UNIT 14   TRANSPORT IN THE PHLOEM

Structure

14.1   INTRODUCTION

So far you have learnt that one of the basic necessities of plants, water, is taken up by the roots. Another purpose served by the roots is to absorb water soluble mineral nutrients from the soil. Mineral nutrients move together with water in long distance pathways provided by the vascular system to reach the entire plant. Roots cannot feed themselves in the darkness of soil. Several other tissues in the plant body also lack photosynthetic apparatus completely or possess it partly in the sense that they cannot manufacture enough food required to support their life processes. Leaves on the other hand rely on roots for water and minerals but manufacture more food than they actually need. Hence, leaves serve as the source of food for other tissues which may store excess of it so that it can be used by plant for the perpetuation and spread of species. Now, how is such a complementary division of labour in tissues particularly between roots and leaves made possible? And how are the organic molecules made by photosynthesis and other biosynthesis are distributed in various parts of plants?

In this unit you will learn about the delivery of food from leaves to various parts of plants such as seeds, fruits and storage tissues. What sort of questions come to your mind when you think about transport of food? Perhaps you would like to know the following: i) Where does the translocation occur in plants? ii) What sort of materials are transported? iii) What is the mechanism of translocation? iv) What are the factors, internal or external, influencing the transport? For instance, how do water melons or grapes manage to be so juicy while the leaves just below are papery and non-tasty?

In this unit we will try to find answers to the above questions.

Objectives

- describe transport network for the translocation of food material,
- explain the concept of source and sink with respect to translocation,
- sketch and describe the structural and functional organisation of phloem particularly near the region of loading and unloading in the sieve tubes,
- list substances transported by phloem conduits,
- describe various experiments performed for the study of phloem transport,
- explain and compare various models proposed for the mechanism of translocation through phloem.

Study Guide

For the study of this unit you should have at least a rudimentary knowledge of hydrodynamics: flow of viscous fluids in capillaries, concept of turgor pressure, osmotic pressure and water potential. Some of these have already been covered in the previous units. You should also know the anatomy of root, stem and leaves and the various types of cells that constitute them; so keep Block 4 of Cell Biology course handy for ready reference.

14.2 WHY IS TRANSPORT NECESSARY?

As you know leaves produce photoassimilates and support various tissues including roots. The excess photoassimilates and metabolites stored in specialised tissues produce fruits and seeds which germinate and regenerate the plant in the appropriate season. The leaves at the canopy of a tree are at a distance from roots. This can vary from a few millimeters to more than a 100 meters. All in all we need an extensive transport system to carry the products of photosynthesis and nitrogen metabolism over medium and long distances. Diffusion is too slow a process to achieve this task over such large distances; what is required is a convective flow in the specialised vascular system so that the photosynthates reach all the needy tissues. The transport system has to be as extensive and ramified as the arterial and venous network in an animal body. However, plants are devoid of a specialised pump such as heart meant for blood circulation. Though we have not yet fully understood how plants achieve this goal, they do carry out this exceedingly difficult task without a heart. Leaves manage to feed the tissues over vast expanses of the plant body with photosynthates necessary to fulfil their requirement.

14.3 THE TRANSPORT NETWORK

You may know that plants have elaborate plumbing network which serves to link their various parts. Phloem forms such a network for the transport of food in higher

Light CO_2

Proteins synthesised
Vitamins and harmones formed

Sugars formed →

Water vapour

Starch, Proteins and fats stored →

Water and minerals

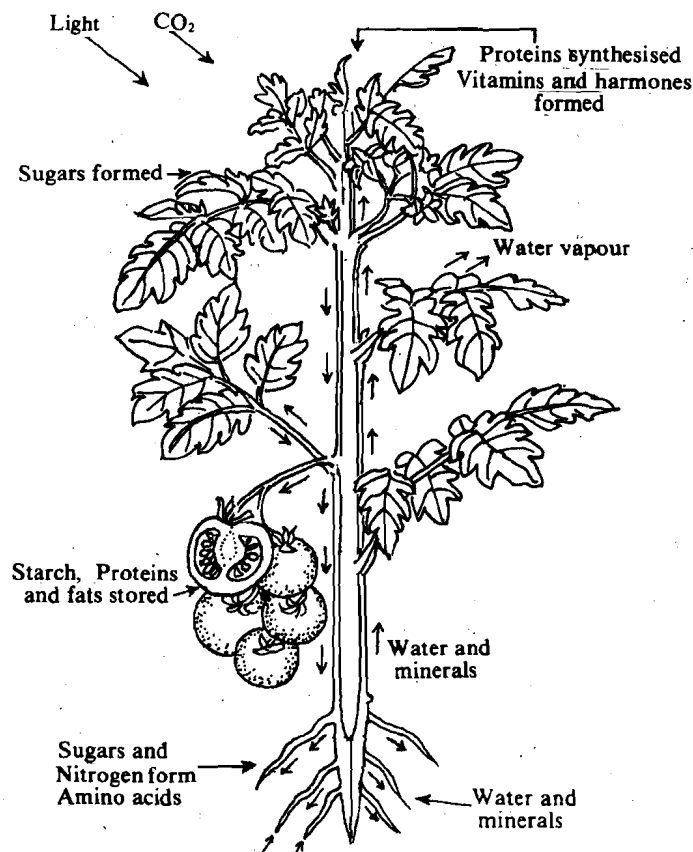Sugars and Nitrogen form Amino acids →

Water and minerals

Fig. 14.1 : Plants are devoid of a heart but carry out massive transport processes within their body. Transpiration stream (→) transports water and inorganic nutrients from their subsoil roots to the shoots, sometimes more than a 100 meter high. A viscous solution of metabolites generated in the leaves from the assimilation of carbon from CO_2 by the capture of solar energy in the process of photosynthesis, is distributed to sink tissues by translocation (- - →).

plants. It runs parallel to other major transport system — the xylem (Fig. 14.1) which takes up water and mineral nutrients from roots and distributes them throughout the plant. The sieve tubes in phloem are joined into long interconnecting pipelines. Unlike water conducting xylem cells, sieve tube members are alive at maturity. The two long distance transport systems and their radial branching establish supply lines to every small region of the plant body.

The direction of transport in phloem varies during the developing stages of the plant. For example, a young seedling moves food upwards from seed to juvenile leaves until they begin to synthesise food. While during fruit formation or for storage in roots or stem the food moves in downward direction. So food moves from the tissues where it is in excess called source to those where it is needed — called sink (Fig. 14.2).
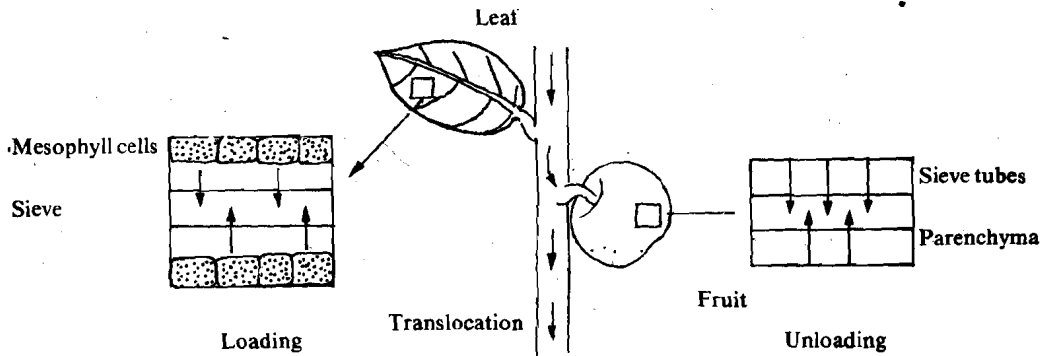

Fig. 14.2 : Source and sink, a schematic diagram.

Essentially, the phloem transport can be subdivided into the following:

i)   The "loading" of the organic nutrients from the mesophyll cell into the phloem of the leaves,

ii) Its translocation over long distances to the tissues awaiting supply,

iii) The "unloading" of the nutrients from the phloem into the cells of the sink.

