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LECTURE 7: SUGAR TRANSPORT

The diagram illustrates the structural differences between xylem and phloem vessels. The xylem vessel is shown on the left with thick, lignified walls and no end walls between cells, allowing for one-way flow of water and minerals. The phloem vessel is shown on the right with thinner walls and perforations between cells, allowing for two-way flow of water and food.

xylem vessel phloem vessel

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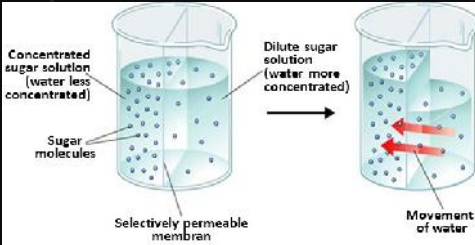
Pressure Flow Hypothesis

- 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

<http://i.ytimg.com/vi/wIAhsMvavx8/maxresdefault.jpg>

The diagram illustrates the Pressure Flow Hypothesis. It shows a cross-section of a plant stem with a tip and a root. At the tip, sugar enters sieve tubes, creating high turgor pressure. Water follows by osmosis from the xylem. The phloem then moves the sugar solution to the root, where it leaves the sieve tube for metabolism and storage, and water follows by osmosis.

OSMOSIS



Concentrated sugar solution (water less concentrated)

Dilute sugar solution (water more concentrated)

Sugar molecules

Selectively permeable membrane

Movement of water

Water potential ($\Psi = \Psi_w$)

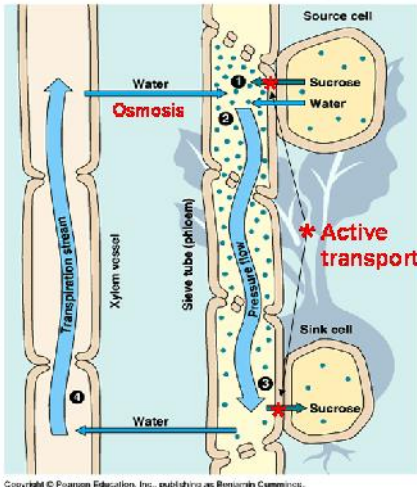
$j = j_p + j_s$

Ψ_p = pressure/turgor potential

Ψ_s = solute/osmotic potential

Source (left): <http://files.lcbiology.weebnode.com/200000125-09bd00ab86/osmosisss.jpg>

XYLEM PHLOEM



Water

Osmosis

Transpiration stream

Xylem vessel

Sieve tube (phloem)

Pressure flow

Source cell

Sucrose

Water

* Active transport

Sink cell

Sucrose

Water

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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 OUTCOME

Students, after mastering materials of the present lecture, 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

1. Phloem Structure
2. Sieve Elements
3. Sieve Element Features

2. SUGAR TRANSLOCATION

1. Early Evidence
2. Structure of Sieve Elements

3. TRANSPORT PROCESS

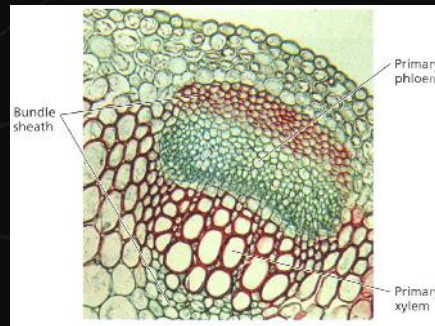
1. Direction of Flow
2. Mechanism of Phloem Transport
3. Pressure Flow Mechanism

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.)

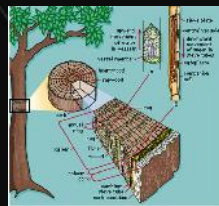


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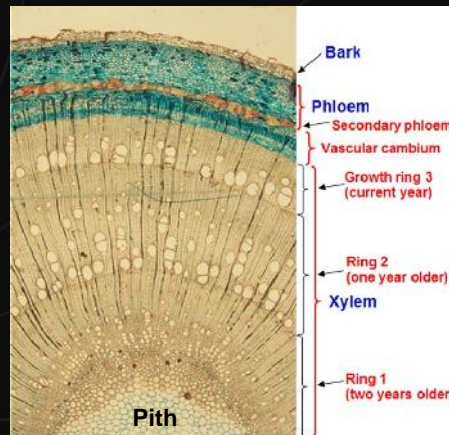
- In plants with secondary growth, the **phloem** constitutes the **inner bark** (Fig. 10.2).



Where is the position of phloem ?

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.)



