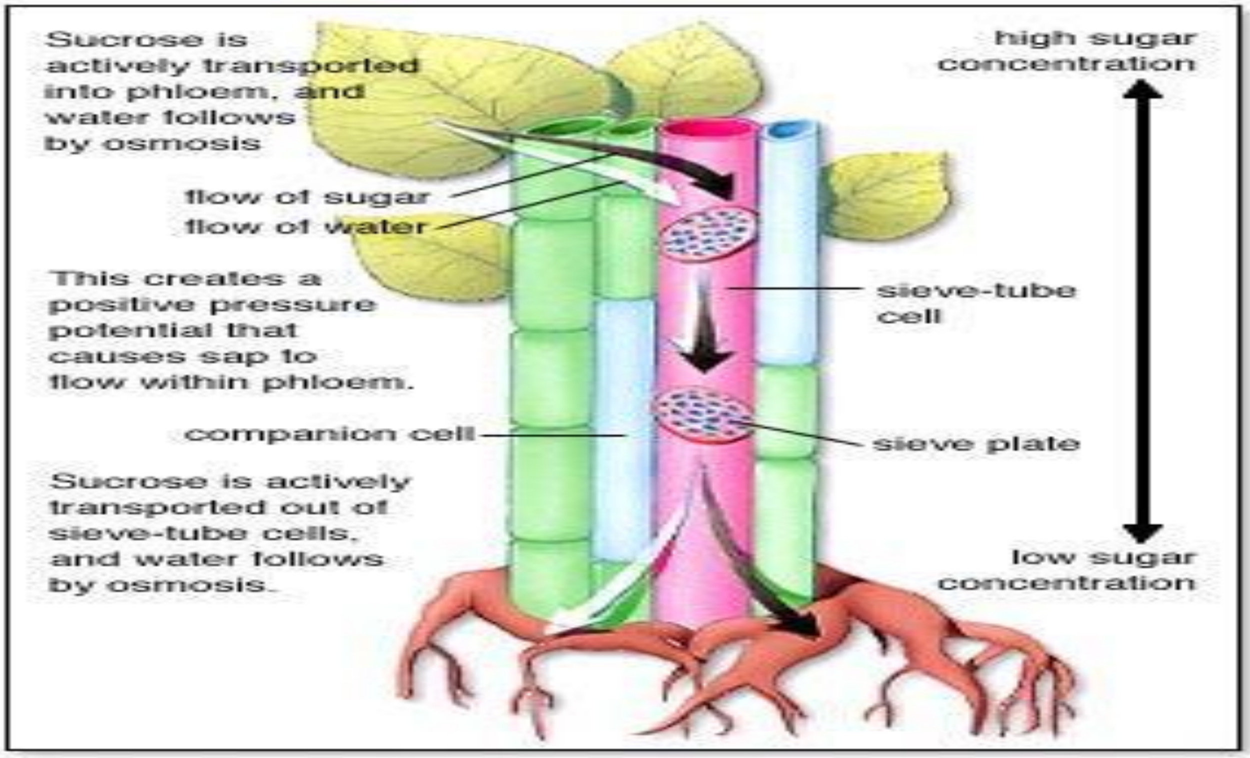
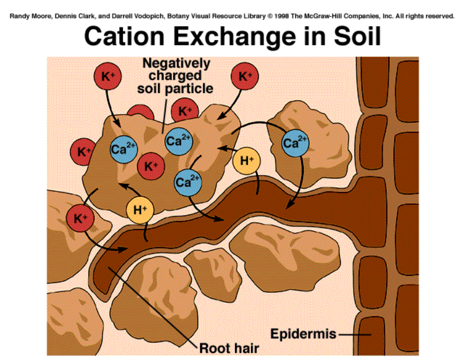
Introductory Crop Physiology





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3. Introductory Crop Physiology (HBP 100) 2(1+1)

Water Relations in Plants: Role of water in plant metabolism, osmosis inhibition, diffusion, water potential and its components, measurement of water potential in plants, absorption of water, mechanism of absorption and ascent of sap. Stomata: Structure, distribution, classification, mechanism of opening and closing of stomata. Osmotic pressure, guttation, stem bleeding; transpiration methods and mechanism and factors affecting transpiration. Drought: Different types of stresses; water, heat and cold tolerance; mechanism of tolerance. Plant Nutrition: Essentiality, mechanism of absorption and its role in plant metabolism. Photosynthesis, structure and function of chloroplast, dark and light reactions, cyclic and non-cyclic electron transfer, CO_2 fixation – C3, C4 and CA metabolism, advantages of C4 pathway. Photorespiration and its implications, factors affecting photosynthesis. Phytohormones, physiological role in controlling plant processes. Environmental stimuli for plant development.

__Practical__: Measurement of water potential, osmosis, root pressure, structure of the stomata, distribution, opening and closing of the stomata, measurement, transpiration and calculation of transpirational pull demonstration. Importance of light and chlorophyll in photosynthesis, pigment identification in horticultural crops and studying the enzyme activity of catalase, estimation of phenols, studying plant movements, root initiation in cuttings.

Lecture - 1
PLANT-WATER RELATIONS

Water is known as the liquid gold or elixir of life. Water is the major constituent of all living cells. Water content in cell ranges from 70 to 90 per cent. Water is dynamic in plant. It forms the major constituent of living things (cells) and all the vital processes of the life are carried out in it. In living tissue, water is the medium for many biochemical reactions and extraction processes. Inorganic nutrients, photosynthates and hormones are transported in aqueous solution. Movement of water form soil solution to root, stem and then to atmosphere, this continuous movement from soil to atmosphere is called as soil-plant-atmosphere water continuum [SPAC]. Evaporation of water can control the temperature of leaf on canopy. Soil nutrients are available to plant roots only when dissolved in water.

Functions of water in plant system

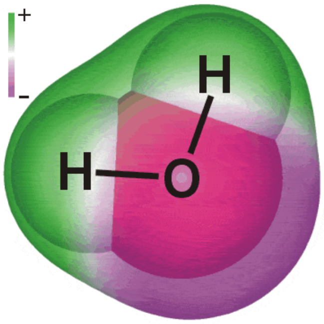
1. Water is the main constituent of protoplasm comprising up to 90-95 per cent of its total weight. In the absence of water, protoplasm becomes inactive.
2. Organic constituents of plants such as carbohydrates, proteins, nucleic acids, enzymes etc. lose their physical and chemical properties in the absence of water.
3. Water participates directly in many metabolic processes. Inter-conversion of carbohydrates and organic acids depend upon hydrolysis and condensation reactions.
4. Water increases the rate of respiration. Seeds respire fast in the presence of water.
5. Water is the source of hydrogen atom for the reduction of CO_2 in the reaction of photosynthesis.
6. Water acts as a solvent and acts as a carrier for many substance. It forms the medium in which several reactions take place.
7. Water present in the vacuoles helps in maintaining the turgidity of the cells which is a must for proper activities of life and to maintain the form and structure.
8. Water helps in translocation of solutes.
9. In tropical plants, water plays a very important role of thermal regulation against high temperature.
10. The elongation phase of cell growth depends on absorption of water.

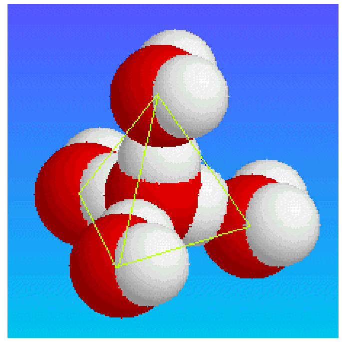
Properties of water

Water as a chemical it is a small molecule. Water has a low MW: 18, melting point :0°C, boiling point :100°C and it has apparent diameter of 2.5 A^o.

Principle property of water is dipolar nature and hydrogen bonding.

Structure which has both positive and negative charges on the same surface area is called as **Polar/bipolar/dipolar structure**.





Tetrahedral Structure of Water Molecule

www1.lsbu.ac.uk/water/molecule.html www.ch.ic.ac.uk/rzepa/mim/environmental/gifs/tetra.gif

Water has high specific heat, heat of vaporization and heat of fusion.

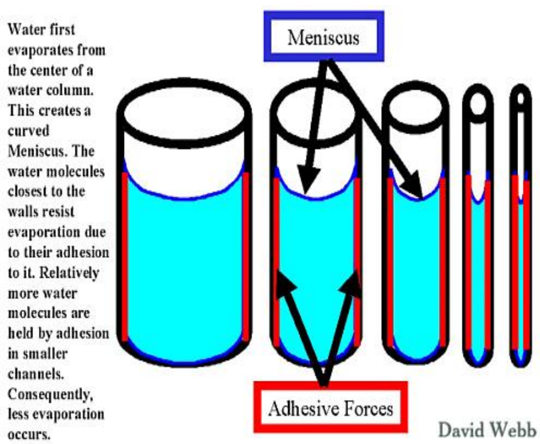
Amount of energy required to raise the temperature by one gram of water by 1^{o} C is called **specific heat**. Energy required 4.184 J.

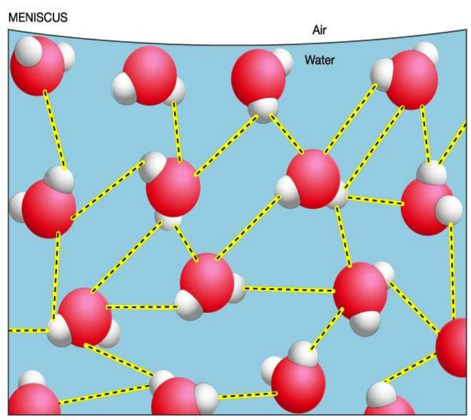
Amount of energy required to change one gram of liquid water to water vapour is called as **latent heat of vaporization**. Energy required is 2452 J at 20^{o}C.

Amount of energy required to change one gram of liquid water to ice is called as **latent heat of fusion**. Energy required is 335J.

Water shows very high adhesive and cohesive property. Attraction between the unlike molecules [water and other charged molecules] or ability of a substance to have intermolecular attraction between dissimilar particles are called **adhesive property**.

Ability of substance to have high enter molecular attraction between similar molecules is called **cohesion property**.





Adhesive property of Water **Cohesive Property of Water**

http://www.botany.hawaii.edu http://www.uic.edu

Due to adhesive and cohesive property of water, it develops other four properties.

1. Water develops high **tensile strength**: Ability of group of water molecules to withstand high levels of tension or negative pressure without getting separated itself. This property helps in bulk movement of water in plant system.
2. Water has high **surface tension**: Force acting invert within the molecules to keep the surface area as small as possible is called as surface tension.

3. Water develops high **capillary force**: Ability of liquid to raise to different levels in tubes of narrow diameter is called as capillary force.
4. Water has low **viscosity**: Ability of liquid to flow from one region to other region due to cohesion and adhesive property of water is called as viscosity.
5. Water has high **dielectric constant**: It is the ability of substance to neutralise the charges present on the surface of another substance is called as dielectric constant. Due this property water is called as **universal solvent**.

Diffusion, osmosis and imbibition

The movement of materials in and out of the cells in plants takes place in solution or gaseous form. Although the exact process of this is not very clear, three physical processes i.e., diffusion, osmosis and imbibition are usually involved in it.

Diffusion

The movement of particles or molecules or ions from a region of higher concentrations to a region of lower concentration due to random kinetic motion of the particles is called as ***diffusion***. The rate of diffusion of gases is faster than liquids or solutes. The diffusing particles have a certain pressure called as the ***diffusion pressure*** which is directly proportional to the number or concentration of the diffusing particles. Therefore the diffusion takes place always from a region of higher diffusion pressure to a region of lower diffusion pressure i.e., along a diffusion pressure gradient.

Animation for diffusion:

http://highered.mcgraw-hill.com/sites/0072495855/student_view0/chapter2/animation__how_diffusion_works.html

Factor which influences the diffusion are

1. Spatial factors; which includes
   a) Path length of diffusion
   b) Area through which diffusion is occurring.
   c) Resistance against free diffusion
2. Higher temperature will increase the diffusion rate.
3. Pressure.
4. Molecular weight: lighter molecules will diffuse faster than the heaver molecules

The rate of diffusion increases if,

a. the diffusion pressure gradient is steeper
b. the temperature is increased
c. the density of the differing particles is lesser
d. the medium through which diffusion occurs is less concentrated.

Diffusion of more than one substance at the same time and place may be at different rates and in different direction, but is independent of each other. A very common example of this is the *gaseous* (CO_2 and O_2*) exchange* in plants. Besides osmotic diffusion, the above mentioned simple diffusion also plays a very important role in the life of the plants.

Significance of diffusion

1. It is an essential step in the exchange of gases during respiration and photosynthesis
2. During passive salt uptake, the ions are absorbed by diffusion
3. It is important in stomatal transpiration as the last step in the process where, diffusion of water vapour from the intercellular space into the outer atmosphere occurs through open stomata.

Animation: How Diffusion Works

http://leavingbio.net/OSMOSIS%20AND%20DIFFUSION.htm#difan
http://www.wiley.com/legacy/college/boyer/0470003790/animations/membrane_transport/membrane_transport.htm

Reference:

1. Plant physiology – III Ed. Taiz and Zeiger: http://4e.plantphys.net/
2. Plant physiology – Salisbury and Rose.
3. www.**tnau**.ac.in/
4. Textbook of Plant physiology – Malik C. P and Srivastava.A. K.

Lecture -2

Osmosis

The movement or diffusion of water molecules from a region of higher concentration to lower concentration through a semi-permeable membrane is called as *osmosis*. It is also referred as *Osmotic diffusion*. In case there are two solutions of different concentrations separated by the semi permeable membrane, the diffusion of solvent will take place from the less concentrated solution into the more concentrated solution till both the solutions attain equal concentration.

Animation: How Osmosis Works

http://highered.mcgraw-hill.com/sites/0072495855/student_view0/chapter2/animation__how_osmosis_works.html

Osmosis and Turgor: **http://www.kscience.co.uk/animations/turgor.htm**

http://leavingbio.net/OSMOSIS%20AND%20DIFFUSION.htm#difan

Osmotic pressure

As a result of the separation of two solutions by the semi permeable membrane, a pressure is developed in solutions due to the presence of dissolved solutes in it. This is called as ***osmotic pressure*** (OP). OP is measured in terms of atmospheres and is directly proportional to the concentration of dissolved solutes in the solution. More concentrated solution has higher OP. The OP of a solution is always higher than its pure solvent.

During osmosis, the movement of solvent molecules takes place from the solution whose osmotic pressure is lower i.e., less concentrated or *hypotonic* into the solution whose osmotic pressure is higher i.e., more concentrated or *hypertonic*.

Osmotic diffusion of solvent molecules will not take place if the two solutions separated by the semi permeable membrane are of equal concentration having equal *osmotic pressures* (i.e., they are *isotonic*). In plant cells, plasma membrane and tonoplast act as selectively permeable or differentially permeable membrane. Depending on this, the solution have been classified as;

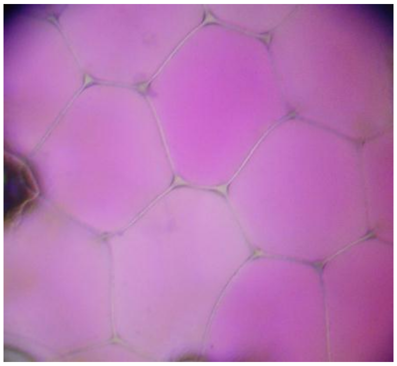
Hypertonic solution: A solution having a concentration such that it gains water or solvent by osmosis across a semi-permeable membrane from some other solution is termed as hypertonic solution (more concentrated solution)

Hypotonic solution: A solution having a concentration such that it loses water or solvent by osmosis across a semi-permeable membrane to some other solution is termed as hypotonic solution (less concentrated solution)

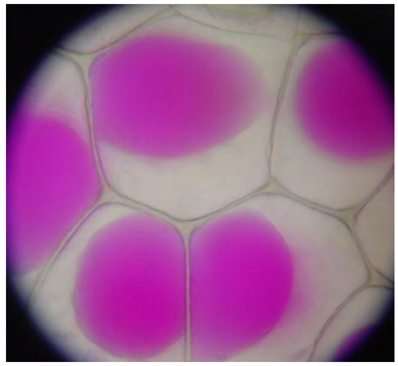
Isotonic solution: A solution having a concentration such that it neither gains nor loses water or solvent by osmosis when separated by a semi permeable membrane from another solution is termed as isotonic solution

If a living plant cell is placed in water or hypotonic solution whose OP is lower than cell sap, water enters into the cell sap through osmosis and the process is called ***endosmosis***. Due to the entry of water within the cell sap, a pressure is developed which press the protoplasm against the cell wall and the cell becomes turgid. This pressure is called as ***turgor pressure***. Consequence of the turgor pressure is the ***wall pressure*** which is exerted by the elastic cell wall against the expanding protoplasm. At a given time, turgor pressure (TP) equals the wall pressure (WP) i.e. TP=WP.

If the plant cell is placed in hypertonic solution (whose OP is higher than cell sap) the water comes out of the cell sap into the outer solution and the cell becomes flaccid. This process is known as ***exosmosis***. During the exosmosis, the cell membrane will be separated from the cell wall and this condition is called as plasmolysis. In the case of isotonic solution, cell (or) tissue will remain as such as there is no movement of water molecules.



Normal cell (A)



Plasmolysed cell (B)

(A) http://upload.wikimedia.org/wikipedia/commons/2/21/Rhoeo_Discolor_epidermis.jpg
(B) http://upload.wikimedia.org/wikipedia/commons/0/01/Rhoeo_Discolor_-_Plasmolysis.jpg

Significance of osmosis in plants

1. Large quantities of water are absorbed by roots from the soil by osmosis
2. Cell to cell movement of water and other dissolved substances involves osmosis
3. Opening and closing of stomata depend upon the turgor pressure of guard cells
4. Due to osmosis, the turgidity of the cells and hence the shape or form of the organs is maintained.
5. The resistance of plants to drought and frost increases with increase in osmotic pressure.
6. Turgidity of the cells of the young seedling allows them to come out of the soil.

Differences between diffusion and osmosis

	Diffusion	**Osmosis**
1	It is defined as the movement of molecules or ions of a solute or a solvent, be it a solid, liquid or gas from the region of its higher concentration to the region of lower concentration	The movement of molecules of water or solvent from the region of higher potential to lower potential through a semi permeable membrane
2	The diffusion may occur in any medium and the diffusing particle may be solid, liquid or gas.	Osmosis occurs only in liquid medium and only the solvent molecules move from one place to another.

Imbibition

Certain substances, if placed in a particular liquid absorb it and swell up. For example, when some pieces of grass or dry wood or dry seeds are placed in water they absorb the water quickly and swell up considerably so that their volume is increased. These substances are called as *imbibants* and the phenomenon as *imbibition is also called as* ***hydration***. Certain force of attraction is existing between imbibants and the involved substance. In plants, the hydrophilic colloids *viz*., protein and carbohydrates such as starch, cellulose and pectic substances have strong attraction towards water. Imbibition plays a very important role in the life of plants.

The first step in the absorption of water by the roots of higher plants is the imbibition of water by the cell walls of the root hairs. Dry seeds require water by imbibition for germination.

As a result of imbibition, a pressure is developed which is called as imbibition pressure or matric potential (ψ_m). It is analogous to the osmotic potential of a solution. With reference to pure water, the values of ψ_m are always negative. The water potential of an imbibant is equal to its matric potential plus any turgor or other pressure (pressure potential) which may be imposed upon the imbibant.

$$\psi_w = \psi_m + \psi_P$$

If the imbibant is unconfined to turgor or any such pressure, the equation will be $\psi_{w:}\ \psi_m$

There are three major physical changes will takes place during hydration. They are,

1. Change in volume.
2. Change in temperature.
3. Change in pressure.

Significance of imbibition

1. Imbibition is the first step in germination of seeds. When the seeds are soaked in water, they imbibe water and swell. The water is imbibed by the seed coat and then by other tissues of embryo and endosperm. Thus, the process of imbibition initiates the seed germination.
2. The water is first adsorbed by the walls of root hairs which are then absorbed by the root hair.
3. During imbibition, heat energy is released which further increases the metabolic activities of cells of seeds.

Reference:

1. Plant physiology – III Ed. Taiz and Zeiger: http://4e.plantphys.net/
2. Plant physiology – Salisbury and Rose.
3. www.**tnau**.ac.in/
4. Textbook of Plant physiology – Malik C. P and Srivastava.A. K.

Lecture 3.

Water potential

Every component of a system possesses free energy capable of doing work under constant temperature conditions. For non-electrolytes, free energy / mole is known as chemical potential. ***With reference to water, the chemical potential of water is called as water potential.*** The chemical potential is denoted by a Greek letter Psi, ψ.

The water molecules possess free energy and the free energy of pure water is greater than the free energy of other solutions prepared in water. The difference between the free energy of water molecules in pure water and the free energy of water molecules in any other system is termed as ***water potential***.

For pure water, the water potential is zero (the maximum value). The presence of solute particles will reduce the free energy of water or decrease the water potential. Therefore it is expressed in negative value. The water potential of any solution is always less than zero and hence expressed in negative value. For cell, water potential is determined by three internal factors i.e.

ψ_w : $\psi_m + \psi_s + \psi_p$

Where, ψ_m : is the matric potential.

ψ_S : solute potential or osmotic potential

ψ_p : pressure potential or turgor potential

Matric potential: It is the term used for the surface to which the water molecules are adsorbed. The matric potential is the component of water potential influenced by the presence of a matrix. In plant system, the matric potential is disregarded as it is not significant in osmosis. Matric potential can be measured for the water molecules adhering on the soil particles and cell wall. It has got a negative value. Therefore, $\psi_w = \psi_s + \psi_p$

Solute potential: It is also known as ***osmotic potential***. The amount of solute present in water is called as solute potential. It can also be defined as the amount by which the water potential is reduced as a result of the presence of solute. It has got a negative value.

In 1887, Vant Hoff, J. H., discovered an empirical relationship that allows calculation of an approximate osmotic potential form the molal concentration of a solution. He ploted osmotic potential from direct osmometer reading as function of molal concentration and obtained the following relationship which has the exact form as the law for perfect gases.

$\pi = -miRT$ where, π = osmotic potential

m = molality of solution

i = a constant that accounts for ionization of solution.

R = Gas constant (8.3144621 J K^{-1} mol^{-1})

T = Absolute temperature (K) = $^{o}C + 273$

If m, i and T is known for any solution, then osmotic potential can be easily calculated.

Osmotic potential for a complex solution such as cell sap is the sum of all osmotic potential caused by all solutes, it is expressed as **osmolality**.

Osmotic pressure: Osmotic pressure in a solution results due to the presence of solutes that lower the water potential. Osmotic pressure and osmotic potential are numerically equal but opposite in sign. Osmotic pressure has positive sign but osmotic potential has negative sign.

Pressure potential: The hydrostatic pressure exerted by the protoplasm against the cell wall as a result of entry of water is called as turgor pressure**.** The potential created by such pressures is called pressure potential. The pressure potential is usually positive and operates in plants as wall pressure and turgor pressure

In a partially turgid cell, ψ_w: $\psi_s + \psi_p$ (High water potential)

In a fully turgid cell, ψ_w: Zero (Highest water potential)

In a flaccid or plasmolysed cell, $\psi_w = \psi_s$ (Lowest water potential)

Water potential in a system can be decreased by;

1. Addition of water soluble solutes.
2. Negative pressure /tension [in plant system i.e., xylem]
3. Reduction in temperature

Water potential in a system can be increased by;

1. Positive pressure.
2. Increase in temperature.

Water potential is experimentally determined by the following methods.

1. Tissue-volume method
2. Gravimetric method
3. Vapour pressure or thermocouple method
4. Pressure bomb method
5. Chardakov's method

ABSORPTION OF WATER

Soil water is the most important constituent of soil as it provides the medium for the absorption of nutrient elements and organic matter by the roots and activates various physiological processes. There are five categories of water depending upon their availability.

1. Gravitational water

After a heavy rainfall, surface soil is temporarily saturated and it displaces air from large spaces between soil particles and gradually penetrates up to the root zone within few days under the influence of gravity. This gravitational water is not available to the plants. Plants can absorb this water only when there is continuous shower.

2. Capillary water

It refers to the bulk of water remaining in the soil after gravitational water has drained away. It occurs in the form of film coating smaller than colloidal soil particles and retained by the forces of surface tension. It is readily available to the plants and is the main source of water to the plants.

3. Hygroscopic or imbibed water

It is held by colloidal soil particles due to the adhesive forces. Plants absorb only very small quantity of this water.

4. Runaway water

The major part of water that flows on the surface of the soil is called runaway water. Plants fail to avail this water.

5. Chemically bound water

Some of the water molecules are chemically combined with soil minerals like iron, aluminium etc. This is also not available to the plants.

Field capacity or water holding capacity of the soil

After heavy rain fall or irrigation, some water is drained off along the slopes and a little amount of water is retained by the soil. This amount of water retained by the soil is called as *field capacity or water holding capacity* of the soil. Field capacity is affected by soil profiles, soil structure and temperature. Water potential at field capacity will be -0.03 MPa or -0.3 bars

Permanent wilting percentage or wilting coefficient

The percentage of soil water left after the plants growing in that soil has permanently wilted is called as *permanent wiling percentage or the wilting coefficient.* Wilting is the reduction in the volume of water in the plant cells sufficient enough to cause them to lose their turgor. The wilting may be visible in plant as drooping, rolling, folding of leaves or young stems.

Wilting may occur for two reasons:

1. If the rate of transpiration exceeds the rate of absorption of water from the soil.
2. If the soil is not having adequate amount of water for the survival of plants

Mechanism of water absorption

In higher plants, water is absorbed through root hairs that are in contact with soil water and form a root hair zone a little behind the root tips. Root hairs are tubular hair like prolongations of the cells of the epidermal layer (when epidermis bears root hairs, it is also known as piliferous layer) of the roots. The walls of root hairs are permeable and consist of pectic substances and cellulose which are strongly hydrophilic in nature. Root hairs contain vacuoles filled with cell sap. When roots elongate, the older root hairs die and new root hairs are developed so that they are in contact with fresh supplies of water in the soil. Kramer (1949) proposed that water is absorbed by two mechanisms.

1. Active absorption of water

In this process the root cells play active role in the absorption of water and metabolic energy released through respiration is consumed. Active absorption may be of two kinds.

(a) Osmotic absorption: Water is absorbed from the soil into the xylem of the roots according to osmotic gradient.

(b) Non-osmotic absorption: Water is absorbed against the osmotic gradient.

2. Passive absorption of water

It is mainly due to transpiration; the root cells do not play active role and remain passive.

Active absorption of water

a. Active osmotic absorption of water

Atkins (1916) and Priestley (1922) postulated the active osmotic absorption of water. The first step in osmotic absorption of water is the imbibition of soil water by the hydrophilic cell walls of root hairs.

Osmotic pressure (OP) of the cell sap of root hairs is usually higher than the OP of the soil water. Therefore, the diffusion pressure deficit (DPD) and suction pressure in the root hairs become higher and water from the cell walls enters into them through plasma membrane by osmotic diffusion. As a result, OP, suction pressure and DPD of root hairs now become lower, while their turgor pressure is increased.

Now, the cortical cells adjacent to root hairs have high OP, SP and DPD in comparison to the root hairs. Therefore, water is drawn into the adjacent cortical cells from root hairs by osmotic diffusion. In the same way, by cell to cell osmotic diffusion water gradually reaches the inner most cortical cells and the endodermis.

Osmotic diffusion of water into endodermis takes place through special thin walled cells called *passage cells* because the other endodermal cells have *casparian strips* (is a band of cell wall material deposited on the radial and transverse walls of the endodermis, which is chemically different from the rest of the cell wall. It is used to block the passive flow of materials, such as water and solutes into the stele of a plant) on thin walls which are impervious to water. Water from endodermal cells is drawn into the cells of pericycle by osmotic diffusion which now become turgid and their suction pressure in decreased.

In the last step, water is drawn into xylem from turgid pericycle cells. It is because in the absence of turgor pressure of the xylem vessels, the SP of xylem vessels becomes higher than SP of the cells of the pericycle when water enters into xylem from pericycle and a positive pressure is developed in the xylem of roots which can raise the water to a certain height in the xylem. This pressure is called as *root pressure*.

b. Active non-osmotic absorption of water

Sometimes, it has been observed that absorption of water takes place even when OP of soil water is high than OP of cell sap. This type of absorption which is non-osmotic and against the osmotic gradient requires the expenditure of metabolic energy probably through respiration. Bennet Clark *et al* (1936), Thimann (1951) and Bogen and Prell (1953) observed that absorption of water against the gradient requires extra energy supplied by cellular respiration. However, Kramer (1969) reported that active absorption of water has negligible importance in the water economy of almost all plants. Aquaporins (are proteins embedded in the cell membrane that regulate the flow of water) are also associated with non osmotic absorption of water.

Passive absorption of water

Passive absorption of water takes place when rate of transpiration is usually high. Rapid evaporation of water from the leaves during transpiration creates a tension in water in the xylem of the leaves. This tension is transmitted to water in xylem of roots through the xylem of stem and water rises upward to reach the transpiring surfaces. As a result, soil water enters into the cortical cells through root hairs to reach the xylem of roots to maintain the supply of water. The force of this entry of water is created in leaves due to rapid transpiration and hence, the root cells remain passive during this process.

Animation on water absorption:

http://www.kscience.co.uk/animations/water_movement.swf

Animation on water and mineral uptake in plants:

http://academic.kellogg.edu/herbrandsonc/bio111/animations/0034.swf

Factors affecting absorption of water

External factors

1. Available soil water

Sufficient amount of water should be present in the soil in the form that can easily be absorbed by the plants. Usually the plants absorb capillary water i.e. water present in films in between soil particles. Other forms of water in the soil e.g. hygroscopic water, combined water and gravitational water are not easily available to plants.

Higher amount of water in the soil results in poor aeration of the soil retarding metabolic activities such as respiration in root cells and thereby the rate of water absorption is reduced.

2. Concentration of soil solution

Increased concentration of soil solution (due to presence of more salts in the soil) results in higher OP. If OP of soil solution will become higher than the OP of cell sap in root cells, the water absorption particularly the osmotic absorption of water will be greatly suppressed. eg. poor absorption of water in alkaline and saline soils.

3. Soil air

Absorption of water is reduced in poorly aerated soils due to the deficiency of O_2 and consequently, the accumulation of CO_2 will retard the metabolic activities like respiration in roots. This also inhibits rapid growth and elongation of the roots and deprived of fresh supply of water in the soil. Water logged soils are poorly aerated and hence, are physiologically dry.

4. Soil temperature

Increase in soil temperature up to about 30°C favours water absorption. At higher temperature, water absorption is decreased. At low temperature also water absorption decreased and at about 0°C, it is almost stopped. This is because at low temperature,

a. The viscosity of water and protoplasm is increased
b. Permeability of cell membrane is decreased
c. Metabolic activity of root cells are decreased
d. Root growth and elongation of roots are checked.

Internal Factors

1. Transpiration

The rate of absorption of water is directly proportional to transpiration. The higher transpiration rates produce a tension or pull that is transmitted to roots through hydrostatic system of plants creating a favourable condition for entry of water.

2. Absorbing root systems

The number of root hairs accounts for the entry of water in the plant system. The development of root hairs depends upon the environment, especially moist condition.

3. Metabolism

The metabolism and absorption are closely related. The factors inhibiting rate of respiration such as poor aeration, anesthetics and KCN reduces the absorption rate.

Differences between active and passive water absorption

	Active water absorption	**Passive water absorption**
1.	It is due to the activity of the roots and particularly root hairs	It is due to the activity of the upper part of the plant such as shoot system.
2.	Osmotic and non osmotic mechanisms are involved	Passive absorption is due to transpiration in the upper part
3.	In active absorption, the osmotic process involves diffusion pressure deficit (DPD) of the cells. The root hairs have more DPD as compared to soil solution.	It occurs due to the *tension* created in the xylem sap by transpiration pull
4.	Active absorption involves *symplastic* movement of water in root hairs. The water first enters the cell sap and then passes from one cell to another. Such type of movement, where living protoplasm involved is called as *symplast*	In passive absorption, water moves probably through the free spaces or *apoplast* of root. The *apoplastic* movement of water includes cell wall and intercellular spaces, which are fully permeable. The water can reach up to endodermis through *apoplast* but it moves through the endodermis by *symplast*.
5.	The evidences for active absorption are root pressure, bleeding and guttation.	The evidence for passive absorption can be given by cutting the roots under water. The absorption of water continued even if all the roots are removed.

