PLANT PHYSIOLOGY
Sugar Transport in Plants

Prof. Dr. S.M. Sitompul
Lab. Plant Physiology, Faculty of Agriculture, **Universitas Brawijaya**
Email : dl@ub.ac.id

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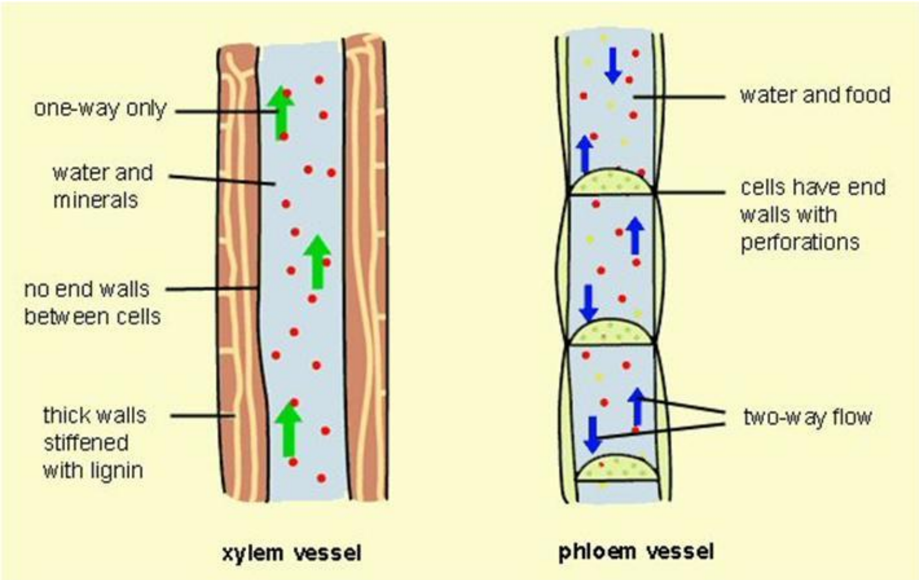
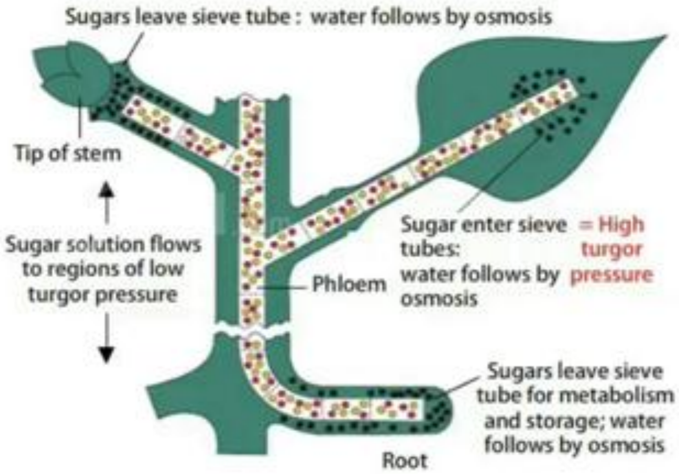
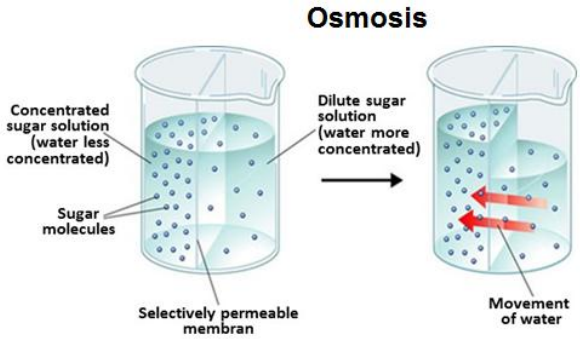


*Komponen utama dari jaringan vakular (pembuluh) pada tanaman adalah xylem (pembuluh kayu) dan phloem (pembuluh tapis). Xylem adalah jaringan yang berfungsi untuk transport air dan mineral dari akar ke bagian atas tanaman. Phloem adalah jaringan yang berfungsi untuk transport senyawa organik serperti gula dari sumber (**sources**) seperti daun yang aktif dalam fotosintesis ke lubuk (sink) yaitu tempat pertumbuhan dan penyimpanan termasuk akar. **Pressure Flow Hypothesis** adalah mekanisme yang dipertimbangkan untuk pergerakan gula melalui phloem.*

Pressure Flow Hypothesis
Water in the adjacent xylem moves into the phloem by **OSMOSIS**. As osmotic pressure (potential) builds up, the phloem sap will move to areas of lower pressure.



At the sink, osmotic pressure must be reduced. Again active transport is necessary to move the sucrose out of the phloem sap and into the cells which will use the sugar – converting it into energy, starch, cellulose, or other substances

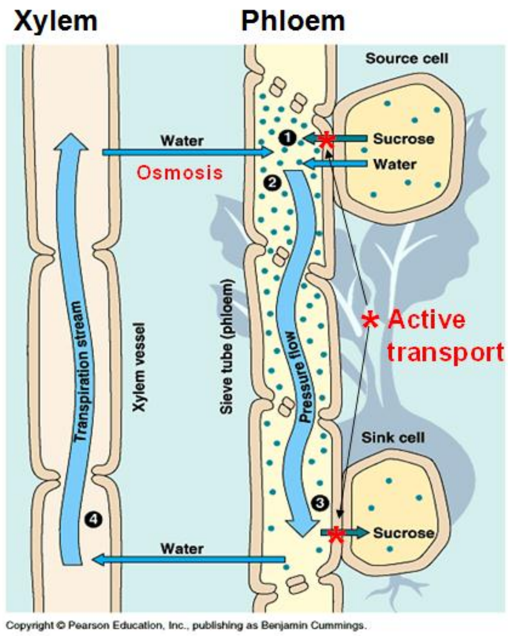


Water potential ($\Psi = \Psi_W$)

$$\Psi = \Psi_P + \Psi_S$$

Ψ_P = pressure/turgor potential

Ψ_S = solute/osmotic potential



***Osmosis**: Air bergerak dari larutan dengan konsentrasi zat terlarut yang tinggi ke yang rendah. Sukrose dari sumber sel (daun) dimuat (loaded) secara aktif dengan bantuan energy (x) ke floem pada bagian sumber (source) yang menghasilkan konsentrasi sukrosa yang tinggi dalam floem pada bagian sumber. Keadaan demikian mengakibatkan aliran air dari xilem ke floem yang diikuti dengan peningkatan tekanan turgor yang mengakibatkan aliran sucrose dari bagian sumber ke bagian lubuk (pressure flow). Sukrose dalam floem pada bagian lubuk dibongkar (unloaded) secara aktif dengan bantuan energy (x) ke lubuk (sink) yang mengakibatkan penurunan tekanan turgor dan aliran air dari floem kembali ke xilem.* Source (left): http://files.lcbiology.webnode.com/200000125-09bd00ab86/osmosisss.jpg

HOW FAR HAVE WE GONE?

