Plant Physiology
Translocation in the Phloem
Unite VI

Land colonization

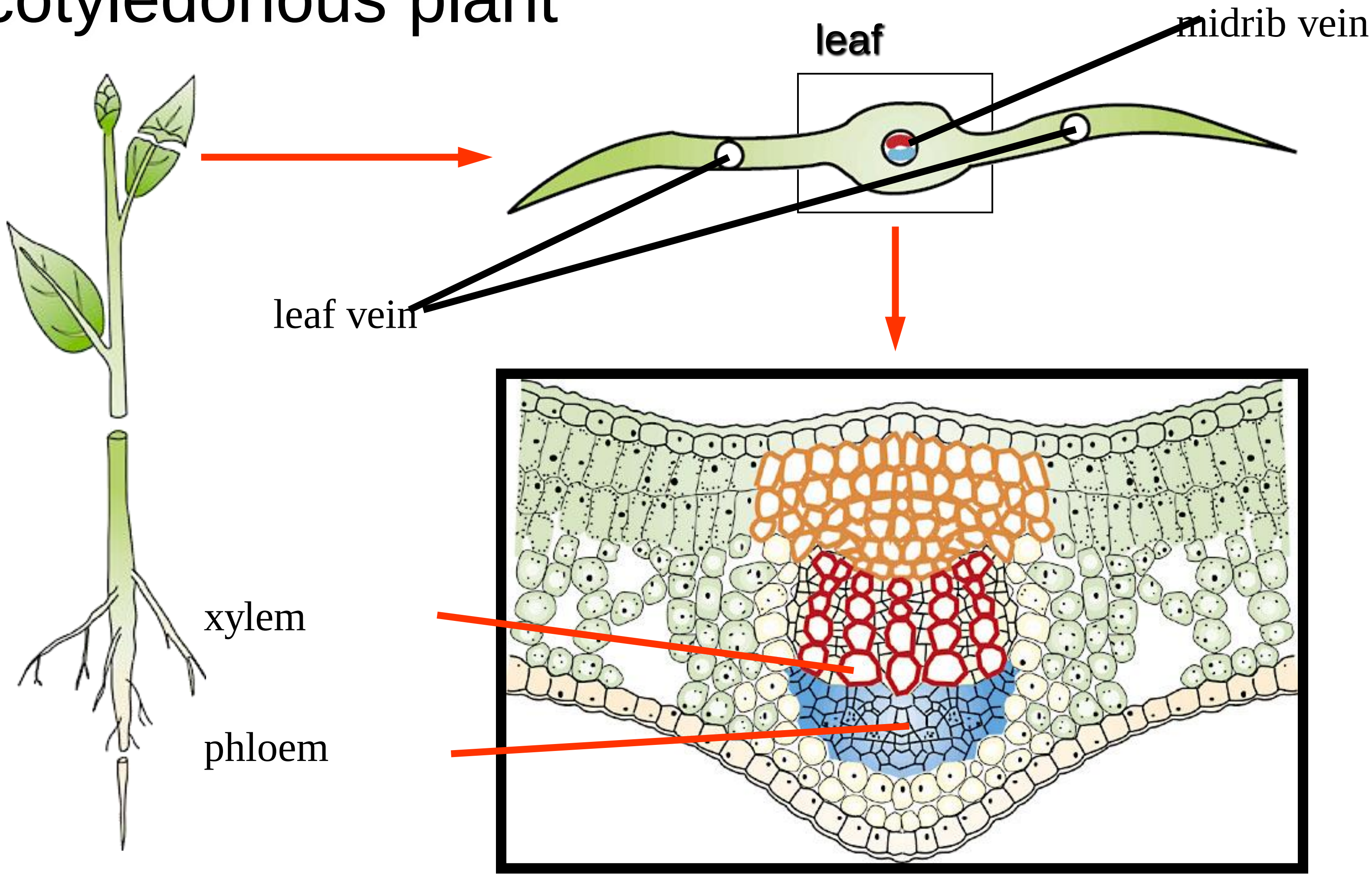
- **Prompted greater shoot growth to reach and compete for sunlight**
- **Prompted development of a deeper root system**
- **Separates photosynthesizing regions from areas where sugars are used**
- **Requires a driving force for this long-distance transport**

Phloem transport

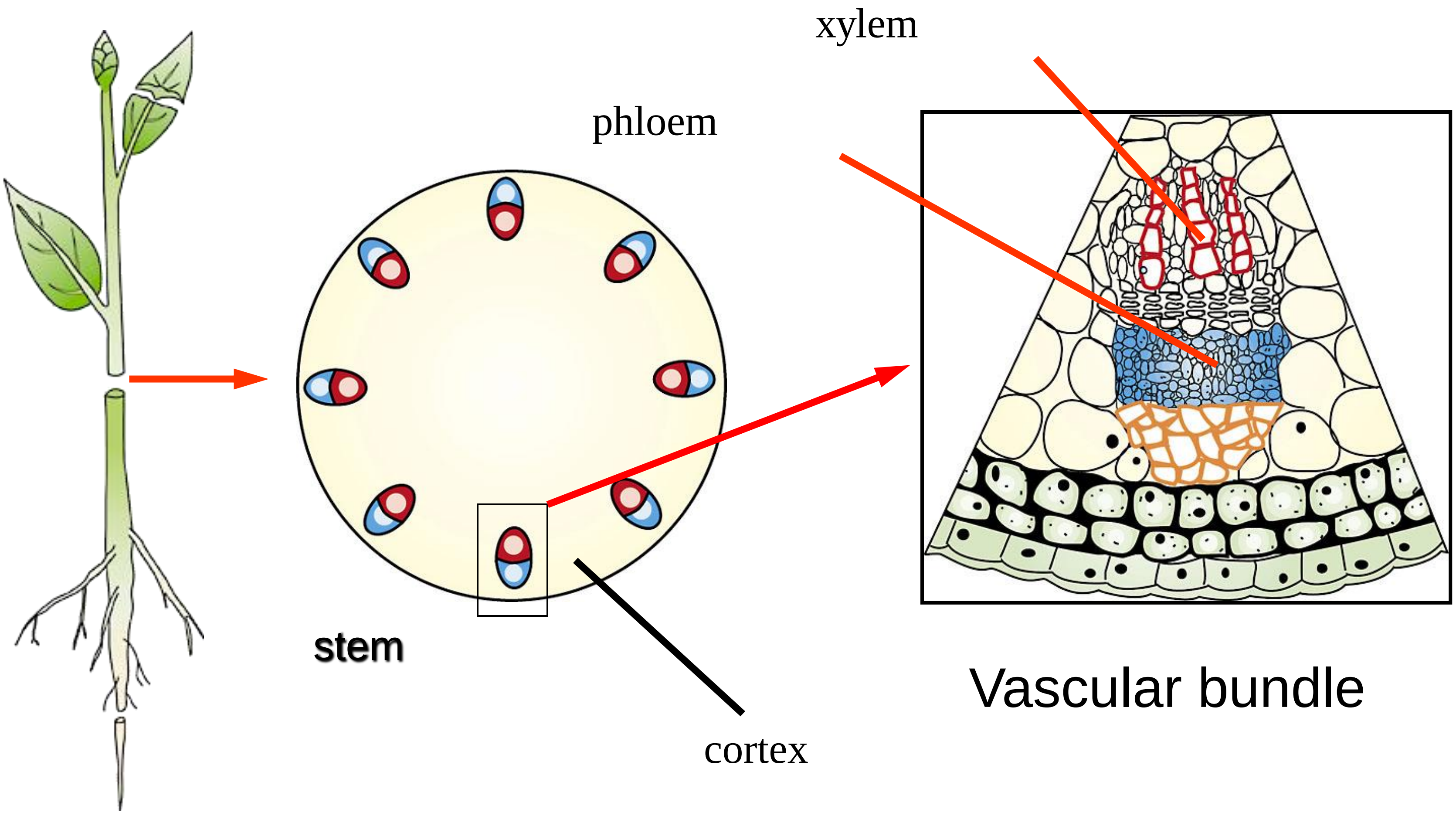
- A highly specialized process for redistributing:
  - **Photosynthesis products**
  - **Other organic compounds (metabolites, hormones)**
  - **some mineral nutrients**