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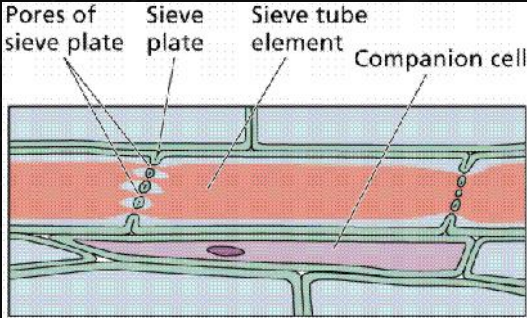
- Although **phloem** is commonly found in **a position** external to the xylem, it is also found on the **inner side** in many eudicot families.
- In these families the phloem in the two positions is called **external** and **internal** phloem, respectively. M

2. Sieve Elements

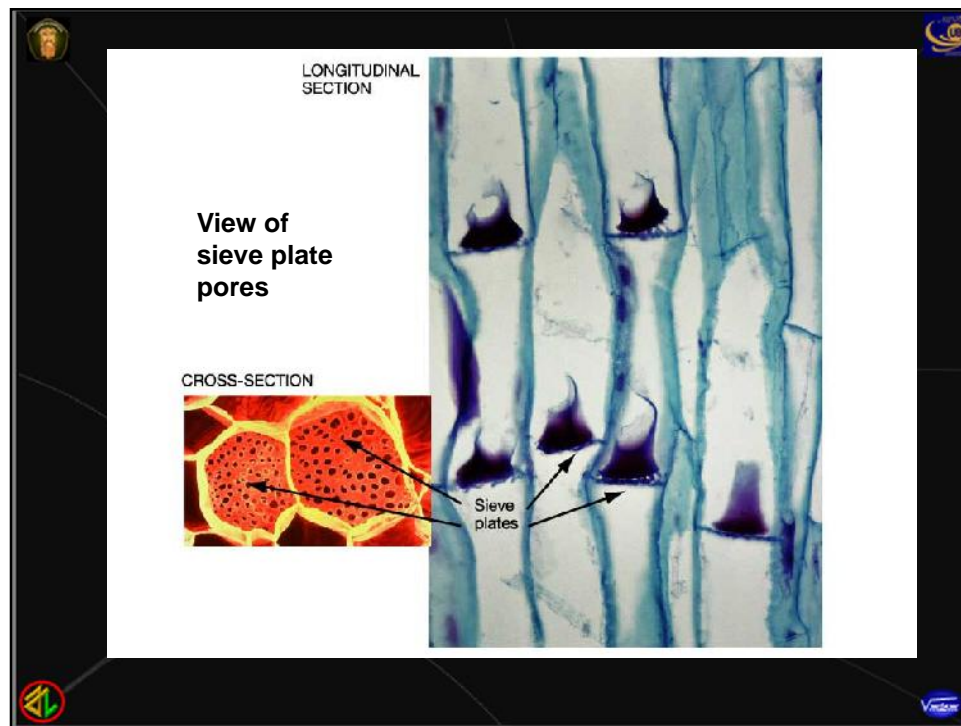
- The **cells of the phloem** that conduct sugars and other organic materials throughout the plant are called **sieve elements**.
- *Sieve element* is a comprehensive term that includes both the highly differentiated **sieve tube elements** typical of the **angiosperms** and the relatively unspecialized **sieve cells** of **gymnosperms**.

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- 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.

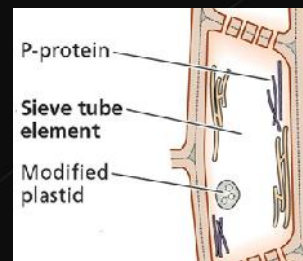


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3. Sieve element features

- 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.



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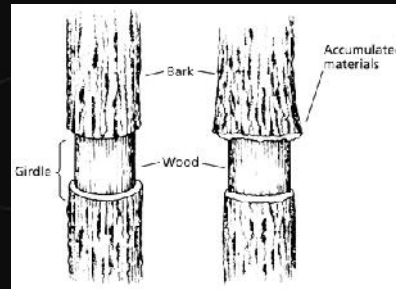
2. SUGAR TRANSLOCATION

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.



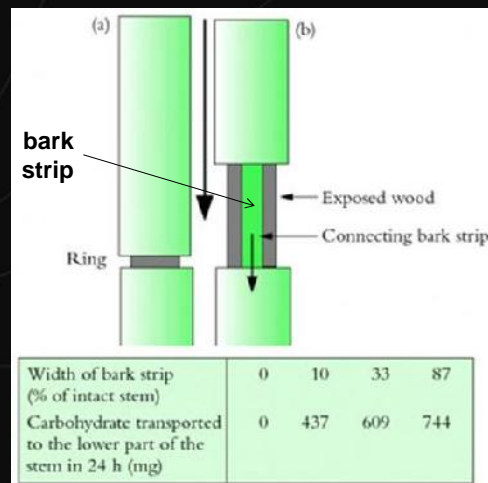
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- a) Mason and Maskell (1928) demonstrated that removing a complete ring of bark, while leaving the wood (xylem) intact, prevented downward movement of sugars.

- 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**



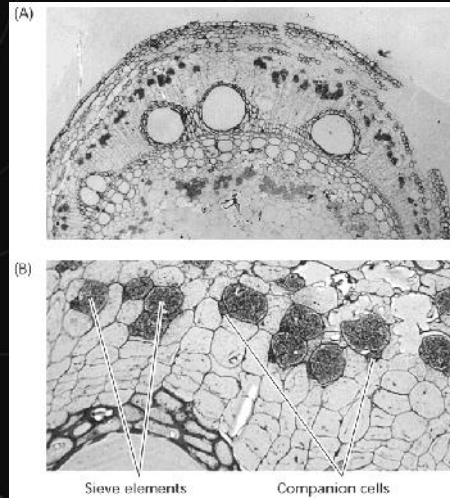
Evidence 2



- When radioactive compounds became available, $^{14}\text{CO}_2$ was used to show that sugars made in the photosynthetic process are translocated through the phloem sieve elements.

