Laboratoř růstových regulátorů

Miroslav Strnad

Floémový transport [kap 10]

- Univerzita Palackého & Ústav experimentální botaniky AV CR

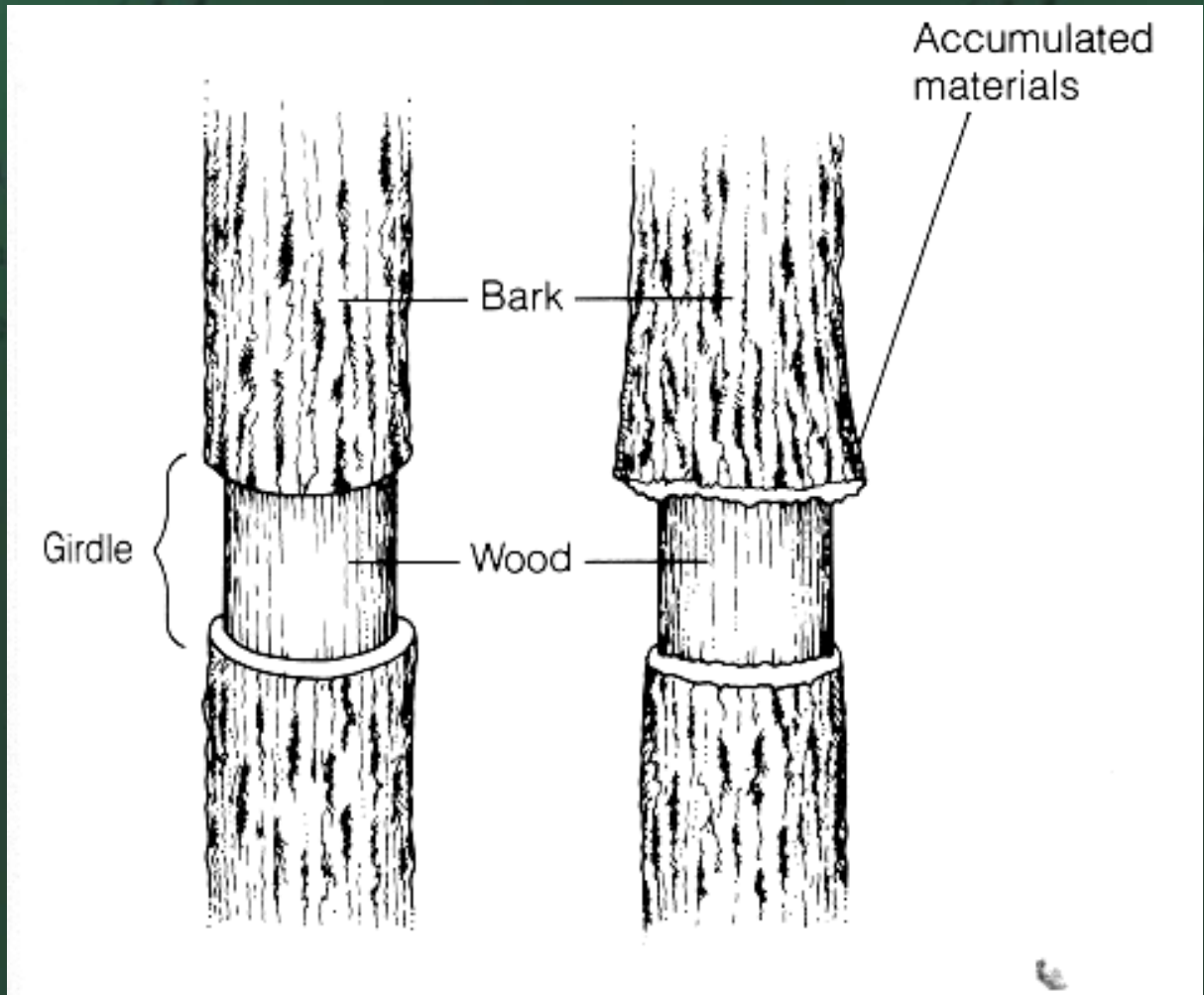
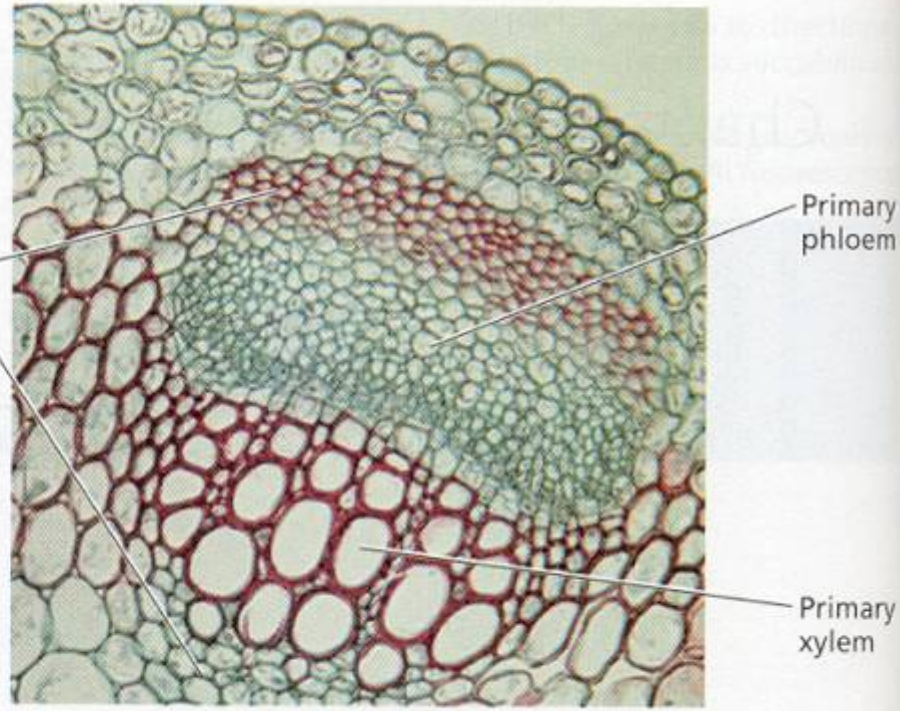


FIGURE 7.3. Tree trunk immediately after girdling (left) and after a longer period of time (right). Girdling is the removal of the bark of a tree in a ring around the trunk. Materials translocated from the leaves have accumulated in the region above the girdle and caused it to swell.

FIGURE 10.1 Transverse section of a vascular bundle of trefoil, a clover (*Trifolium*). (130×) 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.)



PATHWAYS OF TRANSLOCATION

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 (Figures 10.1 and 10.2). In plants with secondary growth the phloem constitutes the inner bark.

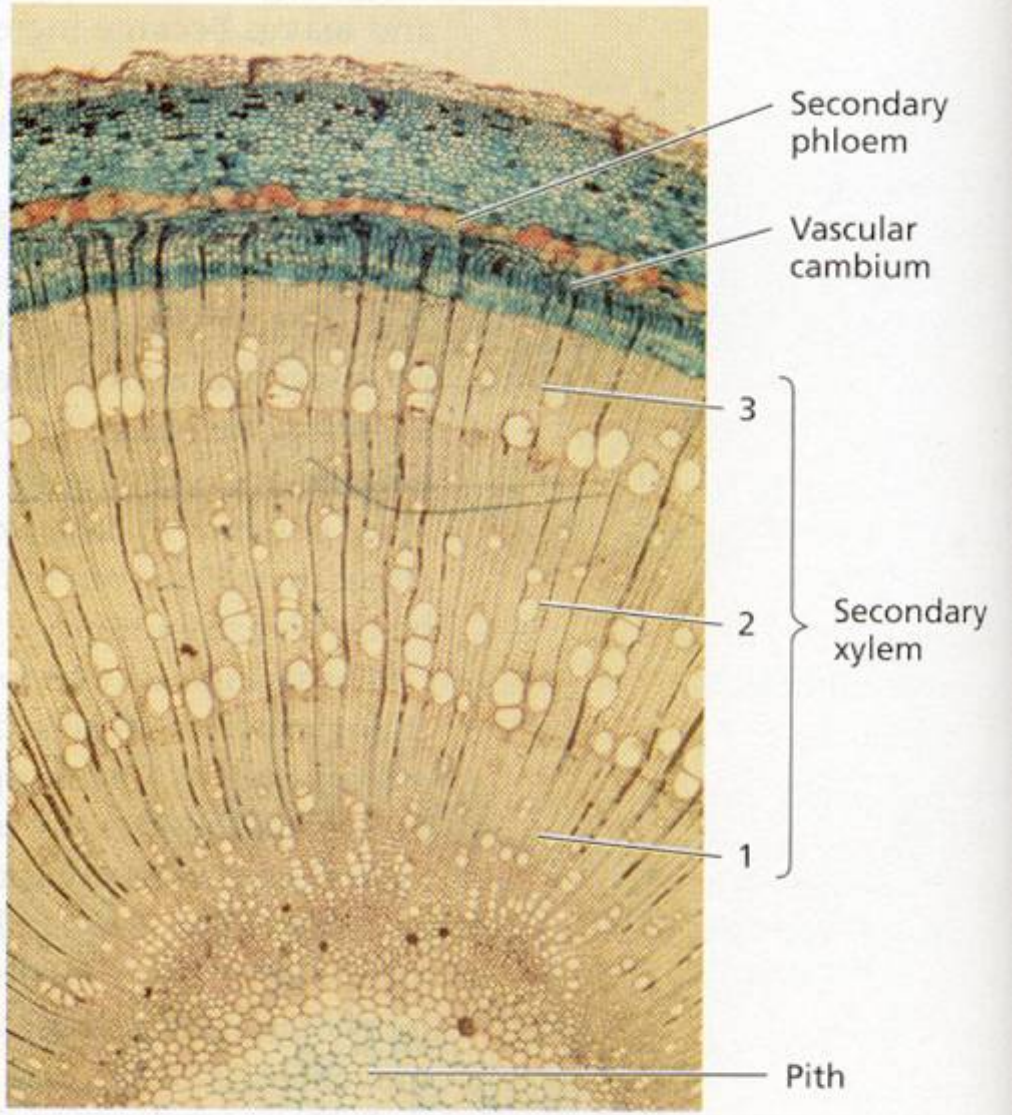


FIGURE 10.2 Transverse section of a 3-year-old stem of an ash (*Fraxinus excelsior*) tree. (27×) The numbers 1, 2, and 3 indicate growth rings in the secondary xylem. The old secondary phloem has been crushed by expansion of the xylem. Only the most recent (innermost) layer of secondary phloem is functional. (© P. Gates/Biological Photo Service.)

