Translocation

**Translocation** is the transport of products of photosynthesis, mainly sugars, from mature leaves to areas of growth and storage. **Phloem** is the tissue through which translocation occurs.

*Sieve elements* are the cells of the phloem that conduct sugars.

Sieve elements have large pores in the cell wall that interconnect the conducting cells.
Sieve elements lose their nuclei and tonoplasts during development. Walls are nonlignified.

Companion cells play a role in transport of photosynthetic products, and also take over some of the critical metabolic functions such as protein synthesis that are lost or reduced during differentiation of sieve elements. In addition, companion cells contain numerous mitochondria that may supply ATP to sieve elements.
Three types of companion cells:

- **Ordinary companion cells**
- **Transfer cells**
- **Intermediary cells**

Ordinary companion cells have cell walls with a smooth inner surface, and are symplastically isolated from surrounding cells, except their own sieve elements.

Transfer cells have wall ingrowths that increase the surface area of the plasma membrane. This increases the potential for solute transfer across the membrane.
Ordinary companion cells and transfer cells are specialized for **apoplastic transport** of solutes. They are found in plants where transport sugars enter the apoplast in movement from mesophyll cells to sieve elements.

Intermediary cells have numerous plasmodesmata that connect them to bundle sheath cells, and are well-suited for taking up solutes via cytoplasmic connections.

Intermediary cells are found in plants where no apoplastic pathways appear to occur in the source leaf.
Sugars and other metabolites are translocated from areas of supply (sources) to areas of metabolism or storage (sinks). Translocation can occur in any direction, and is not defined with respect to gravity.

Sources are generally mature leaves capable of producing photosynthate (products of photosynthesis) in excess of their own needs. Storage organs can also function as sources.

Sinks include any organs that do not produce enough photosynthate to support their own growth or storage needs.

Upper mature leaves usually provide photosynthate to the growing shoot tip, and young, immature leaves. Lower leaves supply predominantly the root system. Intermediate leaves export in both directions.

Shoots and root apices are the major sinks during the vegetative stage, whereas seeds and fruits generally become the dominant sinks during the reproductive stage.

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

<table>
<thead>
<tr>
<th>Component</th>
<th>Concentration (mg mL⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sugars</td>
<td>80.0–106.0</td>
</tr>
<tr>
<td>Amino acids</td>
<td>5.2</td>
</tr>
<tr>
<td>Organic acids</td>
<td>2.0–3.2</td>
</tr>
<tr>
<td>Protein</td>
<td>1.45–2.20</td>
</tr>
<tr>
<td>Potassium</td>
<td>2.3–4.4</td>
</tr>
<tr>
<td>Chloride</td>
<td>0.355–0.675</td>
</tr>
<tr>
<td>Phosphate</td>
<td>0.350–0.550</td>
</tr>
<tr>
<td>Magnesium</td>
<td>0.109–0.122</td>
</tr>
</tbody>
</table>

Source: Hall and Baker 1972.

Sucrose is the most commonly transported sugar. It is less reactive than glucose and fructose.
Triose phosphate can be utilized in starch formation in the chloroplast, or transported into the cytosol in exchange for Pi.

In the cytosol, triose phosphate can be converted into sucrose for storage in the vacuole, or transport.
Pressure Flow Model

Transport is driven by an osmotically-generated pressure gradient between source and sink.

In source tissues, phloem loading leads to an accumulation of sugars in sieve elements, lowering osmotic and total water potentials. Water flows into sieve elements, increasing turgor pressure.

At the receiving end, phloem unloading reduces sugar concentrations in sieve elements, increasing osmotic and total water potentials. Water flows out of the sieve elements and turgor decreases.
Steps of Phloem Loading

1. Triose phosphate formed by photosynthesis during the day is transported from the chloroplast to the cytosol, where it is converted to sucrose. During the night, carbon from stored starch leaves the chloroplast primarily in the form of maltose, and is converted to sucrose.

Steps of Phloem Loading

2. Sucrose moves from producing cells in the mesophyll to cells in the vicinity of sieve elements in the smallest veins of the leaf. This short-distance transport pathway covers a distance of only a few cell diameters.

