Organic Translocation:

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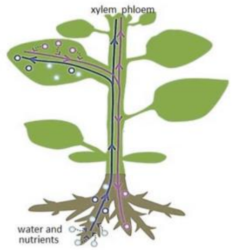
Introduction

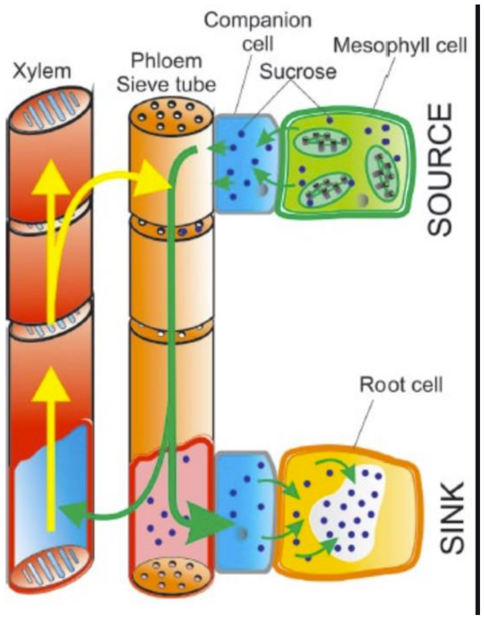
- Plant cells are separated from their environment by a plasma membrane that is only two lipid molecules thick.
- They form a hydrophobic barrier to diffusion.
- But the membrane must facilitate and continuously regulate the inward and outward traffic of selected molecules and ions:
  - The cell takes up nutrients,
  - Exports wastes, and
  - Regulates its turgor pressure.
- The same is true for the internal membranes that separate the various compartments within each cell.
- The cell's only contact with its surroundings is the plasma membrane
- It must also relay information
  - About its physical environment,
  - About molecular signals from other cells, and
  - About the presence of invading pathogens.



Transportation in plants

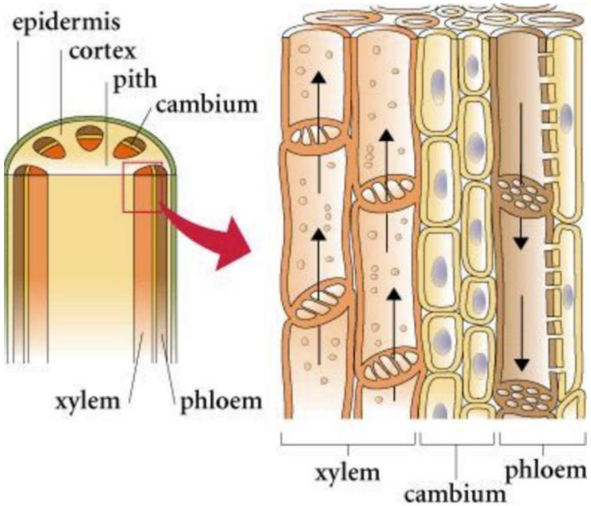
- Often these signal transduction processes are mediated by changes in ion fluxes across the membrane.
- Molecular and ionic movement from one location to another is known as **transport**.

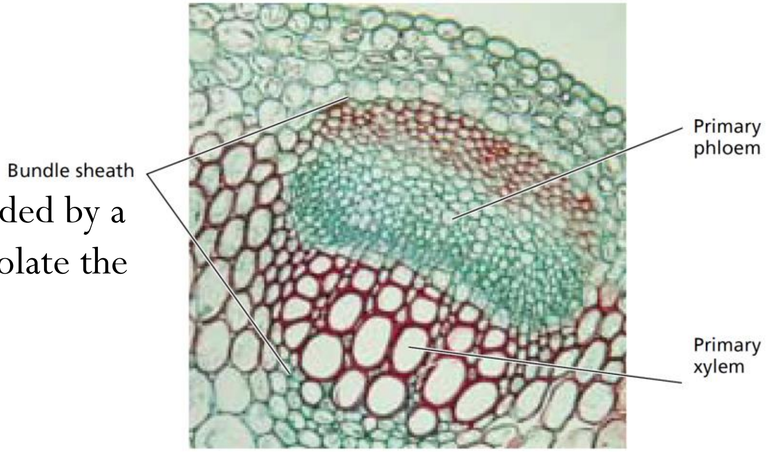
- Local transport of solutes into or within cells is regulated mainly by membranes.
- Larger-scale transport between plant and environment, or between leaves and roots, is also controlled by membrane transport at the cellular level.
- The transport of sucrose from leaf to root through the phloem, referred to as ***translocation***.
- Translocation is driven and regulated by membrane transport **into** the phloem cells of the **leaf**, and **from** the phloem to the storage cells of the **root**.
- The xylem: transports water and minerals from the root system to the aerial portions of the plant.
- The phloem: translocates the products of photosynthesis from mature leaves to areas of growth and storage, including the roots.



Pathways of Translocation

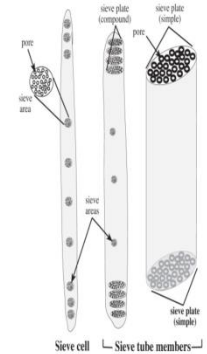
- The two long-distance transport pathways extend throughout the plant body
  - The xylem.
  - The phloem
- The phloem is generally found on the outer side of both primary and secondary vascular tissues.
- In plants with secondary growth the phloem constitutes the inner bark.
- Transverse section of a vascular bundle of trefoil, a clover (*Trifolium*).
  - The primary phloem is toward the outside of the stem.
  - Both the primary phloem and the primary xylem are surrounded by a **bundle sheath** of thick-walled sclerenchyma cells, which isolate the vascular tissue from the ground tissue.

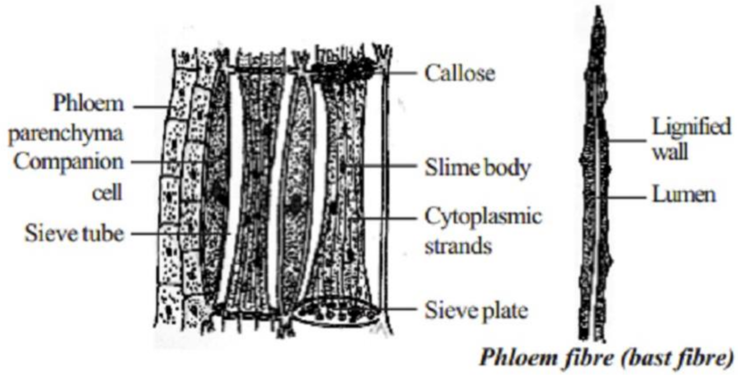




The cells of the phloem

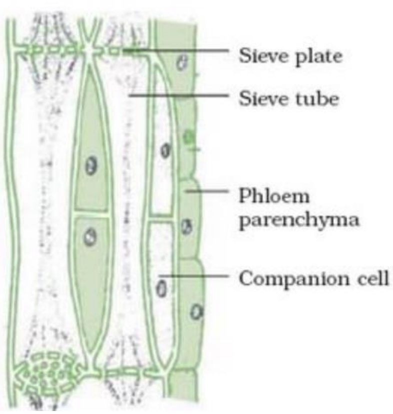
- The cells of the phloem that conduct sugars and other organic materials throughout the plant are called **sieve elements**.
- Sieve elements are typically elongate cells which bear sieve areas on their walls which contain pores through which pass cytoplasmic connections with adjacent cells.
- Sieve element includes both:
  - The highly differentiated sieve tube elements (the angiosperms) and
  - The relatively unspecialized sieve cells (gymnosperms).
- In addition to sieve elements, the phloem tissue contains:
  - Companion cells and
  - Parenchyma cells (which store and release food molecules).
- In some cases the phloem tissue also includes
  - Fibers
  - Sclereids (for protection and strengthening of the tissue) and
  - Laticifers (latex-containing cells).
- Only the sieve elements are directly involved in translocation.
- The small veins of leaves and the primary vascular bundles of stems are often surrounded by a **bundle sheath.**
- In the vascular tissue of leaves, the bundle sheath surrounds the small veins all the way to their ends, isolating the veins from the intercellular spaces of the leaf.





