Plant physiology

Unit I:

PLANT-SOIL RELATIONSHIP

1.1 Component of soil

All parts of soil are essential to plant for growth and development as well as to survive. The main components of soil are minerals, water, air and organic material. Another important component of soil, which isn't always recognized, is the living world that exists under the ground *i.e.* the biological component.

(a) Minerals: All soil is composed of sand, silt and clay. The minerals found in soil come from non-living, inorganic materials. Sand comes from small fragments of quartz and other minerals and water can easily pass through it. Silt is a combination of quartz and other rocks. Silt particles are smaller than sand. Clay is the richest of soil minerals, containing nutrients like iron, potassium and calcium. The smallest soil particles come from clay.

(b) Water: Plants cannot survive without water. Water in soil usually contains dissolved salts and other chemicals. Water retaining capacity varies with the variation of soil types, like clay retains water much better than others.

(c) Air: Air is a combination of gaseous elements that are found naturally in Earth's atmosphere, which supports the underground living organism to survive. In soil, air pockets allow water to pass through the soil and help the plants to grow above and below the soil line.

(d) Organic or Biological Materials: Through decomposition of the dead and decaying plants and animal parts, organic materials are broken down and turned into nutrients for the plants.

1.2. Classification of soil

Based on the proportion of clay present, the soil may be classified as follows-

(a) **Sandy soil:** This fraction of soil contains almost 10% of each of clay and silt with a large proportion of sand particles. Due to larger size, empty spaces remain in between sand particles and through these empty spaces, air and water can easily pass and can retain only 25-30 parts of water by weight. Sandy soil is not suitable for the growth of the plant.

(b) **Silt soil**: It consists of medium textured soil particles of size intermediate in between sanand clay. It is like flour in dry condition whereas like plastic in wet condition, it is. It contains enough quantity of nutrients with greater water holding capacity, hence it is fertile.

(c) **Clay soil**: It contains 40% or more of clay. Clay particles are mainly made up of oxides of aluminium with some important minerals like K, Ca and Mg. It has highest water holding capacity and stores considerable amount of nutrients for plants.

(d) **Loam**: Such soil contains 30-50% of silt, 5-25% clay and rest being sand. It can retain 50 parts of water by weight. This soil is sufficiently aerated and has good water holding capacity which enhance the luxurious growth of plants.

PLANT-WATER RELATIONSHIP

1.3 Types of water in soil

Rain is the principle source of soil water. The amount of water present or stored in the soil varies greatly in different soil types and under different conditions. Following are the five categories of such types of water in relation to soil.

(a) **Run-away water:** After a heavy rainfall some amount of water drains away along the slopes which is called run-away or run-off water. Plant cannot use such type of water.

(b) **Gravitational water:** When the upper soil layer becomes highly saturated with rain water, the remaining water percolates downwards through the pores present within the soil particles under the influence of gravity until it reaches the water table. This is called gravitational water and it is unusable for the plants.

(c) **Capillary water:** On the way to the downward movement of water, a portion of water retains in the spaces among the soil particles due to surface tension. This water is known as capillary water and it is the main source of available water for plants that can be easily absorbed by the roots.

(d) **Hygroscopic water:** Some amount of water is present as thin film around the soil particles which is not evaporated even in strong sunlight. This is called the hygroscopic water which is not available for the plants.

(e) **Chemically combined water:** A small amount of water in the soil is bound to the molecules of some soil minerals by strong chemical bonds is known as chemically combined water. This water is practically unavailable to the plants.

1.4. Water Potential

Water potential is the potential energy of water in a system compared to pure water at the same temperature and pressure. It can also be described as a measure of how freely water molecules can move in a particular environment or system. The chemical potential of water is referred to as water potential and it is measured in kilopascals (kPa) and is represented by the Greek letter Psi (ψ) or more accurately ψ_w. The maximum value of water potential is zero, which is that of pure water at atmospheric pressure. In solutions the value of water is always negative. Water always moves from the area of high water potential to the area of low water potential *i.e.* from less negative potential to more negative potential. Water potential can be calculated as $\psi_w = \psi_s + \psi_p$, where ψ_s is the solute potential which is negative and ψ_p is pressure potential which is positive or zero.