Steps of Phloem Loading

3. Sugars are then transported into sieve elements and companion cells (phloem loading). Once inside the sieve elements, sucrose and other solutes are translocated (exported) away from the source through the vascular system to the sink. This is long-distance transport. Phloem loading can occur via the apoplast or symplast.
Apoplastic loading requires energy.

Apoplastic loading involves a sucrose-H⁺ symporter.

Symplastic loading occurs because of concentration differences.
Polymer Trapping Model

Symplastic loading of sucrose is driven by concentration gradients. How is that gradient maintained?
Sucrose diffuses from bundle sheath cells into intermediary cells through plasmodesmata. In the intermediary cells, raffinose and stachyose are synthesized from sucrose and galactose. These polymers cannot diffuse back into bundle sheath cells because they are too large, but they can diffuse into the sieve elements. Utilization of sucrose in the intermediary cells maintains the sucrose concentration gradient.

**Table 16.3 Patterns in apoplastic and symplastic loading (Part 1)**

<table>
<thead>
<tr>
<th>Feature</th>
<th>Aposaplastic loading</th>
<th>Symplastic polymer trapping</th>
<th>Passive symplastic loading</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transport sugar</td>
<td>Sucrose</td>
<td>Raffinose and stachyose in addition to sucrose</td>
<td>Sucrose</td>
</tr>
<tr>
<td>Characteristics of companion cells</td>
<td>Ordinary companion cells or transfer cells</td>
<td>Intermediary cells</td>
<td>Ordinary companion cells</td>
</tr>
<tr>
<td>Number and connectivity of cells connecting the SE-CG complex to surrounding cells</td>
<td>Low</td>
<td>High</td>
<td></td>
</tr>
</tbody>
</table>

*Note: Plasmolysis of plasmodesmata of plasmolysis may alter transport sugar alcohols. In addition, some species may load into symplastically and passively, thus utilizing types of companion cell complexes within the vessel system. SE-CG complex, sieve elements-companion cell complex.*

**Table 16.3 Patterns in apoplastic and symplastic loading (Part 2)**

<table>
<thead>
<tr>
<th>Feature</th>
<th>Aposaplastic loading</th>
<th>Symplastic polymer trapping</th>
<th>Passive symplastic loading</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dependence on active carriers in SE-CG complex</td>
<td>Transporter driven</td>
<td>Independent of transporters</td>
<td>Independent of transporters</td>
</tr>
<tr>
<td>Overall concentration of transport organs in source leaves</td>
<td>Low</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>Cell type in which driving force for long-distance transport is generated</td>
<td>Stone element-companion cell complex</td>
<td>Intermediary cells</td>
<td>Mesophyll</td>
</tr>
<tr>
<td>Growth habit</td>
<td>Mainly herbaceous</td>
<td>Herbaceous woody species</td>
<td>Mainly trees</td>
</tr>
</tbody>
</table>

*Note: Some mechanisms of plasmolysis may affect transport sugar alcohols. In addition, some species may load into symplastically and passively, thus utilizing types of companion cell complexes within the vessel system. SE-CG complex, sieve elements-companion cell complex.*
Steps of Phloem Unloading

1. Imported sugars leave sieve elements of sink tissues.
2. After unloading, sugars are transported to cells in the sink through a short-distance transport pathway.
3. Sugars are stored or metabolized in sink cells.

Growing leaves, roots, and storage sinks, in which carbon is stored in starch or protein, use symplastic phloem unloading and short distance transport. Transport sugars are used as substrate for respiration, and are metabolized into storage polymers and into compounds needed for growth. Sucrose metabolism results in a low sucrose concentration in sink cells, thus maintaining a concentration gradient for sugar uptake.

No membranes are crossed during sugar uptake, and transport through plasmodesmata is passive, driven by concentration gradients.

In some sink organs, part of the short-distance pathway is apoplastic. When an apoplastic step occurs, the transport sugar can cross the apoplast unchanged, or it can be partly metabolized in the apoplast. For example, sucrose can be hydrolized into glucose and fructose by invertase, and then these sugars would enter the sink cells.