All these three processes are interlinked. The rate of transport is not constant but depends on the metabolic needs of the sinks on one hand and on the rate of photosynthesis in the leaves — the sources on the other. Phloem transport is a very complex phenomenon and we may indicate, at the beginning itself, that in spite of intensive research, it is not fully understood even today. As such this field offers a very challenging subject for future research in plant anatomy and physiology.

14.4 ORIGIN AND DELIVERY — THE SOURCE AND THE SINK

We have stated above that transport of photosynthates starts from leaves and ends up in one or the other sink tissue. Though this is true, however, it is necessary to define the concept of sinks and sources at any given point of time. For this consider an experiment on the plant *Saxifraga* (Fig. 14.3). This plant spreads by giving out long offshoots with a bunch of leaves and a potential root system at the end. If the latter comes in contact with moist soil, it develops into a self-sufficient shoot-root system. However, so long this has not happened, the long link provides water and minerals taken up by the root of the parent plant to the juvenile bunch of leaves. The phloem transport system initially provides the buds of the distant shoot with the necessary nutrition. When fully grown, the new cluster of leaves becomes excess producers of photosynthates and contributes their output to the parent plant. If we shut off the light falling on the parent plant or the off-shoot (Fig. 14.3b and c) over a substantial period of time, so that either of them is incapable of photosynthesis, which way will the phloem translocate the food? We are sure that you have already arrived at the correct answer. It is observed that translocation is from the system in which photosynthesis takes place to that in which it is prevented. Thus, the two systems of leaves can be sink at one time and source at another. The direction of phloem transport in the above case is, therefore, dependent on the relative production of photosynthates in the two systems of leaves.

Similar situations among typical sinks also exist. In tropics when the new leaves in deciduous plants emerge in the spring on a denuded tree, they need the supply of nutrients. What could be the possible source of nutrients in the absence of pre-existing mature leaves? Naturally from the stored stock of metabolites in sink tissues. In spring, both the xylem and the phloem receive metabolites from all over the plant body and deliver them to the buds.
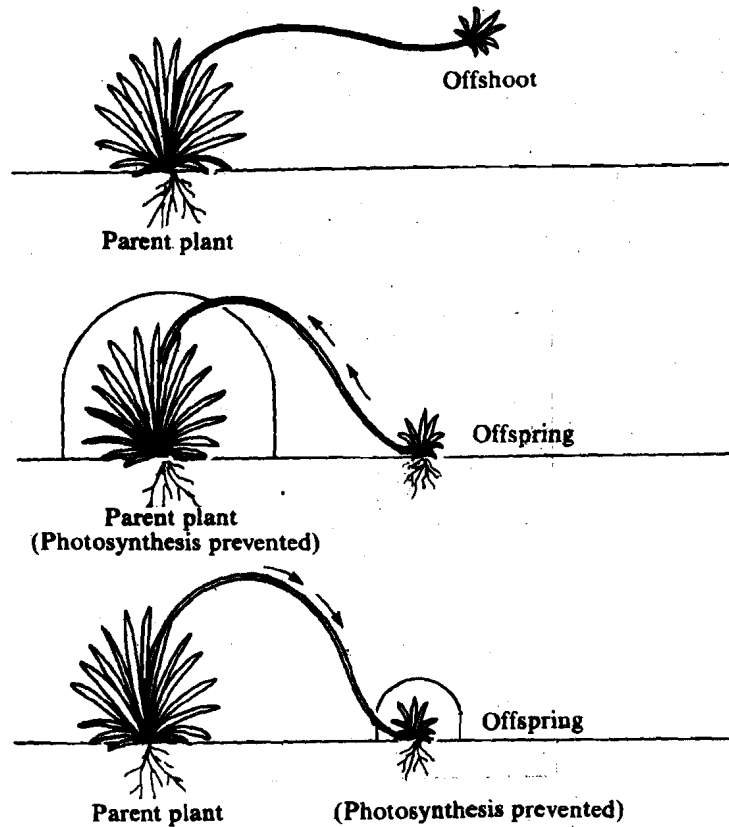

Fig. 14.3 : a) *Saxifraga* **plant with an offshoot, b) Supply of food by the offspring, c) Supply of food by the parent plant.**

SAQ 1

i) Plants need extensive and ramified transport system to carry the products of .... and .... metabolism to their various parts.

ii) The two elaborate transport networks .... and .... run parallel to each other in plants.

iii) .... are arranged in a linear array running vertically through the length of phloem.

iv) Phloem translocates food from .... to ....

v) Loading in sieve tube takes place at the .... and unloading at the ....

14.5 PHLOEM — STRUCTURAL AND FUNCTIONAL RELATIONSHIP

In this section we will explain the structural and functional relationship of phloem and compare it with xylem. The location of phloem with respect to other tissues can be examined by a single transverse section, but to get an idea of their longitudinal route from stem to various branches requires a painstaking study of innumerable serial transverse sections along the height of the plant. Fig. 14.4 shows a schematic drawing envisaged from serial sections. Note the branching, criss-crossing and ramification of vascular bundles. The longitudinal branching and fusion of phloem, particularly at the node show that phloem of one side of a stem can effectively cross

Callose : It is a special carbohydrate polymer which is deposited at the sieve plate usually around plasmodesmata and forms artefacts in the pores.
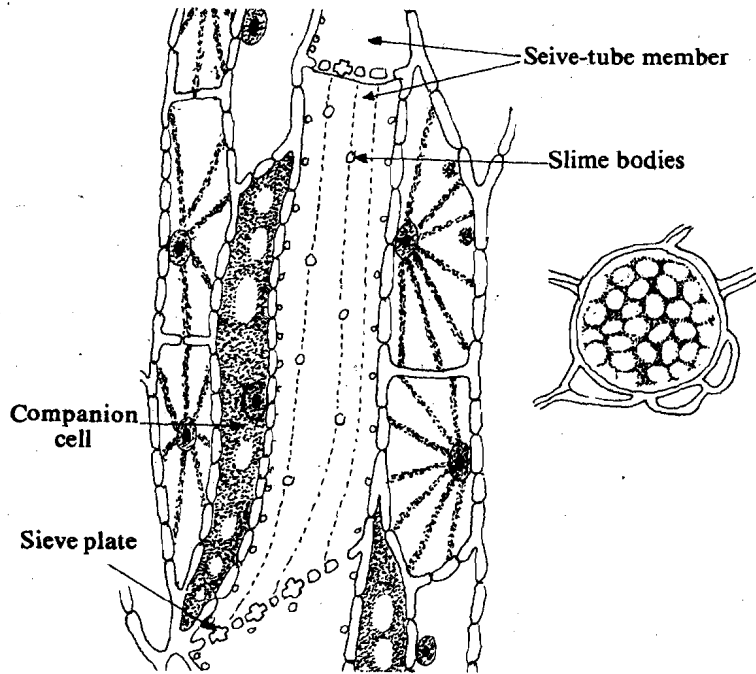
Fig. 14.5 : **Fine structure of phloem showing a full sieve tube element, its companion cell and other cells of phloem. The sieve plate pores are circular openings in the cell walls of adjacent sieve element (inset).**

over to the opposite side on its longitudinal path. We know that phloem consists of 4 types of cells: i) sieve elements, ii) companion cells, iii) phloem parenchyma and sometimes iv) phloem fibres. The metabolites flow only in sieve elements which resemble hollow pipelines referred to as cellular channels (Fig. 14.5). The sieve tube elements are devoid of nucleus but plastids and mitochondria are present. The cell lumen of the sieve element appears open except for transcellular strands that merge with neighbouring sieve cells at the sieve pore plate via plasmodesmata (Fig. 14.6). The continuity of plasmalemma and cytoplasm makes the sieve tubes a longitudinally extending symplast. Do you remember as to what the xylem vessels form, symplast or apoplast?

