PAPER-VIII -PLANT PHYSIOLOGY

Subject Code: **18MBO32C**

Unit - II:

Mineral nutrition:

- Criteria of essentiality of elements
- Macro and Micro- nutrients
- Role of essential elements
- Mineral deficiency symptoms

Mineral salt absorption

- Nutrient uptake and transport mechanism
- Role of cell membrane, Ion pump carrier.

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Criteria of essentiality of elements; Macro and Micro- nutrients

MINERAL NUTRITION

The term, mineral nutrient is generally used to refer to an inorganic ion obtained from the soil and required for plant growth. The chemical form in which elements are applied to plants is called as nutrient. Nutrition may be defined as the supply and absorption of chemical compounds needed for plant growth and metabolism The nutrients indispensable for the growth and development of higher plants are obtained from three sources viz., atmosphere, water and soil. The atmosphere provides carbon and oxygen as carbon dioxide. Carbon is reduced during photosynthesis and oxygen is utilized during aerobic respiration. Soil provides the mineral ions.

Essential elements

The term essential mineral element was proposed by Arnon and Stout (1939). These are the composition of both macro and microelements, in the absence of any one of these elements the plant cannot maintain its normal growth and develops deficiency symptoms, affects metabolism and die prematurely. Of the many elements that have been detected in plant tissues, only 16 are essential for all higher plants. They are C, H, O, N, P, K, Ca, Mg, S, Zn, Cu, Fe, Mn, B, Cl and Mo. In the absence of each of the essential elements, plants develop deficiency symptoms characteristic of the deficient element and die prematurely.

Macronutrients

The nutrient elements which are required for the growth of plants relatively in larger quantities are called as major nutrients or macronutrients. The major elements required for growth of plants are C, H, O, N, P, K, Ca, Mg and S. Among these nutrients, C, H and O are taken up by the plants from the atmosphere and water. The N, P, K, Ca, Mg and S are taken up by the plants from the soil and they are applied in the form of chemical fertilizers either through the soil or foliage.

Micronutrients

The nutrient elements which are required comparatively in small quantities are called as minor or micro nutrients or trace elements. The micronutrients required for the plant growth are Zn, Cu, Fe, Mn, Mo, B and Cl.

Tracer elements

The nutrient elements that are required for plants are sometimes labeled and used to study their movement or tracing out the involvement of such nutrients in metabolism in different organs of plants, are called as tracer elements. They may either be stable or radioactive types and they are also called as isotopic elements.

E.g. Stable isotopes: 15N, 12C, 31P

Radioactive: 14C, 32P, 65Zn, 56Fe, 60Co, etc.

Hidden hunger

When the plants are not able to meet their requirement either one or more of these essential elements, the plants will undergo starvation for such elements. At the initial stage of deficiency of such elements plants will not show any characteristic symptoms which could be exhibited morphologically and due to want of those elements some activities of plants would rather be affected and the internal deficiency is called as Hidden hunger.

General role of essential elements

In general, an element is essential to the life of a higher green plant for one or more of the following three reasons.

1. It may perform a nutritive role by being a component of one or more of the major classes of plant constituents.

2. It may be a catalytic role either as an action for of an enzyme or as an integral component of an enzyme.

3. It may function as a free ion and thereby exert a balancing role in maintaining electroneutrality within plant cells (e.g. Potassium).

Criteria for essentiality of elements

The demonstration of the essentially several elements (macro and micronutrients), especially, micronutrients is rather very difficult. In view of the technical difficulties associated with demonstrating the essentiality of elements required in very small amounts, Arnon and Stout (1939) suggested the adoption of the following three criteria of essentiality for judging the exact status of a mineral in the nutrient of a plant

1. The element must be essential for normal growth or reproduction and the plant processes cannot proceed without it.

2. The element cannot be replaced by another element.

3. The requirement must be direct i.e., not the result of some indirect effect such as relieving toxicity caused by some other substance.

Another recent suggestion to the criteria of essentiality is that some elements might better be called functional or metabolic elements rather than essential elements. This is intended to indicate that an element that is metabolically active, functional or metabolic may or may not be essential. For example in chlorine-bromine, chlorine is designated as a functional element rather than an essential element as chlorine can be substituted with bromine.

Based on the mobility in phloem, elements are also classified into three types.

1. Mobile elements: N, K, P, S and Mg

2. Immobile elements: Ca, Fe and B

3. Intermediate: Zn, Mn, Cu, Mo

Role 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

Phosphorus content is found to be 0.2 to 0.8% of the total dry weight.

1. It is found abundantly in the growing and storage organs such as fruits and seeds.
2. It promotes healthy root development and fruit ripening through translocation of carbohydrates.

3. 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.
4. It is also found in plants as a constituent of nucleic acids, phospholipids, and the coenzymes like NAD etc.
5. Phospholipids along with protein may be important in cell membrane.
6. 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

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.

1. It acts as an activator of many enzymes involved in carbohydrate metabolism and protein synthesis.
2. It is actively involved in the opening and closing of stomata.
3. It takes an important role in drought tolerance of crops through water relations.
4. It offers resistance to pest and disease which affects the crops.
5. It is present in the soluble forms and mostly contain in the cell sap and cytoplasm.
6. 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

It is a constituent of chlorophyll, and therefore, essential for its synthesis.

1. It acts as a phosphorus carrier in the plant.
2. It is essential for the synthesis of fats and metabolism of carbohydrate and phosphorus.
3. It is required in binding two subunits of ribosome during protein synthesis.
4. It acts as an activator for many enzymes in phosphate transfer reactions in carbohydrate metabolism and nucleic acid synthesis.
5. It is involved in the formation of seeds of high oil contents containing a compound called lecithin
6. 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

It is an important constituent of some amionacids (cystine, cysteine and methionine), vitamins (biotine, thiamine), coenzyme A and volatile oils.

1. It participates in protein synthesis
2. Sulfohydryl groups are necessary for the activity of many enzymes
3. Disulphide linkages help to stabilize the protein structure.
4. It adversely affects chlorophyll synthesis.
5. Sulphur affects the nodule formation in roots of leguminous plants.
6. Characteristic odour of Cruciferous plants (onion, garlic etc.) is due to the Sulphur as constituent of volatile oils.

7. 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

It is the important constituent of middle lamella in the cell wall

1. It is essential in the formation of cell membranes.
2. It helps to stabilize the structure of chromosomes.
3. It is also an activator of many enzymes (ATPase, kinases, succinate dehyrogenase)
4. It provides a base for the neutralization of organic acids.
5. It is concerned with the growing root apices.
6. It is essential for fact metabolism, carbohydrate metabolism and binding of nucleic acids with proteins.
7. It is also essential in the counteraction of metal toxicity
8. 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 CO_2, 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.

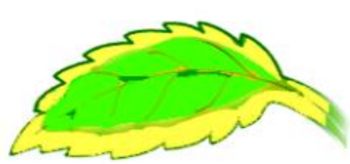
Mineral deficiency symptoms

Plants need the right combination of nutrients to live, grow and reproduce. When plants suffer from malnutrition, they show symptoms of being unhealthy. Too little or too much of any one nutrient can cause problems. Plant nutrients fall into 2 categories:

macronutrients and micronutrients. Macronutrients are those elements that are needed in relatively large amounts. They include nitrogen, potassium, sulfur, calcium, magnesium and phosphorus. Micronutrients are those elements that plants need in small amounts (sometimes trace amounts), like iron, boron, manganese, zinc, copper, chlorine and molybdenum. Both macro- and micronutrients are naturally obtained by the roots from the soil. Plant roots require certain conditions to obtain these nutrients from the soil. First, the soil must be sufficiently moist to allow the roots to take up and transport the nutrients. Sometimes correcting improper watering strategies will eliminate nutrient deficiency symptoms. Second, the pH of the soil must be within a certain range for nutrients to be release-able from the soil particles. Third, the temperature of the soil must fall within a certain range for nutrient uptake to occur. The optimum range of temperature, pH and moisture is different for different species of plants. Thus, nutrients may be physically present in the soil, but not available to plants. A knowledge of soil pH, texture, and history can be very useful for predicting what nutrients may become deficient. Too much of any nutrient can be toxic to plants. This is most frequently evidenced by salt burn symptoms.

