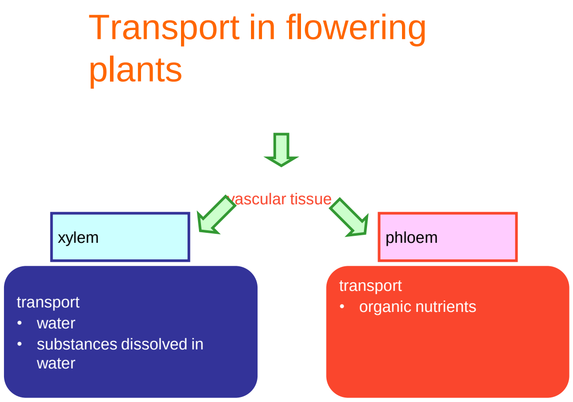
Phloem Transport

As in case of water and minerals translocation up ward through specialized tissues (xylem),the products of photosynthesis are also translocated from leaves to the rest of plant parts through specialized sieve tubes, that consists of rows of cells arranged longitudinally ,and each one is called sieve element separated by sieve plate.



In addition to those (sieve elements, sieve plate), the phloem consists of other types of cells including phloem parenchyma (storage of starch substances), companion cells, phloem fibers, sclereids and ray cells.

Sieve elements differ from xylem vessels in that it contains living protoplasm although it does not have nucleus, absence of mitochondria (or rare presence of mitochondria), and most of the protoplasm is present in the form of protein called p-protein (or phloem protein) that connect the sieve elements together.

Composition of phloem

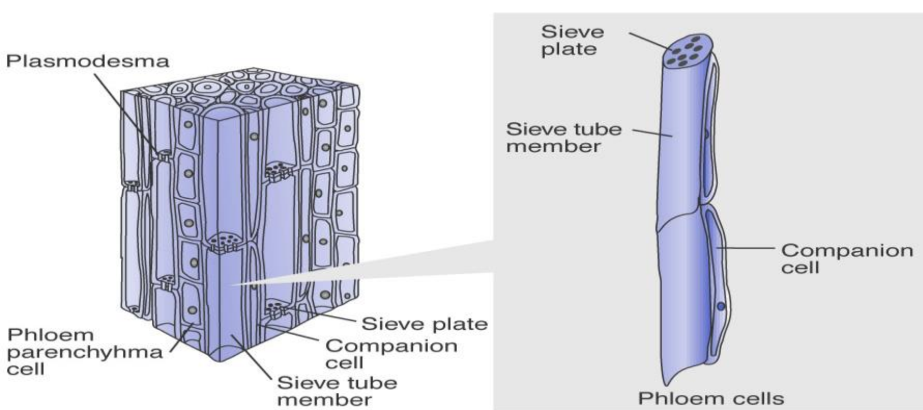
Phloem, like xylem, is a complex conducting tissue of vascular plants. Its main function is the long distance transport of sugars and other photosynthates from the source (mature leaves), or reserves (the cotyledons of germinating seedlings) towards the sinks, e.g. roots, developing reproductive structures (flowers, fruits and seeds), meristems and young leaves.

Table 36.1 *Mechanisms of Sap Flow in Plant Vascular Tissues*

36.1 Mechanisms of Sap Flow in Plant Vascular Tissues

	XYLEM	PHLOEM
Driving force for bulk flow	Transpiration from leaves	Active transport of sucrose at source
Site of bulk flow	Non-living vessel elements and tracheids (cohesion)	Living sieve tube elements
Pressure potential in sap	Negative (pull from top; tension)	Positive (push from source; pressure)

Phloem is also the primary trafficking pathway in vascular plants for the movement of plant growth regulators and other compounds that signal and direct accumulations or responses at sites remote from their origin. Phloem almost always accompanies xylem, and their elements run parallel to each other in vascular bundles. Phloem consists of several types of cells, including conducting and parenchyma cells, phloem fibers, sclereids and, in some plants, secretory ducts and laticifers.