1. INTRODUCTION
   - PLANT FUNCTION: CARBOHYDRATE
2. CARBOHYDRATE PRODUCTION
   - Lecture 2: Light Reaction (NADPH Synthesis)
   - Lecture 3: Light Reaction (ATP Synthesis)
   - Lecture 4: Dark Reaction (C3 plants)
   - Lecture 5: Dark Reaction (C4 & CAM plants)
3. CARBOHYDRATE USE
   - Lecture 6: Respiration
4. CARBOHYDRATE TRANSPORT
   - Lecture 7: Sugar Transport

LECTURE OUTCOMES

After the completion of this lecture and mastering the lecture materials, students should be able;

1. To explain the pathway of sugar transport in plants
2. To explain physical structure of transport pathway of sugars
3. To explain evidence supporting the transport pathway of sugars
4. To explain water potential as the driving force of sugar transport
5. To explain the mechanism of sugar transport in the pathway

LECTURE OUTLINE

1. INTRODUCTION - Phloem Structure - Sieve Elements - Sieve Element Features 2. SUGAR TRANSLOCATION - Early Evidence - Structure of Sieve Elements	3. TRANSPORT PROCESS - Direction of Flow - Mechanism of Phloem Transport - Pressure Flow Mechanism

1. INTRODUCTION

1. Phloem Structure

- The two long-distance transport pathways-the phloem and the xylem-extend throughout the plant body. The phloem is generally found on the outer side of both primary and secondary vascular tissues (Fig. 10.1 & 10.2).

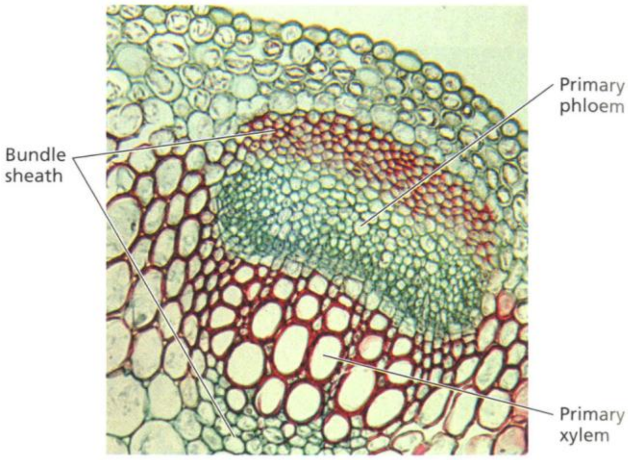


Fig. 10.1 Transverse section of a vascular bundle of trefoil, a clover (*Trifolium*). (130x) The primary phloem is toward the outside of the stem. Both the primary phloem and the primary xylem are surrounded by a bundle sheath of thick-walled sclerenchyma cells, which isolate the vascular tissue from the ground tissue. (© J. N. A. Lott/Biological Photo Service.)

- In plants with secondary growth, the phloem constitutes the inner bark (Fig. 10.2).

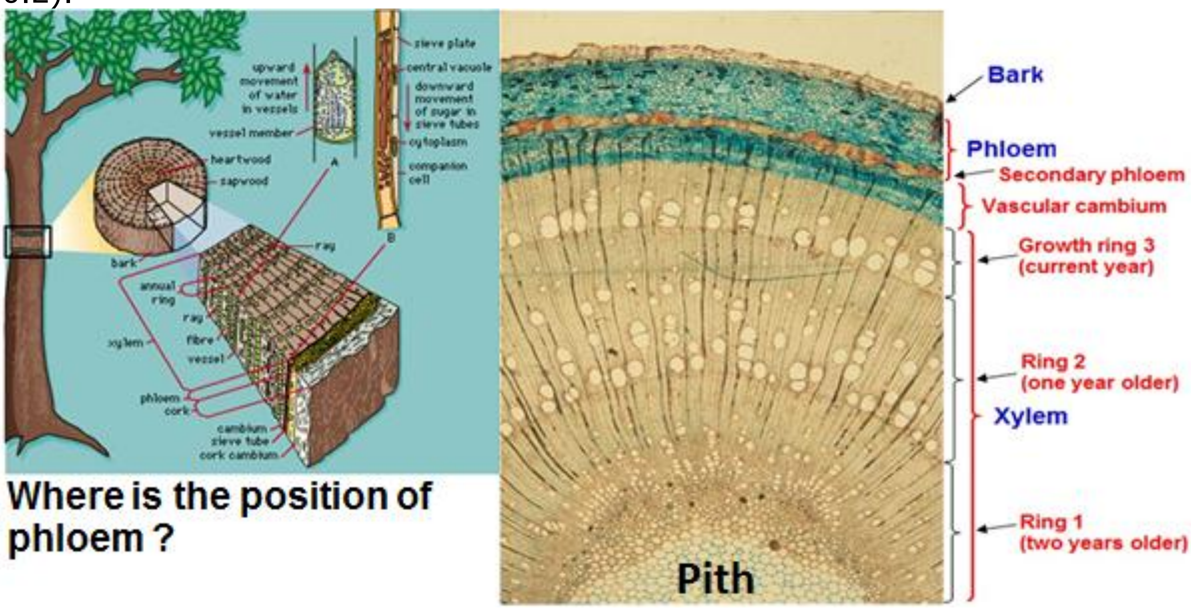


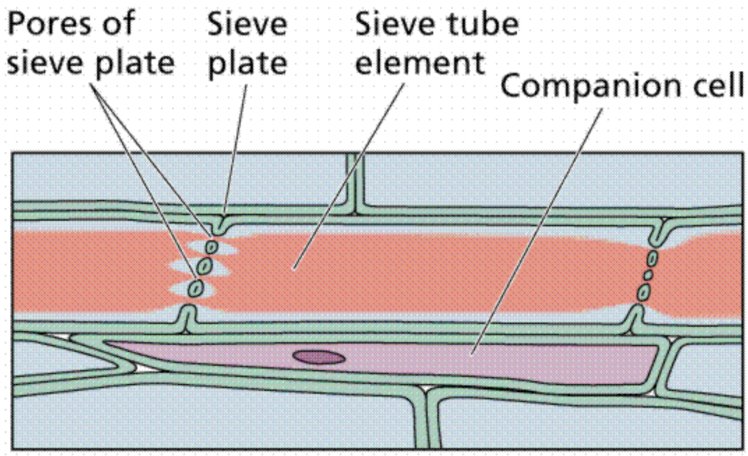
Fig 10.2 Transverse section of a 3-year-old stem of an ash (*Fraxinus excelsior*) tree. (27x) The numbers 1, 2, and 3 indicate growth rings in the secondary