- ***Redistributed from***
  - **SOURCE → SINK**

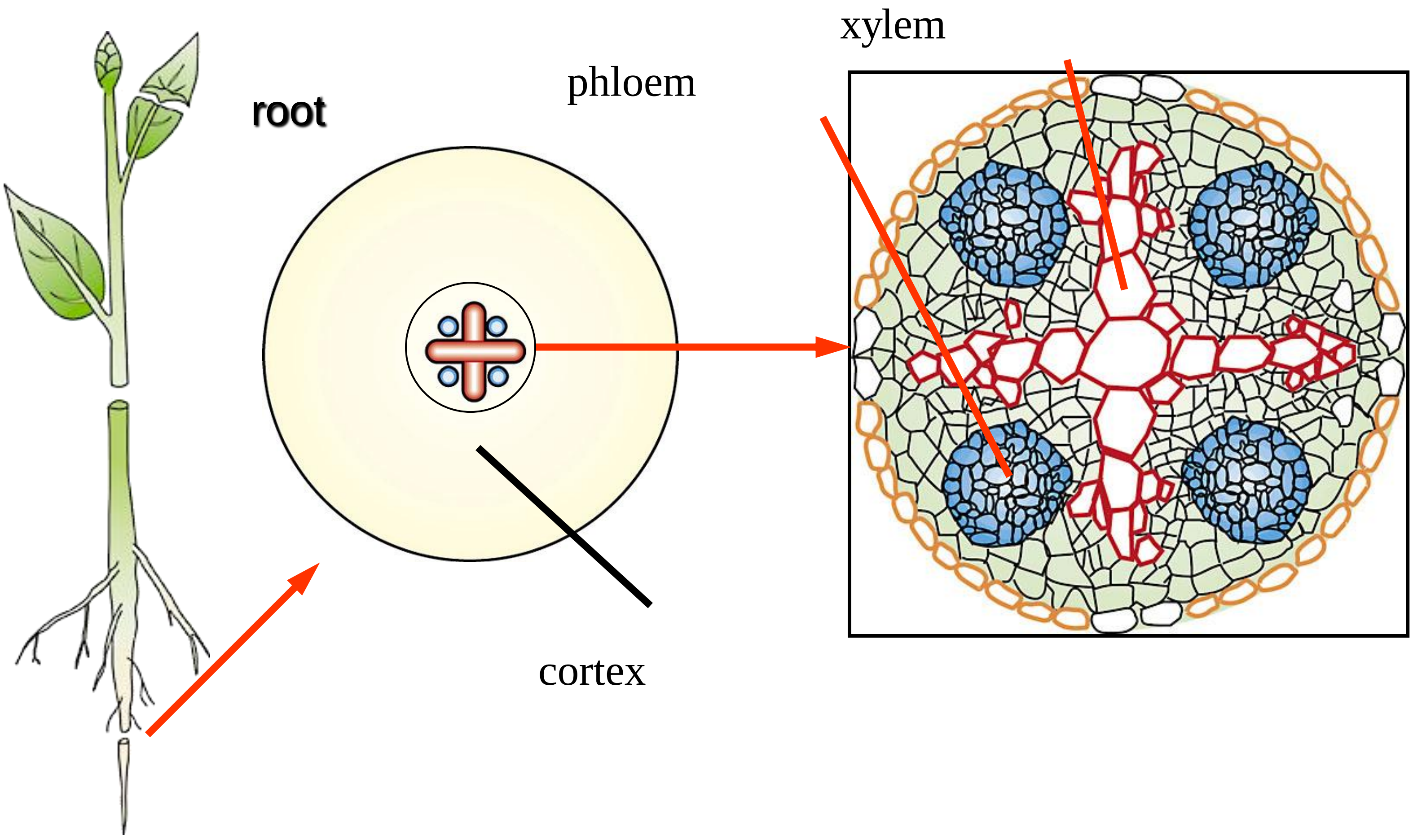
Distribution of vascular tissue in dicotyledonous plant