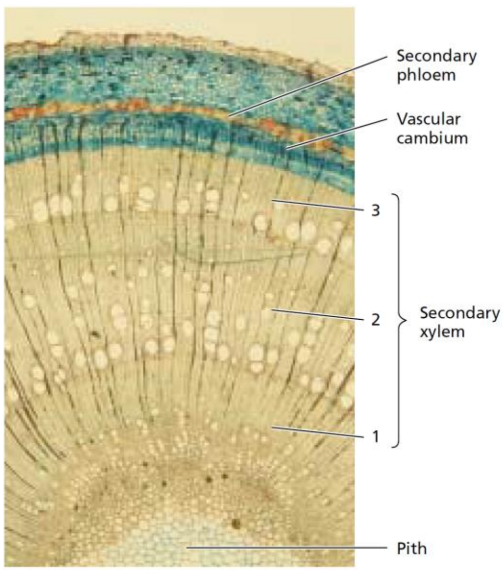
Phloem fibre (bast fibre)

Phloem tissue

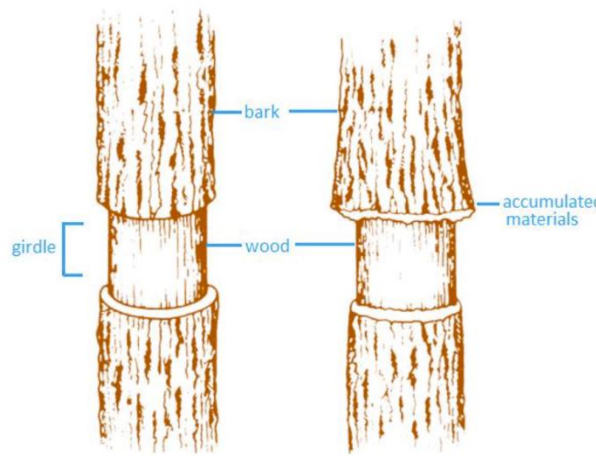


Sugar Is Translocated in Phloem Sieve Elements

- Early experiments on phloem transport demonstrated that removal of a ring of bark around the trunk of a tree, which removes the phloem, effectively stops sugar transport from the leaves to the roots without altering water transport through the xylem.
- Radioactive compounds (radiolabeled $^{14}CO_2$) were used: Showed that sugars made in the photosynthetic process are translocated through the phloem sieve elements.



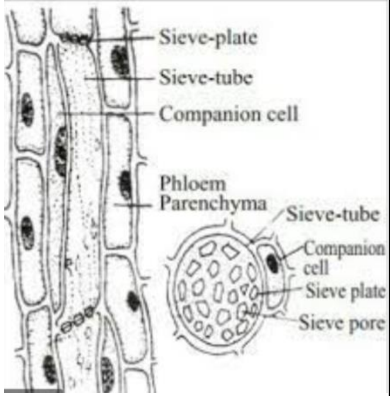
Transverse section of a 3-year-old stem of an ash (*Fraxinus excelsior*) tree.



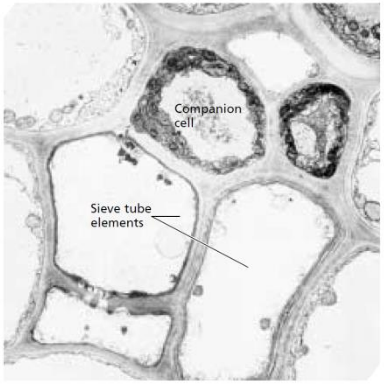
Girdling experiment

Mature Sieve Elements Are Specialized for Translocation

- Mature sieve elements are unique among living plant cells.
- They lack many structures normally found in living cells.
  - Sieve elements lose their nuclei and tonoplasts (vacuolar membrane) during development.
  - Microfilaments, microtubules, Golgi bodies, and ribosomes are also absent from the mature cells.
  - In addition to the plasma membrane, organelles include modified mitochondria, plastids, and smooth endoplasmic reticulum.
  - The walls are non-lignified, though they are secondarily thickened in some cases.



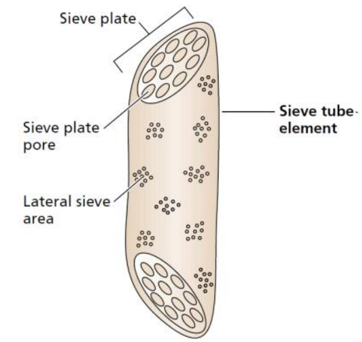
- Sieve elements are different from that of tracheary elements of the xylem:
  - They are dead at maturity,
  - They lack a plasma membrane, and
  - They have lignified secondary walls.
- Sieve elements are different from living cells are critical to the mechanism of translocation in the phloem.

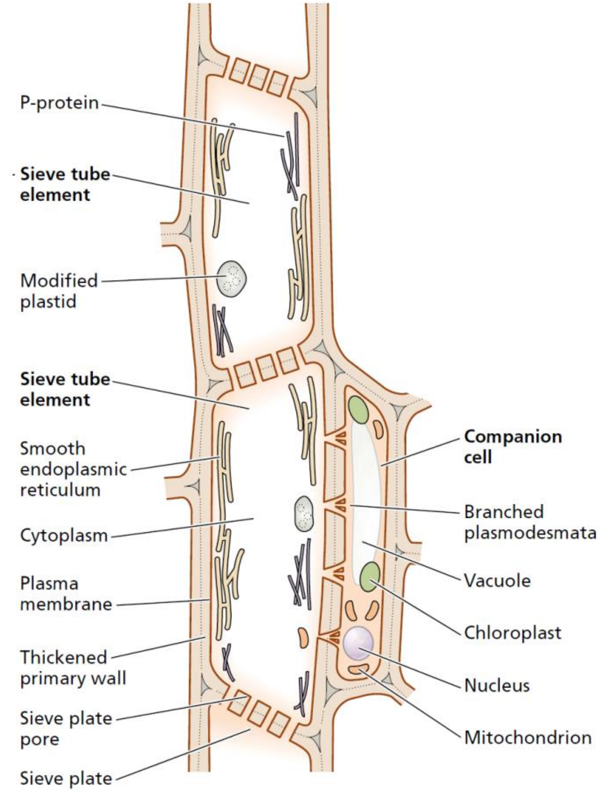


- Electron micrograph of a transverse section of companion cells and mature sieve tube elements:
  - Shows cellular components are distributed along the walls of the sieve tube element

Mature sieve elements (sieve tube elements)

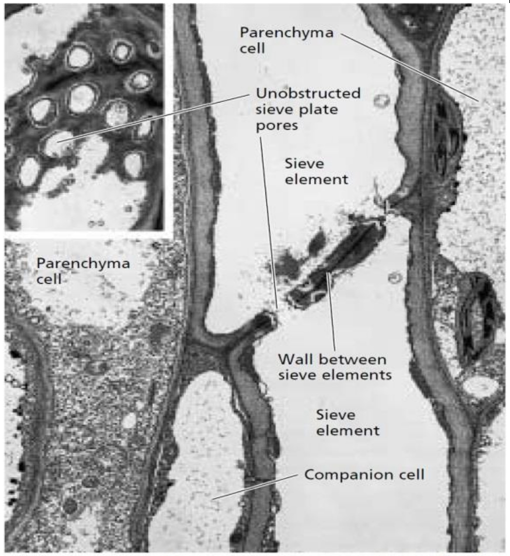
- External view: shows sieve plates and lateral sieve areas.
- Longitudinal section:
  - Two sieve tube elements joined together to form a sieve tube.
  - The pores in the sieve plates between the sieve tube elements are open channels for transport through the sieve tube.
  - The plasma membrane of a sieve tube element is continuous with that of its neighboring sieve tube element.
  - Each sieve tube element is associated with one or more companion cells, which take over some of the essential metabolic functions that are reduced or lost during differentiation of the sieve tube elements.
  - The companion cell has many cytoplasmic organelles, whereas the sieve tube element has relatively few organelles.
- The cellular components are distributed along the walls of the sieve tube elements



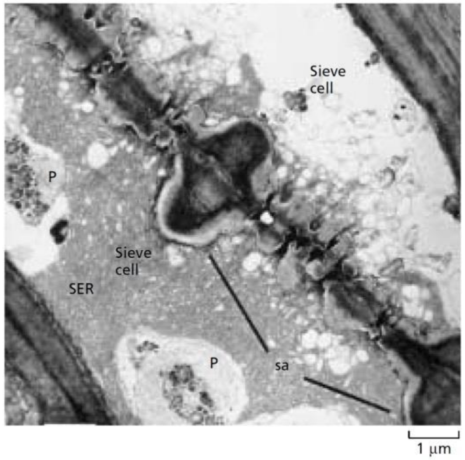


Sieve Areas Are the Prominent Feature of Sieve Elements

- Sieve elements (sieve cells and sieve tube elements) have characteristic sieve areas in their cell walls, where pores interconnect the conducting cells.
- The sieve area pores range in diameter from less than 1 μm to approximately 15 μm.
- Unlike sieve areas of gymnosperms, the sieve areas of angiosperms can differentiate into sieve plates.
- **Sieve tube elements found in angiosperms:**
  - Some sieve areas are differentiated into sieve plates; individual sieve tube elements are joined together into a sieve tube.
  - Sieve plate pores are open channels.
  - P-protein is present in all dicots and many monocots.
  - Companion cells are sources of ATP and other compounds
- **Sieve cells found in gymnosperms**
  - There are no sieve plates; all sieve areas are similar.
  - Pores in sieve areas appear blocked with membranes
  - There is no P-protein.
  - Albuminous cells sometimes function as companion cells.