Nutrient	Deficiency Symptoms	Comments	Fertilizer Sources
MACRONUTRIENTS **Replace macronutrients in soils regularly (at least once per growing season)**			
calcium (Ca)	New leaves (top of plant) are distorted or irregularly shaped. Causes blossom-end rot.	Desert soils and water generally have plenty of calcium, so deficiency problems are rare. Excessive calcium can limit the availability of other nutrients.	Anything with the word "calcium"; also gypsum.
nitrogen (N)	General yellowing of older leaves (bottom of plant). The rest of the plant is often light green.	Most plants absorb nitrogen in the form of ammonium or nitrate. These forms readily dissolve in water and leach away.	Anything with the words "ammonium," "nitrate," or "urea." Also manures.
magnesium (Mg)	Older leaves turn yellow at edge leaving a green arrowhead shape in the center of the leaf.	Plants absorb magnesium as an ion (charged particle), which can be readily leached from soil. May be readily leached from soil if calcium is not present.	Anything with the word "magnesium"; also Epsom salts (magnesium sulfate).
phosphorus (P)	Leaf tips look burnt, followed by older leaves turning a dark green or reddish-purple.	Plants absorb phosphorus in the form of phosphate. This form dissolves only slightly in water, but pH strongly affects uptake.	Anything with the words "phosphate" or "bone." Also greensand.
potassium (K)	Older leaves may wilt, look scorched. Interveinal chlorosis begins at the base, scorching inward from leaf margins.	Plants absorb potassium as an ion, which can be readily leached from soil. Desert soils and water generally have plenty of potassium, so deficiency problems are rare.	Anything with the words "potassium" or "potash."
sulfur (S)	Younger leaves turn yellow first, sometimes followed by older leaves.	Plants absorb sulfur in the form of sulfate. This readily leaches from the soil. Sulfur may acidify the soil (lower the pH).	Anything with the word "sulfate."

MICRONUTRIENTS *Replace when deficiency symptoms are evident.*			
boron (B)	Terminal buds die, witches' brooms form.	Plants absorb boron in the form of borate. Problems are seen in intensely cropped areas.	Anything with the words "borax" or "borate."
copper (Cu)	Leaves are dark green, plant is stunted.	Plants absorb copper as an ion. Arizona soils have plenty of copper, so problems are rare.	Anything with the words "copper," "cupric," or "cuprous."
iron (Fe)	Yellowing occurs between the veins of young leaves.**	Plants absorb iron as an ion through their foliage as well as their roots. Uptake is strongly affected by pH. Chelated iron is readily available for use by the plant, other forms of iron may be tied up in the soil.	Anything with the word "iron chelate."
manganese (Mn)	Yellowing occurs between the veins of young leaves. Pattern is not as distinct as with iron. Palm fronds are stunted and deformed, called "frizzle top." Reduction in size of plant parts (leaves, shoots, fruit) generally. Dead spots or patches.	Plants absorb manganese as an ion through their foliage as well as their roots.	Anything with the words "manganese" or "manganous." Often required with zinc application.
molybdenum (Mo)	General yellowing of older leaves (bottom of plant). The rest of the plant is often light green.	Plants absorb molybdenum in the form of molybdate. Problems are rare in Arizona soils but are occasionally seen on legumes where it mimics nitrogen deficiency.	Anything with the words "molybdate" or "molybdic."
zinc (Zn)	Terminal leaves may be rosetted, and yellowing occurs between the veins of the new leaves.	Plants absorb zinc as an ion through their foliage as well as their roots. High pH may limit availability.	Anything with the word "zinc."



* Magnesium deficiency symptom in leaf evident in yellow parts of leaf.

** Interveinal chlorosis, a symptom of iron, zinc and manganese deficiencies, evident in yellow parts of leaf.

Mineral salt absorption: Nutrient uptake and transport mechanism

Mechanism of Mineral Salt Absorption:

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 different 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 the tips.

However, some mineral salts may also be absorbed at other locations on the root surface or over the entire root surface including zone of elongation and root hairs that depends upon the high availability of such minerals around them and/or strong tissue demand at such locations.

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 the process of Ion-Exchange which does not require metabolical energy but greatly facilitates mineral salt absorption.

Ion-Exchange:

The ions adsorbed on the surface of the walls or membranes of root cells may be exchanged with the ions of 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 regarding the mechanism of ion exchange:

(i) Contact Exchange Theory:

According to this theory, the ions adsorbed on the surface of root cells and clay particles (or clay micelles) are not held tightly but 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 the oscillation volume of ions adsorbed on clay particles, and the ions adsorbed on clay particle may be exchanged with the ions adsorbed on root-surface directly without first being dissolved in soil solution (Fig. 7.1 A).

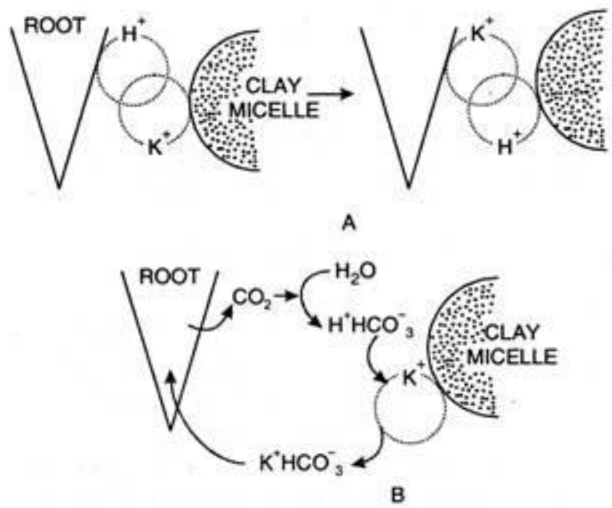


Fig. 7.1. Diagrammatic representation of (A) the contact-exchange theory and (B) the carbonic acid exchange theory.

(ii) Carbonic Acid Exchange Theory:

According to this theory, the CO_2 released during respiration of root cells combines with water to form carbonic acid (H_2CO_3). Carbonic acid dissociates into H^+ and an anion HCO_3^- in soil solution. These H^+ ions may be exchanged for cations adsorbed on clay particles.

The cations thus released into the soil solution from the clay particles, may be adsorbed on root cells in exchange for H^+ ions or as ion pairs with bicarbonate (Fig. 7.1 B). Thus, soil solution plays an important role in carbonic acid exchange theory.

The further process of the absorption of mineral salts may be of two types:

(1) Passive and

(2) Active

(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.

It is now known that during passive absorption, the mineral salts may diffuse through cell membranes directly through lipid bilayer but mainly through trans-membrane ion-selective protein channels or trans-membrane carrier proteins. Carrier or channel mediated passive transport of mineral salts across the membrane is also called as facilitated diffusion (Fig. 7.6).

(2) Active Absorption of Mineral Salts:

It has often been observed that the cell sap in plants accumulates large quantities of mineral salts ions against the concentration gradient. For example in alga Nitella the cell sap accumulated K^+ and phosphate ions to such an extent that their concentrations were thou-sands and hundreds times greater than in the pond water in which the plant was growing.

This cannot be explained by simple diffusion or Donnan's Equilibrium and has led people to believe that absorption and accumulation of mineral salts against the concentration gradient is an active process which involves the expenditure of metabolic energy through respiration.

Following evidences favour this view:

(i) The factors like low temp., deficiency of O_2, metabolic inhibitors etc. which inhibit metabolic activities like respiration in plants also inhibit accumulation of ions.

(ii) Rate of respiration is increased when a plant is transferred from water to salt solution (Salt Respiration).

It has now been accepted that active absorption of mineral salts involves the operation of a carrier compound present in the plasma membrane of the cells.

The Carrier Concept:

According to this theory the plasma membrane is impermeable to free ions. But some compound present in it acts as carrier and 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 up fresh ions (Fig. 7.2).

