This is another force of adhesion which holds water to the walls of xylem vessels.
- Continuous water column: A continuous column of plat. The continuity of water column is maintained in the plants because of cohesive force of water molecules. Dixon described this water column in the stem as a net or rop. Water column is present in tracheary elements. These tracheary elements from this continuous system through their unthickened areas. Since, a large number, no breakage in the continuity of water occurs for the blockage of one or few of them.
- Transpiration pull: According to this theory, due to transpiration, the water column inside the plant occurs under tension. This is called 'transpiration pull'. On account of this tension, the water column is pulled up passively from below to the top of the plant. A tension of one atmosphere is sufficient to pull water to a height of about 10 metres.
- During transpiration in plants, water is lost in form of water vapour, from the mesophyll cells to exterior, through stomata.
- As a result the turgor pressure of these cells decreases and the diffusion pressure deficient increases. Now these cells take water from adjoining cells decreases. This process is repeated and ultimately water is absorbed from nearest xylem vessels of leaf. As there is a continuous water column inside the xylem elements, a tension or pull is transmitted down and finally transmitted to root, resulting in upward movement.
- So, this theory suggests that the transport of water takes place at low pressure and high tension. However, under this condition, the dissolved gases in xylem sap comes out of solution and they form bubbles due to low solubility. This phenomenon is known as 'cavitation'. It may occur during water stress. These bubbles definitely prevent the transport of water. As this condition, an alternative route for the transpiration stream would be needed. This theory was criticized due to the fact these bubbles may break up the water column. However, it is revealed that even in extreme dry conditions these air bubbles could not enter in water column and if they entered, they do not block the whole system.

VITAL THEORIES

- According to vital theories, upward movement of water takes place due to activity of living cells of plant bordering xylem.
- Godlewski's relay pup theory: According to Godlewski's (1984) ascent of sap takes place due to rhythmatic change in the osmotic pressure of rhythmatic change in the osmotic pressure of living cells of xylem parenchyma and medullar rays and are responsible for bringing about a pumping action of water in upward direction. Living cells absorb water due to osmosis from bordering vessels and finally water is pumped into xylem vessel due to lowering of pressure in living cells. Thus, a staircase type of pressure in living cells. Thus, a staircase type of movement occurs. Hanse (1887) supported the theory and showed that if flower part of the shoot is killed upper leaves were affected.
- Criticism: Theory was discarded due to following reasons:
- Strasburger (1893), Overton (1911) and MacDougal (1966) showed that transport of water was independent of living cells. They found that water continued to rise even after living cells were killed at high temperature and poison treatments.
- Xylem structure does not support the Godlewsk's theory. For pumping action living cells should be in between two xylem vessels and not on the lateral sides as found.
- Pulsation theory: Sir J.C.Bose (1923) said that living cells of inner most layer of cortex, just outside the endodermis were in rhythmatic pulsations. Such pulsations are responsible for pumping the water in upward direction. He inserted a fine needle into a stem of Desmodium. The needle was connected to galvanometer and an electric circuit. The fine needle touched the innermost layer of cortex oscillations turned violent indicating that cells in this layer were pulsating i.e. expanding and contracting alternately. According to Bose, the pulsatory cells pump the water into vessels.
- Criticism: However, this theory was criticized by several workers including Shull (1923) and Benedict (1927). The living cells do not seem to be involve in the ascent of sap because when a plant is placed in poisonous liquid, like picric acid, even then water continues to rise upward in plant.

TRANSPIRATION

- Loss of water in the vapour state from the aerial parts of plants is known as transpiration.
- Transpiration is similar to evaporation in the loss of water vapour but differs from the same in

(i) Formation of water vapour internally.
(ii) Being controlled by a number of plant factors
(iii) Occurrence of it even when the air is saturated.
(iv) Influence of light

- 98-99 % of water absorption by a plant is lost through transpiration. Over 90% of the transpiration occurs through leaves and is called foliar transpiration. A minor amount of transpiration occurs through barks of plants and is called bark transpiration.

CUTICULAR TRANSPIRATION

- It is the loss of water in the vapour from the general surface through the layer of cuticle. Cuticular transpiration is appreciable only in case the cuticle is thin as in mesophytic plants growing in humid areas. Commonly, it is 3-10% of the total. Cuticular transpiration continues through day and night.

STOMATAL TRANSPIRATION

- It is the loss of water in the vapour form stomata present on the surface of leaves and lesser extent on the surface of flowers and young stems. It is the major form of transpiration constituting 50-97% of total. It, however, occurs only when stomata are open.

LENTICULAR TRANSPIRATION

- This is lose of water in vapour form from lenticles or aerating pores present in the bark of stem. It is hardly 0.1% of the total.

STOMATA.

- They are minute pore complexes which occur on the soft aerial parts of the plants, especially the leaves. They hardly occupy 1-2% of leaf surface but due to perimeter diffusion, the exchange capacity of stomata is very high almost equal to whole surface area of the leaf.