Distribution of vascular tissue in dicotyledonous plant



Distribution of vascular tissue in dicotyledonous plant



Phloem cells

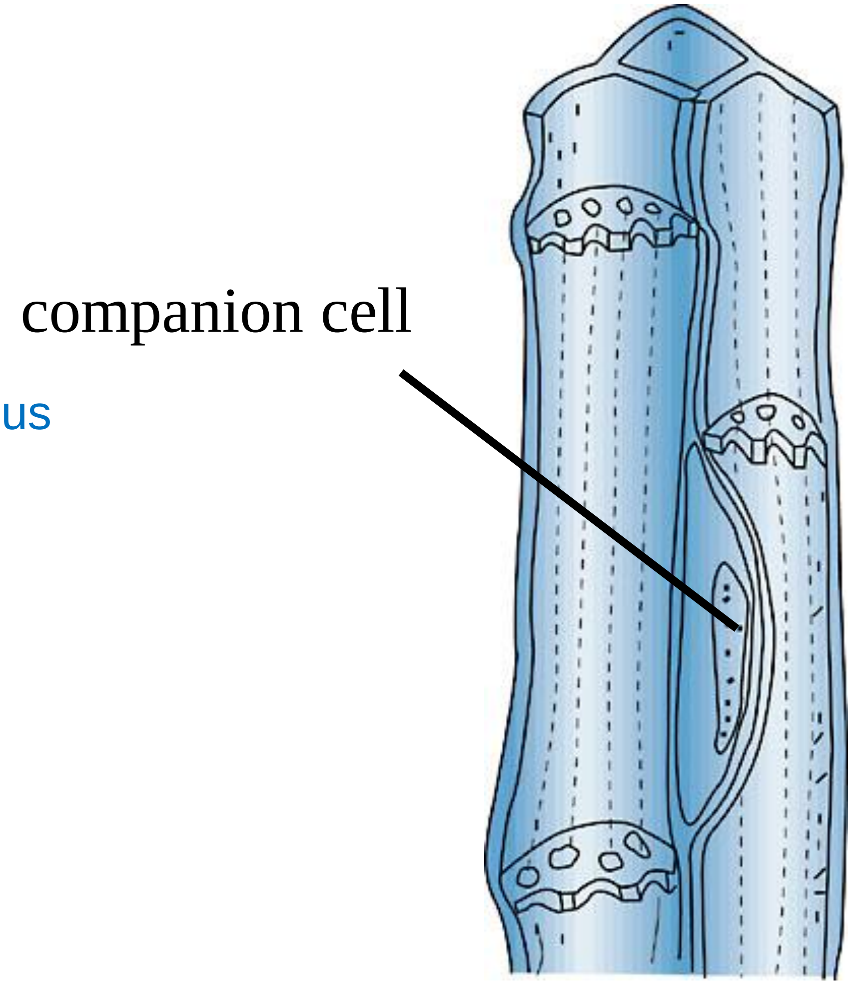
phloem tissue made up of

1. sieve tubes

2. companion cells

- narrow cell with a nucleus / numerous organelles

- support the metabolic activities of the sieve tubes



phloem cells

Sieve Plate

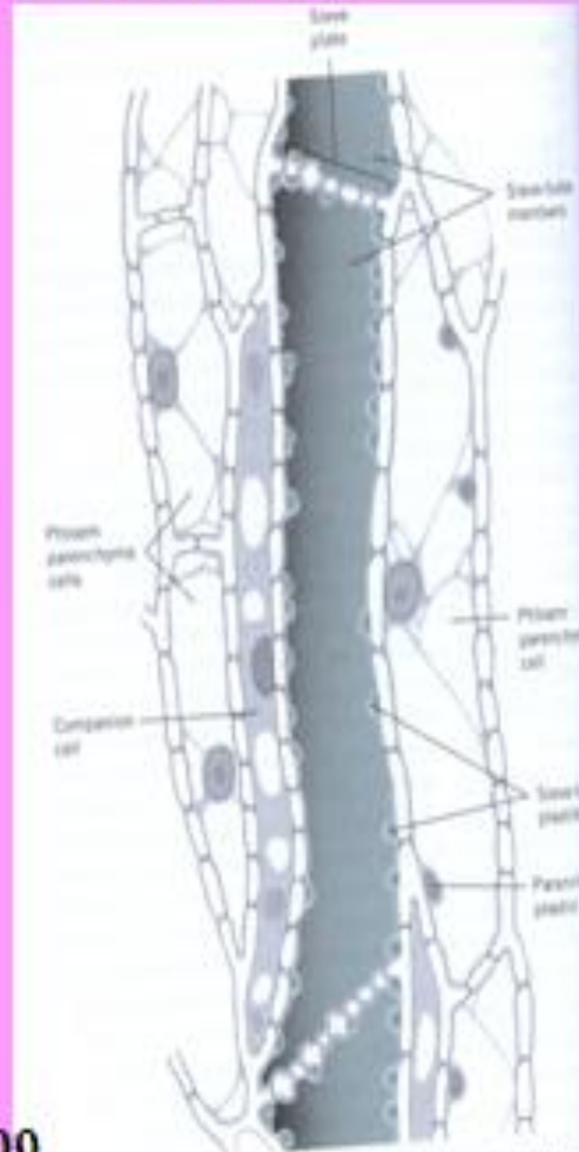


FIGURE 11.4 Phloem tissue from the stem of tobac

Sieve tube members

Phloem Parenchyma cells

Phloem Parenchyma cells

Sieve Tube Plastids

Companion Cell

Parenchyma plastids

From Hopkins, 1999

Phloem transport: Sources and sinks

- ***Source***:
  - Any exporting region that produces photosynthate above and beyond that of its own needs
- ***Sink***:
  - any non-photosynthetic organ or an organ that does not produce enough photosynthate to meets its own needs

Source-sink pathways follow patterns

- Although the overall pattern of transport can be stated as ***source*** to ***sink***
- Not all ***sources*** supply all ***sinks*** in a plant
- Certain sources preferentially supply specific sinks
- In the case of herbaceous plant, such as Sugar-beet, the following occurs:

Source-sink pathways follow patterns

- ***Proxity***: – 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

Exactly what is transported in phloem?

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.

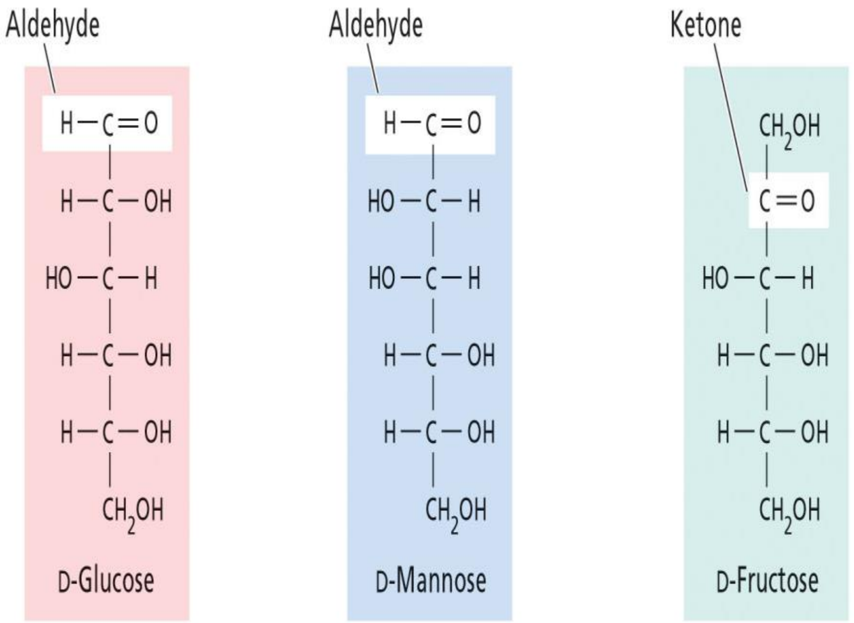
Sugars that are not generally in phloem

- 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***

(A) **Reducing sugars, which are not generally translocated in the phloem**

The reducing groups are aldehyde and ketone groups.



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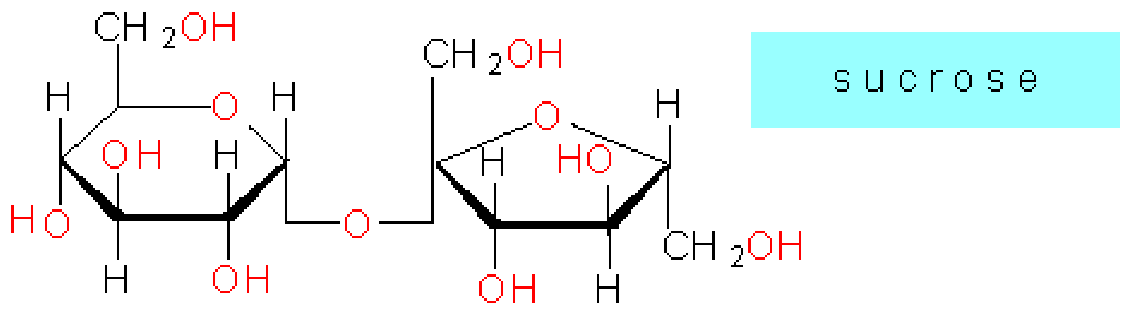
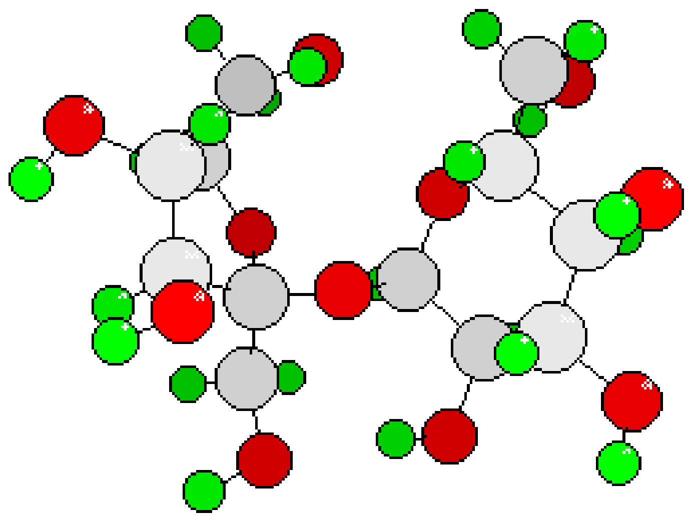
Sucrose

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



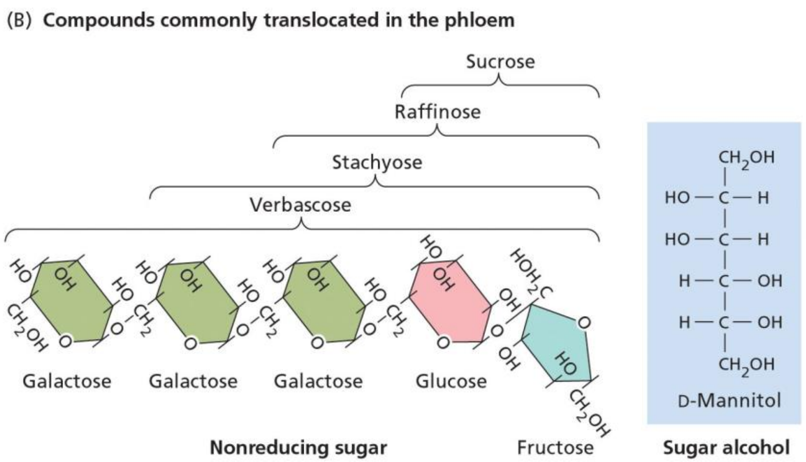
Sucrose - is not a rigid structure, but mobile in itself.