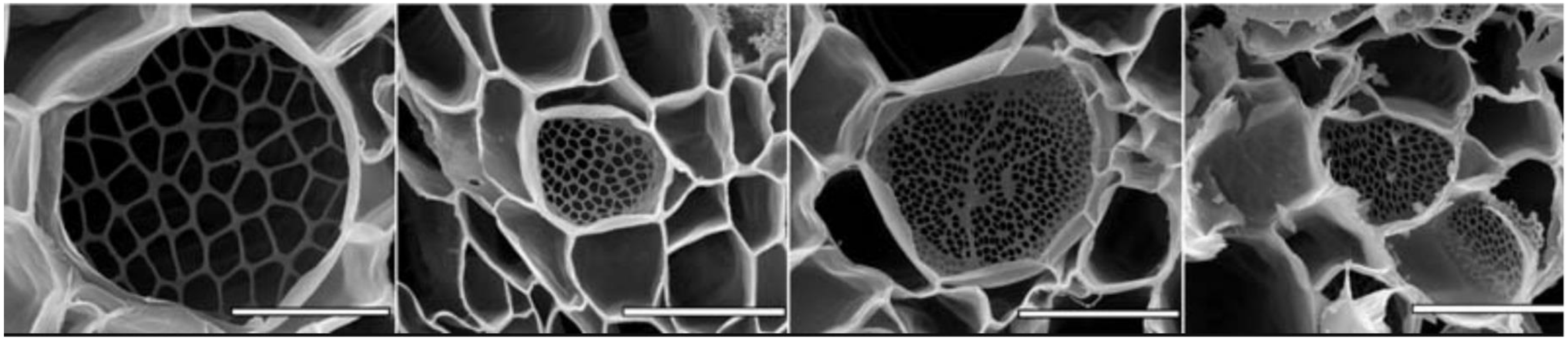
Sieve elements and open sieve plate pores: longitudinal section of two mature sieve elements (sieve tube elements), showing the wall between the sieve elements (called a sieve plate) in the hypocotyl of winter squash (*Cucurbita maxima*).



Electron micrograph showing a sieve area (sa) linking two sieve cells of a conifer (*Pinus resinosa*). Smooth endoplasmic reticulum (SER) covers the sieve area on both sides and is also found within the pores and the extended median cavity. Plastids (P) are enclosed by the SER.

Sieve plates

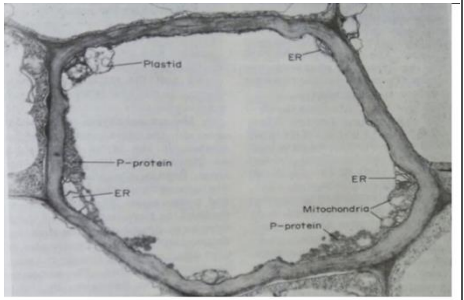
- They have larger pores than the other sieve areas in the cell.
- They are generally found on the end walls of sieve tube elements.
- The individual cells are joined together to form a longitudinal series called a **sieve tube**
- The sieve plate pores of sieve tube elements are open channels that allow transport between.
- The pores of gymnosperm sieve areas meet in large median cavities in the middle of the wall.
- Smooth endoplasmic reticulum (SER) covers the sieve areas.
- It is continuous through the sieve pores and median cavity, as indicated by ER-specific staining.



Pumpkin Green bean Castor bean Tomato.

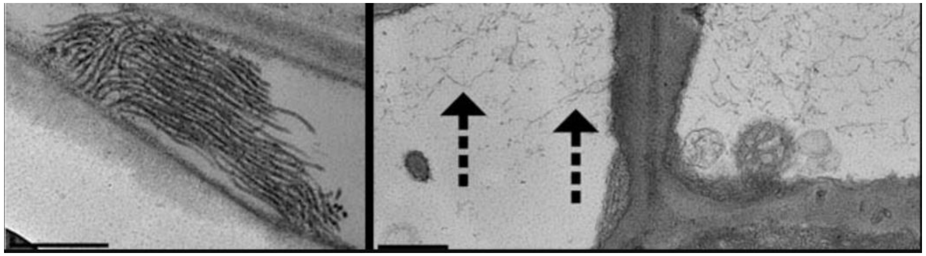
(Mullendore et al. (2010) Sieve tube geometry in relation to phloem flow. Plant Cell 22, 579-593. Copyright American Society of Plant Biologists)

Deposition of P-Protein and Callose Seals Off Damaged Sieve Elements



Electron micrograph of cross cection of sieve tube of *Cucurbita maxima*

- **P-protein:** The sieve tube elements of most angiosperms are rich in a phloem protein.
- P-protein is found in all dicots and in many monocots, and it is absent in gymnosperms.
- It occurs in several different forms: depending on the species and maturity of the cell.
  - Tubular,
  - Fibrillar,
  - Granular, and
  - Crystalline.
- In immature cells, P-protein is most evident as discrete bodies in the cytosol known as **P-protein bodies**.
- P-protein bodies may be:
  - Spheroidal,
  - Spindle-shaped, or
  - Twisted and coiled.



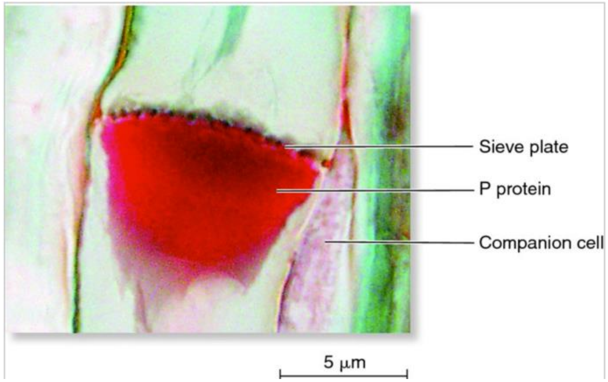
- They generally disperse into tubular or fibrillar forms during cell maturation.

P-proteins at the molecular level

- *Cucurbita:* P-proteins consist of two major proteins:
  - PP1: the phloem filament protein, and
  - PP2: the phloem lectin (plant defense proteins).
- The gene that encodes PP1 in pumpkin (*Cucurbita maxima*) has sequence similarity to genes encoding ***cysteine proteinase inhibitors***.
- It suggests a possible role in defense against phloem-feeding insects.
- Both PP1 and PP2 are thought to be synthesized in companion cells and transported via the plasmodesmata to the sieve elements, where they associate to form P-protein filaments and P-protein bodies.

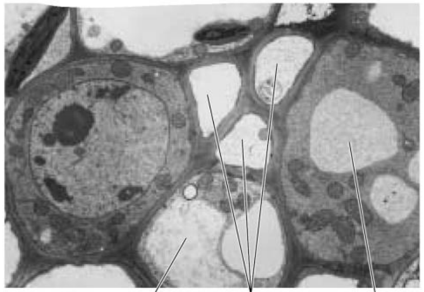
P-protein appears to function

- In sealing off damaged sieve elements by plugging up the sieve plate pores.
- Sieve tubes are under very high internal turgor pressure, and the sieve elements in a sieve tube are connected through open sieve plate pores.
- When a sieve tube is cut or punctured the release of pressure causes the contents of the sieve elements to surge toward the cut end, from which the plant could lose much sugar-rich phloem sap if there were no sealing mechanism.
- Sap is a general term used to refer to the fluid contents of plant cells.
- When surging occurs, P-protein and other cellular inclusions are trapped on the sieve plate pores, helping to seal the sieve element and to prevent further loss of sap.



Companion Cells Aid the Highly Specialized Sieve Elements

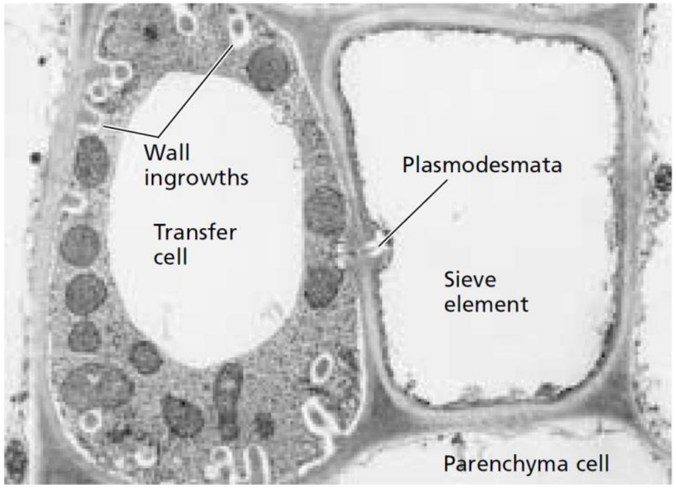
- Each sieve tube element is associated with one or more **companion cells**.
- The division of a single mother cell forms the sieve tube element and the companion cell.
- Numerous plasmodesmata penetrate the walls between sieve tube elements and their companion cells, suggesting a close functional relationship and a ready exchange of solutes between the two cells.
- The plasmodesmata are often complex and branched on the companion cell side.
- Companion cells play a role in the transport of photosynthetic products from producing cells in mature leaves to the sieve elements in the minor (small) veins of the leaf.
- The numerous mitochondria in companion cells supply energy as ATP to the sieve elements.
- Three different types of companion cells in the minor veins of mature exporting leaves:
  1. "Ordinary" companion cells
  2. Transfer cells.
  3. Intermediary cells.
- All three cell types have dense cytoplasm and abundant mitochondria.
- Ordinary companion cells:
  - Have chloroplasts with well-developed thylakoids and a cell wall with a smooth inner surface.
  - Relatively few plasmodesmata connect this type of companion cell to any of the surrounding cells except its own sieve element.



