ONLINE CLASS-(E content) TDC III BOTANY HONOURS

Translocation of organic solutes

Movement of inorganic and organic solutes from one part of the plant to another part is called translocation of solutes. As we know that carbohydrates are synthesized in leaves by photosynthesis and all the body cells require sugars for metabolic processes. Therefore, sugars present in the leaf mesophyll tissues reach all the parts through conducting tissues of phloem. This aspect has been a matter of research and debate among scientists, in the 19^{th} century scientists, such as Dutrochet(1827), Sachs(1874), De Vries(1885), Strasburger(1891), and in the 20^{th} century Schmidt(1917), Curtis and Clark(1927-50), Munch(1927) Mason and Muskel(1928), Esau(1966), Fensom1972) etc.

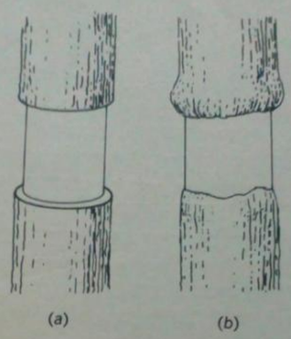
Path of translocation

Solutes are translocated through the sieve tubes of phloem. There are two translocatory tissues namely xylem vessels and phloem sieve tubes. Besides them , they also consist of some other tissues for their functioning. Xylem vessels are dead tissues without protoplasm, whereas sieve tubes are living ones. Experimentally this has been established that xylem vessels are responsible for conduction of water from root cells to all the parts and the apex of the plant. Movement of water takes place in the upward direction. In contrast, sieve tubes conduct the organic solutes from top part, where leaves are borne, to the tissues present below, such as branches ,flowers,fruits and roots. Therefore the movement is downwards. However, scientists have opined that the movement of organic solutes takes place through sieve tubes in both downward and upward direction.

Experimental evidences in support of that translocation of sugars takes place through phloem are many. Following are some experiments in its support-

1. Ringing or girdling experiment-

Curtis (1925), experimentally showed that complete removal of bark (which includes phloem) from a woody stem caused swelling of the bark just above the removed portion, due to accumulation of food material coming from top. When inner part of the stem including xylem was removed, leaving bark intact, no accumulation of food or swelling occurred.



9-1 (a) A trunk of a tree immediately after a circle of bark has been removed. (b) The same trunk after a period of time. Note that the materials being translocated from the leaves have accumulated above the girdle, causing this.area to bulge.

Fig. Courtesy: Plant Physiology, R.M.Devlin (East-West Press,Pvt. Ltd.)

2. Chemical analysis of phloem contents

3. Evidences from tracer techniques-

Burr et al. (1945) using isotopic $^{14}CO_2$ in photosynthesis found the presence of ^{14}C labelled sugar in the phloem. This clearly confirms that organic solutes (sugars) are translocated through sieve tubes.

Mechanism of translocation

The mechanism of translocation of solutes has been a debatable aspect among scientists. Different theories have been put forward to explain the transport of organic solutes in plants. These can be categorized as

I. Short distance translocation

II. Long distance translocation

Short distance transport can be explained by

1. Protoplasmic streaming theory

2. Transcellular streaming theory

3. Contractile proteins, and

4. Electro-osmosis theory

1. Protoplasmic streaming theory- This theory was proposed by De Vries(1885) and supported by Curtis (1935).According to this theory, diffusion and cytoplasmic streaming are involved in the translocation process. Since, sieve tubes are interconnected with each other forming a continuous channel, diffusion of solutes can easily take place through the sieve pores. Further the movement of

solutes takes place due to cytoplasmic streaming. This theory has merit to explain bidirectional translocation.

2. Transcellular streaming- A modified version of the previous theory was proposed by Thaine (1964). He observed the presence of Transcellular strands in sieve tubes which contains particles. These strands move up and down. There is Transcellular streaming or movement of the particulate and fluid constituents of cytoplasm through these linear files. Transcellular strands are proteinaceous which show rhythmic contraction. This theory was also supported by Aikman and Anderson (1971).This theory is also able to explain the bidirectional translocation in plants at the same time. However, this theory needs explanation of availability of physical driving force due to metabolic energy in the sieve tubes. Furthermore, such strands have not been observed under electron microscope.

3. Contractile Proteins- Fensom and Williams (1974) observed a network of interlinked microfibrils in the sieve tubes which oscillated in a manner like moving flagella in other organisms. They opined that particles attached to microfibrils move. These movements suggest that the microfibrils are composed of contractile threads of p-proteins.