The most important components of phloem tissue are the cells conducting photosynthates, represented in flowering plants by the sieve elements. This term is explained by the presence of areas within the cells that contain specialized pores "sieve pores" in their walls. Unlike dead treachery elements of xylem, sieve elements are typically living cells with an intact, osmotically active plasmalemma, some mitochondria, modified leucoplasts and endoplasmic reticulum. However, in the conducting state they lack cytosol, ribosomes, Golgi apparatus, a nucleus and the central vacuole with its tonoplast.

A unique filamentous protein termed P-protein ("P" derived from "phloem") is formed in the sieve elements of many plants during differentiation. Sieve elements, unlike tracheary elements, do not usually possess lignified secondary walls.

Two types of sieve elements are recognized: sieve cells and sieve tube elements, which may be considered analogous to tracheids and vessel members of tracheary elements in xylem. Sieve pores are modified plasmodesmata and, like plasmodesmata, they interconnect sieve cells. A series of sieve elements arranged end-to-end and interconnected through sieve plates forms a sieve tube, analogous to a vessel in the xylem. Gymnosperms and lower vascular plants have sieve cells, while sieve tubes are characteristic of flowering plants (angiosperms)

Types of Companion cells

- ***Ordinary Companion cells***:
  - Chloroplasts with well developed thylakoids, smooth inner cell wall, relatively few plasmodesmata.
    - ***Connected only to it's own sieve plate***
- ***Transfer cells***:
  - Well developed thylakoids
  - Have fingerlike cell wall ingrowths –increase surface area of plasma membrane for better solute transfer.
- **Both of these types are specialized for taking up solutes from apoplast or cell wall space**

Types of Companion Cells

- ***Intermediary cells***:
  - Appear well suited for taking up solutes via cytoplasmic connections
  - Have many plasmodesmata connects to surrounding cells
    - ***Most characteristic feature***
  - Contain many small vacuoles
  - Lack starch grains in chloroplast
  - Poorly developed thylakoids
- **Function in symplastic transport of sugars from mesophyll cells to sieve elements where no apoplast pathway exists**

Types of Sieve Elements

TABLE 10.1
Characteristics of the two types of sieve elements in seed plants

Sieve tube elements found in angiosperms
1. Some sieve areas are differentiated into sieve plates; individual sieve tube elements are joined together into a sieve tube.
2. Sieve plate pores are open channels.
3. P-protein is present in all dicots and many monocots.
4. Companion cells are sources of ATP and perhaps other compounds and, in some species, are transfer cells or intermediary cells.
Sieve cells found in gymnosperms
1. There are no sieve plates; all sieve areas are similar.
2. Pores in sieve areas appear blocked with membranes.
3. There is no P-protein.
4. Albuminous cells sometimes function as companion cells.

PLANT PHYSIOLOGY, Third Edition, Table 10.1 © 2002 Sinauer Associates, Inc.

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Protective mechanisms in phloem

- Sieve elements are under high internal turgor pressure
  - When damaged the release of pressure causes the contents of sieve elements to surge towards the damage site
    - ***Plant could lose too much of the hard worked for sugars if not fixed***
- Damaged is caused by
  - Insects feeding on manufactured sugars
  - Wind damage, temperature (hot and cold)
  - Pollution causing a change in light wavelength

Protective mechanisms in phloem

- ***P proteins***:
  - Occurs in many forms (tubular, fibrillar, chrystaline – depends on ***plant species*** and ***age*** of cell)
  - Seal off damaged sieve elements by plugging up the sieve plate pores
  - Short term solution
- ***Callose***:
  - Long term solution
  - This is a β-(1,3)-glucan, made in functioning sieve elements by their plasma membranes and seals off damaged sieve elements

Each sieve tube element in angiosperms is accompanied by one or more usually dense-cytoplasmic cells called companion cells. The companion cells lie along the sieve element and, in fact, are the product of longitudinal division from a common mother cell. Companion cells are thought to play an important part in loading sieve tubes with photosynthates in source area and unloading in sink areas. Companion cells and sieve elements together constitute a functional unit in food conductance. In gymnosperms, typical companion cells are lacking in the phloem, but have specialized cells called albumineous cells.