Evidence 3

Radioactive labeling with $^{14}\text{CO}_2$ can trace movement of sugars in the phloem, and from source leaves to sinks throughout the plant.



- The phloem is the **vascular system** for moving (translocating) sugars produced in photosynthesis (photosynthate) and other substances throughout the plant.

Evidence 4

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

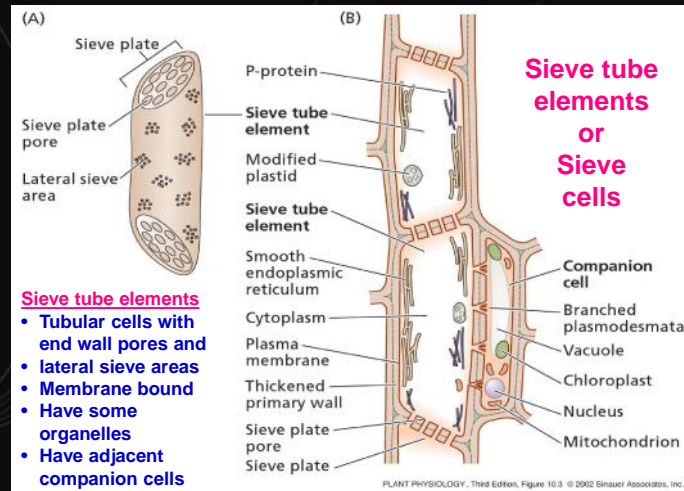
Component	Concentration (mg mL ⁻¹)
Sugars	80.0–106.0
Amino acids	5.2
Organic acids	2.0–3.2
Protein	1.45–2.20
Potassium	2.3–4.4
Chloride	0.355–0.675
Phosphate	0.350–0.550
Magnesium	0.109–0.122

Source: Hall and Baker 1972.

PLANT PHYSIOLOGY, Third Edition, Table 10.2. © 2002 Sinauer Associates, Inc.

2. Structure of Sieve Elements

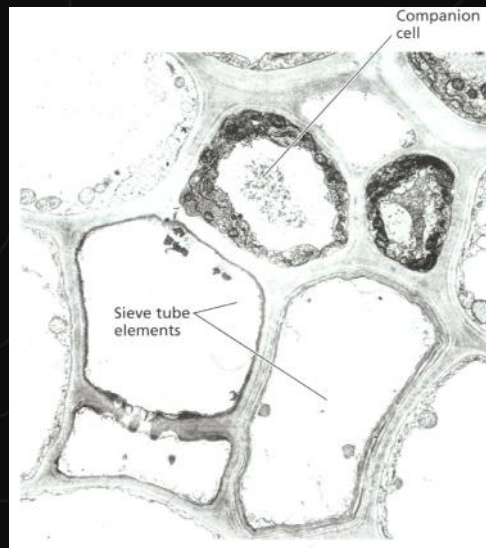
- Mature sieve elements are unique among living plant cells (Figs. 10.3 & 10.4).



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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.)



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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.



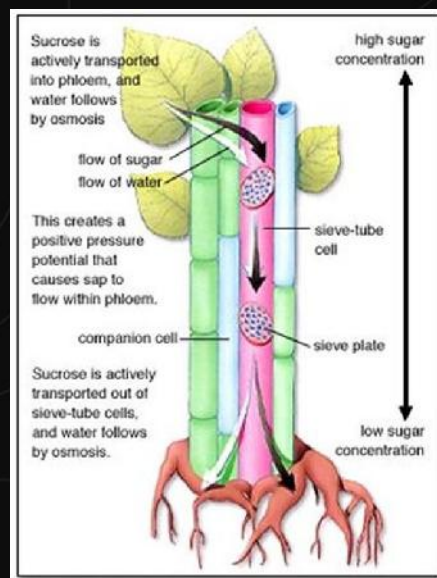
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1. Leaves:

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

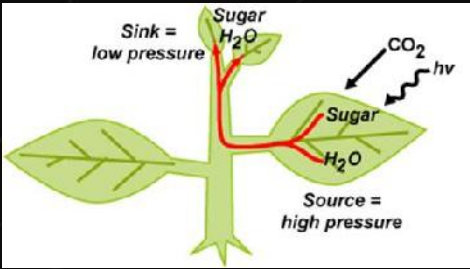


2. Roots: typically **sinks** (fed by phloem).

- 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.

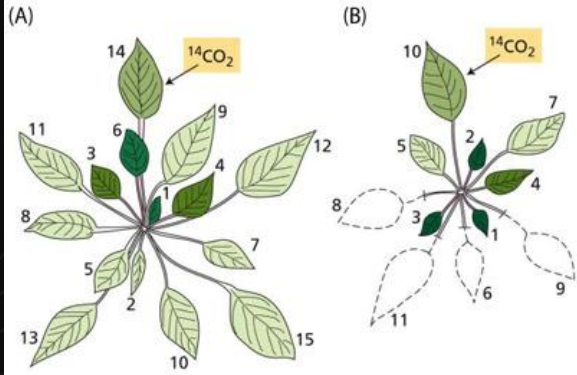
- If seed germinates, or the storage organs become sources when the bulb sends out shoots in the spring.