1.5. Osmotic potential

The osmotic potential is also known as solute potential. The decrease in water potential brought about by dissolved substances in solution is referred to as solute potential or the potential with which pure water will diffuse towards a solution is osmotic potential ($\psi\pi$) of that solution. As water potential of pure water is zero and it has to move according to the concentration gradient, the osmotic potential of a solution is less than zero or it is negative. With the increase in the concentration of solute in a solution, lower is its osmotic potential. Thus, for a solution at atmospheric pressure osmotic potential is equal to water potential. Its value is calculated by using the formula OP or SP = C x R x T, where C is the concentration of solute particles in moles per litre, R is gas constant with a value of 0.083 and T is the absolute temperature.

1.6. Pressure potential

In a closed osmotic system like in plant cell, a pressure called turgor pressure, is imposed on water which increases the water potential. The potential created by such pressure is called pressure potential and is represented by ψ_p. The value of this pressure is always towards positive started from zero.

Plasmolysis and deplasmolysis

MOVEMENT OF WATER WITHIN THE PLANT BODY

1.7. Water absorption

The water is essential for plant to survive as well as for various metabolic activities. Terrestrial plants get their water from soil that takes place mostly through the roots with the help of root hairs those can enter to the capillary micropores. Some important factors like diffusion, imbibition, suction pressure and osmosis, are related with this absorption. Once water is absorbed by root hairs it can enters to the xylem inside the roots by two pathways- Apoplast and Symplast.

(a) Apoplast pathway- Here water passes from root hairs to xylem of roots through the wall of intervening cells without crossing any membrane or cytoplasm. The movement of water is fast in this pathway due to least resistance in cell wall except in impermeable casparian strips.

(b) Symplast pathway- Here water passes from cell to cell through the protoplasm and plasmodesmata, that's why it is also called transmembrane pathway. Cytoplasmic movement helps in symplastic movement and it comparatively slower than apoplastic movement.

1.7.1. Mechanism of water absorption

Mechanism of water absorption is of two types: 1. Active absorption and 2. Passive absorption

1. **Active absorption** : Active absorption refers to the absorption of water by roots with the help of metabolic energy generated by respiration. Two theories have been put forwarded to explain the mechanism of active absorption-
   - **(a) Osmotic theory**- This theory was proposed by Atkins (1916) and Priestley (1922). According to them water moves from dilute soil solution to concentrated xylem sap by the process of osmosis through various tissues of roots and it causes the development of root pressure. But there are certain objections regarding the movement of water from the cortical cells to xylem cells as xylem contains less concentrated sap than cortical cells. Due to the absence of semipermeable membrane in tracheids water cannot enter into it unless some other mechanism exists. Although starting of this process does not require energy but to maintain the flow of solute in these cells must require some energy.
   - **(b) Non-osmotic theory**- According to Thimann (1951) and Kramer (1959) non-osmotic absorption of water occurs even the osmotic pressure of soil water is higher than that of cell sap. The energy required for this absorption may be supplied by the metabolic energy evolved during respiration. The supporting evidences of this theory are- (i) the factors which inhibit respiration also decrease water absorption, (ii) the treatments of roots with metabolic inhibitors reduce the rate of absorption and (iii) auxins which increase metabolic activities of cells stimulate absorption of water.

2. **Passive absorption:** Passive absorption of water takes place when rate of transpiration is high. Rapid evaporation of water from the leaves during evaporation creates a tension of water in the xylem of the leaves which is transmitted to water in xylem of roots and the water rises upward to reach the transpiring surfaces. As a result, soil water enters to the xylem of the roots through cortical cells of root hairs to maintain the constant supply of water. The force for this entry of water is created in leaves due to rapid transpiration and hence it may be called as passive absorption.