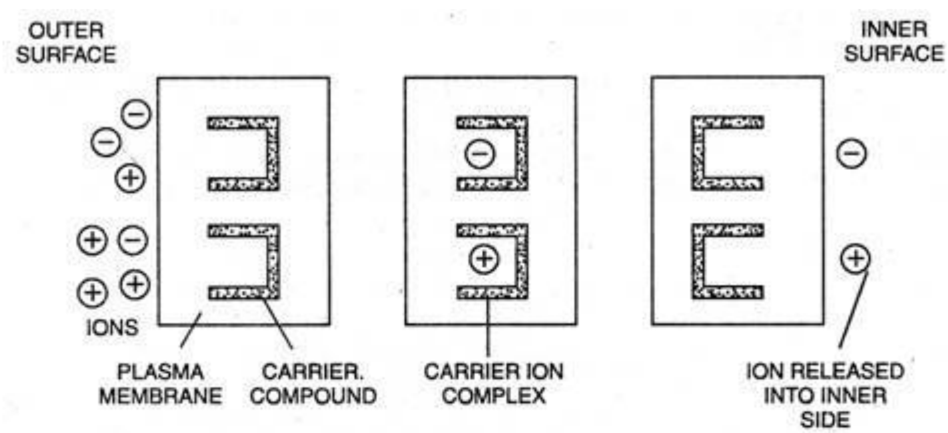


Fig. 7.2. Diagrammatic representation of a model illustrating the carrier concept.

Following observations strongly support the carrier concept of active absorption of mineral salts:

(i) Isotopic Exchange:

Several times, it has been found that actively absorbed radioactive ions (such as $^{35}S0_4$) cannot diffuse back or be exchanged with other ions in the outer solution indicating thereby that the plasma membrane is not permeable to free ions.

(ii) Saturation Effects:

Beyond a certain limit, increased concentration of salts in outer solution does not bring about an increase in the rate of mineral salt absorption. It is because the active sites on the carrier compound become saturated with ions.

(iii) Specificity:

Active sites on carrier compound may be specific which can bind only some specific ions. This also explains the selective and unequal absorption of ions by the plants. There are two common hypotheses based on the carrier concept to explain the mechanism of active salt absorption, although they are not universally accepted.

(1) Lundegardh's Cytochrome Pump Theory:

Lundegardh and Burstrom (1933) believed that there was a definite correlation between respiration and anion absorption. Thus when a plant is transferred from water to a salt solution the rate of respiration increases. This increase in rate of respiration over the normal respiration has been called as anion respiration or salt respiration.

The inhibition of salt respiration and the accompanying absorption of anions by CO and cyanides (which are known inhibitors of cytochrome oxidase of electron transport chain in mitochondria), later on led Lundegardh (1950, 54) to propose cytochrome pump theory which is based on the following assumptions:

(i) The mechanism of anion and cation absorption is different.

(ii) Anions are absorbed through cytochrome chain by an active process.

(iii) Cations are absorbed passively.

According to this theory (Fig. 7.3):

(i) Dehydrogenase reactions on inner side of the membrane give rise to protons (H^+) and electrons (e^-).

(ii) 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 oxidised (Fe^{++}) on the inner surface.

(iii) On the outer surface, the reduced cytochrome is oxidised by oxygen releasing the electron (e^-) and taking an anion (A^-).

(iv) The electron thus released unites with H^+ and oxygen to form water.

(v) The anion (A^-) travels over the cytochrome chain towards inside.

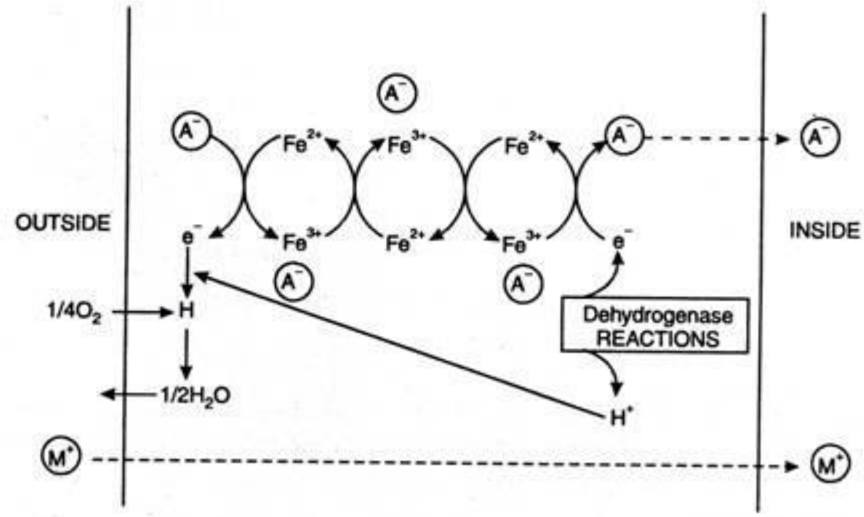


Fig. 7.3 Diagrammatic representation of the Lundegardh's cytochrome pump theory.

(vi) On the inner surface the oxidised cytochrome becomes reduced by taking an electron produced through the dehydrogenase reactions, and the anion (A^-) is released.

(vii) As a result of anion absorption, a cation (M^+) moves passively from outside to inside to balance the anion.

Main defects of the above theory are:

(i) It envisages active absorption of only anions.

(ii) It does not explain selective uptake of ions.

(iii) It has been found that cations also stimulate respiration.

(2) Bennet-Clark's Protein-Lecithin Theory:

In 1956, Bennet-Clark suggested that because the cell membranes chiefly consist of phospholipids and proteins and certain enzymes seem to be located on them, the carrier could be a protein associated with the phosphatide called as lecithin. He also assumed the presence of different phosphatides to correspond with the number of known competitive groups of cations and anions (which will be taken inside the cell).

According to this theory (Fig. 7.4), (i) the phosphate group in the phosphatide is regarded as the active centre binding the cations, and the basic choline group as the anion binding centre.

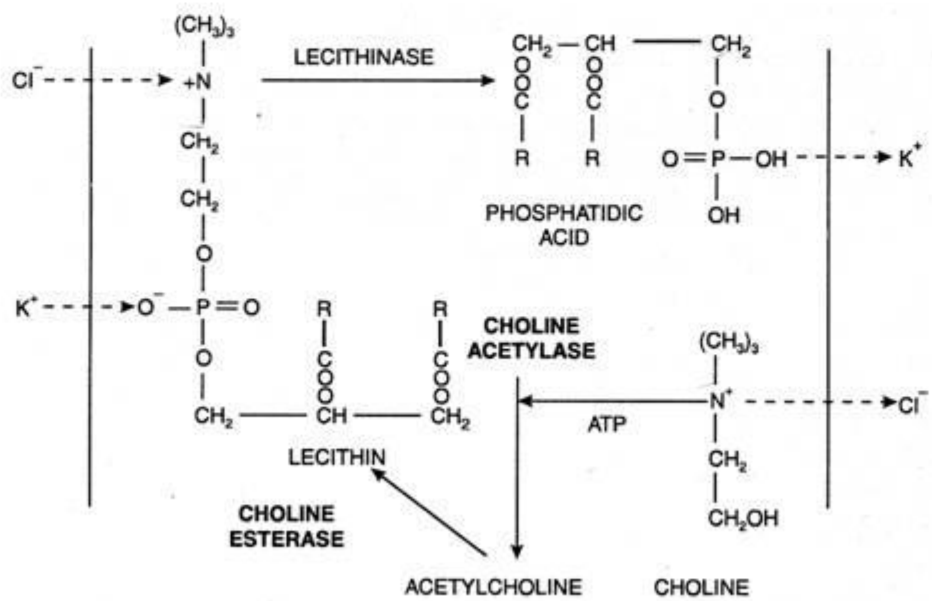


Fig. 7.4. Diagrammatic representation of the Bennet-Clark's Protein-Lecithin theory.

(ii) The ions are liberated on the inner surface of the membrane by decomposition of the lecithin by the enzyme lecithinase.

(iii) 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 latter acts as a source of energy.