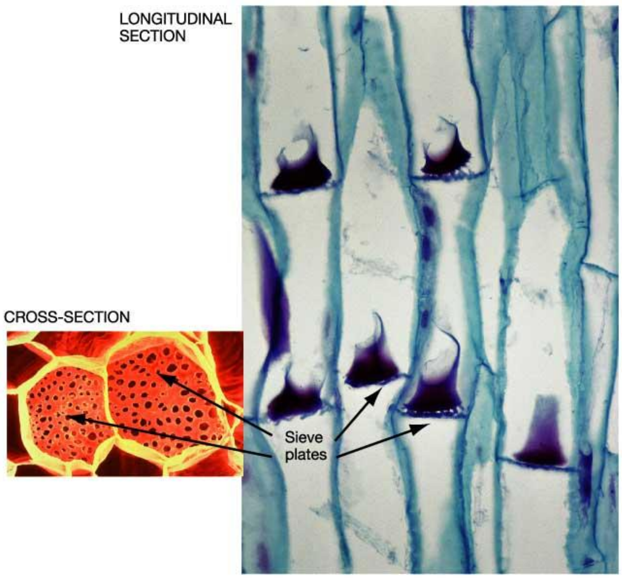
xylem. The old secondary phloem has been crushed by expansion of the xylem. Only the most recent (innermost) layer of secondary phloem is functional. (© P. Gates/Biological Photo Service.)

- Although phloem is commonly found in a position external to the xylem, it is also found on the inner side in many eudicot families.
- In these families the phloem in the two positions is called external and internal phloem, respectively.

2. Sieve Elements

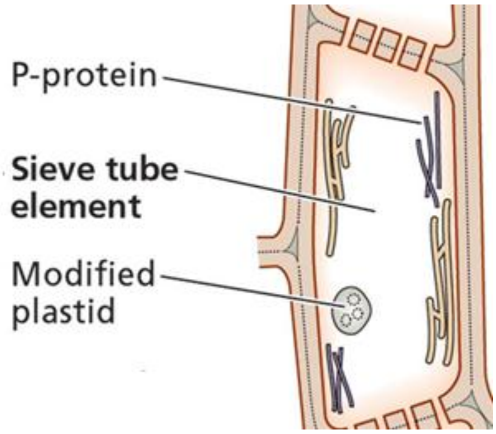
- The cells of the phloem that conduct sugars and other organic materials throughout the plant are called **sieve elements**.
- *Sieve element* is a comprehensive term that includes both the highly differentiated **sieve tube elements** typical of the angiosperms and the relatively unspecialized **sieve cells** of 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 and sclereids (for protection and strengthening of the tissue) and laticifers (latex-containing cells).
- However, only the sieve elements are directly involved in translocation.





3. Sieve element features

- living, membrane-bound cells (compare to tracheary elements of xylem)
- lack some structures and organelles in most living cells - no nuclei, vacuole, Golgi, ribosomes, microtubules, microfilaments
- associated with companion cells that have full set of structures and organelles
- have sieve areas or pores that interconnect adjacent sieve elements
- Sieve tube elements in angiosperm are called sieve cells in gymnosperms

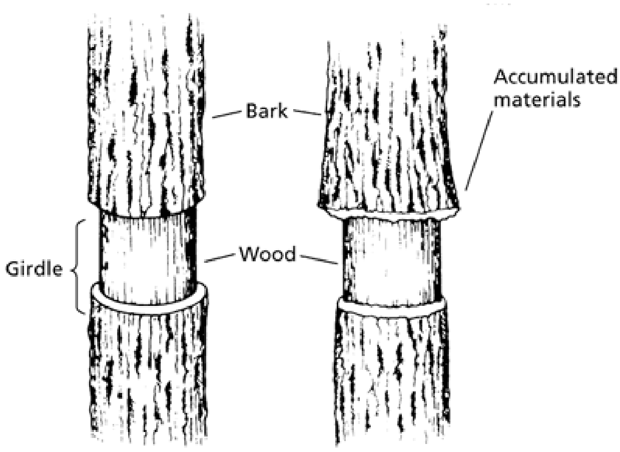


2. SUGAR TRANSLOCATION

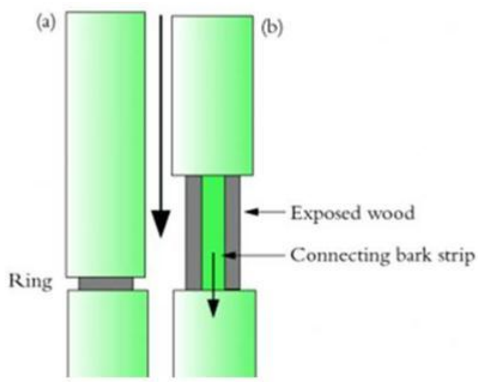
1. Early Evidence

- These classical experiments 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.

  Evidence 1: A classic experiment – girdling. "Girdling" a woody plant causes swelling of stem above the point of damage, indicating a blockage of phloem transport.



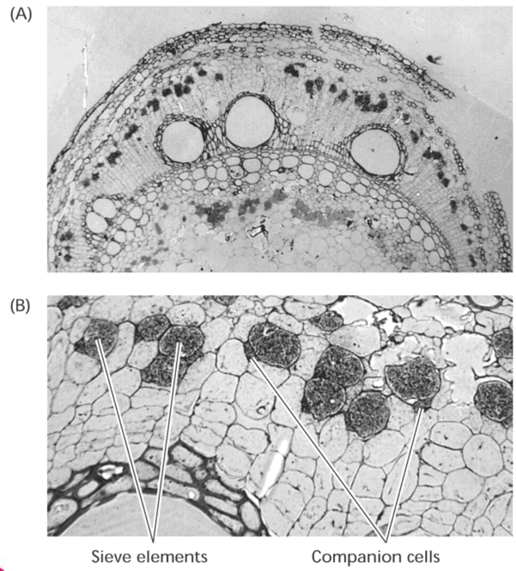
  a) Mason and Maskell (1928) demonstrated that removing a complete ring of bark, while leaving the wood (xylem) intact, prevented downward movement of sugars.
  b) When a strip of bark was retained between upper and lower stem parts, sugars flowed downwards in direct proportion to the width of the remaining bark



Width of bark strip (% of intact stem)	0	10	33	87
Carbohydrate transported to the lower part of the stem in 24 h (mg)	0	437	609	744

  Evidence 2:

- When radioactive compounds became available, $^{14}CO_2$ was used to show that sugars made in the photosynthetic process are translocated through the phloem sieve elements.