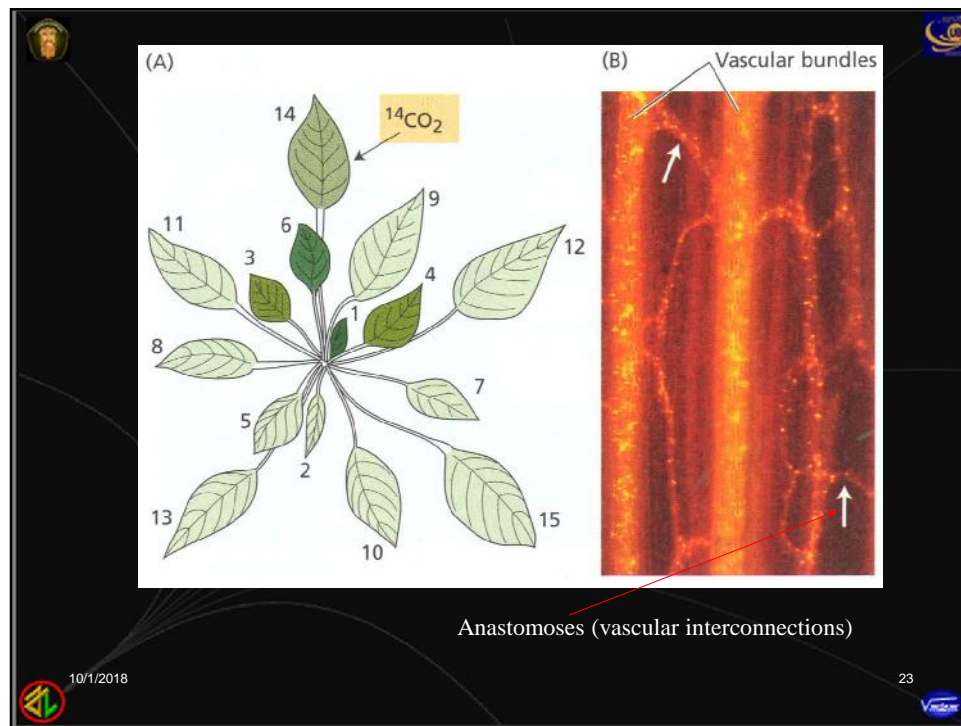
Sugar derived from CO_2 and light energy is loaded with H_2O into the phloem of mature leaves to establish a region of high pressure. Growing tips (represented by developing leaves) utilize sugars to create a region of low pressure, causing bulk flow from source to sink tissues.

– 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 $^{14}\text{CO}_2$ was supplied for **4 hours** to a single source leaf (arrow).

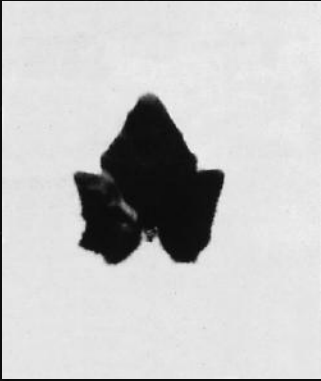


The degree of radioactive labeling is indicated by the intensity of shading of the leaves. Leaves are numbered according to their age; the youngest, newly emerged leaf is designated 1



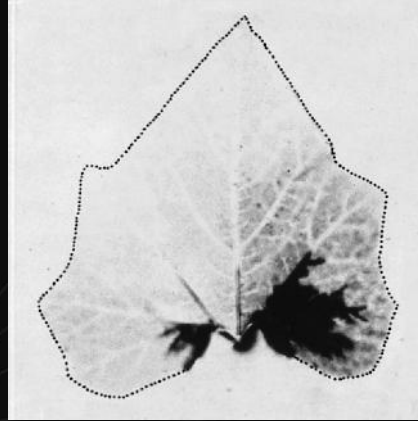
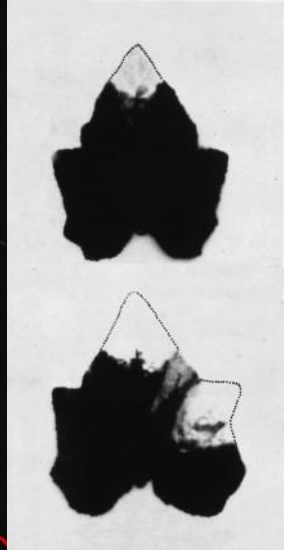
Anatomical and developmental determinants of the direction of source-sink translocation.

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.

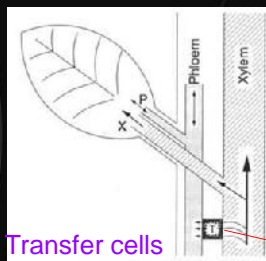
As the leaf grows it increasingly provides for its own carbohydrate needs.



Mature leaf is largely a carbohydrate exporter (source)

2. Mechanism of Phloem Transport

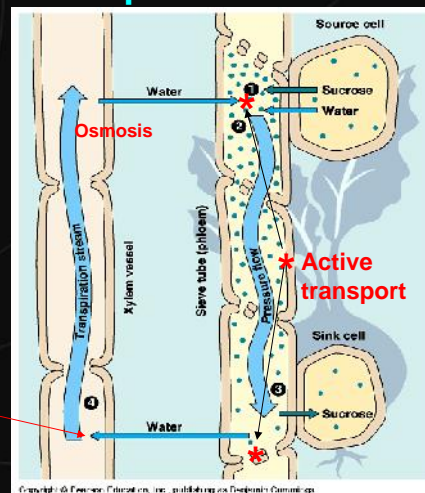
- What is the mechanism of phloem transport?
- What causes flow?, and What's the source of energy?