Lachenmeir (1932) and Kramers (1937) forwarded some evidences in favour of passive absorption and these are- (i) the rate of absorption is almost equal to the rate of transpiration, (ii) it satisfies critically the movement of water against osmotic gradients, (iii) in some plants the cut ends of stem are capable of absorbing water, (iv) it is purely a physical process and (v) the movement of water across cells is faster than simple osmotic diffusion whereby excess demand of water can be maintained during fast transpiration.

Passive absorption is more common means of water absorption as compared to active absorption.

1.8. TRANSPIRATION

Transpiration is the removal of excess water in the form of water vapour from the internal tissues of aerial parts of plants such as leaves, stems and flowers under the influence of sunlight. When transpiration occurs through surface of leaves is known as **foliar transpiration**. The transpiration is called **cauline transpiration** when it occurs from stems. Generally, transpiration is of following three types-

(i) Stomatal transpiration: Stomatal transpiration takes place through the epidermal pore of leaves and young stems known as stomata. More than 90% of total plant transpiration occurs through stomata during day time.

(ii) Cuticular transpiration: Though cuticle is an impervious layer to water, a maximum of about 10% of total transpiration takes place through this layer generally present in leaves and herbaceous stems.

(iii) Lenticular transpiration: Very little amount may be lost by woody stems through lenticels which is called as lenticular transpiration.

1.8.1. Significance of transpiration: Plant utilize a huge amount of energy in water absorption, but maximum of this energy is wasted through transpiration. According to some people transpiration is advantageous whereas other regard it as an unavoidable but harmful process.

Advantages-

(a) Ascent of sap mostly occurs due to transpiration pull exerted by transpiration of water and indirectly helps in absorption of water.

(b) Transpiration remove the excess amount of water which is not of use for the plants.

(c) During day time the temperature of plants increases and by evaporating water transpiration reduces this temperature by 10^0-15^0C.

(d) The development of mechanical tissue is favoured by the increase in transpiration.

(e) The distribution of mineral salts throughout the plant body may be facilitated by transpiration through translocation of water in the xylem elements.

(f) The loss of excess water through transpiration increase the concentration of mineral salts in the plants.

(g) Transpiration helps in better development of root system, requires for support and absorption of mineral salts.

(h) The fruits quality is enhanced with the increase in transpiration.

(i) Excessive transpiration induces hardening and resistance to moderate drought.

(j) Transpiration maintains the shape and structure of plant parts by keeping cell turgod.

(k) Transpiration is responsible for pulling of water into the mesophyll cells of leaves from the xylem thereby help in providing continuous supply of water for photosynthesis.

Disadvantages-

(i) Wilting is quite common when the rate of transpiration is higher than the water absorption which may lead to the death of the plants.

(ii) High rate of transpiration creates water deficit inside the plants which may gives stunted appearance.

(iii) According to Tumarov (1925), a single wilting reduces the formation flowers, frits and seeds by 50%.

(iv) Water stress created by excessive transpiration produces abscisic acid that promotes the abscission of leaves, flowers and fruits.

(v) The energy used in absorption and conduction of water is wasted when more than 90% of absorbed water is lost through transpiration.

(vi) Many xerophytes have to develop structural modifications and adaptation to check transpiration.

(vii) During autumn the deciduous trees shed their leaves to check the loss of water by stomal transpiration.

But in spite of having various disadvantages transpiration cannot be checked till the stomata open for gaseous exchange for photosynthesis and respiration. Similarly, cuticular and lenticular types of transpiration cannot be avoided as there is no such methods for their control. Therefore, many scientists like Curtis (1926) have regarded transpiration as necessary evil.

1.8.2. Factors affecting transpiration:

The factors affecting may be external and internal. The external factors related with the environmental whereas the internal factors related with the physiological structure of the plant.

External factors-

(i) Humidity of the air- In an environment saturated with water vapour the rate of transpiration from the leaves is negligible. Whereas the rate increases in drier atmosphere. The lower the relative humidity of the air the more rapid is the transpiration and *vice versa*.

(ii) Temperature- A high temperature lowers the relative humidity of the air whereby increases the rate of transpiration and low temperature decreases the transpiration rate by increasing the humidity on the surrounding atmosphere.