Once inside the epidermal cells of the root, the mineral salts in their ionic form move from one cell to another by:

(i) Apoplastic pathway (i.e., through cell walls and intercellular spaces),

(ii) Trans membrane pathway (i.e., by crossing the membranes) and

(iii) Symplastic pathway (i.e., through plasmodesmata), and ultimately reach to xylem vessels and tracheids (Fig. 7.5) from where they are carried to different parts of the shoot along with ascent of sap.

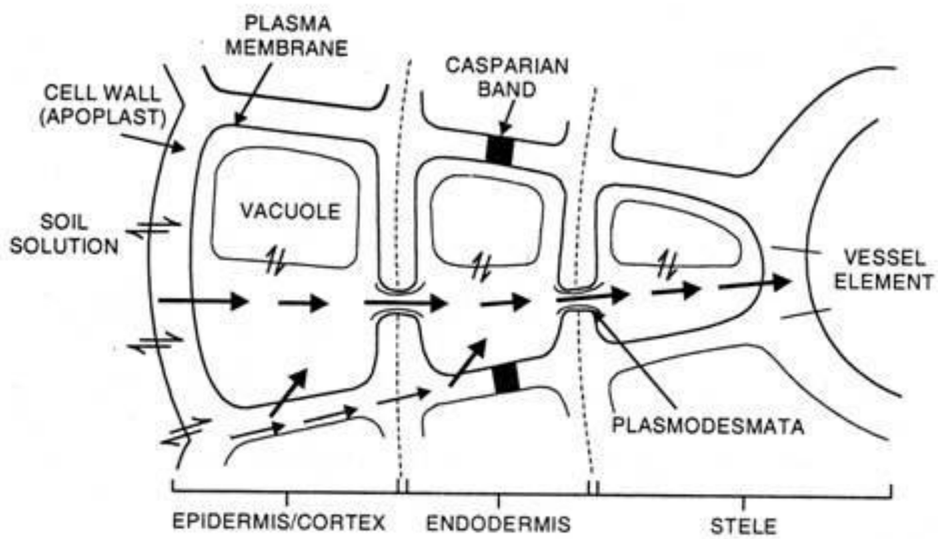
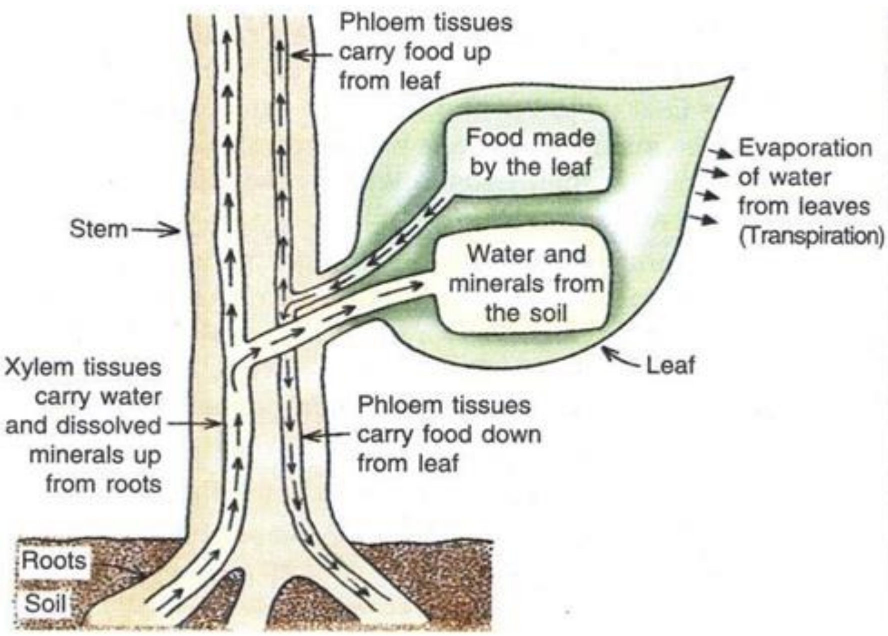


Fig. 7.5. Radial paths of movement of mineral nutrient ions in root

Transport system in plants

Transport in biology means carrying substance absorbed or made in the body of an organism to all other parts of its body.

In plants, it is only water and minerals that need to be transported to its other parts. Another thing that needs to be transported to other parts of the plants is the food prepared in leaves. This is because a plant has a branching shape so it gets carbon dioxide for photosynthesis and oxygen for respiration from air directly through diffusion.



The two types of conducting tissues that perform the function of transport system in plants are:

1) Xylem

2) Phloem

Transport of water and minerals

Plants need water to make food through the process of photosynthesis and minerals for making proteins. Thus, a plant absorbs water and minerals from soil through roots and transport it other parts like stem, leaves, flowers etc. It is through two kinds of elements of xylem tissue called, xylem vessels and tracheid that water and minerals move from roots of a plant to its leaves.

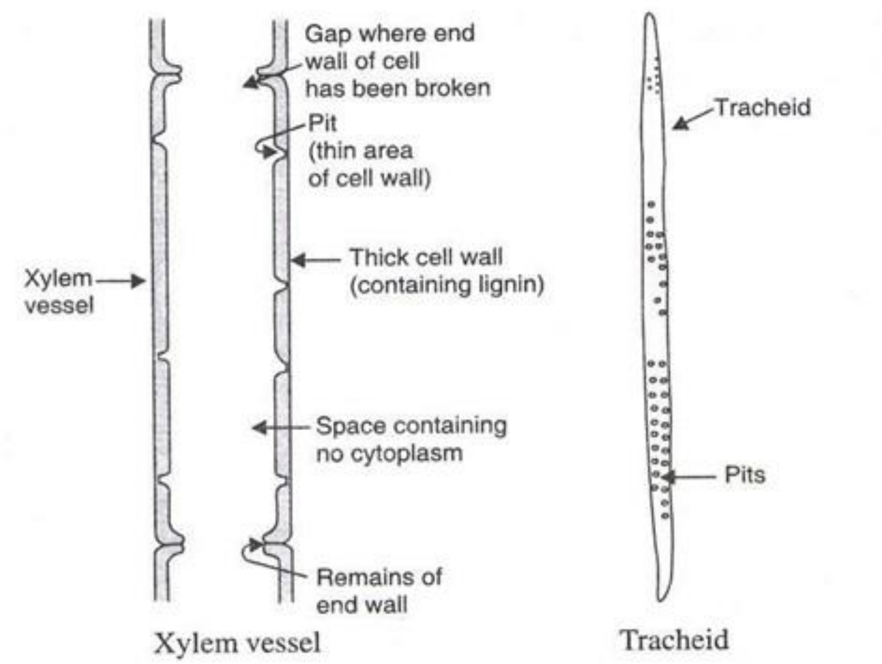
Xylem vessels

Xylem vessel is a long tube made up of dead cells joined end to end. It is a non-living tube which runs from roots of the plants and runs through the stem and reaches every leaf. The end walls of the cells are broken so that an open tube is formed.

Xylem vessels do not have cytoplasm or nuclei and the walls of the vessels are made of cellulose or lignin. Other than transporting water and minerals, xylem vessel also provides strength to the stem and keeps it upright. This is because lignin is very hard and strong. Wood is made of lignified xylem vessels. Xylem vessels have pits in their cell walls where lignin is not deposited. Either xylem vessel or both xylem vessel and tracheid transport water in flowering plants.

Tracheids

In non-flowering plants tracheids are the only water conducting tissues. Tracheids are dead cells with lignified walls with no open ends. They are long, thin and spindle shaped cells. They have pits in them and it is through pits only that water flows from one tracheid to another. All the plants have tracheid in them.



Before understanding the mechanism of transport of water and minerals in a plant it is necessary to know the meaning of some important terms:

Epidermis: The outer layer of the cells in the root of a plant is called epidermis. The thickness of epidermis is equal to one cell.