Reference:

1. Plant physiology – III Ed. Taiz and Zeiger: http://4e.plantphys.net/
2. Plant physiology – Salisbury and Rose.

3. www.**tnau**.ac.in/
4. Textbook of Plant physiology – Malik C. P and Srivastava.A. K.

Lecture 4.
ASCENT OF SAP

Sap is a liquid containing water and dissolved mineral salts. The upward movement of water from the root system to the aerial parts of the plant through the xylem is known as ***ascent of sap***. Xylem is the main water conducting tissue and the ascent of sap take place through the xylem.

The ringing experiment of *Malphigi* proved that ascent of sap takes place through xylem. A ring of bark (all tissues outside the xylem) is removed from the stem and the plant is left as such for a few days. The leaves above the ringed part of the stem remain fresh and green. This shows that the ascent of sap occurs through xylem. Similarly, if a portion of xylem is removed by making a hole in the stem, the leaves above that portion showed wilting symptom. This again confirms the ascent of sap is through xylem.

Mechanism of ascent of sap

A number of theories have been put forward to explain the mechanism of ascent of sap as follows.

1. Vital theories
2. Root pressure theory
3. Physical force theories

1. Vital theories

According these theories, the living cells of the plants are responsible for the ascent of sap. Vital theories include two theories:

a. Relay pump theory **(Godlewski, 1884)**

According to this theory, the living cells of xylem pump the water upwards and the xylem tracheids and vessels act as reservoirs.

b. Pulsation theory **(J.C. Bose, 1923)**

According to this theory, ascent of sap takes place due to pulsatory activity of the living cells of inner most cortical layer, just outside the epidermis. Here, the cells absorb water from outside and pump the same to the vessels. The objection to this theory was put forward by *Strasburger* that the ascent of sap can take place even if the living cells are killed by treating with poisons like picric acid.

2. Root Pressure theory (Priestley Stocking, 1956)

According to this theory, the ascent of sap is due to a hydrostatic pressure developed in the roots by the accumulation of absorbed water. The pressure developing in the tracheary elements of the xylem as a result of the metabolic activities of root is referred as *root pressure*. If a plant system is cut a few inches above its base, the xylem sap is seen flowing out through the cut end. This phenomenon is called *exudation or bleeding*. Some scientists believe that root pressure is responsible for ascent of sap. But, it does not seem to be an effective force in the ascent of sap due to following reasons.

1. Root pressure is not observed in plants grown in cold, drought or less aerated soil, where ascent of sap is normal.
2. *Strasburger* observed ascent of sap in plants in which the roots are removed.
3. The magnitude of root pressure is very low (about 2 atm.)
4. In many tall plants, there is no root pressure. In gymnosperms, root pressure has been rarely observed.

3. Physical Forces Theories

According to this theory, the dead cells of the xylem are responsible for the ascent of sap. There are four theories to support this mechanism

a. Atmospheric pressure theory **(Boehm, 1800)**

The theory says that ascent of sap takes place due to atmospheric pressure. But, it is not accepted because the atmospheric pressure cannot raise water beyond 34 feet.

b. Imbibition theory **(Unger, 1868; Sachs, 1978)**

According to this theory, ascent of sap takes place by imbibition through the walls of xylem but, it was observed later that ascent of sap take place through the lumen of the xylem and not through walls.

c. Capillary theory **(Boehm, 1868)**

This theory states that water rises in narrow tubes due to surface tension. In plants, the xylem vessels are placed one above the other forming a sort of continuous channel. This can be compared with long capillary tubes and water rises in the capillary tube due to capillary force. However, the following objections are observed.

1. For capillarity, a free surface is required.
2. The magnitude of capillary force is very low.
3. In gymnosperms, the vessels are usually absent. Other xylem elements do not form continuous channels

4. Transpiration Pull theory/ Cohesion hypothesis/Cohesion- Tension theory (Dixon and Jolly, 1834)

According to this theory, the ascent of sap is due to transpiration and the cohesion and adhesion of water. This theory is very convincing and supported by many scientists as it involves two important aspects.

1. Cohesive and adhesive properties of water

Animation showing "Cohesion – tension model of xylem transport" :

http://academic.kellogg.edu/herbrandsonc/bio111/animations/0031.swf

The attraction between water molecules is called cohesion. The cohesive force developed between the water molecules make the water remain in the form of continuous water column in the xylem and the magnitude of cohesive force is very high (350 atm.) The adhesive properties of the water molecules and the walls of the xylem further ensure the continuity of water column in the xylem. The xylem vessels are tubular structures extending from roots to the top of the plants. Cells are place one above the other, with their end walls perforated forming a continuous tube. One end of the xylem tube is connected with the root hairs via pericycle, endodermis and cortex and another end is connected with the sub stomatal cavity in the leaves via mesophyll cells. This tube is filled with water and due to the cohesion and adhesion properties, it forms continuous water column.

2. Transpiration pull

Animation on transpiration pull:

http://www.kscience.co.uk/animations/transpiration_pull.swf

The pulling force developed in the water column of xylem due to transpiration is called transpiration pull. When transpiration takes place in the upper part of the plant, water evaporates from the inter cellular spaces of the leaves to the outer atmosphere through the stomata. More water is released into the intercellular spaces from the mesophyll cells and in turn, mesophyll cells draw water from the xylem of the leaf. Due to this, a tension is created in water in the xylem elements of the leaves and this tension is transmitted downward to water in the xylem of root through xylem of stem. Now, the water is pulled upward in the form of a continuous unbroken water column to reach the transpiring surface up to the top of the plants.

This theory was also objected by Milburn and Johnson (1966) and other scientists that the presence of air bubbles in the conducting channels due to variation in the day and night temperature will break the continuity of the water column.

Factors affecting ascent of sap

1. Water movement is regulated by root pressure and transpiration. All those factors which affect the rate of water absorption and transpiration also influence the ascent of sap.
2. High temperature, atmospheric pressure, wind velocity and low atmospheric humidity influence the ascent of sap as that of transpiration.
3. Soil water deficit also decrease the ascent of sap indirectly by influencing the absorption of water.

Root Pressure

The father of Plant Physiology, Stephen Hales (1727) proposed *root pressure*. It is a pressure developed in the tracheary elements of xylem as a result of metabolic activities of roots. Root pressure is an osmotic phenomenon developed due to the activity of root cells and it is an active process. The factors that affect transpiration also affect root pressure.

Significance of root pressure

1. Exudation (bleeding) and guttation are caused by root pressure.
2. It helps in ascent of sap

Reference:

1. Plant physiology – III Ed. Taiz and Zeiger: http://4e.plantphys.net/
2. Plant physiology – Salisbury and Rose.
3. www.**tnau**.ac.in/
4. Textbook of Plant physiology – Malik C. P and Srivastava.A. K.

Lecture 5.
TRANSLOCATION OF ORGANIC SOLUTES

The process of movement of dissolved organic food materials from one place to another in plants is called ***translocation of organic solutes***. In plants, the green parts of the plants such as leaves synthesize organic food materials like carbohydrates. They move in solution to the non-green parts such as roots for utilization and storage. Generally, they move from the region of synthesis to the region of utilization. The region of synthesis is called **supply end or source** and the region of utilization is called **consumption end or sink**. The organic food materials move from source to sink. Translocation of organic solutes always takes place from the region of higher concentration to the region of lower concentration. Translocation of organic solutes occurs in the *soluble* from and it occurs mainly through *phloem.*

Significance of Translocation

Translocation of organic solutes brings out the following functions:

1. The synthesized food is supplied to non-green parts of the plants by translocation.
2. By translocation, food is served to the areas of utilization such as buds, growing leaves, etc.
3. The excess food materials are transported to the areas of storage such as fruits, seeds, underground stems, bulbils, etc.
4. During germination of seeds, stored food materials are transported to the growing seedlings.

Direction of Translocation

The movement of organic solutes takes place in all directions. It may occur *downward* or *upward* or *radially.* The food materials synthesized in the leaves move *downwards* to the stems and roots. The *upward* and *downward* translocation takes place through the *phloem.* The *upward movement* of food materials occurs from the leaves to the buds, growing leaves, flowers, fruits and seeds. During the germination of seeds, the stored food is supplied to the growing seedlings, through upward translocation. *Radial* translocation is the lateral movement of organic solutes. It occurs from the cells of *pith* to the cells of *cortex* and *epidermis.* The radial translocation occurs through the *medullary rays.*

Conditions Essential for Translocation

Two conditions are essential for conduction of food materials.

i) The food materials must be in *water soluble form.* For this purpose, even in storage tissues, the reserve food materials which are in the form of insoluble starch will be converted into soluble sugars with-the help of enzymes before they are conducted.

ii) The supply end (source) must have higher concentration of food materials when compared with the consumption end (sink).

Path of Translocation (or) Tissue Concerned with Translocation

As early as 1837, *Hartig* discovered the importance of *phloem* in the conduction of food materials. Since then, there are number of evidences to prove that the phloem tissues are well suited for the conduction of food materials.

There are number of evidences to prove the concept that phloem is the tissue concerned with transport of food materials.

Evidences: The following are some of the evidences to prove the above concept. .

1. Phloem- Tissue concerned with Translocation

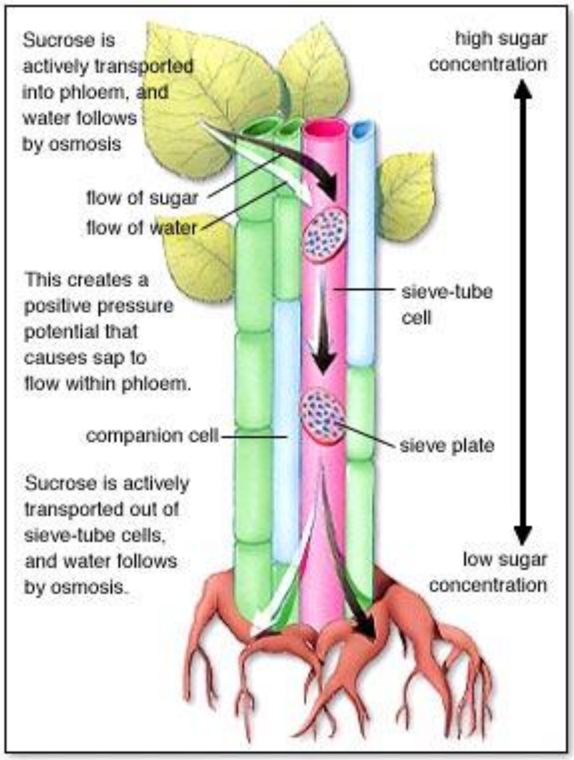
The cells of ground tissues like parenchyma, collenchyma etc. is comparatively poor in organic substances. The existing food materials are also in insoluble form. This clearly indicates that these tissues are not well suited for conduction because they never form a continuous system between supply end and consumption end. They have been well suited for storage only. *Xylem* is also *not well suited* because the cells are dead and they have a rapidly moving water current upwards, from root to stem and leaves. So food materials cannot move downwards through this tissue.

From this it is clear that the remaining phloem tissue is the actual path for the downward flow of organic food materials.

2. Structure and distribution of phloem

In higher plants, the *sieve tubes* constitute the chief component of phloem tissue. The sieve tubes are elongated, placed end to end and their end walls are provided with *sieve plates.* The sieve plates are *perforated* and through the pores protoplasmic connections are established between the sieve tubes above and below. In *cucurbits* large amount of food materials have to be conducted through a narrow stem. Hence, they are provided with *bicollateral vascular bundles* i.e. with phloem on either side of the xylem.

Thus the structure of phloem and its distribution in plants clearly indicate that phloem tissue is the only most suitable tissue for conduction of food material.



http://www.mhhe.com/biosci/esp/2001_gbio/folder_structure/pl/m4/s3/assets/images/plm4s3_1.jpg

3. Chemical Analysis of Phloem Tissue

The phloem cells contain comparatively large amount of carbohydrates and they are present in soluble state. This clearly indicates that these food materials are not' for storage but for translocation only.

Mason and *Maskel* (1928) by chemical analysis of phloem tissues showed that there was a diurnal (day and night) variation in the sugar content of the phloem tissue. High concentration of sugar was observed in the phloem tissues during noon time when the photosynthetic rate and food production are maximum.

4. Evidence from Ringing Experiment

Malpighi (1679) demonstrated that the removal of a ring of bark (with phloem tissue) from the stem of the trees, blocked the movement of sap down the trees and this caused a swelling of the tissues above the ring. This type of swelling is due to the accumulation of food materials. Since the continuity of phloem tissue is cut off due to ringing, food materials cannot be transported below the ring. The downwardly moving food materials accumulate above the ring and cause swelling.

This also clearly indicates that phloem tissue is concerned with conduction of food materials. .

5. Effect of Blocking the Phloem Tissues

If the path of phloem tissue is blocked by means of liquid paraffin, the conduction of food materials becomes blocked. Similar conditions are noticed if the phloem tissue is injured or blocked due to diseases.

6. Evidence from the Use of Radioactive Isotopes

i) *Biddulph* and *Markle* (1944) studied the translocation of radioactive isotopes of phosphorus (P^{32}) after it had been introduced into the leaves of cotton plants. They separated the xylem and phloem tissue at a particular place by introducing a wax paper in order to prevent lateral conduction. After a short period, they found the presence of greater amount of P^{32} in the phloem tissue. These results clearly indicate that the downward movement of P^{32} labeled organic compounds occurred in the phloem.

ii) *Rabideau* and *Burr* (1945) supplied the bean plant with CO_2 marked with radioactive C^{14}. They traced the path of C^{14}. Carbon-di-oxide, with C^{14} was used by the plants to prepare the organic food materials. Thus the path of organic food materials with C^{14} was traced. By this method they proved that the phloem was concerned with the translocation of organic solutes.

iii) *Biddulph* (1956) by the use of radioactive tracers and autoradiography has shown that sieve cells of conifers and the sieve tubes of angiosperms is the path of movement of organic food materials.

7. Evidence from Aphid Stylet Studies

Aphids are parasite insects, parasitic on the food materials translocated in plants. The aphids insert their stylet to feed on. They are anaesthetized and their stylet is cut off when it is feeding on the plants. The exudates from such cut stylets directly are related to the food materials being translocated in the phloem. Microscopic examination of sections of the stem, on which the aphid was allowed to feed, always revealed that it was the sieve tubes or a group of sieve elements which were punctured and which supplied the exudates.

All the above given evidences proved beyond doubt that phloem is the only tissue that conducts organic food materials.

Mechanism of Translocation of Solutes

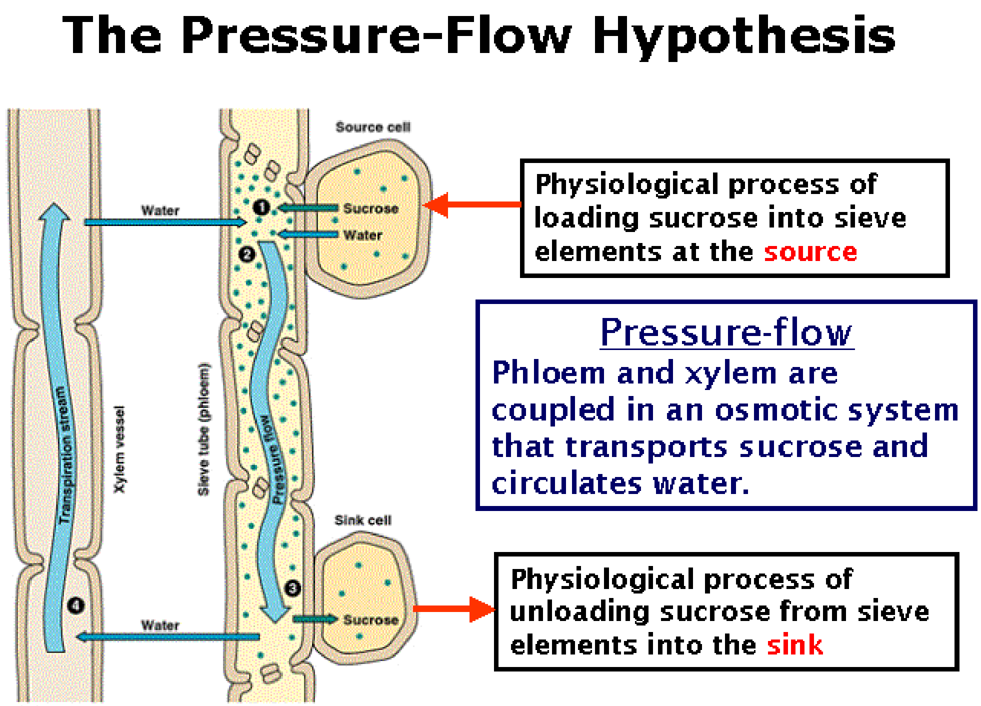
Basically, there are three theories to explain the mechanism of translocation of solutes. They are:

1. Munch's mass flow or pressure flow hypothesis
2. Diffusion hypothesis
3. Protoplasmic streaming hypothesis

1. Munch's Mass flow Hypothesis (or) Pressure Flow Hypothesis

Animation showing pressure-flow model of phloem transport:

http://academic.kellogg.edu/herbrandsonc/bio111/animations/0032.swf



http://www.desktopclass.com/wp-content/uploads/2011/02/pressureflow.gif

According to this theory translocation is a kind of blood circulation within the plant body and the mesophyll cells of the leaves acting as a heart. The pumping force is provided by the Osmotic concentration of the solutes to be translocated in phloem which is supported by the hydrostatic pressure developed due to entry of water from xylem.

According to this theory, carbohydrates like sucrose is produced in the mesophyll cells of leaves during photosynthesis. This causes an increase in the osmotic concentration of these cells. Hence, these cells absorb water from the neighbouring xylem cells. This in turn brings about an increased hydrostatic (turgor) pressure in these cells. This pressure forces the solution of mesophyll cells into the sieve tubes of phloem tissue. Through the sieve tubes which form a continuous net work within the plant body, food materials are transported from the leaf to root through the stem.

In the leaves, food materials are continuously produced by photosynthesis and thus the concentration of food materials is always kept high. At the stem and roots, the food materials are continuously utilized for various metabolic activities and thus the concentration of solutes in stem and root are always kept at low level. Thus a gradient of hydrostatic pressure is established between the leaf and the root. Because of the gradients of hydrostatic pressure there will be a bulk or mass flow of solution and dissolved solutes from the leaves to the stem through the phloem. Hence, a mass flow of solutes occurs continuously from the leaf to the root through the stem. The tissue concerned in translocation is phloem tissue of root, stem and leaf. This can be easily represented by an experiment.

Such a mechanism may be illustrated by means of a simple physical model.

Two cells A and B have membranes which are permeable only to water. They are connected by a glass tube C. Cell A contains a solution of high osmotic pressure such as sucrose solution. Cell B contains only water. When these two cells are placed in water in a vessel D, water will enter into cell A from the vessel D as a result of endosmosis. This will create a hydrostatic or turgor pressure in cell A. This causes the sucrose solution to move out of cell A along the tube C. This in turn will force water out of the cell B.

This process will continue until the concentration of sucrose in both cells is equal at which time the flow will cease. Cell A may be regarded as a *source* and cell B as a *sink.* If the sucrose solution in B is continuously removed, then the flow will continue from cell to cell B through the tube C.

This theory is comparatively better in explaining the translocation of solutes and the model also gives positive results. However, there are some serious objections against this most accepted theory also. They are:

1. This theory explains the unidirectional flow of solutes, whereas in plants, the flow of food materials is bidirectional at the same time.
2. This theory explains the translocation as a non physiological process.
3. It calls for excessive turgor pressure to account for the flow through the pores of the sieve plates.
4. The cross walls present in between the sieve tubes offer a considerable resistance and thus prevent a rapid mass flow of food materials with in the phloem tissue.

Even though there are some demerits, mass flow hypothesis is the most widely supported theory.

2. Diffusion Hypothesis

Diffusion is a simple process by which substances will move from its region of higher concentration to the region of lower concentration.

Diffusion hypothesis believes that translocation is fundamentally by simple diffusion and translocation will take place only if there is a concentration gradient between the supply end and consumption end. If there is no concentration on gradient there is no translocation. The rate of translocation will be greater when the concentration of the solutes in the supply end is also greater. The only merit of the theory is that it explains the simultaneous flow of organic compounds in opposite directions.

But this theory is also not accepted because; translocation of solute is a rapid process whereas diffusion is a very slow process. So it cannot account for the rapid movement of food materials.

Activated Diffusion Hypothesis

In 1937, *Mason* and *Phillis proposed that the transport of food materials takes place through stationary cytoplasm by activated diffusion.* According to them, diffusion is hastened by activating the diffusing molecules or by decreasing the resistance to diffusion through the protoplasmic medium. This theory is not accepted because no such activation has been demonstrated experimentally.

3. Protoplasmic Streaming Hypothesis

This theory was proposed first by de Vries in 1885 and *elaborated by Curtis and her associates in* 1935. *According to them, moving protoplasm carries the solutes within the sieve elements and the protoplasmic fluid moves from cell to cell through large protoplasmic connections across the sieve plates.*

A circular movement or *Cyclosis* of living protoplasm has been observed in many different plant cells. (e.g.) Chara, *Nitella*, Staminal hairs of Tradescantia.

The *evidences* in support of this theory are:

1. Streaming of granular substances is observed in all living cells.
2. Streaming will allow a rapid transport than that of diffusion.
3. The solutes will be easily carried from one place to another by the streaming protoplasm
4. Protoplasmic connections are observed between adjacent sieve tubes through the pores present in the sieve plate
5. A recent evidence in favour of this theory comes from the works of Thaine (1967).

Transcellular cytoplasmic strands are existing between phloem cells and food particles moving within transcellular strands. Thaine (1967) suggests that the force or energy for this movement might be provided in the form of Adenosine Tri Phosphate (ATP) by mitochondria.

The major *objections* against this theory are:

i) The cytoplasmic streaming has never been observed in mature sieve elements

ii) *The* rate-of streaming cannot account for the rapid translocation of solutes.

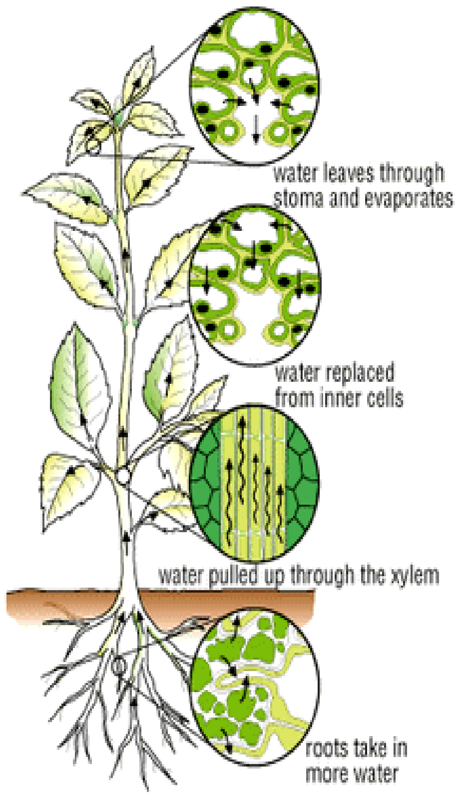
Reference:

1. Plant physiology – III Ed. Taiz and Zeiger: http://4e.plantphys.net/
2. Plant physiology – Salisbury and Rose.
3. www.**tnau**.ac.in/
4. Textbook of Plant physiology – Malik C. P and Srivastava.A. K.

Lecture 6
TRANSPIRATION

Transpiration is the evaporation of water from cell surfaces and its loss through the anatomical structures of the plant (stomata, lenticels and cuticles). The total water loss by transpiration may be very great. The daily water loss of large, well watered tropical tress may run as high as 500 litres. A corn plant may loose 3 to 4 litres of water per day. Whereas a tree sized desert cactus may loose water less than 25 ml per day. In general about 99 per cent of water absorbed by a plant during the growth is lost in transpiration (necessary evil). Water lost by a growing field of corn would be about 8-11 inches of water per acre during the growing season. Transpiration is mostly taking place through the stomata.

Although large quantities of water are absorbed by plant from the soil, only a small amount is utilized. The excess of water is lost from the aerial parts of plants in the form of water vapour and this process is called as transpiration. Nearly >95 per cent of water absorbed by the plants is lost through transpiration and only <5 per cent is utilized by the plant. In general, there are 3 types of transpiration i.e. stomatal, cuticular and lenticular transpirations.



http://graphpad.co.uk/images/Plant_transpiration_intro.jpg

Animation on transpiration: http://www.kscience.co.uk/animations/transpiration.swf

1. Stomatal transpiration

Most of the transpiration takes place through stomata. Stomata are usually confined in more numbers on the lower sides of the leaves. In most of the monocots, they are equally distributed on both sides of leaves. While in aquatic plants, stomata are present on the upper surface of the floating leaves. Stomatal transpiration accounts for 80-90 per cent of the total water loss from the plants.

2. Cuticular transpiration

The loss of water through the impervious cuticle is called as cuticular transpiration. It may contribute a maximum of about 10 ten per cent of the total transpiration.

3. Lenticular transpiration

The loss of water through the lenticels of woody stems is called as lenticular transpiration. It accounts for about 0.1 per cent of the total transpirational loss of water.

Distribution of stomata

The position and distribution of stomata on the two surfaces of the leaf are variable in plants and there are five types.

Kidney shaped are found in the most of the plants including mosses, gymnosperms, dicots and many monocots. Dumbbell shaped or bone shaped guard cells are characteristic of grasses and hence it is also refereed as "*grass type*". Lantern types of stomata are present mostly in the CAM plants

Different Types of Stomata

A. Types of Stomata based on Distribution

1. Apple or mulberry type: Stomata are found distributed only on the lower surface of the leaves. eg., apple, peach, mulberry, walnut etc. Such leaves are called as **hypostomatic type**.

2. Water lily type: Stomata are distributed only on the upper epidermis of the leaves. eg., water lily, Nymphaea and many aquatic plants. These plants are **epistomatic type**.

3. Potato type: In this type, the stomata are found more on the lower surface (multistomatic) and less on the upper leaf surface (paucistomatic type). eg., Potato, cabbage, bean, tomata, pea etc. Such leaves are called as **amphistomatic** and **anisostomatic type.**

4. Oat type: Stomata are equally distributed on the both lower and upper surface of the leaves. These leaves are referred as **isostomatic type**.

5. Potamogeton type: In this case, stomata are altogether absent or if present, they are vestigial. eg., Potamogeton and other submerged aquatics. Such leaves are called as **astomatic type.**

B. Types of Stomata based on Movement

Loftfield (1856) classified three main groups of stomata in accordance with their daily movement:

1. Alfalfa Type: The stomata remain open throughout the day and closed all night, eg., peas, bean, mustard etc.

2. Potato Type: The stomata will open throughout the day and night except for few hours in the evening, eg., Allium, cabbage, pumpkin, etc.

3. Barley Type: The stomata open only for a few hours in a day, eg., Barley and other cereals.

C. Types of Stomata based on Behavior

Considering the behavior of the stomatal movements, five categories have been recognized:

1. Photo-active movements: Light directly or indirectly controls stomatal movements. Such stomata remain open during day time and closed in nights (dark).

2. Skoto-active movements: Stomata remain closed during day time and open during night. Such cases are found in succulent plants and other CAM Plants.

3. Hydro-active movements: In some cases, stomata open due to excessive loss of water from the epidermal cells and close due to turgid conditions of epidermal cells. This is usually found during mid-day.

4. Autonomous movements: In certain cases, stomata open and close at a rate of 10-15 minutes showing diurnal or rhythmic pulsation.

5. Passive and Active movements: Opening of stomata is considered as active process and closing is the passive process and this is caused by the turgor changes in the guard cells.

Mechanism of stomatal transpiration

The mechanism of stomatal transpiration can be studied in 3 steps.

1. Osmotic diffusion of water in the leaf, from xylem to intercellular space above the stomata through the mesophyll cells.
2. Opening and closing of stomata (stomatal movement).
3. Simple diffusion of water vapour from intercellular spaces to outer atmosphere

Osmotic diffusion

Inside the leaf, the mesophyll cells are in contact with xylem, and with intercellular spaces above the stomata. When mesophyll cells draw water from the xylem they become turgid and their diffusion pressure deficit (DPD) and osmotic pressure (OP) decreases. Then, water is released in the form of vapour into intercellular spaces close to stomata by osmotic diffusion. Now, the OP and DPD of mesophyll cells become higher and hence, they draw water form xylem by osmotic diffusion.

Opening and closing of stomata (Stomatal movement)

Animation on stomatal movement:

http://academic.kellogg.edu/herbrandsonc/bio111/animations/0021.swf

Stomatal movements

(Night) stomata closed

↓ Light

CO_2 content reduced in guard cells (…………)*

↓

Bicarbonate increased (+ phosphoenol pyruvic acid)

↓

malic acid

↓

dissociate into H^+ and malate ions

↓

Influx of K^+ and efflux of H^+ ions

↓

Potassium malate transported into vacuole

↓

Water potential decrease

↓

Entry of water

↓

Turgidity increased

↓

Stomata open

$$* (CO_2 + H_2O \longrightarrow H_2CO_3 \longrightarrow H^+ + HCO_3^-)$$

The stomata will be opened by the action of light. When the light falls on the leaf the CO_2 content of guard cells will be converted into bicarbonates which results in a decrease of CO_2 concentration. Bicarbonate formed will be combined with phosphoenol pyruvic acid to form malic acid. The malic acid will be dissociated into H+ and malate ions. H+ ions will be exchanged with the K+ ions from other epidermal cells. With the result there will be an influx of K+ ions into the guard cells. This K+ ion combines with malate ions to form potassium malate. This will be transported into the vacuoles. Thus the solute potential will be decreased which leads to a decrease in the water potential also. Because of this decrease in water potential a gradient in water potential will be developed between guard cells and other epidermal cells. With the result water will be taken into the guard cells. Thus the turgidity of guard cells increases which leads to the opening of stomata.

The stomata are easily recognized from the surrounding epidermal cells by their peculiar shape. The epidermal cells that immediately surround the stomata may be similar to other epidermal cells or may be different and specialized. In the latter case, they are called as subsidiary cells. The guard cells differ from other epidermal cells also in containing chloroplasts and peculiar thickening on their adjacent surface (in closed stomata) or on surfaces.

Consequent to an increase in the osmotic pressure (OP) and diffusion pressure deficit (DPD) of the guard cells (which is due to accumulation of osmotically active substances), osmotic diffusion of water from surrounding epidermal cells and mesophyll cells into guard cells follows. This increase the turgor pressure (TP) of the guard cells and they become turgid. The guard cells swell, increase in length and their adjacent thickened surfaces stretch forming a pore and thus the stomata open.

On the other hand, when OP and DPD of guard cells decrease (due to depletion of osmotically active substances) relative to surrounding epidermal and mesophyll cells, water is released back into the latter by osmotic diffusion and the guard cells become flaccid. The thickened surfaces of the guard cells come close to each other, thereby closing the stomatal pore and the stomata.

Osmotic diffusion of water into guard cells occur when their osmotic pressure increases and water potential decreases (i.e. become more negative) related to those of surrounding epidermal and mesophyll cells. The guard cells become flaccid when their osmotic pressure decreases relative to the surrounding cells (Movement of water takes place from a region of higher water potential to a region of lower water potential).

The different mechanisms that create osmotic potential in the guard cells and control stomatal movements are,

a. Hydrolysis of starch into sugars in guard cells

b. Synthesis of sugars or organic acids in guard cells
c. The active pumping of K^+ ions and, Cl^- ions or organic acid counter ions into the guard cells

a. Hydrolysis of starch into sugars in guard cells

Starch – Sugar Interconversion theory

This classical theory is based on the effect of pH on starch phosphorylase enzyme which reversibly catalyses the conversion of starch + inorganic phosphate into glucose -1 phosphate.

During the day, pH in guard cells in high. This favours hydrolysis of starch (insoluble) into glucose -1- phosphate (soluble) and osmotic pressure is increased 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, the reverse process occurs. Glucose 1- phosphate is converted back into starch in the guard cells thereby decreasing osmotic pressure. The guard cell release water, become flaccid and stomata become closed.

$$\underset{\text{(insoluble)}}{\text{Starch}} + \text{Pi} \underset{\text{Dark, low pH}}{\overset{\text{Light, high pH}}{\rightleftharpoons}} \underset{\text{(Soluble)}}{\text{Glucose-1-phosphate}}$$

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 osmotically.

In this scheme it is 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.