Phloem carries a viscous solution of metabolites mainly sucrose. The sieve tube elements are of a much smaller radius than xylary vessels and tracheids. The free flow of the viscous phloem sap is apparently not affected by the narrow sieve plate pores.
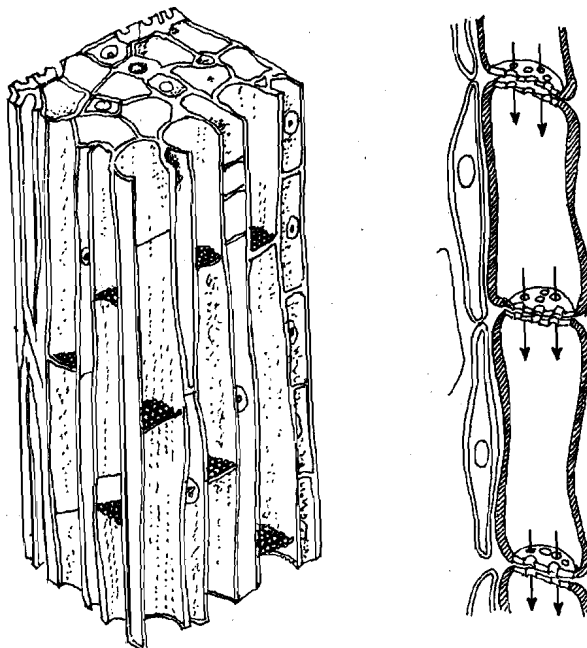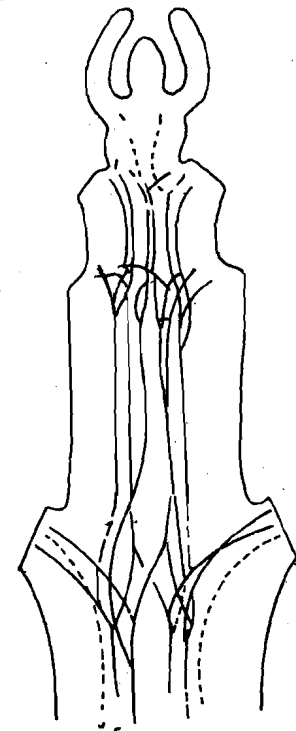

Fig. 14.4 : **Branching, criss-crossing and remification of vascular bundles in a stem of clematis vitalba (schematic).**

Fig. 14.6 : **Detailed 3-dimensional schematic representation of phloem.**

EM pictures reveal that sieve plate pores are callose-lined and are often occluded with endoplasmic reticulum and phloem protein (P-Protein). Earlier it was not conclusively known whether the sieve plate pores are normally occluded or the occlusions were possible artefacts introduced while preparing specimens for electron microscopic studies. Later, using special techniques (that avoid artefacts) it has been suggested that sieve pore plates are open in normal growing plants and flow of solutes occurs through unplugged sieve plate pores. When plants are cut or injured, P-proteins flow to the sieve plate thereby blocking the pores. In their absence, metabolites would continue to flow out of the wounded part and plant will eventually die. The P-protein apparently play a role similar to blood protein fibrin. In the absence of fibrin the person would bleed to death.

Each sieve element is compulsorily associated with a neighbouring companion cell. Both are usually connected with many plasmodesmata. The two arise from a common cell. The function of companion cells is not known but they live as long as the sieve cells live. In this sense, they are true companions. They contain the same concentration of sucrose and have the same osmotic potential as the sieve tube elements. The companion cells have dense cytoplasm and numerous cell organelles, specially mitochondria which indicate that they have a high metabolic activity. It is very likely that companion cells support translocation. Furthermore, the numerous plasmodesmatal connections between the two cells support the idea that companion cells supply large quantities of food materials to the sieve tube elements and provide the latter with proteins and enzymes which they cannot synthesise.

In some species at the phloem loading (near the sieve tubes of leaves) and unloading sites (near the sieve tubes into any sink) there are special kinds of cells called **transfer cells**. As the name suggests they play a major functional role in the transfer of metabolites from the source to the sink. These cells are modified companion cells or cells of phloem parenchyma. Their location in xylem or in phloem varies depending on the part of the plant but in general they are located at the critical sites of heavy transport of inorganic solutes or metabolites. The plasma membrane of transfer cells is highly convoluted which serves to increase the surface area for solute exchange across the cell wall (apoplast) as well as through numerous plasmodesmata (symplast). Moreover, the cells have dense cytoplasm and numerous mitochondria which indicate a high level of metabolic activity.

14.6 LOADING AND UNLOADING OF SIEVE TUBES

In order to understand the loading of food from manufacturing leaf cells to sieve tubes we must examine the anatomy of a minor vein shown in Fig. 14.7. We can see
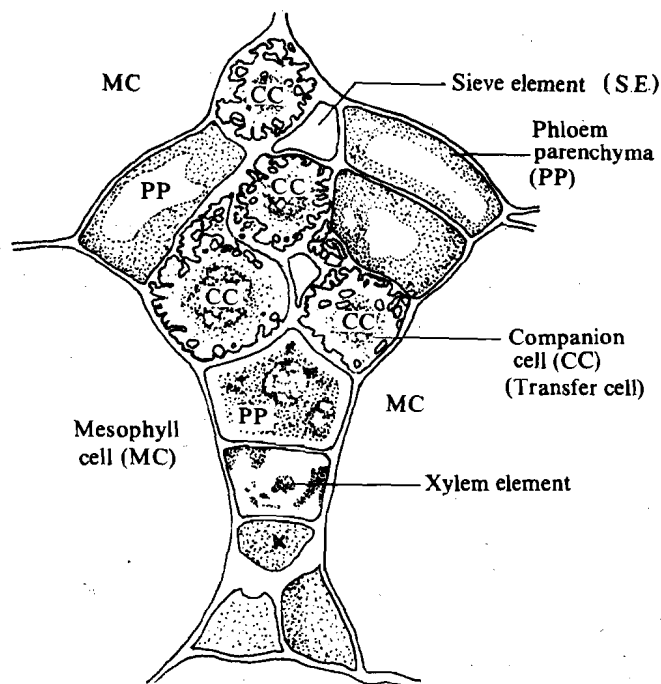

Fig. 14.7 : A cross-section of a minor leaf vein. (MC—Mesophyll Cell, XE—Xylem Elements, SE—Sieve Element, TC—Transfer Cells, PP—Phloem Parenchyma cell.

a xylem vessel (X), two sieve elements (SE) which are relatively smaller than other cells and without cytoplasm, the modified companion cells or transfer cells (TC) with dense cytoplasm and phloem parenchyma (PP) which is less dense and vacuolated. The transfer cells are associated with bundle sheath and mesophyll cells. The ingrowths of cell walls in the companion cells of leaves occur as the leaf matures, perhaps to increase its efficiency to load the sieve tube elements. The metabolites of all the mesophyll cells around the sieve elements join in a common pool to load via the surrounding transfer cells. The path of metabolites and other solutes is shown in Fig. 14.8. Presumably the metabolites are poured in the sieve tubes by the following three types of transport processes:

i) Symplastic transport via the plasmodesmatal connections,
ii) apoplastic transport through the cell wall (passive transport), and
iii) active transport (symport and antiport).

The latter two occur across the plasma membrane of the transfer cells.

All the non-photosynthetic cells and young buds which require more energy than they produce by photosynthesis are the sites of delivery (unloading points) of phloem sap. Grossly speaking, roots are the major importers of metabolites. Buds, phloem and xylem-parenchyma get their supply along the whole length of the vascular system. Seeds, fruits, tubers etc. become the major importers during their growth and development. The morphology of phloem at the sites of transfer of metabolites to seeds, buds, fruits etc. becomes specialised because of the layer of transfer cells which are arranged similar to the placenta of an animal embryo. The process of unloading is similar to loading except that the events occur in reverse direction.
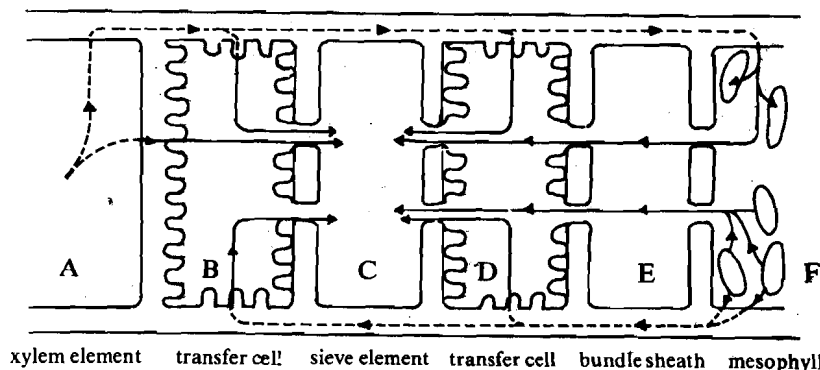

| xylem element | transfer cell | sieve element | transfer cell | bundle sheath | mesophyll |

Fig. 14.8 : The role of transfer cells in a minor vein of a leaf is to mediate solute fluxes from leaf mesophyll cells via leaf apoplasm, into the sieve elements ("loading"). Water and mineral nutrients reach mesophyll cells through the cell wall phase (apoplasm). Membrane permeable metabolites and K^+ released into the apoplasm by the mesophyll cells enter sieve elements via the transfer cells.