Evidence 3: Radioactive labeling with $^{14}CO_2$ can trace movement of sugars in the phloem, and from source leaves to sinks throughout the plant.

2. Structure of Sieve Elements

- Mature sieve elements are unique among living plant cells (Figs. 10.3 & 10.4).

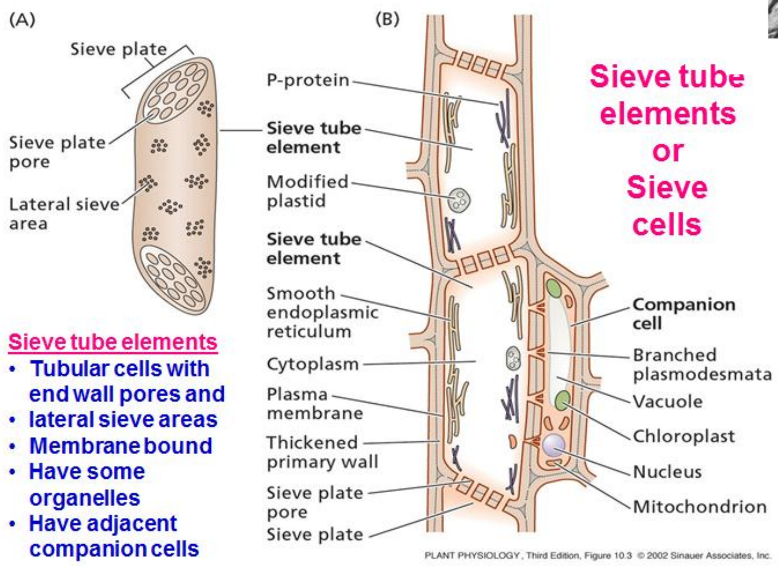
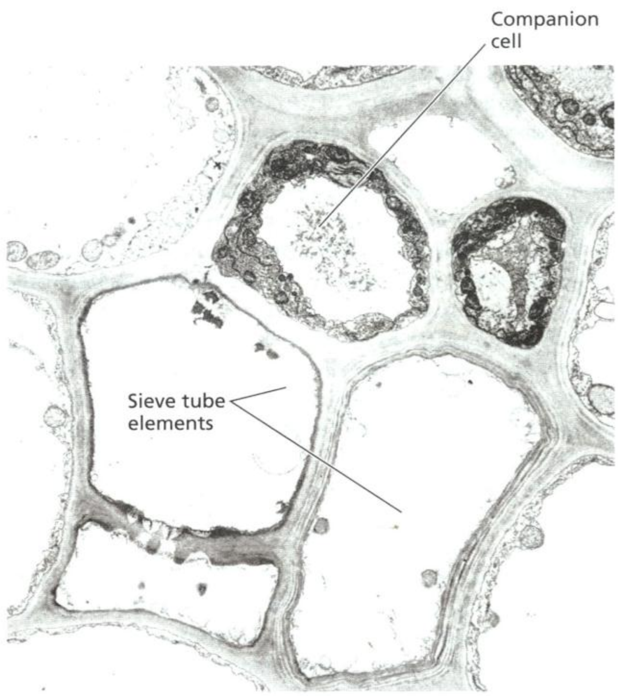


Fig. 10.4 Electron micrograph of a transverse section of ordinary companion cells and mature sieve tube elements. (3600x) The cellular components are distributed along the walls of the sieve tube elements, where they offer less resistance to mass flow. (From Warmbrodt 1985.)



3. TRANSPORT PROCESS

1. Direction of Flow

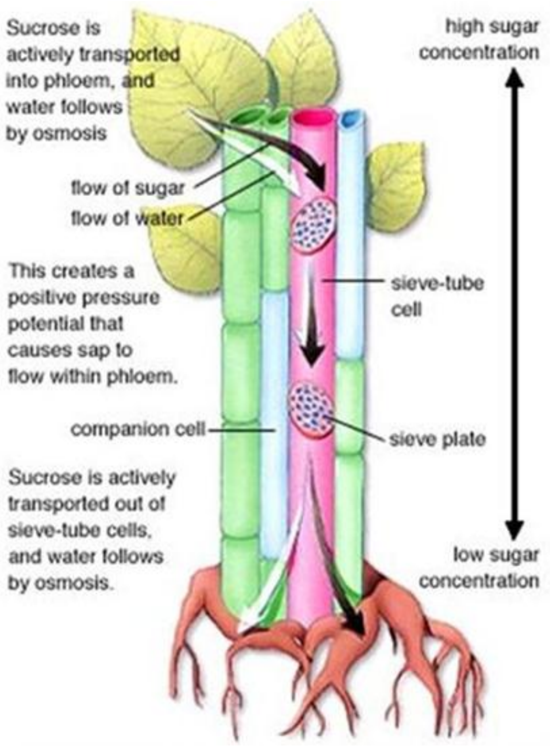
- Sap in the phloem is not translocated exclusively in either an upward or a downward direction, and translocation in the phloem is not defined with respect to gravity.
- Rather, sap is translocated from areas of supply, called **sources**, to areas of metabolism or storage, called **sinks**.

Source → Sink

Source - produces more carbohydrates than required for its own needs.
Sink - produces less carbohydrates than it requires.

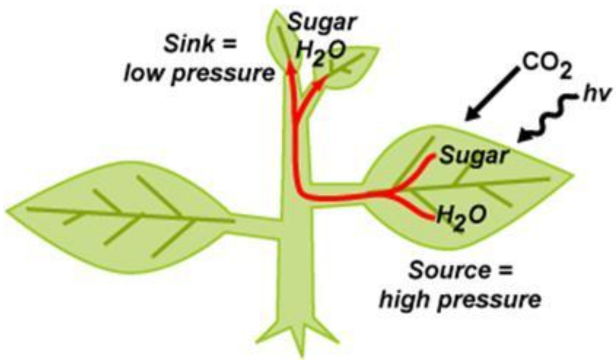
1. Leaves:

- typically sources (supply roots, meristems, fruits), but
- when just forming, are briefly sinks and nutrients enter via phloem rather than xylem.



2. Roots: typically sinks (fed by phloem).

- May become sources when trees leaf out in the spring
- Then assimilated nutrients supply leaves rather than nutrients from soil.