Three sieve elements abut two intermediary cells and a ordinary companion cell in a minor vein from *Mimulus cardinalis*.

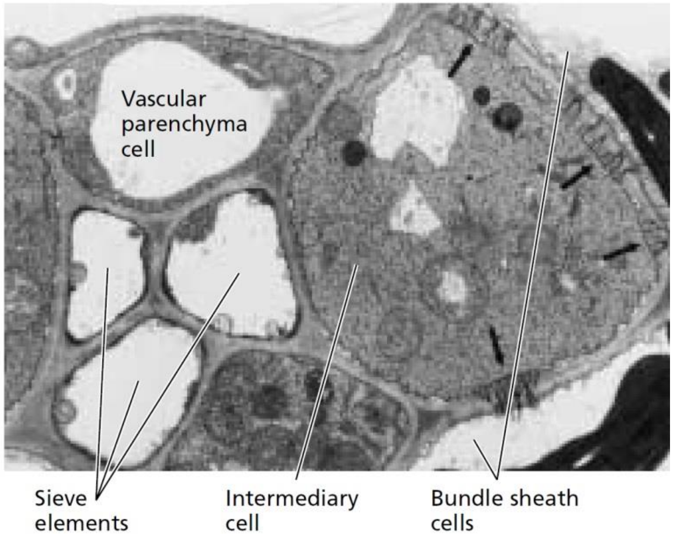
Specialized Companion Cells ……

1. Transfer cells: they develop fingerlike wall ingrowths, particularly on the cell walls that face away from the sieve element. These wall ingrowths greatly increase the surface area of the plasma membrane, thus increasing the potential for solute transfer across the membrane.



A sieve element adjacent to a transfer cell with numerous wall ingrowths in pea (*Pisum sativum*).

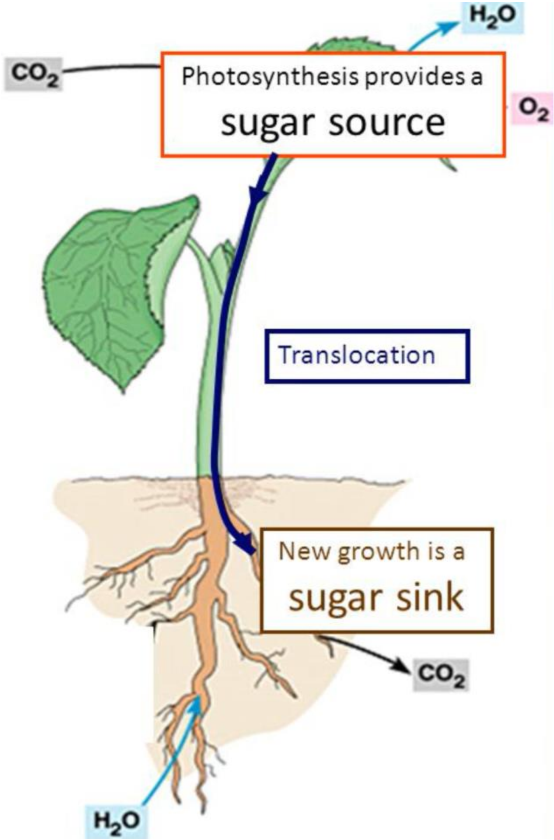
2. Intermediary cells: well suited for taking up solutes via cytoplasmic connections. They have numerous plasmodesmata connecting them to surrounding cells, particularly to the bundle sheath cells.



A typical intermediary cell with numerous fields of plasmodesmata (arrows) connecting it to neighboring bundle sheath cells.

PATTERNS OF TRANSLOCATION: SOURCE TO SINK

- Sap is translocated from areas of supply, called ***sources***, to areas of metabolism or storage, called ***sinks***.
- ***Sources*** include any exporting organs: Mature leaves, that are capable of producing photosynthate in excess of their own needs.
- **Sinks** include any non-photosynthetic organs of the plant and organs that do not produce enough photosynthetic products to support their own growth or storage needs.
  - Roots,
  - Tubers,
  - Developing fruits, and
  - Immature leaves.

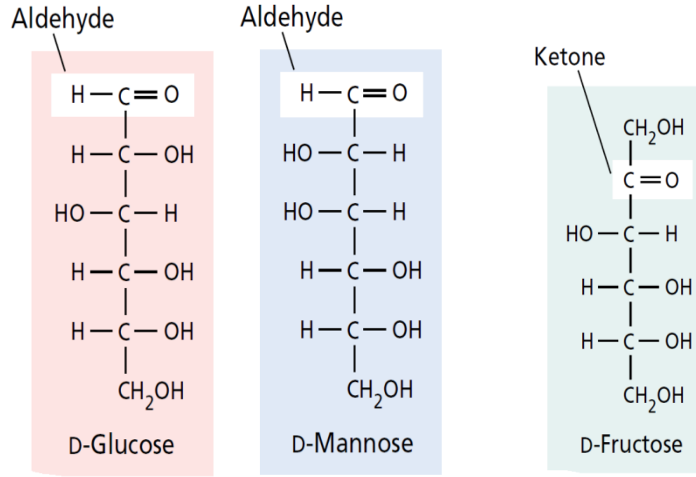


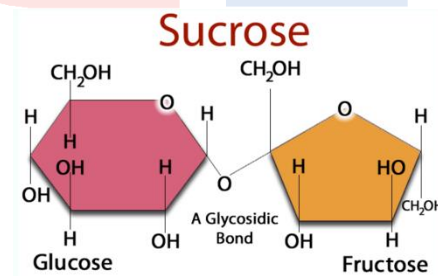
MATERIALS TRANSLOCATED IN THE PHLOEM

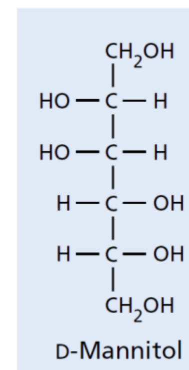
- Materials translocated in the Phloem:
  - Sucrose, Amino acids, Hormones, and Some inorganic ions
- Water is the most abundant substance transported in the phloem.
  - Dissolved in the water are the translocated solutes, mainly carbohydrates.
  - Sucrose is the sugar most commonly transported in sieve elements.
  - There is always some sucrose in sieve element sap, and it can reach concentrations of 0.3 to 0.9 *M*.
- Nitrogen is found in the phloem.
  - Largely in amino acids and amides, especially glutamate and aspartate and their respective amides, glutamine and asparagine.
- Almost all the endogenous plant hormones:
  - Auxin,
  - Gibberellins,
  - Cytokinins, and
  - Abscisic acid
- Nucleotide phosphates and proteins have also been found in phloem sap.
- Proteins found in the phloem
  - Filamentous P-proteins,
  - Protein kinases,
  - Thioredoxin, ubiquitin, chaperones (protein folding), and protease inhibitors.
- Inorganic solutes: They include potassium, magnesium, phosphate, and chloride.
- In contrast, nitrate, calcium, sulfur, and iron are relatively immobile in the phloem.

Sugars Are Translocated in Non-reducing Form

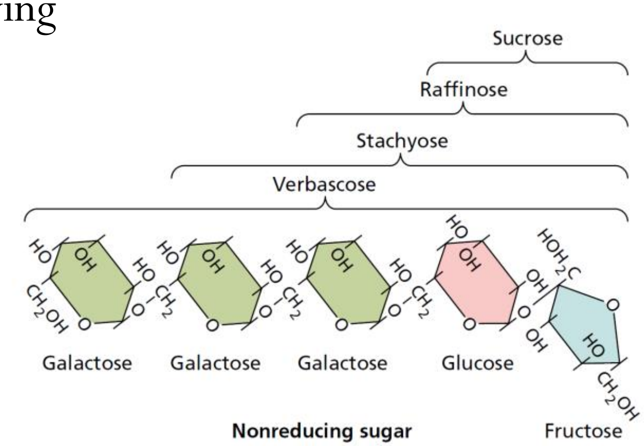
- The translocated carbohydrates are all ***non-reducing sugars.***
- Reducing sugars, such as glucose and fructose, contain an exposed aldehyde or ketone group.
- In a non-reducing sugar (sucrose), the ketone or aldehyde group is reduced to an alcohol or combined with a similar group on another sugar.
- The non-reducing sugars are the major compounds translocated in the phloem because they are less reactive than their reducing counterparts.
- Sucrose is the most commonly translocated sugar
- Mobile carbohydrates contain sucrose bound to varying numbers of galactose molecules.
    - Raffinose: Sucrose and one galactose molecule.
    - Stachyose: Sucrose and two galactose molecules.
    - Verbascose: Sucrose and three galactose molecules
- Translocated sugar alcohols include mannitol and sorbitol.