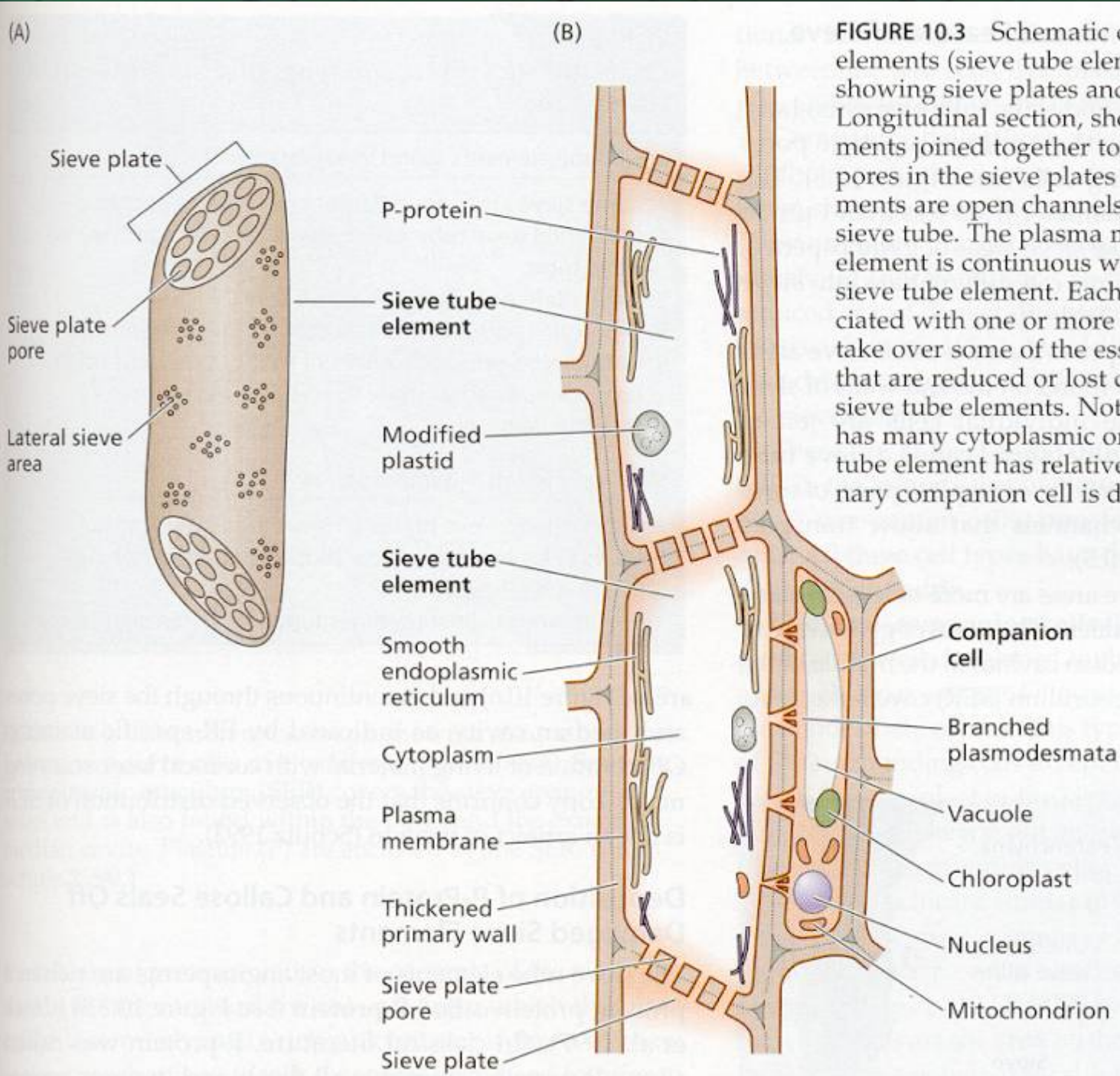


FIGURE 10.3 Schematic drawings of mature sieve elements (sieve tube elements). (A) External view, showing sieve plates and lateral sieve areas. (B) Longitudinal section, showing two sieve tube elements joined together to form a sieve tube. The pores in the sieve plates between the sieve tube elements are open channels for transport through the sieve tube. The plasma membrane of a sieve tube element is continuous with that of its neighboring sieve tube element. Each sieve tube element is associated with one or more companion cells, which take over some of the essential metabolic functions that are reduced or lost during differentiation of the sieve tube elements. Note that the companion cell has many cytoplasmic organelles, whereas the sieve tube element has relatively few organelles. An ordinary companion cell is depicted here.

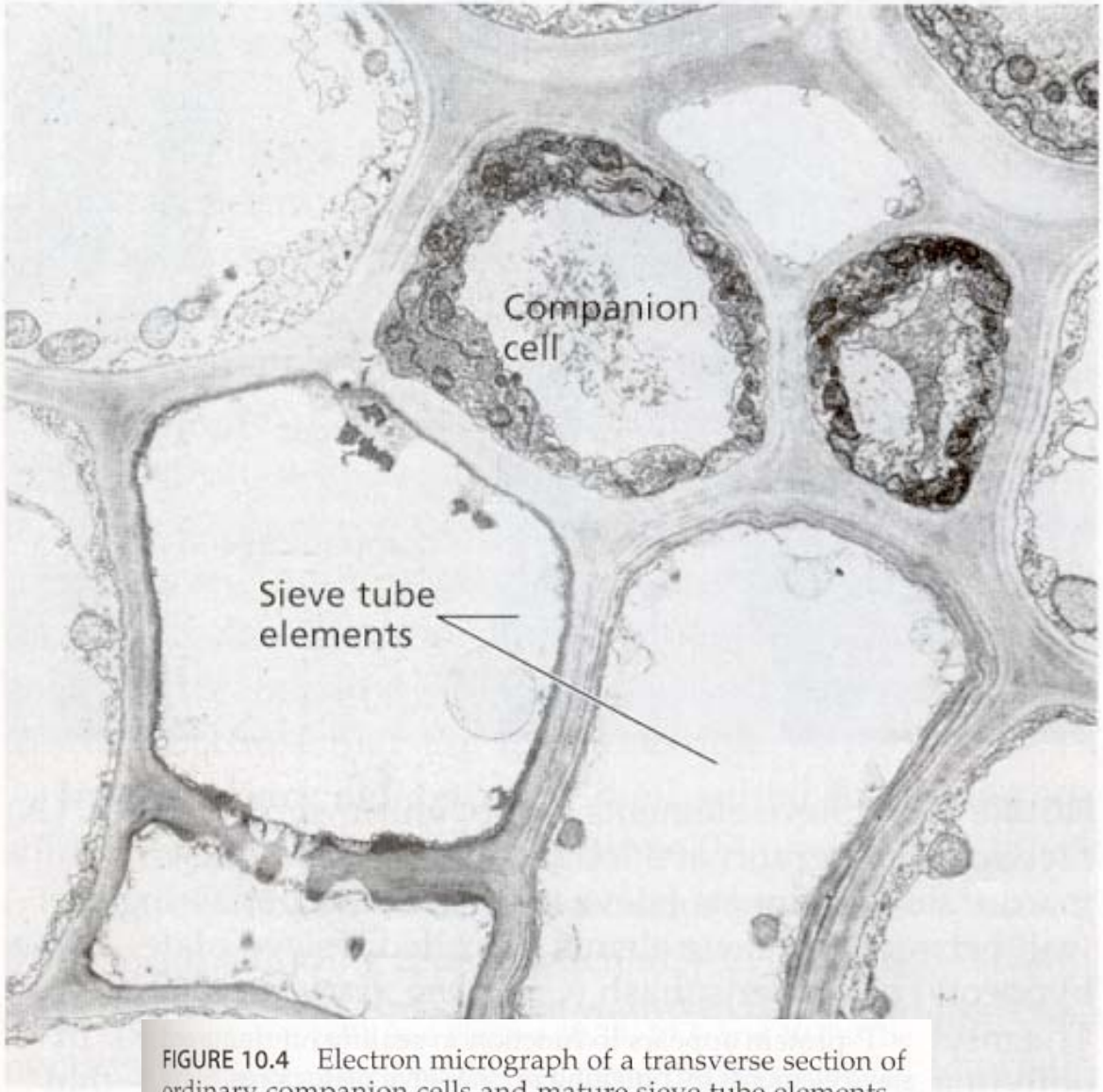


FIGURE 10.4 Electron micrograph of a transverse section of ordinary companion cells and mature sieve tube elements. (3600×) The cellular components are distributed along the walls of the sieve tube elements. (From Warmbrodt 1985.)