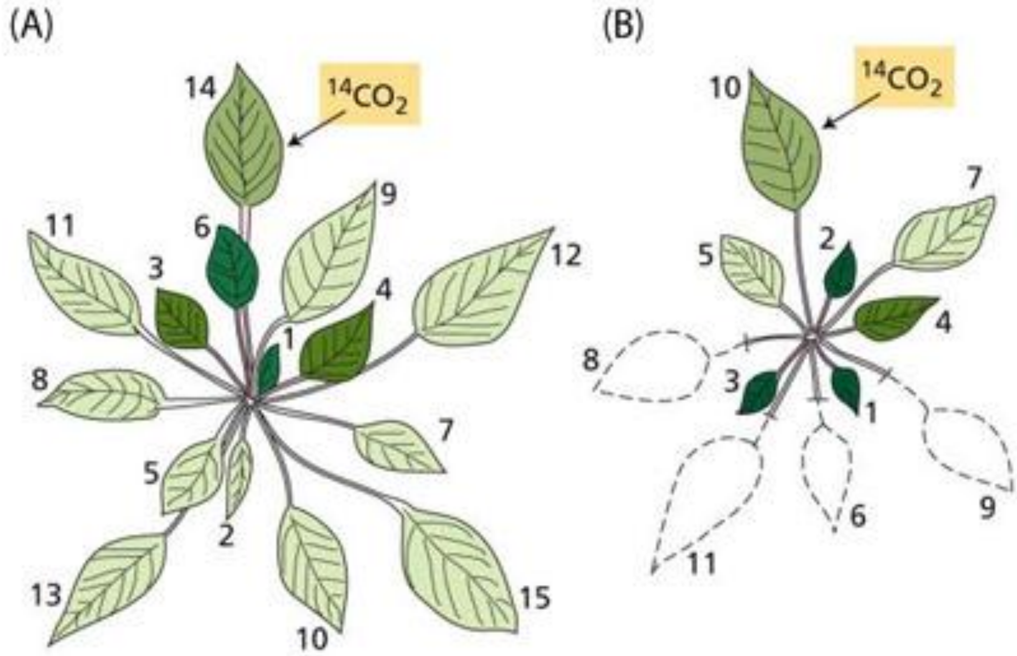
3. Fruits, or storage organs: are sinks as they develop.

- If seed germinates, or the storage organs become sources when the bulb sends out shoots in the spring.

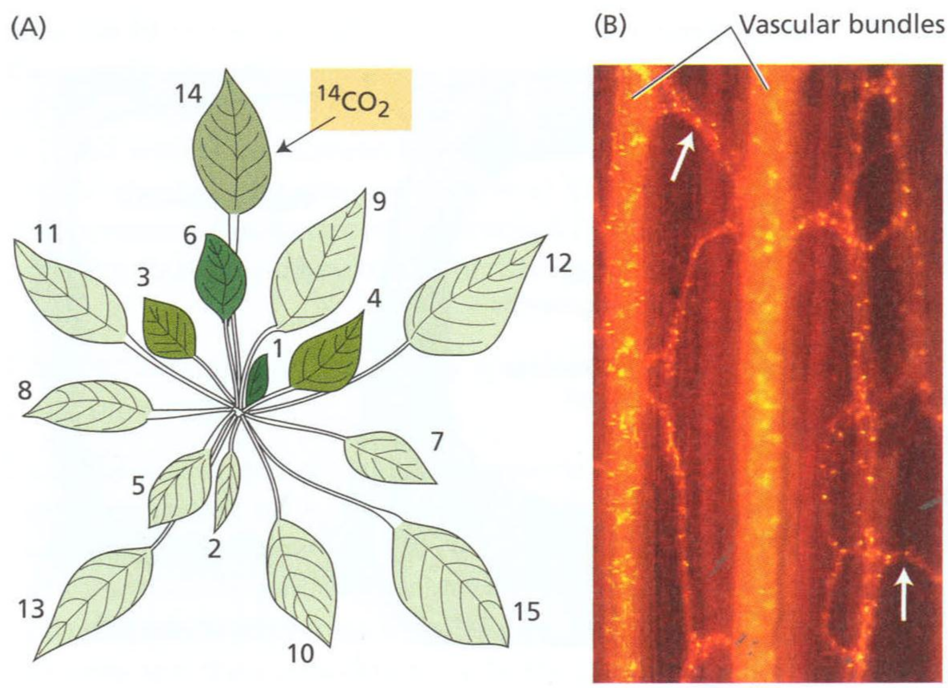
  Sugar derived from CO_2 and light energy is loaded with H_2O into the phloem of mature leaves to establish a region of high pressure. Growing tips (represented by developing leaves) utilize sugars to create a region of low pressure, causing bulk flow from source to sink tissues.

The direction of phloem translocation within the plant can be explained by source-sink relationships.

Distribution of radioactivity from a single labeled source leaf in an intact sugar beet plant (*Beta vulgaris*) . This was determined 1 week after $^{14}CO_2$ was supplied for 4 hours to a single source leaf (arrow).



The degree of radioactive labeling is indicated by the intensity of shading of the leaves. Leaves are numbered according to their age; the youngest, newly emerged leaf is designated 1



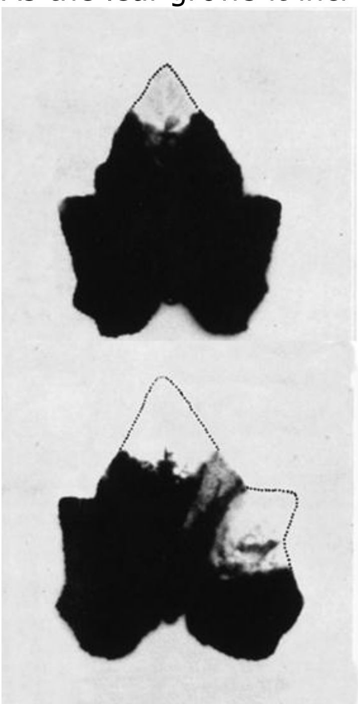
Anatomical and developmental determinants of the direction of source-sink translocation.

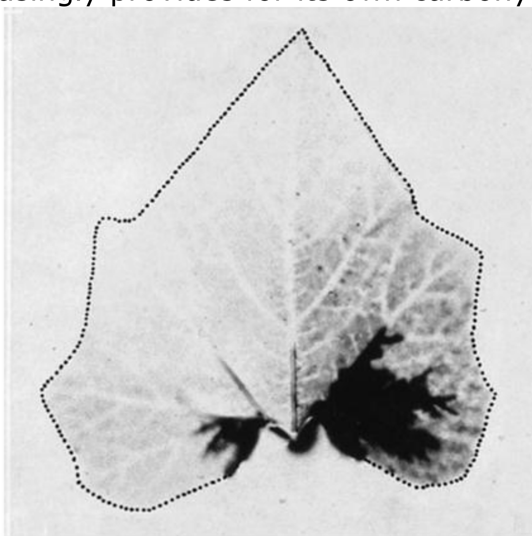
1. **Proximity** - sinks tend to be supplied by closer sources

2. **Vascular connections** may cause distinct source-sink patterns that counter proximity
3. **Source-sink relationships** may shift during development

Young leaf is completely dependent on carbohydrates from other sources. It is a strong sink.