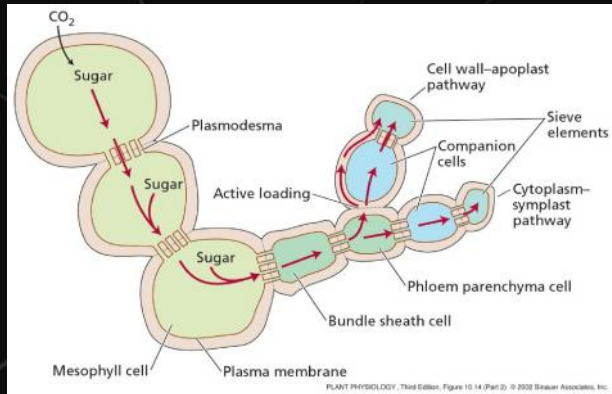
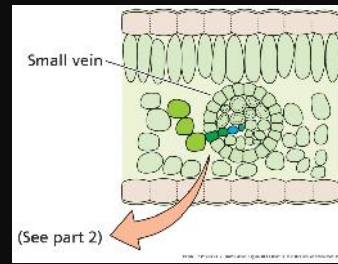
Transfer cells

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})



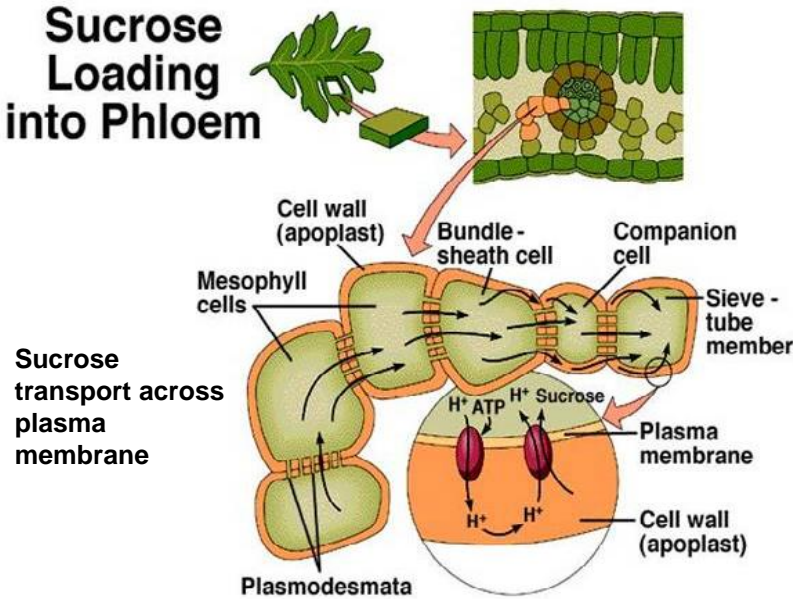
Sugars are moved from photosynthetic cells and actively (energy) loaded into companion & sieve cells.