What is transported in phloem?

TABLE 10.2
The composition of phloem sap from castor bean (*Ricinus communis*), collected as an exudate from cuts in the phloem

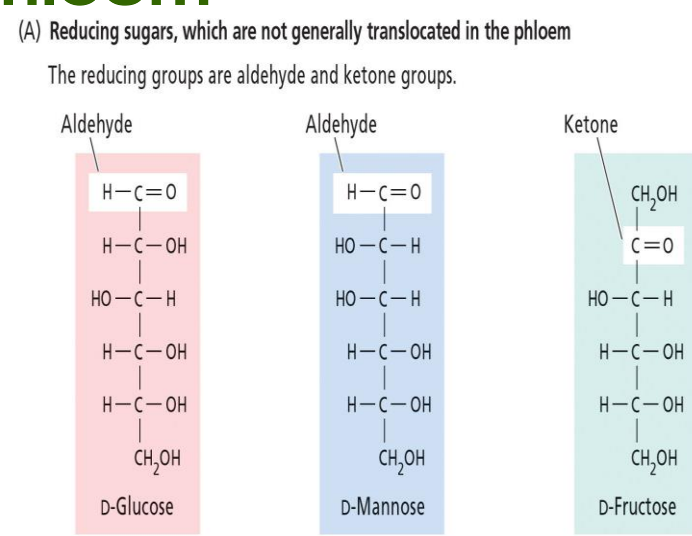
Component	Concentration (mg mL^{-1})
Sugars	80.0–106.0
Amino acids	5.2
Organic acids	2.0–3.2
Protein	1.45–2.20
Potassium	2.3–4.4
Chloride	0.355–0.675
Phosphate	0.350–0.550
Magnesium	0.109–0.122

Source: Hall and Baker 1972.

Composition of Phloem sap

Sugars that are not generally in phloem

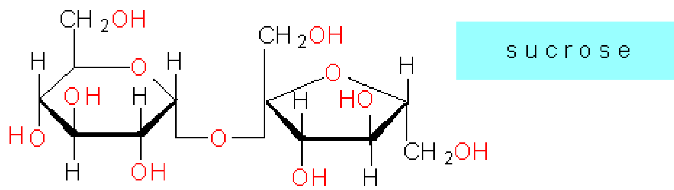
- Carbohydrates transported in phloem are all ***nonreducing*** sugars.
  - ***This is because they are less reactive***
- Reducing sugars, such as ***Glucose***, ***Mannose*** and ***Fructose*** contain an exposed aldehyde or ketone group
  - ***Too chemically reactive to be transported in the phloem***



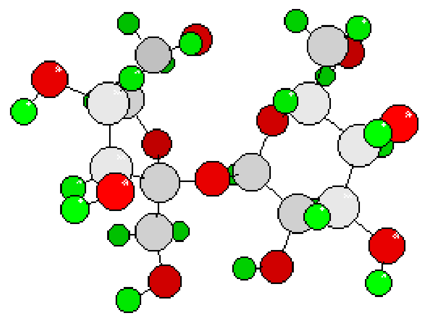
Sucrose

The sugar that is most important in translocation is sucrose

Sucrose is a disaccharide, i.e., made up of two sugar molecules – an additional synthesis reaction is required after photosynthesis