4. Electrosmosis theory- Spanner and Jones (1958,70) suggested that translocation of solutes is linked with electrosmotic mechanism. They stated that a current of K^+ ionspasses through the sieve pores by electrosmosis and the sugar molecules adhered tightly to K^+ ions are carried along with them. This process utilizes ATP, which is derived from neighbouring cells. Thus, each sieve plate acts as an electro osmotic pumping station, which boosts mass flow of sugar solution at intervals along the sieve tube.

5. Mass flow theory/ Pressure Flow theory- This theory was proposed by Munch (1926).According to him translocation is analogous to blood circulation. The mesophyll cell lacks like heart. During photosynthesis, the cell sap concentration in mesophyll cells is high and as a result high osmotic pressure exists in them. Due to high osmotic concentration, mesophyll cells absorb water from the adjacent tissues. This creates a high turgor pressure. Mesophyll cells are connected to sieve tubes through small pores, known as plasmodesmata. This makes a continuous channel through which the solutes flow in bulk under the osmotic influence.

Mass flow theory can be experimentally demonstrated. In this experiment two bulb like vessels A and B having semi permeable membranes are taken. These vessels are interconnected with a channel C. The vessel A contains concentrated sugar solution, where as vessel B contains pure water. Both the vessels are dipped in a container having pure water. Water is in continuity in the container having vessels A and B. Here A corresponds to mesophyll cell, which acts as source and the vessel B acts as the organ/ cell, where the sugar is utilized acting as sink. Since, vessel A contains high conc. of sugar solution it absorbs water rapidly in large quantity and results in a high turgor pressure. As a result, the solution flows in mass in the direction from vessel A to B via C under turgor pressure gradient. This flow continues until the equilibrium of concentrations in both the chambers A and B becomes equal. Then the process will stop. This process may continue if the chamber A is added with concentrated solution, as this happens in the mesophyll cells naturally. The water will diffuse from chamber B into water vessel and can again pass through to chamber A.

Munch theory was supported by Crafts (1961) and Esau (1966). This is supported by the fact that sap exudations containing higher sugar contents takes place from the cut end of stem from phloem.

Objections t to this theory were also raised based on the following facts-

1. This explains only unidirectional flow of solutes and cannot justify the bidirectional flow. However, bidirectional flow has been explained by Crafts considering presence of two sinks, one at the apex and the other at the roots, in separate sieve tubes. Both operate simultaneously. But it does not seem reasonable.

2. Present findings support that during translocation of solute the cytoplasm participates actively which is clarified by the experiment conducted with low temperature and metabolic inhibitors, where it retards the or stops altogether.

3. For the uninterrupted movement of sugar from one end to the other end overcoming the resistance offered by the cross walls- plasmodesmata, the turgor pressure must be very high, which is naturally not possible.

4. There is no such heart like pump in plants. Arisz (1952) proposed that this system does not exist in mesophyll cells as the turgor pressure gradient is from sieve tubes to mesophyll cells instead of reverse. Warmer (1953) reported that concentration of sugar in sieve tube is 23 times higher than in the mesophyll cells. This fact eliminates the operation of mass flow as proposed in Munch hypothesis.

Modifications of Pressure flow Hypothesis-

Some modifications in Munch pressure flow theory were put forward, which are Volume flow, solution flow, and active mass flow theory.

Volume flow- This theory was proposed by Eschrich, Evart and Young (1972). They believe that pressure differences which act as a driving force were more localised, even at the levelof individual sieve tubes. So it is not an overall pressure gradient that causes mass flow as proposed by Munch. They considered solution flow in closed turgid tubes and in open tubes without turgor. Their experimental observations were based on the basis of hydrostatic and osmotic pressure difference across the semi permeable membranes of these tubes.It was noted that hydrostatic pressure gradient along the direction of solution flow was not required.

Solution flow- Marshall and Wardlaw (1973) proposed that materials move in the form of solution. Both the solute and solvent travel concurrently. According to them different solutes should move at the same speed because they are moving under physical influence as a solution. They observed simultaneous translocation of ^{14}C- labelled assimilates and ^{32}P-labelled phosphate in wheat plants.

Active mass flow- Mason and Phillis (1936) found that oxygen is required to maintain some special state of cytoplasm which enables translocation to occur. They calculated the movement of sugar along living stems was 40,000 times faster than could be accounted for by diffusion through a column of water standing in a glass tube. Thus, they proposed the hypothesis of activated diffusion of sugars. The theory was also supported by Qureshi and Spanner (1973).