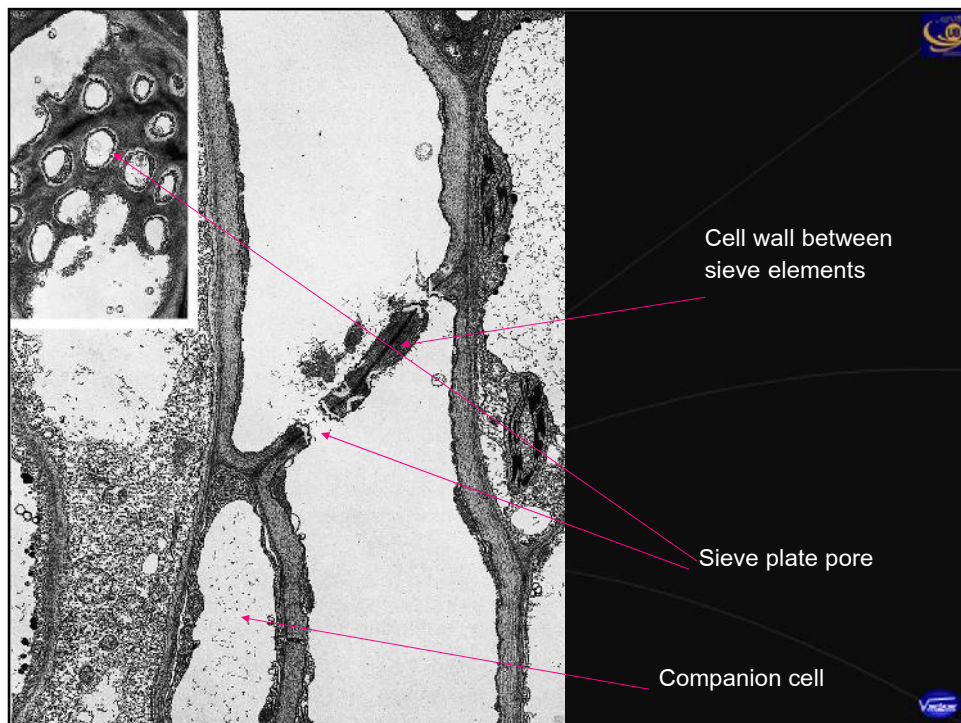
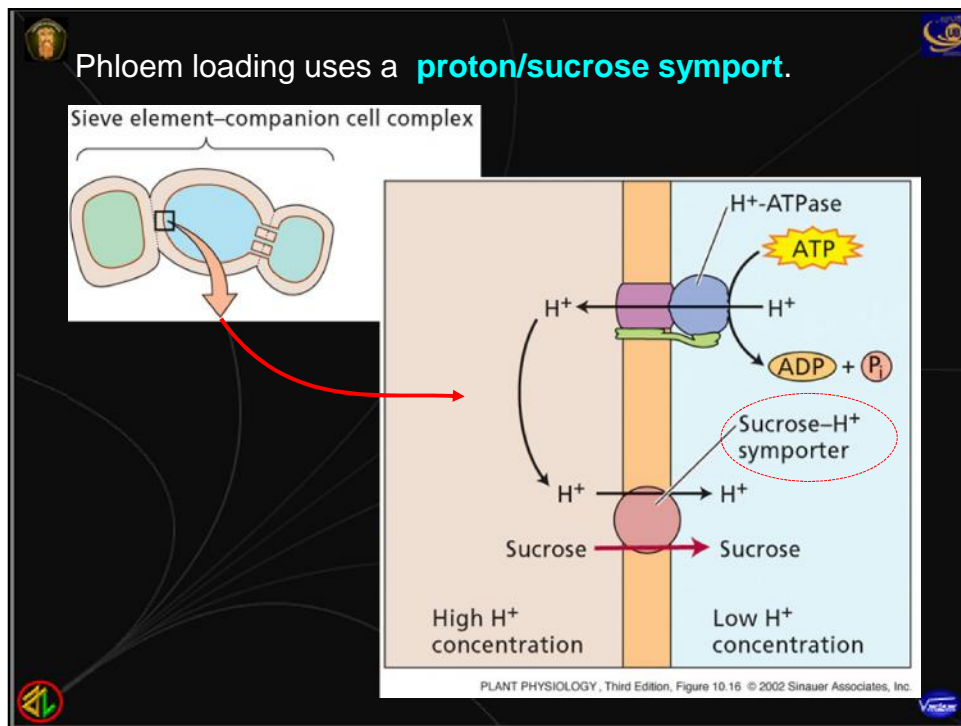


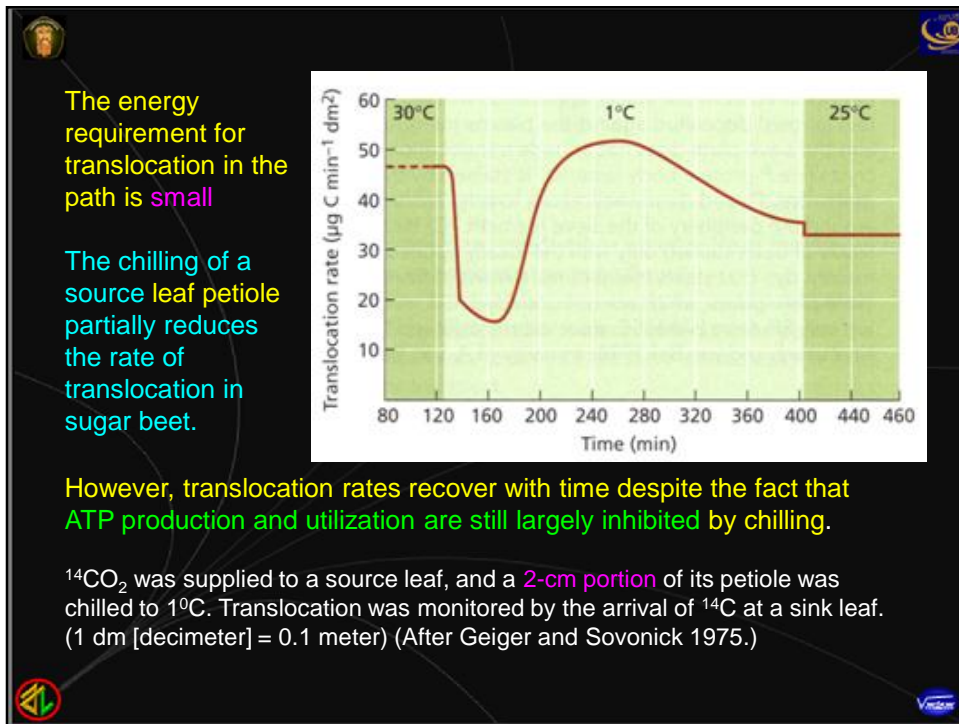
The concentrating of sugars in sieve cells **drives** the osmotic uptake of water.

Sucrose Loading into Phloem

Randy Moore, Dennis Clark, and Darrell Vodopich, Botany Visual Resource Library © 1998 The McGraw-Hill Companies, Inc. All rights reserved.