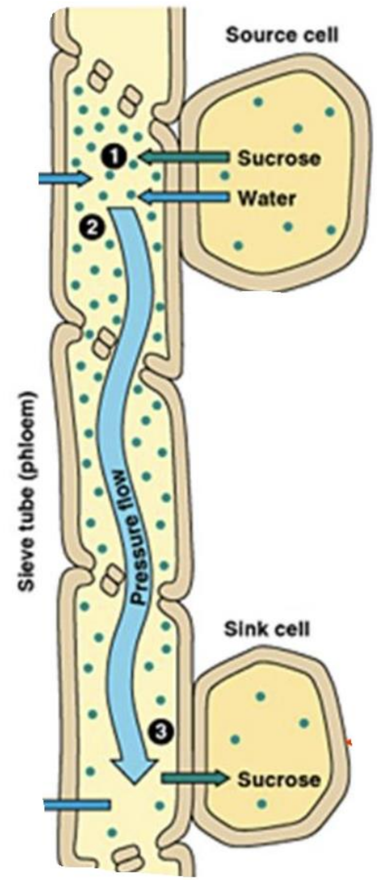


Mannitol is a sugar alcohol formed by the reduction of the aldehyde group of mannose.



The Mechanism of Translocation In The Phloem

- **The pressure-flow model:**
  - It explains phloem translocation as a flow of solution (bulk flow) driven by an ***osmotically generated pressure gradient*** between source and sink.
  - Energy is required in both sources and sinks.
  - In sources:
    - Energy is necessary to move photosynthate from producing cells into the sieve elements.
    - This movement of photosynthate is called ***phloem loading***.
  - In sinks:
    - Energy is essential for movement from sieve elements to sink cells, which store or metabolize the sugar.
    - This movement of photosynthate from sieve elements to sink cells is called ***phloem unloading.***
  - The passive mechanisms of phloem transport assume that energy is required in the sieve elements of the path between sources and sinks simply to maintain structures such as the cell plasma membrane and to recover sugars lost from the phloem by leakage.
  - The pressure-flow model is an example of a passive mechanism.
  - The active theories, on the other hand, postulate an additional expenditure of energy by path sieve elements in order to drive translocation itself.

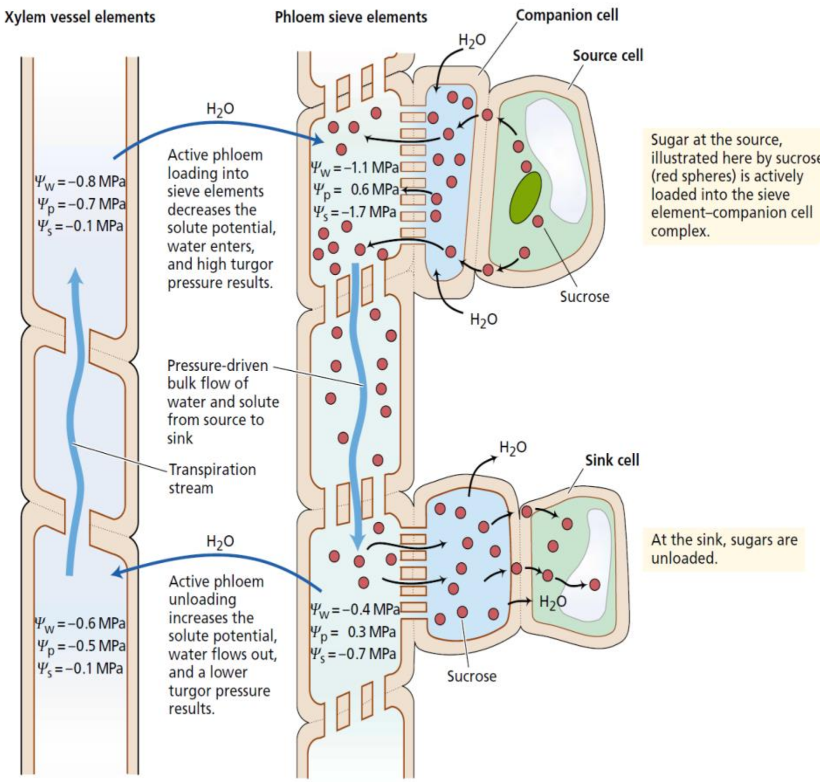


A Pressure Gradient Drives Translocation

- Diffusion is far too slow to account for the velocities of solute movement observed in the phloem.
- The pressure-flow model, first proposed by Ernst Münch in 1930:
  - States that a flow of solution in the sieve elements is driven by an osmotically generated pressure gradient between source and sink ($\Delta\Psi p$).
  - The pressure gradient is established as a consequence of phloem loading at the source and phloem unloading at the sink.
  - We know, $\Psi w = \Psi s + \Psi p$ (Ψw=Water potential, Ψs = the effects of solutes, Ψp= the the effects of pressure). So, $\Psi p = \Psi w - \Psi s$
  - In source tissues, energy-driven phloem loading leads to an accumulation of sugars in the sieve elements, generating a low (negative) solute potential ($\Delta\Psi s$) and causing a steep drop in the water potential ($\Delta\Psi w$).
  - In response to the water potential gradient, water enters the sieve elements and causes the turgor pressure (Ψp) to increase.
  - At the receiving end of the translocation pathway, phloem unloading leads to a lower sugar concentration in the sieve elements, generating a higher (more positive) solute potential in the sieve elements of sink tissues.
  - As the water potential of the phloem rises above that of the xylem, water tends to leave the phloem in response to the water potential gradient, causing a decrease in turgor pressure in the sieve elements of the sink.

- If no cross-walls were present in the translocation pathway—
  - The entire pathway were a single membrane-enclosed compartment.
  - The different pressures at the source and sink would rapidly equilibrate.
- The presence of sieve plates:
  - Greatly increases the resistance along the pathway.
  - It results in the generation and maintenance of a substantial pressure gradient in the sieve elements between source and sink.
  - The sieve element contents are physically pushed along the translocation pathway as a bulk flow.

- The water in the phloem is moving against a water potential gradient from source to sink.
- The water is moving by bulk flow not by osmosis.
- No membranes are crossed during transport from one sieve tube to another.
- Solutes are moving at the same rate as the water molecules.
- Water movement in the translocation pathway is driven by the pressure gradient.
- This passive, pressure-driven, long-distance translocation in the sieve tubes ultimately depends on the active, short-distance transport mechanisms involved in phloem loading and unloading.
- These active mechanisms are responsible for setting up the pressure gradient.

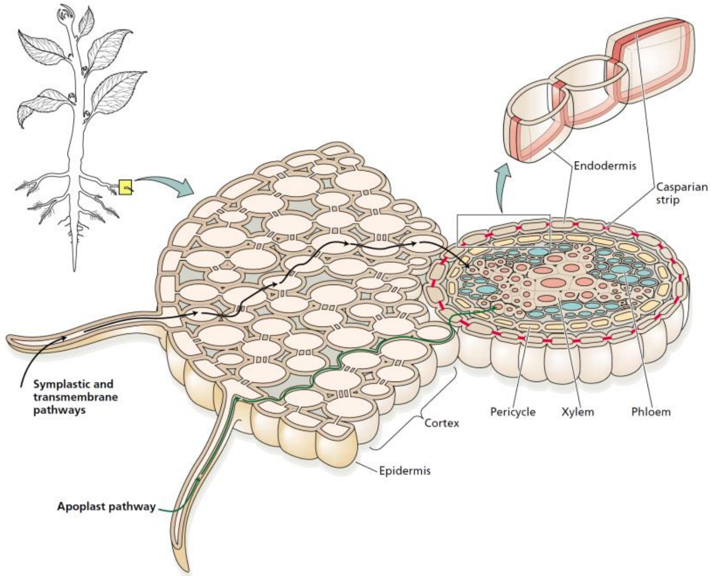


Phloem Loading

- From chloroplasts to sieve elements.
- ***Phloem loading:*** Several transport steps that are involved in the movement of photosynthate from the mesophyll chloroplasts to the sieve elements of mature leaves.
- Triose phosphate formed by photosynthesis during the day is transported from the chloroplast to the cytosol, where it is converted to sucrose.
- During the night, carbon from stored starch exits the chloroplast probably in the form of glucose and is converted to sucrose.
- Sucrose moves from the mesophyll cell to the vicinity of the sieve elements in the smallest veins of the leaf : ***Short-distance transport pathway***.
- It usually covers a distance of only two or three cell diameters.
- Sugars are transported into the sieve elements and companion cells.
- Sugars become more concentrated in the sieve elements and companion cells than in the mesophyll.
- The sieve elements and companion cells are considered a functional unit: The ***sieve element–companion cell complex***.
- Once inside the sieve elements, sucrose and other solutes are translocated away from the source: ***export***.
- Translocation through the vascular system to the sink is referred to as ***long-distance transport***.

