Plant Physiology

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1.http://www.cls.zju.edu.cn/sub/classroom/physiology/content/ketang.htm
2.http://jpkc.zju.edu.cn/k/437/content/ketang.htm
Chapter 5  Translocation and partitioning of photoassimilates

p123-143

Focus on:

• 1. The allocation of fixed carbon (photoassimilate)
• 2. Photoassimilate transport systems
• 3. Phloem translocation: structure, direction (source-sink), power---the pressure-flow hypothesis, phloem loading and unloading
• 4. Partitioning of photoassimilate in the different organs
• 5. Factors that regulate the distribution of photoassimilate
• Section 1  Starch and sucrose are biosynthesized in two different compartments

• The appropriation of carbon fixed by the PCR cycle into either starch or sucrose biosynthesis is called carbon allocation.

• Starchy leaf: soybean, spinach, tobacco
• Sugar leaf: wheat, barley, oat
Fig 5-1 Allocation of photoassimilate
• 1. Starch is biosynthesized in the stroma.
• The dominant storage carbohydrate in higher plants is the polysaccharide starch.

• Amylose

• Amylopectin
Fig 5-2  The structure of starch

- Amylose
- Amylopectin
2. Sucrose is biosynthesized in the cytosol

A soluble disaccharide: G + F.

The more abundant natural products not only play a vital role in plant life but is also a leading commercial commodity.

Translocation to other nonphotosynthetic tissues for direct metabolic use or for conversion to starch.

Storage products in sugarbeet or sugarcane
• 3. Sucrose synthesis is regulated by fructose-2,6-biphosphate (F2,6P).

F-2,6-P regulates conversion of F1,6P to F6P
Section 2 Translocation systems of assimilate in plant

• Figure 5-3 shows compartmentation in plant cell
• Fruit stores photoassimilate

Leaf makes photoassimilate

• Figure 5-4 shows compartmentation in plant organs
2.1 Photoassimilates are translocated by the two systems

- Short-distance transport systems
- Long-distance transport system
• **2.1.1** Transport systems in short distance.

• **1. Intracellular transport** → diffusion, protoplasmic streaming, transporters—Pi.

• **2. Intercellular transport** throughout apoplast and symplast (see chapter 1 water relationship).
Intercellular transport pathway

Plasmodesma consist of endoplasmic reticulum, plama membrane, central rod, spoke-like extensions, desmotubule and cytoplasmic sleeve (figure 5-5).
Figure 5-5 The structure of plasmodesma
• $10^6$~$10^7$/mm² in plant
  The plasmodesma is φ3nm, can transport the limited molecule of 800-1000D, but virus 10000D.
Figure 5-6 shows conceptual model for the cell-to-cell trafficking of viral RNA (vRNA) in uninfected plants.

**MP:** Move protein
Figure 5-7 shows a conceptual model for cell-to-cell trafficking of specific proteins of a size larger than passive SEL.
Plasmodesma function:

- Substance transport and information transduction.
- Less resistance to substance transport cell by cell because of no transmembrane transport.
- Such as the resistance for plasma membrane is 0.31 \( \Omega / \text{m}^2 \), for tonoplast 0.1 \( \Omega / \text{m}^2 \) and for plasmadesma 0.05/ \( \Omega \) m\(^2\).
• 3. Short distance translocation is alternative between apoplast and symplast

Fig 5-8 alternative transport between apoplast and symplast
4. Transfer cells play a vital role in phloem loading and unloading of photoassimilates.
• Transfer cells: A group of specific cells exist in the terminal in conduct tissue, flower or fruits

• Characteristics in structure and metabolism:
  • Large surface area of cell because cell wall and plasma membrane show rugocity (ingrowth).
  • Abundant cytosol and organelles, high metabolic activity.
• Companion cells and intermediary cells are considered as transfer cells.

• Main function: Loading assimilate into phloem from source and unloading assimilate into sink cell from phloem or other conduct tissue.
Figure 5-10 Sieve elements and companion cells
• **2.1.2 long distant translocation of Photoassimilates via phloem**

![Diagram of ring girdling](image)

- **Ring girdling**
- **Ring girdling for certain time forms a hump**

- **Figure 5-11** Ring girdling results in the hump
Figure 5-11 conduct tissue
• 1. Sieve tube and companion cell (SE/CC) are in angiosperm

Figure 5-12 a model of sieve element and companion cells
Figure 5-13 Photograph of sieve element and companion cell by electron microscope
• **Longevity**: 1 growth season to several years

• **Companion cell**: it tightly contacts with sieve elements and link with plasmadesma.