(iii) Light- The rate of transpiration increases in light and decreases in dark. Light affects transpiration in two ways- by raising temperature of the leaves and by opening the stomata.

(iv) Wind- Dry winds lower the amount of air moisture and support transpiration.

(v) Atmospheric pressure- Low atmospheric pressure enhances evaporation, produces air currents and increases the rate of transpiration.

(vi) Availability of soil water- The rate of transpiration can be maintained if the plant can absorbed enough water that is available in the soil.

Internal factors-

(i) Leaf area- The transpiration is more in plants with large leaf than in plants with small leaves.

(ii) Structural features- The number, size and position of the stomata affect the rate of transpiration. Sunken stomata help in reducing the rate of transpiration.

In xerophytic plants the leaves are reduced in size and number to check the foliar transpiration. Formation of prickles, leaf spines, scaly leaves, phyllodes, phylloclades are some other modifications found in xerophytes to reduce the rate of transpiration.

Thick cuticle and waxy coating on exposed parts of plants reduces cuticular transpiration.

Leaves with compact mesophyll, the transpiration is less as compared to that with loose mesophyll.

(iii) Root and shoot ratio- A low root/shoot ratio decreases the transpiration rate while a high ratio increases the transpiration.

(iv) Mucilage and solutes- Presence of mucilage and solutes present in the plants are responsible for decreasing the rate of transpiration.

1.8.3. Mechanism of transpiration:

The mechanism of stomatal transpiration that takes place during the day time can be studied in three steps.

(i) Osmotic diffusion of water in the leaf from xylem to intercellular space below the stomata through the mesophyll cells- When mesophyll cells draw water from the xylem they become turgid and their diffusion pressure deficit (DPD) and osmotic pressure (OP) decreases and as a result, they release water to intercellular spaces close to stomata by osmotic diffusion. Now in turn, the O.P and D.P.D of mesophyll cells become higher and hence, they draw water from xylem by osmotic diffusion.

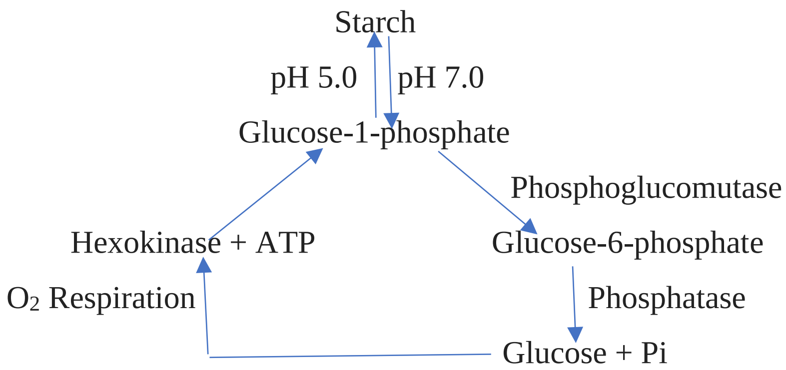
(ii) Opening and closing of stomata- Each stomata is surrounded by two guard cells which contain chloroplasts and have peculiar thickening on their adjacent surface. Consequently, an increase in the osmotic pressure (OP) and diffusion pressure deficit (DPD) of the guard cells due to accumulation of osmotically active substances, osmotic diffusion of water takes place to guard cells from surrounding epidermal cells and mesophyll cells. This increases the turgor pressure (TP) of the guard cells and become turgid. The outer thin walls are stretched out while the inner thick walls, being inelastic, are pulled apart and become concave. This increases the gap between guard cells and stomata becomes open. On the other hand, when OP and DPD of guard cells decrease, water is come out from the guard cells and become flaccid.

