



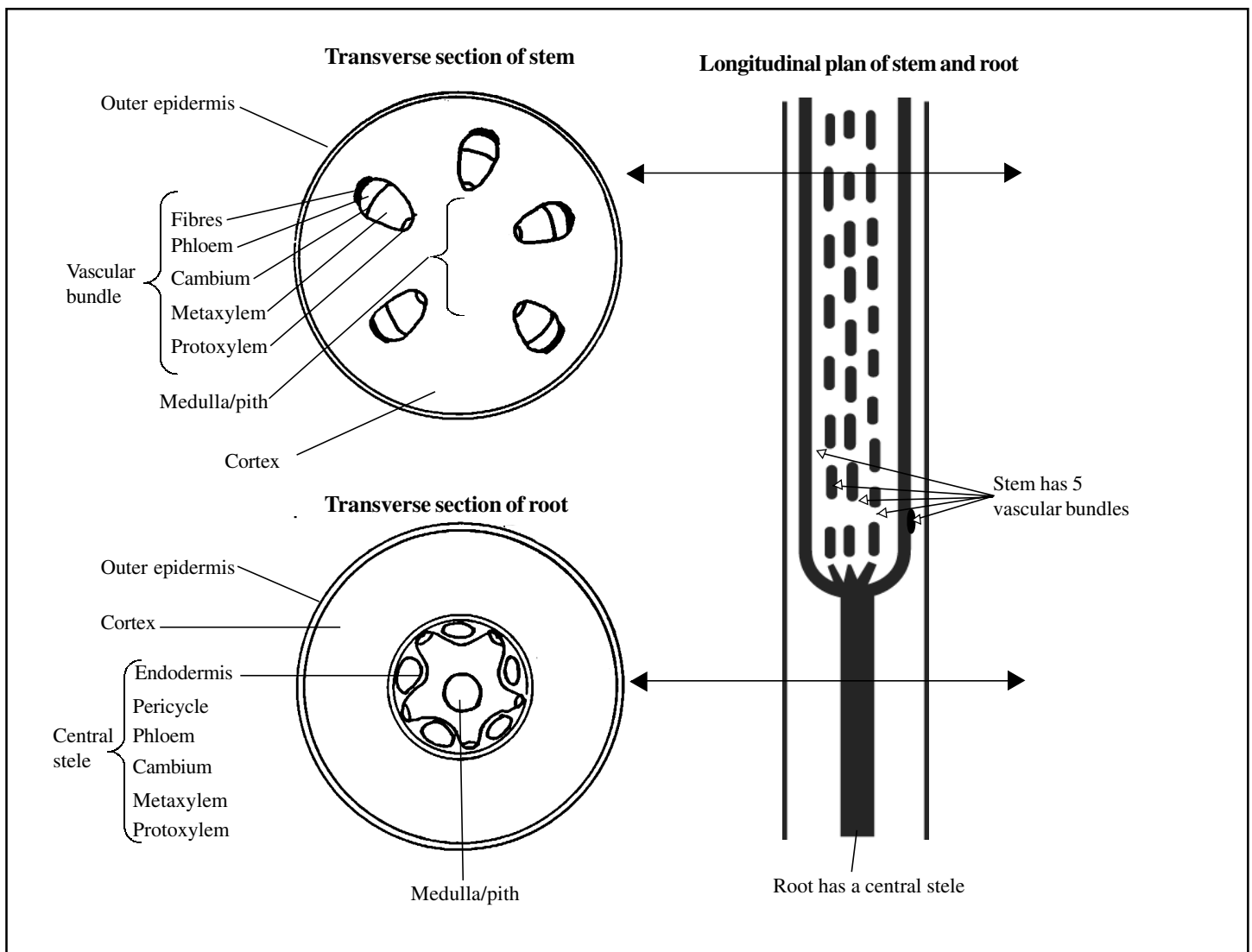
Tracheids, Vessels and Sieve Tubes

Tracheids, vessels and sieve tubes are found in the **vascular tissue** of the plant.

- Tracheids and vessels are found in the **xylem** tissue and conduct water and dissolved mineral ions from the roots to the aerial parts of the plant.
- Sieve tubes are found in the **phloem** tissue and conduct organic solutes, for example, sugars and amino acids, up and down the plant, from where they are synthesised to where they are required.