As the leaf grows it increasingly provides for its own carbohydrate needs.

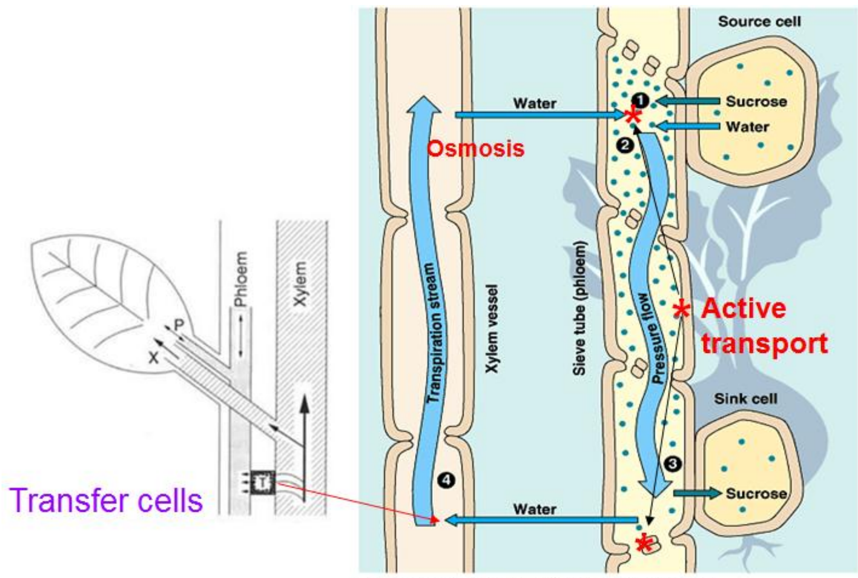




Mature leaf is largely a carbohydrate exporter (source)

2. Mechanism of Phloem Transport

- *What is the mechanism of phloem transport?*
- *What causes flow?, and What's the source of energy?*



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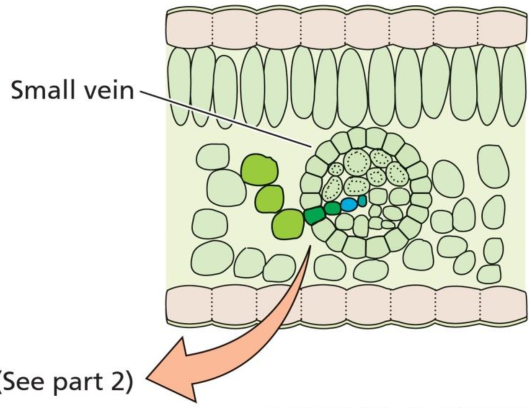
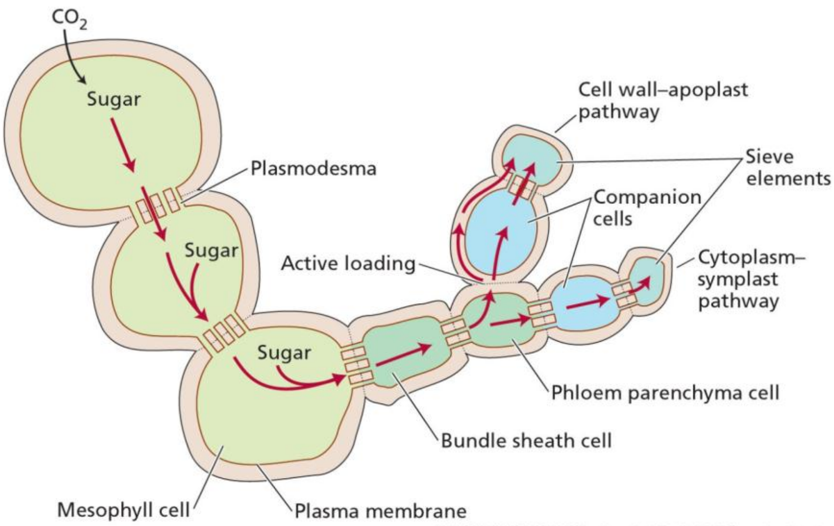
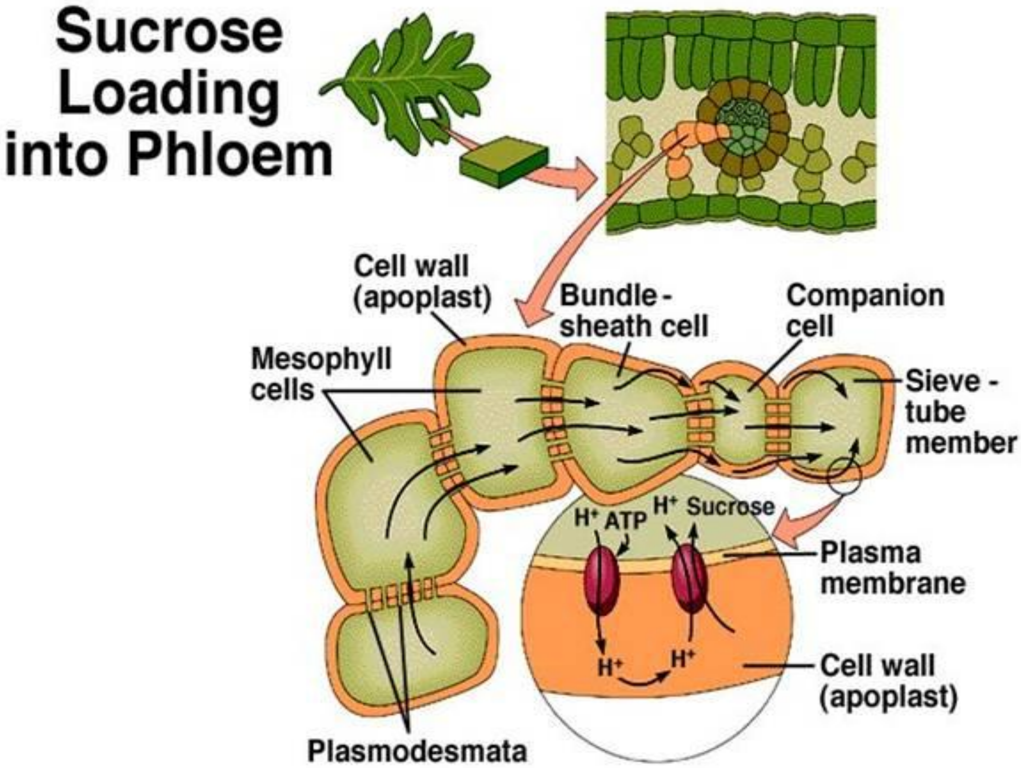
Velocities ≈ 1 m hour^{-1}, much faster than diffusion.
More recent measurements of velocity using NMR spectrometry and magnetic resonance imaging yielded an average velocity for castor bean of 0.25 mm sec^{-1} (equivalent to 90 cm h^{-1})

Sugars are moved from **photosynthetic cells** and actively (energy) loaded into companion & sieve cells.