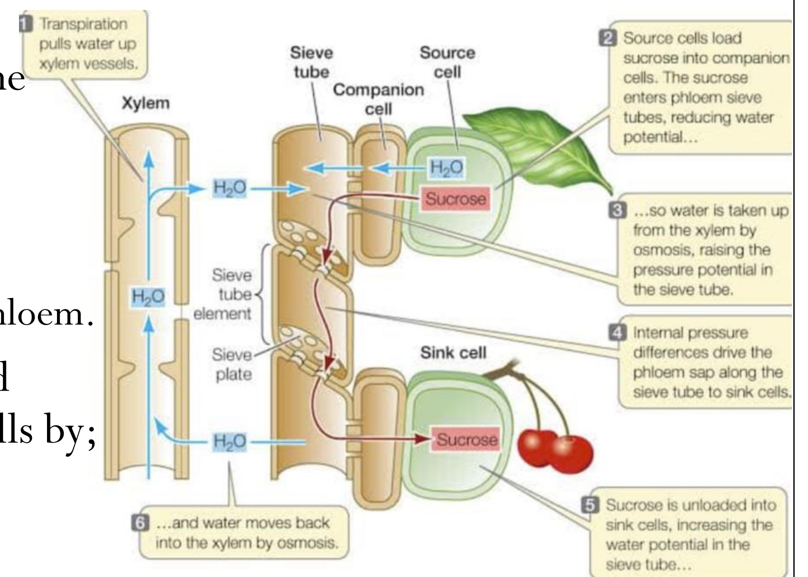
Pathways for water uptake by the root: Apoplast and the Symplast

- Through the cortex, water may travel via
  - The apoplast pathway: the transmembrane pathway, and
  - The symplast pathway.
- The symplast pathway:
  - Water flows between cells through the plasmodesmata and
  - Without crossing the plasma membrane.
- In the apoplast or transmembrane pathway:
  - Water moves across the plasma membranes, with a short visit to the cell wall space.
  - At the endodermis, the apoplast pathway is blocked by the Casparian strip.



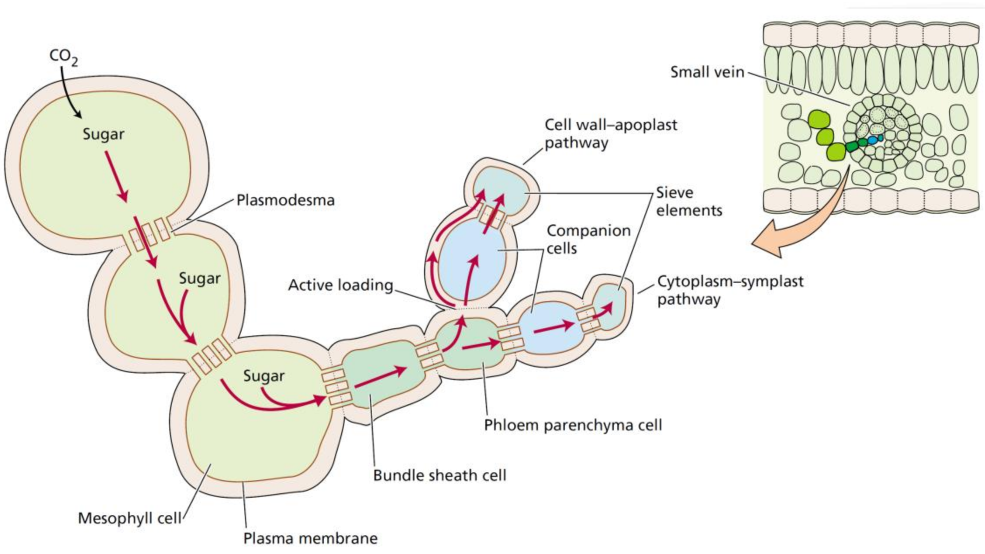
Translocation: Apoplast and the Symplast

- Photosynthate can move from mesophyll cells to the sieve elements via the apoplast or the symplast.
- Solutes (mainly sugars) in source *leaves:* must move from the photosynthesizing cells in the mesophyll to the veins.
- Sugars might move entirely through:
  - The ***symplast*** (cytoplasm) via the plasmodesmata, or
  - They might enter the ***apoplast*** at some point en route to the phloem.
- ***In the apoplastis movement***: The sugars are actively loaded from the apoplast into the sieve elements and companion cells by;
  - An energy-driven, selective transporter located in the plasma membranes of these cells.
  - Sucrose uptake in the apoplastic pathway requires metabolic energy.
- In source leaves, sugars become **more** concentrated in the **sieve elements and companion** cells than in the mesophyll.
- The higher concentration of in the sieve element–companion cell complex than in surrounding cells indicates that sucrose is actively transported against its chemical-potential gradient.
- Treating source tissue with respiratory inhibitors both decreases ATP concentration and inhibits loading of exogenous sugar.



Schematic diagram of pathways of phloem loading in source leaves.

- ***In the totally symplastic pathway***: sugars move from one cell to another in the plasmodesmata, all the way from the mesophyll to the sieve elements.
- ***In the partly apoplastic pathway***: sugars enter the apoplast at some point.
- Here, sugars are entering the apoplast near the sieve element–companion cell complex,
- But they could also enter the apoplast earlier in the path and then move to the small veins.
- The sugars are actively loaded into the companion cells and sieve elements from the apoplast.
- Sugars loaded into the companion cells are thought to move through plasmodesmata into the sieve elements.



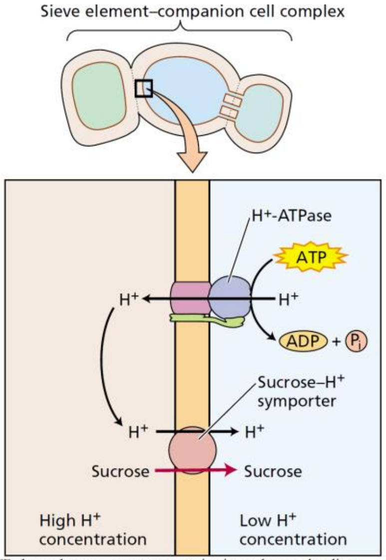
Sieve Element Loading Involves a Sucrose–H^+ Symporter

- In the Apoplastic Pathway, Sieve Element Loading Involves a ***Sucrose–H^+ Symporter***.
- A sucrose–H^+ symporter mediate the transport of sucrose from the apoplast into the sieve element–companion cell complex.
- *Arabidopsis*: The H^+-ATPases in companion cells is correlated with the distribution of a sucrose–H+ symporter (called SUC2).
- In *Plantago major (*broad-leaved plantain): The SUC2 transporter has also been localized in companion cells.
- SUC2 is one of several sucrose–H^+ symporters that have been cloned and localized in the phloem.
- The carriers are found in plasma membranes of either sieve elements (SUT1, SUT2, and SUT4) or companion cells (SUC2).
- **Sucrose–H^+ symporters in the phloem**:

Carrier	Location	Species
SUT1	Sieve elements	Tobacco, tomato, potato
SUT2	Sieve elements	Tomato
SUT4	Sieve elements	Arabidopsis, tomato, potato
SUC2	Companion cells	*Arabidopsis*, plantain

Regulating sucrose loading

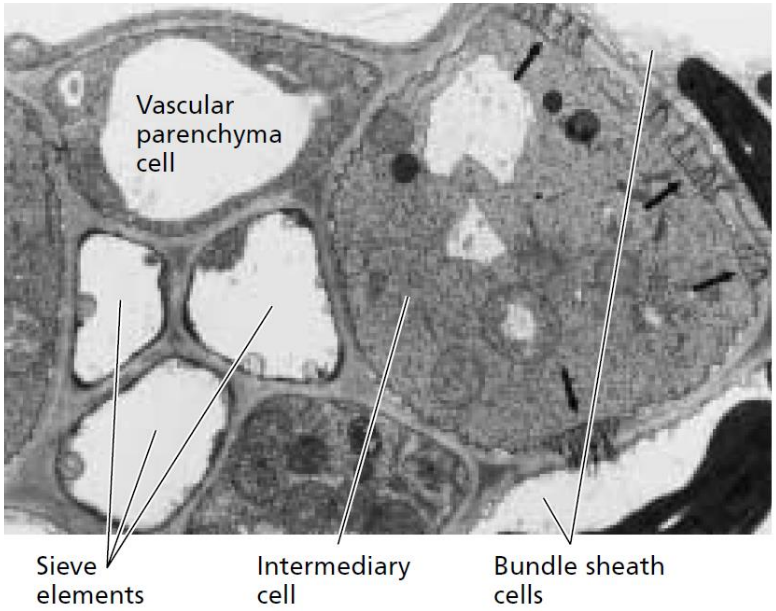
- The mechanisms that regulate the loading of sucrose from the apoplast to the sieve elements by the sucrose–H^+ symporter include the following factors:
  - The solute potential or the turgor pressure of the sieve elements: A decrease in sieve element turgor below a certain threshold would lead to a compensatory increase in loading.
  - Sucrose concentration in the apoplast: High sucrose concentrations in the apoplast would increase phloem loading.
  - The available number of symporter protein molecules:
    - The levels of SUT1 transporter mRNA and protein have been shown to be lower after 15 hours of darkness than after a light treatment.
    - These data suggest that the concentration of SUT1 transporter molecules could regulate loading.