Xylem and phloem are characteristic of the higher plants called Tracheophytes, which include ferns, conifers and flowering plants. Lower plants such as liverworts and mosses do not develop xylem or phloem. The special water conducting cell known as the tracheid is characteristic of the xylem tissue in ferns and conifers. In flowering plants, although some tracheids may be present, a more specialised system of water conducting xylem vessels has evolved.

Fig 1. Distribution of vascular tissue in stem and root of a dicotyledonous flowering plant, for example, buttercup

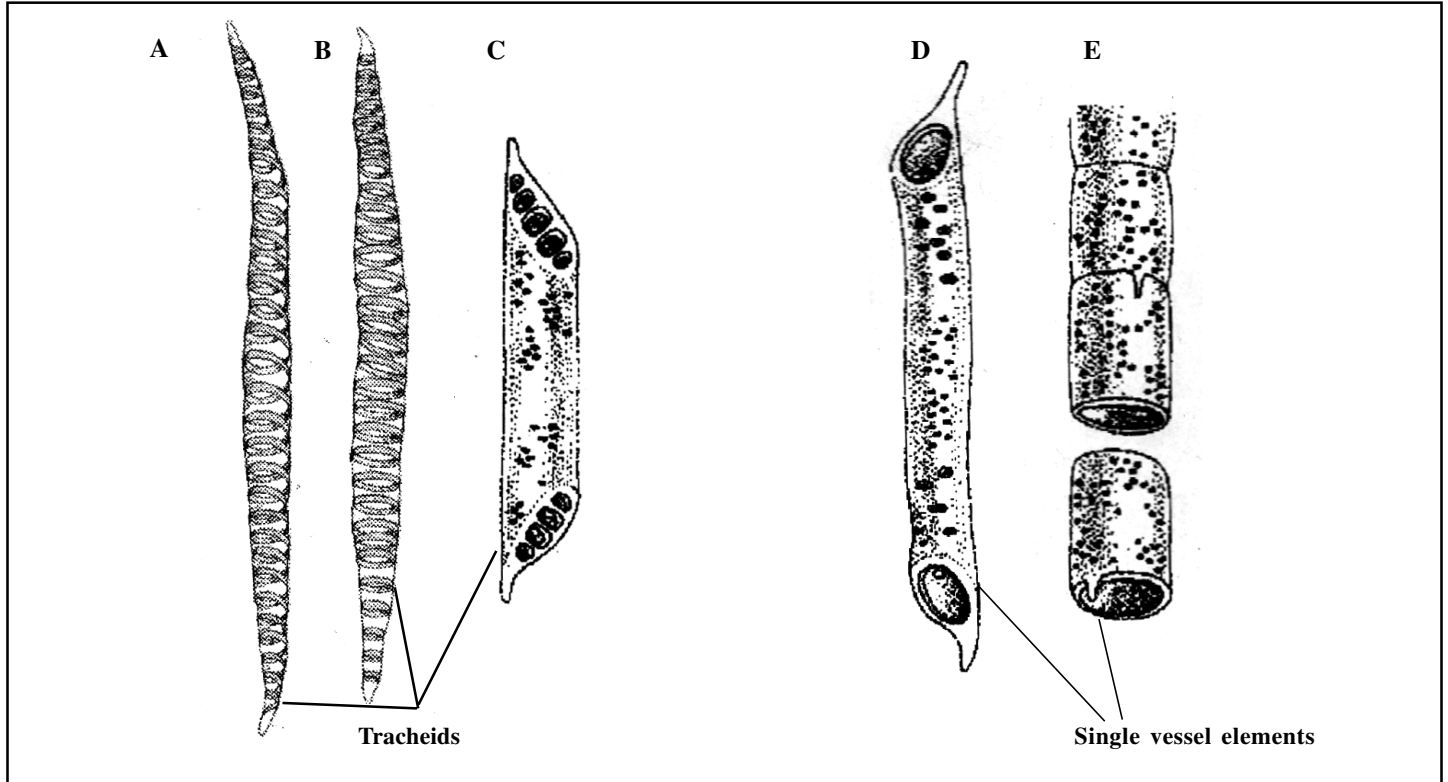


- Protoxylem is the first to differentiate and has a structure, which although suitable for conducting water and dissolved minerals up the plant, enables the growing plant to still elongate.
- Metaxylem develops later and in greater bulk than protoxylem. It will not allow further elongation of the plant, but besides being adapted to transport water and minerals it also has a mechanical strengthening and supporting function in the plant.
- Fibres are additional elongated, lignified (see below) cells which provide extra strength and stability to the stem and to the soft phloem tissue in particular. The pericycle in many roots is also made up of fibres.
- Cambium consists of cells that can divide by mitosis and then differentiate into extra xylem and phloem tissue. This happens in plants (trees) that become woody and is referred to as 'secondary growth'.