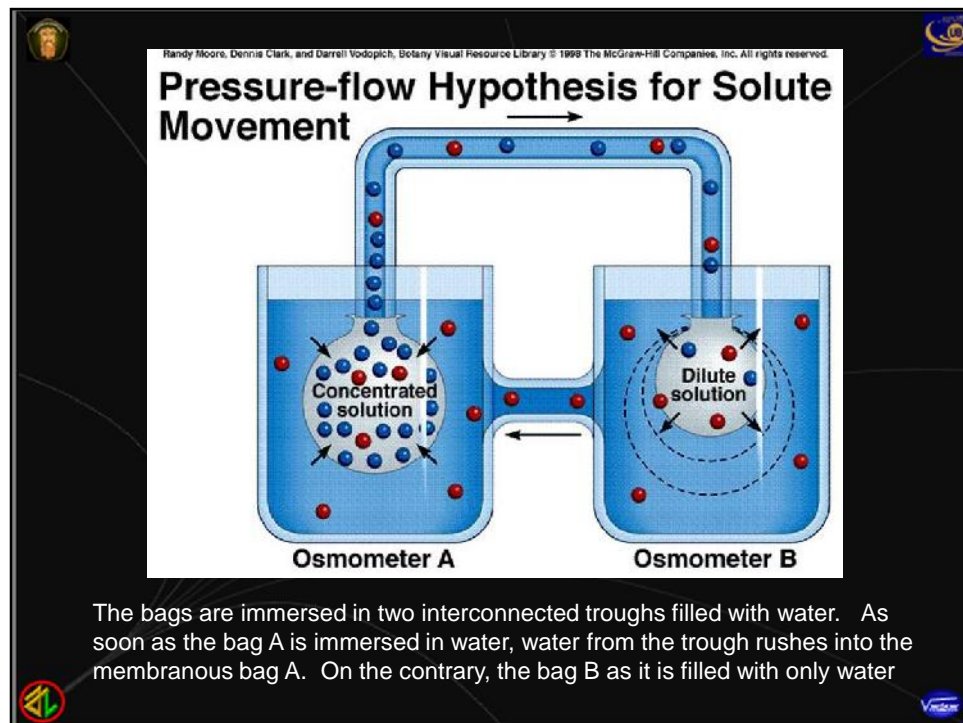
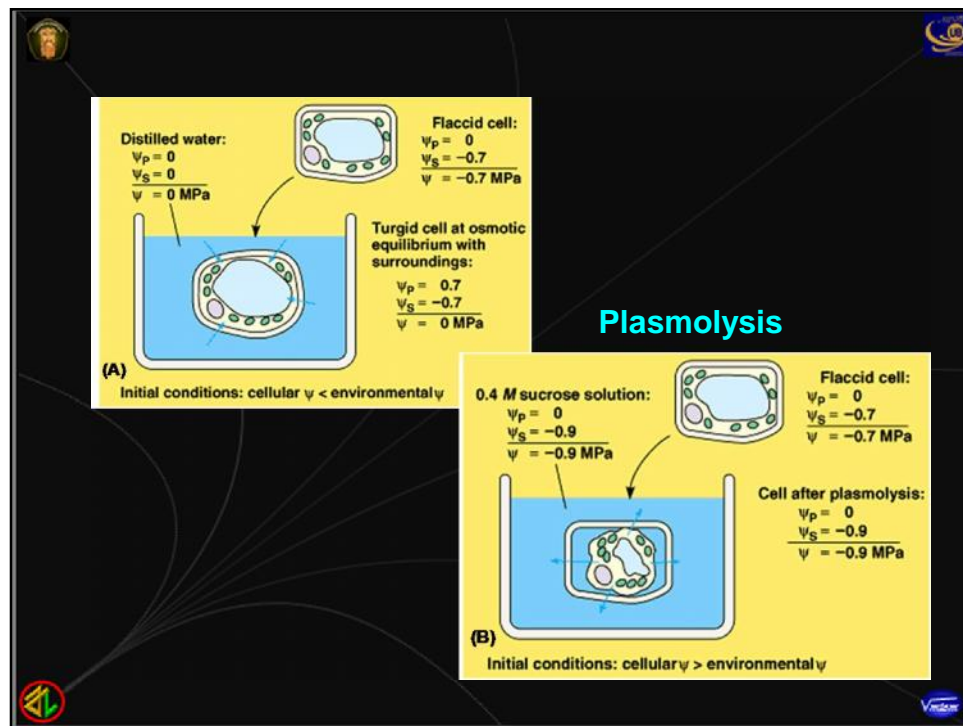
3. Pressure-flow Mechanism

Pressure flow model was first proposed by Ernst Műch in 1930.

$$\mathcal{E}_W = \mathcal{E}_P + \mathcal{E}_S$$

$\mathcal{E} = \mathcal{E}_W$ = water potential
 \mathcal{E}_P = pressure potential (turgor pressure)
 \mathcal{E}_S = solute (osmotic) potential