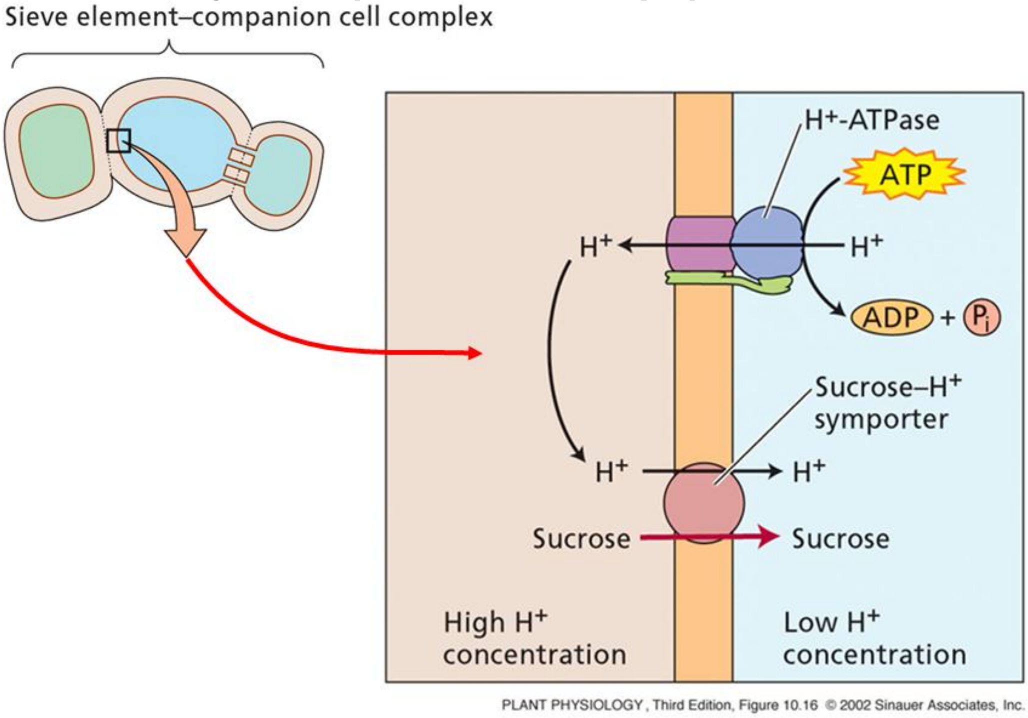
The concentrating of sugars in sieve cells drives the osmotic uptake of water.

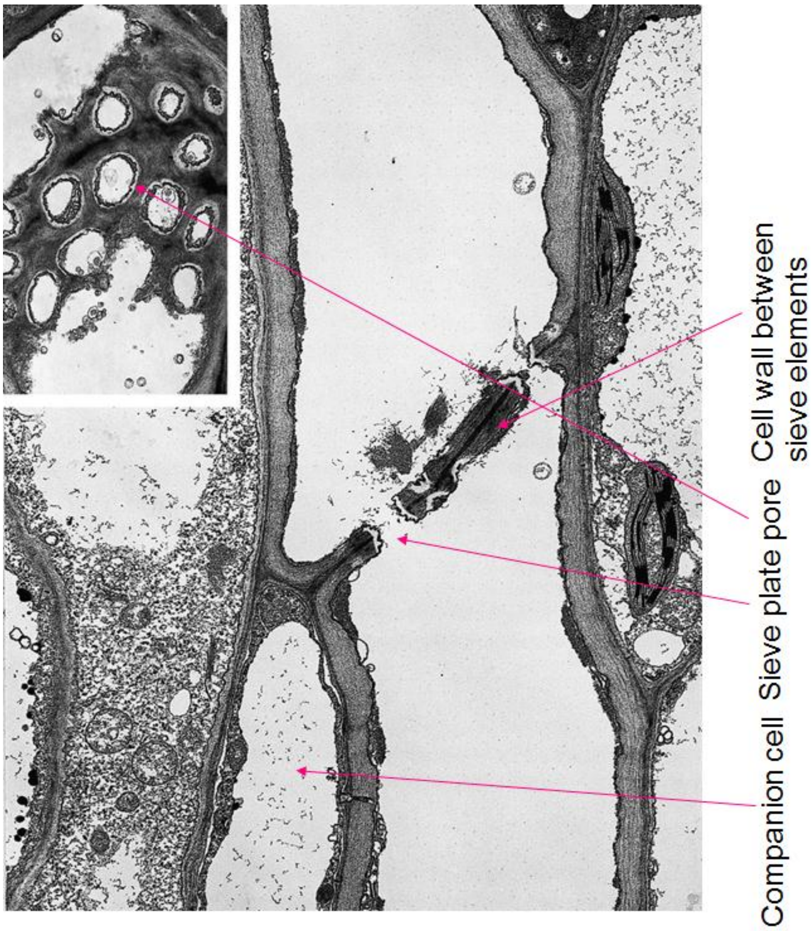




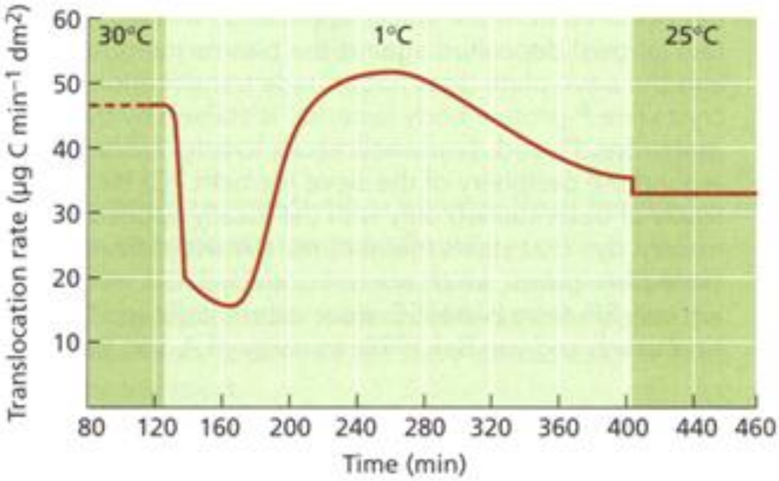


Phloem loading uses a **proton/sucrose symport**.





The energy requirement for translocation in the path is small
The chilling of a source leaf petiole partially reduces the rate of translocation in sugar beet.