Steward's scheme of reactions involved in the opening and closing of stomata

At higher pH (7.0) the opening of the stomata is caused in the following sequence.

$$\text{Starch} + PO_4 \xrightarrow{\text{Phosphorylase}} \text{Glucose -1-}\ PO_4$$

$$\text{Glucose -1-}\ PO_4 \xrightarrow{\text{Phosphoglucomutase}} \text{Glucose -6-}\ PO_4$$

$$\text{Glucose -6-}\ PO_4 \xrightarrow{\text{Phosphatase}} \text{Glucose} + PO_4$$

The closing of stomata is brought about by the conversion of glucose into glucose -1-PO_4 with the help of ATP in the presence of the enzyme hexokinase and oxygen.

$$\text{Glucose} + \text{ATP} \xrightarrow{\text{Hexokinase}} \text{Glucose -1-}\ PO_4$$

$$\text{Glucose -1-}\ PO_4 \xrightarrow{\text{Phosphorylase}} \text{Starch} + PO_4$$

However, starch – sugar inter-conversion theory is not universally applicable as this scheme operates under certain circumstances.

Difference between epidermal cells and guard cells:

1).Guard cells have chloroplast, epidermal cells do not.
2) Guard cells are much smaller than the epidermal cells
3) They have bean or Kidney shape in dicots and dumbell shape in monocots especially grasses
4) The cell walls of guard cells are not uniform . Inner walls are thicker than the outer walls . Epidermal cells are uniformly thin .

Reference:

1. Plant physiology – III Ed. Taiz and Zeiger: http://4e.plantphys.net/
2. Plant physiology – Salisbury and Rose.
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Lecture. 7. Transpiration cont.

Transpiration (Continued)

The different mechanisms that create osmotic potential in the guard cells and control stomatal movements are,

a. Hydrolysis of starch into sugars in guard cells

b. Synthesis of sugars or organic acids in guard cells

c. The active pumping of K+ ions and, Cl- ions or organic acid counter ions into the guard cells

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.
- There may be some build up of organic acids, chiefly malic acid during this period in guard cells.

- The formation of malic acid would produce proton that could operate in an ATP-driven H+/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 (decreasing water potential) of the guard cells and leading to stomatal opening.
- The reverse process would occur in darkness.

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 in to the adjacent epidermal cells and in exchange K+ ions are pumped in to the guard cells from epidermal cells.
- The exchange of H+ and K+ ions is mediated through ATP and thus it is an active process.
- ATP is generated in non-cyclic photo phosphorylation in photosynthesis in the guard cells.
- The ATP required in ion exchange process may also come through respiration.
- The accumulation of K+ ion along with Cl- ions and organic acid is sufficient 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 guard cells in dark.

ABA Signaling Also Involves Ca2+-Independent Pathways

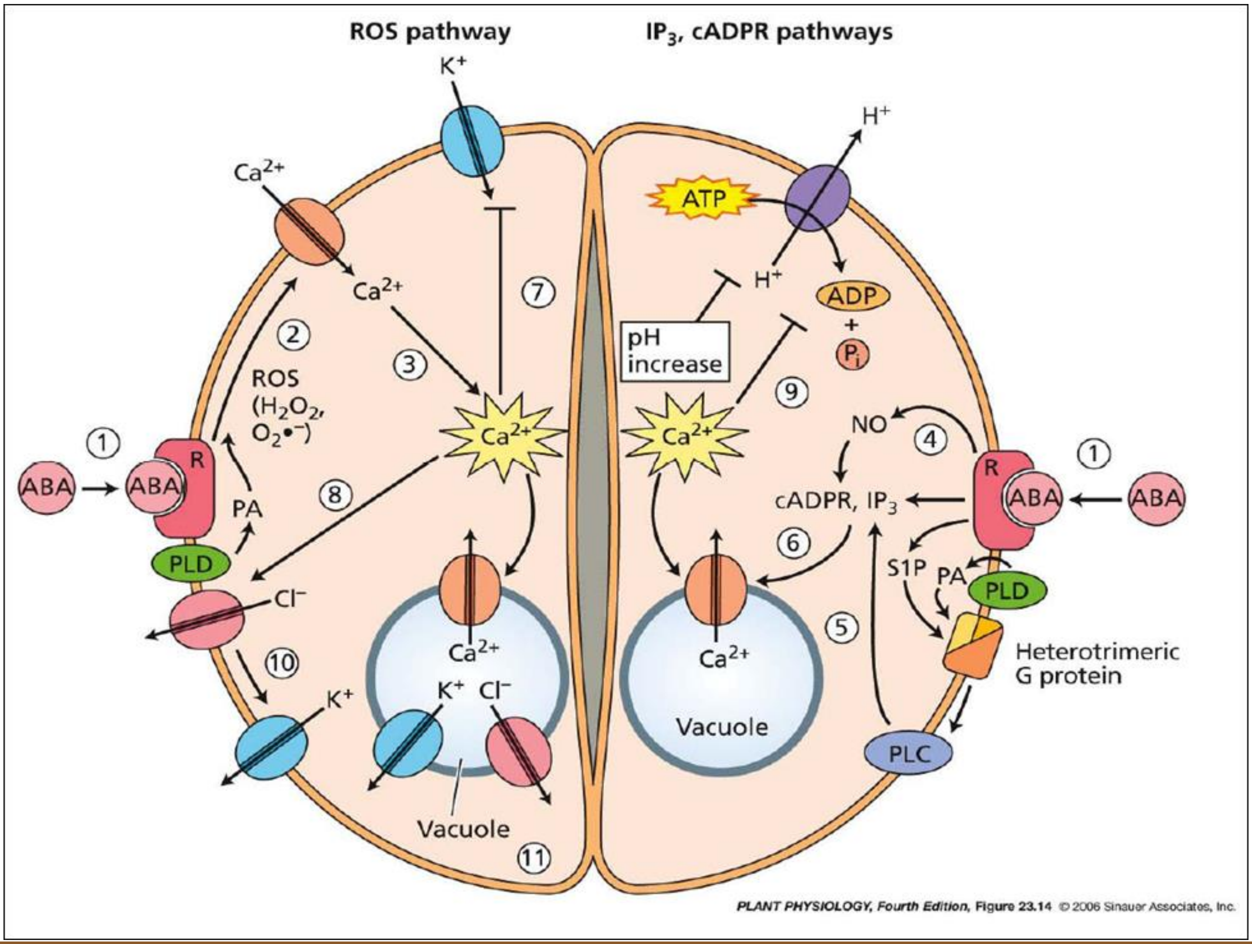
- Although an ABA-induced increase in cytosolic calcium concentration is a key feature of the current model for ABA-induced guard cell of stomat closure, ABA is able to induce stomatal closure even in guard cells that show no increase in cytosolic calcium (Allan et al. 1994). In other words, ABA seems to be able to act via one or more calcium-independent pathways.
- In addition to calcium, ABA can utilize cytosolic pH as a signaling intermediate. As previously discussed, a rise in cytosolic pH can lead to the activation of outward K+channels, and one effect of the abi1 mutation is to render these K+ channels insensitive to pH.
- Such redundancy in the signal transduction pathways explains how guard cells are able to integrate a wide range of hormonal and environmental stimuli that affect stomatal aperture, and such redundancy is probably not unique to guard cells.A simplified general model for ABA action in stomatal guard cells is shown in Figure For clarity, only the cell surface receptors are shown.

1. ABA binds to its receptors. **2.** ABA-binding induces the formation of reactive oxygen species, which activate plasma membrane Ca2+ channels. **3.** ABA increases the levels of cyclic ADP-ribose and IP3, which activate additional calcium channels on the tonoplast. **4.** The influx of calcium initiates intracellular calcium oscillations and promotes the further release of calcium from vacuoles. **5.** The rise in intracellular calcium blocks K+ in channels. **6.** The rise in intracellular calcium promotes the opening if Cl–out (anion) channels on the plasma membrane, causing membrane depolarization. **7.** The plasma membrane proton pump is inhibited by the ABA-induced increase in cytostolic calcium and a rise in intracellular pH, further depolarizing the membrane. **8.** Membrane depolarization activates K+ out channels. **9.** K+ and anions to be released across the plasma membrane are first released from vacuoles into the cytosol.

TOP

3. Simple diffusion of water vapour from intercellular spaces to outer atmosphere through stomata.

The last step in the mechanism of transpiration is the simple diffusion of water vapours from the intercellular spaces to the atmosphere through open stomata. The intercellular spaces are more saturated with moisture on comparison to the outer atmosphere in the vicinity of stomata and the difference in the moisture content causes the diffusion of water vapour.



Significance of Transpiration

Significance of Transpiration

- Plants waste much of their energy in absorbing large quantities of water and most of which is ultimately lost through transpiration.
- Transpiration is a unique feature in the plant system and referred as necessary evil as it is advantageous to plant under certain circumstances and harmful in some other situations.

I. Transpiration is necessary

1. Role in the movement of water

- Water plays an important role in the upward movement of water i.e. Ascent of sap in plants.
- But, it does not mean that the translocation of water will be stopped without it.

2. Role in the absorption and translocation of mineral salts

- Absorption of water and mineral salts are entirely independent process.
- Therefore transpiration has nothing to do with the absorption of mineral salts.
- However, once mineral salts have been absorbed by the plants, their further translocation and distribution may be facilitated by transpiration through translocation of water in the xylem elements.

3. Role of regulation of temperature

- Some of the light energy absorbed by the leaves is utilized in photosynthesis, rest is converted into heat energy which raise the leaf temperature.
- Transpiration plays an important role in controlling the temperature of the plants.
- Rapid evaporation of water from the aerial parts of the plant through transpiration brings down the temperature and thus prevents them from excessive heating.

- Transpiration is one of the chief ways for the dissipation of excess energy, which the plant receives from the sun.
- Shull (1930) estimated that approximately 0.8 cal of energy is received upon each square cm of leaf surface per minute, of which about 10% is reflected and 25% is transmitted.
- The remaining 65% (0.52 cal) will increase the temperature of the leaves very rapidly.
- If the weight of the leaf tissue is 0.02g/cm2 with the specific heat of 0.879, then the rise in temperature would be at 32°C per minute.
- With this rate of increase in temperature, the plants will be killed in less than two minutes, if there is no dissipation of energy.
- Transpiration plays a significant role here.
- It helps in dissipating this excess energy which will otherwise raise the temperature.

4. Role on growth and development:

- Winneberger (1958) has observed that the buds of hardy pear cease to grow under conditions of high humidity and that under the same conditions growth of the sunflower plant is reduced to about half of the normal.
- So it is clear that transpiration is necessary factor in the normal growth of these two plants.
- Most important point is that cell growth depends on absorption of water

which is passively absorbed by the roots of plants due to transpiration pull.

- Plants showing high rate of transpiration exhibit adequate development of mechanical tissues. Transpiration also shows that plants showing high rate of transpiration exhibit extensive root system.

5. Involves in improvement in the quality of fruits:

- Increased sugar and mineral contents of fruits follows high rate of transpiration.

6. Transpiration help in hardening process:

- Transpiration induces hardening which imparts resistance of plant to drought.

7. Transpiration help in removal of excess water:

- It has been held that plants absorb far more amount of water than is actually used by the plant by the plant. Transpiration removes excess of water.

TOP

Transpiration as a Necessary evil

- It is a vital and unavoidable phenomenon of plants.
- The loss of water does not serve any good purpose in plant life. Besides,

the transpiration also consumes energy and causes unnecessary absorption of excess water by roots. Nevertheless, the internal structure is basically meant for the exchange of gases during photosynthesis and respiration.

- When the rate of transpiration is high and soil is deficient in water, internal water deficit is created in the plants which may affect metabolic processes.
- Many xerophytes have developed structural modification and adaptation to check transpiration.
- Deciduous trees have to shed their leaves during autumn to check loss of water.

But, in spite of the various disadvantages,

- The plants cannot avoid transpiration due to their peculiar internal structure, particularly those of leaves.
- Their internal structure although basically mean for gaseous exchange for respiration, photosynthesis etc., it cannot check the evaporation of water.
- Therefore, many workers like Curtis (1926) have called transpiration as necessary evil.

Factors affecting Transpiration

The factors affecting rate of transpiration can be categorized under two groups:

1. **External or Environmental factors** (eg. atmospheric humidity, temperature, wind velocity, light, water supply, atmospheric pressure, sprays and dusts and vital activities)
2. **Internal or Structural factors** (eg. stomatal apparatus and its frequency, water content of mesophyll cells and structural peculiarities of the leaf).

A. External factors

1. Atmospheric humidity

- When the atmosphere is humid, the rate of transpiration is reduced.
- It is because atmosphere is more saturated with moisture and retards the diffusion of water vapour from the intercellular spaces of the leaves to the outer atmosphere through stomata.
- In dry atmosphere, the RH is low and the air is not saturated with moisture and hence, the rate of transpiration increases.

2. Temperature

- An increase in temperature brings about an increase in the rate of transpiration by lowering the relative humidity and wider opening of stomata.

3. Wind

- When wind is stagnant (not blowing), the rate of transpiration remains normal
- When the wind is blowing gently, the rate of transpiration increases as it removes moisture from the vicinity of the transpiring parts of the plant thus facilitating the diffusion of water vapour from the intercellular spaces of the leaves to the outer atmosphere though stomata.
- When the wind is blowing violently, the rate of transpiration decreases as it creates hindrance in the outward diffusion of water vapours from the transpiring part and it may also close the stomata.

4. Light

- Light increases the rate of transpiration as stomata remain open under light conditions coupled with increased temperature.
- In dark, due to closure of stomata, the stomatal transpiration is almost stopped.

5. Available soil water

- The rate of transpiration will decrease if the available soil water is not sufficient enough for easy absorption by the roots.

6. CO2

- An increase in the atmospheric CO2 concentration and the concentration inside the leaf causes stomatal closure and reduced transpiration.

TOP

B. Internal factors

1. Internal water conditions

- It is very essential for transpiration.
- Deficiency of water in the plants results in decrease of transpiration rate.
- Increased rate of transpiration continuing for longer periods often create internal water deficit in plants as absorption of water does not keep pace with it.

2. Structural features

- The number, size, position and the movement of stomata affect rate of transpiration.
- In dark, stomata are closed and stomatal transpiration is checked.
- Sunken stomata help in reducing the rate of stomatal transpiration.
- In xerophytes, the leaves are reduced in size or may even fall to check transpiration.
- Thick cuticle and the presence of wax coating on exposed parts reduce

cuticular transpiration.

(a) Leaf area

- Greater the leaf area greater will be the magnitude of transpiration.
- On the per unit basis smaller plants often transpire at a greater rate than do larger plants.
- Larger plants loose more but on per unit area basis smaller plants loose more.

(b) Leaf structure

Leaf structure determines the rate of transpiration in three ways.

(1) Thickness of cuticle

(2) Number, density and thickening of the epidermal hairs.

(3) The ratio of internal exposed surface area to the external exposed surface area of the leaf. Cuticular transpiration depends on the degree of its thickness. The epidermal hairs increase the thickness of the adherent stationary air. They reduce the rate of transpiration. If more of the leaf cells are exposed to the intercellular spaces the internal air of the leaf will tend to become saturated rapidly losing more water in transpiration.

(c) Stomata

- The Rte of transpiration is influenced by the number, spacing, distribution structural peculiarities, size of the stomatal aperture and the periodicity of the stomatal opening.
- The rate of transpiration in is little in xerophytes because their stomata remain open during the night and closed during the day.
- Sunken stomata reduce the rate of transpiration.

(d) Leaf orientation

- Solar radiations cause more heating when the flat surface of the leaf lies perpendicular to the incident light.
- The effect is minimum when it lies parallel to it as found in compass paints Lactuca.
- Leaves of Eucalyptus hang downwardly to avoid overheating during the hot periods of the day.

(e) Leaf size and shape

- With the decrease in the leaf size the rate of transpiration decreases.
- It is very little in needle shaped leaves

(f) Leaf modifications

  - Like spines, thorns and scales show reduced rate of transpiration.

(g) Root shoot ratio

- Parker found that transpiration increases with increase in root shoot ratio.
- Sorghum typically transpires at higher rate than corn plant per unit of leaf surface.
- Muller has pointed out that the secondary root development is much more advanced in Sorghum than that in corn.

Mucilage and solutes

- They decrease the rate of transpiration by holding water tenaciously.

(i) Water content of the leaves

- Optimum transpiration continues only when the leaves have sufficient moisture.
- Low water content of the leaf generally brings down the rate of transpiration by decreasing water vapor pressure inside the leaf and closure of the stomata.

(j) Diseases

- The rate of transpiration is generally higher in the diseased plants as compared to healthy ones.

TOP

Lecture. 17. Stress Physiology Cont..

Tolerance of stress in plants

Mechanism of tolerance of plant to stress

- In general two types of stress resistance are recognized and these are avoidance and tolerance. In the avoidance an internal environment is created within the plants so that, its cells are not put under stress. In case of tolerance, plant has the capacity to withstand stress. In some species both the characters may be present.
- Plants experience usually drought which is one of the commonest stress. Plants have developed several mechanisms to tide over this stress such as development of thick cuticle, sunken stomata, formation of seeds with low water contents, completion of life cycle in short duration by the desert plants are some of the measures adopted by plants against drought.
- In some plants water is retained in enough quantities, or the leaves are reduced to scales.
- Dehydration leads to loss of water molecules and thus proteins are disrupted.
- Water molecules have several functions to perform and one of these is to help to keep complex fluids in a stable configuration.
- Water loss leading to high concentration of cell sap and intercellular fluid

causes a greater decrease in the water potential of the fluid, this cause stress on the protoplasm and change in the cell pH also be there.

- Most of the biochemical processes are adversely affected because of the water imbalance.

On the basis of plant's response to available water, the plants are usually classified into three categories

- 1. *Hydrophytes*: the plants growing at a place where water is always available e.g., in a ponds.
- 2. *Xerophytes*: the plants growing at places such as deserts, where water is scarce at most of the time.
- 3. *Mesophytes*: the plants growing at places where water availability is intermediate.

- Plants have developed several mechanisms to tolerate drought conditions. One of these is the presence of hydrophilic substances in the protoplasm like high molecular weight protein, some carbohydrates (eg alginic acid), low molecular compound like polyhydric alcohols acts as hydrophilic compounds.
- These attributes are very common in sea weeds which are subjected to high and low tides. Sugars are usually accumulated in drought conditions

in such plants, since their presence in solution directly lowers the water potential of cell sap. This helps the plants to retain and conserve water and save the protoplasm from desiccation.

- Xerophytes in the desert are actually exposed to wide range of water potentials.
- Plants such as palms that grow at an oasis where, their roots reaches the water table or other plants such as mesquit (Prosopis glandosa) and alfalfa (Medicago sativa) that have roots that extend as much as 50 m down to the water table never experience extremely negative water potential. They are called as water spenders. They certainly avoid the drought. Of course seeds plants must be able to use the available soil water while they are extending their roots to the water table.
- So called desert ephemerals (is one marked by short life cycles, usually six to eight weeks. The word ephemeral means transitory or quickly fading.) are annual plants that escape the drought by existing only as dormant seeds during the dry season. When enough rainfall to wet the soil to a considerable depth, these seeds often germinates, perhaps in response to the leaching away of germination inhibitors.
- Many of these plants grow to maturity and set at least one seed per plant before all soil moisture has been exhausted. They are well suited to dry region and thus are xerophytes in the true sense of the word, yet their active and metabolizing protoplasm is never exposed to extremely negative water potential and is not drought hardy.

- Succulent species such as cacti, century plant (Agave americana) and various other CAM plants are water saver. They resist the drought by storing water in their succulent tissue. Enough water is stored and its rate of loose is so extremely low (because of an exceptionally thick cuticles and sotmatal closure during the day times) that they can exist for long periods without added moisture.
- Succulents are drought avoidance but not truly drought tolerant. The water potential in this tissue is often -1.0 MPa. Some of the succulents especially the cacti have extensive shallow root system, which is capable of absorbing surface moisture after a storm. Of course the moisture is then stored in these succulent tissue.
- Many other desert plants also have several adaptations that reduce water loss, although they don't actually store water in succulent tissue. The adaptations are small leaf blades, increases heat transfer by convection, lowering leaf temperature and thus reducing transpiration.
- Other adaptation that apparently reduces transpiration includes sunken stomata, shedding of leaves during dry periods and have heavy pubescences on leaf surface. Although these modification may reduce the water lose, they never completely prevent it and are by themselves insufficient to protection against extreme drought.

Sunken stomata of spruce needle conifer

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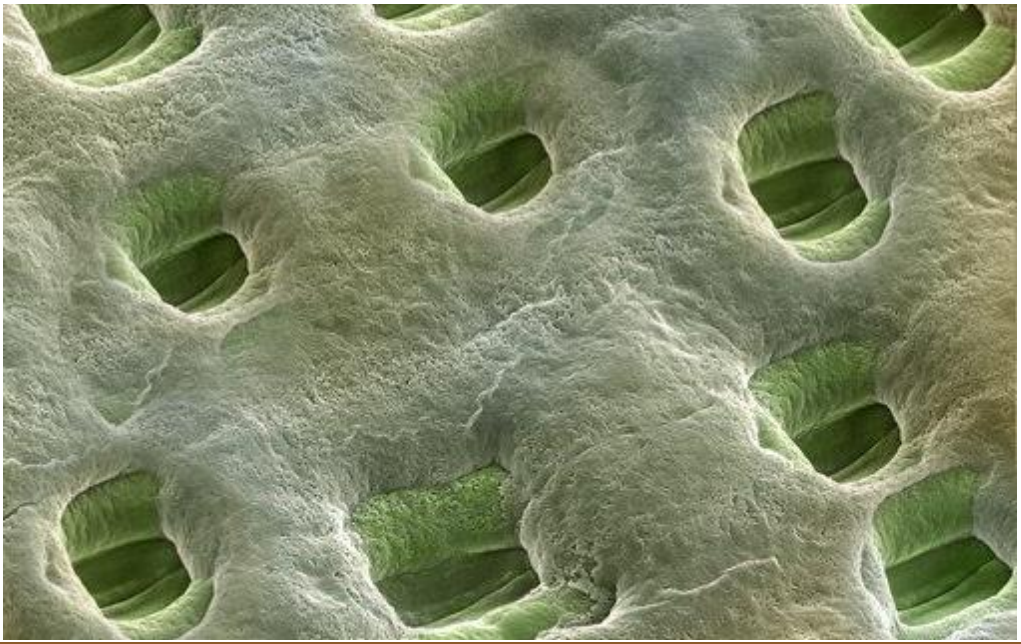


Drought Resistance

Drought resistance

1. Drought avoidance/ drought postponement
2. Drought tolerance

Drought avoidance/ drought postponement: Ability to maintain tissue hydration or plants ability to maintain a high level of water status or turgor under conditions of increasing soil water deficits.

Dehydration tolerance: Ability to function while dehydrated is called as dehydration tolerance mechanism which maintains tissue hydration during drought

Reduction in water loss

a) Reduction in transpiration area

b) Stomatal behaviour: It is governed by

- Uptake/lose of K – changes in osmotic potential of guard cells
- Metabolic changes involving organic acids ex: Malate
- Hormones – ABA and cytokinines

c) Waxiness

d) Leaf rolling

e) High hydraulic resistance by decreasing the diameter of xylem

f) Root to shoot signaling: (Conservative approach) ABA synthesized in drying roots moves to the shoot and regulates leaf conductance, leaf expansion and thus brings about reduction in water lose (Drought postponement)

- Water is conserved for further use in later stages
- Early warning/signal

g) WUE: Balance between water used or water availability with respect to biomass production (at canopy level). At whole plant level it is the ratio between the photosynthesis and transpiration. When there is decline water potential- shoot growth is completely ceased but root growth will continue even under severe stress condition

h) Root characteristics: Uptake of water

Mechanism which are related to the ability to function while dehydrated

1. *Membrane integrity*: Ability of a cell to maintain structure and function of membrane especially to prevent electrolyte leakages.

2. *Osmotic adjustment*: Adaptional response to decrease the water potential in the extreme environment resulting in increased accumulation of compounds like proline, glycine betain, manitol, sorbitol, etc in the cell is called as osmoregulation or osmotic adjustment. Mechanism to maintain the turgor even at low water potential is extremely important for saline adaptation.

3. *Stress proteins*: Proteins of smaller molecular weight are synthesized by organisms as a physiological response to environmental stress for cellular protection. eg., heat shock proteins, dehydrins, osmotins, etc

TOP

Lecture 8
Plant antitranspirants

The chemicals or substances applied to the transpiring surface with the aim to reduce transpiration are called antitranspirants. Antitranspirants will reduce transpiration without reducing the assimilation rate

Examples: ABA (5 to 10 ppm), CCC (1000 ppm), Alar (200 ppm), Simazine (50 ppm), Silicon (100 ppm), etc

There are three types of antitranspirants.

i) Stomatal closing type

These antitranspirants reduce the closure of stomata and reduce the rate of transpiration. Since the stomata are made to close, the rate of CO_2 diffusion into the leaf is also reduced leading to low photosynthetic rates.

eg. Phenyl Mercuric Acetate (PMA), Abscisic Acid (ABA) and high CO_2 concentration

CO_2 is an effective antitranspirant. A little rise in CO_2 concentration from the natural 0.03% to 0.05% induces partial closure of stomata. Its higher concentration cannot be used as this result in complete closure of stomata affecting adversely, the photosynthesis and respiration.

PMA is widely used chemical for stomatal closer. It has the ability to close the stomata but it has a disadvantage that it is toxic to fruits and vegetables. This chemical also inhibits phosphorylation and hence damages the foliage by blocking photosynthesis

Herbicides such as triazine, atrazine, simazine which are the inhibitors of ETC at QA and QB sites but at the lower concentration they can also be used as antitranspiratns.

ii) Film forming type

This type forms a thin film coating on the surface of leaf and inhibits the loss of water vapour from the leaf. But they allow CO_2 to pass into the leaf through lower epidermis.

E.g. Waxes, Plastic films, Silicone oils

Disadvantages:

- Affects only at low temperature but not at high temperature
- Comes in the way of gas exchange.
- Form the mechanical barrier for stomatal movement

iii) Reflective type

The principle of using this type of chemicals is to increase the light reflection by the leaves, thus decreasing the leaf temperature or head load on the leaf. The water loss is reduced without affecting the CO_2 assimilation. E.g. Kaolinite (Kaolin), Lime water (Lime wash)

Kaoline when applied it forms white thin film. Usually it is sprayed at 2-5 per cent and forms thin coating on the leaf

Function: Reflects radation falling on the leaf and reduces heat load on leaf. When heat load is reduced amount of water to maintain temperature is also reduced. Therefore water conservation occurs. Kaoline doesn’t come in the way of any metabolic activity.

Features of ideal antitranspirent

1. Non toxic to plants
2. Non permanent damages to stomatal mechanism. Specific effect should be on guard cells and not to the other cells
3. Chemical should be cheaply and readily available

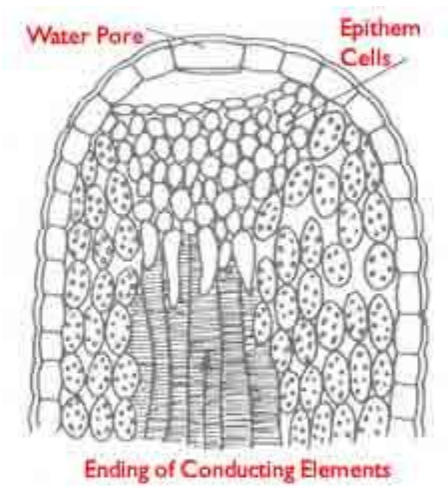
Use of antitraspirants

1. To reduce transpiration of high value fruits and vegetable plants.
2. Helps in ornamental horticulture
3. Usage in water curing for lawns

GUTTATION

In some plants such as tomato and *colocasia*, water drops ooze out from the uninjured margins of the leaves where a main vein ends. This is called as *guttation* and takes place usually early in the morning when the rate of absorption and root pressure are high while the transpiration is very low.

The phenomenon of guttation is associated with the presence of special types of cellsat the margins of the leaves which are called as *water stomata or hydathodes*. Each hydathode consists of a water pore that remains permanently open. Below this, there is a small cavity followed by a loose tissue called as *epithem*. This epithem is in close association with the ends of the vascular elements of veins. Under high root pressure, the water is given to the epithem by the xylem of the veins and from epithem, water is released into the cavity. When this cavity is completely filled with watery solution, it begins to ooze out in the form of watery drops through the water pore.



http://www.studentsguide.in **http://www.bio.miami.edu**

Under higher root pressure, water is given to the epithem by the xylem of the veins. From epithem, the water is released into the cavity. When this cavity is completely filled with the watery solution, the latter begins to ooze out in the form of watery drops through the water pore.

Differences between Transpiration and Guttation

	Transpiration	Guttation
1.	Transpiration takes place throughout the day and the rate is maximum at noon.	Guttation takes place at night and in the early morning
2.	It does not depend on root pressure	Depends on root pressure
3.	Water is lost from aerial parts of plants in the form of invisible water vapour	Watery solution oozes out from uninjured margins of aerial leaves.
4.	Transpiration occurs mostly through stomata. It may also take place through cuticle and lenticels	It occurs only through hydathodes (water stomata)
5.	Transpired water is pure	Guttation fluid contains salts and sugars as aqueous solution.
6.	The leaf temperature is reduced	There is no such effect

Differences between Transpiration and Evaporation

	Transpiration	Evaporation
1.	It is a physiological process that occur in plants	It is a physical process that occur on any free surface
2.	Living cells are involved	Both living and non living cells are involved
3.	It causes wetness on the surface of leaves and young stems	It causes dryness of the surface
4.	Vapour pressure, diffusion pressure and osmotic pressure are involved	No osmotic pressures are involved

BLEEDING

The exudation of water and cell sap through the cuts or wound of plants is called as *bleeding*. It also happens due to positive root pressure. In certain plants the pressure is developed either in the phloem elements or in the cells surrounding the cut or wounds. The exudations of toddy juice form the wounded stem of Borassus and latex form rubber stem are the examples of bleeding. It has been utilized in the production of various economically important products link rubber, sugar and alcoholic drinks.

FIGURE 1 - Exudation of reddish-brown liquid through cracks on a coconut trunk.

http://www.scielo.br/img

Rubber latex

http://img.alibaba.com

Reference:

1. Plant physiology – III Ed. Taiz and Zeiger: http://4e.plantphys.net/
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Lecture 9
MINERAL NUTRITION

In order to complete the life cycle normally, the living organism requires large number of substances from outside. This is called as **nutrition.** Thus, the plant growth and development can proceed only when the plants are applied with the chemical elements referred as **Essential Elements.** These nutrients are absorbed by plant root from the soil. Chemical analysis of the plant ash has shown that plants contain about 40 different elements. Some of them are indispensable or necessary for the normal growth and development of the plants and they are called as **Essential Elements**. Rests of the elements are called as **Non-essential elements.** It is now known that the following 16 elements are essential for majority of the plants: C, H, O, N, P, K, Ca, S, Mg, Fe, Zn, B, Cu, Mu, Cl and Mo. Besides these, Al, Si,, Na, Co and Ga may be essential for some plants.

Essential elements may be classified into three groups:

1. Major elements or Primary nutrients

The essential elements, which are required by the plants in comparatively larger amounts, are called **Major Elements or Primary Nutrients.** C, H, O, N, P and K.

2. Secondary elements or Nutrients

These elements are also required by the plant in larger quantity next to primary nutrients. Examples are: Ca, Mg and S.

3. Minor elements or Micronutrients or Trace elements

The essential elements required in smaller amounts or traces by the plants are called as Minor or Trace Elements. They are: Fe, Mn, Cu, Zn, Mo, B and Cl. Apart from these elements, recently some more elements have also been shown to the essential for the normal growth of some plants such as Na for Atriplex, Si for rice and Cl for coconut and Al, Va and Co for ferns.