14.7 THE NATURE OF METABOLITES IN SIEVE TUBES

The phloem sap contains three major classes of organic compounds — organic acids, amino acids and sucrose besides some cations, anions and hormones. Their concentrations are represented in the histogram shown below (Fig. 14.9). Sucrose — the major energy source in plants is the major metabolite transported from leaves to sinks. Rarely unusual sugars such as raffinose or mannitol are transported in some species. Of the total solute content in phloem, sucrose content ranges from 50 to 90%. The reason why sucrose is the major transporter of energy is not known. It is loaded by active transport because of its high concentration in sieve tubes. Amino acids and organic acids, mainly malate, are also substantial components of phloem sap. Among cations, the concentration of K^+ is much higher. In the xylem sap the concentrations of NO_3^- and K^+ are about the same, but in phloem concentration of NO_3^- is very small.

Can you think where the NO_3^- could disappear? Nitrate is reduced in the leaves and used for the synthesis of amino acids and several other nitrogen containing

compounds. Now, can you guess why there is so much K^+ in the phloem sap? Unlike NO_3^-, K^+ is not incorporated into organic molecules. Due to transpiration there is a persistent influx of K^+ in the leaves. Because water evaporates leaving K^+ behind, its enhanced levels in the shoot require recycling in the xylem.

The presence of excess of ions in root tissues in turn affects the uptake of these mineral nutrients from soil by influencing the ionic relationships of the cells of the root. Here, we would like to emphasise that ions that accumulate in excess in the leaf apoplasm are passed on to the sieve elements via the transfer cells. The presence of K^+ is important as a counter ion to organic acids and amino acids within the cytoplasm of all cells and it is gradually assimilated in the cells of growing plant tissues.
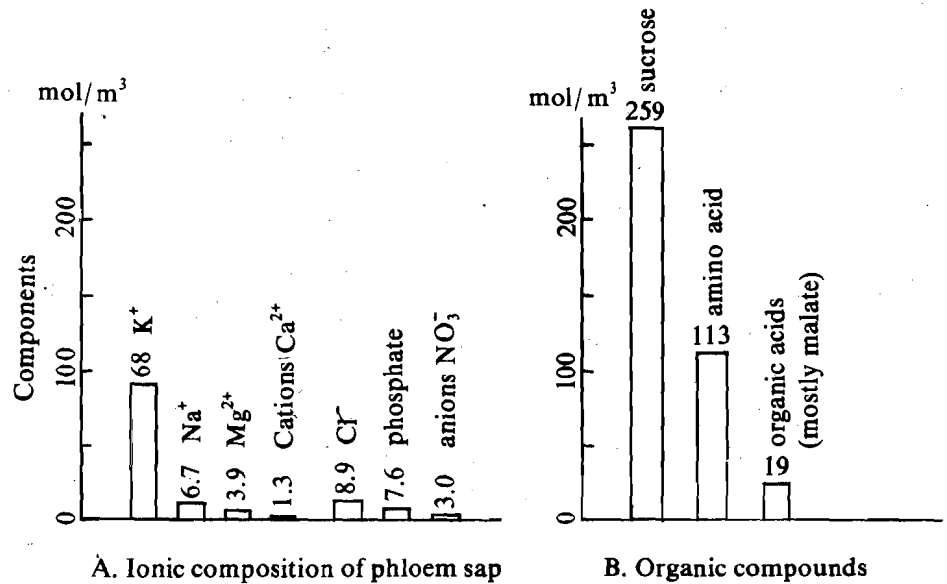
Fig. 14.9 : Ionic and organic compounds of phloem sap of _Ricinus_. In general phloem sap is alkaline (pH 7.2-8.5).

SAQ 2

a) Match the items given in column 1 with those listed in column 2.

Column 1	Column 2
i) Sieve tubes	a) prevent the flow of phloem sap from injured cells
ii) Xylem vessels	b) cellular channels running throughout the plant
iii) P-proteins	c) alive at maturity
iv) Sieve tube element	d) cellulose pipelines running throughout the plant

b) Which of the following statements are true? Write T for true and F for false in the given boxes.

i) Sieve tube elements are smaller in radius than xylem vessels and tracheids. ☐

ii) Sieve tube elements can carry out protein synthesis. ☐

iii) Companion cells have numerous mitochondria to carry high metabolic activity. ☐

iv) Transfer cells are located at the site of heavy transport of organic solutes and metabolites. ☐

v) Transfer cells transfer metabolites to mesophyll cells and load them into the sieve tubes. □

vi) Sugars are transported via both symplastic and apoplastic route. □

14.8 EXPERIMENTS ON PHLOEM TRANSPORT

To begin with, it was necessary to establish the basic fact that the metabolites flow from the source to the sink through phloem. One of the earliest experiments was to cut the bark of a stem (to remove phloem) in the form of a ring leaving the xylem intact. After a few weeks, the bark on the upper side showed swelling while the lower side retained the initial diameter (Fig. 14.10), thereby suggesting that the food, materials moved via the phloem and accumulated in the upperpart.

(a) **(b)**
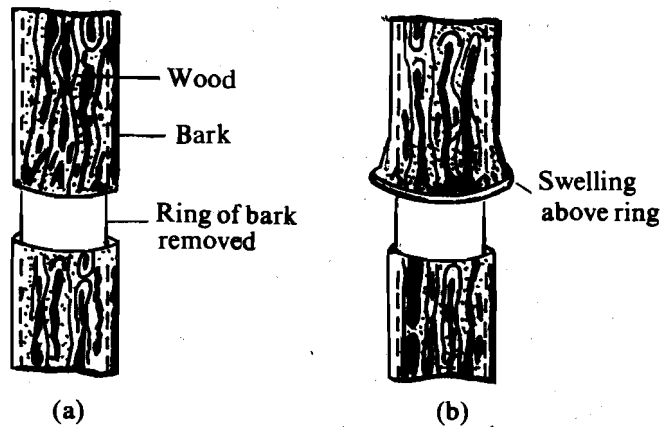
Fig. 14.10 : Ringing (girdling) a tree. a) A ring of bark is removed from the tree, stripping the bark away, down to the xylem. b) Swelling in the bark above the ring is thought to occur from accumulation of downwardly transported material and the continued rapid development of cells just above the ring as compared with those below the ring. The tree eventually dies as the lower part does not receive food material synthesised in the leaves.