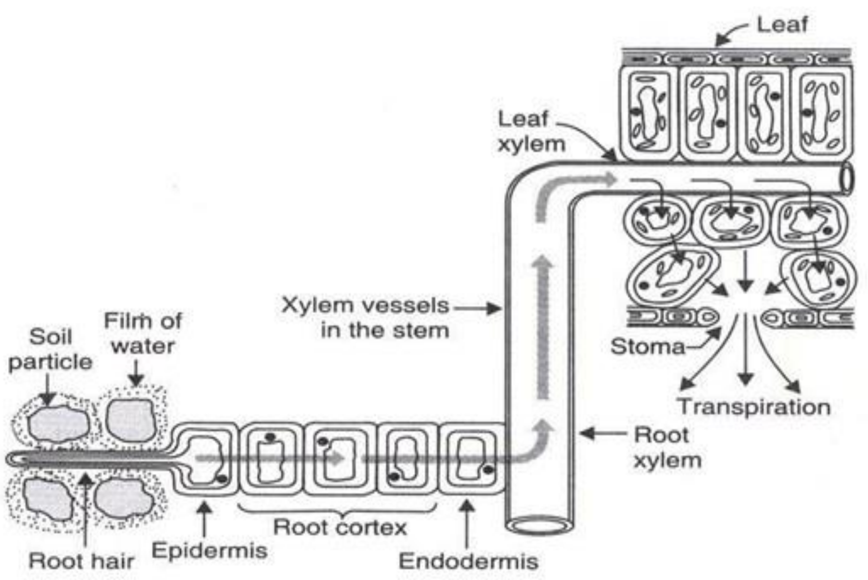
Endodermis: It is the layer of cells around the vascular tissue (xylem and phloem) in the root of a plant. Endodermis is the innermost layer of cortex.

Root cortex: It is the part of root between the epidermis and endodermis.

Root xylem: It is the xylem tissue present in the roots. It is present at the centre of the root. Epidermis, root cortex and endodermis are present between the root hair and root xylem. So, the water which is absorbed by the root hairs from soil first passes through epidermis, root cortex and endodermis and then finally reaches to root xylem.

Also, minerals are present in soil. Plants take these minerals from soil in inorganic form such as nitrates and phosphates. Minerals from soil gets dissolve in water to form an aqueous solution. So, when water is transported from roots to leaves, minerals dissolved in water is also transported.

Mechanism of transport of water and minerals in a plant



Root hair absorbs the water containing dissolved minerals from the soil. Root hair is directly in contact with the film of water present in-between the soil particles. Water containing minerals gets into the root hair and passes from cell to cell through the process of osmosis and reaches epidermis, root cortex, endodermis and root xylem.

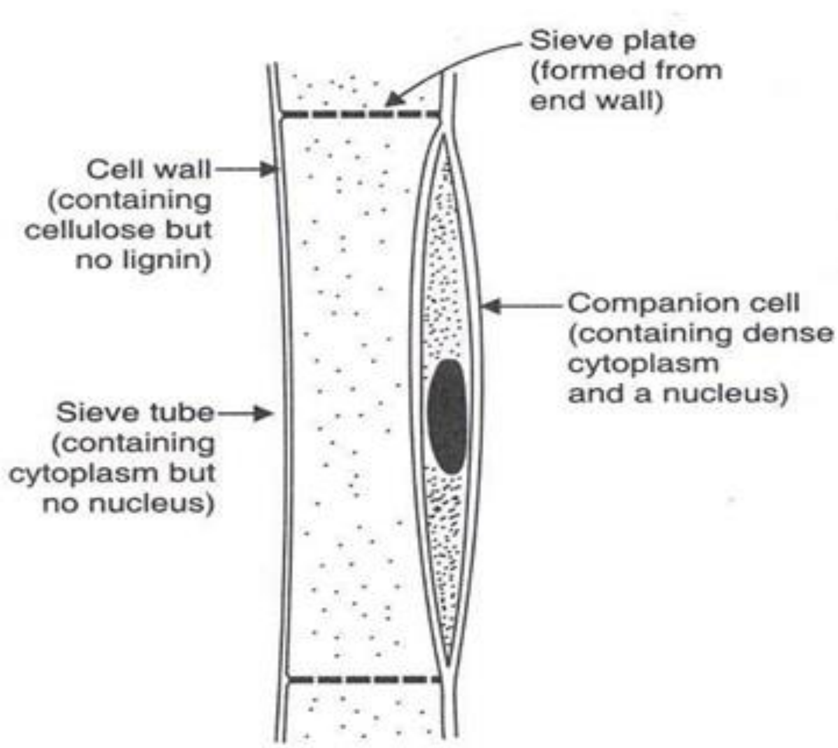
Xylem vessels of the root are connected with the xylem vessel of the stem of a plant. So the water enters from root xylem vessel to the stem xylem vessel and further reaches into the leaves of the plant from petiole. The plant uses only one or two per cent of the water in photosynthesis. The remaining water is lost in air as water vapour.

Water is sucked up by the xylem vessel

The pressure at the top of the plant (in the leaves) is low whereas pressure at the bottom of the plant is high. It is due to transpiration that the pressure is low at the top of a plant. And it is because of low pressure at the top of the plant that water flows up the xylem vessel into the leaves of a plant.

The continuous evaporation of water from the leaves of a plant is called transpiration. The leaves of a plant have tiny pores called stomata. It is through them that the water evaporates into the air. This reduces the pressure at the top of xylem vessels and thus water flows up into them.

Transport of food and other substances



The food which is prepared by the process of photosynthesis in the leaves of a plant has to be transported to other parts like stem, roots, branches etc. Therefore this food is transported to other parts of the plant through a kind of tubes called phloem. The transport of food from leaves to other parts of a plant is called translocation. The food made by the leaves is in the form of simple sugar.

Phloem is present in all the parts of a plant.

Phloem contains Sieve Tubes

Phloem is a long tube made of many living cells joined end to end. The living cells of phloem are called sieve tubes. The end walls of cells in the phloem have sieve plates which have tiny holes in them. It is through these holes that the food passes along the phloem tubes. Sieve tubes contain cytoplasm in them but have no nucleus. Each sieve tube cell has a companion cell which has a nucleus and many other organelles. The cell wall of sieve tubes contains cellulose but no lignin.

The food is made by the mesophyll cells of a leaf and from there it enters into the sieve tubes of the phloem. These phloem tubes are interconnected and once the food reaches the phloem tube of a leaf, it is then transported to all other parts of a plant.

The transport of food is necessary because every part of a plant needs food for:

- Energy
- Building its parts
- Maintaining its life

Other substance like hormones made in the tips of roots and shoots are also transported through phloem tubes.

Mechanism of transport of food in a plant

It is by using the energy from ATP that the food made in the leaves of a plant is loaded in sieve tubes of phloem tissue. Then by the process of osmosis water enters into sieve tubes that contain sugar. This raises pressure in phloem tissue. This high pressure produced in phloem tissue moves the food to all other parts of a plant having less pressure. In this way food is transported to all parts of a plant through phloem tissue.

Role of cell membrane

A cell is the structural and functional working unit of life and also been described as building blocks and fundamental unit of an organism. The term cell was coined by an English scientist Robert Hooke in the year 1665. The shape and size of the cells vary according to their functions and compositions. There are different types of cells and can be differentiated based on the presence and absence of few cell organelles.

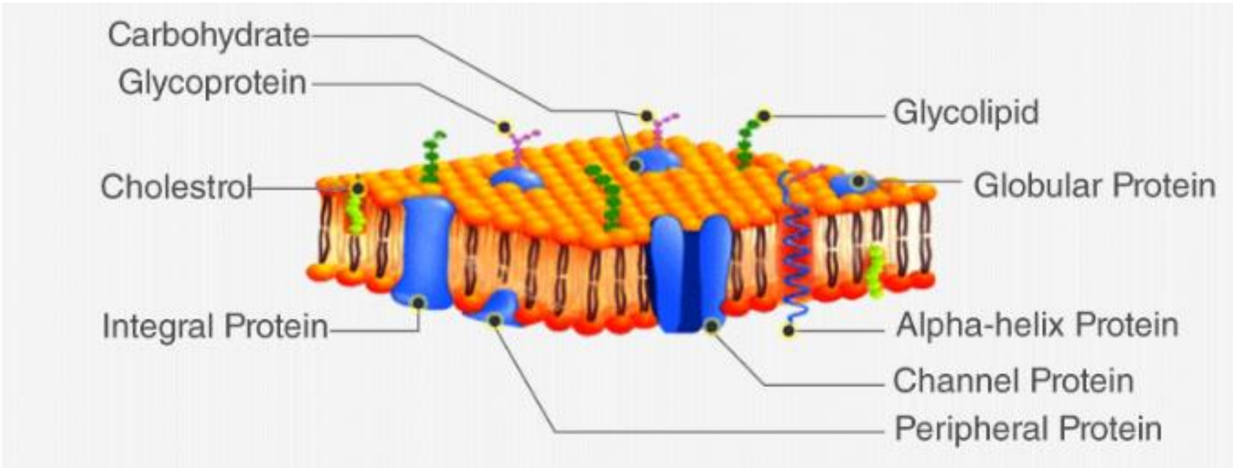
The **cell wall** is present only in plants, fungi and bacteria. The image above represents a plant cell wall

The cell wall is the outermost covering of plant cells. It is present outside the cell membrane and is tough, flexible and sometimes rigid in its texture. It is mainly composed of cellulose, long fibres of carbohydrates including hemicellulose, lignin and pectin.