Development of Xylem

Xylem (and phloem) develop first in the zone of differentiation behind the apical meristems (growing points). Xylem develops from undifferentiated living plant cells which have cellulose walls. The cells become **elongated** and their walls become impregnated with **lignin**.

Lignin is a complex non-carbohydrate polymer which is laid down on the primary cellulose walls of the water-transporting cells and tubes of xylem. The process is called **lignification** and because lignin is impermeable the contents of lignified cells die, leaving hollow tubes for water transport.

Fig 2. Types of xylem water-conducting elements

A and B: These cells are tracheids because their ends are not yet perforated with one large hole. These primitive tracheids are characteristic of the protoxylem of conifers, and the lignin is laid down in rings (annular thickening) or in a spiral (spiral thickening). This enables further elongation of the stem or root during growth. If the lignin was laid down in a solid fashion it would prevent elongation. The water and dissolved salts can pass from cell to cell through the non-lignified areas of the wall, particularly at the non-lignified tapering ends.

Protoxylem vessels in flowering plants also have annular and spiral thickening.

C: This is a more advanced type of tracheid, characteristic of the metaxylem of conifers. This type of cell may also be found dispersed amongst the vessels in the xylem of some flowering plants. The lignin is laid down in a solid mass, but has pits which align with pits on adjacent tracheids to allow lateral transport of water. The end walls are perforated with several large holes to allow easy passage of water upwards, from tracheid to tracheid.

D and E: D is a single vessel element. The end wall has completely perforated so that water can easily pass up the vessel. E shows a vessel in which several vessel elements are joined end to end. Such a vessel may contain hundreds of vessel elements and stretch from the roots to the leaves of a tall tree. Vessels of this sort are characteristic of the metaxylem and secondary xylem (wood) of flowering plants.

Mechanism of water movement up the xylem of a tall plant

The stream of water (and dissolved salts) which passes up the xylem from the water absorbing areas of the root to the leaves is called the **transpiration stream**.

The transpiration stream in tall plants is unique in that it flows uphill. The force of gravity is overcome by strong forces caused in the leaves by **transpiration**. This process is driven by heat from the Sun, which causes water on the external surfaces of the mesophyll cells to evaporate, forming water vapour, which diffuses from the leaves, mainly via stomata. The loss of water from a mesophyll cell lowers the water potential of that cell causing water to move into the mesophyll cell, by osmosis, from an adjacent cell. Thus a water potential gradient becomes established, causing water to be drawn from the xylem into the mesophyll cells.

The continuous, unbroken column of water in the xylem vessels, from the deepest roots to the highest shoot tips, is thought to be maintained by **cohesion and adhesion**.

- Water has unique **cohesive** properties, by which hydrogen bonds between water molecules hold the water molecules together, giving the water column high tensile strength. This prevents the water column from breaking apart as it is pulled upwards. The loss of water from the xylem to the mesophyll creates a pulling force (**tension**) in the water column. The tension is transmitted all the way down to the roots, maintaining the integrity of the entire water column.
- **Adhesion**, which is a force of attraction between unlike molecules, occurs between the water molecules and the lignified walls of the xylem vessels. This force prevents the water column from slipping back down towards gravity. Therefore, by a combination of tension, cohesion, and adhesion, water moves up the stem.

Remember – atmospheric pressure will help to support the column of water in the xylem. However, a pressure of 1 atmosphere at sea level will only support a column of water 10.4 metres high. Some trees reach a height of around 120 metres and so, if relying on atmospheric pressure, would need a pressure of around 11.5 atmospheres to maintain the water column in the xylem. Thus cohesion and adhesion are of paramount importance.