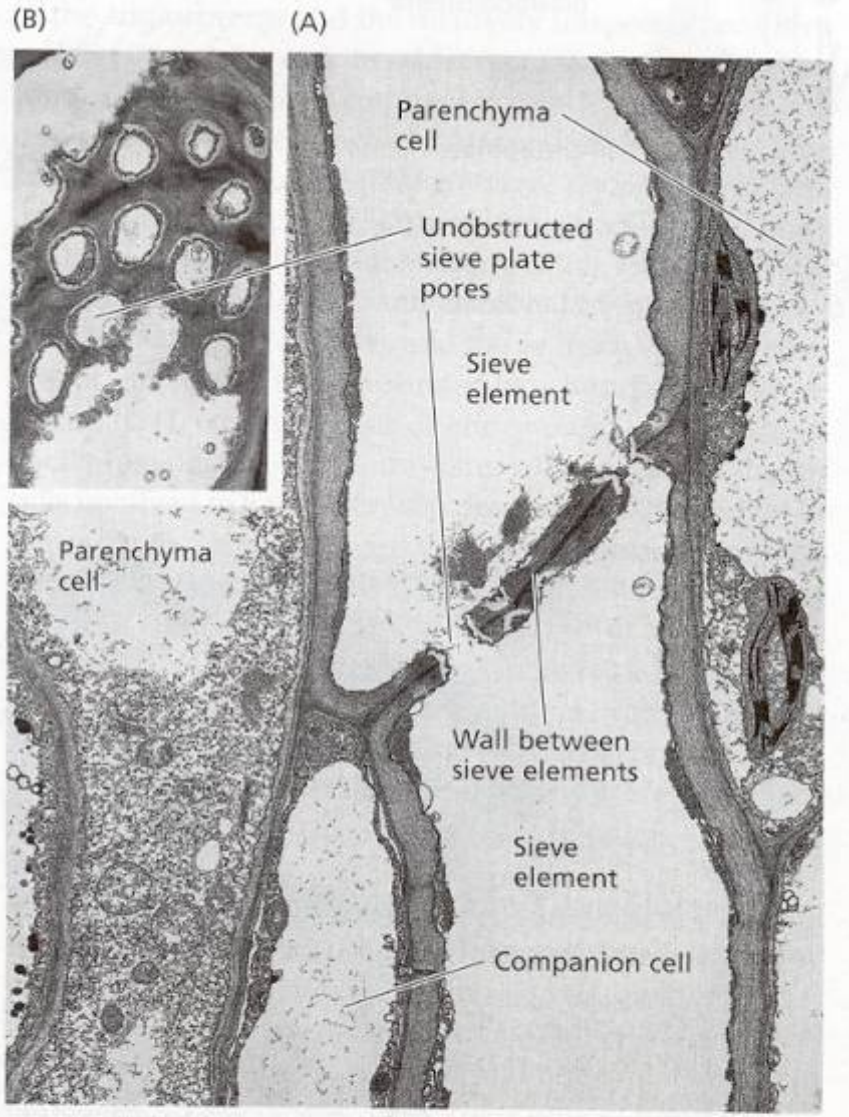


FIGURE 10.5 Sieve elements and open sieve plate pores. (A) Electron micrograph of a longitudinal section of two mature sieve elements (sieve tube elements), showing the wall between the sieve elements (called a sieve plate) in the hypocotyl of winter squash (*Cucurbita maxima*). (3685×) (B) The inset shows sieve plate pores in face view (4280×). In both images A and B, the sieve plate pores are open—that is, unobstructed by P-protein. (From Evert 1982.)

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.

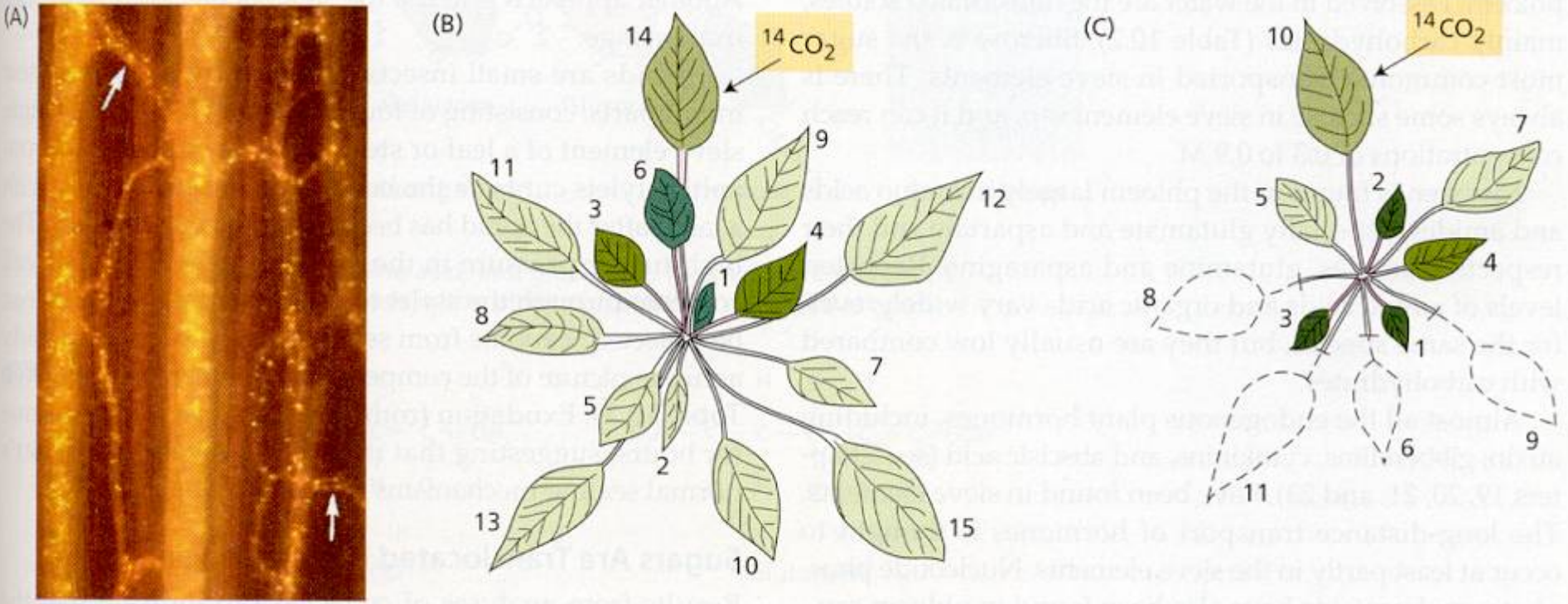


FIGURE 10.8 (A) Longitudinal view of a typical three-dimensional structure of the phloem in a thick section (from an internode of dahlia [*Dahlia pinnata*]). View here after clearing, staining with aniline blue, and observing under an epifluorescent microscope; the sieve plates are seen as numerous small dots because of the yellow staining of callosa in the sieve areas. Two large longitudinal vascular bundles are prominent. This staining reveals the delicate sieve tubes forming the phloem network; two phloem anastomoses are marked by arrows. (B) Distribution of radioactivity from a single labeled source leaf in an intact plant. The distribution of radioactivity in leaves of a sugar beet plant (*Beta vulgaris*) was determined 1 week after $^{14}CO_2$ 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. The ^{14}C label was translocated mainly to the sink leaves directly above the source leaf (that is, sink leaves on the same orthostichy as the source; for example, leaves 1 and 6 are sink leaves directly above source leaf 14). (C) Same as B, except all source leaves on the side of the plant opposite the labeled leaf were removed 24 hours before labeling. Sink leaves on both sides of the plant now receive ^{14}C-labeled assimilates from the source. (A courtesy of R. Aloni; B and C based on data from Joy 1964.)

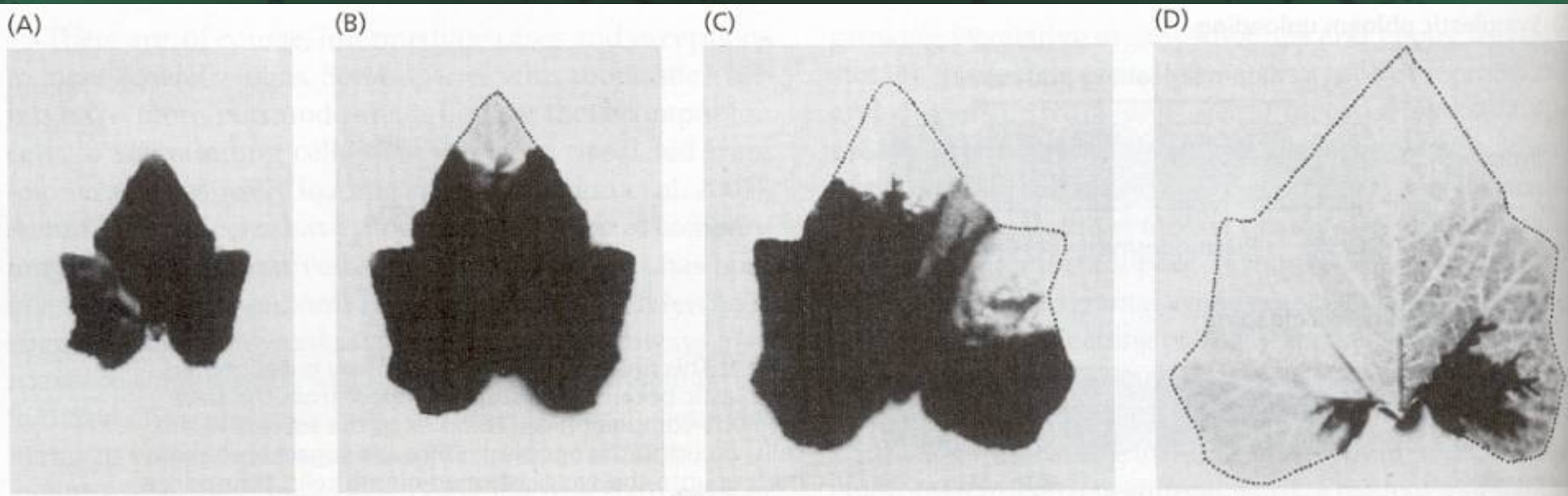


FIGURE 10.19 Autoradiographs of a leaf of summer squash (*Cucurbita pepo*), showing the transition of the leaf from sink to source status. In each case, the leaf imported ^{14}C from the source leaf on the plant for 2 hours. Label is visible as black accumulations. (A) The entire leaf is a sink, importing sugar from the source leaf. (B–D) The base is still a sink. As the tip of the leaf loses the ability to unload and stops importing sugar (as shown by the loss of black accumulations), it gains the ability to load and to export sugar. (From Turgeon and Webb 1973.)