Classification of Plant mineral nutrients according to their Biochemical functions	
Mineral Nutrient	**Functions**
Group 1	**Nutrients that are part of carbon compounds**
N	Constituent of amino acids, amides, proteins, nucleic acids, nucleotides, coenzymes, hexoamines, etc.
S	Component of cysteine, cystine, methionine, and proteins. Constituent of lipoic acid, coenzyme A, thiamine pyrophosphate, glutathione, biotin, adenosine-5'-phosphosulfate, and 3-phosphoadenosine.
Group 2	**Nutrients that are important in energy storage or structural integrity**
P	Component of sugar phosphates, nucleic acids, nucleotides, coenzymes, phospholipids, phytic acid, etc. Has a key role in reactions that involve ATP.
Si	Deposited as amorphous silica in cell walls. Contributes to cell wall mechanical properties, including rigidity and elasticity.
B	Complexes with mannitol, mannan, polymannuronic acid, and other constituents of

	cell walls. Involved in cell elongation and nucleic acid metabolism.
Group 3	**Nutrients that remain in ionic form**
	Required as a cofactor for more than 40 enzymes. Principal cation in establishing cell turgor and maintaining cell electroneutrality.
Ca	Constituent of the middle lamella of cell walls. Required as a cofactor by some enzymes involved in the hydrolysis of ATP and phospholipids. Acts as a second messenger in metabolic regulation.
Mg	Required by many enzymes involved in phosphate transfer. Constituent of the chlorophyll molecule.
Cl	Required for the photosynthetic reactions involved in 0_2 evolution.
Mn	Required for activity of some dehydrogenases, decarboxylases, kinases, oxidases, and peroxidases. Involved with other cation-activated enzymes and photosynthetic 0_2 evolution.
Na	Involved with the regeneration of phosphoenolpyruvate in C_4 and CAM plants. Substitutes for potassium in some functions.
Group 4	**Nutrients that are involved in redox reactions**
Fe	Constituent of cytochromes and nonheme iron proteins involved in photosynthesis, N_2 fixation, and respiration.
Zn	Constituent of alcohol dehydrogenase, glutamic dehydrogenase, carbonic anhydrase, etc.
Cu	Component of ascorbic acid oxidase, tyrosinase, monoamine oxidase, uricase, cytochrome oxidase, phenolase, laccase, and plastocyanin.
Ni	Constituent of urease. In N_2-fixing bacteria, constituent of hydrogenases.
Mo	Constituent of nitrogenase, nitrate reductase, and xanthine dehydrogenase

Source: http://xa.yimg.com/kq/groups/21666630/1921577070/name/CH--Mineral-Nutrition.pdf

Adequate tissue levels of elements that may be required by plants			
Element	**Chemical symbol**	**Concentration in dry matter (% or ppm)**	**Relative number of atoms with respect to molybdenum**
Obtained from water or carbon dioxide			
Hydrogen	H	6	60,000,000
Carbon	C	45	40,000,000
Oxygen	0	45	30,000,000
Obtained from the soil			
Macronutrients			
Nitrogen	N	1.5	1,000,000
Potassium	K	1.0	250,000
Calcium	Ca	0.5	125,000
Magnesium	Mg	0.2	80,000
Phosphorus	P	0.2	60,000

Sulfur	S	0.1	30,000
Silicon	**Si**	0.1	30,000
Micronutrients			
Chlorine	Cl	100	3,000
Iron	Fe	100	2,000
Boron	B	20	2,000
Manganese	Mn	50	1,000
Sodium	Na	10	400
Zinc	Zn	20	300
Copper	Cu	6	100
Nickel	Ni	0.1	2
Molybdenum	Mo	0.1	1

The values for the non mineral elements (H, C, O) and the macronutrients are percentages. The values for micronutrients are expressed in parts per million.

Source: *http://xa.yimg.com/kq/groups/21666630/1921577070/name/CH--Mineral-Nutrition.pdf*

Micronutrients are usually present in the plants in different chemical forms as:

1. Inorganic ions
2. Undissociated molecules or
3. Organic complexes as chelates

Criteria of Essentiality of Elements (Arnon and Stout, 1939)

In order to show that element is truly essential, it is necessary to show that:

i. A deficiency of the element makes it impossible for a plant to complete its vegetative and reproductive cycle
ii. It cannot be replaced by another element and
iii. The element should also have some part to play in metabolism of the organism etc.

Nutrient Availability in Soil Solution

Soil serves as a main source of mineral salts in which clay crystals are present in colloidal form. These crystals have a central nucleus called **micelle.** The micelles are negatively charged and in order to maintain a balance, they attract and hold positively charged ions on the surface of the colloidal clay crystals. Thus, the balance is always maintained.

The available minerals of soil occur in ionic forms.

The common cationic forms are : K,Mg,Ca, Fe,Mn,Cu,Zn and Co while anionic forms and N,P,B,S and Cl. These ions are found either in the form of loosely absorbed ions or firmly absorbed ions on the colloidal particles. The order of cation retentive capacity of colloids is as follows:

H+ > Ca++ > Mg++ > K+ > NH4 + > Na+

The loosely absorbed ions can be easily displaced by decreasing their own concentration in the soil solution while the firmly absorbed ions can be replaced by other ions which have more affinity for the colloid or ion exchange. The ion exchange may be either cation exchange or anion exchange.

Availability of Mineral Salts

Mineral salts are found either as soluble fraction of soil solution or as adsorbed ions on the surface of colloidal particles. It is believed that the uninterrupted supply of mineral nutrient from the absorbed fractions is possibly done by ionic exchange.

Ion Exchange

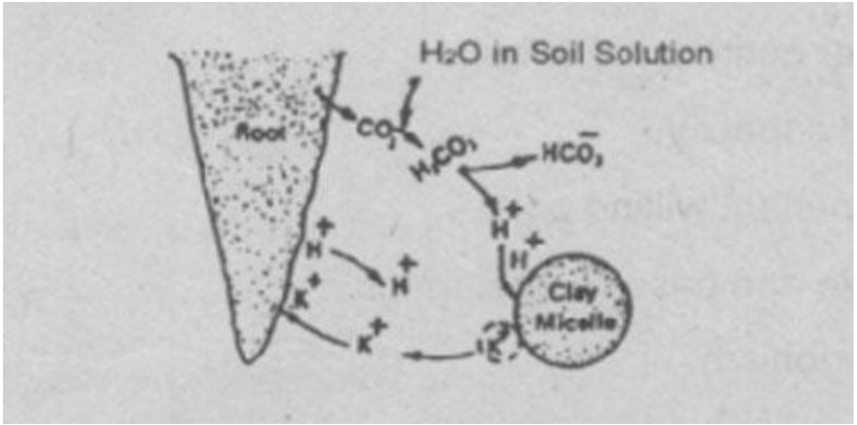
First step in the absorption of mineral salts is the process of **Ion-Exchange** which does not require metabolic energy but greatly facilitates mineral salt absorption. The ions adsorbed on the surface of the wall or membranes of root cells may be exchanged with the ions of the same sign from external solution. For example, the cation K+ of the external soil solution may be exchanged with H+ ion adsorbed on the surface of the root cells. Similarly, an anion may be exchanged with OH- ion.

There are two theories proposed to explain the mechanism of ion exchange:

a. CO_2 hypothesis (or) Carbonic Acid Exchange Theory
b. Cation Exchange hypothesis (or) Contact Exchange Theory.

a. CO_2 hypothesis

According to this theory, CO_2 released by the roots during respiration, combines with water to produce carbonic acid (H_2CO_3). The carbonic acid dissociates into hydrogen ions (H^+) and bicarbonate ions (HCO_3). These hydrogen ions may be exchanged for cations adsorbed on clay particles. The cations thus released into the soil solution from the clay particles may be absorbed on root cells in exchange for H^+ ions. While the dissociated bicarbonate ions release the adsorbed anions. Thus, both cations and anions are made available to the closeness of the roots of plants. Thus, soil solution plays an important role in carbonic acid exchange theory.

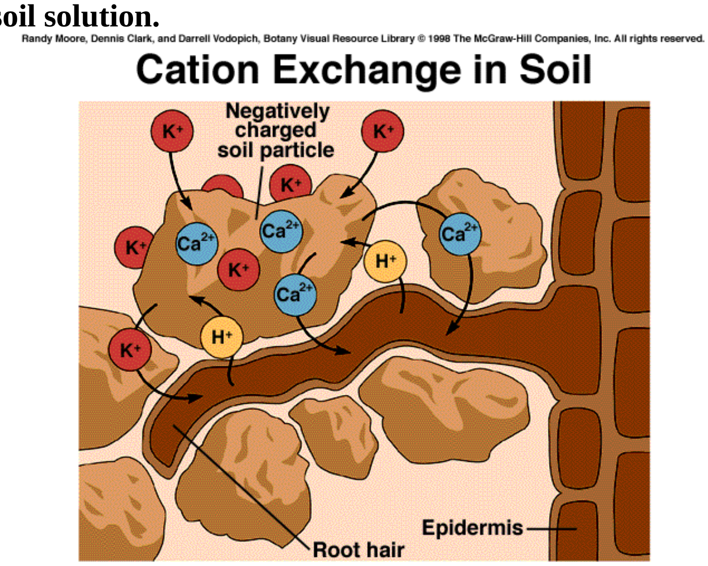


CO_2 hypothesis

http://www.about-knowledge.com/wp-content/uploads/2009/05/carbonic-acid-exchange.jpg

b. Cation Exchange hypothesis

This theory states that the ions adsorbed on the surface of root cells and clay particles (micelles) are not held tightly but always oscillate within small volume of space. If the roots and clay particles are in close contact with each other, the oscillation volume of ions adsorbed on root-surface may overlap volume of ions adsorbed on clay particles. Then, the ions adsorbed on clay particle may be exchanged with the ions adsorbed on root surface **directly without first being dissolved in soil solution.**



Cation exchange theory

http://www.mhhe.com/biosci/pae/botany/uno/graphics/uno01pob/vrl/images/0662.gif

Mechanism of Mineral uptake by Plants

Previously, it was thought that the absorption of mineral salts from the soil took place along with the absorption of water, but it is now well established that the mineral salt absorption and water absorption are two independent processes. Mineral salts are absorbed from the soil solution in the form of ions. They are chiefly absorbed through the

meristematic regions of the roots near tips. Plasma membrane of the root cells is not permeable to all the ions. It is **selectively permeable.** All the ions of the same salt are not absorbed at equal rate but there is **unequal absorption of ions.**

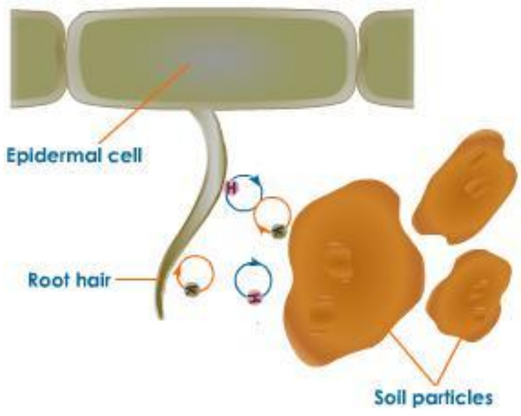
First step in the absorption of mineral salts is by Ion Exchange. Once the nutrients come and adsorb on the surface of the walls or the membranes of root cells, then the further process of the absorption of mineral salts may be of two types. They are:

1. Passive Absorption
2. Active Absorption

Various theories have been proposed to explain the mechanism of mineral salt absorption, which can be of two categories:

1. Passive Absorption of Mineral Salts

When the concentration of mineral salts is higher in the outer solution than in the cell sap of the root cells, the mineral salts are absorbed according to the concentration gradient by simple process of **diffusion.** This is called as passive absorption because it does not require expenditure of metabolic energy. This can also be called as **Physical Absorption.** This process is not affected by temperature and metabolic inhibitors. This theory is based on the movements of ions from the region of its higher concentration to the lower concentration. Therefore, the direction of the initial uptake gets reversed if the tissues are transferred back to a low concentration. Important theories are Mass Flow, ion exchange and Donnan equilibrium.



Contact Exchange Theory

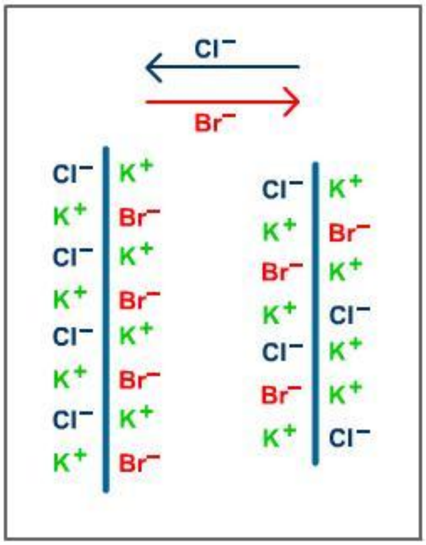
http://image.wistatutor.com/content/plant-nutrition/contact-excahnge-theory-illustration.jpeg

i. Mass Flow Theory (Bulk Flow)

According to this theory, the ions are taken up by the roots along with mass flow of water under the influence of transpiration. Therefore, transpiration effect on salt absorption is direct.

ii. Ion Exchange Theory

According to this theory, ions from the external solution in which the tissue is immersed may exchange with the ions absorbed on the surface of the cell wall or membranes of the tissue.



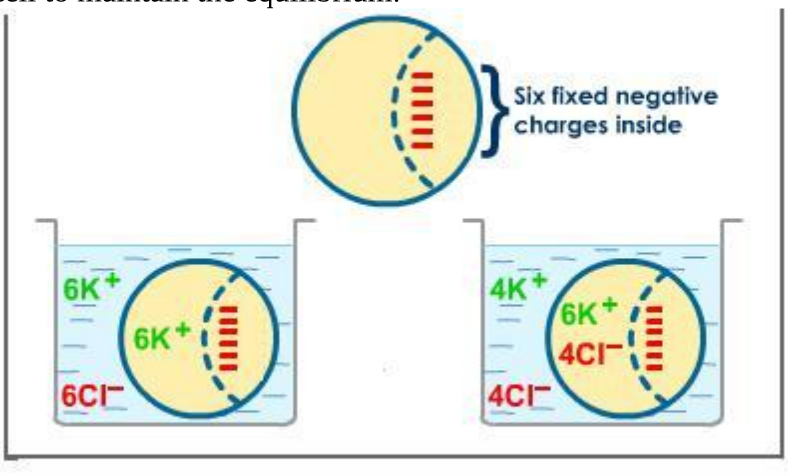
Ion Exchange Theory

Negatively charged Cl^- and Br^- are exchanged without disturbing the electrical neutrality

http://image.wistatutor.com/content/plant-nutrition/ion-exchange-theory.jpeg

iii. Donnan Equilibrium

This theory explains the accumulation of ions inside the cells without involving the expenditure of the metabolic energy. According to this theory, there are certain preexisting ions inside the cell, which cannot diffuse outside through membrane. However, the membrane is permeable to both anions and cations of the outer solution Normally, equal number of anions and cations would have diffused into the cell through an electrical potential to balance each other, but to balance the fixed anions already present in the cell (pre-existing), more cations will diffuse into the cell, and this equilibrium is known as **Donnan's Equilibrium.** In this particular case, there would be more accumulation of cations inside the cell. However, if there are fixed cations (preexisting) inside the cell, then the Donnan's equilibrium will result in more accumulation of anions inside the cell to maintain the equilibrium.



Explanation of Donnan's Equilibrium

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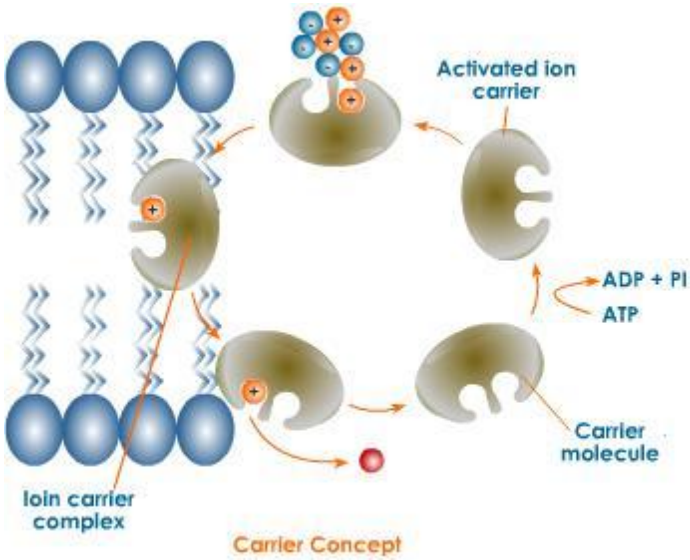
2. Active Absorption of Mineral Salts

This processes involves the metabolic energy for the transport of ions from soil solution to the plants. Based on the nature of participation of metabolic energy, various theories have been proposed. It includes the theories related with carrier concept such as Cytochrome Pump hypothesis, ATP theories, Protein-Lecithin as carrier theories etc.

i. Carrier Concept Theory (Honert, 1973) (for movement of both cation & anion)

According to this theory, the ion transport process is carried out by means of carriers, which may be organic molecules or vesicles. This theory explains that the plasma membrane is impermeable to free ions. The carrier combines with ions to form **carrier ion complex,** which can move across the membrane. On the inner surface of the membrane, this complex breaks releasing ions into the cell while the carrier goes back to the outer surface to pick fresh ions. Here, the metabolic energy is required in the process of formation of carrier-ion complex, its transport, and breakdown of complex, regeneration of carrier and movement of carrier molecules back.

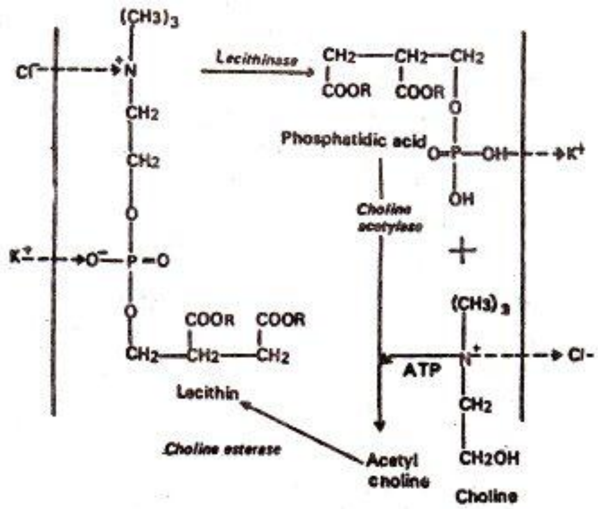


Explanation of carrier mechanism of ion uptake.

http://image.wistatutor.com/content/plant-nutrition/carrier-mechanism.jpeg

ii. Protein-lecithin as Carrier (Bennet-Clark, 1956) for uptake of both cation & anion

It is suggested that because the cell membranes chiefly consist of phospholipids and proteins and also certain enzymes seem to be located on them, the carrier could be a protein associated with the phosphotide (One of a large group of naturally occurring phospholipids that are derivatives of glycerol phosphate and which normally contain a nitrogenous base.) called as **lecithin.** This theory believes in the participation of some **amphoteric compounds** as carriers with which both cations and anions can combine.



Diagrammatic Schemes of Protein-lecithin theory

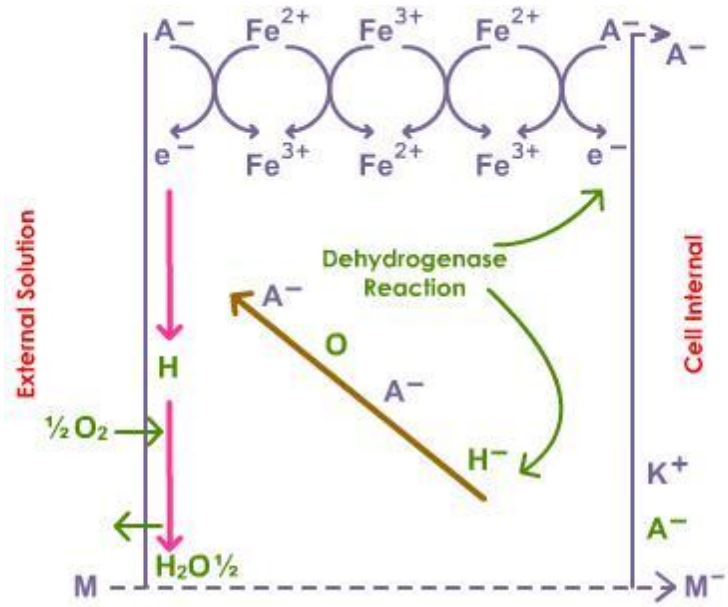
According to this theory,

1. The acidic phosphate group in the phosphatide is regarded as the active centre **binding the cation,** and the **basic choline group** (N+) as the **anion binding centre.**
2. The **ions are liberated** on the inner surface of the membrane by decomposition of the lecithin by the enzyme **lecithinase.**
3. The regeneration of the carrier lecithin from phosphatidic acid and choline takes place in the presence of the enzymes choline acetylase **and choline esterase and ATP.** The **ATP** acts as a source of energy.

iii. Cytochrome-pump Theory (For the movement of anions only)

Lundegardh and Burstrom (1933) claimed that a quantitative relaionship exists between anion absorption and respiration. When a plant is transferred from water to salt solution, the rate of respiration will increases. They called this increase in respiration as **Salt Respiration**. The actual transport of anions occurs through a cytochrome system.

1. Dehydrogenase reactions on inner side of the membrane give rise to protons (H^+) and electrons (e^-).
2. The electron travels over the cytochrome chain towards outside the membrane, so that the Fe of the cytochrome becomes reduced (Fe^{++}). on the outer surface and oxidized (Fe^{+++}) on the inner surface.
3. On the outer surface, the reduced cytochrome is oxidised by oxygen releasing the electron (e^-) and taking an anion (A^-)
4. The electron thus released unites with H^+ and oxygen to form water.
5. The anion (A^+) travels over the cytochrome chain towards inside.
6. On the inner surface, the oxidised cytochrome becomes reduced by taking an electron produced through the dehydrogenase reactions and the anion (A^+) is released.
7. As a result of anion absorption, a cation (M^+) move passively from outside to inside to balance the anion.



Diagrammatic representation of cytochrome pump hypothesis on salt absorption, anions (A^-) is actively absorbed via a cytochrome pump and cations (M^+) are passively absorbed.

http://image.wistatutor.com/content/plant-nutrition/cytochrome-pump-hypothesis-diagram.jpeg

iv. ATP Theories

According to this theory, ion uptake into the cell is energized by ATP molecules. The energy from hydrolysis of ATP molecules can be made available to energies ion pumps through the action of enzymes.

Case I

Here, the organic compound is first phosphorylated which on dephosphorylation makes the organic compound capable to combine with cation. The cation is released when phosphorylation occurs again.

Case II

In this case, the phosphorylated organic compound combines with cation and the cations are released on hydrolysis of the complex (dephosphorylation). Thus, the role of ATP in this theory is of two kinds. i.e., by removal or addition of phosphate group.

Reference:

1. Plant physiology – III Ed. Taiz and Zeiger: http://4e.plantphys.net/
2. Plant physiology – Salisbury and Rose.
3. www.**tnau**.ac.in/
4. Textbook of Plant physiology – Malik C. P and Srivastava.A. K.

Lecture 10

Factors Affecting Salt Absorption

Absorption of salt by the plants is affected by several factors. Some of them are discussed below.

i. Temperature

The increase in temperature increases both active and passive salt absorption processes and lowering of temperature decreases them.

ii. pH

It indirectly affects the salt absorption as the pH affects the availability of ions in the medium.

iii. Light

As opened stomata allow more transpiration and increased mass flow and photosynthesis provides energy and O_2 for salt uptake, light indirectly affects the rate of salt absorption by affecting the opening and closing of stomata and the process of photosynthesis.

iv. O_2 content

The deficiency of O_2 decreases salt uptake as the active phase of salt absorption is inhibited by the absence of O_2.

v. Interaction of other ions

The absorption of one ion may be influenced by the presence of other ion. The interaction may be associated with the availability and specificity of binding sites on carriers.

vi. Growth

Different types of growth affect salt absorption in different ways, eg., growth involving increase in surface area, number of cells, synthesis of new binding sites or carriers and volumes of water uptake stimulate salt absorption. Heavily suberised root is unable to absorb salts. Vegetative growth and increased metabolic activity accompanied with more water uptake enhance salt absorption.

Physiological Roles of Essential Elements

1. Nitrogen (N)

Source

Soil is the chief source of nitrogen. Plants absorb N either in the form of nitrate or ammoniacal salts. Some bacteria and heterocyst containing blue green algae fix N of atmosphere, which can be utilized by the plants.

Physiological Roles

1. Present in the structure of the protein molecule
2. It is found in important molecules like purines, pyrimidines (which are essential in protein synthesis)etc.
3. It is also found in the porpyrines found in chlorophyll and cytochrome enzymes and hence it is essential for photosynthesis.
4. It is participated in the co-enzymes essential for the function of many enzymes.

5. It is readily mobile within the plant tissues. When its deficiency occurs, it is transferred from older to younger tissues where it can be reutilized in growth process. As a result symptoms develop first on older leaves.

2. Phosphorus (P)
Source

The plant absorbs P in the form of soluble phosphates such as H3PO4and HPO4. The absorption ability differs from plant to plant, e.g. cabbage and alfalfa can absorb phosphate from rocks whereas barley, corn and oats cannot absorb so efficiently.

Physiological Roles

1. Phosphorus content is found to be 0.2 to 0.8% of the total dry weight.
2. It is found abundantly in the growing and storage organs such as fruits and seeds.
3. It promotes healthy root development and fruit ripening through translocation of carbohydrates.
4. It is an essential element participating in the skeleton of plasma membrane, nucleic acids and organic molecules such as ATP (Adenosine Tri Phosphate) and other phosphorylated compounds.
5. It is also found in plants as a constituent of nucleic acids, phospholipids, and the coenzymes like NAD etc.
6. Phospholipids along with protein may be important in cell membrane.
7. It is readily mobile within the plant.

3. Potassium (K)
Source

Potassium is widely distributed in soil minerals. Forms such as potash felspar, mica and glauconite are slowly converted into soluble forms by weathering processes. It is strongly fixed in soils, largely as an exchangeable base. The K is found in less available forms. Small amounts are normally present in the soil in an exchangeable form.

Physiological Role

i. It is concerned with the formation of carbohydrate and protein synthesis, photosynthesis, transpiration regulation, enzyme action, synthesis of nucleic acids and chlorophyll, oxidative and photo phosphorylation, translocation of solutes etc.
ii. It acts as an activator of many enzymes involved in carbohydrate metabolism and protein synthesis.
iii. It is actively involved in the opening and closing of stomata.
iv. It takes an important role in drought tolerance of crops through water relations.
v. It offers resistance to pest and disease which affects the crops.
vi. It is present in the soluble forms and mostly contain in the cell sap and cytoplasm.
vii. It is readily mobile within the plant tissues.

4. Magnesium (Mg)
Source

Magnesium occurs as carbonates and held in soils as an exchangeable base. It is easily leached and for this reason may become deficient in sandy soils during wet periods. Heavy application of K fertilizers reduces its absorption.

Physiological Roles

i. It is a constituent of chlorophyll, and therefore, essential for its synthesis.
ii. It acts as a phosphorus carrier in the plant.
iii. It is essential for the synthesis of fats and metabolism of carbohydrate and phosphorus.
iv. It is required in binding two subunits of ribosome during protein synthesis.
v. It acts as an activator for many enzymes in phosphate transfer reactions in carbohydrate metabolism and nucleic acid synthesis.
vi. It is involved in the formation of seeds of high oil contents containing a compound called **lecithin**
vii. It is readily **mobile** within the plant tissues.

5. Sulphur (S)

Source : It is available to plants in the form of soluble suphates of soil.

Physiological Role

i. It is an important constituent of some amionacids (cystine, cysteine and methionine), vitamins (biotine, thiamine), coenzyme A and volatile oils.
ii. It participates in protein synthesis
iii. Sulfohydryl groups are necessary for the activity of many enzymes
iv. Disulphide linkages help to stabilize the protein structure.
v. It adversely affects chlorophyll synthesis.
vi. Sulphur affects the nodule formation in roots of leguminous plants.
vii. Characteristic odour of Cruciferous plants (onion, garlic etc.) is due to the Sulphur as constituent of volatile oils.
viii. It is immobile in the plant tissues. When its deficiency occurs, it is not transferred to the younger leaves but accumulated in the older leaves only. As a result, deficiency symptoms develop first on younger leaves.

6. Calcium (Ca)

Source

Calcium occurs in soil with variety of minerals. The soil derived from stone or chalk rocks contains larger percentage of carbonates of lime (calcium carbonate), while sandy soils show Ca deficiency which is met by adding lime or lime stone. The presence of CO2 dissolved in the soil water promotes solubility of carbonate of lime in soil ensuring the quick Ca absorption.

Physiological Roles

i. It is the important constituent of middle lamella in the cell wall
ii. It is essential in the formation of cell membranes.
iii. It helps to stabilize the structure of chromosomes.
iv. It is also an activator of many enzymes (ATPase, kinases, succinate dehyrogenase)
v. It provides a base for the neutralization of organic acids.
vi. It is concerned with the growing root apices.
vii. It is essential for fact metabolism, carbohydrate metabolism and binding of nucleic acids with proteins.
viii. It is also essential in the counteraction of metal toxicity
ix. It is immobile in the plant tissues.

Micronutrients

1. Iron (Fe)

Source: In well-irrigated soils, Fe is present predominantly as ferric form and in waterlogged soils, ferrous compounds are formed. The availability of Fe to plants increases with acidity and is decreased by phosphates. It is **absorbed in ferric state;** but, **ferrous form is only metabolically active** form for the plants.

Physiological Role

1. It is an important constituent of iron-porphyrin proteins like, cytochromes, peroxidases, catalases etc.
2. It is essential for the synthesis of chlorophyll.
3. It acts as a catalyst and electron carrier during respiration.
4. It also acts as an activator of nitrate reductase and aconitase enzymes.
5. It is a very important constituent of ferredoxin, which plays an important role in biological nitrogen fixation and primary photochemical reaction in photosynthesis.
6. It is immobile in the plant tissues. Its mobility is affected by several factors like presence of magnesium, potassium deficiency, high phosphorus and high light intensity.

2. Manganese (Mn)

Source: Like iron, the oxide forms of Mn are common in soil but the more highly oxidized forms (manganous dioxide) are of very low availability to plants. Its solubility increases with increased acidity and in strongly acid soils. Absence of organic matter and poor drainage condition of soil cause unavailability of Mn in the soil. Sometimes, Oxidising bacteria in the soils may also cause Mn unavailable over the pH range of 6.5 to 7.8.

Physiological Roles

1. It acts as an activator of some respiratory enzymes like oxidases, Peroxidases, dehyrogenases, kinases, decarboxylases etc.
2. It is essential in the formation of chlorophyll
3. It decreases the solubility of iron by oxidation; in certain cases, abundance of Mn leads to Fe deficiency.
4. It is necessary for the evolution of O2 during photosynthesis.
5. It is immobile in the plant tissues. When its deficiency occurs, it is not transferred to the younger leaves but accumulated in the older leaves only. As a result, deficiency symptoms develop first on younger leaves.

3. Copper (Cu)

Source : Copper is found in smaller quantity in soils due to the additions of growing plants and its added residue. Organic matter, soil organism and pH are the important factors affecting the availability of copper. Soils neighboring the copper deposits are normally toxic to plants.

Physiological Roles

1. It acts as a catalyst and regulator
2. It is a constituent of several oxidizing enzymes like ascorbic oxidase, lactase, tyrosinase, phenoloxidase, plastocyanin etc.
3. It is essential for photosynthesis, respiration and to maintain carbon/ nitrogen balance.
4. Its higher concentration is toxic to plants.

5. It is **immobile** in the plant tissues.

4. Zinc (Zn)
Source: Like copper, it is also found in soils in very small quantities and largely it results from the concentration and addition from growing plants and added residue. Its uptake is reduced by large or prolonged supply of phosphate fertilizers. It is generally found to be toxic in the neighborhood of zinc deposits.

Physiological Role

1. It is a component of enzymes like carbonic anhydrase, alcohol dehyrogenase, glutamic dehydrogenase, lactic dehydrogenase, alkaline phosphatase and carboxy pepsidase.
2. It is essential for the evolution and utilization of CO2, carbohydrate and phosphorus metabolism.
3. It is also essential for the biosynthesis of the growth hormone, Indole-3-acetic acid (IAA) and also for the synthesis of RNA.
4. It is readily mobile within the plant tissues.
5. It is closely involved in the chlorophyll formation.

5. Molybdenum (Mo)
Source: It is found widely distributed in small amounts in soils and plants and relatively higher concentration occurs in mineral oils and coal ashes.

Physiological Roles

1. It is associated with the prosthetic group of enzyme, nitrate reductase and thus involved in nitrate metabolism.
2. It acts as an activator of some dehydrogenases and phosphatases and as cofactors in synthesis of ascorbic acid.
3. It is necessary in the formation of nodules in legumes for the fixation of atmospheric nitrogen.

6. Boron (B)
Source: Boron occurs in rocks and marine sediments. It is absorbed in the form of borate ions and it has some sort of antagonistic effect with other cations like, calcium, potassium and others.