As water is drawn up the xylem, by the transpiration pull, it is replaced because water is drawn into the xylem from the cortex cells of the root. This maintains a water potential gradient across the root cortex to the root hairs and causes the root hairs to absorb more water from the soil solution.

Exam Hint: Candidates sometimes refer to the sum of the forces interacting to hold water in the xylem tubes is as **capillarity**. This is not quite true. Capillarity is a force that will hold a column of water in a narrow glass tube which has water compatible (hydrophilic) surfaces. Although capillarity may aid support of the water column in small herbaceous plants it is not great enough to support a column of water the height of a tree.

Remember: that xylem tubes need to be narrow so that forces of adhesion, cohesion, tension and capillarity are great relative to the small water volume but need to be wide enough to carry the volumes of water required. This is why xylem tends to contain many small vessels rather than a few large ones.

Another force, not completely understood, involved in water transport up the xylem is **root pressure**. This force rarely exceeds 2 atmospheres and so can only support a water column of up to a metre. The pushing force requires ATP and apparently originates from active transport mechanisms transferring ions from root cortex to xylem across the pericycle and endodermis.

Structure of phloem tissue

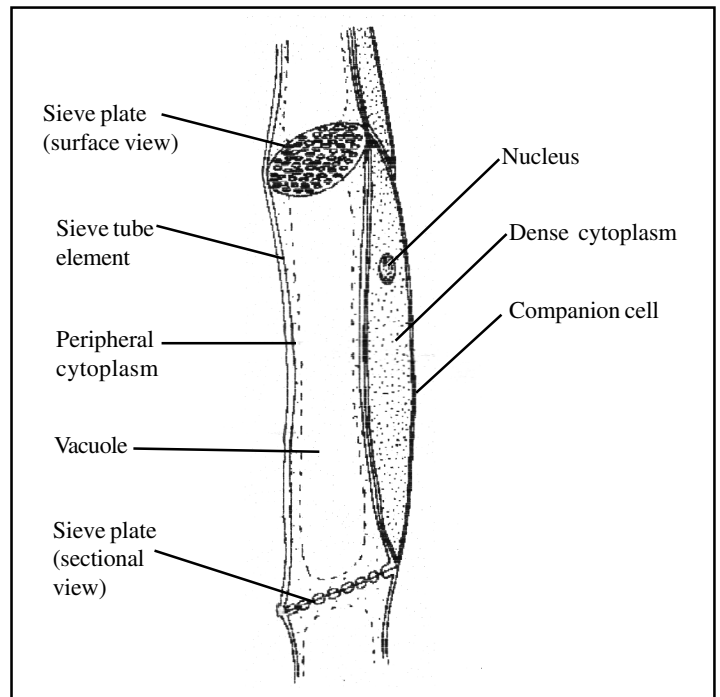
The main structures found in phloem are **sieve tubes** and **companion cells**. Each sieve tube is a cylindrical column of sieve tube elements, joined end to end.

- Each sieve tube is a cylindrical column of **sieve tube elements** joined end to end. The end walls are perforated by pores, through which pass enlarged **plasmodesmata** (cytoplasmic strands passing through the cell walls), forming structures called **sieve plates**, so called because they look like a sieve. When maturing, a sieve tube element loses its nucleus and its cytoplasm becomes pushed to the sides of the cell. Sieve tube elements are kept alive and supported in their function by **companion cells**.
- A typical companion cell has dense cytoplasm containing the normal organelles, but it has an unusually thin cellulosic cell wall and a vacuole, is usually absent. Companion cells have a very high number of mitochondria, indicating that they have a high metabolic rate. Companion cells are closely connected to sieve tube elements via numerous plasmodesmata.

A sieve tube and its companion cells forms a functional unit for **translocation** of organic solutes in the phloem. Sieve tubes will not work without their companion cells. A sieve tubes may consist of hundreds of sieve tube elements and stretch from the leaves to the roots or stem tips or flowers.

In deciduous trees the phloem sieve plates become blocked with callose just prior to leaf fall. Thus the phloem becomes inoperative during the dormant, unfavourable, leafless seasons.

Fig 3. Longitudinal section of a sieve tube element and its companion cell



Translocation of organic solutes in the phloem

The solution carried in the phloem is called **sap**. It contains organic solutes, for example, the disaccharide sucrose, amino acids, plant growth substances and some inorganic salts which have been transferred from the xylem.