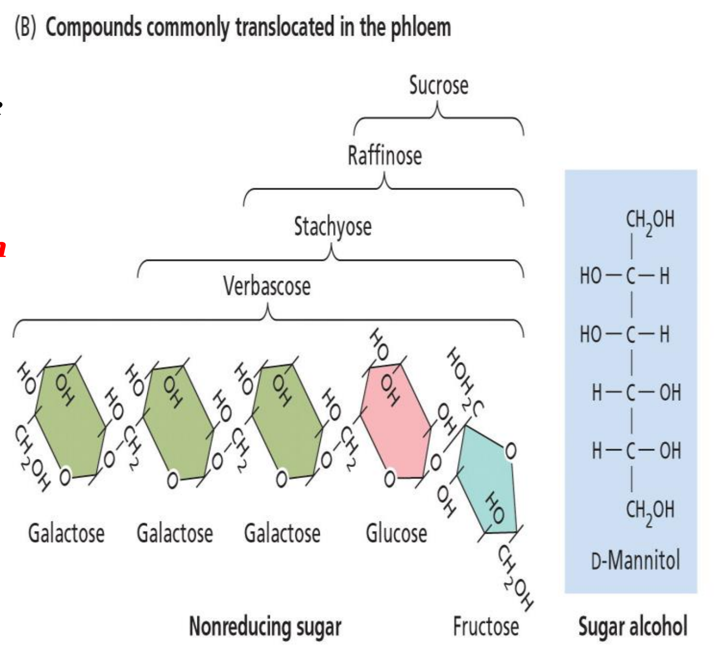
Sucrose - is not a rigid structure, but mobile in itself.



http://www.biologie.uni-hamburg.de/b-online/e16/16h.htm#sucr

Sugars that are in phloem (polymers)

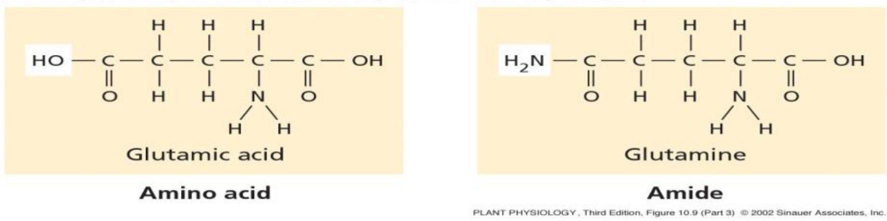
- The most common transported sugar is ***sucrose***.
  - *Made up from glucose & Fructose*
- This is a reducing sugar
  - ***The ketone or aldehyde group is combined with a similar group on another sugar***
  - ***Or the ketone or aldehyde group is reduced to an alcohol***
    - **D-Mannitol**
- Most of the other mobile sugars transported contain Sucrose bound to varying numbers of ***Galactose*** units



OTHER COMPOUNDS

- **Water!!!!!!!!!**
- **Nitrogen** is found in the phloem mainly in:
  - ***amino acids*** (Glutamic acid)
  - ***Amides*** (Glutamine)
- Proteins (see later)

Glutamic acid and glutamine are important nitrogenous compounds in the phloem, in addition to aspartate and asparagine.



Translocation in phloem

Source: any organ or tissue that the organic compounds are translocated from it through the phloem.

Sink: any organ or tissue that the organic compounds are translocated to it through the phloem. What determine whether the organ or tissue is source or sink depends on its contents of organic compounds (mostly soluble sugars) capable for translocation, as compared with other sites?

Source-sink pathways follow patterns

- ***Proximity*****:** – of source to sink is a significant factor.
  - Upper nature leaves usually provide photosynthesis products to growing shoot tip and young, immature leaves
  - Lower leaves supply predominantly the root system
  - Intermediate leaves export in both directions
- ***Development*****:** – Importance of various sinks may shift during plant development
  - Roots and shoots major sinks during vegetative growth
  - But fruits become dominant sinks during reproductive development

Source-sink pathways follow patterns

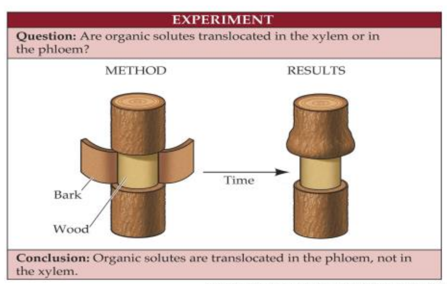
- ***Vascular connections*:** –Source leaves preferentially supply sinks with direct vascular connections
  - A given leaf is connected via vascular system to leaves above and below it on the stem
- ***Modifications of translocation pathways*: -** Interference with a translocation pathway by mechanical wounding (or pruning)
  - vascular interconnections can provide alternate pathways for phloem transport

Direction of translocation

The directions of translocation in xylem vessels is upward only and does not go in two directions (i.e. water moves from downward to the top of plant). In phloem, the direction is variable and is affected by metabolic activities and moves to all plant parts that can store the food (or storage organs).