However, translocation rates recover with time despite the fact that ATP production and utilization are still largely inhibited by chilling.

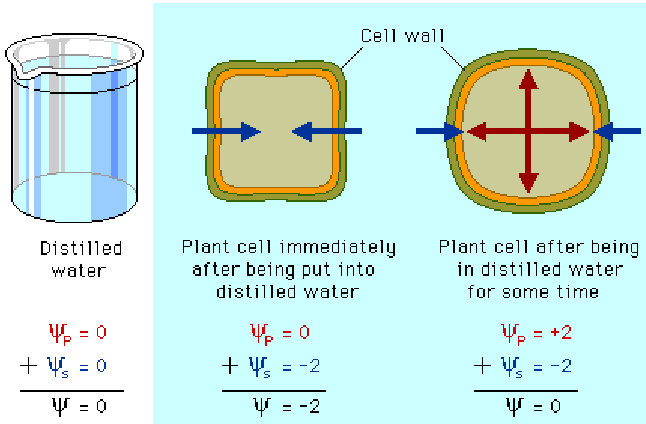
$^{14}CO_2$ was supplied to a source leaf, and a 2-cm portion of its petiole was chilled to 1^0C. Translocation was monitored by the arrival of ^{14}C at a sink leaf. (1 dm [decimeter] = 0.1 meter) (After Geiger and Sovonick 1975.)

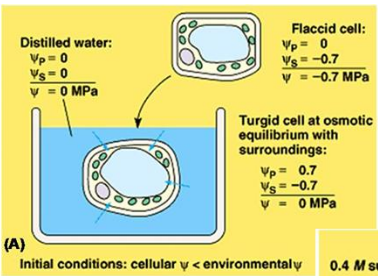
3. Pressure-flow Mechanism

- Pressure flow model was first proposed by Ernst Müch in 1930.

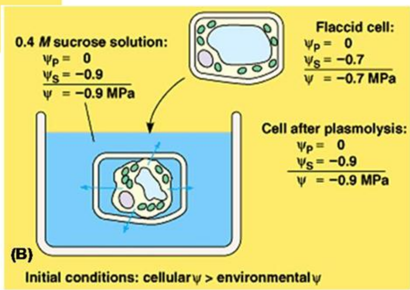
$\psi_W = \psi_P + \psi_S$

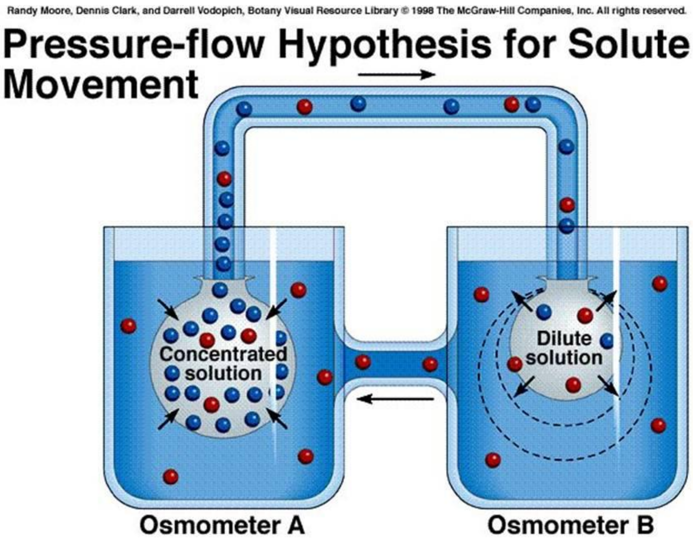
$\psi = \psi_W$ = water potential
ψ_P = pressure potential (turgor pressure)
ψ_S = solute (osmotic) potential





Plasmolysis



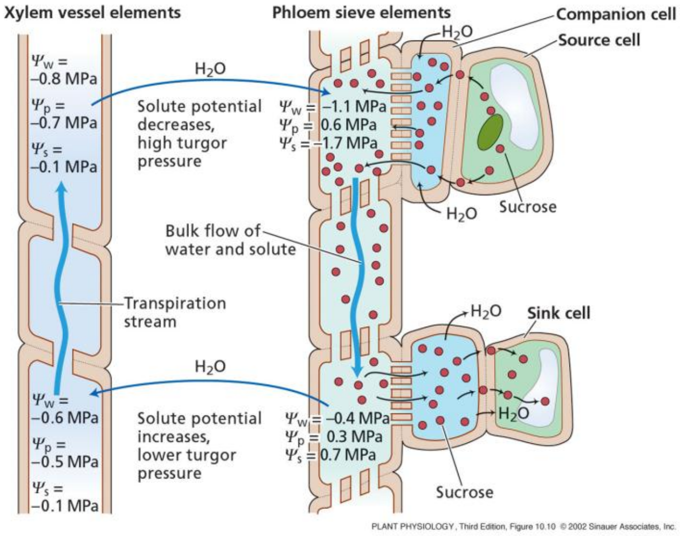


The bags are immersed in two interconnected troughs filled with water. As soon as the bag A is immersed in water, water from the trough rushes into the membranous bag A. On the contrary, the bag B as it is filled with only water

The pressure-flow model of phloem translocation

1. Flow is driven by a gradient of pressure, **Y_P**.
2. At source end of pathway
   - Active transport of sugars into sieve cells
   - Y_s and Y_w decrease
   - Water flows into sieve cells and turgor increases
3. At sink end of pathway
   - Unloading (active transport again) of sugars
   - Y_s and Y_w increase
   - Water flows out of sieve cells and turgor decreases

Phloem solution moves along a gradient of pressure generated by a solute concentration (osmotic potential, ψ_s) difference between source and sink ends of the pathway



1. Sugar is actively loaded into the sieve tube at the source
2. With the increased concentration of sugar, the water potential is decreased, and water from the xylem enters the sieve tube by osmosis.

3. Sugar is removed (unloaded) at the sink, and the sugar concentration falls; as a result, the water potential is increased, and water leaves the sieve tube.
4. With the movement of water into the sieve tube at source and out at the sink, the sugar molecules are carried passively by the water along the concentration gradient between source and sink.
5. Note that the sieve tube between source and sink is bounded by a differentially permeable membrane, the plasma membrane. Consequently, water enters and leaves the sieve tube not only at the source and sink, but all along the pathway.
6. Evidence indicate that few if any of the original water molecules entering the sieve tube at the source end up in the sink, because they exchanged with other water molecules that enter the sieve tube from the phloem apoplast along the pathway.

REFERENCE

Taiz, L. and Zeiger, E., 2010. Plant Physiology Chapter 8: The Carbon Reaction. Benjamin/Cummings, Company, Inc., Redwood City, California