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



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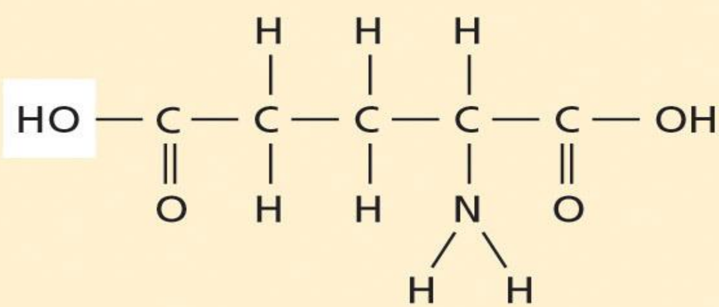
Other compounds

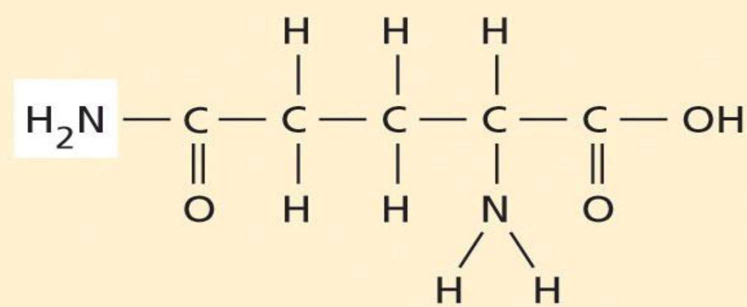
- **Water!!!!!!!!!**
- **Nitrogen** is found in the phloem mainly in:
  - ***amino acids*** (Glutamic acid)
  - ***Amides*** (Glutamine)
- Proteins (see later)

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



Glutamic acid

Amino acid



Glutamine

Amide

Phloem Structure

- The main components of phloem are
  - ***sieve elements***
  - ***companion cells***.
- Sieve elements have no nucleus and only a sparse collection of other organelles . *Companion cell provides energy*
- so-named because end walls are perforated - allows cytoplasmic connections between vertically-stacked cells .
- conducts sugars and amino acids - from the leaves, to the rest of the plant

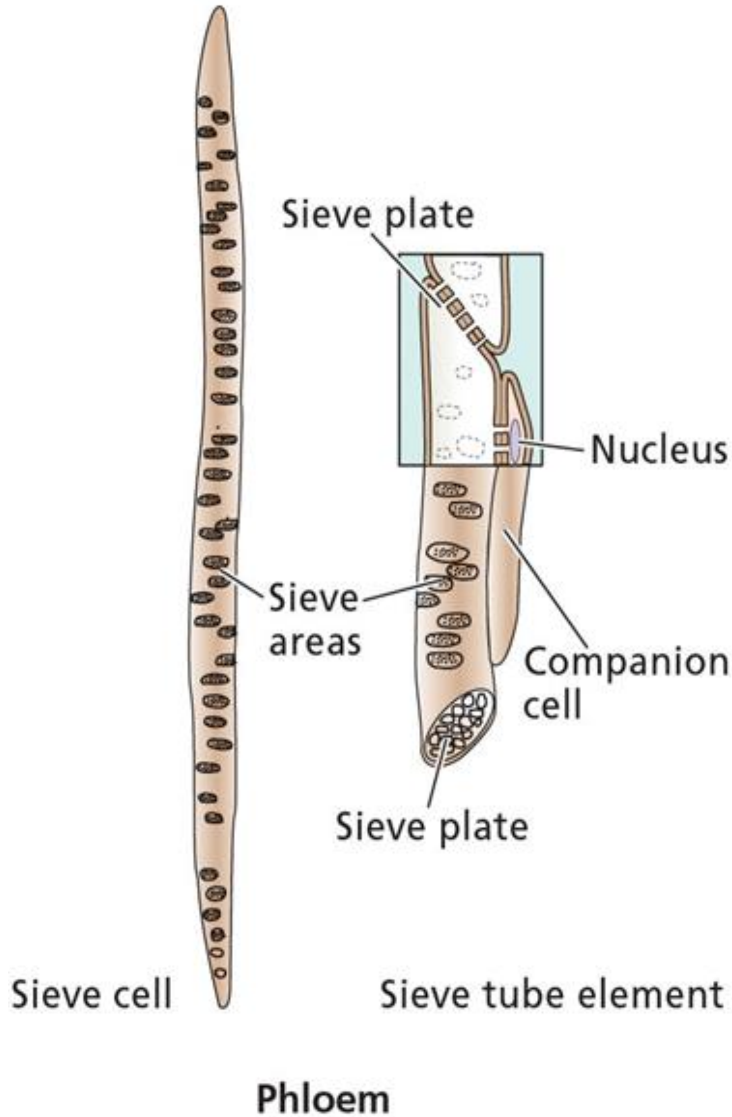


Table 36.1 *Mechanisms of Sap Flow in Plant Vascular Tissues*

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)

LIFE: THE SCIENCE OF BIOLOGY, Seventh Edition, Table 36.1

Girdling experiments

Girdling a tree, i.e., removing a complete ring of bark and cambium around a tree, has no immediate effect on water transport, but sugar accumulates above the girdle and tissue swells while tissue below the girdle dies.

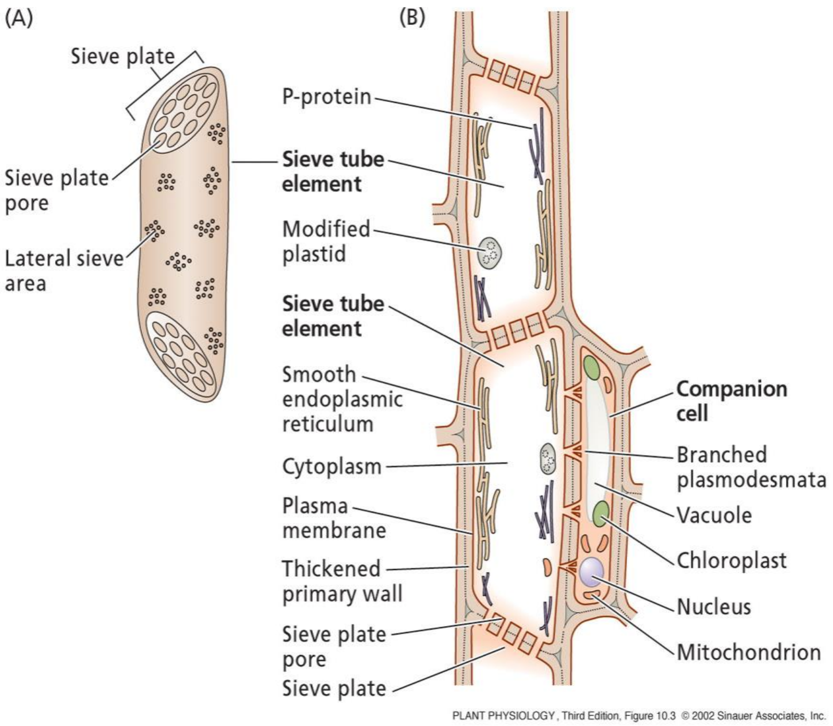
Girdling is sometimes used to enhance fruit production.

Radio active tracer experiments

Application of $^{14}CO_2$ to a photosynthesizing leaf, or application of ^{14}C-sucrose, then visualization of the path of the radioactive tracer through photographing cross sections of the plant’s stem indicates that photosynthate moves through phloem sieve elements.