Physiological Roles

1. It is necessary for the translocation of sugars within the plant system
2. It is involved in reproduction and germination of pollens (tube)
3. It is concerned with water reactions in cells and regulates intake of water into the cell
4. It keeps Ca in soluble form within the plant and may act as a regulator of K ratios (K/Ca etc.)
5. It is also concerned with the nitrogen metabolism and with oxidation and reduction equilibrium in cells.
6. It is **immobile** in the plant tissues.

7. Chlorine

Chlorine occurs in soils as chlorides and moves freely in soil solution and form which it is available to the plant. Chlorine increases the water content of tobacco cells; it affects carbohydrate metabolism and speeds up photosynthesis.

Cobalt is needed by the leguminous crop in the absence of nitrogen because; it is required by the symbiotic bacteria for fixation of atmospheric nitrogen. Elements like, aluminum (Al), silica (Si) and selenium (Se) possess stimulating effects of certain nonessential elements by counteracting the toxicity of certain elements present in soil.

Animation minerals which requires for plant growth :

http://www.kscience.co.uk/animations/minerals.swf

Reference:

1. Plant physiology – III Ed. Taiz and Zeiger: http://4e.plantphys.net/
2. Plant physiology – Salisbury and Rose.
3. www.**tnau**.ac.in/
4. Textbook of Plant physiology – Malik C. P and Srivastava.A. K.

Lecture 11
Nutritional Disorders in Crops

Low supply or complete absence of any of the essential elements will exhibit typical symptoms, which are specific to the particular elements(s). This condition is called as **nutrient deficiency** and the symptoms as **deficiency symptoms.**

In absence or low supply of elements (deficiency), following common symptoms generally develop in the plants.

General Deficiency Symptoms

1. Chlorosis:

It is a physiological disease that occurs due to deficiency of mineral elements. (eg. N, K. Mg, Fe, Zn, Mn, S). Leaves become abnormally yellow or white due to reduction of chlorophyll contents.

2. Mottling:

It is a condition of plant surface marked with coloured spots due to anthocyanin pigmentation (eg. due to deficiency of N, K, Mg, P, and S).

3. Necrosis:

It refers to the patch of dead tissues, due to deficiency of K, Mg, Zn, Ca, Mo, Mn, Fe, or B.

4. Bronzing:

Development of bronze/copper colour on the leaves and various parts (eg. K)

5. Die back:

Collapse of growing tip, affecting the youngest leaves and buds (eg. K, Ca, B or Cu)

6. Scorching:

Burning of tissues accompanied by light brown colour. (eg. K, Ca, B or Cu)

7. Firing:

Burning of tissues accompanied with dark brown or reddish brown colour (eg. Mg)

8. Rosetting:

Clustering of leaves due to reduced leaf size and shorter internodal distance (eg. Cu, K, Zn)

9. Distortion of leaves:

Irregular shaping of leaves like cupping, twisting, hooking or curling and also wavy margins.

Cupping: B or Mo
Twisting / Hooking: Zn / Ca / B
Curling: Ca, B or Zn
Head distortion: Cu (rice), Mn (Sunflower)
Wavy: Zn

10. Gummosis:

Oozing out of cell sap in the form of gummous nature (eg. Cu as in coconut etc.)

Occurrence of Deficiency Symptoms

Deficiency symptoms of various nutrient elements will appear either on older or on younger leaves depending on mobility of the nutrient. Thus, the relative mobility of the nutrient influences the site of appearance of the deficiency symptoms.

Deficiency symptoms of mobile elements will appear on the older leaves because, these elements will move rapidly from older leaves to younger leaves. eg. N, P, K, Mg, Zn. On the other hand, the deficiency symptoms of the non-mobile elements will appear on the young leaves because of their accumulation on the older leaves due to their immobile nature. eg. Ca, B, Cu, Mn, Fe and S.

Specific deficiency symptoms of various nutrient elements and their corrective measures are given below:

1. Nitrogen (N)

1. Plant growth is stunted and poorly developed (because protein content, cell division and cell enlargement are decreased)
2. Nitrogen deficiency causes yellowing (chlorosis) of leaves. Older leaves are affected first
3. Flowering and fruiting are reduced
4. Protein and starch contents are decreased
5. Prolonged dormancy and early senescence appear
6. Root gets more lengthened as in wheat
7. Veins turn purple or red due to development of abundant anthocyanin pigment (eg. tomato, apple)
8. The angle between stem and leaves is reduced.
9. Plants look so sickly and conspicuously pale that the condition is called as general starvation.
10. Symptoms first occur on the older leaves due to its mobility.

Nitrogen Deficiency

Potato Plant in Sand
http://www.hbci.com/~wenonah/min-def/list.htm

Corrective Measures:

For correcting N deficiency, fertilizers like ammonium suphate, calcium nitrate, urea etc. are supplied. Foliar spray of 1-2% urea is a quick method of ameliorating N deficiency.

2. Phophorus (P)

1. Young plants remain stunted with dark blue green or some times purplish leaves.
2. P deficiency may cause premature leaf fall
3. Dead necrotic areas are developed on leaves and fruits.
4. Leaves sometimes develop anthocyanin in veins and may become necrotic; leaves will be dark green in colour.
5. Cambial activity is checked
6. Tillering of crops is reduced
7. Dormancy is prolonged
8. P deficiency may cause premature fall of leaves
9. Growth is retarded
10. *Sickle leaf disease* is caused in P deficiency, which is characterised by chlorosis adjacent to main veins followed by leaf asymmetry.

Sugar Beet Plant

Potato Plant in Sand Culture

http://www.hbci.com/~wenonah/min-def/list.htm

Corrective Measures:

Spraying 2% DAP or application of Phosphatic fertilizers will correct the deficiency.

3. Potassium (K)

The deficiency symptoms vary with the degree of shortage of the element.

i. In mild deficiency cases,
   a. thin shoots may develop and
   b. there may be restricted shoot growth
ii. In acute deficiency cases,
   a. shoots may die back, eventually plant may die
   b. Plants may become stunted with numerous tillers and
   c. there may be little or no flowering
iii. Leaf will be dull or bluish green in colour.
iv. Chlorosis occurs in interveinal regions **(interveinal chlorosis)**
v. In older leaves, browning of tips (tip burns), marginal scorching (leaf scorch or development of brown spots near the margins occur.
vi. Necrotic areas develop at the tip and margins of the leaf which curve downward.

vii. In broad leaved plants, shortening of internodes and poor root system are important.

Potato Culture

Plant in Sand Tomato

Leaf

http://www.hbci.com/~wenonah/min-def/list.htm

Corrective Measures:

Supply of muriate of potash or foliar spray of 1% potassium chloride is commonly used to overcome K deficiency.

4. Magnesium (Mg)

i. Mg deficiency causes interveinal chlorosis. The older leaves are affected first and proceed systematically towards the younger leaves.
ii. Dead necrotic spots appear on the leaves.
iii. Severely affected leaves may wither and shed or absciss without the withering stage.
iv. Defoliation is quite severe
v. Carotene content is reduced.
vi. Stem becomes yellowish-green, often hard and woody.

Plant in Tomato

Sand Leaf

Potato Culture

http://www.hbci.com/~wenonah/min-def/list.htm

Corrective Measures:

Magnesium sulphate is usually applied for redressing the deficiency. The malady can be readily corrected as foliar spray @ 2% of MgSO4.

5. Calcium (Ca)

Classic symptoms of calcium deficiency include blossom-end rot of tomato (burning of the end part of tomato fruits), Tip burn of lettuce, blackheart of celery and death of the growing regions in many plants. All these symptoms show soft dead necrotic tissue at rapidly growing areas, which is generally related to poor translocation of calcium to the tissue rather than a low external supply of calcium. Very slow growing plants with a deficient supply of calcium may re-translocate sufficient calcium from older leaves to maintain growth with only a marginal chlorosis of the leaves. This ultimately results in the margins of the leaves growing more slowly than the rest of the leaf, causing the leaf to cup downward. This symptom often progresses to the point where the petioles develop but the leaves do not, leaving only a dark bit of necrotic tissue at the top of each petiole. Plants under chronic calcium deficiency have a much greater tendency to wilt than non-stressed plants.

Culture

Potato Tomato

Plant in Sand Truss

http://www.hbci.com/~wenonah/min-def/list.htm

Corrective Measures:

Calcium ammonium nitrate (CAN) or super phosphate or gypsum is supplied in deficient soils. In Indian soils, Ca deficiency is not a serious problem.

6. Sulphur (S)

i. Sulphur deficiency causes yellowing (Chlorosis) of leaves. Young leaves are affected first.
ii. Tips and margins of leaves roll inward.
iii. Marked decrease in leaf size, general paling with red or purple pigmentation aregeneral symptoms.
iv. Necrosis of young leaf tips develop
v. Internodes are shortened'
vi. Apical growth is inhibited and lateral buds develop prematurely
vii. Young leaves develop orange, red or purple pigments.
viii. Leaf tips are characteristically bent downwards. The leaf margins and tips roll

ix. inwards. (eg. tomato, tobacco and tea)
x. Fruit formation is suppressed.
xi. Sclerenchyma, xylem and collenchyma formation gets increased and hence the stem becomes unusually thick due to S deficiency.


Sulfur (S) deficiency in Lucerne **Cabbage plant**
www.dpi.qld.gov.au **www.sulphurindia.com**

Corrective Measures:

Common fertilizers used for supplying nitrogen and phosphorus contain appreciable amount of sulphur sufficient to meet the crop requirement. In case of severe deficiency, gypsum is added to the soil @ 500Kg/ha.

Micronutrients

7. Iron (Fe)

i. Interveinal chlorosis of the younger leaves occurs. The veins remain green.
ii. Leaf chlorosis may produce a mottled appearance.
iii. Leaf may show complete bleaching or often becoming necrotic.
iv. In extreme conditions, scorching of leaf margins and tips may occur
v. *Lime induced chlorosis is the common disease* found in fruit trees like citrus. It is also fund in beet, spinach, brassicas and cereals. The younger leaves become white or yellowish white.


To ma to

Foliage **Turnip Plant**

http://www.hbci.com/~wenonah/min-def/list.htm

Corrective Measures

Foliar spray of 0.5% ferrous sulphate along with lime (50% requirement) will remove the deficiency in the plant and soil. Chelated iron compounds such as Fe-EDTA, give a very good response in ameliorating Fe deficiency.

8. Manganese (Mn)

i. Deficiency causes **interveinal chlorosis** and necrotic spots of the leaf.
ii. Dead tissue spots are found scattered over the leaf.
iii. Severely affected tissues turn brown, the brown areas may also twist in the form of spirals and they may wither also.
iv. Root system is often poorly developed and badly affected and the plants may die.
v. Grain formation is also reduced and the heads may be blind (as in sulphur)
vi. Four diseases are found due to its deficiency:
   a. Grey Speck also called as grey stripe, grey spot or dry spot
   b. Pahla blight of sugarcane
   c. Marsh spot of pea
   d. Speckled yellow of sugar beet.

Sugar Beet

Plant **Potato**

Leaves

http://www.hbci.com/~wenonah/min-def/list.htm

Corrective Measures

Foliar spray of 0.5% manganous sulphate plus 50% lime requirement is quite effective and it should be applied in the early stage of the crop. Soil application of 15-30 kg $MnSO_4$ per ha (mixed with sand) is sufficient.

9. Copper (Cu)

i. It causes necrosis of the tip of the young leaves.
ii. Both vegetative and reproductive growth is retarded.
iii. Wilting of terminal shoots occur which is followed by frequent death
iv. Leaf colour is often faded due to reduction of carotene and other pigments.

v. Foliage shows burning of margins or chlorosis or rosetting and multiple bud formation.
vi. Gumming may also occur **(gummosis)**
vii. Younger leaves wither and show marginal chlorosis (yellowish grey) of tips. It is called as **Yellow tip or reclamation disease.**
viii. Following two diseases are common:

a. ***Exanthema or die back of fruit tree:*** It is commonly found in citrus, plum, apple and pear.

The symptoms include formation of strong water-shoots bearing large leaves, gummous tissue or the bark and longitudinal breaks. Fruits become brown, glossy and splitted. Affected shoots loose their leaves and die back and lateral shoots produce bunchy appearance.

b. Reclamation disease: It is also called as **White Tip disease** and is found in legumes, cereals, oats and beet. The tips of leaves become chlorotic followed by a failure of the plants to set seed.

Copper deficiency symptoms in tomato.
www.mjindiaexports.net

Corrective Measures:

Foliar spray of 0.5% of $CuSO_4$ is recommended.

10. Zinc (Zn)

i. Older leaves show chlorosis which starts from tips and the margins
ii. Leaves become leathery
iii. Plants show rosetting due to shortening of internodes and premature shedding.
iv. Whitening of upper leaves in monocots and chlorosis of lower leaves in dicots are often found.
v. Leaf margins distorted, become twisted or wavy which later curl and look sickle shaped *(Sickle leaf)*
vi. Seed production and fruits size is greatly reduced.
vii. The following diseases are commonly notice:
    a. Khaira of paddy: The entire older leaves show rusty brown appearance (due to chlorosis) and ultimately die.

b. *White bud (tip) of maize:* Unfolded newer leaves are often pale yellow to while. There is appearance of light yellow streaks between the veins of older leaves followed by white necrotic spots.

c. *Rosette of fruit trees:* It is also called as little leaf disease. Yellow mottling of leaves, reduction of leaf size with rosette appearance (due to reduced internodal distance) and die back of the affected branches are symptoms of the disease.

d. ***Frenching of citrus:*** Initially, yellow spots develop between the veins. Leaves become progress evenly smaller and develop chlorophyll at the basal end of mid rib.

Zinc deficiency in tomato
www.progressivegardens.com

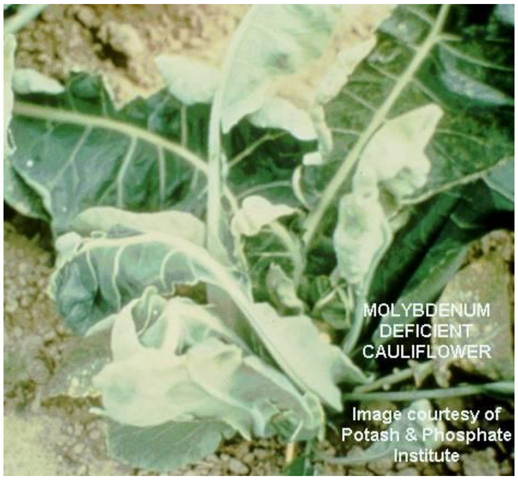
Corrective Measures

Foliar spray of 0.5% $ZnSO_4$ twice at 7-10 days interval during early stages of growth will alleviate the problem. Also, soil application of 25 kg $ZnSO_4$ per ha is also found beneficial.

11. Molybdenum (Mo)

i. Deficiency causes chlorotic interveinal mottling of the older leaves.
ii. Leaves often show light yellow chlorosis and leaf blades fail to expand.
iii. In acute deficiency cases, necrosis of leaf tissues occurs.
iv. Flower formation is inhibited.
v. Failure of grain formation occurs (as in oats)
vi. Its deficiency causes two diseases:

a. **Whiptail of Cauliflower and Brassica*:*** The symptoms begin as appearance of translucent areas near the midrib which become ivory tinted or necrotic. The leaf margins become ragged with upward curling. Before the death of the growing point, the leaf elongates and lamina remains suppressed thus gives a typical whip tail condition.



Cauliflower
http://enst2.umd.edu

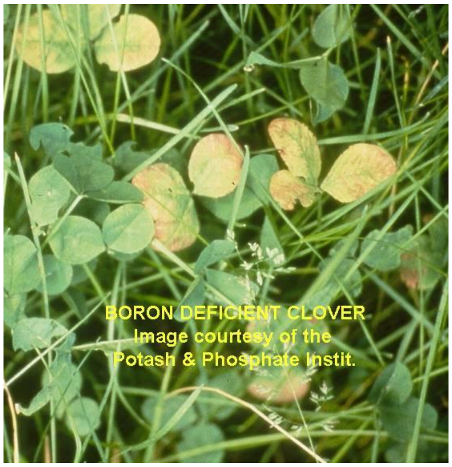
Tomato Leaves
www.progressivegardens.com

Corrective Measures :

The Mo deficiency is commonly found in cauliflower, legumes, oats and other *brassicas* which can be corrected by soil application of 0.5 to1.0 Kg/ha sodium or ammonium molybdate or by its foliar spray@ 0.01-0.02% conc.

12. Boron (B)

i. It causes death of shoot tip
ii. Flower formation is suppressed.
iii. Root growth is stunted.
iv. Leaves become coppery in texture.
v. Plants become dwarf, stunted with apical meristem blacken and die followed by general breakdown of meristematic tissue.
vi. Terminal leaves become necrotic and shed prematurely
vii. Leaves show symptoms like distortion such as cupping and curling, appearance of white stripe, scorching, pimpling, splitted midrib and reduced growth.
viii. Stem shows symptoms like die-back of apex, abnormal tillering, and appearance of various forms of deformities such as curling and brittle lesions, pimpling etc.
ix. Fruits are severely deformed and develop **typical cracking or splitting.**
x. Following *diseases* are commonly found due to B deficiency:
   a. Heart rot of sugar beet and marigold
   b. Canker and internal black spot of garden pea
   c. Browning of cauliflower
   d. Top sickness of tobacco
   e. Hard fruit of citrus.



Clover leaves **Cauliflower** **Tomato**

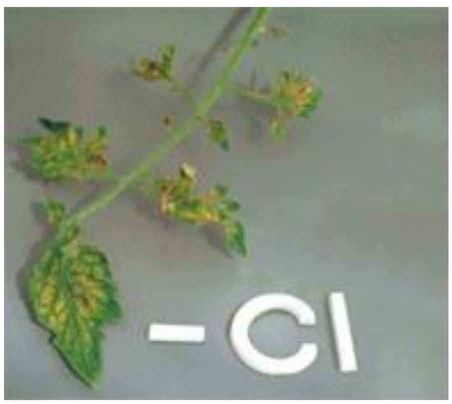
http://enst2.umd.edu **http://www.hbci.com**

Corrective Measures:

Foliar spray of 0.2% borax acid will be effective for quick recovery. Liming of soil should be strictly avoided when boron-containing fertilizers are applied.

13. Chlorine (Cl)

Distinct interveinal chlorosis. Plants require relatively high chlorine concentration in their tissues. Chlorine is very abundant in soils, and reaches high concentrations in saline areas, but it can be deficient in highly leached inland areas. The most common symptoms of chlorine deficiency are chlorosis and wilting of the young leaves. The chlorosis occurs on smooth flat depressions in the interveinal area of the leaf blade. In more advanced cases there often appears a characteristic bronzing on the upper side of the mature leaves.



http://4e.plantphys.net/

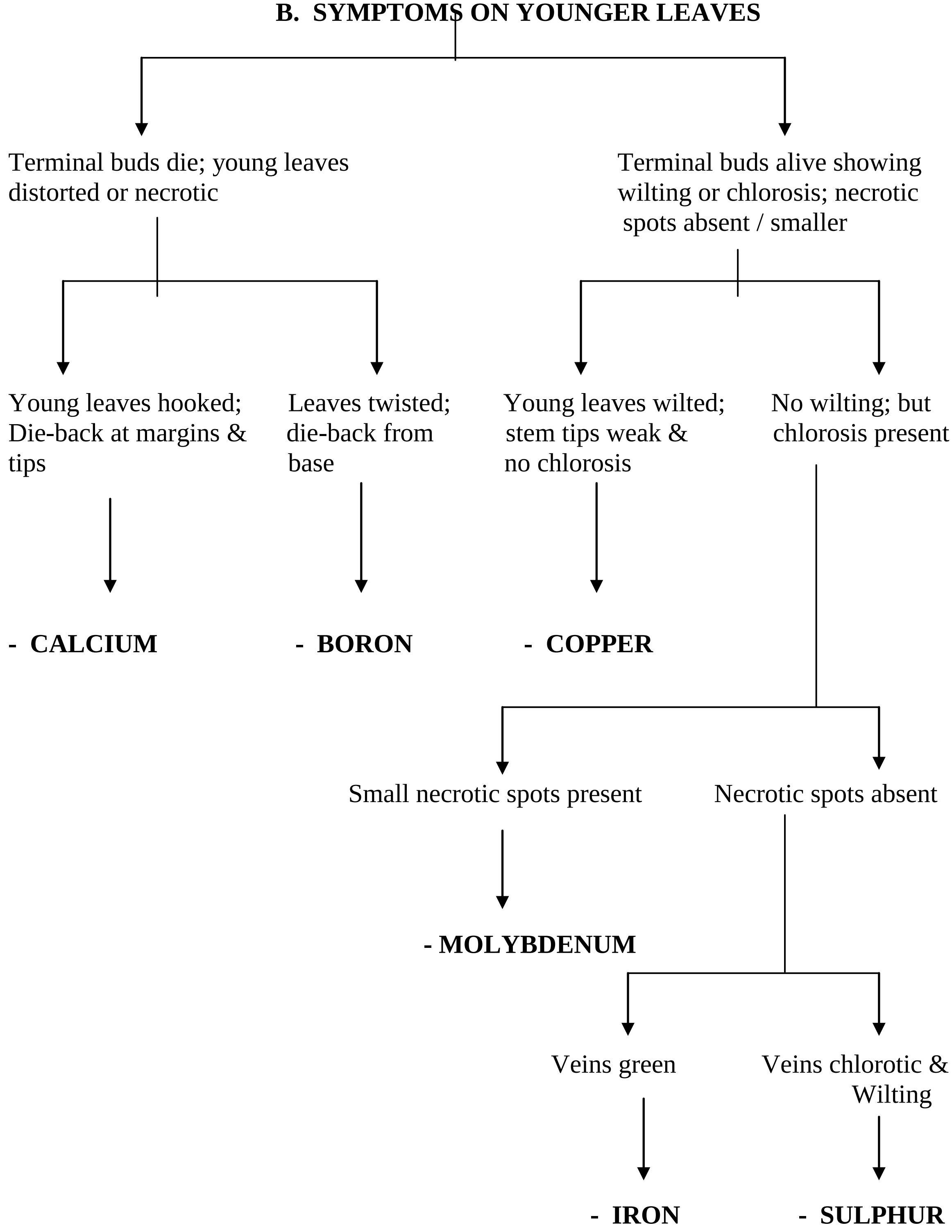
KEY FOR IDENTIFICATION OF NURIENT DEFICIENCY SYMPTOMS IN CROPS

(Mc Murbery, 1952)

A. SYMPTOMS ON OLDER LEAVES

- Effects throughout plant body; Lower leaves dry up
  - Plants light / pale green; lower Leaves yellow, stalks small, Stunted growth; abundant Anthocyanin pigments → **- NITROGEN**
  - Leaves dark green; lower leaves usually red or yellow; stalks small → **- PHOSPHORUS**
- Effects localised; lower leaves mottling or chlorosis; no dry up of leaves / margin
  - Lower leaves chlorotic/mottled; Larger necrotic spots; severe Defoliation; interveinal chlorosis absent or restricted → **- MAGNESIUM**
  - Leaves chlorotic; interveinal chlorosis; necrotic spots small or between veins, tips or margins → **- POTASSIUM**
  - Larger necrotic spots develop & spread to veins; leaves thicker and leathery and small **("Little leaf")** → **- ZINC**

B. SYMPTOMS ON YOUNGER LEAVES



INDICATOR CROPS

Some of the crops are known to be specific for the occurrence of symptoms of a particular deficient nutrient element exhibiting characteristic symptoms. Such crops are called as Indicator Crops for the deficiency of that particular element(s). This is mainly due to the greater demand of the element in the respective Indicator Crops. Some of the Indicator Crops are furnished in the following Table along with the element:

Table. Indicator plants for deficiencies of some nutrients

S.No.	Nutrient Element	Indicator Crops
01.	Nitrogen	Cereals like, maize, sorghum and pulses
02.	Phosphorus	Tomato, maize, cereals, Leucerne
03.	Potassium	Potato, banana, cotton, Leucerne
04.	Magnesium	Cotton (leaf reddening)
05.	Zinc	Maize, paddy ("khaira" disease), citrus, beans
06.	Sulphur	Cereals, leucerne, tea (yellowing)
07.	Copper	Citrus, cereals
08.	Iron	Sugarcane, sorghum, citrus, ornamental plants
09.	Manganese	Citrus, sunflower, sugarbeet
10.	Calcium	Cauliflower, tomato (blossom end rot of fruits), sugarbeet
11.	Molybdenum	Cauliflower (whiptail)

Reference:

1. Plant physiology – III Ed. Taiz and Zeiger: http://4e.plantphys.net/
2. Plant physiology – Salisbury and Rose.
3. www.**tnau**.ac.in/

Lecture 12
PHOTOSYNTHESIS

Photosynthesis is a vital physiological process where in the chloroplast of green plants synthesizes sugars by using water and carbon dioxide in the presence of light. Photosynthesis literally means *synthesis with the help of light* i.e. plant synthesize organic matter (carbohydrates) in the presence of light.

Photosynthesis is sometimes called as carbon assimilation (assimilation: absorption into the system).This is represented by the following traditional equation.

$$6CO_2 + 12H_2O \xrightarrow[\text{Green pigments}]{\text{Light}} 6O_2 + \underset{\text{carbohydrates}}{C_6H_{12}O_6}$$

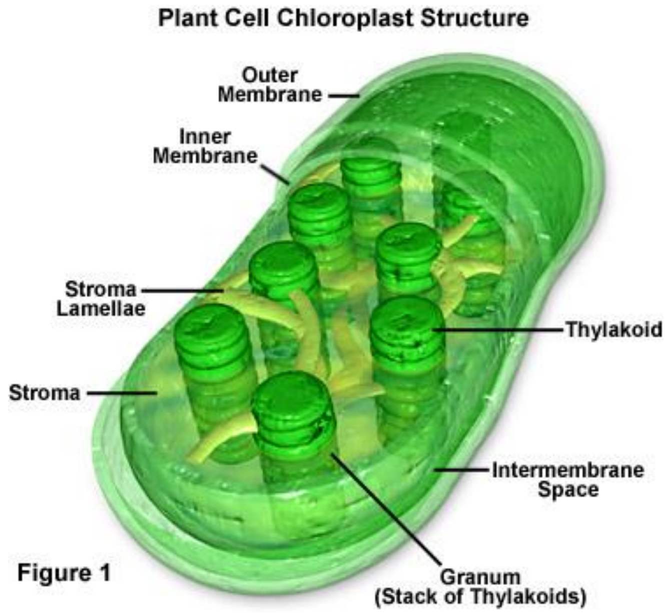
During the process of photosynthesis, the light energy is converted into chemical energy and is stored in the organic matter, which is usually the carbohydrate. One molecule of glucose for instance, contains about 686 K Calories energy. CO_2 and water constitute the raw material for this process and oxygen and water are formed as the by products during photosynthesis. *Stephen Hales* (1727) first explained the relationship between sunlight and leaves and *Sachs* (1887) established that starch was the visible product of photosynthesis.

Of the total world's photosynthesis 10 per cent is carried marine water algae and aquatic plants (ocean).

Basically, photosynthesis is process of conversion of light energy into chemical energy. Light not only behaves as a wave but also has energy particles called **photons**. The energy of photons is different for light of different wavelengths.

Atmosphere contains about 2.2 x 10^3 tonnes of CO_2, while, oceans have high CO_2 concentration 11 x 10^3 tonnes. Only about 10^{11} or 100 billion tones of carbon is converted into organic forms of about 225 billion tones of organic matter. According to old concept aquatic photosynthesis is 90% and 10% is terrestrial photosynthesis. But according to new concept 40% of total photosynthesis is aquatic photosynthesis.

Photosynthetic apparatus



http://micro.magnet.fsu.edu/cells/chloroplasts/images

The chloroplast in green plants constitutes the photosynthetic apparatus. In higher plants, the chloroplast is discoid in shape, 4-6 µ in length and 1-2µ thick. The chloroplast is bounded by two unit membranes of approximately 50°A thickness and consists of lipids and proteins. The thickness of the two membranes including the space enclosed by them is approximately 300°A (1 Angstrom: 0.1 cm).

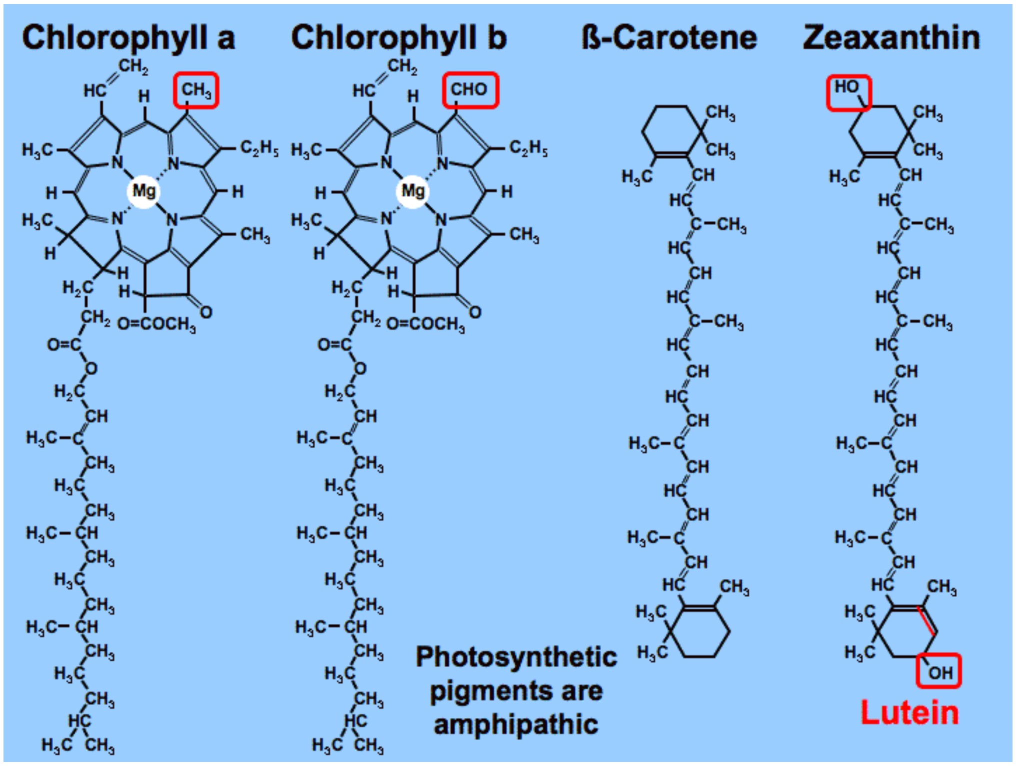
Internally, the chloroplast is filled with a hydrophilic matrix called as *stroma* embedded with *grana.* Each grana consists of 5-25 disk shaped grana lamellae (thylakoids) placed one above the other like the stack of coins. Each grana lamella of thylakoid encloses a space called *loculus* and the thylakoid membrane consists of alternating layer of lipids and proteins. Some of the grana lamella of thylakoids of grana are connected with thylakoids of other grana by somewhat thinner *stroma lamella or fret membrane*. Chlorophyll and other photosynthetic pigments are confined to grana. The chlorophylls are the site of photochemical reactions.

Photosynthetic pigments

Photosynthetic pigments are of three types;

1. Chlorophylls
2. Carotenoids and
3. Phycobillins.

- Chlorophylls and carotenoids are insoluble in water and can be extracted only with organic solvents such as acetone, petroleum ether and alcohol.
- Phycobilins are soluble in water
- Carotenoids include carotenes and xanthophylls. The xanthophylls are also called as *carotenols.*



Chlorophylls (green pigments)

Chlorophylls are magnesium porphyrin compounds. The porphyrin ring consists of four pyrrol rings joined together by CH bridges. Long chain C atoms called as phytol chain is attached to porphyrin ring at pyrrol ring IV.

The chemical structure of chlorophyll *a* and chlorophyll *b* are well established. The molecular formula for chlorophyll *a*: $C_{55}H_{72}O_5N_4$ Mg and chlorophyll *b*: $C_{55}H_{70}O_6N_4$ Mg. Both of them consist of Mg porphyrin head which is hydrophilic and a phytol tail which is lipophilic. The two chlorophylls differ because in chlorophyll *b* there is a –CHO group instead of CH_3 group at the 3rd C atom in pyrrol ring II. Chlorophyll is formed from protochlorophyll in light. The protochlorophyll lacks 2H atoms one each at 7th and 8th C atoms in pyrrol ring IV. Difference between two chlorophylls is in chlorophyll b there is -CHO (aldehyde) group, instead of a _CH3 (acetyl) group in chlorophyll a molecule.