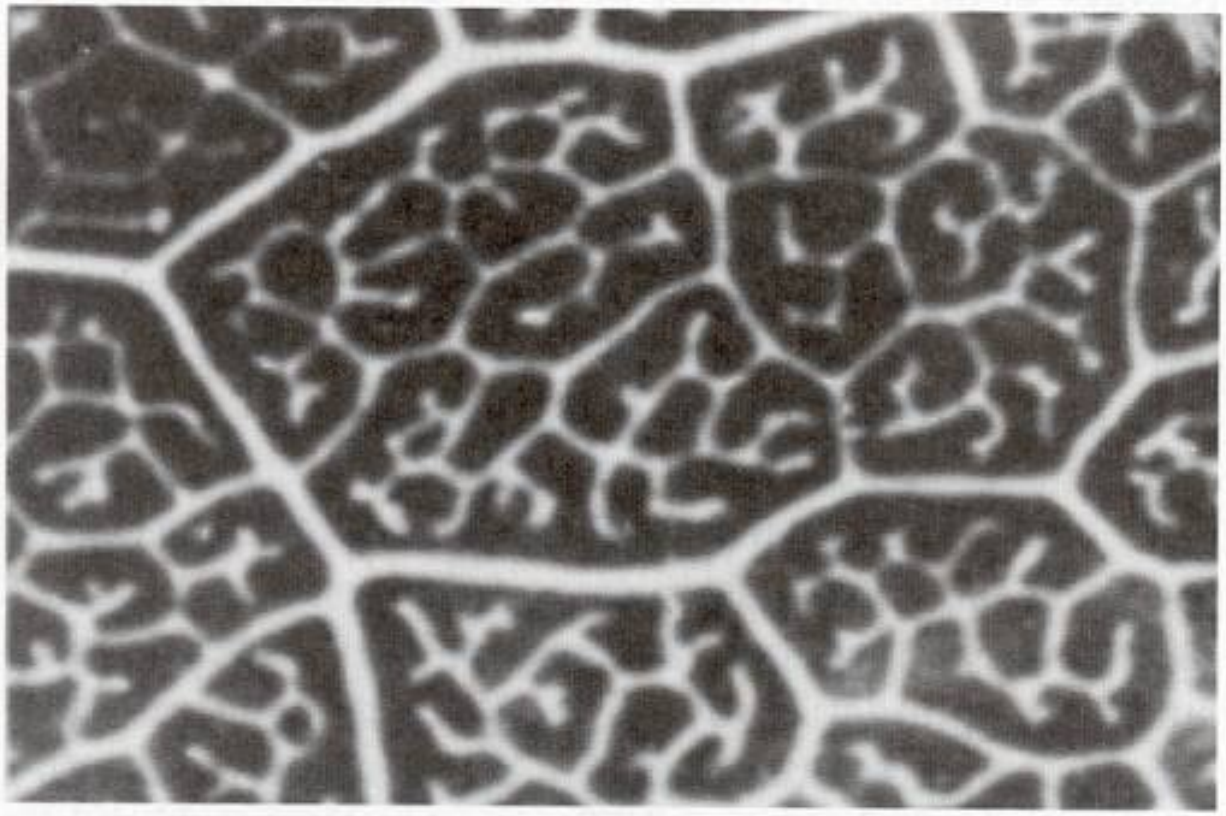
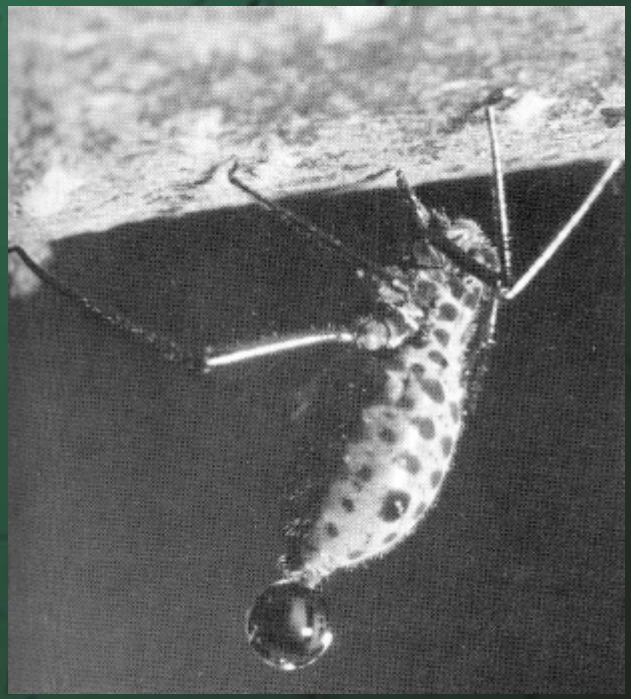
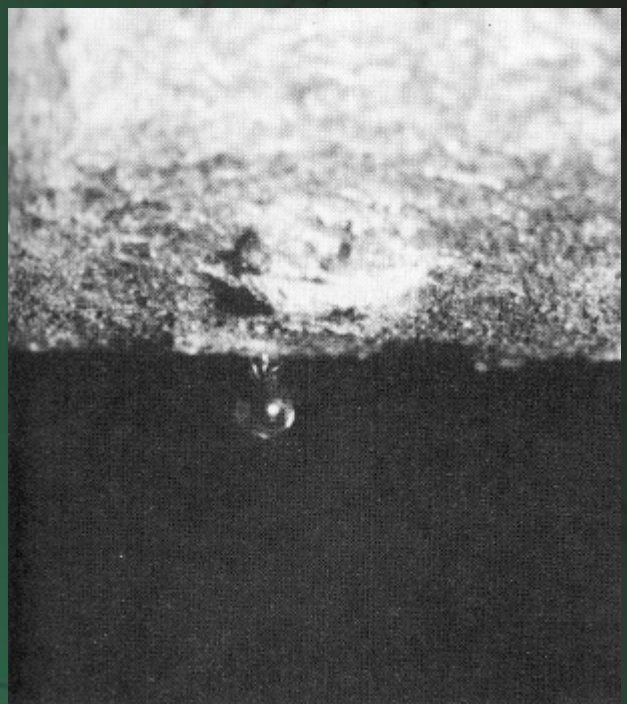
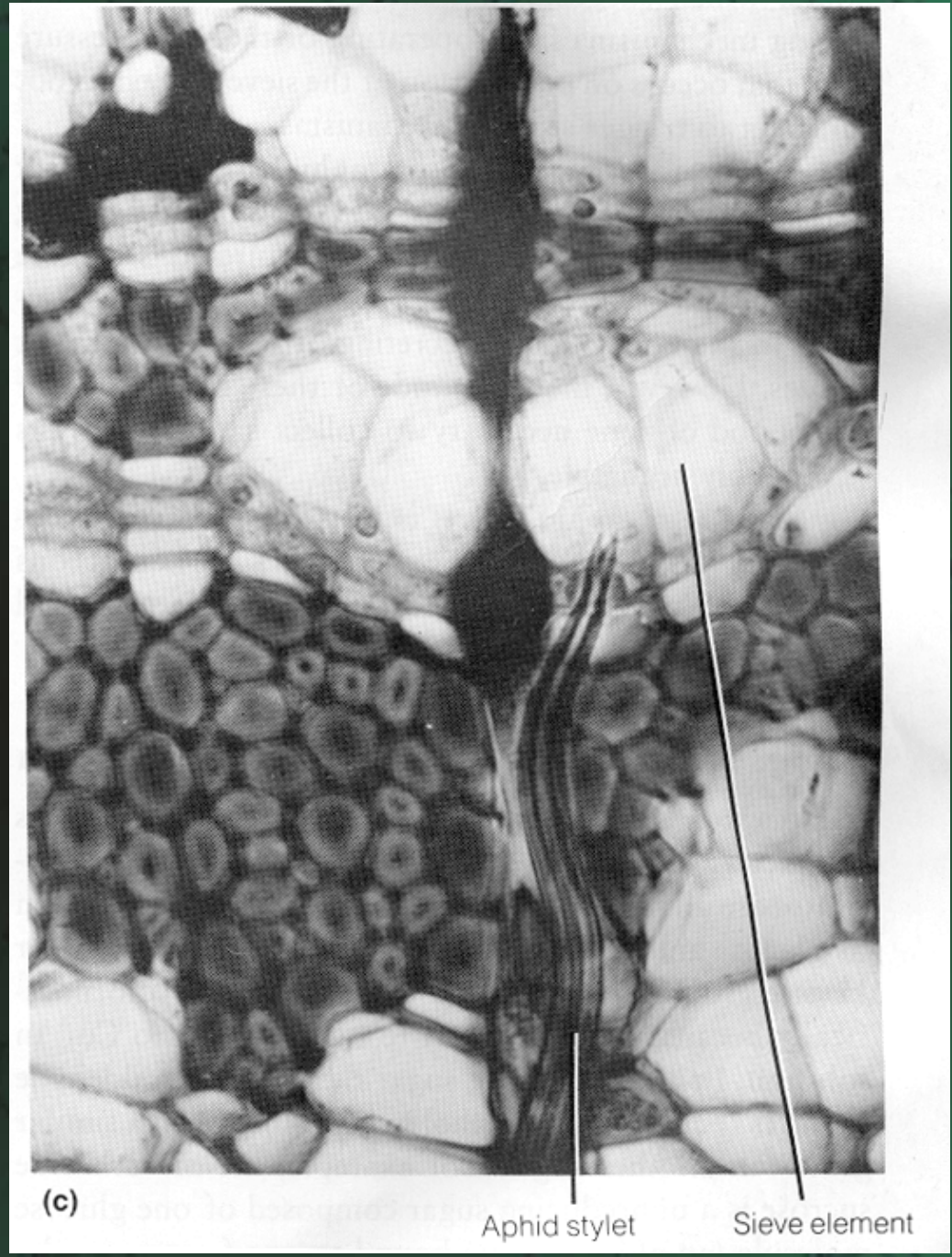


FIGURE 10.15 This autoradiograph shows that labeled sugar moves from the apoplast into sieve elements and companion cells against its concentration gradient. A solution of ^{14}C-labeled sucrose was applied for 30 minutes to the upper surface of a sugar beet (*Beta vulgaris*) leaf that had previously been kept in darkness for 3 hours. The leaf cuticle was removed to allow penetration of the solution to the interior of the leaf. 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.)






(c)
Aphid stylet
Sieve element

Složení floémové šťávy

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.