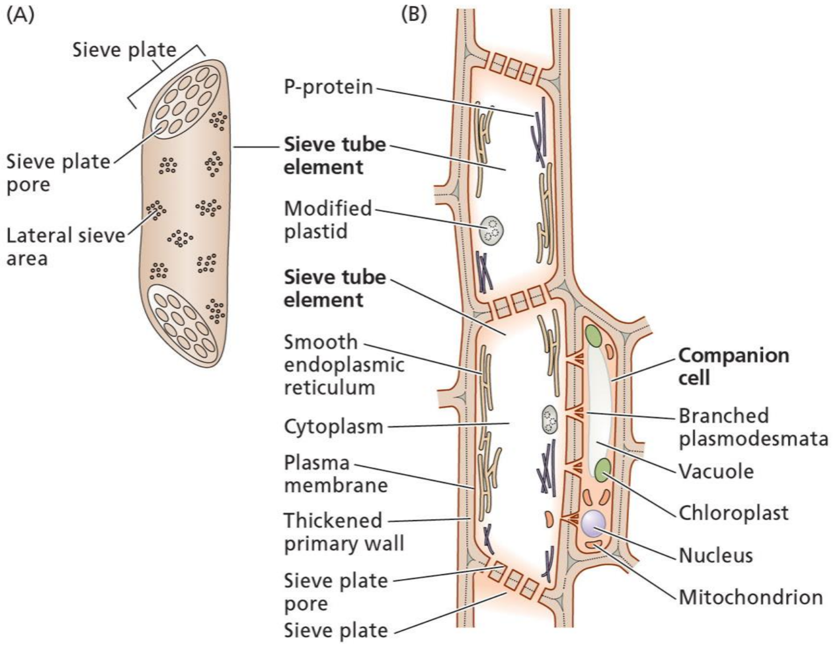
Phloem transport requires specialized, living cells

- 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



Phloem transport requires specialized, living cells

- ***Companion cells***:
  - Role in transport of photosynthesis products from producing cells in mature leaves to sieve plates of the small vein of the leaf
  - Synthesis of the various proteins used in the phloem
  - Contain many, many mitochondria for cellular respiration to provide the cellular energy required for active transport
  - There are three types
    - Ordinary companion cells
    - Transfer cells
    - Intermediary cells



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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 in growths –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.

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)

Protective mechanisms in phloem

- ***P proteins***:
  - Occurs in many forms (tubular, fibrillar, crystalline – 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

The mechanism of phloem transport

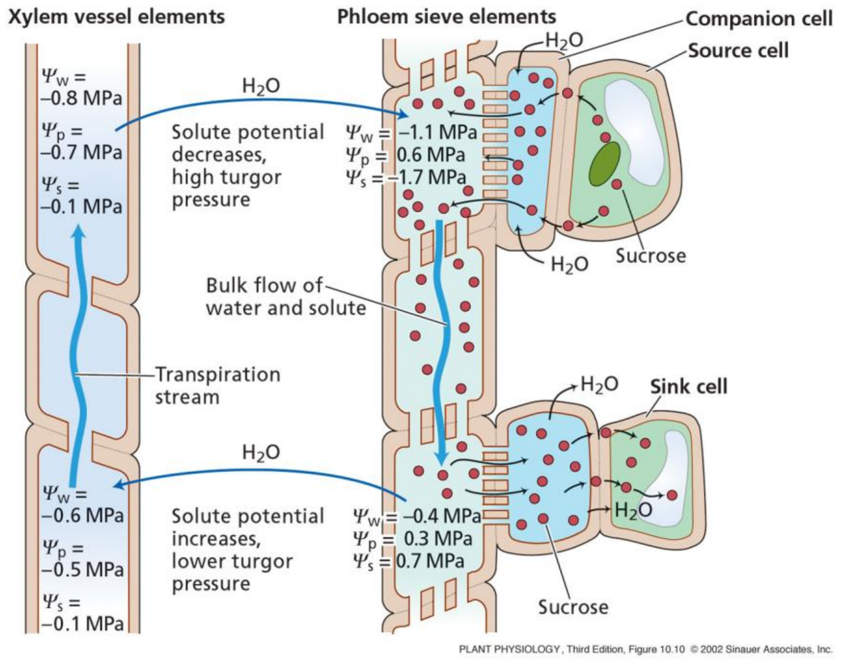
The Pressure-Flow Model

The Pressure-Flow Model

Translocation is thought to move at 1 meter per hour

- *Diffusion too slow for this speed*

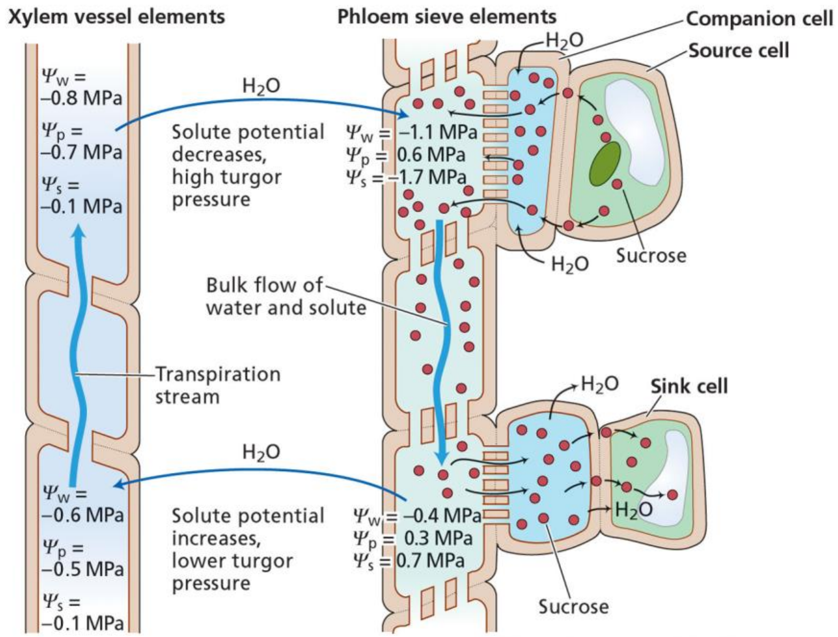
- The flow is driven by an osmotically generated pressure gradient between the ***source*** and the ***sink***.
- **Source**
  - Sugars (red dots) is actively loaded into the sieve element-companion cell complex
    - *Called phloem loading*
- **Sink**
  - Sugars are unloaded
    - *Called phloem unloading*



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 potentia
  - Water potential **increases**
  - Water leaves phloem and enters sink sieve elements and xylem
    - ***Thus phloem turgor pressure decreases***



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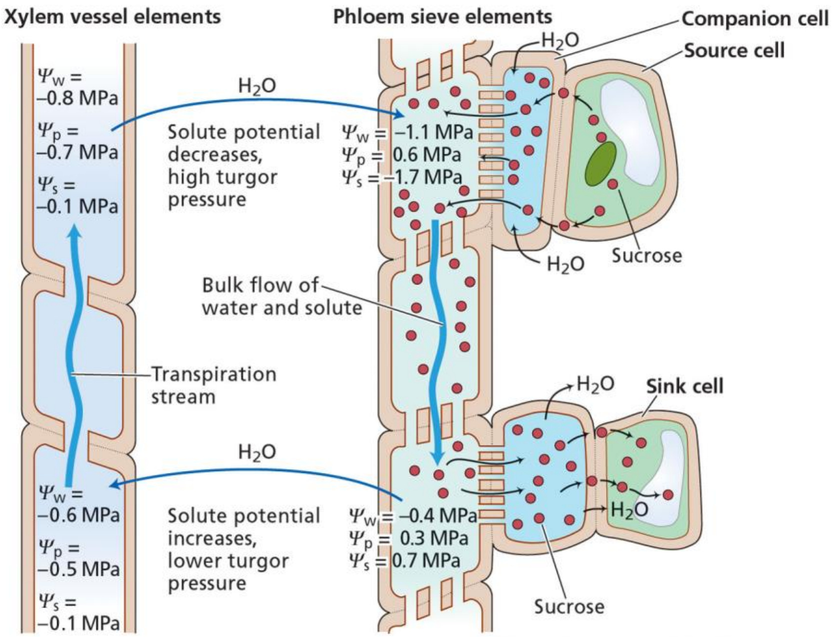
The Pressure-Flow Model