Carotenoids (yellow or orange pigments)

1. Carotenes: Carotenes are hydrocarbons with a molecular formula $C_{40}H_{56}$

2. Xanthophylls (carotenols)

They are similar to carotenes but differ in having two oxygen atoms in the form of hydroxyl or carboxyl group. The molecular formula is $C_{40}H_{56}O_2$.The role of carotenoids is absorption of light energy and transfer the light energy to chlorophyll *a* molecules. They also play a very important role in preventing photodynamic damage within the photosynthetic apparatus.

Photodynamic damage is caused by O_2 molecules which is very reactive and is capable of oxidizing whole range of organic compounds such as chlorophylls and thereby making them unfit for their normal physiological function.

Phycobilins (red and blue pigments)

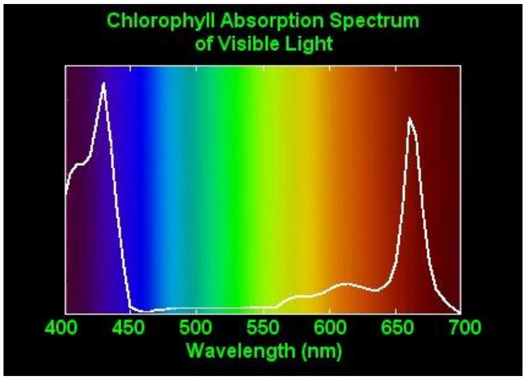
These also contain four pyrrol rings but lack Mg and the phytol chain.

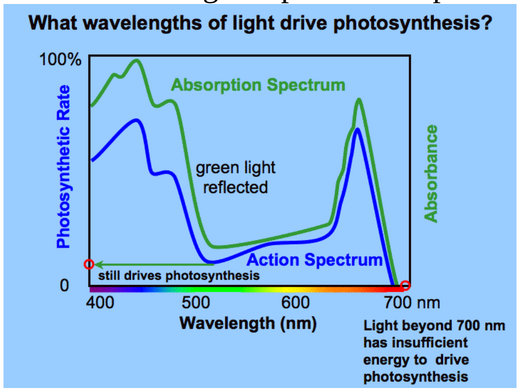
Location of photosynthetic pigments in chloroplast

The photosynthetic pigments are located in grana portions of the chloroplast. They are present in the thylakoid membrane or membrane of grana lamella. The membrane of thylakoid is made up of proteins and lipids or the membrane consists of both lipid layer and protein layer. The hydrophilic *heads* of the chlorophyll molecules remain embedded in the protein layer while lipohilic phytol tail in the lipid layer. The other pigments are thought to be present along with chlorophyll molecules.

Absorption spectra of chlorophyll

The absorption of different wavelengths of light by a particular pigment is called **absorption spectrum**. Chlorophylls absorb maximum light in the violet blue and red part of the spectrum. The absorption peaks of chlorophyll *a* are 410 and 660nm, for chlorophyll *b* 452 and 642nm. Carotenoids absorb light energy in blue and blue green part of the spectrum.





www.arborsci.com http://plantphys.info/plant_physiology

Transfer of light energy absorbed by accessory pigments to chlorophyll *a*

All pigments except chlorophyll *a* are called as **accessory pigments or antenna pigments**. The light energy absorbed by accessory pigments is transferred to chlorophyll *a* molecule. The transfer of light energy from accessory pigments to chlorophyll *a* is called as **resonance or forster transfer** and takes part in primary photochemical reaction in photosynthesis. Chlorophyll *a* molecules also absorb light energy directly. As a result of absorbing the light energy, the chlorophyll molecule gets *excited*.

Excited states of atoms or molecules (*fluorescence* and *phosphorescence*)

The normal state of the chlorophyll molecule or atom is called as *ground state or singlet state.* When an electron of a molecule or an atom absorbs a quantum of light, it is raised to a higher energy level which is called as *excited second singlet state*. This state is unstable and has a life time of 10^{-12} seconds.

The electron comes to the next higher energy level by the loss of some of its extra energy in the form of heat. This higher energy level is called as *excited first singlet state* and is also unstable with a half life of 10^{-9} seconds. From the first singlet state, the excited electron may return to the ground state in two ways viz., either losing its remaining extra energy in the form of heat or in the form of radiant energy. The second process is called **fluorescence**. The chlorophyll molecules exit the extra energy in the form of fluorescent light when they are exposed to incident light. Fluorescent light is of longer wavelength than the incident light.

The excited molecule or the atom may also lose its excitation energy by internal conversion and comes to another excited state called as **triplet state** which is metastable with a half life of 10^{-3} seconds. From the triplet state, the excited molecule or the atom may return to the ground state in three ways.

(i) by losing its remaining extra energy in the form of heat

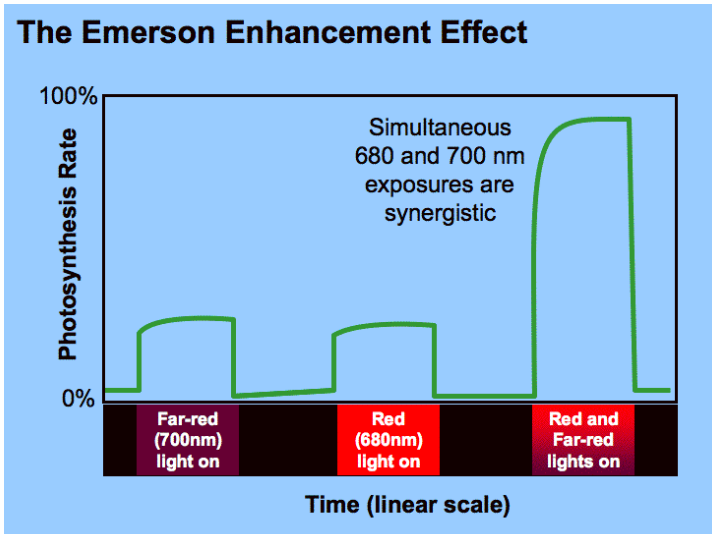
(ii) by losing extra energy in the form of radiant energy (**phosphorescence**) and the chlorophyll molecules emit phosphorescent light even after the incident radiant light is cut off. The phosphorescent light is of longer wavelength than incident light and also fluorescent light.

(iii) electrons carrying the extra energy may be expelled from the molecule and is consumed in some further photochemical reaction and the fresh normal electron returns to the molecule.

Quantum requirement and quantum yield

Light rays consist of tiny particles called **photons** and the energy carried by a photon is called **quantum**. The number of photons (quantum) required to release one molecule of oxygen in photosynthesis is called **quantum requirement**. On the other hand, the number of oxygen molecules released per photon of light in photosynthesis is called as **quantum yield**. The quantum yield is always in fraction of one.

Red drop and Emerson's enhancement effect

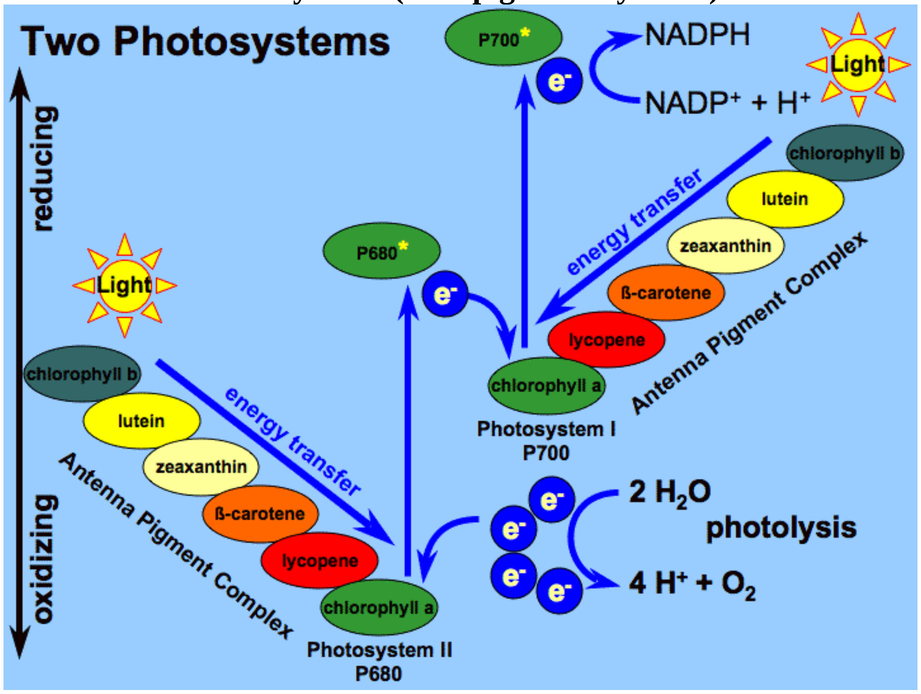


http://plantphys.info/plant_physiology

Robert Emerson noticed a sharp decrease in quantum yield at wavelength greater than 680 nm, while determining the quantum yield of photosynthesis in *chlorella* using monochromatic light of different wavelengths. Since this decrease in quantum yield took place in the red part of the spectrum, the phenomenon was called as **red drop**.

Later, they found that the inefficient far-red light beyond 680 nm could be made fully efficient if supplemented with light of shorter wavelength (blue light). The quantum yield from the two combined beams of light was found to be greater than the sum effects of both beams used separately. This enhancement of photosynthesis is called as **Emerson's Enhancement**.

Photosystems (Two pigments systems)



http://plantphys.info/plant_physiology

The discovery of red drop and the Emerson's enhancement effect led the scientists to suggest that photosynthesis is driven by two photochemical processes. These processes are associated with two groups of photosynthetic pigments called as **pigment system I** and **pigment system II**. Wavelength of light shorter than 680 nm affect both the pigments systems while wavelength longer than 680 nm affect only pigment system I.

In green plants, pigment system I contains chlorophyll *a*, *b* and carotene. In this pigment system, a very small amount of chlorophyll *a* absorbing light at 700 nm, known as P700 however constitutes the reaction centre of **photosystem I**.

The pigment system II contains chlorophyll *b* and some forms of chlorophyll a (such as chlorophyll *a* 662, chlorophyll *a* 677 and chlorophyll *a* 679) and xanthophylls. A very small amount of special form of chlorophyll called P680 constitute the reaction centre of pigment system II. Carotenoids are present in both the pigment systems

The two pigment systems I and II are interconnected by a protein complex called cytochrome b_6–f complex. The other intermediate components of electron transport chain *viz*., plastoquinone (PQ) and plastocyanin (PC) act as mobile electron carriers between the complex and either of the two pigment systems. The light energy absorbed by other pigment is ultimately trapped by P700 and P680 forms of chlorophyll *a* which alone take part in further photochemical reaction.

Pigment system I (PSI) complex consists of 200 chlorophylls, 50 carotenoids and a molecule of chlorophyll *a* absorbing light at 700 nm(P700) and this constitute the reaction centre of photosystem I. Pigment system II (PSII) complex consists of 200 chlorophylls, 50 carotenoids and a mole of chlorophyll a absorbing light at 680 nm, called P 680 at the centre. This constitutes the reaction centre of pigment system II.

Mechanism of photosynthesis

The biosynthesis of glucose by the chloroplast of green plants using water and CO_2 in the presence of light is called photosynthesis. Photosynthesis is a complex process of synthesis of organic food materials. It is a complicated oxidation- reduction process where water is oxidized and CO_2 is reduced to carbohydrates. The mechanism of photosynthesis consists of two parts.

1. Light reaction / Primary photochemical reaction / Hill's reaction/ Arnon's cycle
2. Dark reaction / Black man's reaction / Path of carbon in photosynthesis.

1. Light reaction or Primary photochemical reaction or Hill's reaction

In light reaction, ATP and $NADPH_2$ are produced and in the dark reaction, CO_2 is reduced with the help of ATP and $NADPH_2$ to produce glucose. The light reaction is called primary photochemical reaction as it is induced by light. Light reaction is also called as Hill's reaction as Hill proved that chloroplast produce O_2 from water in the presence of light. It is also called as Arnon's cycle because Arnon showed that the H^+ ions released by the break down of water are used to reduce the coenzyme NADP to NADPH. Light reaction includes photophosphorylation as ATP is synthesised in the presence of light. The reaction takes place only in the presence of light in **grana** portion of the chloroplast and it is faster than dark reaction. The chlorophyll absorbs the light energy and hence the chlorophyll is called as **photosystem or pigment system.** Chlorophylls are of different types and they absorb different wavelengths of light. Accordingly, chlorophylls exist in two photosystems, Photosystem I (PSI) and Photosystem II (PS II). Both photosystems are affected by light with wavelengths shorter than 680nm, while PS I is affected by light with wavelengths longer than 680nm.

The components of photosystems

Photosystem I	**Photosystem II**
Chlorophyll *a* 670	Chlorophyll *a* 660
Chlorophyll *a* 680	Chlorophyll *a* 670
Chlorophyll *a* 695	Chlorophyll *a* 680 or P680
Chlorophyll *a* 700 or P700	Chlorophyll *b*
Chlorophyll *b*	Phycobilins
Carotenoids	Xanthophylls
P700 form of Chlorophyll *a* is the active reaction centre	P680 form of Chlorophyll *a* is the active reaction centre

The light reaction can be studied under the following headings.

i. Absorption of light energy by chloroplast pigments

Different chloroplast pigments absorb light in different regions of the visible part of the spectrum.

ii. Transfer of light energy from accessory pigments to chlorophyll *a*

All the photosynthetic pigments except chlorophyll *a* are called as accessory or antenna pigments. The light energy absorbed by the accessory pigments is transferred by resonance to chlorophyll *a* which alone can take part in photochemical reaction. Chlorophyll *a* molecule can also absorb the light energy directly. In pigment system I, the photoreaction centre is P700 and in pigment system II, it is P680.

iii. Activation of chlorophyll molecule by photon of light

When P700 or P680 forms of chlorophyll *a* receives a photon (quantum) of light, becomes an excited molecule having more energy than the ground state energy. After passing through the unstable second singlet state, and first singlet stage the chlorophyll molecules comes to the metastable triplet state. This excited state of chlorophyll molecule takes part further in primary photochemical reaction i.e. the electron is expelled from the chlorophyll *a* molecule.

$$\text{Chlorophyll } a \xrightarrow{\text{light}} \text{Excited triplet state of chlorophyll } a$$

$$\text{Excited triplet state of chlorophyll } a \longrightarrow \textit{Chlorophyll } a^{+} + e^{-}$$

iv. Photolysis of water and O_2 evolution (oxidation of water)

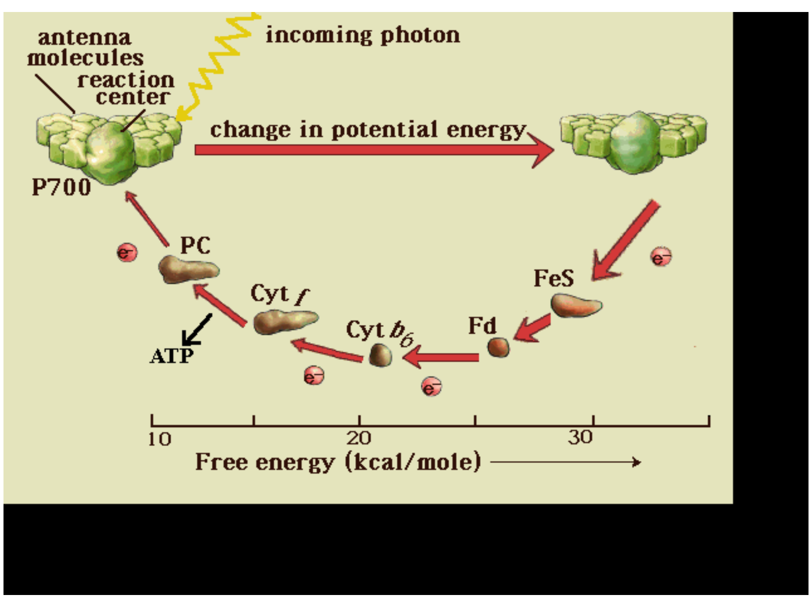
These processes are associated with pigment system II and are catalyzed by Mn^{++} and Cl^{-} ions. When pigment system II is active i.e it receives the light, the water molecules split into OH^{-} and H^{+} ions (*Photolysis of water*). The OH^{-} ions unite to form some water molecules again and release O_2 and electrons.

$$4H_2O \rightarrow 4H^{+} + 4\,(OH^{-})$$
$$4(OH^{-}) \rightarrow 2H_2O + O_2 + 4e^{-}$$
$$2H_2O \rightarrow 4H^{+} + O_2 + 4e^{-}$$

v. Electron transport and production of assimilatory powers ($NADPH_2$ and ATP)

It has already been observed that when chlorophyll molecule receives the photon of light, an electron is expelled from the chlorophyll *a* molecule along with extra energy. This electron after traveling through a number of electron carriers is utilized for the production of $NADPH_2$ from NADP and also utilized for the formation of ATP molecules from ADP and inorganic phosphate (Pi). The transfer of electrons through a series of coenzymes is called **electron transport** and the process of formation of ATP from ADP and Pi using the energy of electron transport is called as **photosynthetic phosphorylation** *or* **photophosphoryration**. The types of Phosphorylation include *cyclic and non- cyclic.*

Cyclic electron transport and cyclic photophosphorylation



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The electrons released from photosystem I goes through a series of coenzymes and returns back to the same photosystem I. This electron transport is called **cyclic electron transport.** The synthesis of ATP occurring in cyclic electron transport is called **cyclic photophosphorylation.** The cyclic electron transport involves only pigment system I. This situation is created when the activity of pigment system II is blocked. Under this condition,

1. Only pigment system I remain active
2. Photolysis of water does not take place
3. Blockage of noncyclic ATP formation and this causes a drop in CO_2 assimilation in dark reaction
4. There is a consequent shortage of oxidized NADP

Thus, when P700 molecule is excited in pigment system I by absorbing a photon (quantum) of light, the ejected electron is captured by ferredoxin *via* FRS. From ferredoxin, the electrons are not used up for reducing NADP to NADPH + H^+ but ultimately it falls back to the P700 molecule via number of other intermediate electron carriers. The electron carriers are probably cytochrome b_6, cytochrome *f* and plastocyanin.

During this electron transport, phosphorylation of ADP molecule to form ATP molecule take place at two places i.e., between ferredoxin and cytochrome b_6 and between cytochrome b_6 and cytochrome *f*. Thus, two ATP molecules are produced in this cycle. Since the electron ejected from P700 molecule is cycled back, the process has been called as **cyclic electron transport** and the accompanying phosphorylation as the **cyclic photophosphorylation.**

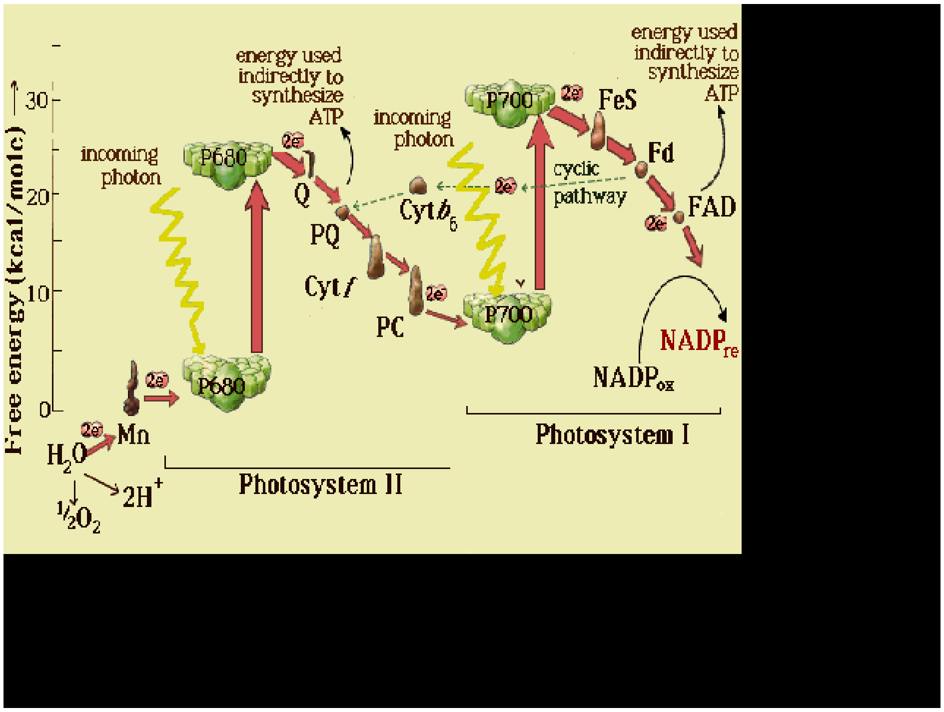
Significance of cyclic photophosphorylation

1. During cyclic electron transport and phosphorylation, photolysis of water, O_2 evolution and reduction of NADP do not take place.
2. The electron returns or cycles back to original position in the P700 form of chlorophyll *a*. Here, chlorophyll molecule serves both as donor and acceptor of the electron.
3. It generates energy rich ATP molecules at two sites and as such cannot drive dark reactions of photosynthesis

On the other hand, non- cyclic photophosphorylation does not produce sufficient ATP in relation to NADPH to operate the dark phase of photosynthesis. Therefore, the deficiency of ATP molecule in non–cyclic photophosphorylation is made up by the operations of cyclic photophosphorylation.

Secondly, the cyclic photophosphorylation may be an important process in providing ATP for photosynthesis and other processes such as synthesis of starch, proteins, lipids, nucleic acids and pigments within the chloroplast.

Non cyclic photophosphorylation



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The electron released from photosystem II goes through a series of enzymes and co-enzymes to photosystem I. This is called **non cyclic electron transport** and the synthesis of ATP in non-cyclic electron transport is called **non-cyclic photophosphorylation**. The main function of non cyclic electron transport is to produce the assimilatory powers such as $NADPH_2$ and ATP and the process occurs in photosystem I and II.

This process of electron transport is initiated by the absorption of a photon (quantum) of light by P680 form of chlorophyll *a* molecule in the pigment system II, which gets excited and an electron is ejected from it so that an electron deficiency or a hole is left behind in the P680 molecule.

The ejected electron is trapped by an unknown compound known as Q. From Q, the electron passes downhill along a series of compounds or intermediated electron carriers such as cytochrome b_6, plastoquinone, cytochrome *f* and a copper containing plastocyanin and ultimately received by pigment system I. At one place during electron transport i.e. between plastoquinone and cytochrome *f*, one molecule of ATP is formed from ADP and inorganic phosphate.

Now, when a photon of light is absorbed by P700 form of chlorophyll molecule in the pigment system I, this gets excited and an electron is ejected from it. This ejected electron is trapped by FRS (Ferredoxin Reducing Substance) and it is then transferred to a non-heme iron protein called ferredoxin. From ferredoxin, electron is transferred to NADP so that NADP is reduced to $NADPH + H^+$

The hole in pigment system I has been filled by electron coming from pigment system II. But, the hole or an electron deficiency in pigment system II is filled up by the electron coming from photolysis of water where, water acts as electron donor.

In this scheme of electron transport, the electron ejected from pigment system II did not return to its place of origin, instead it is taken up by pigment system I. Similarly, the electron ejected from pigment system I did not cycle back and was consumed in reducing NADP. Therefore, this electron transport has been called as *non–cyclic electron transport* and accompanying phosphorylation as *non–cyclic photophosphorylation.*

The non cyclic electron transport (photophosphorylation) takes the shape of Z and hence it is called by the name Z–scheme. Non cyclic photophosphorylation and O_2 evolution are inhibited by CMU (3-(4'-Chlorophyl) – 1-1dimethyl urea and 3-(3-4-dichlorophenyl)-1, 1-dimethyl urea (DCMU).

Significance of non cyclic electron transport

1. It involves PS I and PSII
2. The electron expelled from P680 of PSII is transferred to PS I and hence it is a non cyclic electron transport.
3. In non cyclic electron transport, photolysis of water (Hill's reaction and evolution of O_2) takes place.
4. Phosphorylation (synthesis of ATP molecules) takes place at only one place.
5. The electron released during photolysis of water is transferred to PS II.
6. The hydrogen ions (H^+) released from water are accepted by NADP and it becomes $NADPH_2$
7. At the end of non cyclic electron transport, energy rich ATP, assimilatory power $NADPH_2$ and oxygen from photolysis of water are observed.
8. The ATP and $NADPH_2$ are essential for the dark reaction wherein, reduction of CO_2 to carbohydrate takes place.

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Lecture 13

2. Dark reaction or Blackman's reaction or Path of carbon in photosynthesis

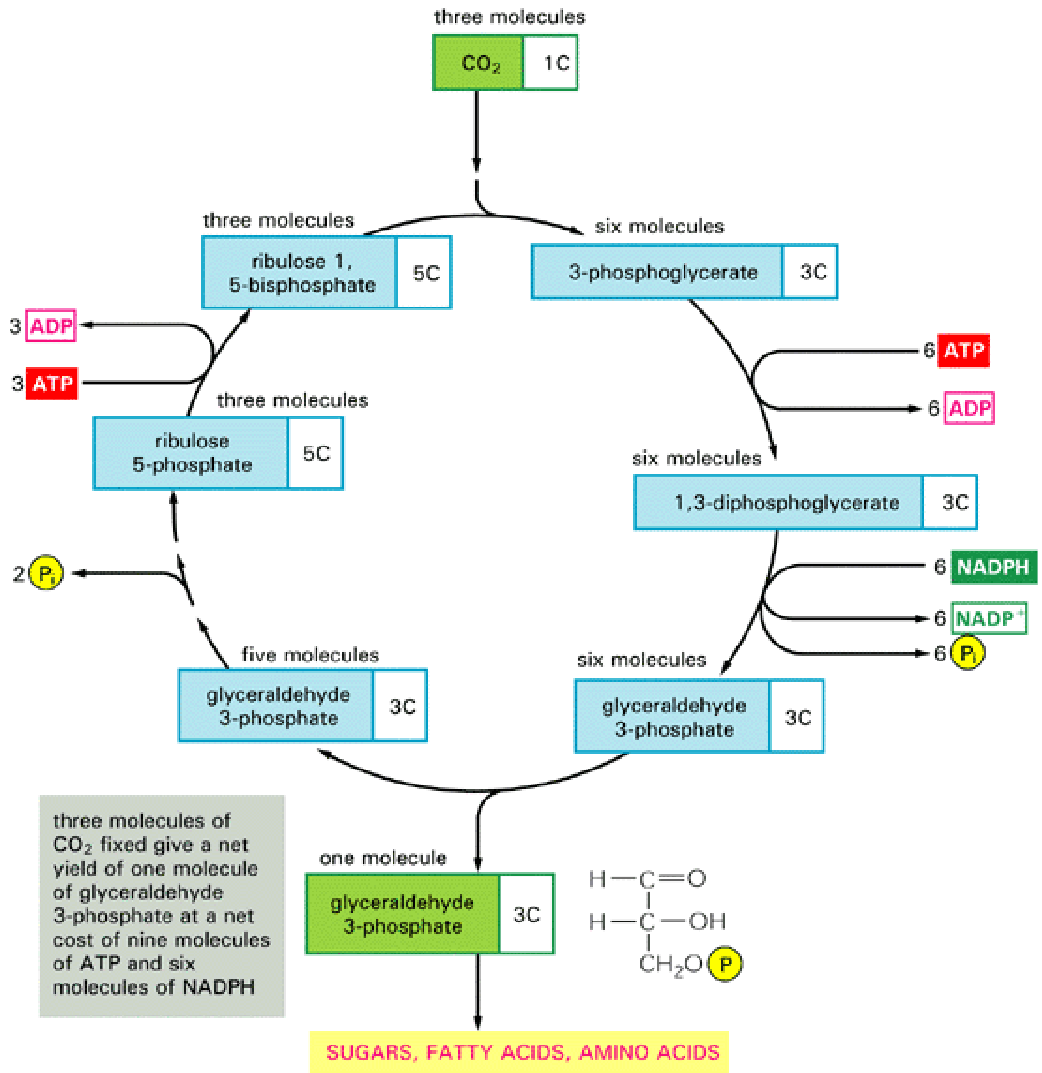
This is the second step in the mechanism of photosynthesis. The chemical processes of photosynthesis occurring independent of light is called **dark reaction**. It takes place in the stroma of chloroplast. The dark reaction is purely enzymatic and it is slower than the light reaction. The dark reactions occur also in the presence of light. In dark reaction, the sugars are synthesized from CO_2. The energy poor CO_2 is fixed to energy rich carbohydrates using the energy rich compound, ATP and the assimilatory power, $NADPH_2$ of light reaction. The process is called carbon fixation or carbon assimilation. Since Blackman demonstrated the existence of dark reaction, the reaction is also called as **Blackman's reaction**. In dark reaction two types of cyclic reactions occur

1. Calvin cycle or C3 cycle
2. Hatch and Slack pathway or C4 cycle

Calvin cycle or C3 cycle

It is a cyclic reaction occurring in the dark phase of photosynthesis. In this reaction, CO_2 is converted into sugars and hence it is a process of carbon fixation. The Calvin cycle was first observed by Melvin Calvin in chlorella, unicellular green algae. Calvin was awarded Nobel Prize for this work in 1961. Since the first stable compound in Calvin cycle is a 3 carbon compound (3 phosphoglyceric acid), the cycle is also called as C3 cycle. The reactions of Calvin's cycle occur in three phases.

1. Carboxylative phase
2. Reductive phase
3. Regenerative phase



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1. Carboxylative phase

Three molecules of CO_2 are accepted by 3 molecules of 5C compound viz., ribulose diphosphate to form three molecules of an unstable intermediate 6C compound. This reaction is catalysed by the enzyme, carboxydimutase

3 CO_2 + **3 Ribulose diphosphate** $\xrightarrow{\text{Carboxydimutase}}$ **3 unstable intermediate 6 carbon compound**

The three molecules of the unstable 6 carbon compound are converted by the addition of 3 molecules of water into six molecules of 3 phosphoglyceric acid. This reaction is also catalysed by the enzyme carboxy mutase.

3 unstable intermediate 6 C compound + **3 H_2O** $\xrightarrow{\text{Carboxydimutase}}$ **3 phosphoglyceric acid**

3 phosphoglyceric acid (PGA) is the first stable product of dark reaction of photosynthesis and since it is a 3 carbon compound, this cycle is known as C3 cycle.

2. Reductive phase

Six molecules of 3PGA are phosphorylated by 6 molecules of ATP (produced in the light reaction) to yield 6 molecules of 1-3 diphosphoglyceric acid and 6 molecules of ADP. This reaction is catalysed by the enzyme, Kinase

3 Phospho glyceric acid + ATP —Kinase→ 1,3 diphospho glyceric acid + ADP

Six molecules of 1,3 diphosphoglyceric acid are reduced with the use of 6 molecules of $NADPH_2$ (produced in light reaction) to form 6 molecules of 3 phospho glyceraldehyde. This reaction is catalysed by the enzyme, triose phosphate dehydrogenase.

1,3 diphospho glyceric acid + $NADPH_2$ —Triose phosphate Dehydrogenase→ 3 phospho glyceraldehyde + NADP + H_3PO_4

3. Regenerative phase

In the regenerative phase, the ribose diphosphate is regenerated. The regenerative phase is called as **pentose phosphate pathway or hexose monophophate shunt**. It involves the following steps.

1. Some of the molecules of 3 phosphoglyceraldehyde isomerise into dihydroxy acetone phosphate. Both 3 phosphoglyceraldehyde and dihydroxy acetone phosphate then unite in the presence of the enzyme, aldolase to form fructose, 1-6 diphosphate.

   3 phospho glyceraldehydes (3PGA) —Triose phosphate isomerase→ Dihydroxy acetone PO_4 (DHAP)

   3PGA + DHAP —Aldolase→ Fructose 1,6 diphosphate

2. Fructose 6 phosphate is converted into fructose 6 phosphate in the presence of phosphorylase

   Fructose 1,6 diphosphate —Phosphorylase→ Fructose 6 phosphate

3. Some of the molecules of 3 phosphoglyceraldehyde instead of forming hexose sugars are diverted to regenerate ribulose 1-5 diphosphate

   3 phospho glyceraldehyde → Ribulose 1,5 diphosphate

4. 3 phosphoglyceraldehyde reacts with fructose 6 phosphate in the presence of enzyme transketolase to form erythrose 4 phosphate (4C sugar) and xylulose 5 phosphate(5C sugar).

   3 phospho glyceraldehydes + Fructose 6 phosphate —Transketolase→ Erythrose 4 phosphate + Xylulose 5 phosphate

5. Erythrose 4 phosphate combines with dihydroxy acetone phosphate in the presence of the enzyme aldolase to form sedoheptulose 1,7 diphosphate(7C sugar).