- Number of stomata on a leaf is about 1,000 to 60,000 in per sq.cm. The size of stomatal pore (fully open) measures about 3-12μm in length.
- Each stomata is surrounded by two small specialized green epidermal cells called guard cells. Guard cells are small in size, therefore, rapidly influenced by turgor changes. They are kidney-shaped in outline and joined at their ends.
- Guard cells contain chloroplasts while the same are generally absent from other epidermal cells. In some plants the guard cells are surrounded by a group of specialized epidermal cells known as accessory or subsidiary cells. In Poaceace, members of Cyperaceae and many palms the guard cells are dum-bell shaped with thin end walls and thick middle parts. In other guard cells are reniform or kidney shaped. Their outer wall are thinner and more elastic while the inner walls are thick and less elastic. They grow out into one or two pair of ledges to protect stoma from water drops. Guard cells are connected with other epidermal cells through plasmodesmata.

TYPES OF STOMATA

There are four categories of stomata.

(i) Barley or cereal type : The guard cells are dum-bell shaped. Stomata are found equally on both surfaces (amphistomatic leaf). They usually remain open during the day for a few hours e.g. maize, wheat and other cereals
(ii) Leucerne or alfalfa type: They open during day and close during night under mesophytic conditions. E.g. pea, apple, radish, grapes, turnip, mustard
(iii) Potato type : Stomata are present on both the surface, more on lower surface than on upper surface. Under mesophytic conditions, the stomata can remain open throughout the day and night, but close down for different periods and at various time for different periods and at various time under conditions of less water availability e.g cucurbits, portulaca, tulip, onion, banana, potato.
(iv) Equisetum type: The stomata remains open and seldom close. E.g. amphibious plants or emergent hydrophytes.

GUARD CELL PHOTOSYNTHESIS THEORY

- This theory was proposed by von mohe (1856). During day time, photosynthesis occurs in guard cells because they contain chloroplast. The soluble sugar formed by this process decreases the water potential of the guard cells and hence resulting in stomatal opening. However, very small amount of soluble sugar has been extracted from the guard cells which are insufficient to affect the water potential.

- During day time at lo CO_2 concentration, pH of guard cells rises. Some organic acid chiefly the malic aid is build up during this period in guard cells. The formation of malic acid would produce proton that could operate in an ATP-driven-proton-K^+ exchange pump, moving protons into the adjacent epidermal cells and K^+ ions into the guard cells. This helps in decreasing water potential of the guard cells and results into the opening of stomata. The reverse process would occur in dark and would lead to closing of stomata.

STARCH HYDROLYSIS THEORY (CLASSICAL THEORY) [Sayre, 1923]

- Guard cells contain starch which is hydrolysed to form glucose under high pH and reduced carbon dioxide concentration. Glucose increases osmotic concentration and hence D.P.D. of guard cells.
- Guard cells absorb water from epidermal cell, swell up and create pore. Closing of stomata is caused by polymerization of glucose to form starch and reduction of osmotic concentration of guard cells. The guard cells lose water to epidermal cells, contract and close the pore.
- Objections:
  (i) Glucose does not occur in detectable quantity in the guard cells of open stomata.
  (ii) Starch and sugar inter-conversion is too slow to account for rapid stomatal opening and closing.

MALATE OR K^+ ION PUMP HYPOTHESIS (MODERN THEORY) [Levitt, 1974]

- Rise in pH of guard cells causes hydrolysis of starch to form phosphoenol pyruvate. The latter combines with carbon dioxide with the help of PEP case (Phosphoenol pyruvate carboxylae) forms oxalic acid which gets changed into malic acid.
- H^+ ions pass out of the guard cells actively while K^+ ions of epidermal cells pass into guard cells. K^+ combines with malate and passes into small vacuoles. Cl^- ions also absorbed from outside to maintain electro-neutrality. The ions exert an osmotic potential. It results in absorption of water from adjacent cells. Development of turgor and hence opening of stomata. Cytokinins and cyclic AMP are required. During closure movement, K^+ ions are pumped out of guard cells and malate is changed back to starch. It reduces osmotic concentration of guard cells. Water is lost. Turgidity of guard cell decreases and pore is closed. Abscisic acid or ABA promotes closure.

- Evidences
  (i) Guard cells of the opened stomata posses abundant K^+ ions
  (ii) At the time of stomatal opening starch is changed to organic acids.