• It provides energy and substance for sieve and constructs a sieve element—companion complex (SE/CC), as the transfer cell, participates in assimilate transport—loading and unloading.
2. Sieve cell and albuminous cell in gymnosperm and pteridophyte

Without P- protein in sieve cell
albuminous cell as a function of companion.
Fig 5-14 Confocal microscope shows phloem transport
• 3.1 Elements of phloem sap
• How to get phloem sap?
Figure 5-15 harvest phloem sap
<table>
<thead>
<tr>
<th>Component</th>
<th>Concentration (mg mL(^{-1}))</th>
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<tbody>
<tr>
<td>Sugars</td>
<td>80.0–106.0</td>
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<tr>
<td>Amino acids</td>
<td>5.2</td>
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<tr>
<td>Organic acids</td>
<td>2.0–3.2</td>
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<tr>
<td>Protein</td>
<td>1.45–2.20</td>
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<tr>
<td>Potassium</td>
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<tr>
<td>Chloride</td>
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<tr>
<td>Phosphate</td>
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<tr>
<td>Magnesium</td>
<td>0.109–0.122</td>
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*Source: Hall and Baker 1972.*
<table>
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<th>Component</th>
<th>Value</th>
<th>Component</th>
<th>Value</th>
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<tr>
<td>Total dry matter</td>
<td>17.1-19.2(%)</td>
<td>K</td>
<td>1.68</td>
</tr>
<tr>
<td>EC (ms/cm)</td>
<td>1.03</td>
<td>Mg</td>
<td>0.051</td>
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<tr>
<td>pH</td>
<td>8.0-8.2</td>
<td>Ca</td>
<td>0.014</td>
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<tr>
<td>Components (mg/ml)</td>
<td></td>
<td>Na</td>
<td>0.0014</td>
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<tr>
<td>Sucrose</td>
<td>150-165</td>
<td>Zn</td>
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<tr>
<td>Glucose</td>
<td>2-4</td>
<td>Fe</td>
<td>0.0041</td>
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<tr>
<td>Fructose</td>
<td>2-4</td>
<td>Mn</td>
<td>0.0005</td>
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<td>Protein</td>
<td>0.5-0.8</td>
<td>Cu</td>
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<tr>
<td>Amino acid</td>
<td>6.3-10.1</td>
<td>Mo</td>
<td>0.00001</td>
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<tr>
<td>Total P</td>
<td>0.301</td>
<td>Nitrate</td>
<td>0</td>
</tr>
<tr>
<td>Pi</td>
<td>0.105</td>
<td>Nitrate</td>
<td>0</td>
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**Amino acid (%)**

<table>
<thead>
<tr>
<th>Amino acid</th>
<th>Value</th>
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<tr>
<td>Gln</td>
<td>58</td>
</tr>
<tr>
<td>Val</td>
<td>10</td>
</tr>
<tr>
<td>Ser, Gly</td>
<td>7</td>
</tr>
<tr>
<td>(Iso-)Leu</td>
<td>6</td>
</tr>
<tr>
<td>Lys</td>
<td>5</td>
</tr>
<tr>
<td>Glu</td>
<td>4</td>
</tr>
<tr>
<td>Ala</td>
<td>2</td>
</tr>
<tr>
<td>Asn</td>
<td>trace</td>
</tr>
<tr>
<td>Pro</td>
<td>trace</td>
</tr>
</tbody>
</table>
• Components in phloem sap:
• 1. Sugars. Sucrose >90%, a small number of sorbitol, mannitol and oligose including raffinose and stachyose.

• Main sorbitol in rose plant phloem.
(B) Compounds commonly translocated in the phloem

Sucrose is a disaccharide made up of one glucose and one fructose molecule. Raffinose, stachyose, and verbascose contain sucrose bound to one, two, or three galactose molecules, respectively.

Mannitol is a sugar alcohol formed by the reduction of the aldehyde group of mannose.

Glutamic acid, an amino acid, and glutamine, its amide, are important nitrogenous compounds in the phloem, in addition to aspartate and asparagine.
• **2. Amino acids and Amides.** Glu or Asp and their amides.

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

Species with nitrogen-fixing nodules also utilize ureides as transport forms of nitrogen.

- Allantoic acid
- Allantoin
- Citrulline
• 3. proteins (enzymes, ATPase) and nuclear acid (small mRNA).

• 4. Plant hormones, ATP, glucolipid, vitamins.

• 5. organic acids. Mal.
• **inorganic ions:** cations > anions, most $K^+$ for cations, most $Pi$ for anions, and without $NO_3^-$

Lower $H^+$, higher pH(7.5-8.5) and $K^+$ concentration in sieve element;

Higher $H^+$ concentration, lower pH(5-6) and $K^+$ concentration outside sieve element.
3.2 Transport direction is determined by sink-source

- 1. From source to sink---bidirectional way.