Erythrose 4 phosphate + DHAP —Aldolase→ Sedoheptulose 1 ,7 diphosphate

6. Sedoheptulose 1, 7 diphosphate loses one phosphate group in the presence of the enzyme phosphatase to form sedoheptulose 7 phosphate.

Sedoheptulose 1 ,7 diphosphate + ADP —Phosphatase→ Sedoheptulose 7 phosphate + ATP

7. S
e
doheptulose phosphate reacts with 3 phosphoglyceraldehyde in the presence of transketolase to form xylulose 5 phosphate and ribose 5 phosphate (both % c sugars)

Sedoheptulose 7 phosphate + 3 PGA —Transketolase→ Xylulose 5 phosphate + Ribose 5 phosphate

8. Ribose 5 phosphate is converted into ribulose 1, 5 diphosphate in the presence of enzyme, phosphopentose kinase and ATP. Two molecules of xylulose phosphate are also converted into one molecule of ribulose monophosphate. The ribulose monophosphate is phosphorylated by ATP to form ribulose diphosphate and ADP, thus completing Calvin cycle.

Ribose-5-phosphate + ATP —Phophopentokinase→ Ribulose 1,5 diphosphate + ADP

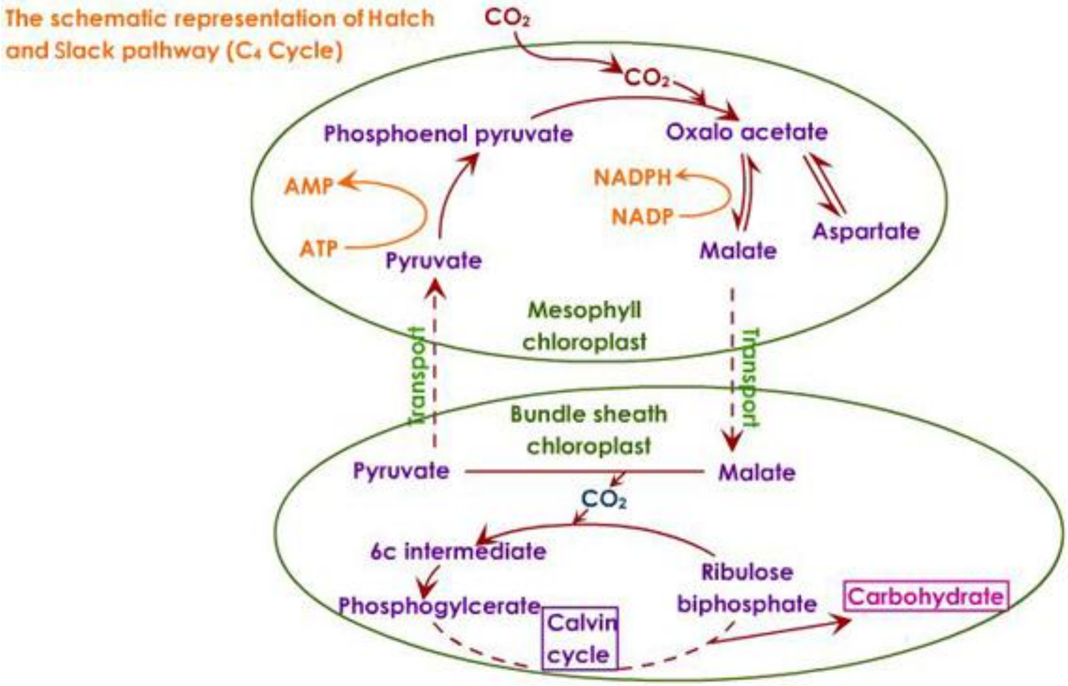
2 mols of Xylulose phosphate —Phophopentokinase→ 1 mol of Ribulose mono phosphate

Ribulose mono phosphate + ATP —Phophopentokinase→ Ribulose diphosphate + ADP

In the dark reaction, CO_2 is fixed to carbohydrates and the CO_2 acceptor ribulose diphosphate is regenerated. In Calvin cycle, 12 $NADPH_2$ and 18 ATPs are required to fix 6 CO_2 molecules into one hexose sugar molecule (fructose 6 phosphate).

6 CO_2 + 12 $NADPH_2$ + 18 ATP → Fructose 6 phosphate + 12 NADP+ 18 ADP+ 17 Pi

C4 cycle or Hatch and Slack pathway



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It is the alternate pathway of C3 cycle to fix CO_2. In this cycle, the first formed stable compound is a 4 carbon compound viz., oxaloacetic acid. Hence it is called **C4 cycle**. The path way is also called as Hatch and Slack as they worked out the pathway in 1966 and it is also called as C4 dicarboxylic acid pathway. This pathway is commonly seen in many grasses, sugar cane, maize, sorghum and amaranthus.

The C4 plants show a different type of leaf anatomy. The chloroplasts are dimorphic in nature. In the leaves of these plants, the vascular bundles are surrounded by bundle sheath of larger parenchymatous cells. These bundle sheath cells have chloroplasts. These chloroplasts of bundle sheath are larger, lack grana and contain starch grains. The chloroplasts in mesophyll cells are smaller and always contain grana. This peculiar anatomy of leaves of C4 plants is called Kranz anatomy. The bundle sheath cells are bigger and look like a ring or wreath. Kranz in German means wreath and hence it is called Kranz anatomy. The C4 cycle involves two carboxylation reactions, one taking place in chloroplasts of mesophyll cells and another in chloroplasts of bundle sheath cells.

There are four steps in Hatch and Slack cycle:

1. Carboxylation
2. Breakdown
3. Splitting
4. Phosphorylation

The C4 pathway is known to operate in two types of cells:

1. Chloroplasts of mesophyll cells.
2. Chloroplasts of bundle sheath cells.

1. Carboxylation

It takes place in the chloroplasts of mesophyll cells. Phosphoenolpyruvate, a 3 carbon compound picks up CO_2 and changes into 4 carbon oxaloacetate in the presence of water. This reaction is catalysed by the enzyme, phosphoenol pyruvate carboxylase.

$$\text{Phosphoenol Pyruvate (3C)} + CO_2 + H_2O \xrightarrow[\text{carboxylase}]{\text{PEP}} \text{Oxaloacetate} + \text{(4C)} \quad H_3PO_4$$

2. Breakdown

Oxaloacetate breaks down readily into 4 carbon malate and aspartate in the presence of the enzyme, transaminase and malate dehydrogenase.

$$\text{Oxaloacetate (4C)} \xrightarrow[\text{Malate dehydrogenase}]{\text{Transaminase}} \text{Aspartate (4C)} + \text{Malate (4C)}$$

These compounds diffuse from the mesophyll cells into sheath cells.

3. Splitting

In the sheath cells, malate and aspartate split enzymatically to yield free CO_2 and 3 carbon pyruvate. The CO_2 is used in Calvin's cycle in the sheath cell.

$$\text{Malate} \xrightarrow{\text{Decarboxylation}} CO_2 + \text{Pyruvate}$$

The second carboxylation occurs in the chloroplast of bundle sheath cells. The CO_2 is accepted by 5 carbon compound ribulose diphosphate in the presence of the enzyme, carboxydimutase and ultimately yields 3 phosphoglyceric acid. Some of the 3 phosphoglyceric acid is utilised in the formation of sugars and the rest regenerate ribulose diphosphate.

4. Phosphorylation

The pyruvate molecule is transferred to chloroplasts of mesophyll cells where, it is phosphorylated to regenerate phosphoenol pyruvate in the presence of ATP. This reaction is catalysed by pyruvate phosphokinase and the phophoenol pyruvate is regenerated.

$$\text{Pyruvate} + \text{ATP} \xrightarrow[\text{Phosphokinase}]{\text{Pyruvate}} \text{Phosphoenol pyruvate} + \text{AMP} + \text{Pyrophosphate}$$

In Hatch and Slack pathway, the C3 and C4 cycles of carboxylation are linked and this is due to the Kranz anatomy of the leaves. The C4 plants are more efficient in photosynthesis than the C3 plants. The enzyme, phosphoenol pyruvate carboxylase of the C4 cycle is found to have more affinity for CO2 than the ribulose diphosphate carboxylase of the C3 cycle in fixing the molecular CO2 in organic compound during carboxylation.

Structural Peculiarities of C4 Plants:

1. Presence of bundle sheath cells containing chloroplasts.
2. Bundle sheath cells are radially arranged around a vascular bundle.
3. Bundle sheath cells lack grana in their chloroplasts.

4. Bundle sheath cells are arranged in one or more layers consisting of large thick walled cylindrical cells, around vascular bundle, a characteristic feature of C4 plants.
5. Bundle sheath cells remain surrounded by one or more wreath like layers of mesophyll cells. This anatomical arrangement is called as Kranz type (Kranz=wreath, a German term). (Kranz: Wreath of mesophyll cells around bundle sheath cells)
6. Mesophyll cells have well-developed grana. (Thus, C4 pathway constitutes an example of dimorphism of chloroplasts) But, some C4 plants (bermuda grass) have grana in chloroplasts of bundle sheath cells).
7. The ratio of PS I: PS II activity is three times higher than the bundle sheath cells.
8. The mesophyll cells are almost three times more active in non-cyclic electron transport system than that of bundle sheath cells.
9. For cyclic electron transport, both the cells are equally efficient.
10. Clear cut categorization of enzymes is found in C4 cycle.

Most of the PEP carbocylase occurs in mesophyll cells. While most of ribulose- 1,5-diphosphate carboxylase and malic enzymes are found in bundle sheath cells. The C4 cycle is also referred as the **dicarboxylic acid cycle** or the **□-Carboxylation pathway** or **Hatch-Slack cycle** or **Co-operative Photosynthesis** (Karpilov, 1970). In this Cycle, the characteristic point is the primary carboxylation reaction and the **phosphoenolpyruvate (PEP)** is found to be **CO_2 acceptor molecule.**

Comparison of the plants of C3 and C4 cycle

	C_3 Plant	**C_4 Plant**
1.	Only C_3 cycle is found	Both C_4 and C_3 cycles are found.
2.	The efficiency of CO_2 absorption at low concentration is far less and hence, they are less efficient.	The efficiency of CO_2 absorption at low concentration is quite high and hence, they are more efficient plants.
3.	The CO_2 acceptor is Ribulose-1, 5-diphosphate.	The CO_2 acceptor is phospho enol pyruvate.
4.	The first stable product is phospho glyceric acid (PGA).	Oxaloacetate (OAA) is the first stable product.
5.	Plants show one type of chloroplast (monomorphic type).	Plants show dimorphic type of chloroplast. The chloroplast of parenchymatous bundle sheath is different from that of mesophyll cells (dimorphic type). The chloroplasts in bundle sheath cell are centripetally arranged and lack grana. Leaves show *Kranz type* of anatomy.
6.	In each chloroplast, two pigment systems (Photosystems I and II) are present.	In the chloroplasts of bundle sheath cells, the photosystem II is absent. Therefore, these are dependent on mesophyll chloroplasts for the supply of NADPH + H^+.
7.	The Calvin cycle enzymes are present in mesophyll chloroplast. Thus, the Calvin cycle occurs.	Calvin cycle enzymes are absent in mesophyll chloroplasts. The cycle occurs only in the chloroplasts of bundle sheath cells.
8.	The CO_2 compensation point is 50-150 ppm CO_2.	The CO_2 compensation point is 0-10 ppm CO_2.

9.	Photorespiration is present and easily detectable.	Photorespiration is present only to a slight degree or absent.
10.	The CO_2 concentration inside leaf remains high (about 200 ppm).	The CO_2 concentration inside the leaf remains low (about 100 ppm).
11.	The $^{13}C/^{12}C$ ratio in C-containing compounds remains relatively low (both $^{13}CO_2$ and $^{12}CO_2$ are present in air).	The ratio is relatively high, *i.e.* C_4 plants are more enriched with ^{13}C than C_3 plants.
12.	Net rate of photosynthesis in full sunlight (10,000 – 12,000 ft. c.) is 15-25 mg. of CO_2 per dm^2 of leaf area per hour.	It is 40-80 mg. of CO_2 per dm^2 of leaf area per hour. That is, photosynthetic rate is quite high. The plants are efficient.
13.	The light saturation intensity reaches in the range of 1000-4000 ft. c.	It is difficult to reach saturation even in full sunlight.
14.	Bundle sheath cells are unspecialized.	The bundle sheath cells are highly developed with unusual construction of organelles.
15.	The optimum temperature for the process is 10-25°C.	In these plants, it is 30-45°C and hence, they are warm climate plants. At this temperature, the rate of photosynthesis is double than that is in C_3 plants.
16.	18 ATPs are required to synthesise one glucose molecule.	30 ATPs are required to synthesise one glucose molecule.

Crassulacean Acid Metabolism (CAM) cycle or the dark fixation of CO_2 in succulents.

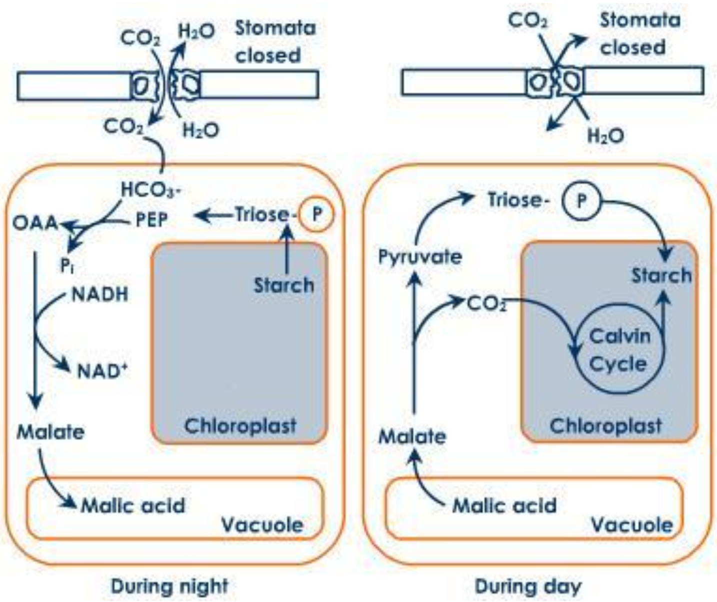
CAM is a cyclic reaction occurring in the dark phase of photosynthesis in the plants of Crassulaceae. It is a CO_2 fixation process wherein, the first product is malic acid. It is the third alternate pathway of Calvin cycle, occurring in mesophyll cells. The plants exhibiting CAM cycle are called CAM plants. Most of the CAM plants are succulents e.g., Bryophyllum, Kalanchoe, Crassula, Sedium, Kleinia etc. It is also seen in certain plants of Cactus e.g. Opuntia, Orchid and Pine apple families.

CAM plants are usually succulents and they grow under extremely xeric conditions. In these plants, the leaves are succulent or fleshy. The mesophyll cells have larger number of chloroplasts and the vascular bundles are not surrounded by well defined bundle sheath cells.

In these plants, the stomata remain open during night and closed during day time. The CAM plants are adapted to photosynthesis and survival under adverse xeric conditions. CAM plants are not as efficient as C4 plants in photosynthesis. But they are better suited to conditions of extreme desiccation.

CAM involves two steps:

1. Acidification
2. Deacidification



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Acidification

In darkness, the stored carbohydrates are converted into phophoenol pyruvic acid by the process of glycolysis . The stomata in CAM plants are open in dark and they allow free diffusion of CO_2 from the atmosphere into the leaf. Now, the phosphoenolpyruvic acid carboxylated by the enzyme phosphoenol pyruvic acid carboxylase and is converted in to oxalaoacetic acid.

Phosphoenol Pyruvate + CO_2 + H_2O $\xrightarrow[\text{carboxylase}]{\text{PEP}}$ Oxaloacetic acid + H_3PO_4

The oxaloacetic acid is then reduced to malic acid in the presence of the enzyme malic dehydrogenase. The reaction requires NADPH2 produced in glycolysis.

Oxaloacetic acid + $NADPH_2$ $\xrightarrow[\text{dehydrogenase}]{\text{Malic}}$ Malic acid + $NADP^+$

The malic acid produced in dark is stored in the vacuole. The malic acid increases the acidity of the tissues.

Deacidification

During day time, when the stomata are closed, the malic acid is decarboxylated to produce pyruvic acid and evolve carbon dioxide in the presence of the malic enzyme. When the malic acid is removed, the acidity decreases the cells. This is called deacidification. One molecule of $NADP^+$ is reduced in this reaction.

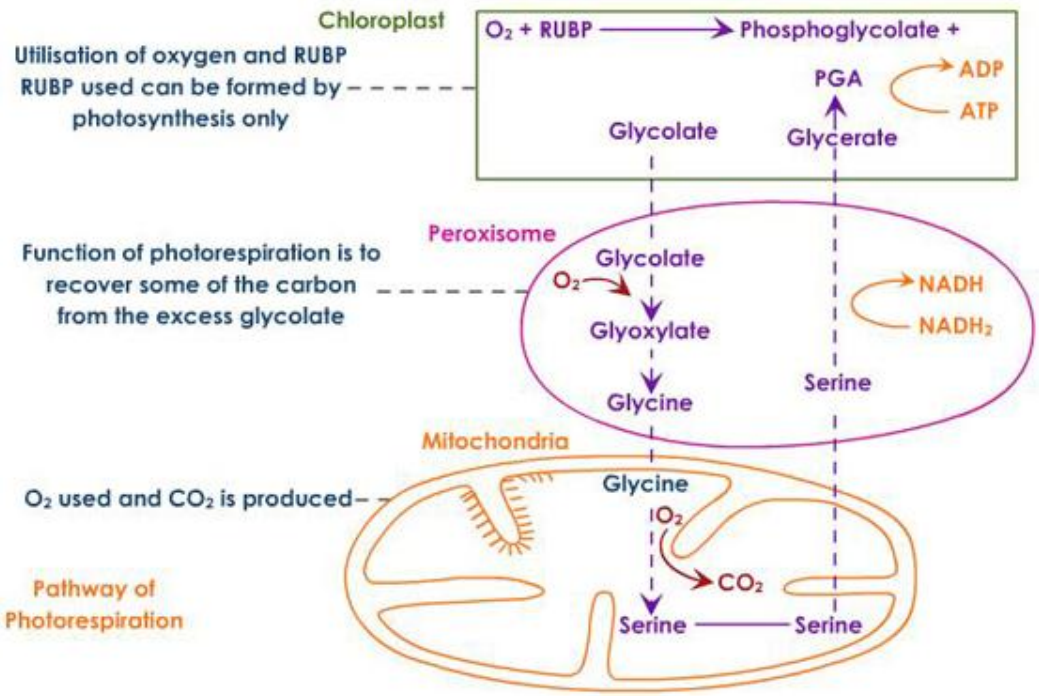
Malic acid + NADP $\xrightarrow{\text{Malic enzyme}}$ Pyruvic acid + $NADPH_2$ + CO_2

The pyruvic acid may be oxidized to CO_2 by the pathway of Kreb's cycle or it may be reconverted to phosphoenol pyruvic acid and synthesise sugar by C3 cycle. The CO_2 released by deacidification of malic acid is accepted by ribulose diphosphate and is fixed to carbohydrate by C3 cycle.

CAM is a most significant pathway in succulent plants. The stomata are closed during day time to avoid transpirational loss of water. As the stomata are closed, CO_2

cannot enter into the leaves from the atmosphere. However, they can carry out photosynthesis during the day time with the help of CO_2 released from organic acids. During night time, organic acids are synthesized in plenty with the help of CO_2 released in respiration and the CO_2 entering from the atmosphere through the open stomata. Thus, the CO_2 in dark acts as survival value to these plants.

Photorespiration



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Photorespiration is a process which involves oxidation of organic compounds in plants by oxygen in the presence of light. Like ordinary respiration, this process also releases carbon from organic compounds in the form of CO_2 but does not produce ATP. Thus, apparently it seems to be a wasteful process, but it must have some functions which are still unknown. This process occurs in C_3 plants and to some extent in C_4. Photorespiratory substrate is glycolate. RuBisco instead of combining with CO_2 it combines with O_2. This type of oxidation of O_2 to RuBP molecule is known as **photosynthetic C-oxidation cycle or glycolate pathway or C_2 photorespiratory carbon oxidation cycle.**

Generally photorespiration is expressed by the term called **CO_2 compensation point** and it is defined as CO_2 concentration at which rate of uptake will be equal to the rate of photosynthetic respiratory CO_2 released. Photorespiration is around 80-100 ppm in case of C_3 plants and 0-10 ppm in C_4 plants.

As alternative substrates for RuBisco, CO_2 and O_2 compete for reaction with ribulose-1,5-bisphostate because of carboxylation (if CO_2 reacts with RuBP then carboxylation takes place) and oxygenation (if O_2 reacts with RuBP then oxygenation takes place) occur within the same active site of the enzyme. Photorespiration occurs usually when there is high concentration of O_2. under such circumstances RuBP carboxylase (or RuBisCo), the enzyme that joins CO_2 to RuBP, functions as oxygenase. As a result oxygen, instead of CO_2, gets attached to the binding site of the enzyme and the latter (ie RuBP) is oxidized. On oxidation, RuBP releases one molecule of C_3 compound, PGA (which enters C_3 cycle) and one molecule of a C_2

compound **phosphoglycolate**. The latter almost immediately changes to glycolate. The glycolate leaves the chloroplast and enters a membrane bound sac of enzymes called peroxisme. Here the glycolate is oxidized into glyoxylate which is aminated into glycine. Further condensation of glycine takes place inside the mitochondria where two molecules of glycine interact and give rise to a molecule of serine and CO_2 each. The later is then released in photorespiration.

Factors controlling photorespiration

1. CO_2 concentration: Higher the CO_2 concentration lesser will be the photorespiration.
2. O_2 concentration: More the O_2 concentration more will be the photorespiration.
3. Temperature: Optimum temperature is 25-35^oC. More the temperature less will be the photorespiration.

Reasons for lack of photorespiration in C_4 plant

1. They have low CO_2 composition point.
2. No or less CO_2 evolution in light.
3. Less response to elevated CO_2 levels with regards to growth rate.
4. Due to lack of synthesis of photorespiratory substrate.
    - i. Photorespiration occure in bundle sheath chloroplast where, RuBisCo present.
    - ii. Due to CO_2 enrichment mechanism higher CO_2 is maintained in bundle sheath cells. Higher CO_2 is maintained due to rapid decarboxylation of malate and aspertate and transferred these from mesophyll cells. Due to higher CO_2 concentration photorespiration is inhibited.

    So in C_4 plants there will no or less photorespiration.

Factors Influencing Photosynthesis

The factors influencing rate of photosynthesis can be classified into two categories,

A. Internal factor and
B. external factor (environmental)

A. Internal Factors

1. Chlorophyll

The amount of chlorophyll present has a direct relationship with the rate of photosynthesis, since, it is the pigment, which is photoreceptive and is directly involved in trapping the light energy.

2. Photosynthetic Enzyme Systems

The amount and nature of enzymes play a direct role on the rate of photosynthesis. Greater enzyme activity at higher light intensity increases the capacity of the leaf to absorb more light and thus increases the photosynthetic rate.

3. Leaf Resistance

Photosynthesis shows close dependence upon leaf resistance. For C4 plants, leaf resistance (primarily controlled by stomatal aperture) appears to regulate photosynthesis, but in C3 plants, the internal resistances including carboxylation efficiency offer greater limitation to CO2 fixation than stomatal resistance. Environmental factors such as light intensity, photoperiod, CO2 concentration, humidity and soil moisture also affect photosynthesis via stomatal resistance.

4. Demand for Photosynthate

Because of the greater demand, the rapidly growing plants show increased rate of photosynthesis in comparison to the mature plants. However, if the demand for photosynthesis is lowered by removal of meristem, then the photosynthetic rate declines.

5. Leaf Age

The Photosynthetic rate is higher in the newly expanding leaves and reaches a maximum as the leaves achieve full size. The rate declines as the leaf ages due to reduced chloroplast functions and other anabolic reactions.

B. External Factors

1. Carbon dioxide

CO_2 is one of the raw materials for photosynthesis; therefore, its concentration affects the rate of photosynthesis markedly. Rate of photosynthesis increases with the increase in the atmospheric CO_2 concentration up to a certain extent. Because of its very low concentration in atmosphere (current level of 350-360ppm), it acts as a limiting factor in natural photosynthesis. Rate of photosynthesis increases with increase in the atm. CO_2 level of upto 1000ppm beyond which, there is a general decline in photosynthesis. At this enhanced level of CO_2, the increase in the photosynthetic rate may be 10 to 30 times more than the normal CO_2 level.

2. Light

Light affects the rate of photosynthesis in several ways. In general, photosynthesis can occur under artificial lights of sufficient intensity. Role of light on photosynthesis can be discussed under the following sub-heads:

a. Intensity of light:

a. Light intensity

Wolkoff (1966) found that the arte of photosynthesis is directly proportional to light intensity. But the extremely high light intensities do not favor for higher photosynthetic rates. The high light intensity which fails to accelerate photosynthesis is called light saturation intensity. Of the light falling on a leaf, about 80 per cent is absorbed, 10 per cent is reflected and 10 % is transmitted. The rate of photosynthesis is greater in intense light than in diffused light. The plants are grouped into two types on the basis of light requirement.

i. Heliophytes (Sun plants)

ii. Sciophytes (Shade plants)

At a specific light intensity, the amount of CO_2 used in photosynthesis and the amount of CO_2 released in respiration are volumetrically equal. This specific light intensity is known as **light compensation point.**

At very high light intensity, beyond a certain point, the photosynthetic cells exhibit *photo oxidation.* This phenomenon is called *solarisation* and a result of this, inactivation of chlorophyll molecules, bleaching of chlorophyll molecules and even inactivation of some enzymes take place resulting in the destruction of whole photosynthetic apparatus. In general, low light intensity favours stomatal closure and in turn reduced rate of photosynthesis.

With the increase in light intensity, the rate of photosynthesis increases, i.e., the rate of photosynthesis is directly proportional to light intensity. However, at stronger light intensity, increase in rate of photosynthesis is not proportional to light intensity. Except on cloudy days, light is never a limiting factor in nature. At certain light intensity, the amount of CO2 used in photosynthesis and the amount of CO2 produced in respiration are volumetrically equal. This point of light intensity is known as Light Compensation Point. Light compensation point is frequently in the order of 100 to 200 f.c. for sun loving leaves; while, the value is 100f.c. for shade-loving leaves. Thus, in shade-loving plants the compensation point lasts for a much shorter period than in sun loving plants.

b. Wavelength of light:

For photosynthesis, the visible range of spectrum of light (PAR: 400 to 700 nm) is essential. Maximum photosynthesis is known to occur in the red part of the spectrum with the next peak in blue part and minimum in the green region (RED ,BLUE and

GRE The region between 575 and 750nm (yellow to red) is quite congenial for photosynthesis. Ultra violet light has a lethal effect on plants if exposure is for a prolonged period.

c. Duration of light:

Photosynthesis may be sustained for relatively long periods of time without any noticeable damaging effect on plants.

d. Photo-oxidation:

When the light intensity for photosynthesizing tissue is increased beyond a certain limit, the cells become vulnerable to chlorophyll photo-oxidation; due to this, many more chlorophyll molecules become excited than can possibly be utilized. This causes damaging effect to the chloroplast membrane system. In presence of O2, the damaging effect of photo-oxidation is severe. It results in bleaching of chlorophyll and inactivation of some important enzyme involved in photosynthesis. Effect to temperature on photosynthesis is little than on other process. Very high and very low temperatures affect the photosynthetic rate adversely. The rate of photosynthesis increases with rise in temperature from 5 to 350C; beyond which, there is a rapid fall in photosynthesis. In the optimum range of temperature, the Temperature Quotient (Q10) is found to be 2.0 for the rate of photosynthesis (Q10=2.0).

4. Water

Water is one of the raw materials in photosynthesis. It has an indirect effect on the rate of photosynthesis. Water availability affects the water relation of plant, thus affecting the rate of photosynthesis. In scarcity of water, cells become flaccid. Depending upon the availability of water, the rate of photosynthesis may be decreased from 10 to 90%.

5. Oxygen

Oxygen is the by-product of photosynthesis. Accumulation of greater amount of oxygen molecules causes substantial inhibition of photosynthesis. Oxygen is also known to have a direct and competitive inhibition for RuBP carboxylase. As a result, glycolate synthesis is enhanced which leads to photorespiration.

Inhibitors of Photosynthetic Process

1. Several urea derivatives such as monuron (or CMU) and diuron (or DCMU) block electron transport between Q and PQ.
2. Simazine, atrazine, bromacil and isocil block the same step.
3. Diquat and paraquat are common photosynthetic inhibitors. These compounds (commonly referred as **viologen dyes**) accept electron from PS I before ferredoxin and produce toxic forms of O_2 (superoxide and hydroxy).

Animation on "overview on photosynthesis":
http://www.wiley.com/college/boyer/0470003790/animations/photosynthesis/photosynthesis.htm

YouTube - Photosynthesis (Light Reactions).flv

Reference:

1. Plant physiology – III Ed. Taiz and Zeiger: http://4e.plantphys.net
2. Plant physiology – Salisbury and Rose.
3. www.**tnau**.ac.in/

Lecture 14
PHYTOHORMONES

Plant hormones or plant growth regulators area organic substances produced by higher plants that alter growth patterns and/or maintenance of the plant. Thimann (1948) proposed the term phytohormone as these hormones are synthesised in plants.

Hormones regulate cellular processes in targeted cells locally and when moved to other locations, in other locations of the plant. Hormones also determine the formation of flowers, stems, leaves, the shedding of leaves, and the development and ripening of fruit. Plants, unlike animals, lack glands that produce and secrete hormones, instead each cell is capable of producing hormones. Plant hormones shape the plant, affecting seed growth, time of flowering, the sex of flowers, senescence of leaves and fruits. They affect which tissues grow upward and which grow downward, leaf formation and stem growth, fruit development and ripening, plant longevity, and even plant death. Hormones are vital to plant growth and lacking them, plants would be mostly a mass of undifferentiated cells.

Characteristics

The word hormone is derived from Greek, meaning 'set in motion.' Plant hormones affect gene expression and transcription levels, cellular division, and growth. They are naturally produced within plants, though very similar chemicals are produced by fungi and bacteria that can also effect plant growth.

Plant hormones are not nutrients, but chemicals that in small amounts promote and influence the growth, [2] development, and differentiation of cells and tissues. The biosynthesis of plant hormones within plant tissues is often diffuse and not always localized.

Plants utilize simple chemicals as hormones, which move more easily through the plant's tissues. They are often produced and used on a local basis within the plant body, plant cells even produce hormones that affect different regions of the cell producing the hormone.

Hormones are transported within the plant by utilizing four types of movements. For localized movement, cytoplasmic streaming within cells and slow diffusion of ions and molecules between cells are utilized. Vascular tissues are used to move hormones from one part of the plant to another; these include sieve tubes that move sugars from the leaves to the roots and flowers, and xylem that moves water and mineral solutes from the roots to the foliage.

Not all plant cells respond to hormones, but those cells that do are programmed to respond at specific points in their growth cycle. The greatest effects occur at specific stages during the cell's life, with diminished effects occurring before or after this period. Plants need hormones at very specific times during plant growth and at specific locations. They also need to disengage the effects that hormones have when they are no longer needed. The production of hormones occurs very often at sites of active growth within the meristems, before cells have fully differentiated. After production they are sometimes moved to other parts of the plant where they cause an immediate effect or they can be stored in cells to be released later. Plants use different pathways to regulate internal hormone quantities and moderate their effects; they can regulate the amount of chemicals used to biosynthesize hormones. They can store them in cells, inactivate them, or cannibalise already-formed hormones by conjugating them with carbohydrates, amino acids or peptides. Plants can also break down hormones chemically, effectively destroying them. Plant hormones frequently regulate the concentrations of other plant hormones. [3] Plants also move hormones around the plant diluting their concentrations.

The concentration of hormones required for plant responses are very low (10^{-6} to 10^{-5}mol/L). Because of these low concentrations, it has been very difficult to study plant hormones, and only since the late 1970s have scientists been able to start piecing together their effects and relationships to plant physiology. [4] Much of the early work on plant hormones involved studying plants that were genetically deficient in one or involved the use of tissue-cultured plants grown *in vitro* that were subjected to differing ratios of hormones, and the resultant growth compared. The earliest scientific observation and study dates to the 1880s; the determination and observation of plant hormones and their identification was spread-out over the next 70 years.