Early in this century Münch cut away two such rings in an apple tree as shown in Fig. 14.11. The apple B with girdles both below and above it stopped growing, while the other two apples A and C grew perfectly well because they could draw their metabolites from above and below respectively.
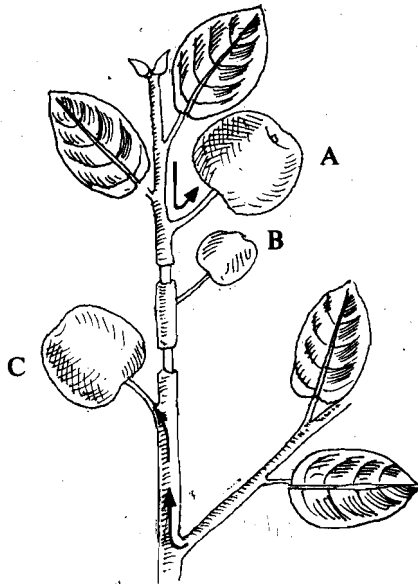
Fig. 14.11 : Girdling (or ringing at two positions), above and below the apple B deprived the apple with organic nutrition and stopped its growth. A and C could obtain photosynthates from the leaves above and below them, respectively

At the end of World War II when radioisotopes were made available as markers, experiments were conducted to trace the pathway of photosynthates using radioactive $^{14}CO_2$. A single leaf was given $^{14}CO_2$ and light so that is would be the only leaf to fix $^{14}CO_2$ by photosynthesis (Fig. 14.12). After a lapse of few hours the stem was cut into a number of segments in order to see the distribution of photosynthate made from $^{14}CO_2$. From the radioactive count of ^{14}C, in the various segments of the stem, it was found that only those parts of plant contained radioactive photoassimilate that were in communication with the leaf receiving $^{14}CO_2$.

Now there are many evidences which prove that photoassimilates and metabolites flow in the sieve tube elements which are the actual channels. Translocation of sugar from leaf to other parts can be followed by placing Geiger tube which detects radioactivity (Fig. 14.12). The velocity of the phloem sap can also be determined by positioning two Geiger tubes against the stem and noting the time required for the movement of radioactivity from tube 1 to tube 2. The values of velocity so obtained usually range from 20 to 100 cm hr^{-1} but occasionally could be as high as three meters hr^{-1}.

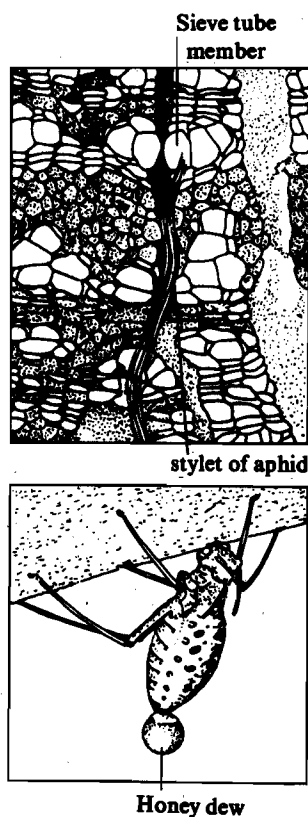**Sieve tube member**

stylet of aphid

Honey dew

Fig. 14.13 : Naturally occurring research tool. a) An aphid penetrating the bark. A honey-dew droplet can be seen at the anal end of aphid. b) The stylets of aphid penetrating into the sieve tube element.

$^{14}Co_2$

Radioactive sugar in phloem
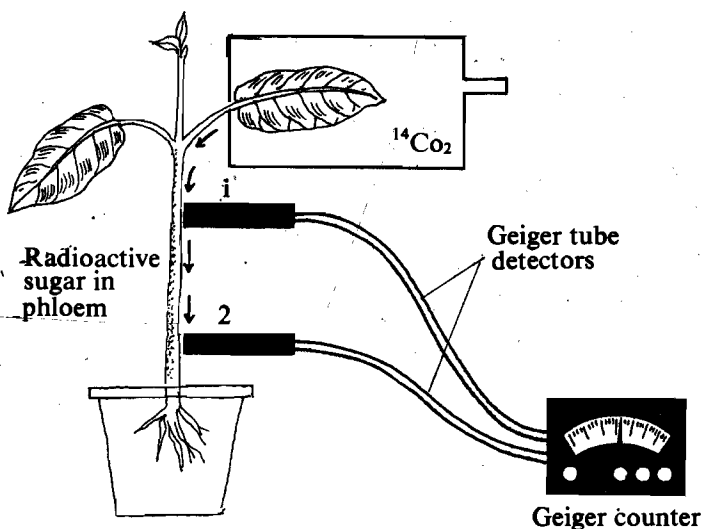
Geiger tube detectors

Geiger counter

Fig. 14.12 : Experimental design for measuring the velocity of phloem sap movement. A leaf is sealed in a closed chamber containing radioactive carbon dioxide ($^{14}CO_2$). The leaf is illuminated and the radioactive carbon dioxide is incorporated into sugar via photosynthesis. The translocation of the radioactive sugar can be detected by a Geiger tube positioned against the stem. The time required for sugar to move a known distance from Geiger tube 1 to Geiger tube 2 can be used to calculate the velocity of phloem sap movement.

The velocity of phloem sap can also be determined by slightly heating small sections of the phloem sap. The sensitive thermocouple is applied further down the stem to detect the arrival of the warmed sap. You may recall that velocities of xylem sap flow is also determined by this method.

The mechanism of transport in phloem is difficult to study because when the cells of phloem are cut, the sieve tube plates get instantly plugged and transport stops altogether. Further, the cellular structure is altered or destroyed.

A simple, neat technique for the study of phloem transport is provided by nature. Aphids, phloem sap sucking insects draw their nutrition from phloem by inserting their stylets right into a sieve tube element (Fig. 14.13). The turgor pressure of the sieve tube is sufficiently high so the sap simply flows into the aphid's alimentary canal. A honey-dew can be seen at the anal end of a well fed aphid. If the insect is cut off from the plant just before the point of entry of stylets, with the stylets still inserted into the bark, phloem sap keeps exuding from the cut end. The exudate called honey dew provides information on the content of the phloem sap. The location of the sharp tip of the stylets is determined by microscopic observations which show that stylets penetrate single sieve element. This simple technique provides valuable information on the transported material and the rate of transport under different conditions (temperature, soil, water content etc.) in a fully functioning intact plant.

Tick mark the correct alternate word(s) given in parenthesis for the statements listed below:

i)   Phloem sap is rich in (amino acid/nucleic acid).

ii) Due to transpiration there is persistent influx of (Ca^{2+}/K^{+}) in leaves.

iii) (Nitrate/Sulphate) is reduced for the synthesis of amino acids.

iv) The technique of (photography/autoradiography) is used to see the location of radioactive carbon in the cell organelles.

14.9   MECHANISM OF PHLOEM TRANSPORT

The efficiency and magnitude of translocation of food material are evident from the annual yields of various crops and fruits. Now, the question is, what is the mechanism of translocation? Diffusion is too slow a process to account for the known velocities of translocation. Moreover, often the direction of movement is from lesser concentration to greater concentration. A few theories proposed for the mechanism of translocation in phloem are discussed below.

14.9.1 Münch Pressure Flow Model

Münch, a German plant physiologist, proposed in 1930, a simple physical model which can be tested in the laboratory for the mechanism of phloem transport. As shown in Fig. 14.14, two osmometers, one containing solute at higher concentration (A) than the other (B), are connected by a tube (C) and dipped in water. Due to high solute concentration in A water flows in to it by the process of osmosis. Consequently, the pressure develops which forces the solution to rise in the connecting tube and the content of A flow into B. This pressure forces water to flow out of B through its membrane in the medium.
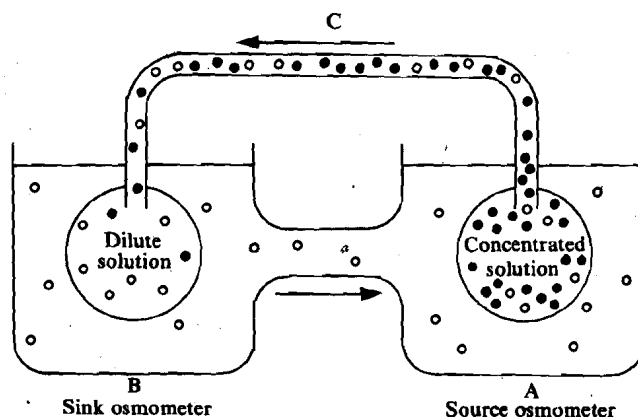

Fig. 14.14 : Model system illustrating Münch pressure flow hypothesis. (See text for details).