The solutes are translocated (carried) from their **sources**, where they are made, to the **sinks**, where they are used. The photosynthetic leaves are the main sources and the growing regions are the main sinks. Storage areas, for example potato or dahlia tubers, act as sinks when the substances brought to them are stored and act as sources when the stored substances are broken down and the products released for use elsewhere in the plant.

Sucrose reaching the storage areas is hydrolysed to glucose and fructose, the fructose is then isomerised to glucose and the glucose is polymerised to the storage polysaccharide, starch. When glucose is required the starch can be broken down to release glucose into the phloem.

Translocation has been experimentally studied in three main ways:-

- **Ringing experiments.** A complete ring of bark, which includes the phloem but not the xylem, is removed from a woody stem. The tissue above the ring swells but the tissue beneath the ring withers. Chemical analysis of the fluid in the swollen tissue shows high concentrations of sugars and other organic solutes, but the tissue beneath the ring is deprived of nutrients, because the removal of the phloem impedes the downward flow of organic solutes. Water and salts can still pass upwards past the ring because the xylem tissue is intact.
- **Sap-sucking aphids.** Aphids feed on the phloem sap by piercing the phloem sieve tubes with their needle-like mouthparts (stylets). If the head of a feeding aphid is detached from the mouthparts, sap continues to exude from the stylet end. The flow can continue for days and the sap can be collected and analyzed. The closer the stylet is to a sugar source (photosynthesizing leaves or starch store) the higher the sugar content of the collected sap and the greater the rate of sap seepage from the stylet. This supports the idea that sugar is actively pumped into the sieve tubes at the source end, generating pressure to cause sap flow. If the phloem is treated with a metabolic inhibitor, such as cyanide, the sap flow ceases. This also suggests an active mechanism for phloem sap flow.

- **Radioactive tracers.** The radioactive isotope ^{14}C can be used to label carbon dioxide which is then utilized by the plant in photosynthesis. The movement of the radioactively labelled photosynthetic products, such as sucrose, can be traced through the stem using photographic film, which blackens where it is exposed to radioactivity. These blackened areas correspond to the position of the phloem. The technique is called **autoradiography**.

The techniques described above have yielded the following information about translocation of organic solutes:-