Translocation of Substances in the Phloem

- Translocation (movement of organic solutes) stops if the phloem is killed.
- Translocation often proceeds in both directions— both up and down the stem simultaneously.
- Translocation is inhibited by compounds that inhibit respiration and the production of ATP.



Mechanism of phloem transport

Any mechanism that explains transport in phloem must coincide with the following transport characteristics

1. Movement of substances in the phloem is rapid and ranges between 20-100 cm /hour (and may reach 2 meters /hour)
2. The amount of transported compounds is relatively large.
3. The direction is always form source to sink (i.e. could take place in both directions).

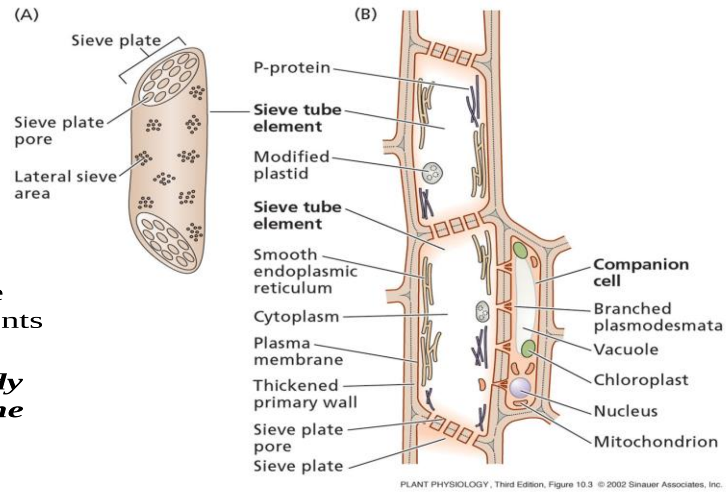
Mechanisms

1. Pressure Flow Mechanism :

This mechanism was suggested by Munch in 1930, and still is the most widely accepted mechanism. It depends on the mass transport of soluble substances from the source to sink according to turgor pressure gradient (from high to low). The organic compounds (i.e. sugars) are accumulated in the sieve elements (usually in the small veins close to the mesophyll which does or conduct photosynthesis). This accumulation leads to increase in solute concentration, which subsequently reduces the osmotic potential (Ψs) which in turn causes the entrance of water osmotically to the sieve elements (from cell walls or close xylem tissue). High turgor pressure (or water pressure) will be generated in the sieve elements (the source). In the meantime, sucrose is removed from the sink (i.e. root or storage cells in stem for example), which leads to reduction in turgor pressure in the sink. As a result, a gradient in turgor pressure is generated between the source and sink in the sieve tubes which leads to the flow of solution. This process (flow of solution) will continue as long as accumulation of sugar is taking place in the source, followed by its removal in the sink. Loading of sugar in the source, and it unloading in the sink is active process and requires metabolic energy.

Phloem transport requires specialized, living cells

- Sieve tubes elements join to form continuous tube
- ***Pores*** in sieve plate between sieve tube elements are open channels for transport
- Each sieve tube element is associated with one or more ***companion cells***.
  - Many plasmodesmata penetrate walls between sieve tube elements and companion cells
  - ***Close relationship, have a ready exchange of solutes between the two cells***