There may be several other theories regarding the mechanisms which create osmotic potential in the guard cells and control stomatal movements are explained as follows:

(a) Starch-sugar interconversion theory- According to this theory during day time, pH in guard cells increases which favours hydrolysis of starch into glucose -1- phosphate so that osmotic potential become lower in guard cells. Consequently, water enters, into the guard cells by osmotic diffusion from the surrounding epidermal and mesophyll cells. Guard cells become turgid and the stomata open. During dark, reverse process occurs. Glucose 1- phosphate is converted back into starch in the guard cells thereby increasing the osmotic potential. The guard cell release water become flaccid and stomata become closed.

$$\underset{\text{(Insoluble)}}{\text{Starch + Pi}} \underset{\text{Dark/ low pH}}{\overset{\text{Light/ high pH}}{=\!=\!=\!=\!=\!=\!=\!=\!=\!=\!=\!=}} \underset{\text{(Soluble)}}{\text{Glucose-1-phosphat}}$$

According to Steward (1964), the conversion of starch and inorganic phosphate into glucose-1-phosphate does not cause any appreciable change in the osmotic pressure because the inorganic phosphate and glucose-1-phosphate are equally active. He suggested that, Glucose-1-phosphate should be further converted into glucose and inorganic phosphate for the opening of stomata. Metabolic energy in the form of ATP would be required for the closing of stomata which probably comes through respiration.



However, this theory does not find much support from the recent workers.

(b) Synthesis of sugars or organic acids in Guard cells- During day light photosynthesis occurs in guard cells as they contain chloroplast. The soluble sugars formed in this process may contribute in increasing the osmotic potential of guard cells and hence resulting in stomatal opening. However, very small amounts of soluble sugars (osmotically active) have been extracted from the guard cells which are insufficient to affect water potential. As a result of photosynthesis CO_2 concentration in guard cells decreases which leads to increased pH, which may lead to build up of some organic acids, chiefly malic acid during this period in guard cells. The formation of malic acid would produce protons that could operate in an ATP-driven proton K^+ exchange pump moving protons into the adjacent epidermal cells and K^+ ions into guard cells and thus may contribute in increasing the osmotic pressure of the guard cells and leading to stomatal opening. Reverse process would occur in dark.

(c) ATP –Driven proton (H^+) – K^+ exchange pump mechanism in Guard cells- According to this mechanism, there is accumulation of K^+ ions in the guard cells during day light period. The protons (H^+) are 'pumped out' from the guard cells into the adjacent epidermal cells and in exchange K+ ions are mediated through ATP and thus are an active process. ATP is generated in non-cyclic photophosphorylation in photosynthesis in the guard cells. The ATP required in ion exchange process may also come through respiration. The accumulation of K ion is enough to significantly decrease the water potential of guard cells during day light. Consequently, water enters into them from the adjacent epidermal and mesophyll cells thereby increasing their turgor pressure and opening the stomatal pore. Reverse situation prevails during dark when stomata are closed. There is no accumulation of 'K' in g cells in dark.

(iii) **Simple diffusion of water vapours from intercellular spaces to outer atmosphere through stomata**- Simple diffusion of water vapour through stomata takes place because the intercellular spaces become more saturated with moisture as compared to outer atmosphere.

Ascent of sap:

Path of ascent of sap: Xylem is a complex tissue consisting of living and non-living cells. The conducting cells in xylem are typically non-living and include vessels members and tracheids. Both of these cell types have thick, lignified secondary cell walls and are dead at maturity. The path of ascent of sap can be shown by the following experiments.

(i) A leafy twig of Balsam plant is cut under water and placed in a beaker containing water with some eosine (a dye) dissolved in it. After some time coloured lines will be seen moving upward in the stem. If sections of stem are cut at this time, only the xylem elements will appear to be filled with coloured water.

(ii) Ringing Experiment: A leafy twig from a tree is cut under water and placed in a beaker filled with water. A ring of bark (all the tissues outer to vascular cambium) is removed from the stem. After sometime it is observed that the leaves above the ringed part of the stem remain fresh and green (Fig. 6.1). It is because water is being continuously supplied to the upper part of the twig through xylem.

B) Mechanism of Ascent of Sap:

In small trees and herbaceous plants the ascent of sap can be explained easily, but in tall trees like Australian Eucalyptus, some conifers such as mighty Sequoias where the water has to rise up to the height of several hundred feet, the ascent of sap, in fact, becomes a problem. Although the mechanism of ascent of sap is not well understood, several theories have been put forward to explain it.