ATP-dependent sucrose transport in sieve element loading:
In the cotransport model of sucrose loading into the symplast of the sieve element–companion cell complex, the plasma membrane ATPase pumps protons out of the cell into the apoplast, establishing a high proton concentration there.
The energy in this proton gradient is then used to drive the transport of sucrose into the symplast of the sieve element–companion cell complex through a sucrose–H+ symporter.

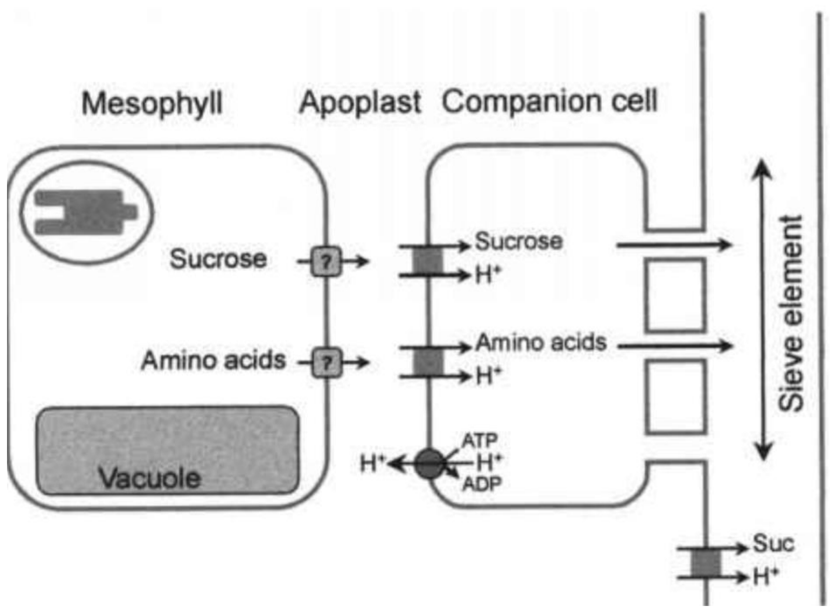
Phloem Loading Appears to Be Symplastic in Plants with Intermediary Cells

- Squash (*Cucurbita pepo*), and melon (*Cucumis melo*):
  - Have ordinary companion cells or transfer cells in the minor veins, and
  - Transport only sucrose or
  - Follow a symplastic pathway that transport raffinose and stachyose in the phloem.
- The operation of a symplastic pathway requires the presence of open plasmodesmata between the different cells in the pathway.
- Many species have numerous plasmodesmata at the interface between the sieve element–companion cell complex and the surrounding cells.
- Experimental studies have demonstrated symplastic continuity in source leaves of some species.



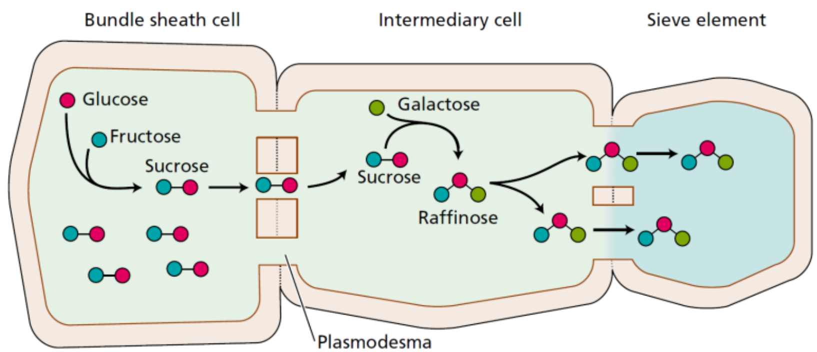
The Polymer-Trapping Model

- This model Explains Symplastic Loading in Source Leaves.
- The composition of sieve element sap is generally different from the solute composition in tissues surrounding the phloem.
- This difference indicates that certain sugars are specifically selected for transport in the source leaf.
- In several species performing symplastic loading: Sieve elements and companion cells have a higher osmotic content than the mesophyll.
- How could diffusion-dependent symplastic loading account for the observed selectivity for transported molecules and the accumulation of sugars against a concentration gradient?



The polymer-trapping model

- Turgeon and Gowan (1990):
  - The sucrose synthesized in the mesophyll diffuses from the bundle sheath cells into the intermediary cells through the abundant plasmodesmata.
  - In the intermediary cells, raffinose ((polymers made of three hexose sugars) and stachyose (polymers made of four hexose sugars) are synthesized from the transported sucrose and from galactose.
  - Because of the anatomy of the tissue and the relatively large size of raffinose and stachyose:
    - The polymers cannot diffuse back into the bundle sheath cells, but
    - They can diffuse into the sieve element.
  - Sucrose can continue to diffuse into the intermediary cells because its synthesis in the mesophyll and its utilization in the intermediary cells maintain the concentration gradient.

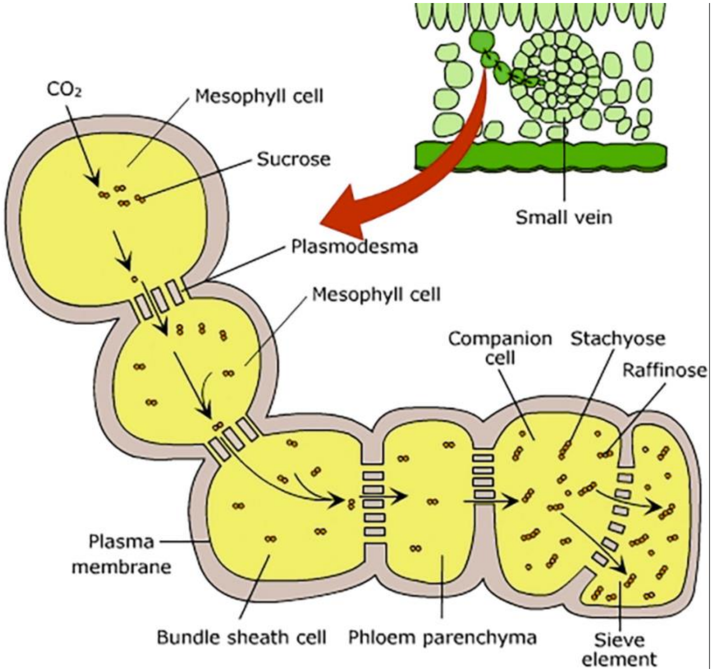


Sucrose, synthesized in the mesophyll, diffuses from the bundle sheath cells into the intermediary cells through the abundant plasmodesmata.

In the intermediary cells, raffinose (and stachyose) are synthesized from sucrose and galactose, thus maintaining the diffusion gradient for sucrose. Because of their larger sizes, they are not able to diffuse back into the mesophyll.

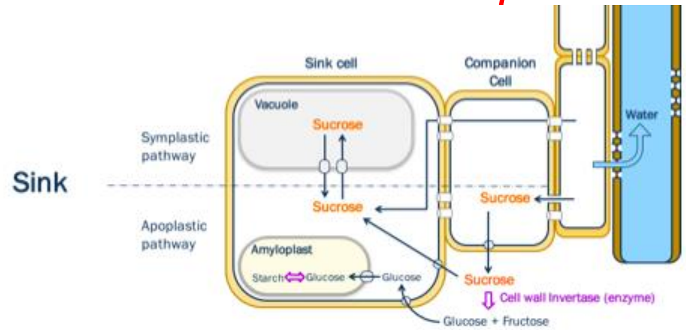
Raffinose and stachyose are able to diffuse into the sieve elements. As a result, the concentration of transport sugar rises in the intermediary cells and the sieve elements.

- The polymer-trapping model makes three predictions:
  1. Sucrose should be more concentrated in the mesophyll than in the intermediary cells.
  2. The enzymes for raffinose and stachyose synthesis should be preferentially located in the intermediary cells.
  3. The plasmodesmata linking the bundle sheath cells and the intermediary cells should exclude molecules larger than sucrose.
- Many studies show:
  - All of the enzymes required to synthesize stachyose from sucrose have been found in intermediary cells.
  - In melon, raffinose and stachyose are present in high concentrations in intermediary cells, but not in mesophyll cells.



PHLOEM UNLOADING AND SINK-TO SOURCE TRANSITION

- So we have learned about the events leading up to the export of sugars from sources.
- Now let's take a look at phloem unloading.
- In many ways the events in sink tissues are simply the reverse of the events in sources.
- Transport into sink organs, such as developing roots, tubers, and reproductive structures, is termed ***import***.
- The following steps are involved in the import of sugars into sink cells.
  1. Sieve element unloading: The imported sugars leave the sieve elements of sink tissues.
  2. Short-distance transport: The sugars are transported to cells in the sink by means of a short-distance transport pathway–sieve element transport.
  3. Storage and metabolism: Sugars are stored or metabolized in sink cells.
- These three transport steps together constitute phloem unloading.
- ***Definition***: The movement of photosynthates from the sieve elements and their distribution to the sink cells that store or metabolize them is called the ***phloem unloading***.