Cukerné alkoholy ve floémové šťávě

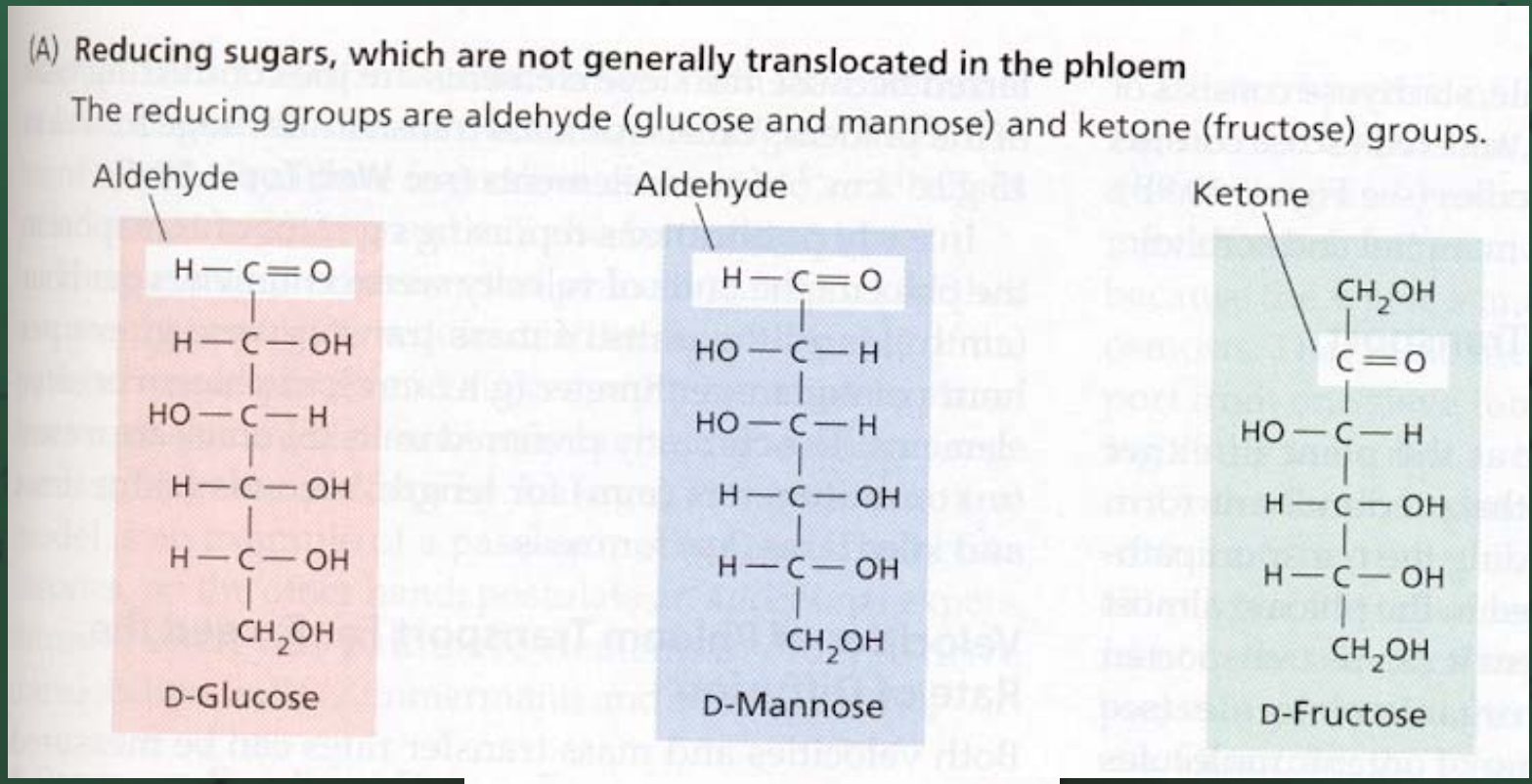
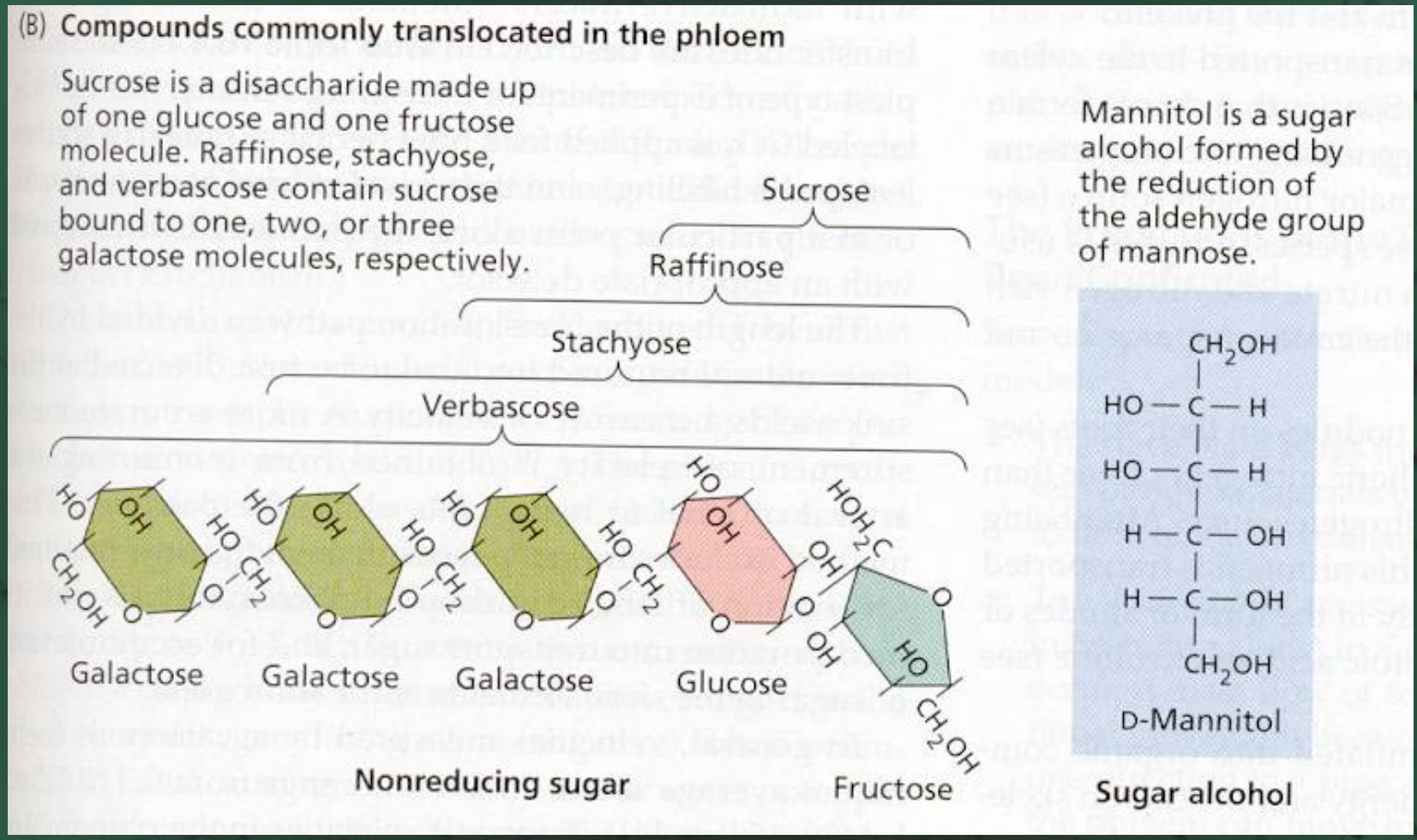


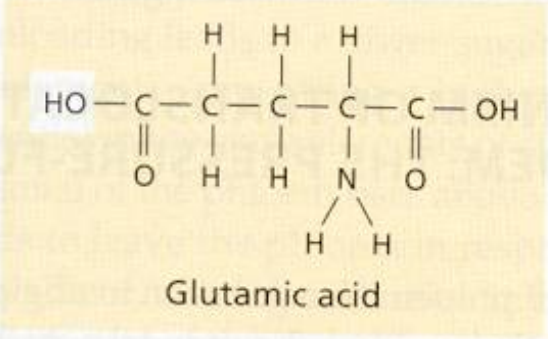
FIGURE 10.9 Structures of compounds not normally translocated in the phloem (A) and of compounds commonly translocated in the phloem (B).