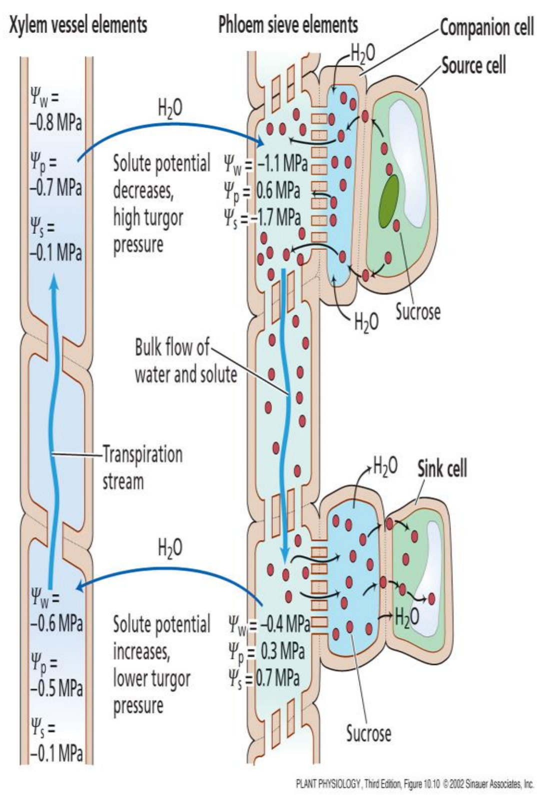


The Pressure-Flow Model

Translocation is thought to move at 1 meter per hour

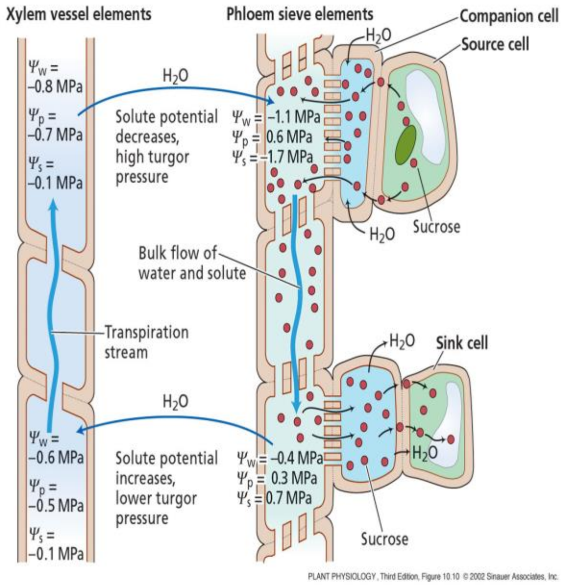
- *Diffusion too slow for this speed*

- The flow is driven by an osmotically generated pressure gradient between the ***source*** and the ***sink***.
- **Source**
  - Sugars (red dots) is actively loaded into the sieve element-companion cell complex
    - *Called phloem loading*
- **Sink**
  - Sugars are unloaded
    - *Called phloem unloading*



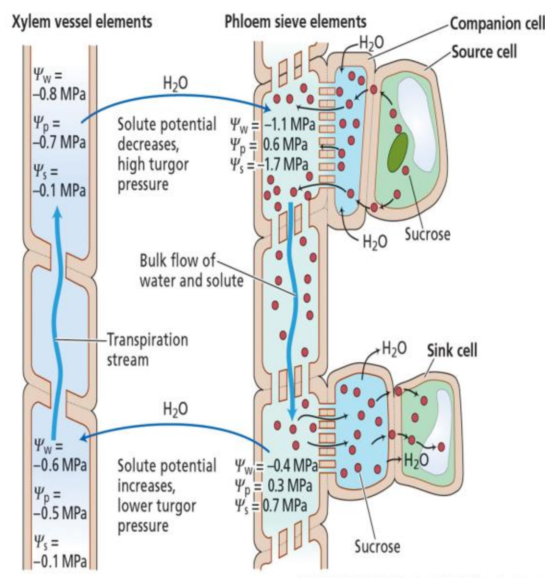
The Pressure -Flow Model

- $\psi w = \psi s + \psi p + \psi g$
- In ***source tissue***, energy driven phloem loading leads to a buildup of sugars
  - Makes **low (-ve)** solute potential
  - Causes a steep **drop** in water potential
  - In response to this new water potential gradient, water enters sieve elements from xylem
    - ***Thus phlem turgor pressure increases***
- In ***sink tissue***, phloem unloading leads to lower sugar conc.
  - Makes a **higher (+ve)** solute potential
  - Water potential **increases**
  - Water leaves phloem and enters sink sieve elements and xylem
    - ***Thus phloem turgor pressure decreases***