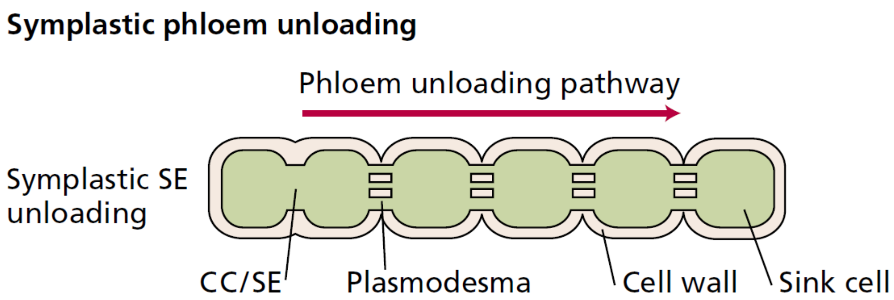


Phloem Unloading: Via Symplastic or Apoplastic Pathways

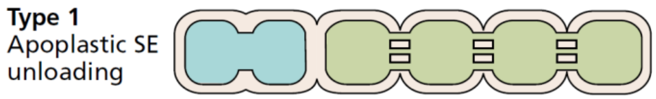
- Sugars move from the sieve elements to the cells that store or metabolize them.
- Sinks vary widely from:
  - Growing vegetative organs (root tips and young leaves)
  - Storage tissues (roots and stems)
  - Organs of reproduction
  - Organs of dispersal (fruits and seeds).
- So sinks vary so greatly in structure and function.
- There is no single scheme of phloem unloading.
- But in sources, the sugars may move
  - Entirely through the symplast via the plasmodesmata, or
  - They may enter the apoplast at some point.

Possible phloem-unloading pathways and their evaluation

- There are several possible phloem-unloading pathways.
- In some young dicot leaves (sugar beet and tobacco): The unloading pathway appears to be completely symplastic
- Evidence:
  - Insensitivity to PCMBS (p-chloromercuribenzenesulfonic acid): A reagent that inhibits the transport of sucrose across plasma membranes but does not permeate the symplastic pathway.
  - Meristematic and elongating regions of primary root tips also appear to unload symplastically.
  - Sufficient plasmodesmata exist in these pathways to support symplastic unloading.

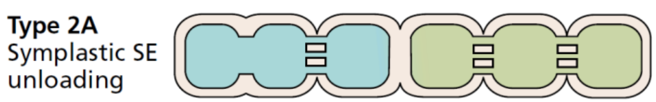


- In some sink organs, part of the phloem-unloading pathway is apoplastic.
- ***Type 1:*** The apoplastic step could be located at the site of the sieve element–companion cell complex (but this pattern has yet to receive experimental support).

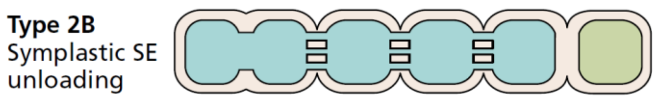


Phloem unloading pathway is designated apoplastic: transport from the sieve element–companion cell complex to the successive sink cells, occurs in the apoplast. Once the sugars are taken back up into the symplast of adjoining cells, transport is symplastic.

- ***Type 2:*** The apoplastic step could also be farther removed from the sieve elements .
  - A typical of developing seeds, appears to be the most common in apoplastic phloem unloading.
  - There are no symplastic connections between the maternal tissues and the tissues of the embryo.
  - Sugars exit the sieve elements (sieve element unloading) via a symplastic pathway and are transferred from the symplast to the apoplast at some point removed from the sieve element–companion cell complex.
  - The apoplastic step permits membrane control over the substances that enter the embryo because two membranes must be crossed in the process.



Sieve element unloading—is symplastic. The apoplastic step occurs later in the pathway. An apoplastic step close to the sieve element–companion cell complex.



Sieve element unloading—is symplastic. The apoplastic step occurs later in the pathway. An apoplastic step that is further removed.

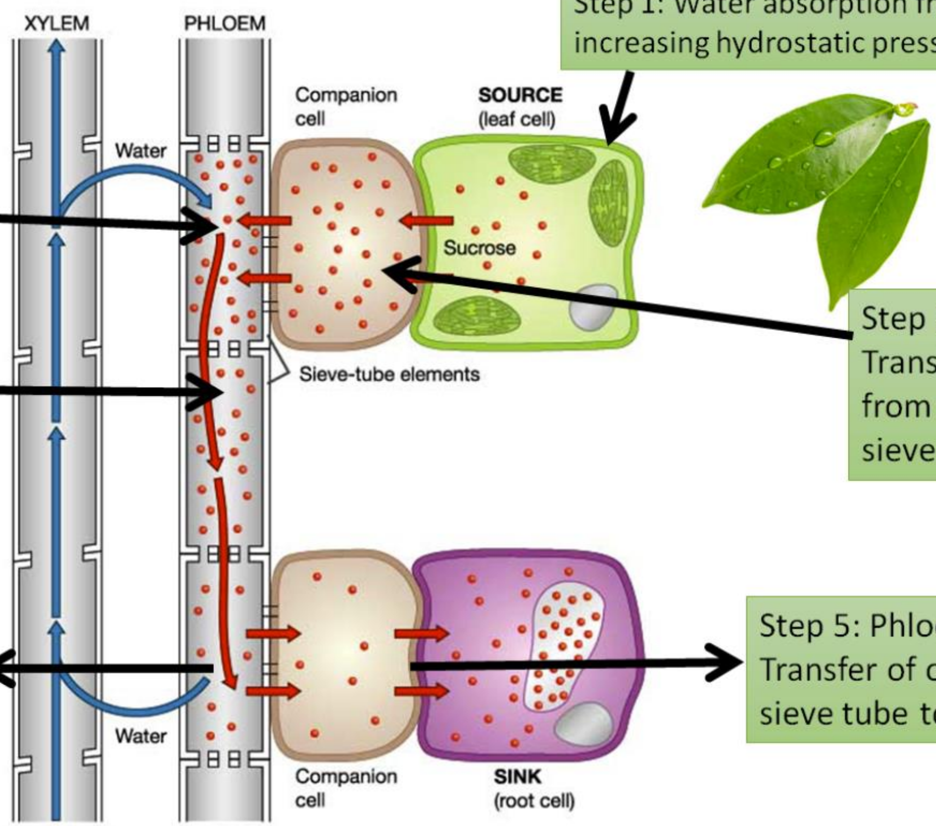
- When phloem unloading is apoplastic, the transport sugar can be partly metabolized in the apoplast, or it can cross the apoplast unchanged.
- Sucrose can be hydrolyzed into glucose and fructose in the apoplast by invertase (a sucrose-splitting enzyme), and glucose and/or fructose would then enter the sink cells.
- Such sucrose-cleaving enzymes play a role in the control of phloem transport by sink tissues.

Transport into Sink Tissues Requires Metabolic Energy

- Inhibitor studies have shown that import into sink tissues is energy dependent.
- Growing leaves, roots, and storage sinks in which carbon is stored in starch or protein utilize symplastic phloem unloading.
- Transport sugars are used as substrate for respiration and are metabolized into storage polymers and into compounds needed for growth.
- Sucrose metabolism results in a low sucrose concentration in the sink cells, thus maintaining a concentration gradient for sugar uptake.
- No membranes are crossed during sugar uptake into the sink cells, and unloading through the plasmodesmata is passive because transport sugars move from a high concentration in the sieve elements to a low concentration in the sink cells.
- Metabolic energy is thus required in these sink organs for ***respiration*** and ***for biosynthesis reactions***.

- In apoplastic phloem unloading, sugars must cross at least two membranes:
  - The plasma membrane of the cell that is exporting the sugar, and
  - The plasma membrane of the sink cell.
- When sugars are transported into the vacuole of the sink cell, they must also traverse the tonoplast.
- Transport across membranes in an apoplastic pathway: may be energy dependent.
- In legumes (soybean): the embryo can be removed from the seed, and unloading from the seed coat into the apoplast can be studied without the influence of the embryo.
- Uptake into the embryo can also be investigated separately.
- Such studies have shown that energy-requiring transporters mediate both
  - Unloading of sucrose into the apoplast and
  - Uptake of sucrose into the embryo in soybean

Mass Flow Hypothesis (Munch, 1930)



Step 1: Water absorption from nearby cells increasing hydrostatic pressure in mesophyll cell

Step 2: Phloem loading Transfer of organic food from mesophyll cells to sieve tube

Step 3: Water entry from xylem to sieve elements by osmosis

Step 4: Hydrostatic pressure difference drives solute movement from sieve tube to sink

Step 5: Phloem unloading Transfer of organic food from sieve tube to sink

Step 6: water moves back to xylem vessels by osmosis and transpiration pulls up water

Thank You