Cukry transportované ve floému

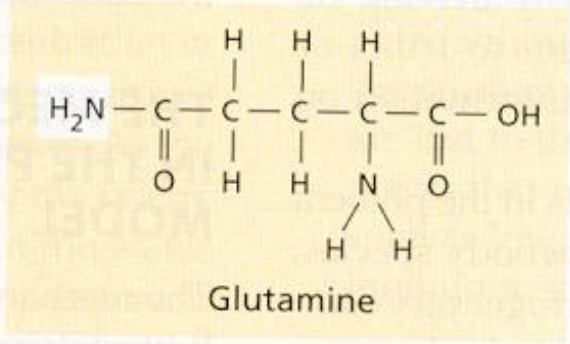


Dusíkaté látky transportované ve floému

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

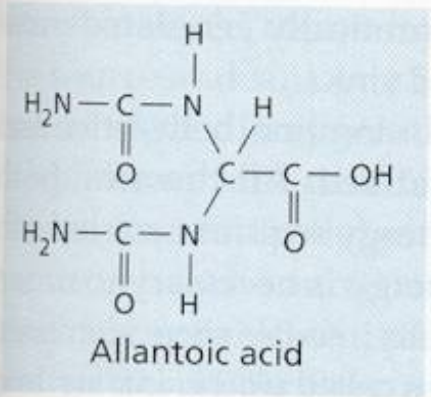


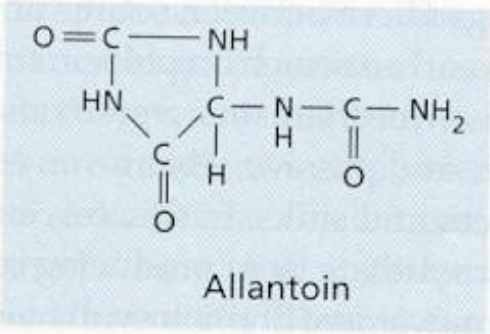
Amino acid

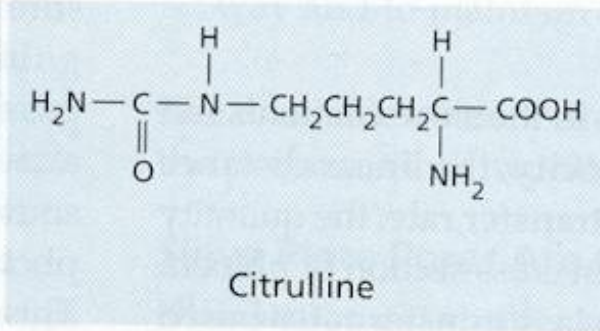


Amide

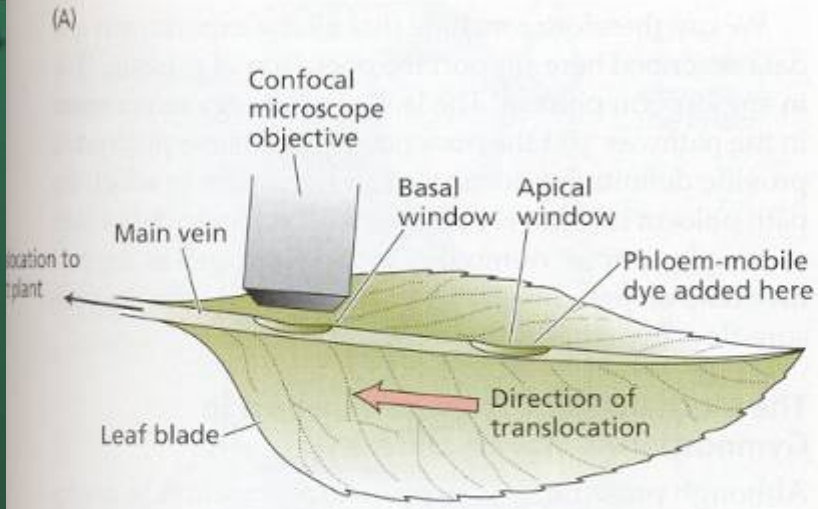
Species with nitrogen-fixing nodules also utilize ureides as transport forms of nitrogen.

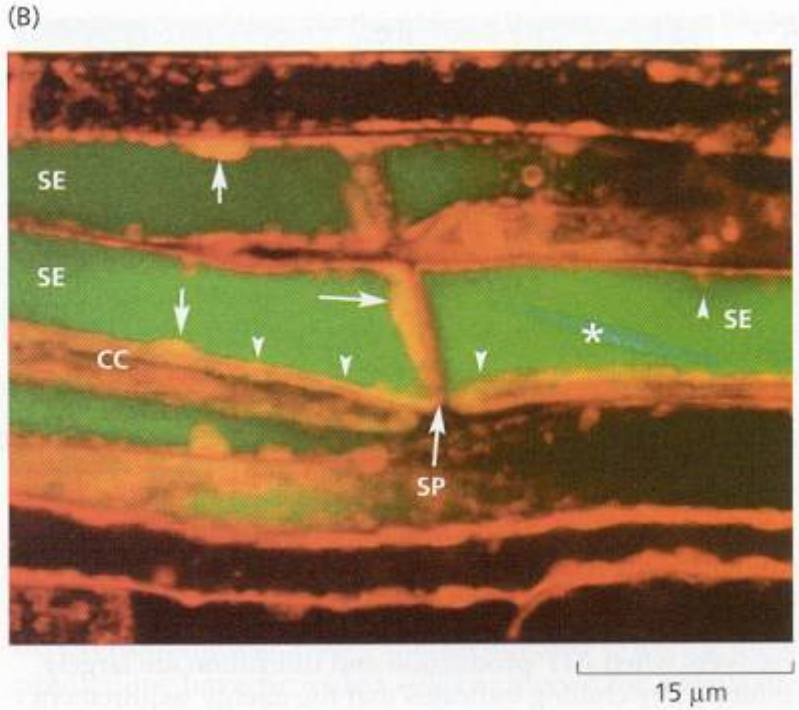






Ureides





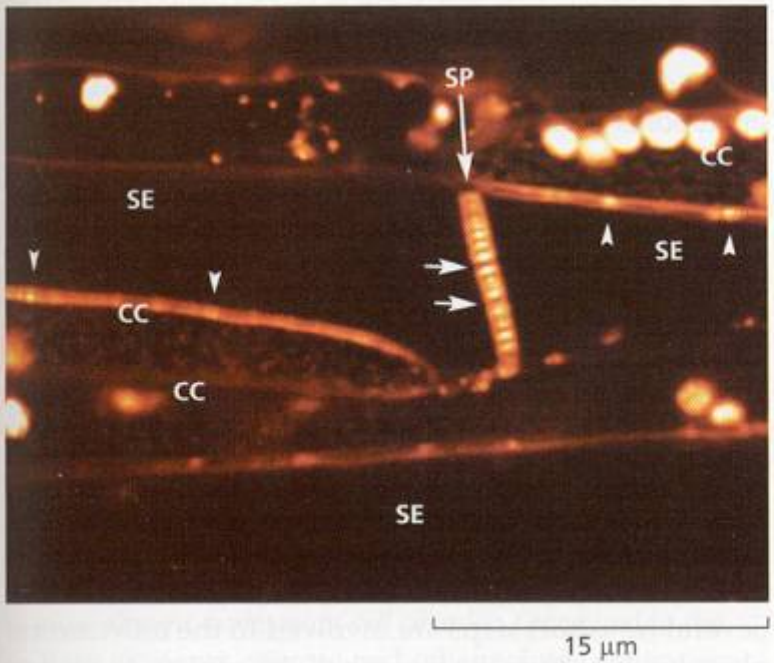


FIGURE 10.11 Translocation in living, functional sieve elements of a leaf attached to an intact broad bean (*Vicia faba*) plant. (A) Two windows were sliced parallel to the epidermis on the lower side of the main vein of a mature leaf, exposing the phloem tissue. The objective of the laser confocal microscope was positioned over the basal window. A phloem-mobile fluorescent dye was added at the apical window. If translocation occurred, the dye would become visible in the microscope at the basal window of the leaf. In this way it could be demonstrated that the sieve elements being observed were alive and functional. (B) Phloem tissue of bean doubly stained with a locally applied fluorescent dye (red) that primarily stains membranes, and a translocated fluorescent dye (green). Protein (arrows) deposited against the plasma membrane and the sieve plate does not impede translocation. A crystalline P-protein body (asterisk) is stained by the green dye. Plastids (arrowheads) are evenly distributed around the periphery of the sieve element. CC = companion cell, SP = sieve plate. See also **Web Topic 10.8.** (From Knoblauch and van Bel 1998; courtesy of A. van Bel.)

Uložení sítkovic v pletivu – asimiláty musí urazit vzdálenost několika buněk

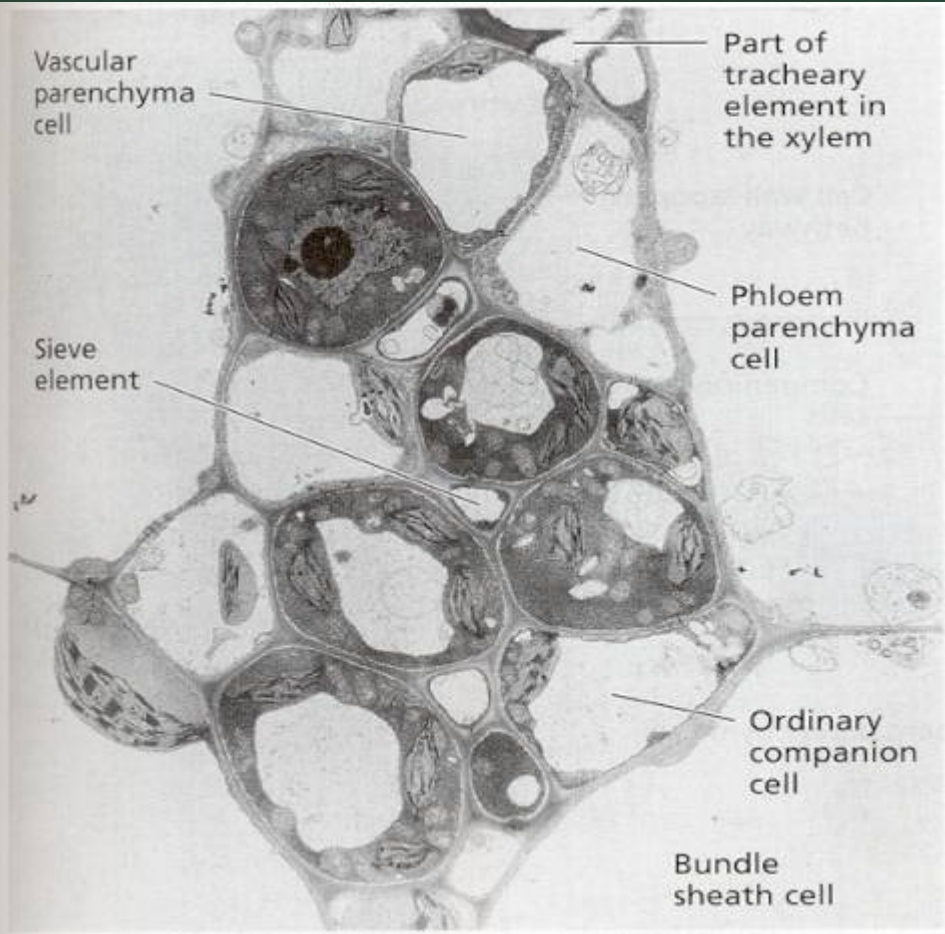


FIGURE 10.13 Electron micrograph showing the relationship between the various cell types of a small vein in a source leaf of sugar beet (*Beta vulgaris*). Photosynthetic cells (mesophyll cells) surround the compactly arranged cells of the bundle sheath layer. Photosynthate from the mesophyll must move a distance equivalent to several cell diameters before being loaded into the sieve elements. (From Evert and Mierzwa 1985, courtesy of R. Evert.)