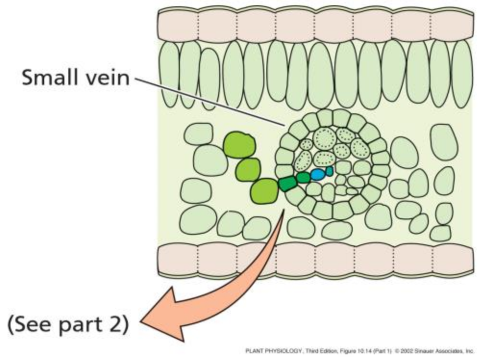
The Pressure-Flow Model

- So, the translocation pathway has cross walls
  - Allow water to move from xylem to phloem and back again
  - If absent- ***pressure difference from source to sink would quickly equilibrate***
- Water is moving in the phloem by ***Bulk Flow***
  - No membranes are crossed from one sieve tube to another
  - Solutes are moving at the same rate as the water
- Water movement is driven by ***pressure gradient*** and **NOT** ***water potential gradient***



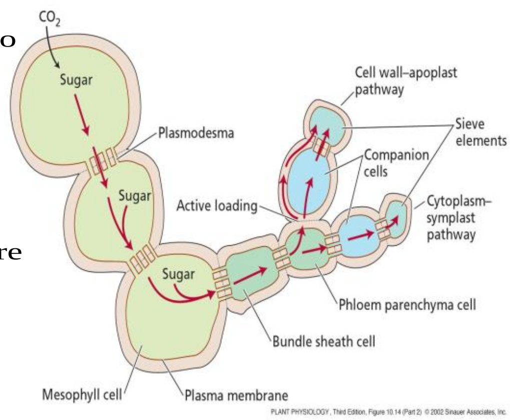
Phloem Loading: Where do the solutes come from?

- Triose phosphate – formed from photosynthesis during the day is moved from chloroplast to cytosol
- At night, this compound, together with glucose from stored starch, is converted to sucrose
  - ***Both these steps occur in a mesophyll cell***
- Sucrose then moves from the mesophyll cell via the smallest veins in the leaf to near the sieve elements
  - Known as short distance pathway – ***only moves two or three cells***



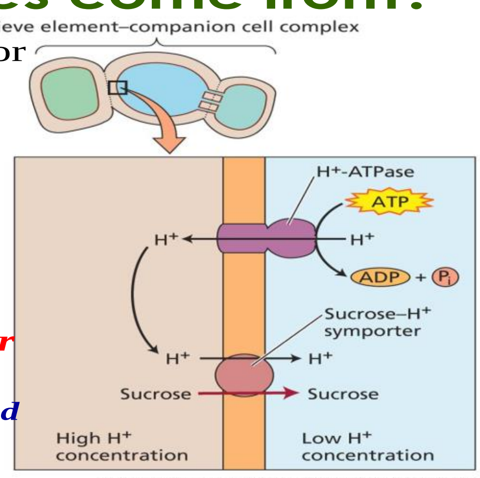
Phloem Loading: Where do the solutes come from?

- In a process called ***sieve element loading***, sugars are transported into the sieve elements and companion cells
- Sugars become more concentrated in sieve elements and companion cells than in mesophyll cells
- Once in the sieve element /companion cell complex sugars are transported away from the source tissue – called ***export***
  - ***Translocation to the sink tissue is called long distance transport***



Phloem Loading: Where do the solutes come from?