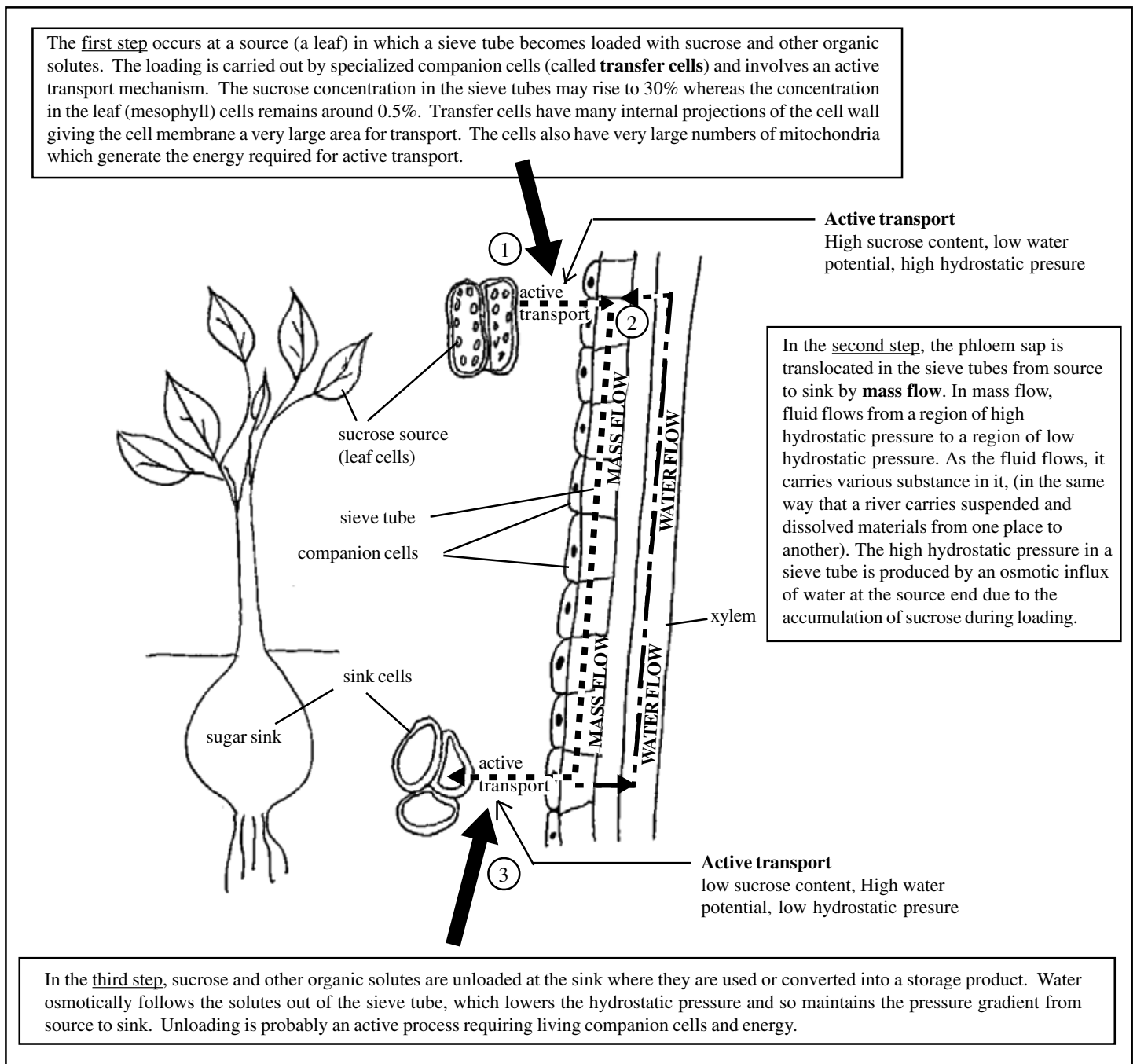
- Translocation takes place mainly in phloem sieve tubes.
- Translocation takes place over large distances.
- It is an active process which only occurs in living tissue.
- It is inhibited by metabolic poisons and lack of oxygen.
- Large quantities of organic substances can be translocated.

- The rate of translocation varies for different organic substances (a distance between 20 and 600 cm travelled per hour).
- Different organic substances can be translocated up and down the plant simultaneously (but probably not in the same sieve tube).
- In temperate plants, an increase in temperature between 10°C and 30°C will increase the rate and amount of translocation.

Translocation does not occur by diffusion because diffusion is too slow to enable the fast rates of translocation or the large quantities translocated. Also, substances that cannot diffuse, for example, viruses, are translocated in the phloem.

The most popular hypothesis used to explain translocation is the **pressure flow hypothesis**. This suggests that translocation involves a combination of active transport and mass flow, and takes place in three steps. These are shown in Fig. 4.

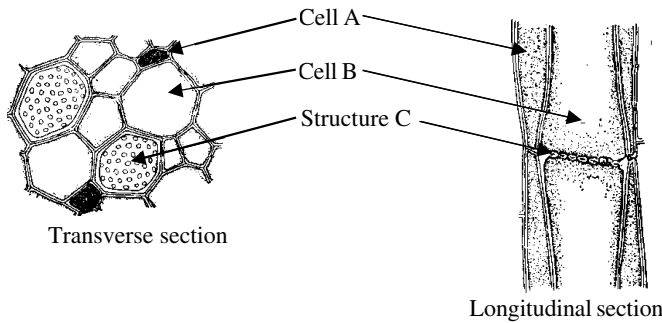
Fig 4. The pressure flow hypothesis



The pressure flow hypothesis is probably only part of the mechanism for phloem transport. For instance, it does not give a role to the sieve plates and does not take into account the cytoplasmic streaming that occurs in sieve tubes.

Practice Questions

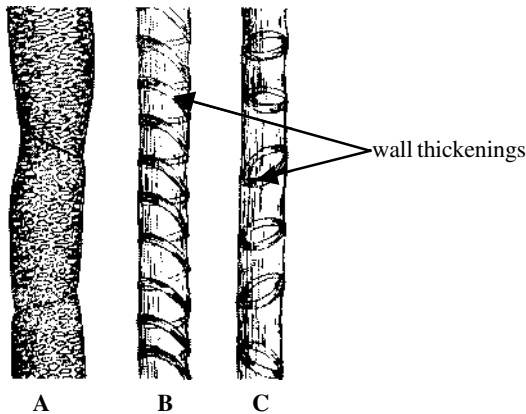
1. The drawings show a plant tissue cut in transverse and longitudinal sections.