Fig. 14.15 : Münch Pressure Flow Model as applied to the plant. (1) Sugar is actively loaded from the leaf into the uppermost sieve tube member. (2) The higher sugar concentration causes water to move in osmotically from the xylem, building up a high water pressure. (3), (4) The high water pressure causes sieve tube sap to flow into the remaining sieve tube members towards the fruit. (5) Sugar is actively unloaded from the lowermost sieve tube member into the fruit. (6) The excess water delivered to the sink enters the xylem and moves back up the plant.

In plants the state of source and sink is analogous to the two osmometers. The source regions have higher solute concentration than the sink region. The phloem conduits in the source region would imbibe water by the process of osmosis and generate a high turgor zone. On the other hand, the phloem in the sink region will be at low turgor. Thus, a pressure gradient exists along the length of the phloem which would cause a mass flow of solvent and solutes with equal velocity.

There are several difficulties in accepting this, otherwise admirably simple and appealing hypothesis. Firstly, the generation of pressure gradient is possible in the above given model only if the water potential is about the same in both regions. However, in plants, water potential is lower in the leaves and higher in the roots. Thus, the tendency of water to enter the phloem in the leaf region is reduced. Whereas in the root region, water can be readily imbibed by sieve elements even at lesser solute concentration of the phloem sap, from neighbouring cells and/or apoplasm. Therefore, it cannot be assumed that the gradient in solute concentration
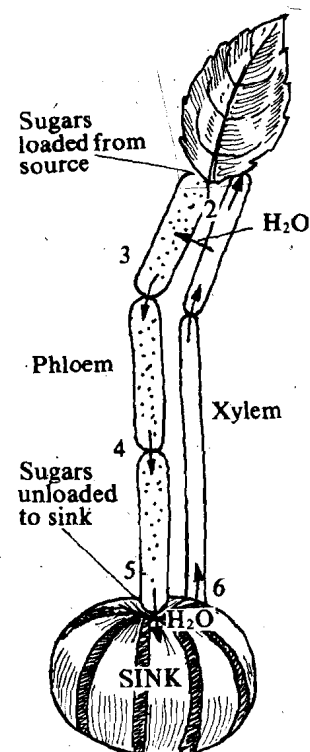
would generate a pressure gradient from sources to sinks. Moreover, the observed differential, mobilities of solute molecules, highest for K^+ and lowest for Ca^{2+}, speak against the pressure flow hypothesis. The original model has been modified, as shown in Fig. 14.15 to remove this problem.

Pressure gradients sufficient for causing mass flow have not been recorded in any plant. Much depends, on the radius of the sieve plate pores, the presence of P-proteins and the degree of callose formation. Hence the debate on the Münch's models is still continuing, primarily because there is still no other alternative model to explain precisely the mechanism of Phloem transport. You may note that at the sites of loading and unloading there is active transport operating which may account for the differential mobilities of ions and accumulation of molecules such as sugars in large amount against concentration gradient.

14.9.2 Fensom and Spanner Electroosmotic Flow Hypothesis

In electroosmosis the ions flow across a membrane in response to electrical gradient. Ions pull along water and other contents because of solvent drag. In this hypothesis it is visualised that sap flows in the lumen of sieve element and electroosmosis occurs across the sieve plate. The basic idea of this model is represented in Fig. 14.16. The pores of sieve are negatively charged and many positive ions are associated with them. The companion cells of consecutive sieve elements are shown to be engaged in K^+ uptake and release. This generates a (K^+) gradient in the direction of phloem sap flux; the fluxes of other solutes are coupled to K^+ flux and move alongwith the electroosmotic flow from one sieve tube to the next.
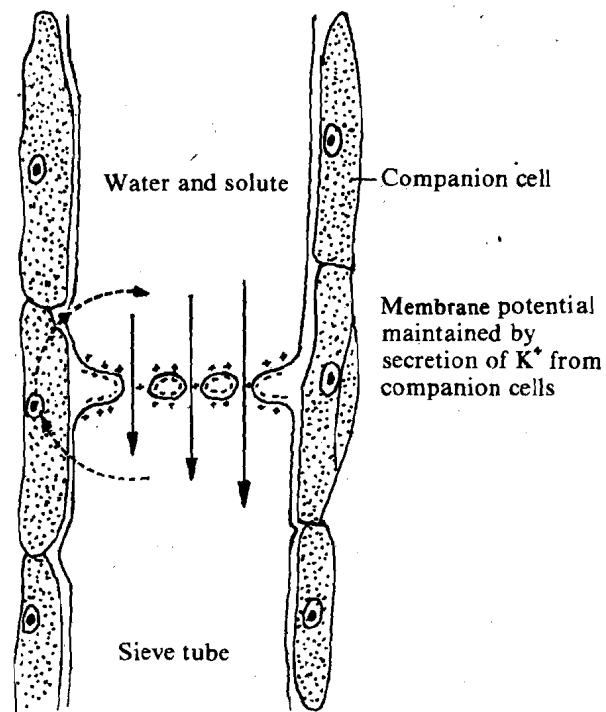
Fig. 14.16 : Active uptake of K^+ by the companion cell from its associated sieve tube on the left and secretion of K^+ into the sieve tube at the right side by its companion cell generate both a potential difference and a K^+ concentration gradient. This causes a flow of K^+ ions and other solutes from right hand side to left.

The model has several advantages over Münch's model. The presence of P-proteins, and the occlusion of sieve plate pores by filaments bearing negative fixed charges are in favour of this model. While these filaments would greatly impede the flow of phloem sap under a pressure gradient, they would make electroosmotic flow more efficient. The negative aspects of this model are:

a) the apparent irrelevance of the source-sink long distance relationship.

b) prohibitively large expenditure of energy (ATP) for K^+ uptake and release by the companion cells and

c) contradiction of the model in respect of anionic fluxes which would be excluded by electroosmosis across channels bearing negative fixed charges.

So long the basic premises of this model are not established by experimental evidences, the model remains an interesting candidate for the mechanism of translocation in phloem.

14.9.3 Protoplasmic Streaming and Tubular Peristaltic Flow Model

The first of the above two models involves the well known phenomenon of cytoplasmic streaming in giant algal cells. Coupling the regular cyclic movement of cytoplasm with active transport across sieve plate pores is thought to lead to a net flux of phloem sap in the direction of sinks. But even the highest estimates of movement by cyclosis are inadequate to explain the observed rates of transport through phloem. The second model is based on the hypothesis of trans-sieve element tubular structures which undergo peristaltic movements similar to the action of our alimentary canal. Both models need experimental support.

14.9.4 Protoosmotic Model

This model as proposed by M.M. Amin (1982), is based on the fact that there exists a metabolically generated pH imbalance between the sinks and the sources. As a rule all cells which use exogenous metabolites and whose metabolism is based on energy derived from respiration generate excess H^+, whereas cells in which photosynthesis and nitrate reduction processes exceed their respiratory activity require uptake of H^+ to maintain the cytoplasm at neutral pH. Thus H^+ flux from sinks (roots) to sources (leaves), is needed (Fig. 14.17). Being a downhill process it provides a source of energy which can be used for phloem transport. The model conceives a long distance translocation of H^+/K^+ antiport process, well known for plant cell membranes. This flux of H^+ from sinks to sources is charge compensated by K^+ Flux (Fig. 14.17). The K^+ flux is electroosmotic in nature which carries other solutes with it (hence named protoosmosis). As against the case of electroosmotic model discussed above, sink-source relationship in exchanging materials as per their metabolic activities is fully incorporated in this model. No experimental evidence has been advanced as yet either to substantiate or refute this model.
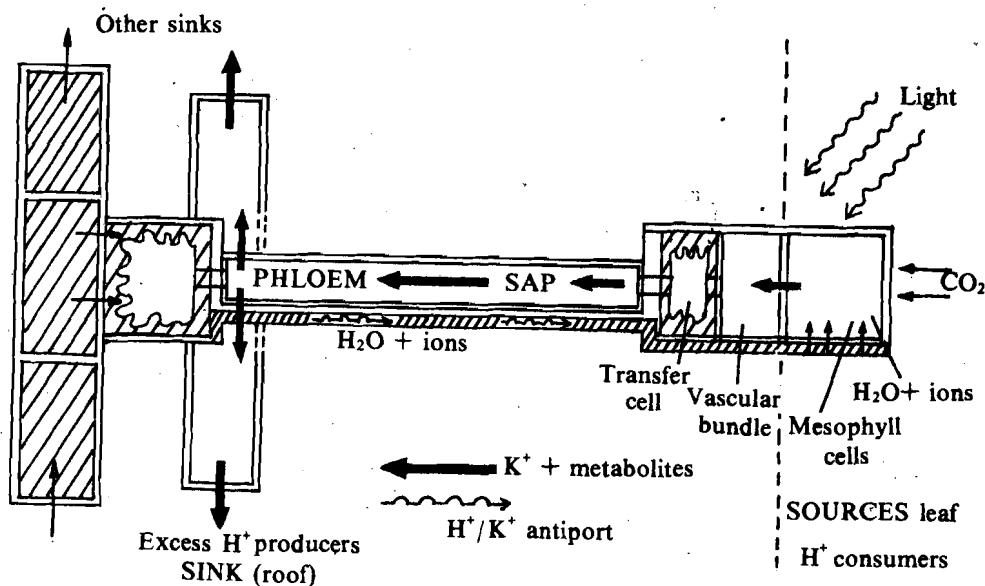
Fig. 14.17 : Proton flux down its gradient from sinks to sources causes K^+ — counter flux in the phloem which is thought to drive metabolites to sinks. The energy for phloem transport is provided by the imbalance in the pH of sources (alkaline) and sinks (acidic), tendencies that arise from their photosynthetic/N-fixing and respiring activities. Potassium ions are recycled in the two vascular systems.