The main functions of the cell wall are:

1. Protecting the cell against physical damage and invading pathogens.
2. Regulates and controls the direction of cell growth.
3. Providing the strength, structural support and maintaining the shape of the cell.
4. Functions as a storage unit by storing carbohydrates for use in plant growth, especially in seeds.
5. It allows entry of smaller molecules through it freely.

Cell Membrane

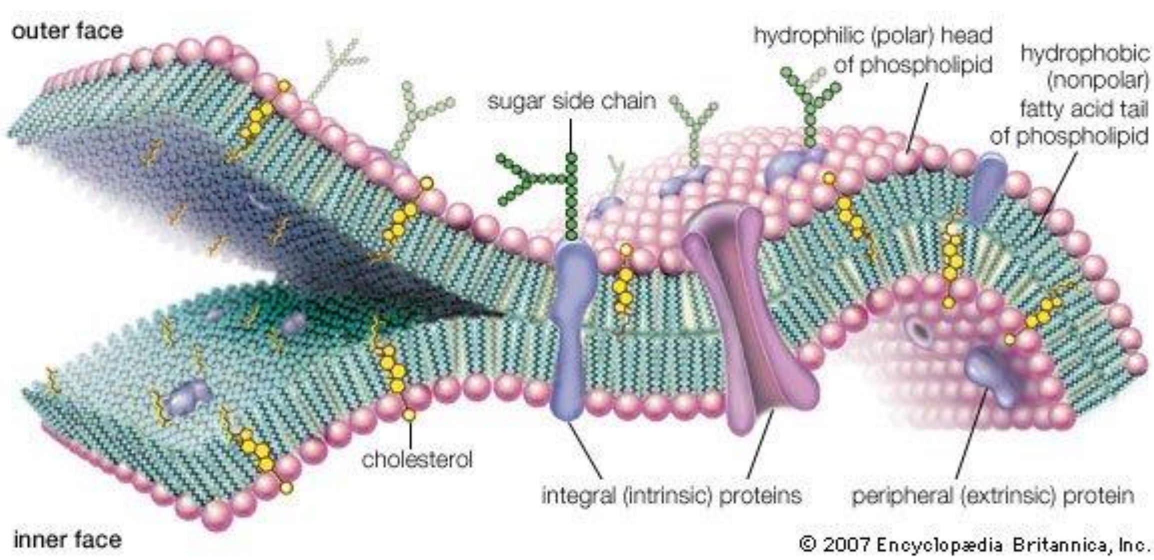


Cell Membrane is present in all organisms including plants

The cell membrane is also known as the plasma membrane. It is the outermost covering of animal cells. It is a semi-permeable membrane composed of lipids and proteins. The main functions of the cell membrane include:

1. Protecting the integrity of the interior cell.
2. Providing support and maintaining the shape of the cell.
3. Helps in regulating cell growth through the balance of endocytosis and exocytosis.
4. The cell membrane also plays an important role in cell signalling and communication.
5. It acts as a selectively permeable membrane by allowing the entry of only selected substances into the cell.

Cell membrane, also called **plasma membrane**, thin membrane that surrounds every living cell, delimiting the cell from the environment around it. Enclosed by this cell membrane (also known as the plasma membrane) are the cell's constituents, often large, water-soluble, highly charged molecules such as proteins, nucleic acids, carbohydrates, and substances involved in cellular metabolism. Outside the cell, in the surrounding water-based environment, are ions, acids, and alkalis that are toxic to the cell, as well as nutrients that the cell must absorb in order to live and grow. The cell membrane, therefore, has two functions: first, to be a barrier keeping the constituents of the cell in and unwanted substances out and, second, to be a gate allowing transport into the cell of essential nutrients and movement from the cell of waste products.



Cell membranes are composed primarily of fatty-acid-based lipids and proteins. Membrane lipids are principally of two types, phospholipids and sterols (generally cholesterol). Both types share the defining characteristic of lipids—they dissolve readily in organic solvents—but in addition they both have a region that is attracted to and soluble in water. This "amphiphilic" property (having a dual attraction; i.e., containing both a lipid-soluble and a water-soluble region) is basic to the role of lipids as building blocks of cellular membranes. Membrane proteins are also of two general types. One type, called the extrinsic proteins, is loosely attached by ionic bonds or calcium bridges to the electrically charged phosphoryl surface of the bilayer. They can also attach to the second type of protein, called the intrinsic proteins. The intrinsic proteins, as their name implies, are firmly embedded within the phospholipid bilayer. In general, membranes actively involved in metabolism contain a higher proportion of protein.

The chemical structure of the cell membrane makes it remarkably flexible, the ideal boundary for rapidly growing and dividing cells. Yet the membrane is also a formidable barrier, allowing some dissolved substances, or solutes, to pass while blocking others. Lipid-soluble molecules and some small molecules can permeate the membrane, but the lipid bilayer effectively repels the many large, water-soluble molecules and electrically charged ions that the cell must import or export in order to live. Transport of these vital substances is carried out by certain classes of intrinsic proteins that form a variety of transport systems: some are open channels, which allow ions to diffuse directly into the cell; others are "facilitators," which help solutes diffuse past the lipid screen; yet others are "pumps," which force solutes through the membrane when they are not concentrated enough to diffuse spontaneously. Particles too large to be diffused or pumped are often swallowed or disgorged whole by an opening and closing of the membrane.

Ion pump carrier.

The mineral salts are absorbed by plants in their ionic form and so is their transport within plants. Certain solutes such as sugars are however transported across the membranes in uncharged state.

For uncharged solutes (non-electrolytes), their movement across the membrane depends upon their concentration gradient i.e., gradient of chemical potential only on two sides of the membrane. But, in case of charged solutes or ions (electrolytes) the situation becomes different.

The movement of solutes into the cytosol through membrane (such as plasma membrane or tonoplast) is called as influx while their exit from the cytosol is termed as efflux. In recent years much work has been done on permeability of cell membranes especially plasma membrane and tonoplast (vacuolar membrane) and various trans membrane transporters (proteins) have been identified in them which enhance movement of solutes across such membranes. These transporter proteins are highly specific with complex structure and different models have been given by scientists to explain their functioning.

These membrane transporter proteins can be grouped in three categories:

(i) Ion-channels,

(ii) Carriers and

(iii) Pumps

1. Ion-Channels:

i. Ion-channels are trans-membrane proteins which function as selective pores through which ions can diffuse easily across the membrane.

ii. Ion-channels are usually highly specific for one or limited number of ion species. The specificity depends upon the size of the pore and density of surface electric charges on its interior lining more than on selective binding of ions.

iii. Transport of ions through channels is always passive.

iv. The channels are not open all the time but are ‘gated’ (Fig. 7.7). The gates open or close in response to external stimuli that include, (i) voltage changes, (ii) light, (iii) hormone binding and (iv) ions themselves. When gates are open, the ions can diffuse through the channels but not when they are closed.

The channel proteins are believed to contain a sensing region or sensor which responds to the appropriate stimulus by changing conformation of channel protein opening the gate.