Figure 5-16 bidirectional way
Source——metabolic source, referred as the organs or tissues which produce or/and transports out assimilate, such as developed leaf, root tuber or tuber during germination.

Sink——metabolic, referred as the organs or/and tissues which consume or/and store assimilate, such as root, seed, fruit, root tuber and tuber during developing.
• Slight ring girdling in branch can enhance fruit setting.
• “树怕剥皮，不怕烂心”? 

**Figure 5-13** Ring girdling results in the hump. 

After ring girdling branch the bark can form a hump (hypertrophic growth).
2. Ipsi-lateral transport of assimilate is dominant

**Figure 5-14** Ipsi-lateral transport of assimilate
• 3. Assimilates in different sources are translocated by different conduct tissues.

• Assimilate made in leaf is transported to root by phloem.

• Assimilate stored in tuber is transported to bud for germination by phloem, too.

• Assimilate stored in the tree root is transported to bud and young leaf by xylem.
• **4. Rate of assimilate transport in phloem**
• **Velocity, mass transfer rate**
• (1) **Velocity**: the linear distance traveled per unit time
• In most plant about 50-250cm/h, such as soybean 84-100, grape 60, sugarcane (C_4 plant) 300-600cm/h.
• Sucrose is 107cm/h, Pi and H_2O are 87cm/h.
• **Mass transfer rate**, the quantity of material passing through a given cross section of phloem or sieve elements per unit time.

• Values for mass transfer rate range from 1 to 15 g h⁻¹ cm⁻² of sieve elements.
• **3.4 Phloem translocation occurs by mass transfer**

• **1. Pressure-flow hypothesis**

• The **pressure-flow model**, first proposed by Ernst Münch in 1930, states that a flow of solution in the sieve elements is driven by an osmotically generated *pressure gradient* between source and sink (\( \Delta Y_p \)). The pressure gradient is established as a consequence of phloem loading at the source and phloem unloading at the sink.
Figure 5-15 A model of pressure flow hypothesis

Osmotic meter A loading, Osmotic meter B unloading
FIGURE 10.10 Pressure-flow model of translocation in the phloem. Possible values for $\Psi_w$, $\Psi_p$, and $\Psi_s$ in the xylem and phloem are illustrated. (After Nobel 1991)
(2) Contractive protein hypothesis
P-protein uses ATP to contract and pushes phloem flow.

Figure 5-16 structure of sieve element
(3) Electroosmotic flow hypothesis

Potential difference

- +

Cation flows

Figure 5-15 illustration of electroosmotic flow hypothesis

cation

anion
3.5 Loading and unloading in phloem

1. Phloem loading is through the sucrose–H$^+$ symporters

- Sucrose from mesophyll cell to apoplast, then to SE/CC into sieve element.
- Requirement for energy and against concentration of sucrose.
Fig 5-17  This autoradiograph shows that labeled sugar moves from the apoplast into sieve elements and companion cells against its concentration gradient in sugar beet (*Beta vulgaris*). Label accumulates in the small veins, sieve elements, and companion cells of the source leaf, indicating the ability of these cells to transport sucrose against its concentration gradient. (From Fondy 1975, courtesy of D. Geiger.)
Figure 5-18 ATP-dependent sucrose transport in sieve element loading.

In the cotransport model of sucrose loading into the symplast of the sieve element–companion cell complex, the plasma membrane ATPase pumps protons out of the cell into the apoplast, establishing a high proton concentration there. The energy in this proton gradient is then used to drive the transport of sucrose into the symplast of the sieve element–companion cell complex through a sucrose–H\(^+\) symporter.
<table>
<thead>
<tr>
<th>Carrier</th>
<th>Location</th>
<th>Species</th>
<th>Affinity</th>
<th>Source</th>
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<tbody>
<tr>
<td>SUT1</td>
<td>Sieve elements</td>
<td>Tobacco, tomato, potato</td>
<td>High</td>
<td>Kuhn et al. 1997</td>
</tr>
<tr>
<td>SUT2</td>
<td>Sieve elements</td>
<td>Tomato</td>
<td>Sensor</td>
<td>Barker et al. 2000</td>
</tr>
<tr>
<td>SUT4</td>
<td>Sieve elements</td>
<td>Arabidopsis, tomato, potato</td>
<td>Low</td>
<td>Weise et al. 2000</td>
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<tr>
<td>SUC2</td>
<td>Companion cells</td>
<td>Arabidopsis, plantain</td>
<td>—</td>
<td>Truernit and Sauer, 1995;</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Stadler et al. 1995</td>
</tr>
</tbody>
</table>
Figure 5-18 Polymer-trapping model of phloem loading.