M = Mesophyll, T = Transfer Cell, B = Bundle sheath

Interestingly this model is applicable to radial transport between phloem and xylem. Xylary sap is always acidic while phloem sap is invariably alkaline and rich in K^+. Flux of H^+ from xylem to phloem would in this case bring K^+ and water into xylem by protoosmosis. This would enrich phloem sap (i.e. enhance the concentration of

sugars) as the sap moves towards a sink, e.g. fruit. Indeed tracer experiments have shown this movement of water (tritium) and K^+ from phloem to xylem in a cyclic form : phloem of stem $\rightarrow$ xylem $\rightarrow$ leaf $\rightarrow$ phloem.

SAQ 4

Give one word for each of the statements listed below:

i) Uptake of organic solutes by sieve elements from adjacent parenchyma cells, companion cells or transfer cells.

ii) The movement of ions across a membrane in response to electrical gradient that pulls along water and other contents because of solvent drag.

iii) The flow of solute from source to sink due to pressure gradient.

iv) The flux of proton down its gradient from sink to source and counter flux of K^+ from source to sink to drive metabolites to sink.

14.10   SUMMARY

In this unit you have learnt that :

● Plants need extensive plumbing network to transport organic material, primarily the products of photosynthesis from the sites where they are synthesised to the sites where they are consumed or stored.

● This transport is carried out through a network of phloem tissue that extends from roots through the stem to the very tip of each and every leaf.

● The sites or the parts of plant from which the organic materials are transported are called the sources and the sites or parts of the plant its receiving the material from the source are called the sinks. A one-time source can also become sink depending on the need of the plant.

● The sieve tube elements are joined together by cytoplasmic connections through holes in the sieve plate, thus forming continuous cytoplasmic channels called sieve tubes.

● Experimental studies show that organic materials move through sieve-tubes.

● The location and special structure of companion cells suggest that they support translocation.

● Transfer cells are modified companion cells. Their convoluted plasma membrane and numerous plasmodesmata are perhaps for increasing the area of loading material in the sieve tubes.

● Phloem sap contains mainly sucrose, amino acids and potassium ions. Some other ions and organic acids are also present.

● The mechanism of phloem transport is poorly understood. According to Münch pressure-flow hypothesis water enters in sieve tube elements by osmosis and creates hydrostatic pressure which pushes the phloem contents from one cell to the next.

● Electroosmotic model visualises the flow of material due to electrical gradient created by uptake and release of K^+ ions by consecutive sieve elements.

● Protoosmotic model proposes a continuous flux of H^+ ions from sink to source compensated by K^+ flux from source to sink. The counter flux of K^+ is thought to drive metabolites to sink.

14.11   TERMINAL QUESTIONS

1) Compare vessels and tracheids of xylem with sieve tube members of phloem.

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2) Why is the phenomenon of translocation of food in sieve element a difficult process to study?

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3) Phloem sap can be collected for the analysis by making incision in the bark. However, the collection of sap by Aphid method is considered to be superior. Why?

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4) Why is cyclosis or diffusion cannot account for the transport of organic solutes in a plant?

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14.12 ANSWERS

Self-assessment Questions

1) i) photosynthesis, nitrogen   ii) xylem, phloem   iii) Sieve tube elements
   iv) source, sink   v) source, sink

2) a) i) b,   ii) d,   iii) a,   iv) c
   b) i) T,   ii) F,   iii) T,   iv) T,   v) F,   vi) F

3) i) amino acid   ii) K^+ iii) Nitrate   iv) autoradiography

4) i) loading   ii) electroosmosis   iii) Munch pressure flow hypothesis
   iv) protoosmotic hypothesis

Terminal Questions

1) Xylem vessels are dead cellulose pipes running through the plant. They form part of apoplastic route whereas the sieve-tubes of phloem are living cytoplasmic channels forming symplasm. Water and mineral ions are tansported through xylem vessels and trachieds, whereas photoassimilates, organic solutes including hormones are translocated through sieve-tubes of phloem.

2) Transport in phloem is difficult to study because the cells involved are very delicate and get easily damaged. When phloem cells are injured, beaded chains of P-protein filaments are formed. Besides a slimy plug of callose develops in each plate pore.

3) Collection of phloem sap does not provide selective sampling of the sieve tube contents, since the phloem contains numerous other cells. Whereas, aphid method provides only sieve tube sap because the stylets are inserted in a single sieve tube element.

4) The observed rates of phloem transport are much higher than the rates that can possibly be achieved by cyclosis or diffusion.

GLOSSARY

Adhesion : The tendency for one substance to cling to another substance due to intermolecular forces.

Bacteriochlorophyll : A type of chlorophyll, occurring in forms a and b, found in photosynthetic bacteria.

Bark : All tissues outside the vascular cambium; in old trees, divided into inner living bark (functional secondary phloem) and dead outer bark.

Bundle sheath : One or more layers of cells surrounding a vascular bundle.

Callose : A complex carbohydrate (1, 3-linked glucan) associated with the pores of sieve tube members, pollen grains, pollen tubes, and primary walls of many living cells.

Capillary water : That portion of soil water that is held in pores of the soil by capillarity.

Carotenoid : Any of a group of fat-soluble, yellow, orange, red, or purple pigments widely distributed among plants. They are subclassified into two groups, carotenes and xanthophylls.

Cell wall : The non-living layer that encloses the plant protoplast, is composed of cellulose, hemicellulose, pectin, lignin, and other substances and consists of a primary cell wall (the outer wall deposited during cell expansion) and a secondary wall (the inner wall layer(s) deposited after expansion has ceased).

Chlorosis : Decreased chlorophyll content due to its loss or reduced production.

Cohesion : The tendency of molecules of the same substance to cling to one another due to intermolecular forces.

Cutin : The fatty layer of cutin on the outer wall of epidermal cells.

Cyclic phosphorylation : ATP synthesis associated with electron transport in a cyclic fashion in photosystem I of chloroplasts.

Cyclosis : The movement of cytoplasm within cells. Also called cytoplasmic streaming.

Dry land farming : Type of agricultural operation involving deep cultivation of the soil to form a sufficient reservoir for the moisture as it falls, surface cultivation to prevent or reduce evaporation.

Electrophoresis : A procedure by which mixture of charged compounds (such as proteins) can be separated in an electrical field on a matrix such as starch gel.

Emerson effect : The experimental olservation made by Robert Emerson in 1957 that photosynthetic efficiency is enhanced in the presence of long wavelength red light when that light is supplemented with shorter wavelength than red light.

Epinasty : Curling and overgrowth of leaves on their upper sides as a result of auxin and ethylene applications.