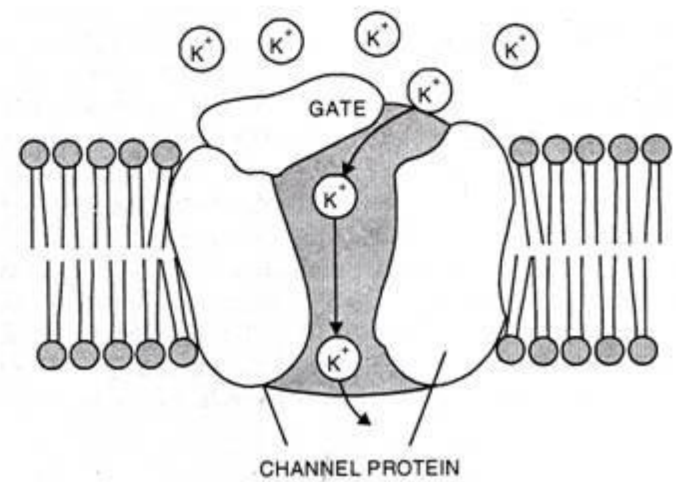


Fig. 7.7. A model showing gated ion-channel

v. Because the ions carry a charge and are mobile, their diffusion across the membrane channel establishes an electric current, which can be detected by a special technique which is known as 'patch-clamp electrophysiology'.

vi. Patch-clamp studies have shown that for a given ion such as K^+, a given membrane has variety of channels which may open in different voltage ranges or in response to different stimuli such as K^+ and Ca^{2+} concentrations, pH, protein kinases and phosphatases etc.
vii. Ions can diffuse through an open channel with rapidity as high as 10^8 s^{-1}.
viii. Those channels which allow inward transport of ions (i.e., towards cytosol side), are called as inward rectifying or inward channels and those which allows outward diffusion (i.e., from cytosol to other side) are called as outward rectifying or outward channels.

ix. Ca^{2+} channels are inward rectifying while anion channels are always outward, (for transport of such ions in reverse direction, active transport mechanisms are required)
x. K^+ is exceptional. It can diffuse inward or outward across the membrane through channels depending upon more negative or more positive membrane potential respectively.
xi. Many channel proteins are inducible i.e., they are synthesized by the cell when a particular solute is available for absorption.

(Some slow vacuolar (SV) channels may be present on tonoplast which allow diffusion of some cations and also anions from vacuole to cytosol).

2. Carriers:

i. These trans-membrane transporter proteins do not form pores in membrane, instead they selectively bind the solute to be transported to a specific site on them. This causes conformational change in carrier protein which exposes the solute to other side of the membrane. After the solute is released from the binding site, the carrier protein reverts back to its original conformation to pick up a fresh solute molecule or ion (Fig. 7.2). Thus, binding and release of solute through carrier is similar to an enzyme catalysed reaction.

ii. Carrier mediated transport of solutes enables transport of much wider range of solutes, but is slower (about $10^4 – 10^5\ s^{-1}$) as compared to channel mediated solute transport.

iii. Carrier mediated solute transport may be of two types:

(i) Passive transport and

(ii) Active transport.

Passive Transport:

Carrier mediated passive transport of solutes occurs along the electrochemical potential gradient and does not require expenditure of energy. This has also been called as facilitated diffusion. According to some scientists, both carrier mediated passive transport and channel mediated transport should come under the purview of facilitated diffusion.

Active Transport:

Carrier mediated active transport of solutes takes place against the electrochemical potential gradient and requires additional input of energy that chiefly comes from hydrolysis of ATP. In such cases, the carrier proteins are called as 'pumps' and the transport of solutes is called as primary active transport because it directly utilizes energy from hydrolysis of ATP.

3. Pumps:

As mentioned earlier, the membrane transporter proteins involved in primary active transport of solute are called as pumps. Most of the pumps transport ions such as H^+ and

Ca^{2+} across the membrane and are known as ion-pumps. Some pumps (such as those of ABC transporters category) may also transport large organic solutes across the membranes.

Ion-pumps may be of two types:

(i) Electro neutral pumps and

(ii) Electro genic pumps.

Electro neutral pumps are those which are associated with transport of ions with no net movement of charge across the membrane. For example H^+/K^+-ATPase of some animal cells, pumps out one H^+ for each K^+ taken in with no net movement of charge. Therefore, it is an electro neutral pump.

Electro genic pumps on the other hand, transport ions involving net movement of charge across the membrane. For example, H^+-ATPase found in plant and animal cells, pumps out H^+ with net movement of one positive charge. Therefore, it is an electro genic pump. (The Na^+/K^+ – ATPase of animal cells such as neurons, is also an example of electro genic pumps because it expels three Na^+ ions for every two K^+ ions taken in resulting in net outward movement of one positive charge.)

H^+-ATPase, H^+-PPase and Ca^{2+}-ATPase are most common electro genic pumps in plant cells and their direction is outward. (Therefore, other mechanisms (secondary active transport) are required for uptake of most of the mineral nutrients).

A brief account of some of the most common pumps in plant cells is as follows:

(i) Proton-ATPase Pumps (H^+-ATPases):

These pumps are also known as P-type ATPases and are found in plasma membrane, tonoplast and possibly other cell membranes. These are structurally distinct and operate in reverse of F-type ATPases i.e., they hydrolyse ATP instead of synthesizing it (ATPases of mitochondria and chloroplast are also known as F-type ATPases)

Fig 7.8 shows a model of plasma membrane H^+– ATPase (also known as P-type ATPase). This enzyme protein is a single chain polypeptide with 10 hydrophobic trans membrane segments or domains (only three of these are shown as helical coils while others are shown as cylinders in the figure).

These segments are joined by hydrophilic loops which project in cytosol and cell wall (apoplast). The ATP binding site is believed to be an aspartic acid residue (D) situated on loop connecting 4th and 5th segments towards cytosilic side. Hydrolysis of ATP causes conformational change in the protein and one H^+ ion is transported from cytosol to outside across the plasma membrane.

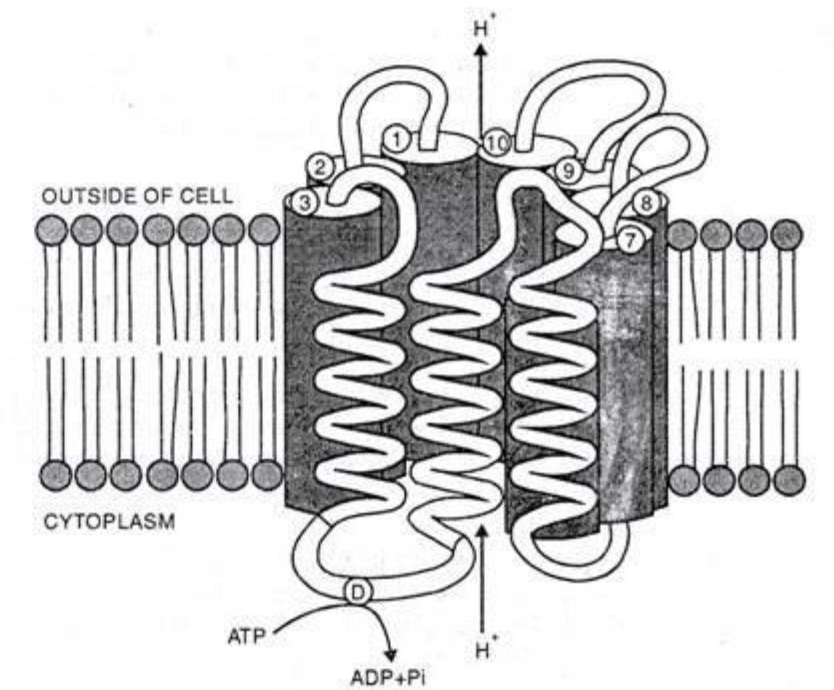


Fig. 7.8. A model of plasma membrane H^+–ATPase. For explanation, see text.

The H+ – ATPases of plasma membrane and tonoplast are different.

Plasma membrane H+-ATPases:

i. These are characteristically inhibited by vandate ions (VO_3^-) but are insensitive to other ions such as NO_3^-.

ii. Single proton (H^+) is trans located for each molecule of ATP hydrolysed.