- Movement is via either apoplast or symplast
- Via ***apoplastic pathway*** requires
- ***Active transport against it's chemical potential gradient***
- ***Involves a sucrose-H+ symporter***
  - ***The energy dissipated by protons moving back into the cell is coupled to the uptake of sucrose***



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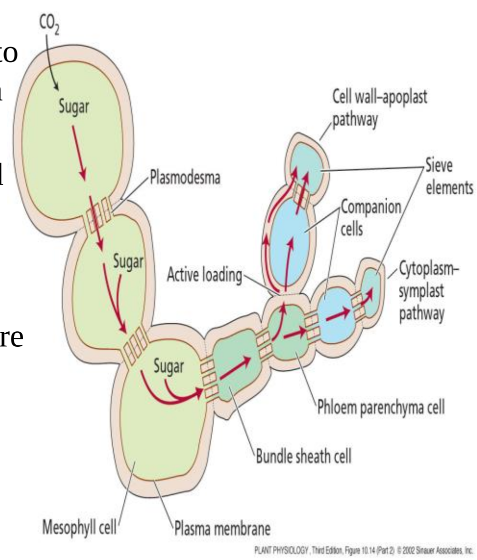
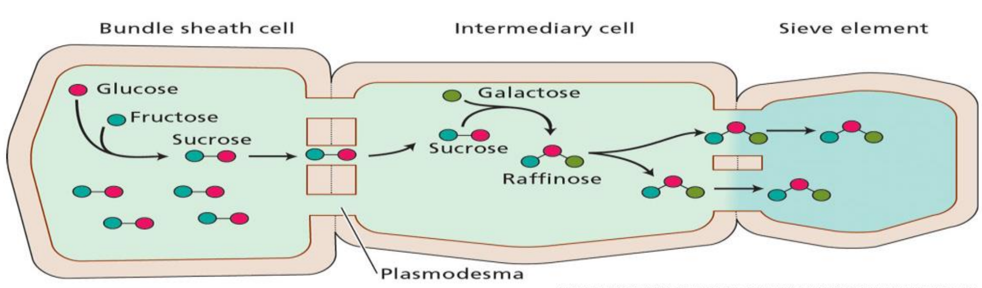


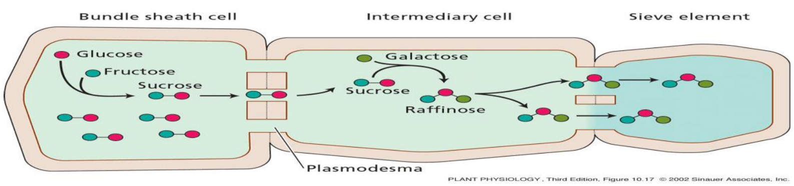
Symplastic phloem loading

- Depends on plant species
  - ***Dependant on species that transport sugars other than sucrose***
- Requires the presence of open plasmodesmata between different cells in the pathway
- Dependant on plant species with intermediary companion cells



Symplastic phloem loading

- Sucrose, synthesized in mesophyll, diffuses into intermediary cells
- Here ***Raffinose*** is synthesized. Due to larger size, can **NOT** diffuse back into the mesophyll
- Raffinose and sucrose are able to diffuse into sieve element



Phloem unloading

- Three steps
- (1) ***Sieve element unloading***:
  - Transported sugars leave the sieve elements of sink tissue
- (2) ***Short distance transport***:
  - After sieve element unloading, sugars transported to cells in the sink by means of a short distance pathway
- (3) ***storage and metabolism***:
  - Sugars are stored or metabolized in sink cells

- **Phloem unloading** also can occur by symplastic or apoplastic pathways
- Varies greatly from growing vegetative organs (root tips and young leaves) to storage tissue (roots and stems) to reproductive organs

Symplastic:

- Appears to be a completely symplastic pathway in young dicot leaves
- Again, moves through open plasmodesmata

Apoplastic: three types

(1) One step, transport from the sieve element-companion cell complex to successive sink cells, occurs in the apoplast. Once sugars are taken back into the symplast of adjoining cells transport is symplastic.

(2) Involves an apoplastic step close to the sieve element companion cell.

(3) Involves an apoplastic step farther from the sieve element companion Cell.