Symplastické nakládání floému

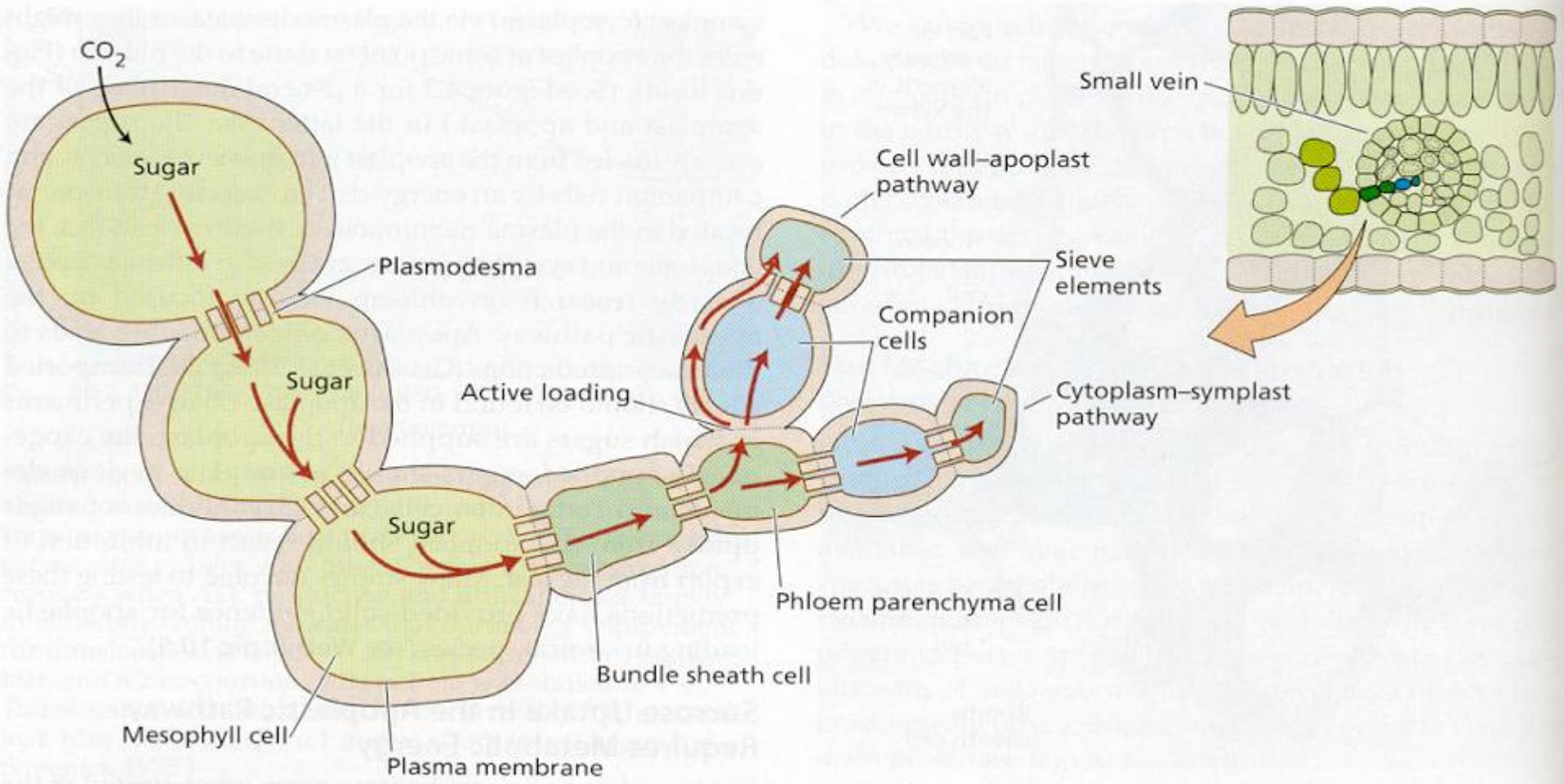


FIGURE 10.14 Schematic diagram of pathways of phloem loading in source leaves. In the totally symplastic pathway, sugars move from one cell to another in the plasmodesmata, all the way from the mesophyll to the sieve elements. In the partly apoplastic pathway, sugars enter the apoplast at some point. For simplicity, sugars are shown here entering the apoplast near the sieve element–companion cell complex, but they could also enter the apoplast earlier in the path and then move to the small veins. In any case, the sugars are actively loaded into the companion cells and sieve elements from the apoplast. Sugars loaded into the companion cells are thought to move through plasmodesmata into the sieve elements.

Apoplastické nakládání floému

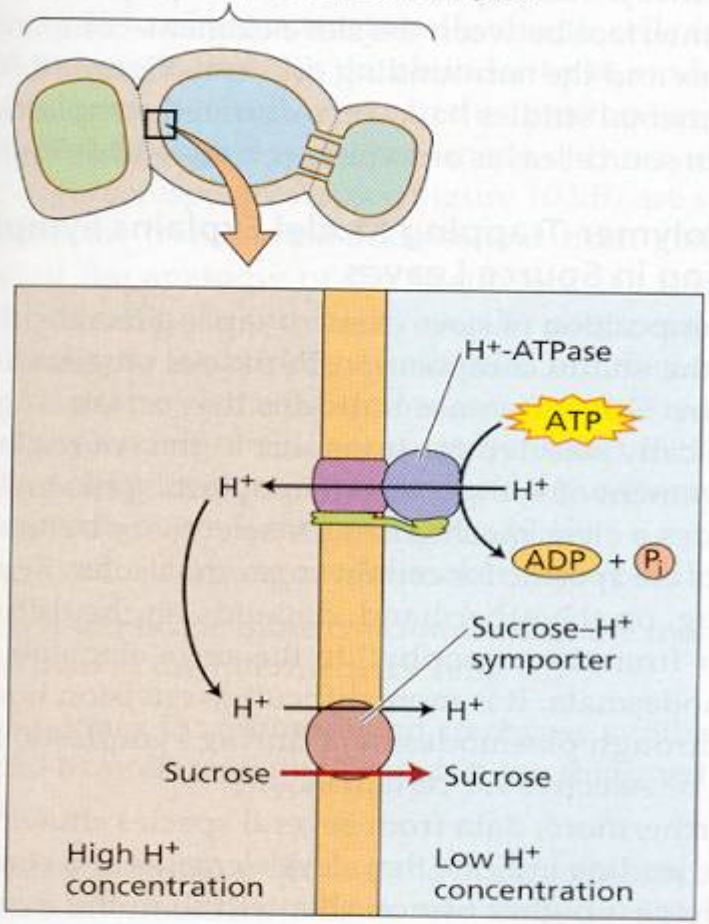
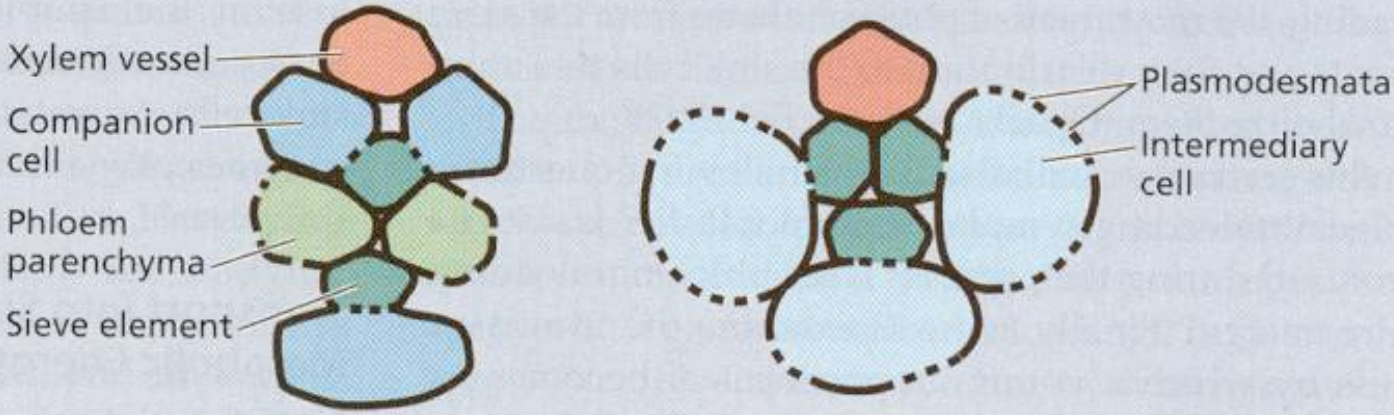


FIGURE 10.16 ATP-dependent sucrose transport in sieve element loading. In the cotransport model of sucrose loading into the symplast of the sieve element–companion cell complex, the plasma membrane ATPase pumps protons out of the cell into the apoplast, establishing a high proton concentration there. 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.

Nakládaní apoplastické (transferové buňky) versus symplastické (zprostředkovatelské bbuňky)

TABLE 10.4
Patterns in apoplastic and symplastic loading

	Apoplastic loading	Symplastic loading
Transport sugar	Sucrose	Oligosaccharides in addition to sucrose
Type of companion cell in the minor veins	Ordinary companion cells or transfer cells	Intermediary cells
Number of plasmodesmata connecting the sieve elements and companion cells to surrounding cells	Few	Abundant



Source: Drawings after van Bel et al. 1992.

Note: Some species may load both apoplastically and symplastically, since different types of companion cells can be found within the veins of a single species.