FACTORS AFFECTING STOMATAL OPENING

1. Light: Most stomata open in light and close in darkness. Light intensity required for stomatal opening is quite low. Even moonlight is sufficient in some cases. Both blue and red light stimulate stomatal opening though blue light is slightly more effective.
   Succulents and some other plants are exceptions to this. Here stomata remains closed during day time. They open only during dark e.g. Agave, opuntia, pineapple.
2. Carbondixoide : Low carbon dioxide concentration induces stomatal opening while high carbon dioxide causes stomatal closure.
3. Oxygen : It is essential for stomatal opening.
4. Humidity: In dry weather, stomata tend to close while in humid environment they remain open for longer period.
5. Plant Hydration: Water deficit in plants causes stomatal closure due to formation of ABA and lowering of water potential in epidermal cells.
6. Hormones: Abscisic acid brings about closure of stomata. It is produced during water stress. Cytokinins are required for keeping stomata open.
7. pH: Acidic pH induces stomatal closure while rise in pH causes stomatal opening.
8. Mechanical shock: It causes stomatal closure.
9. Temperature: Rise in temperature induces stomatal opening while fall in temperature causes closure. At 38^o-40^o C stomata open even in darkness.
10. Potassium : Opening of stomata is due to influx of K^+ while closure depends upon efflux of K^+ from guard cells.

FACTORS AFFECTING TRANSPIRATION

- EXTERNAL FACTORS

i) When relative humidity is high, the rate of transpiration decreases, because the atmosphere is more saturated with moisture. It retards the diffusion of water vapour from the intercellular spaces of the leaves to the outer atmosphere through the stomata.

ii) Transpiration increases with the increase in temperature. High temperature opens stomata even in dark

iii) Light increases with the rate of transpiration because in light, stomata open.
iv) Transpiration is less in still wind because water vapour accumulates around the transpiring organs and reduce the DPD of air. Rate of transpiration increases with the wind velocity.
v) A decrease in amount of available soil water, reduces absorption causing reduction in the rate of transpiration.

- Internal factors

i) The more of leaf surface area, the more is the rate of transpiration.
ii) An increase in root/shoot ratio causes an increase in the rate of transpiration.
iii) Mucilage and solutes decrease the rate of transpiration by holding water tenaciously.
iv) Structural features
(a) Sunken stomata: Help in reducing the rate of stomatal transpiration. The rate of transpiration is further decreased, if they are situated in grooves and sometimes protected by hairs.
(b) Thick cuticle: The thinner the cuticle, the greater is the rate of cuticalar transpiration. Therefore, in xerophytes, thick cuticle is developed by plants. The presence of wax coating exposed parts also reduces cuticalar transpiration.
(c) Leaf modification: Leaf spines, scale leaves, phyllode, phylloclade, prickles are all modifications of leaf and help in reducing transpiration.
(d) Mesophyll: Compact mesophyll cells reduce transpiration, because of fewer intercellular space. Loose mesophyll increases transpiration because of larger intercellular spaces.

MEASUREMENT OF TRANSPIRATION

1. Potometer: It is an instrument for measurement of the rate of transpiration by shoots through measuring the rate of their water absorption.
2. Prometer: An instrument that gives a rough idea about the degree of stomatal opening.
3. Cobalt chloride paper test: Dry cobalt chloride is blue while the moist one is pink. A filter paper slip can be dipped in 3-5% cobalt chloride and dried. It appears blue. The slip is placed over leaf surface and protected from atmospheric humidity by a glass slide or transparent tap. Change in colour of the filter paper slip from blue to pink indicates transpiration.

ADVANTAGES OF TRANSPIRATION

1. It plays an important role in the upward movement of water, i.e. ascent of sap
2. It helps in absorption and translocation of minerals salts.
3. Rapid evaporation of water from the aerial parts of the plant through transpiration brings down their temperature. Thus, it prevents them from excessive heating. This is also known as cooling effect.

ANTITRANSPIRANTS

- They are substances that are employed for reducing the rate of transpiration. It is done by –
  (i) Chemical which reduces the degree of stomatal opening. E.g PMA (Phenyl mercuric acetate). Salicylic acid and ABS (abscisic acid).
  (ii) Formation of ultra –thin surface film of silicon emulsion over leaf surface. It is more permeable to gases than water vapour.
- Importance
  Benefits of transpiration includes cooling of surface area, increased development of mechanical tissues, better development of fruits, increased absorption of salts etc. Its drawbacks include reduced growth, reduced yield, modification and wilting. However, transpiration cannot be checked completely because it will occur to a smaller or larger degree. Whenever stomata open for gaseous exchange. Therefore, it is regarded as necessary evil.

GUTTATION (Bregerstein, 1887)

- Loss of water in the liquid state from uninjured parts of plants is known as guttation. It is usually occurs from the tips and margin of leaves during night or early morning when there is high atmospheric humidity as during wet seasons. Guttation occurs in some plants only (345 genera) e.g. Cucurbita. Potato, tomato and many grasses.
- In the regions of guttation, the leaves posses special pores called hydathodes. Hydathods or water pores are permanently open pores as their guard cells are immobile. Internally a hydathode leads to a loose parenchymatous tissue called epithem. A vein ends below. Root pressure usually causes the flow of sap from the vein to epithem and then hydathode. Guttated water contains minute quantities of both inorganic and organic substances.