- 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 ***<u>Bulk Flow</u>***
  - 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 **<u>NOT</u>** ***water potential gradient***



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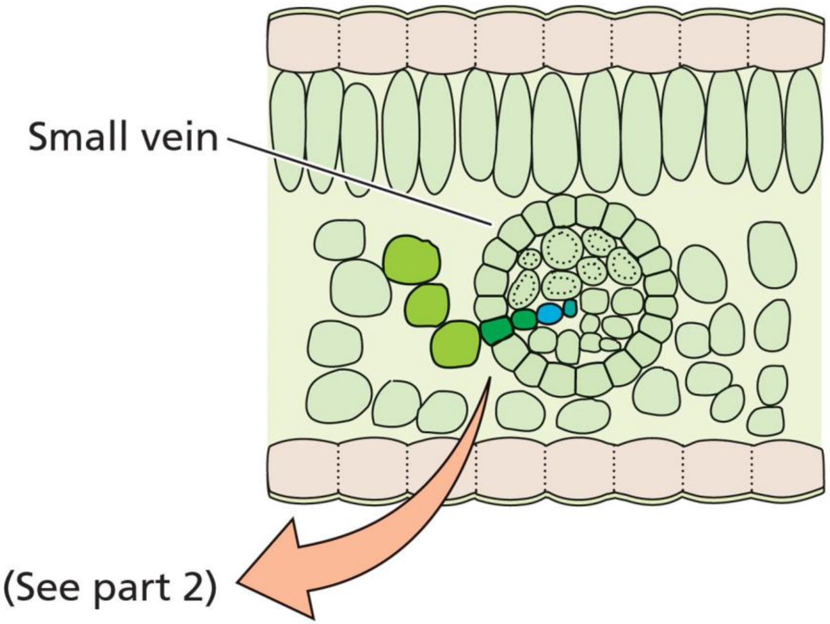
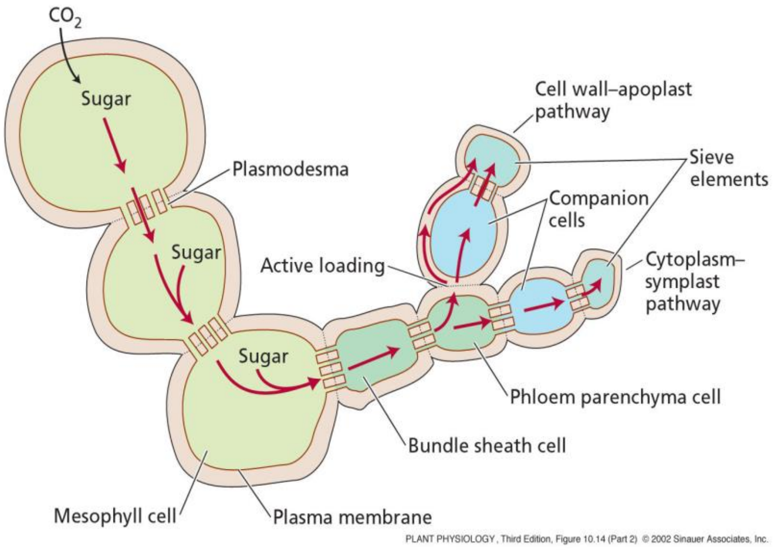
Phloem Loading:
Where do the solutes come from?

- 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***



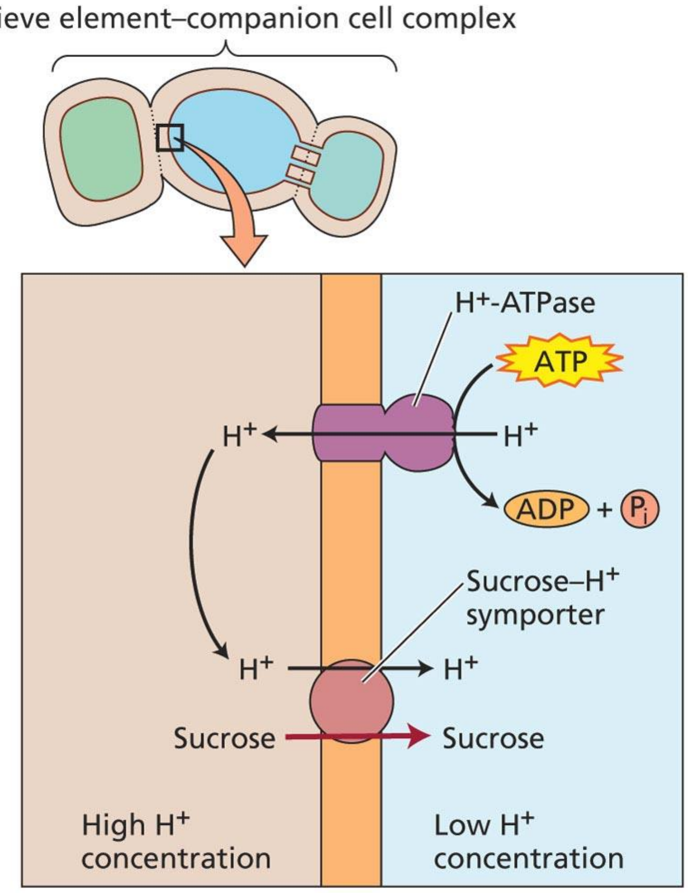
Phloem Loading: Where do the solutes come from?

- 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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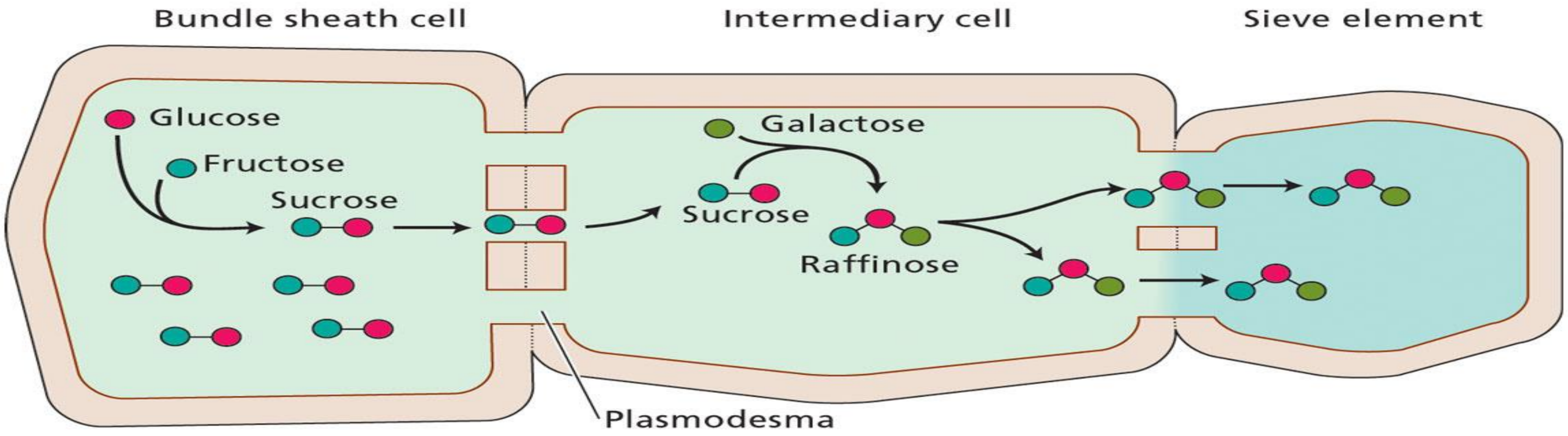
Symplastic phloem loading

