Translocation: Distribution of Assimilates

Transport systems in plants: xylem and phloem

• Xylem
  – tracheids
  – xylem vessels
  – transport driven by gradient in hydrostatic pressure
  – dead cells

• Phloem
  – several cell types (as illustrated in this lecture)
  – what is driving force for transport?
  – live cells

Transport of photosynthate occurs mainly in the phloem

Evidences?
Ringbarking (damaging the phloem, leaving the xylem intact) girdling a tree has no immediate effect on water transport, but sugar accumulates above the girdle and tissue swells, tissue below girdle dies.

Conclusion: sugars are transported in the phloem, but not in the xylem.

- application of 14CO₂ or 14C-sucrose, then visualization of path of radioactive tracer indicates that photosynthate moves through phloem sieve elements.

Transverse sections of a pine needle and of a wheat leaf.

The pine needle has a single central vein with two strands of phloem and xylem.

The wheat leaf has one large vein with three large vessels.

**Bidirectional Flow of Phloem Contents**

How can this occur? Apparently, sieve tubes adjacent to each other can flow in opposite directions. If this occurs in same cell then the mechanisms used to describe phloem transport are suspect.
**Source vs. Sink**

- **Source**: a net exporter of assimilate
- **Sink**: a net importer of assimilate

**Phloem structure**

- **Sieve elements**
  - joined together to form sieve tube, sieve plates in between (not in gymnosperms)
  - lots of plasmodesmata between sieve element and companion cells
  - broken/ruptured sieve tubes are plugged by protein and callose (β-1,3 glucose polymer)
  - sieve elements lack many organelles, DO have mitochondria, ER, modified plastids, plasma membrane
  - Associated with companion cells (albuminous cells in gymnosperms)

**Source vs. Sink**

- **Source**: mostly mature leaves
- **Sink**: apical meristems
  - lateral meristem
  - fruit
  - seed
  - developing leaves etc.

**Phloem structure**

- **Companion cells/transfer cells**
  - perform some of the basic cell functions for the sieve-tube members, like protein synthesis, lots of mitos for ATP synthesis, extensive
  - some plants have transfer cells with invaginations on sides opposite sieve-tube member, increases surface area for better transport
  - neither companion cells or transfer cells have many or any plasmodesmatal connections with cells opposite the sieve elements (they only have plasmodesmatal connections with sieve elements)
**Phloem structure**

- Intermediary cells
  - some plants have intermediary cells that have extensive plasmodesmatal connections to bundle sheath/parenchyma cells (as well as to sieve elements)

**Cell types in the phloem: sieve elements, companion cells, parenchyma cells**

**Sieve Tube Transport**

- Sugars concentrated (up to 25% or 600 mM sucrose = main translocated photosynthate) for transport
  - other sugars may be abundant—raffinose (sucrose+galactose), stachyose
  - some plants have lots of amino acids (glu, asp) and or amides (gln, asn) in phloem sap
  - minerals also cycle through phloem sap
  - pH is relatively high (~8)
- **Transport rate:** 0.5-1.5 m h^{-1}
Sugars in phloem sap

Sucrose is a nonreducing sugar and is therefore less reactive. The bond linking glucose and fructose (the $\beta$-fructoside linkage) has a relatively high negative free energy of hydrolysis (just below ATP).

Why is sucrose used for transport rather than glucose or fructose?

Sucrose is a nonreducing sugar and is therefore less reactive.

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Aphids as a valuable tool for plant scientists

Most of the phloem content appears as 'honey dew'.

The aphid’s stylet can also be cut with a laser beam and pure phloem content can be collected.

P-protein

- Phloem Protein begins as discrete bodies
- Range in mass from 15 to 220 kD
- Its function is not totally clear but it may bind carbohydrates and participate in transport. It is located along inner wall of sieve element and does not block sieve plate.
Callose

- Callose is a 1–3-glucan related to starch.
- Located on surface of the sieve plate or near pores between elements.
- May help “seal off” sieve tube if injured to preserve plant integrity.

Mechanism of phloem translocation

- Transport of Sucrose from site of synthesis (mesophyll cells) and accumulation in the sieve elements (**phloem loading**) can occur by two paths.

How do the sugars move from the mesophyll cells into the sieve elements?

Phloem loading might be **symplasmic**, if there are plasmodesmatal connections between the mesophyll cells and the companion cells and **apoplastic** if there is no connections.

In some species there are such connections....

...in others there are not
Loading of sucrose in species with an apoplastic pathway

1. An ATPase builds up a $H^+$-gradient
2. The $H^+$-gradient is used to ‘drive’ sucrose uptake via sucrose-$H^+$-cotransport

This mechanism is similar to that used for $NO_3^-$ transport across the plasma membrane.

Loading of sucrose in species with a symplasmic pathway

How can the sugar concentration in the sieve tubes be higher than that in mesophyll cells?

The polymerisation trap to explain symplasmic phloem loading

Symplasmic pathway is probably older

- It is common in tropical species: high solubility of oligosaccharides
- Apoplastic pathway in colder climates: low solubility of oligosaccharides
- Arid environments are also inhabited by species with apoplastic pathway
Mechanism of phloem translocation: pressure-flow hypothesis of Ernst Munch (1930)

Phloem Transport: Mass Flow Theory

- Solution is forced to move through phloem
- More sugar continues to be loaded
- Phloem is under positive pressure
- An active sink is required for transport to continue.

From Galston et al., 1980
Recent Findings About Phloem Loading

- Some species may exhibit predominantly apoplastic loading, others may exhibit symplastic loading.
- Some species that load symplastically tend to transport stachyose rather than sucrose.

Phloem unloading can also be symplastic or apoplastic

- symplastic in growing tissues like young roots, young leaves
- apoplastic unloading into storage tissues, like sugar beet roots
- also apoplastic in seeds (no symplastic connections to embryo)
- often involves conversion - like breaking down sucrose to glucose+fructose (enzyme is invertase)
- Apoplastic unloading again requires active transport to accumulate sucrose in the storage cells

Assimilate Distribution

Distribution or Allocation consists of:

1. Leaf Metabolism and Biomass
2. Storage
3. Export from Leaf

Photosynthate Partitioning

- On a whole plant basis, partitioning is called dry matter distribution.
- Transport occurs through the most direct phloem connections
  - sinks closest to a source receive photosynthate first
  - vascular connections usually run vertically, sinks above or below source receive photosynthate first
  - direction of flow can change through development (sink to source transition) or upon pruning/wounding
**Photosynthate Partitioning**

Understanding of "sink strength" and regulation of photosynthate partitioning may lead to development of plants that provide greater harvest yield.

**Sink Strength** = sink size (g) × sink activity

Sink activity refers to the uptake rate/demand, Temperature, rate of phloem unloading, turgor, and concentrations of hormones dictate sink activity.

**Role of Hormones in Photosynthate Partitioning**

Abscisic acid may stimulate growth rate of fruit, translocation of sugar to bean and sugarbeet roots, and unloading of sucrose into apoplast from soybean seed coat.

*From Hopkins, 1999*

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**Xenobiotics**

Xenobiotics are biologically active substances that are “foreign” to a given species. The most practical examples are pesticides.

For many pesticides to be effective, they must enter the phloem. Foliar-applied substances may diffuse into leaf tissue through cuticle or enter stomata.

Movement through the plasmalemma is dependent upon polarity/hydrophobicity. This is why pesticide formulations are so important.

*From Hopkins, 1999*