Vacuolar H^+-ATPases:

i. These are insensitive to VO_3^- but are strongly inhibited by NO_3^-.

ii. Two protons ($2H^+$) are trans located for each molecule of ATP hydrolysed.

iii. Resemble structurally to F-type ATPases of mitochondria and can be separated into two complexes analogous to F_0 and F_1, out unlike the former are not inhibited by oligomycin or azides.

(ii) Proton-pyrophosphatases (H^+– PPases):

i. There are mainly found in tonoplasts but may also occur in membrane of Golgi-bodies. They pump protons into the lumen of vacuole and Golgi-cisternae.

ii. These pumps appear to work in parallel with vacuolar ATPases to create protons gradient across the tonoplast. This enzyme protein consists of a single polypeptide chain with molecular mass of 80 kD and utilizes energy from hydrolysis of inorganic pyrophosphate (PPi).

iii. Free energy released by hydrolysis of PPi is less than that obtained from hydrolysis of ATP. Vacuolar H^+ – PPase transport only one H^+ per PPi molecule hydrolysed.

(iii) Calcium Pumping ATPases (Ca^{2+}-ATPases):

i. These are found in plasma membrane, tonoplast and possibly other cell membranes such as those of chloroplasts and ER.

ii. These pumps couple hydrolysis of ATP with translocation of Ca^{2+} across the membrane.

(iv) ATP-Binding Casette Transporters (ABC Transporters):

Certain large metabolites such as anthocyanin's and other secondary plant products are removed from the cytosol and transported across the tonoplast to the vacuole through ABC-transporters located on tonoplast that consume ATP directly. Recently ABC transporters have also been reported from plasma membrane and also mitochondria.

Secondary Active Transport—Symport and Antiport:

A large number of nutrients are transported across the cell membranes against their chemical potential or electro chemical potential gradients by secondary active transport mechanism that does not utilize energy liberated by hydrolysis of ATP directly but indirectly through the energy stored in proton-electrochemical potential gradient across the membrane or proton motive force.

The electro genic proton-ATPase (H^+-ATPase) pumps serve as proton trans locating carrier proteins and free energy of hydrolysis of ATP is conserved in the form of proton gradient across the membrane (more protons accumulating on outer side). This proton gradient together with normal membrane potential contributes to proton electrochemical potential gradient or a proton motive force which tends to move protons back across the membrane through specific carrier proteins located elsewhere on the same membrane.

When protons return back to cytosolic side, the proton motive force generated by electro genic H^+ transport can be utilized to drive transport of other solute molecules or ions against their chemical or electrochemical potential gradient through the same carrier protein through which H^+ is returning back to cytosol. This is called as secondary active transport and because ions or molecules of two different substances (H^+ and other solute) are being transported at the same time through the some carrier protein, this process of solute transport is also called as cotransport mechanism.

Secondary active transport or cotransport mechanism is of two types:

(i) Symport and

(ii) Antiport.

Symport:

When influx of protons is coupled with movement of other solute in the same direction, the cotransport mechanism is celled as symport and the carrier protein is called as symporter (Fig. 7.9A).

Antiport:

When influx of protons is coupled with efflux of other solute, the cotransport mechanism is called as antiport and the carrier protein involved is called as antiporter (Fig. 7.9 B).

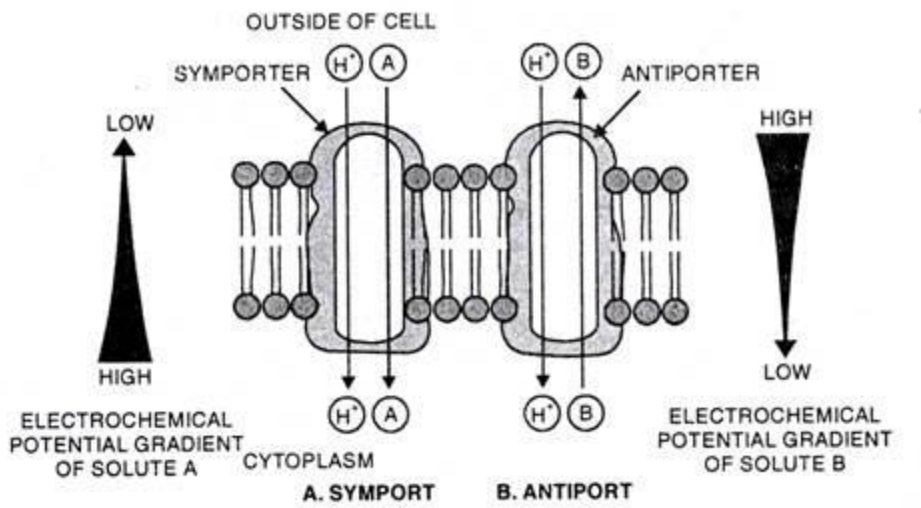


Fig. 7.9. Secondary active transport (Cotransport) **A.** Symport. **B.** Antiport

Fig. 7.10 gives an overview of the various solute transport processes through plasma membrane and tonoplast in plants.

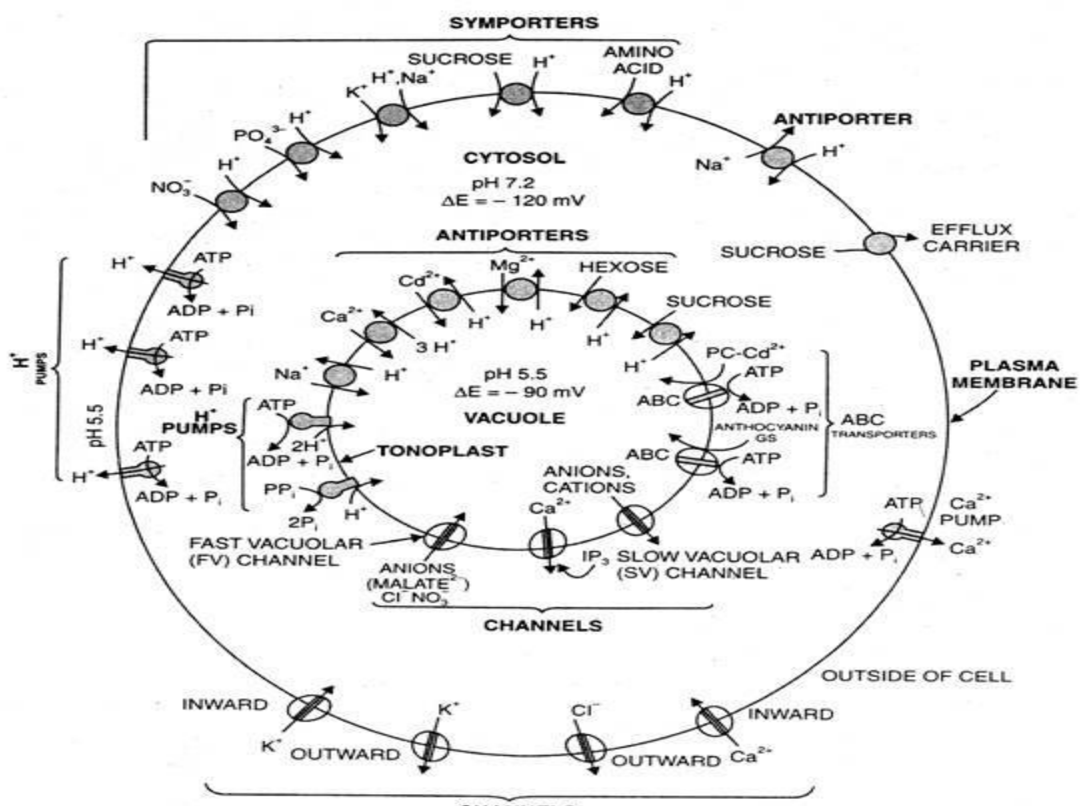


Fig. 7.10. An overview of various solute transport processes through plasmamembrane and tonoplast in plants. IP_3 = inositol triphosphate, a secondary messenger that triggers opening of calcium channels; ΔE = Nernst* potential *i.e.*, electric potential difference at equilibrium in millivolts (mV). The minus sign indicates that the inside is negative relative to the outside