(A) Vital Theories: Supporters of vital theories think that the ascent of sap is under the control of vital activities in the stem. Two such theories are: (1) According to Godlewski (1884) ascent of sap takes place due to the pumping activity of the cells of xylem parenchyma which are living. The cells of the medullary rays which are also living, in some way change their O.P. When their O.P. becomes high they draw water from the lower vessel and their O.P. becomes low. Now due to the low O.P., water from the cells of xylem parenchyma is pumped into the above vessel. This process is repeated again and again, and water rises upward in the xylem.This theory seemed only hypothetical and was further discarded by the experiments of Strasburger. (1891, 1893) who demonstrated that ascent of sap continues even in the stems in which living cells have been killed by the uptake of poisons. (2) According to Bose (1923) upward translocation of water takes plate due to the pulsatory activity of living cells of inner most cortical layer just outside the endodermis. This theory was also rejected because many workers could not repeat his experiment and many others found no correlation between pulsatory activity and the ascent of sap.

(B) Root Pressure Theory: Although, root pressure which is developed in the xylem of the roots can raise water to a certain height but it does not seem to be an effective force in ascent of sap due to the following reasons:

(i) Magnitude of root pressure is very low (about 2 atms).

(ii) Even in the absence of root pressure, absent of sap continues. For example, when a leafy twig is cut under water and placed in a beaker full of water it remains fresh and green for sufficient long time.

(iii) In gymnosperms root pressure has rarely been observed.

(C) Physical Force Theories: Various physical forces may be involved in the ascent of sap:

(1) Atmospheric Pressure: This does not seem to be convincing because:(i) It cannot act on water present in xylem in roots, (ii) In case it is working, then also it will not be able to raise water beyond 34′.

(2) Imbibition: Sachs (1878) supported the view that ascent of sap could take place by imbibition through the walls of xylem. Now it is well known that imbibitional force is insignificant in the ascent of sap because it takes place through the lumen of xylem elements and not through walls.

(3) Capillary Force: In plants the xylem vessels are placed one above the other forming a sort of continuous channel which can be compared with long capillary tubes and it was thought that as water rises in capillary tube due to capillary force, in the same manner ascent of sap takes place in xylem. There are many objections to this theory: (i) For capillarity a free surface is required. (ii) The magnitude of capillary force is low. (iii) In spring when there is more requirement of water due to the development of new leaves, the wood consists of broader elements. While in autumn, when water supply decreases, the wood consists of narrow elements. This is against capillarity. (iv) In Gymnosperms usually the vessels are absent. Other xylem elements do not form continuous channels.

(D) Transpiration Pull and Cohesion of Water Theory: This theory was originally proposed by Dixon and Jolly (1894) and greatly supported and elaborated by Dixon (1914, 1924). This theory is very convincing and has now been widely supported by many workers. It is based on the following features:

(i) Cohesive and Adhesive properties of water molecules to form a continuous water column in the xylem. (ii) Transpiration pull exerted on this water column. Water molecules remain joined to each other due to the presence of H-bonds between them. Although H-bond is very weak but when they are present in enormous numbers as in case of water, a very strong mutual force of attraction or cohesive force develops between water molecules and hence they remain in the form of a continuous water column in the xylem which cannot be broken easily due to the force of gravity or other obstructions offered by the internal tissues in the upward movement of water. The adhesive properties of water i.e. the attraction between the water molecules and the xylem walls further ensure the continuity of water column in xylem. When transpiration takes place in leaves at the upper parts of the plant, more water is released into the intercellular spaces from the mesophyll cells. In turn, the mesophyll cells draw water from the xylem of the leaf. Due to all this, a tension is created in water in the xylem elements of the leaves. This tension is transmitted downward to water in xylem elements of the roots through the xylem of petiole and stem and the water is pulled upward in the form of continuous unbroken water column to reach the transpiring surfaces—up to the top of the plants. According to some workers object as certain air bubbles present in the conducting channels, will break the continuity of the water column. This has been defended by others who say that there are no air bubbles and if present, they will not able to break the water column which will remain continuous through other elements of the xylem.