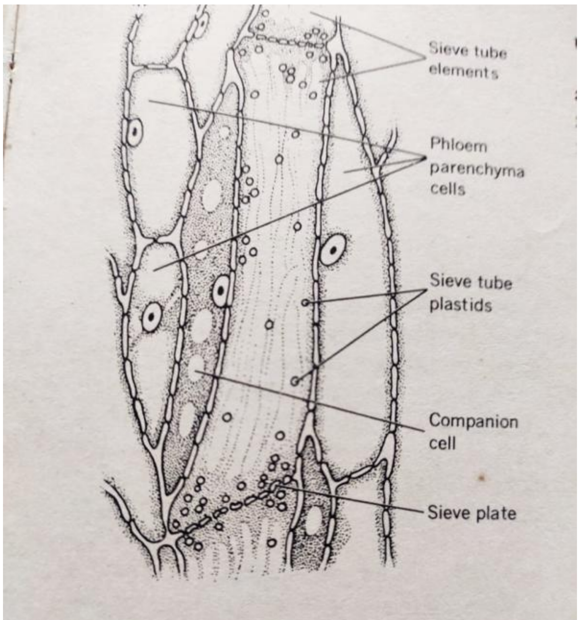
&. Bimodal theory of translocation-

Fenson (1971) proposed a composite theory of translocation. According to his theory, sucrose translocation takes place in two chief modes. The first mode includes micro peristaltic movement along hollow fibrils of contractile proteins. The second mode is considered as a mass flow of solution around the contractile protein fibrils. This is relatively slow and is stopped by callose formation, but it is also stopped if the first mode is inactive. Fenson (1972) stated that microfibrillar material could also participate directly in the movement of sucrose as pulses travelling at about 400cm/. This mode of translocation is not stopped by callose because p-Protein fibrils stretch between successive sieve tubes and about 50-350 microfibrillar strands can pass through a single sieve plate pore.

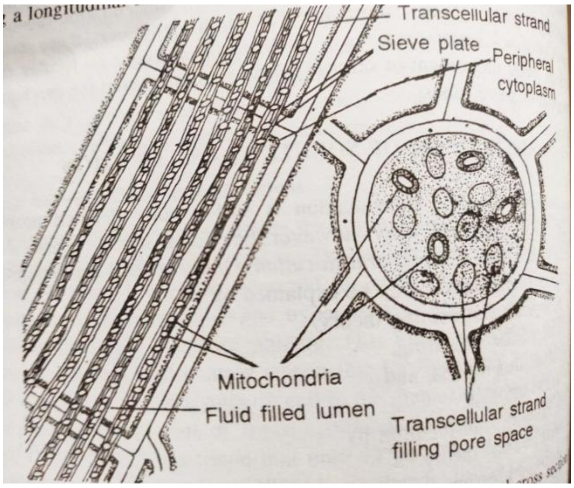
There are some more models to explain the translocation of sugars and other solutes.

Sucrose- Proton model-

According to this model, transport of sucrose takes place through plasma membrane. The membrane contains enzymes ATPase which hydrolyse a molecule of ATP and pumps two protons out of the cell. This makes outside more positive charged and inside more negatively charged. The sucrose-proton carrier in its negatively charged form combines with a proton and a sucrose molecule and undergoes conformational changes. In this way sucrose moves across the membrane. Both sucrose and protons are released into the interior of the cell. This is a symport translocation as there is movement of two entities.



9-3 Phloem tissue from the stem of *Nicotiana tabacum*, showing a sieve tube element, a companion cell, and phloem parenchyma cells. (After R. Holman and W. Robbins. 1938. Textbook of general botany for colleges and universities. Wiley, New



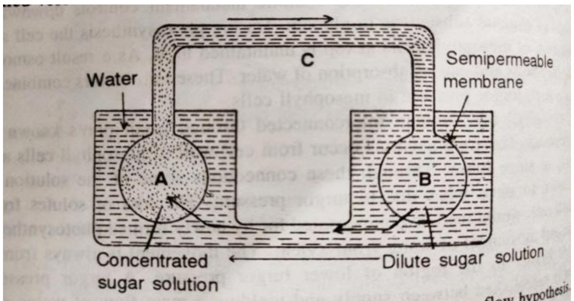


Fig. 15.5. Experimental representation of Münch mass flow hypothesis

Figs. Plant Physiology; S.N.Pandey and B.K.Sinha (Vikash Publ.House,N.Delhi)