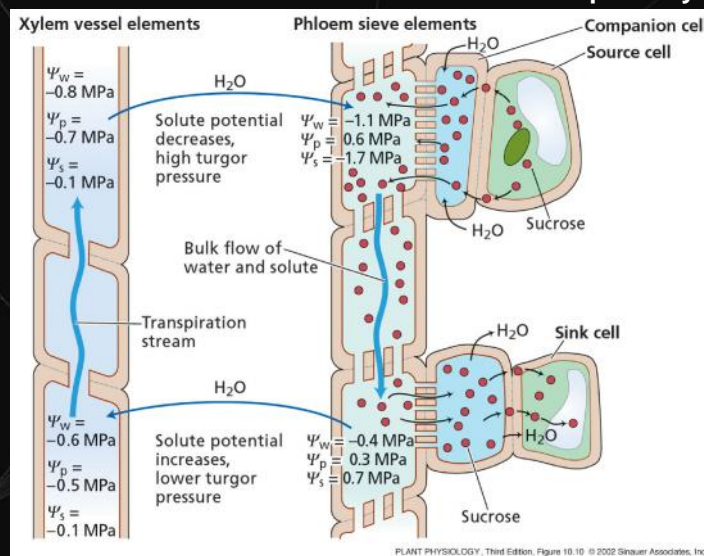
Distilled water	Plant cell immediately after being put into distilled water	Plant cell after being in distilled water for some time
$\psi_p = 0$	$\psi_p = 0$	$\psi_p = +2$
$+ \psi_s = 0$	$+ \psi_s = -2$	$+ \psi_s = -2$
$\psi = 0$	$\psi = -2$	$\psi = 0$






The pressure-flow model of phloem translocation




1. Flow is driven by a gradient of pressure, Ψ_p .
2. At source end of pathway
 - Active transport of sugars into sieve cells
 - Ψ_s and Ψ_w decrease
 - Water flows into sieve cells and turgor increases
3. At sink end of pathway
 - Unloading (active transport again) of sugars
 - Ψ_s and Ψ_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



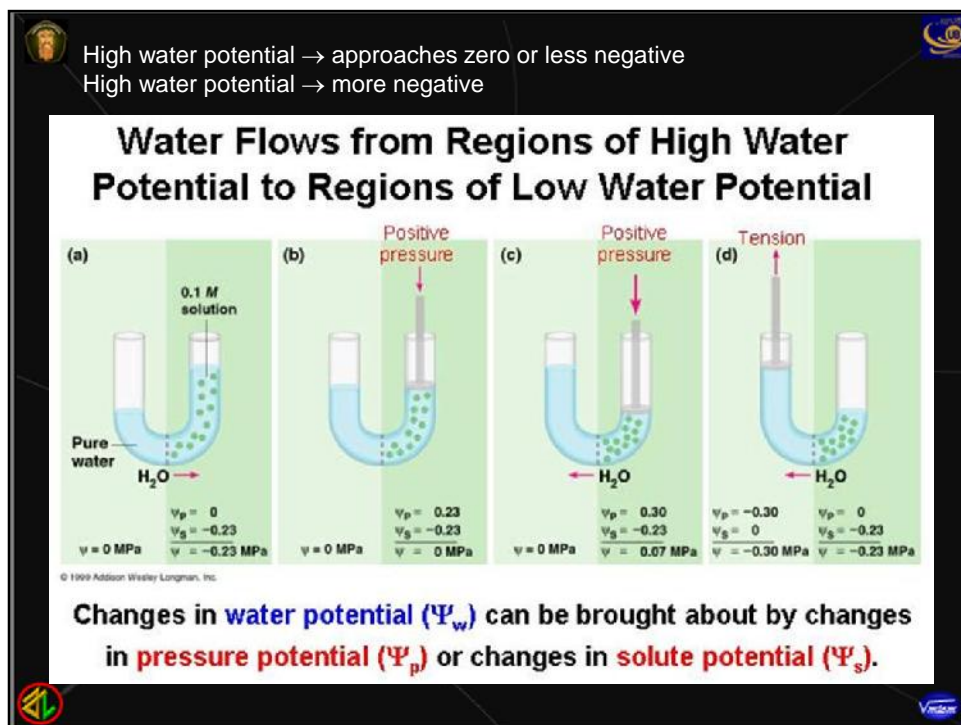


1. Sugar is **actively loaded** into the sieve tube at the source
2. With the increased concentration of sugar, the **water potential** is **decreased**, and water from the xylem enters the sieve tube by osmosis.
3. Sugar is removed (unloaded) at the sink, and the sugar concentration falls; as a result, 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.



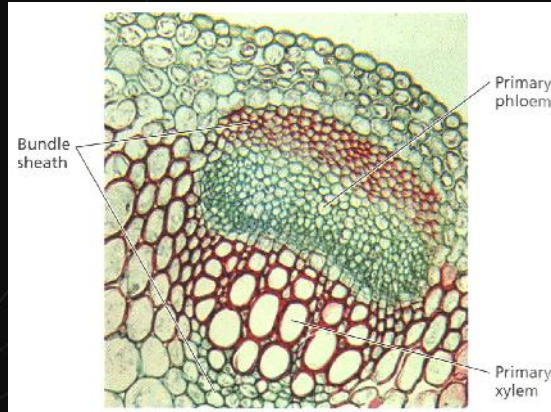
5. Note that the sieve tube between source and sink is bounded by a differentially permeable membrane, the plasma membrane. Consequently, water enters and leaves the sieve tube not only at the source and sink, but all along the pathway.
6. Evidence indicate that few if any of the original water molecules 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





1. Phloem Structure

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.)