- 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



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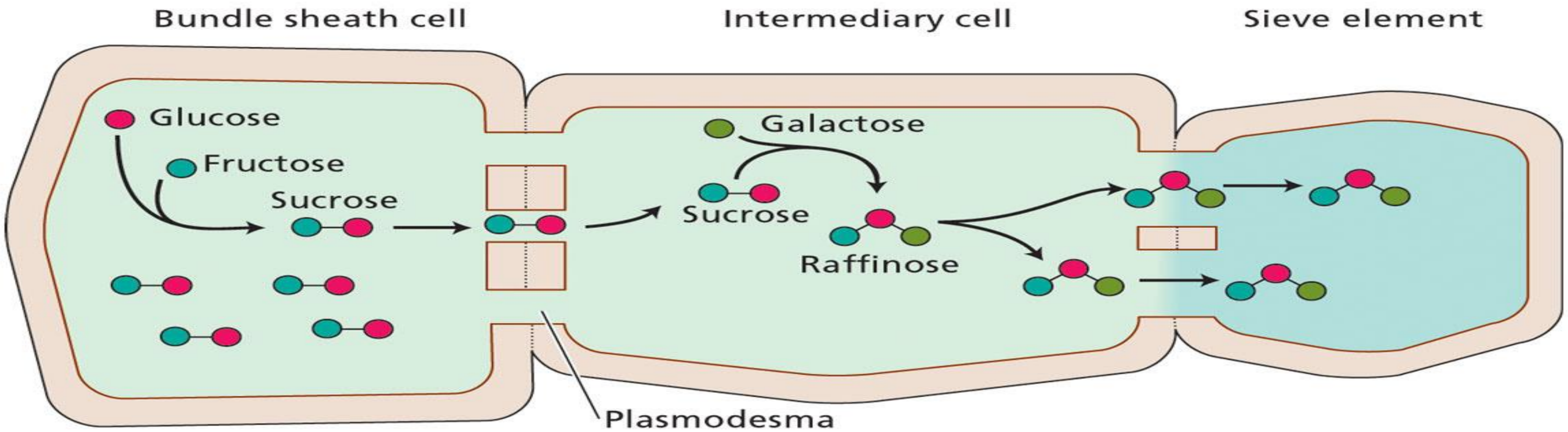
Symplastic phloem loading

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



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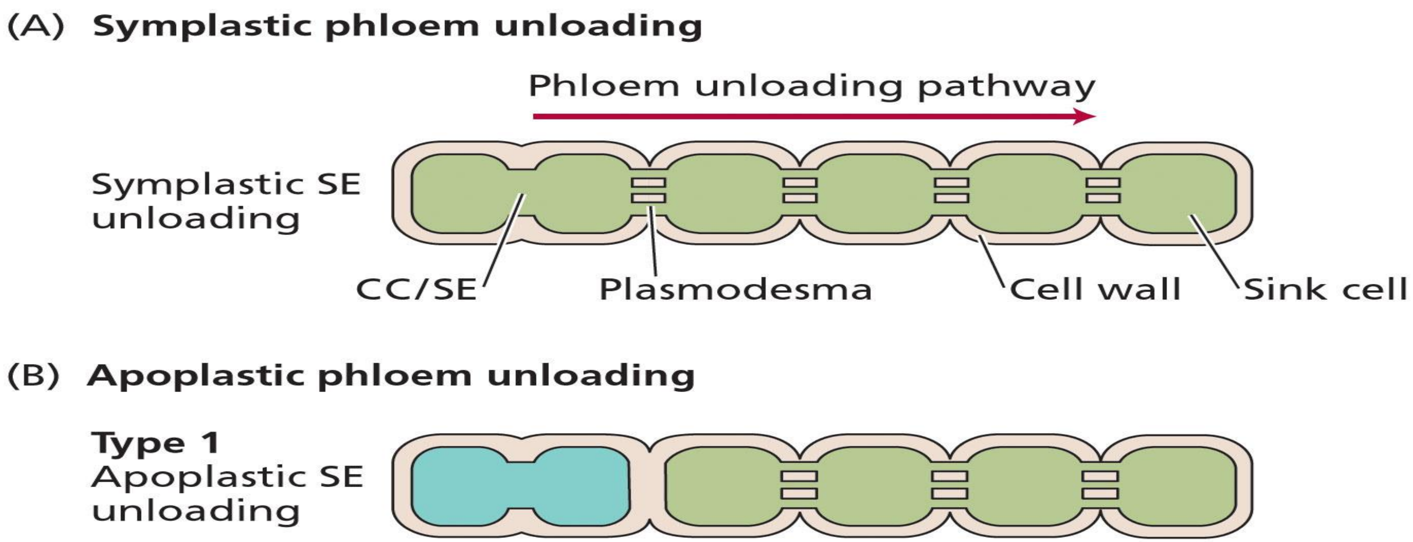
Phloem unloading

- 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



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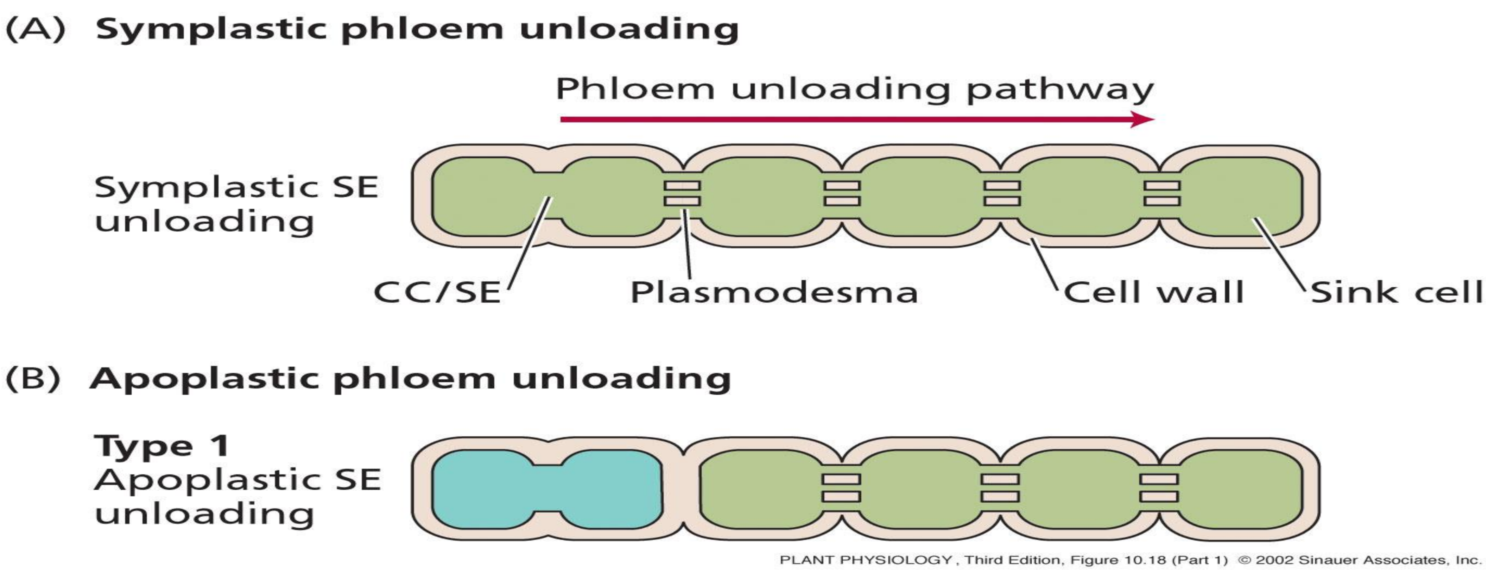
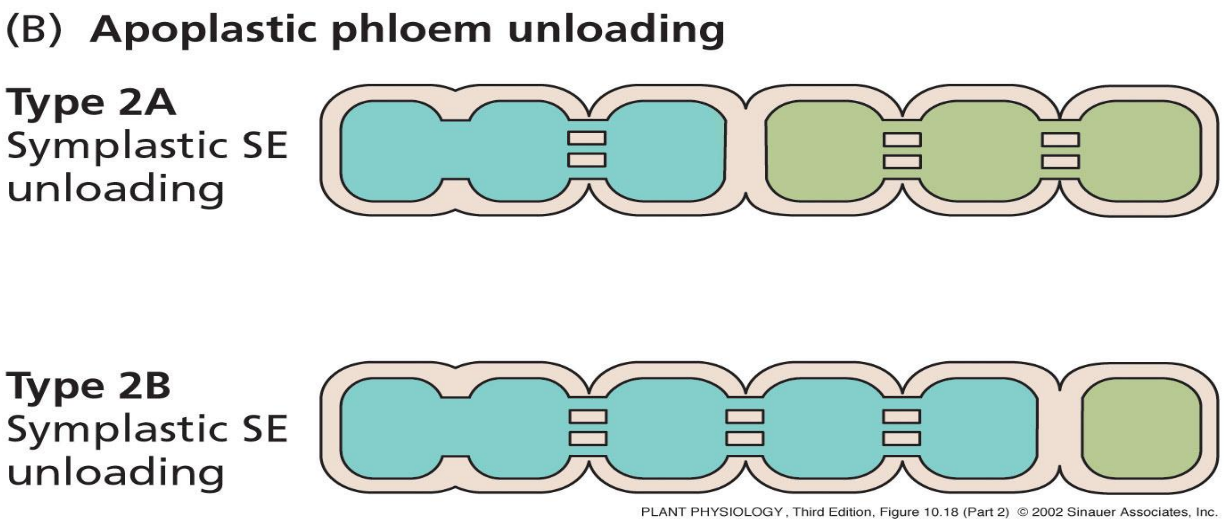
Phloem unloading