- (a) (i) Identify this tissue. 1
 (ii) Name cells A and B and structure C. 3
 (iii) In a deciduous tree what change occurs to structure C just prior to leaf fall? 2
 (b) (i) List three differences in structure between cell A and cell B. 3
 (ii) Outline the 'pressure flow hypothesis' explanation of translocation. 6

Total 15 marks

2. The drawings below show parts of a plant tissue seen in longitudinal view.



- (a) (i) Name the tissue to which these parts belong. 1
 (ii) Name the substance used to thicken the walls and state two of its properties. 3
 (iii) Which of A, B or C are found just behind apical meristems? Explain your answer. 3
 (iv) Are the structures shown vessels or tracheids? Why? 2
 (b) Outline the way in which water is drawn up the plant to the leaves. 6

Total 15 marks

3. Which of the following statements about the 'pressure flow hypothesis' are true?

- A.** The high hydrostatic pressure in a sieve tube is caused by an osmotic influx of water at the sink end.
B. In mass flow water flows from a region of low hydrostatic pressure to a region of high hydrostatic pressure.
C. Active transport is involved in pumping sucrose from source to sieve tube and from sink tube to sieve tube.
D. The high hydrostatic pressure in a sieve tube is caused by an osmotic influx of water at the source end.

4. Suggest reasons why:

- (a) cyanide will inhibit phloem transport, 2
 (b) ringing a plant will inhibit phloem transport but allow xylem transport to continue; 2
 (c) The sap-seepage rate from aphid mouthparts increases the closer the aphids are to the photosynthesizing leaves. 2

Total 6 marks

Answers

1. (a) (i) phloem; 1
 (ii) A = companion cell; B = sieve tube cell; C = sieve plate; 3
 (iii) large plasmodesmata passing through pores; become broken as pores are blocked with callose; 2
 (b) (i) A has a large central vacuole, B has not; A has peripheral cytoplasm, B is full of dense cytoplasm; A has no nucleus, B has; A has few mitochondria, B has many mitochondria; max 3
 (ii) transfer cells load the sieve tube with sucrose at the source end; this causes low water potential in the sieve tube which draws water in osmotically from the xylem; this produces high hydrostatic pressure which pushes sap along the sieve tube/causes mass flow; at the sink end sucrose passes to the sink thus raising the water potential in the sieve tube; thus water leaves the sieve tube thus maintaining the hydrostatic pressure gradient from source to sink; ref to sucrose being moved at source and sink end by active transport; 6

Total 15 marks

2. (a) (i) xylem; 1
 (ii) lignin; impermeable to water and dissolved solutes; mechanically strong; 3
 (iii) B and C; ref annular thickening in C and spiral thickening in B; these types of thickening enable elongation of the stem/proxyloem to lengthen; 3
 (iv) vessels; they have no end walls/open ended; 2
 (b) ref to water drawn from xylem into mesophyll cells which have a low water potential; caused by water loss in transpiration; ref to cohesion of water molecules together tending to keep water column intact; ref to adhesion of water molecules to walls of xylem vessels tending to hold water column up xylem; ref to transpiration pull, cohesion and adhesion producing tension in the xylem water which tends to draw water up from roots to replace that which was lost from leaves; ref to roles of atmospheric pressure/root pressure/capillarity; 6

Total 15 marks

3. **A.** False – water influxes at the source.
B. False – water flows from high to low hydrostatic pressure.
C. True; (sucrose will pass from sink to sieve tube when food reserves in the sink are mobilized)
D. True;

Total 2 marks

4. (a) cyanide is a metabolic inhibitor which will prevent ATP production; mass flow relies on active transport which requires energy from ATP; 2
 (b) ringing removes the bark and the phloem, thus stopping phloem transport; the xylem is to the inside of the phloem and remains intact; 2
 (c) the stylets of the aphids are inserted into the sieve tubes; the hydrostatic pressure in the sieve tubes is greatest near the source/photosynthesizing leaves, due to their high sucrose and water content; 2

Total 6 marks

Acknowledgements:

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