Field capacity : A measure of the water-holding capacity of the soil; soil water content (per cent by weight) after saturating soil with water and allowing gravitational runoff.

Fixation : The incorporation of components of free gas into organic materials. In photosynthesis, the carbon of carbon dioxide is fixed into carbohydrate. In nitrogen fixation, gaseous nitrogen is fixed into ammonia and eventually carbon compounds.

Freeze-fracture : A technique for preparing material for viewing under the electron microscope in which the specimen is frozen and then fractured with a cutting blade often causing membranes to split down the middle revealing internal components.

Gravitational water : That component of water added to the soil which is lost by runoff under the force of gravity.

Guttation : The secretion of liquid water from hydathodes, along the edge and tip of a leaf.

Humus : A complex mixture of colloidal matter in the soil composed of those fractions of the organic matter of plants, animals, and microoganisms that are most resistant to degradation.

Hygroscopic water : The component of soil water that is held by adsorption to the surface of soil particles and is not available to plants.

Lignin : A complex polymer, made up of coniferyl, sinapyl, or p-coumaryl alcohols, which becomes associated with cellulose in primary and secondary cell walls, especially in secondary xylem, and gives strength to the cell wall.

Mass spectrometer : An apparatus for obtaining the mass spectrum of a beam of ions by means of suitably disposed magnetic and electric fields.

Middle lamella : The layer of cementing substance between the primary walls of adjacent cells.

Monochromatic : Having one colour or wavelength only.

Necrosis : Death of a cell or group of cells as a result of injury, disease, or nutrient deficiency.

Net photosynthesis : Photosynthetic carbon fixation minus the carbon released as carbon dioxide by processes such as respiration.

P_{680} : A special molecule of chlorophyll a that accepts energy from the light-harvesting pigments of photosystem II and transfers it by loss of a high-energy electron to an electron acceptor.

P_{700} : A special molecule of chlorophyll a that accepts energy from the light-harvesting pigments of photosystem I and transfers it by loss of a high-energy electron to an electron acceptor.

Parthenocarpy : The development of a fruit in the absence of fertilization.

Parthenogenesis : The development of an egg without fertilization. The production of an organism from an unfertilized egg.

Pectin : A cell wall polymer made of β-1, 4-linked galacturonic acid residues with the carboxyl groups esterified with methanol, rhamnogalacturonan (rhamnose and galactose), and arabinogalactan (arabinose and galactose).

Photoreceptor : Light sensitive spot; eye of vertebrate.

Photosystem : One of two interacting energy-collecting and energy-transferring systems that operate in chloroplasts.

Phycocyanin : Any of several blue, water-soluble protein pigments present in most blue-green algae.

Phycoerythrin : Any of several water-insoluble red protein pigments present in most blue-green algae and all red algae.

Quantum : A discrete unit of electromagnetic energy. An entity having particle like properties. With reference to light, the amount of energy associated with one particle like unit or photon.

Sieve plate : A region of the cell wall of a sieve tube member where pores are concentrated.

Sieve tube: A column of sieve tube members that functions in the transport of organic solutes in the phloem of angiosperms.

Sieve tube member : An elongated cell with pores on its end walls.

Stomatal apparatus : A pair of guard cells and associated subsidiary cells involved in the opening and closing of the pore between the guard cells.

Stroma : The fluid substance within an organelle, such as a plastid. In fungi, a large mass of somatic (vegetative) hyphal tissue.

Thylakoid : A photosynthetic membrane in chloroplasts of eukaryotic cells. A stack of thylakoids in a chloroplast is called a granum.

Tracheid : An elongated, empty cell of the xylem without perforated walls that is active in longitudinal transport of water and mineral nutrients in vascular plants.

Transfer cell : A parenchyma cell modified with internal extensions of the cell wall that greatly increase the surface of the plasma membrane.

Turgor : The positive hydrostatic pressure that develops within plant cells as a result of osmotic water entry. Also, the distension that results from the pressure.

Ureides : The major derivatives of urea which have been found in nodulated plants are allantoin, allantoic acid and citrulline.

Vessel : A long, hollow series of vessel members connected to each other end-to-end in the xylem that functions in longitudinal transport of water and mineral nutrients in angiosperms and some ferns.

Water potential : A measure of the potential energy of osmotic potential and the pressure potential. A measure of the tendency of water to move away from a given location.

Water use efficiency : The ratio of organic material produced by a plant to water utilized (including water taken up from the soil and lost by transpiration).

Wilting : Drooping of leaves or other plant parts due to decreased turgor within the cells as a result of excess water loss by transpiration.

FURTHER READING

1) Noggle, G. Ray and Fritz, George J. *Plant Physiology*, 2nd edition, 1989, Prentice-Hall of India Pvt., New Delhi.

2) Devlin, Robert M. and Witham Francis H. *Plant Physiology*, 4th edition, 1986, CBS Publishers, Delhi.

3) Salisbury, Frank B. and Ross, Cleon W. *Plant Physiology*, 4th edition, 1989, CBS Publishers, Delhi.

Dear Student,

While studying these units you may have found certain portions of the text difficult to comprehend. We wish to know your difficulties and suggestions, in order to improve the course. Therefore, we request you to fill and send us the following questionnaire, which pertains to this block.

QUESTIONNAIRE

LSE-05
Block-3

Enrolment No.

1) How may hours did you need for studying the units?

Unit Number					
No. of Hours					

2) How many hours (approximately) did you take to do the assignments pertaining to this block?

Assignment Number		
No. of Hours		

3) In the following table we have listed 4 kinds of difficulties that we thought you might have come across. Kindly tick (√) the type of difficulty and give the relevant page number in the appropriate columns.

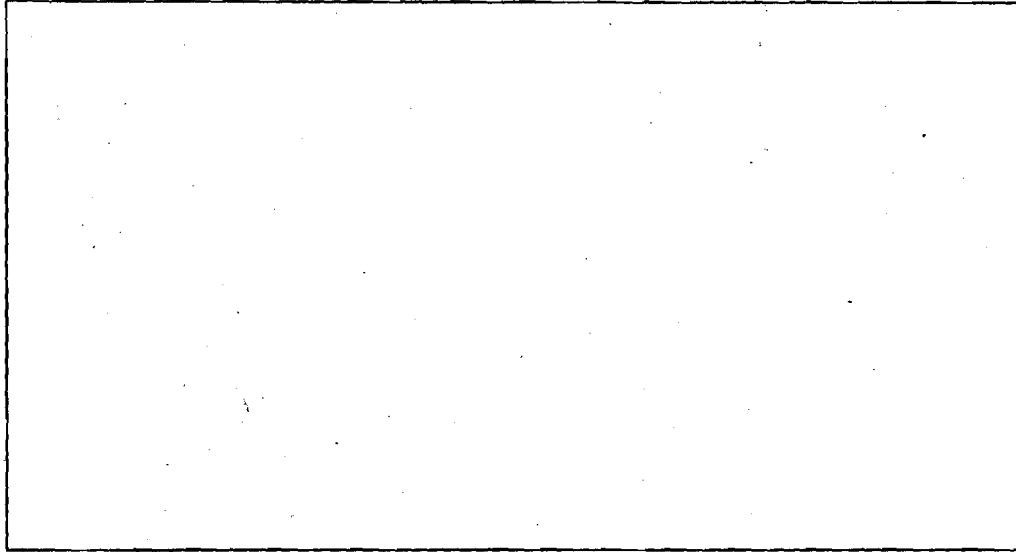| Page Number	Types of difficulties			
	Presentation is not clear	Language is difficult	Diagram is not clear	Terms are not explained

4) It is possible that you could not attempt some SAQs and TQs.
In the following table are listed the possible difficulties. Kindly tick (√) the type of difficulty and the relevant unit and question numbers in the appropriate columns.

Unit No.	SAQ No.	TQ No.	Type of difficulty			
			Not clearly posed	Cannot answer on basis of information given	Answer given (at end of Unit) not clear	Answer given is not sufficient

5) Were all the difficult terms included in the glossary? If not, please list in the space given below.

6) Any other suggestion(s):

To,

The Course Coordinator (LSE-05, Physiology)
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