Classes of plant hormones

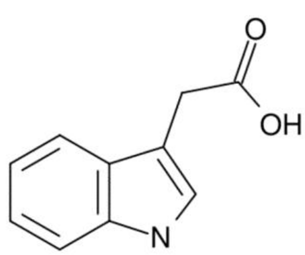
In general, it is accepted that there are five major classes of plant hormones, some of which are made up of many different chemicals that can vary in structure from one plant to the next. The chemicals are each grouped together into one of these classes based on their structural similarities and on their effects on plant physiology. Other plant hormones and growth regulators are not easily grouped into these classes; they exist naturally or are synthesized by humans or other organisms, including chemicals that inhibit plant growth or interrupt the physiological processes within plants. Each class has positive as well as inhibitory functions, and most often work in tandem with each other, with varying ratios of one or more interplaying to affect growth regulation.

The five major classes are:

1. Auxins
2. Cytokinins
3. Gibberellins
4. Ethylene
5. Abscisic acid
6. Brassinosteroids

Auxins:

The concept of chemical messengers in plants was proposed by Charles Darwin and his son, Francis in 1881, who spent time looking at the phenomenon of phototropism in wheat seedlings. Plant shoots are positively phototropic. When a seedling is illuminated from one side the shoot will bend towards the light. The directional growth makes sense, since plants need light for photosynthesis. However, Darwin found that if the coleoptiles of the wheat seedling were removed the plant no longer curved towards light. They did a number of experiments and determined that a chemical located in the colepotile travelled to the region of elongation and effected a differential elongation of cells furthest from the light sources. The chemical was subsequently studied and named it as ***auxin*** by Frits Went in 1926. Chemically auxin is indolacetic acid (IAA) which is synthesised from tryptophan. Auxin promotes growth in molar concentrations of 10^{-3} to 10^{-8}. A primary site of auxin production is the apical shoot meristem. Auxin moves down the stem parenchyma cells by polar transport (auxin become negatively charged) using proton pumps, an energy requiring process



Structure of auxin
http://wapedia.mobi/en/File:Indol-3-ylacetic_acid.svg

Auxin functions:

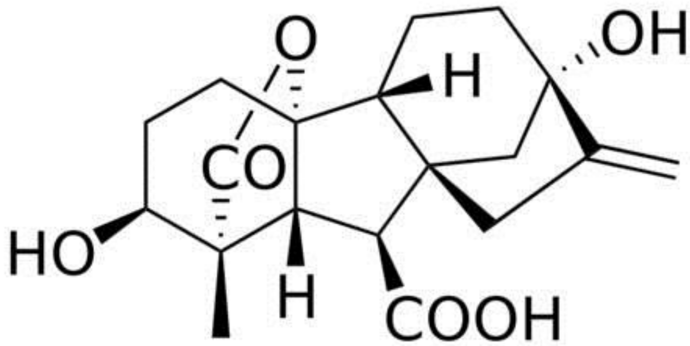
- Stimulates cell elongation
- Stimulates cell division in the cambium and, in combination with cytokinins in tissue culture
- Stimulates differentiation of phloem and xylem
- Stimulates root initiation on stem cuttings and lateral root development in tissue culture
- Mediates the tropistic response of bending in response to gravity and light
- The auxin supply from the apical bud suppresses growth of lateral buds
- Delays leaf senescence
- Can inhibit or promote (via ethylene stimulation) leaf and fruit abscission
- Can induce fruit setting and growth in some plants
- Involved in assimilate movement toward auxin possibly by an effect on phloem transport
- Delays fruit ripening
- Promotes flowering in Bromeliads
- Stimulates growth of flower parts
- Promotes (via ethylene production) femaleness in dioecious flowers
- Stimulates the production of ethylene at high concentrations

Gibberellins

The discovery of gibberellins (GA) is created to Ewiti Kurosawa who found that a fungus was responsible for abnormal rice seedling growth, called the "foolish seedling" disease. The fungus secreted a chemical that caused the rice plant to grow abnormally long and then collapse frm weakness. The fungus was *Gibberella fujikuroi*, hence the hormone named as ***Gibberellin***. Many seeds contain a variety of different gibberellins. Over 100 different GA's (organic acides synthesized from mevalonic acid) are known. GA's are produced in roots and younger leaves. Most effects of GA are shown only in concert with Auxins

The Nature of Gibberellins

Unlike the classification of auxins which are classified on the basis of function, gibberellins are classified on the basis of structure as well as function. All gibberellins are derived from the ent-gibberellane skeleton. The structure of this skeleton derivative along with the structure of a few of the active gibberellins are shown above. The gibberellins are named $GA_1....GA_n$ in order of discovery. Gibberellic acid, which was the first gibberellin to be structurally characterized, is GA_3. There are currently 136 GAs identified from plants, fungi and bacteria. GA's are widespread and so far ubiquitous in both flowering (angiosperms) and non-flowering (gymnosperms) plants as well as ferns.



Structure of GA
http://wapedia.mobi/en

Functions of Gibberellins

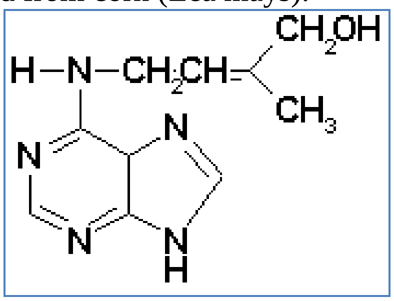
Active gibberellins show many physiological effects, each depending on the type of gibberellin present as well as the species of plant. Some of the physiological processes stimulated by gibberellins are outlined Stimulate stem elongation by stimulating cell division and elongation.

- Stimulates bolting/flowering in response to long days.
- Breaks seed dormancy in some plants which require stratification or light to induce germination.
- Stimulates enzyme production (a-amylase) in germinating cereal grains for mobilization of seed reserves.
- Induces maleness in dioecious flowers (sex expression).
- Can cause parthenocarpic (seedless) fruit development.
- Can delay senescence in leaves and citrus fruits.

CYTOKININS:

Nature of Cytokinins

Cytokinins or CKs are a group of chemicals that influence cell division and shoot formation. Cytokinins are compounds with a structure resembling adenine which promote cell division and have other similar functions to kinetin Kinetin was the first cytokinin discovered and so named because of the compounds ability to promote cytokinesis (cell division). They were called kinins in the past when the first cytokinins were isolated from yeast cells. They also help delay senescence or the aging of tissues, are responsible for mediating auxin transport throughout the plant, and affect internodal length and leaf growth. They have a highly-synergistic effect in concert with auxins and the ratios of these two groups of plant hormones affect most major growth periods during a plant's lifetime. Cytokinins counter the apical dominance induced by auxins; they in conjunction with ethylene promote abscission of leaves, flower parts and fruits. The most common form of naturally occurring cytokinin in plants today is called zeatin which was isolated from corn (Zea mays).



Structure of cytokinins

http://www.plant-hormones.info/cytokinins.htm

Cytokinin Functions

- Stimulates cell division.
- Stimulates morphogenesis (shoot initiation/bud formation) in tissue culture.
- Stimulates the growth of lateral buds-release of apical dominance.
- Stimulates leaf expansion resulting from cell enlargement.
- May enhance stomatal opening in some species.
- Promotes the conversion of etioplasts into chloroplasts via stimulation of chlorophyll synthesis

Role of cytokinins:

1) Cutokinins (together with auxin) probably regulate the cell cycle
2) Cytokinins (together with auxin) may regulate tissue morphogenesis, since the ratio of auxin: cytokinin in tissue culture medium determines root or shoot production
   - High auxin : cytokinin = root production
   - Intermediate auxin : cytokinin = callus growth
   - Low auxin : high cytokinin = shoot production
3) Cytokinins delay senescence and promote nutrient uptake
   - Application of cutokinin to a leaf on an aging plant can allow that leaf to stay green while others turn yellow and die
   - Cytokinin application to later buds can promote their growth
   - Some pathogens produce cutokinins that attract nutrients to that tissue or cause extensive growth of lateral buds (leads to witch's broom)
4) Cytokinins promote chloroplast maturation and cell enlargement in leaf cotyledons
   - Cytokinin application promotes development of chloroplast from etioplasts
   - Sections of leafy cotyledons enlarge when treated with cytoikinin (but not acid growth)

Reference:

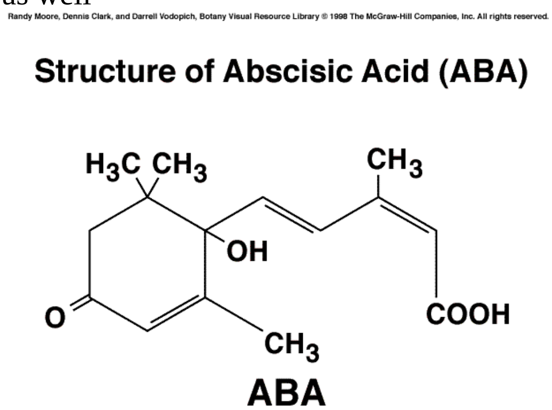
1. Plant physiology – III Ed. Taiz and Zeiger: http://4e.plantphys.net/
2. Plant physiology – Salisbury and Rose.
3. www.**tnau**.ac.in/
4. Textbook of Plant physiology – Malik C. P and Srivastava.A. K.

Lecture 15

Abscisic acid (ABA) is a hormone that functions by inhibiting growth activities in times of environmental stress rather than by promoting growth. It often serves as an antagonist to the other growth promoting hormones in plant. ABA which is also synthesized from mevalonic acid, got its name from erroneous belief that it promoted the formation of abscission layers in leaves and fruits. It does not, although leaf abscission accompanies dormancy in many plants

Nature of Abscisic Acid

Abscisic acid is a single compound unlike the auxins, gibberellins, and cytokinins. It was called "abscisin II" originally because it was thought to play a major role in abscission of fruits. At about the same time another group was calling it "dormin" because they thought it had a major role in bud dormancy. The name abscisic acid (ABA) was coined by a compromise between the two groups. Though ABA generally is thought to play mostly inhibitory roles, it has many promoting functions as well



Structure of ABA
http://www.mhhe.com/biosci/pae/botany/uno/graphics/uno01pob/vrl/images/0629.gif

Functions of Abscisic Acid

The following are some of the physiological responses known to be associated with abscisic acid

- Stimulates the closure of stomata (water stress brings about an increase in ABA synthesis).
- Inhibits shoot growth but will not have as much affect on roots or may even promote growth of roots.
- Induces seeds to synthesize storage proteins.
- Inhibits the affect of gibberellins on stimulating de novo synthesis of a-amylase.
- Has some effect on induction and maintenance of dormancy.
- Induces gene transcription especially for proteinase inhibitors in response to wounding which may explain an apparent role in pathogen defense.

Ethylene

Ethtylene is sole growth regulator known which is a gas of small hydrocarbon molecule, easily synthesized in chemistry labs.

The benefits of ethylene as fruit ripener were known for centuries prior to it being identified as plant product in the early 1900's. Chinese gardeners knew centuries ago that fruits ripened better in rooms with burning incense. Citrus growers used kerosene stoves in the rooms in which they ripened their fruits. During the era of gas lamps, leaking lamps along city streets often promoted leaf abscission. Today, grocer warehouses have ethylene rooms that are used for ripening most of produce of our produce, which shipped unripe. Immature fruits are firmer and less subject to damage.

$$H_2C=CH_2$$

Structure of ethylene

http://www.plant-hormones.info/ethylene.htm

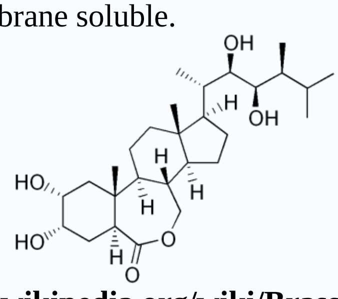
Ethylene is known to affect the following plant processes

- Stimulates the release of dormancy.
- Stimulates shoot and root growth and differentiation (triple response)
- May have a role in adventitious root formation.
- Stimulates leaf and fruit abscission.
- Stimulates Bromiliad flower induction.
- Stimulates flower opening.
- Stimulates flower and leaf senescence.
- Stimulates fruit ripening.
- Ethylene promotes female flower production in some members of the cucurbitaceae, whereas high GA may promote formation of male flowers.

Brassinolides (Brassinosteroids)

Brassinosteroids (BRs) are a class of polyhydroxysteroids which have been recognized as a sixth class of plant hormones. These were first explored nearly forty years ago when Mitchell et al. reported promotion in stem elongation and cell division by the treatment of organic extracts of rapeseed (*Brassica napus*) pollen. Brassinolide was the first isolated brassinosteroid when it was shown that pollen from *Brassica napus* could promote stem elongation and cell divisions and the biologically active molecule was isolated. The yield of brassinosteriods from 230 kg of *Brassica napus* pollen was only 10 mg. Since their discovery, over 70 BR compounds have been isolated from plants.

The BR is biosynthesised from campesterol. The biosynthetic pathway was elucidated by Japanese researchers and later shown to be correct through the analysis of BR biosynthesis mutants in *Arabidopsis*, tomatoes and peas. The sites for BR synthesis in plants have not been experimentally demonstrated. One well-supported hypothesis is that all tissues produce BRs, since BR biosynthetic and signal transduction genes are expressed in a wide range of plant organs, and short distance activity of the hormones also supports this. Experiments have shown that long distance transport is possible and that flow is in an acropetal direction, but it is not known if this movement is biologically relevant. Brassinosteroids are recognized at the cell membrane, although they are membrane soluble.



http://en.wikipedia.org/wiki/Brassinosteroid

BRs have been shown to be involved in numerous plant processes:

- Promotion of cell expansion and cell elongation; works with <u>auxin</u> to do so.

- It has an unclear role in cell division and cell wall regeneration.
- Promotion of vascular differentiation; BR signal transduction has been studied during vascular differentiation.
- Is necessary for pollen elongation for pollen tube formation.
- Acceleration of senescence in dying tissue cultured cells; delayed senescence in BR mutants supports that this action may be biologically relevant.
- Can provide some protection to plants during chilling and drought stress.
- Brassinosteroids activate signal transduction pathways, promote cell elongation and cell division.
- Brassinosteroids promotes differentiation of xylem tissue and perhaps other tissues too.
- Brassinosteroids can also retard leaf abscission abscission.
- Absence of brassinolides results in dwarf plants.
- BRs have been reported to counteract both abiotic and biotic stress in plants. Application of brassinosteroids to cucumbers was demonstrated to increase the metabolism and removal of pesticides, which could be beneficial for reducing the human ingestion of residual pesticides from non-organically grown vegetables.

Other identified plant growth regulators include:

- Salicylic acid - activates genes in some plants that produce chemicals that aid in the defense against pathogenic invaders.
- Jasmonates - are produced from fatty acids and seem to promote the production of defense proteins that are used to fend off invading organisms. They are believed to also have a role in seed germination, and affect the storage of protein in seeds, and seem to affect root growth.
- Plant peptide hormones - encompasses all small secreted peptides that are involved in cell-to-cell signaling. These small peptide hormones play crucial roles in plant growth and development, including defense mechanisms, the control of cell division and expansion, and pollen self-incompatibility.
- Polyamines - are strongly basic molecules with low molecular weight that have been found in all organisms studied thus far. They are essential for plant growth and development and affect the process of mitosis and meiosis.
- Nitric oxide (NO) - serves as signal in hormonal and defense responses.

Reference:

1. Plant physiology – III Ed. Taiz and Zeiger: http://4e.plantphys.net/
2. Plant physiology – Salisbury and Rose.
3. www.**tnau**.ac.in/

Lecture 16
STRESS PHYSIOLOGY

In both natural and agricultural conditions, plants are frequently exposed to environmental stresses. Some environmental factors, such as air temperature, can become stressful in just few minutes; others, such as soil water content, may take days to weeks, and factors such as soil mineral deficiencies can take months to become stressful.

In addition, stress plays a major role in determining how soil and climate limit the distribution of plant species. Thus, understanding the physiological processes that underlie stress injury and the adaptation and acclimation mechanisms of plants to environmental stress is of immense importance to both agriculture and environment.

The concept of plant stress is often used imprecisely, and stress terminology can be confusing, so it useful to start the discussion with some definitions.

Stress physiology: it is an important branch of environmental physiology, is concerned with how plants and animals responds to environmental conditions that deviate significantly from those that are optimal for the organisms in question –or in a broader sense for organism in general.

This sub science of physiology can contribute to our understanding of what limits plants distribution in natural environments. In such a context, it would be a part of physiological ecology. Most of research in the field however is concerned with how adverse environmental conditions limit agricultural yields.

In 1972, **Jacob Levitt** proposed a definition of *biological stress* derived from *physical stress*. Physical **stress** is any force applied to an object (ex: a steel bar); **strain** is the change in the object dimension caused by the stress.

Levitt suggested that **biological stress** *is any change in environmental conditions that might reduce or adversely change plants growth or development* (*its normal function*); ***biological strain*** *is the reduced or changed functions*.

Any change in environmental conditions that results in plant response less than the optimum might be considered stressful. Considering a plant suddenly subjected to reduced light levels. Since photosynthesis is immediately reduced, applying Levitt's definition we say that the reduced light levels are the stress and reduced photosynthesis is strain.

Levitt went on to define ***elastic biological strain*** as those change in an organism's function that returns to the optimal level when conditions return to those best suited to the organism studied (i.e., when biological stress has been removed). If the functions don't returns to normal the organism is said to exhibit ***plastic biological strain***.

In general, plant physiologist have emphasized in their studies such as *plastic strains* as those caused by the stresses of frost, high temperature, limited water, or high salt concentration and *elastic strains* in plants such as photosynthesis.

Levitt (1972) listed some other definitions. He suggested that we should distinguish between **avoidance** and **tolerance (hardiness)** to any given stress factors.

In **avoidance**, the organism responds by somehow reducing the impact of the stress factor. Ex: a plant in the desert might avoid the dry soil by extending its roots down to the water table.

If plant develops **tolerance**, on the other hand it simply tolerates or endures the adverse environment. *Crosote* bush is good example of a desert plant that is tolerant towards the drought. It simple dries out but scurvies anyway; it tolerate or endures the dryness of its protoplasm.

Effect of stress

Plants usually yield to any stress conditions and its reaction may be elastic or plastic. The stress may be immediately made out in the plant or plants may become resistant when exposed to stress conditions. This state is called **hardening**. Sometime the effect produced is carried over in the subsequent generations. Thus pea or bean plants subjected to low temperature tend to become dwarf and this effect is passed on for several generations. However, recent years are witnessing studies on genetic basis of resistant strains. Breeders are also making efforts to evolve the genetic lines which are gradually adapted to diverse climatic conditions. The reactions of plants to the stress conditions are highly complex and are manifested in the form of several physiological responses.

Types of stress

The most common stresses to which the plants are expressed to are **drought, heat, cold and frost**. In addition to these several other stresses also exist eg. *Shade, salt, high altitude etc*. In recent time occurrence of *excessive pollutants, effluents, etc* also gives toxic environments to the plants.

Stress response:

Acclimation : Adjustment to environmental change by an individual. The physiological adjustment or increased tolerance shown by an individual organism to environmental change.

Acclimatization: The physiological adaptation of plant to changes in climate or environment often multiple stress such as light, temperature, altitude, etc

Adaptation: An alteration or adjustment in structure or habits, often hereditary, by which a species or individual improves its condition in relationship to its environment.
or an inherited or acquired modification in organisms that makes them better suited to survive and reproduce in a particular environment

Reference:

1. Plant physiology – III Ed. Taiz and Zeiger: http://4e.plantphys.net/
2. Plant physiology – Salisbury and Rose.
3. Textbook of Plant physiology – Malik C. P and Srivastava.A. K.

Lecture 18

SALT STRESS

A common and important stress factor in desert is the presence of high salt concentrations in the soil. Soil salinity also restricts growth in many temperate regions besides desert.

Millions of acres have gone out of productions as salts from irrigation water accumulate in the soil. A plant face two problems in such areas

1. Obtaining water from a soil of negative osmotic potential
2. Dealing with high concentration of potentially toxic, carbonate and chloride ions.

Some crop plants (eg: beets, tomato, rye) are much more salt tolerant than others (eg: onion, peas)

Classification of plants depending on the tolerance towards the salt concentration.

1. Facultative halophytes
2. Obligate halophytes

1. **Facultative halophytes**: are particularly interesting, several such species grown best where salt levels in the soil are high as in desert or in soils saturated with brackish (Na) waters as in sea coasts or close to shores, where the salt content may be saturated at levels as high as 27 per cent by weight. They also grow in non-saline soils.

The following genera are good examples: iodine bush, pickle weed, sea lavender, etc. these also grow in somewhat less salty soils.

Obligate halophytes:

Barbour *et al*., (1980) reviewed the literature that suggest that there are no obligate halophytes. Plant that cannot grow unless the soil contain salt. So far all halophytes studied have been found growing naturally in non-salty soil and will grow well where planted in non-salty soils. Normally they are not abundant in non-salty soil because they cannot compete with the glycophytes that normally grow there.

Members of genus *Halobacterium* (prokaryotes) accumulates large amount of salts into their cells and cannot survive except in salty environment.

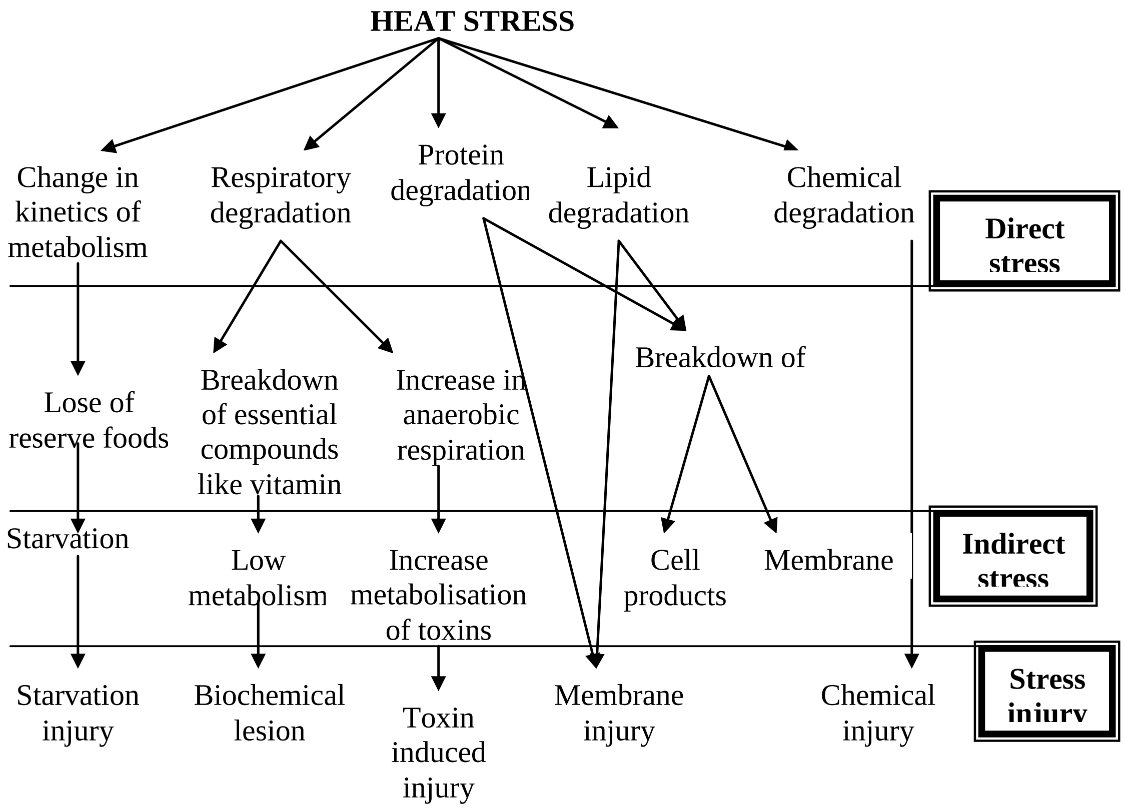
Some halophytes are referred as **salt accumulator**. In these species the osmotic potential continues to become more negative throughout the growing season as salt is absorbed.

Water moves into the plant osmotically and not simply in bulk flow. The endodermal layer in the roots probably provides the osmotic barrier.

Halophytes in which the salt concentration with in the plant does not increase during the growing season are known as **salt regulators**. Often salt enter the plant, but the leaves swell by absorbing water, so concentration don't increases. This leads to development of *succulence* (ratio of high volume/surface), a common morphological feature of halophytes.

Sometime excess salt is exuded on the surface of the leaves, helping to maintain a constant salt concentration within the tissue. In some halophytes, there are readily observable salt glands on the leaves.

Frequently, halophytes synthesis large quantity of the amino acid such as proline as well as other amnio acids and such other compounds as *galactosyl glycerol* and organic acids, these functions in *osmotic adjustment*.



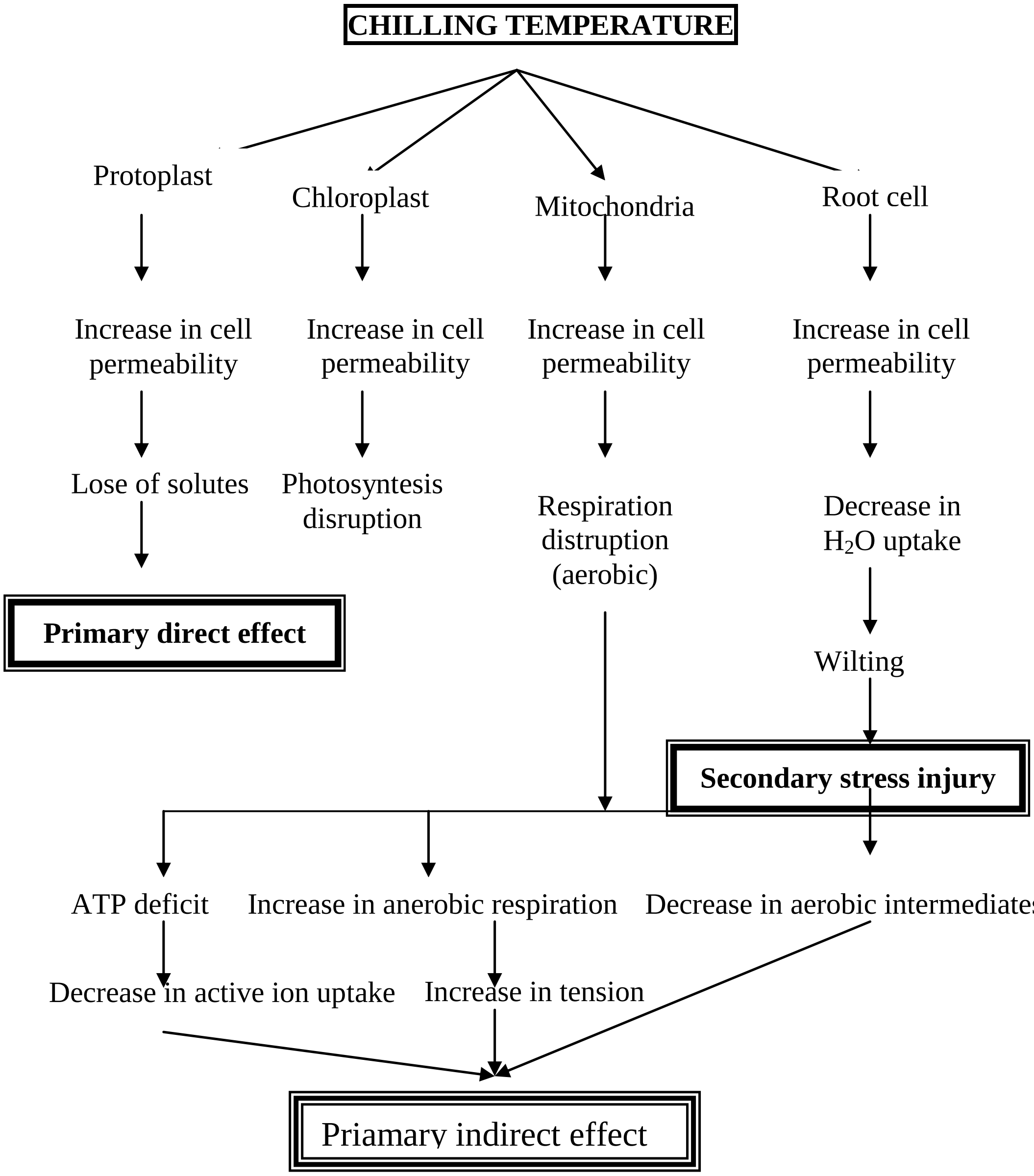
Plant response of heat and their tolerance levels varies. Leaves may help the plant to avoid heat due to transpiration but the process is negligible.

Majority of the plant species survives high temperature because of their internal built up. Some of the thermal algae, cacti and several other desert plants experience as high as 70^{o}C and yet survive. High temperature tends to denature proteins and also heavy water loses. One of the attributes is increased enzyme production to compensate for the destruction.

Some organisms, a rise in temperature slows down some process and when some compounds like **ascorbic acid** and **other vitamins** are added the process is restarted.

In general plants which are temperature tolerant, possesses enzymes which are more stable to high temperature. Infact in these enzymes some of the isozymes develop to high temperature.

In summary it can be stated that most of the plants are heat tolerant because they possess the capacity to produce heat stable proteins. They also have the ability of replace thermal denatured protein immediately.



Like the heat tolerance, plant species also possess the capability to resist freezing. Several processes may be involved in causing freezing injury to the plants.

In general plants growing under tropical climate are more chilling prone. Hence chilling causes damage to their tissue or organs. Such plants also are sensitive to low temperature +12 to 13^{o}C while, low temperature like -0 to -5^{o}C is lethal. Obviously proteins are sensitive to low temperature on the contrary most of the alpine and arctic plants don't experience any damaging effect at this low temperature. In these plants the danger is that their tissues may not undergoes water formation in their cells. Seeds, pollens and embryos can be stored at low temperature such as -190^{o}C obtained through liquid nitrogen.

Freezing damage is done in two ways:

1. There is formation of ice crystals and the damage is due to mechanical effects. There is disruption of membranes and even cell organization.

2. Ice formation reduces the water amount in the cells leading to drought situation.

However, the intercellular water has high potentials whereas, water in the cell cytoplasm or vacuole has nearly negative water potential. To begain with it is the intercellular space that the ice crystals are formed and then with the freezing continuing, water leaves the cell cytoplasm in the plants which are freezing hardy, water tends to remain in the intercellular spaces. In brief following is a set of events which takes place. Crystals formed in the intercellular spaces and protoplast solutes become concentrated due to removal of water from these. The precipitation of solutes in the protoplast causes abrupt shifts in the cell pH. If the temperature is lowered down still further (eg -35 to -45^{o}C) all water in the tissue is crystallized. Gradually, the crystals emerge in size and hence there is mechanical damage to the cell. The freezing may be slow or rapid and different plant exhibit different response.

At low temperature in the frost-hardy plants there is formation of low temperature resistant proteins. This may be due to increased concentration of electrolytes which protect tissue water against its removal by the intercellular ice. Frost hardy plant have high sugar amount and obviously frost hardiness involves synthesis of more sugars. Plant tissue may be made frost-hardy by placing in sugar solution. Thus even though new frost resistant proteins might be synthesized these protein must be resistant to high sugar concentration.

HARDENING (ACCLIMATION)

Plants exposed to low water potential, high light levels and such other factor as high phosphorous and low nitrogen fertilization become drought tolerant or hardy compared to plants of the same species not treated in this way i.e., they become acclimation to drought, a process of considerable importance to agriculture. This is a good example of a conditioning effect.

Actively growing plants, especially herbaceous species, are damaged or killed by temperature of only -1 to -5^{o}C, but many of the plants can be acclimated to survive winter temperature of -25^{o}C or lower.

Frost hardness typically develops during exposure to relatively low temperature (5^{o}C) for several days. Temperature down to -3^{o}C are sometime required for maximum acclimation. Short days also promote acclimation in several species and these are indications that a stimulus may move from leaf tissue to the stem. The development of frost hardiness is a metabolic process required an energy source. Apparently this can be provided by light and photosynthesis. Factors that promote more rapid growth inhibit acclimation: high nitrogen in the soil, pruning irrigations and so on. In general, non-growing or slowly growing plants are more resistant to several environmental extremes, including air pollution. Water stressed plants are more resistant to air pollution partially because their stomates are closed.

Reference:

1. Plant physiology – III Ed. Taiz and Zeiger: http://4e.plantphys.net/
2. Plant physiology – Salisbury and Rose.
3. www.**tnau**.ac.in/
4. Textbook of Plant physiology – Malik C. P and Srivastava.A. K.

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