- ***Apoplastic***: three types
- (1) [B] 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



Phloem unloading

- ***Apoplastic***: three types
- (2) [A] involves an apoplastic step close to the sieve element companion cell.
- (3) [B] involves an apoplastic step father from the sieve element companion cell
- ***Both involve movement through the plant cell wall***



Summary

- ***Pathway of translocation***:
  - Sugars and other organic materials are conducted throughout the plant in the phloem by means of sieve elements
    - ***Sieve elements display a variety of structural adaptations that make the well suited for transport***
- ***Patterns of translocation***:
  - Materials are translocated in the phloem from ***sources*** (usually mature leaves) to ***sinks*** (roots, immature leaves)

Summary

- ***Materials translocated in phloem***:
  - Translocated solutes are mainly carbohydrates
  - Sucrose is the most common translocated sugar
  - Phloem also contains:
    - ***Amino acids, proteins, inorganic ions, and plant hormones***
- ***Rate of translocation***:
  - Movement in the phloem is rapid, well in excess of rates of diffusion
    - ***Average velocity is 1 meter per hour***

Experiment

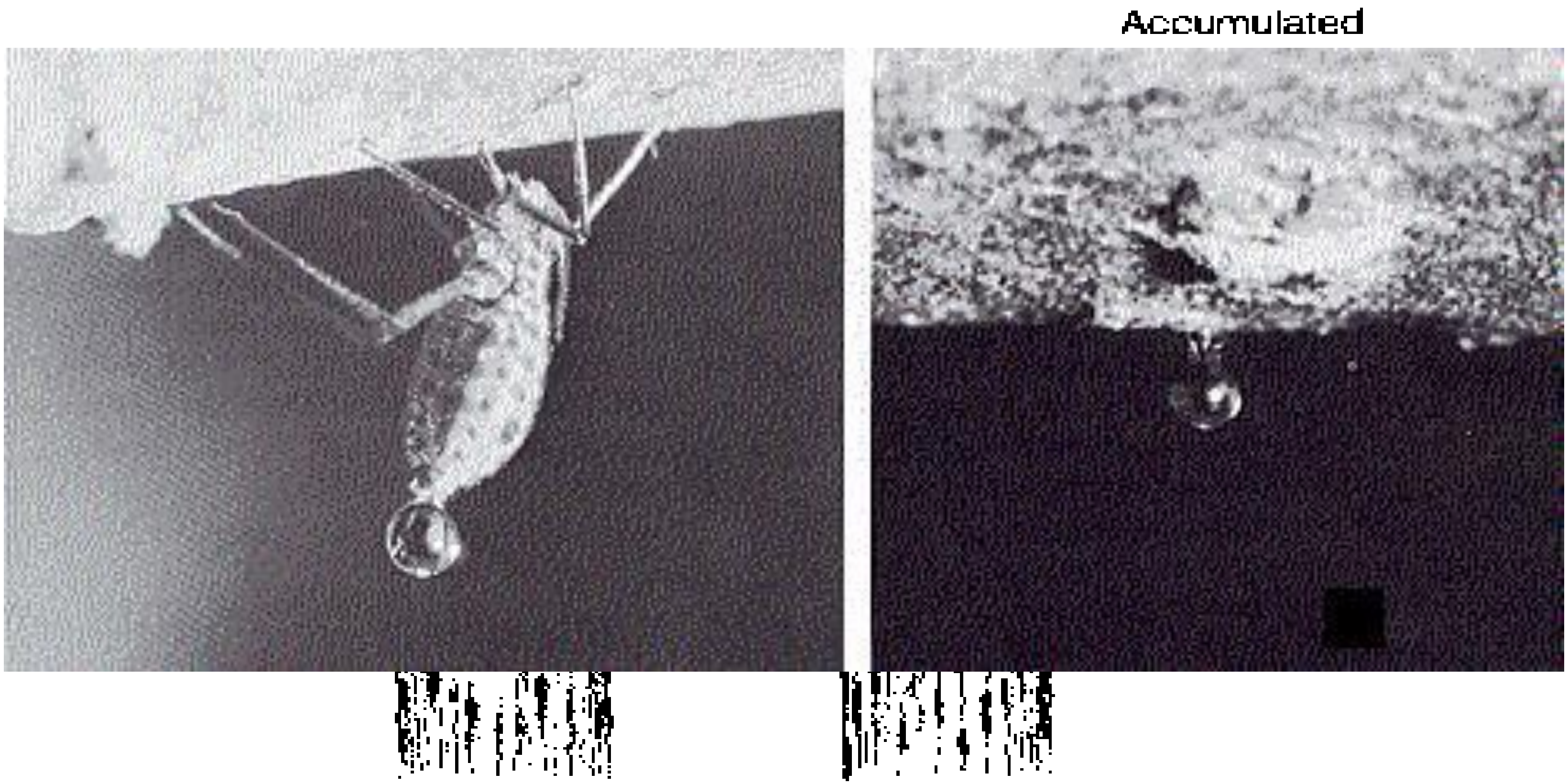


FIGURE 7.3. Tree trunk immediately after girdling (left) and after a longer period of time (right). Girdling is the removal of the bark of a tree in a ring around the trunk. Materials translocated from the leaves have accumulated in the region above the girdle and caused it to swell.

A technique for analyzing phloem sap chemistry is the use of aphid stylets. A feeding aphid is anesthetized and its stylet severed   The phloem sap is under positive pressure and is collected.

Aph
s

http://members.ozemail.com.au/~lblanco/Ap1.htm