Sucrose, synthesized in the mesophyll, diffuses from the bundle sheath cells into the intermediary cells through the abundant plasmodesmata.

In the intermediary cells, raffinose (and stachyose) are synthesized from sucrose and galactose, thus maintaining the diffusion gradient for sucrose. Because of their larger sizes, they are not able to diffuse back into the mesophyll.

Raffinose and stachyose are able to diffuse into the sieve elements. As a result, the concentration of transport sugar rises in the intermediary cells and the sieve elements.
(2) Phloem unloading

Fig 5-19 Pathways for phloem unloading. The sieve element–companion cell complex (CC/SE) is considered a single functional unit. The presence of plasmodesmata is assumed to provide functional symplastic continuity. An absence of plasmodesmata between cells indicates an apoplastic transport step.

(A) Symplastic phloem unloading

Phloem unloading pathway

Symplastic SE unloading
CC/SE Plasmodesma Cell wall Sink cell

(B) Apoplastic phloem unloading

Type 1
Apoplastic SE unloading

Type 2A
Symplastic SE unloading

Type 2B
Symplastic SE unloading

Type 1: This phloem unloading pathway is designated apoplastic because one step, transport from the sieve element–companion cell complex to the successive sink cells, occurs in the apoplast. Once the sugars are taken back up into the symplast of adjoining cells, transport is symplastic. This route has not yet been demonstrated in any sink type.

Type 2: This pathway also has an apoplastic step. However, the exit from the sieve element-companion cell complex—that is, sieve element unloading—is symplastic. The apoplastic step occurs later in the pathway. The upper figure (2A) shows an apoplastic step close to the sieve element-companion cell complex; the lower figure (2B), an apoplastic step that is further removed.
Section 4  Partitioning of photoassimilates in plant

• **4.1 Relationship between sink and source**
  
  1. Sink-source is variable:
  
  • Young leaf—sink, half-developed leaf—sink and source, well developed leaf—source.
  
  • Developing seed, tuber—sink; germinating seed—source.
• (2) Sink-source are promoted and inhibited by each other.

• Small source $\rightarrow$ small sink, small sink inhibits source activity. Such as shading leaf, grain number ↓, empty ↑, small fruit.

• Too strong source makes sink ↓ and too strong sink results in source activity and causes premature of source.

• “Full source, large sink and high transloaction”——high yield physiology.
4.2 The law of assimilate partition

- 1. Source to sink prior to growth center
- Growth center is a part growing fast and getting assimilate easily at that time.
• 2. Ipsi-lateral transport, near supplication prior to the sink next to source.

Maintaining flag leaf and fruit leaf!
3.3 Redistribution and reutilization of assimilate

- Transport from senescence leaf to young part and from vegetative organ to reproductive one.
Fig 5-20 The empty ovule technique for studying phloem unloading in legumes. A flap is cut into the wall of a young bean pod (1), allowing access to the developing seed. The distal (unattached) half of the seed is surgically removed and discarded (2). The embryo tissues of the remaining half-seed are scooped out (3), leaving a cup-shaped structure (the empty ovule) comprised only of maternal seed coat tissue. The cup can then be filled with a buffer or agar, which traps substances from vascular tissue that, in the intact seed, would supply the embryo.
5.1 Internal factors

1. Sucrose content: $S \uparrow$, export $\uparrow$.
• 2. ATP ↑ 、Pi ↑ 、TP ↑ 、export ↑.

• In sugarbeet, K/Na ↑ 、starch ↑ 、S ↓ 、export ↓。
• 3. **Plant hormones**: IAA, GA, CTK ↑, import ↑

• 4. **Size in sink**, sink ↑, import ↑。
4.2 Environmental factors


2. Light: light ↓, Pn ↓, S ↓, export ↓
   - Transport during daytime > one at night.
3. **Temperature**: optimum 20-30°C. T ↓, transport ↓ because of respiration ↓, energy ↓, Pn ↓ photoassimilate ↓, viscosity ↑, callose ↑.

High T, transport ↓, due to respiration ↑, Pn ↓, photoassimilate ↓, viscosity ↑, callose ↑

Larger difference in temperature favors transport because of accumulation of photoassimilate.

4. **Mineral nutrition**: B, P, K.
1. What factors determine whether the product of the PCR cycle will be converted to starch in the chloroplast or sucrose in the cytosol?
2. Describe the structure of mature phloem tissue. What are causes hypertrophic growth above a girdle wound?
3. Describe the source–sink concept. To what extent are source-sink relationships involved in determining the direction and rate of translocation in the phloem?
4. How are sugars loaded into the phloem sieve tubers at the source and removed at the sink?
5. Distinguish between allocation and partitioning. What factors determine allocation of carbon within a source leaf? What factors determine partitioning between more than one potential sink?