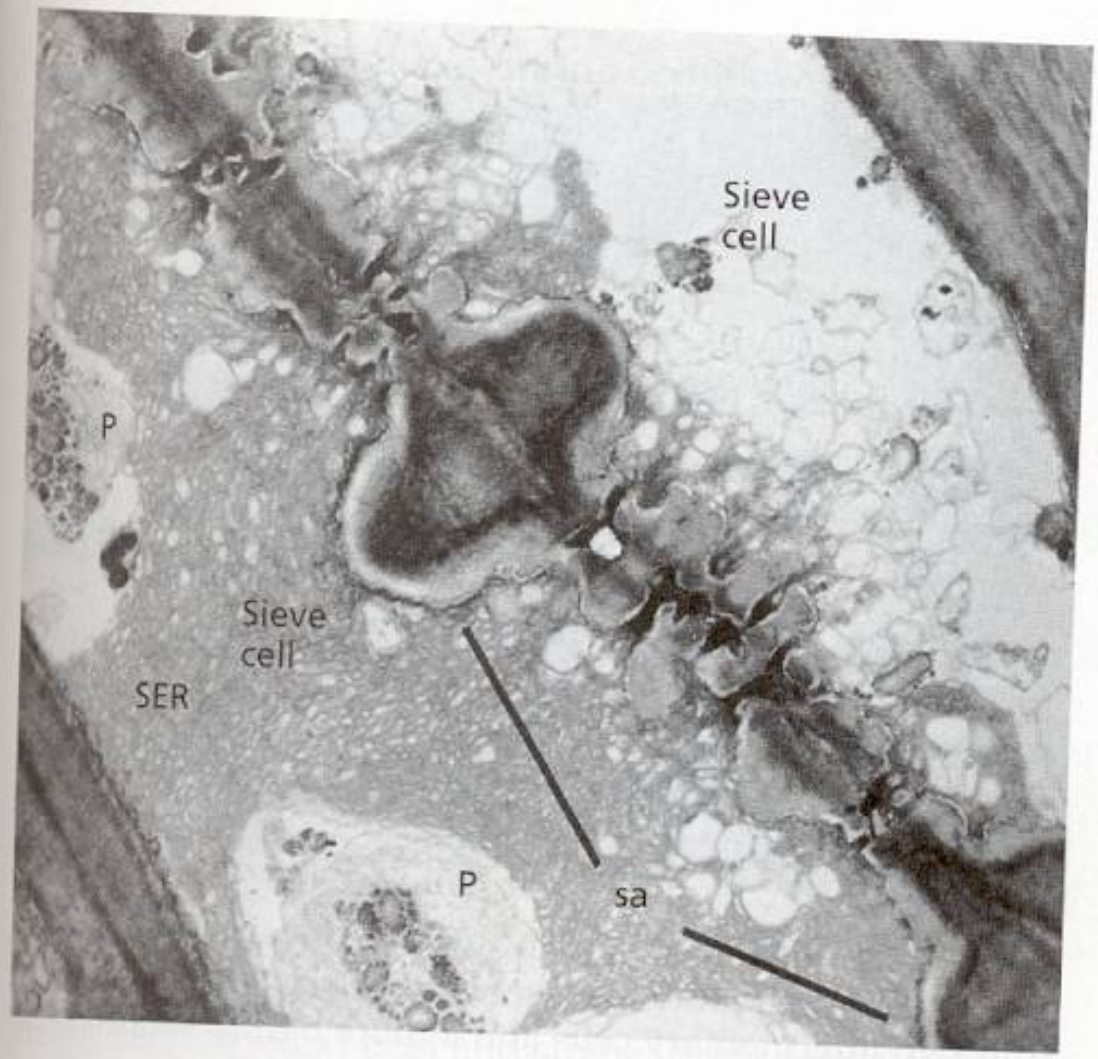
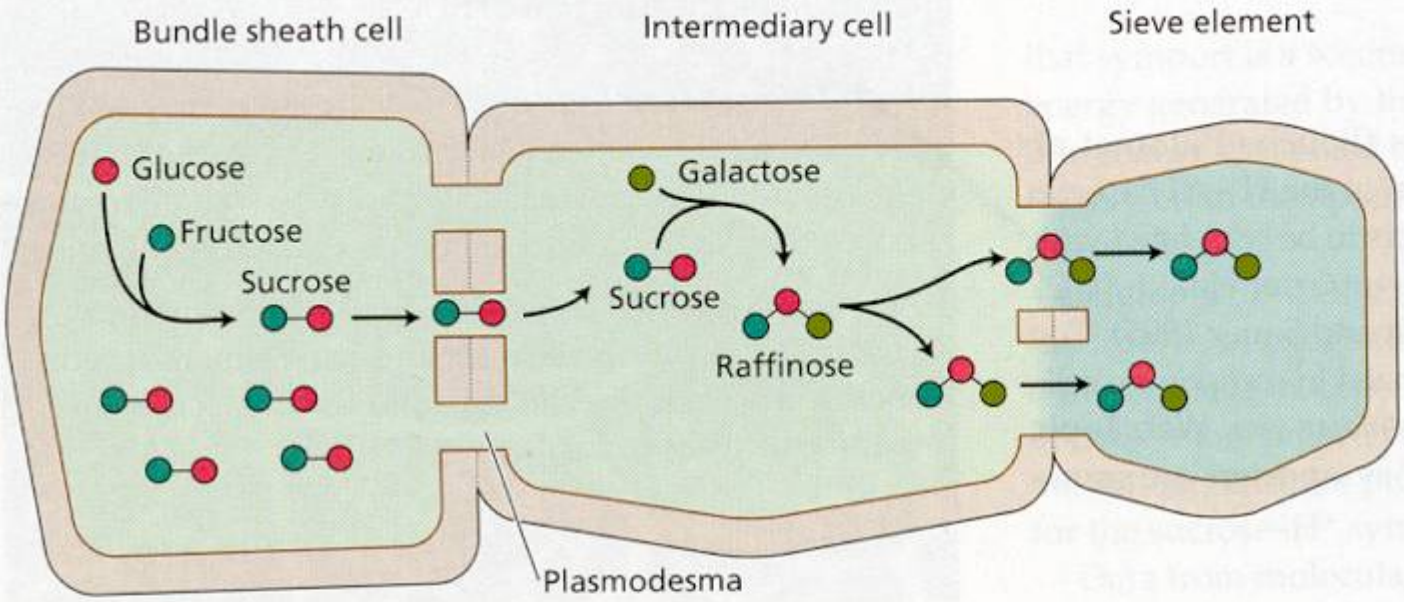


FIGURE 10.6 Electron micrograph showing a sieve area (sa) linking two sieve cells of a conifer (*Pinus resinosa*). Smooth endoplasmic reticulum (SER) covers the sieve area on both sides and is also found within the pores and the extended median cavity. Plastids (P) are enclosed by the SER. (From Schulz 1990.)

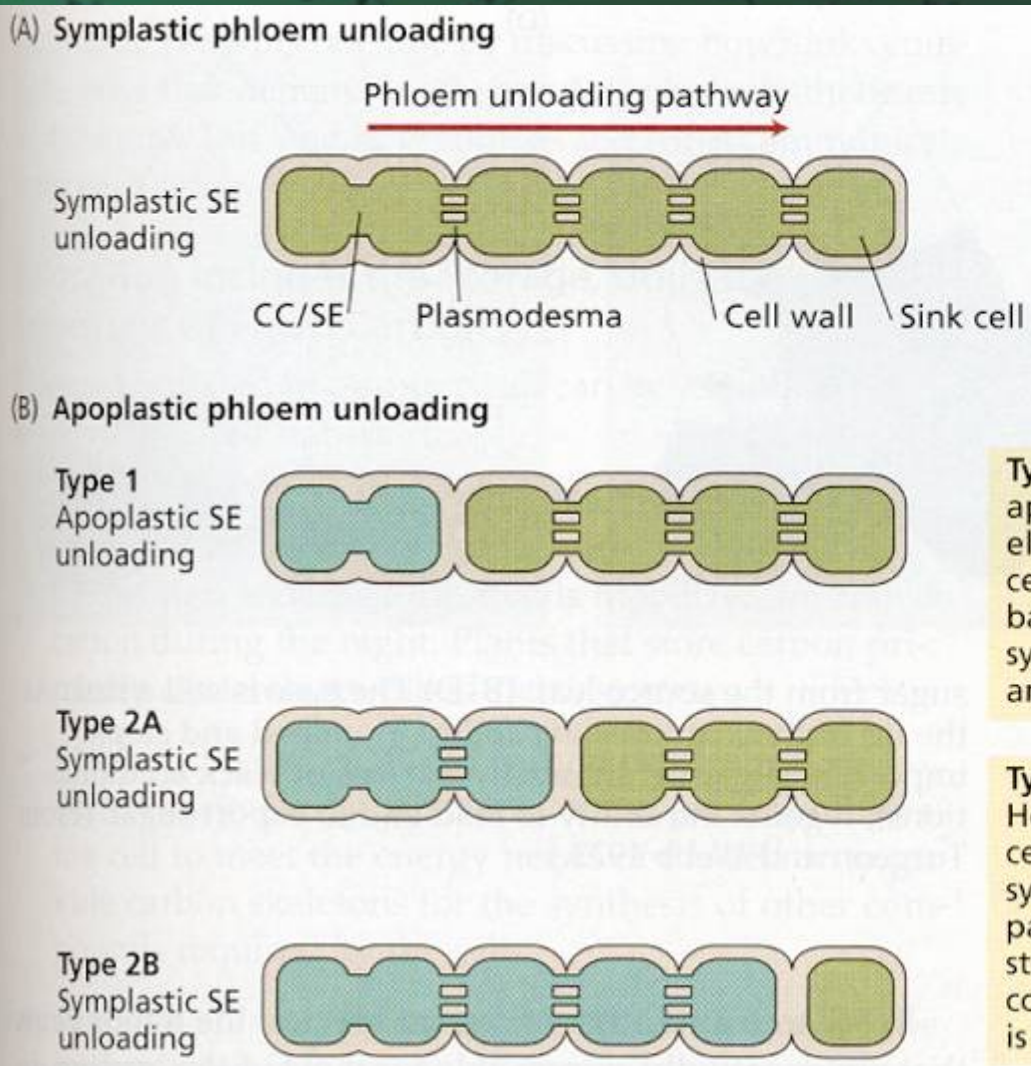


Sucrose, synthesized in the mesophyll, diffuses from the bundle sheath cells into the intermediary cells through the abundant plasmodesmata.

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.

FIGURE 10.17 Polymer-tra
ping model of phloem loa
ing. For simplicity, the tris
charide stachyose is omitt
(After van Bel 1992.)



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.

FIGURE 10.18 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. (B) Three types of apoplastic phloem unloading. (After Oparka and van Bel 1992.)

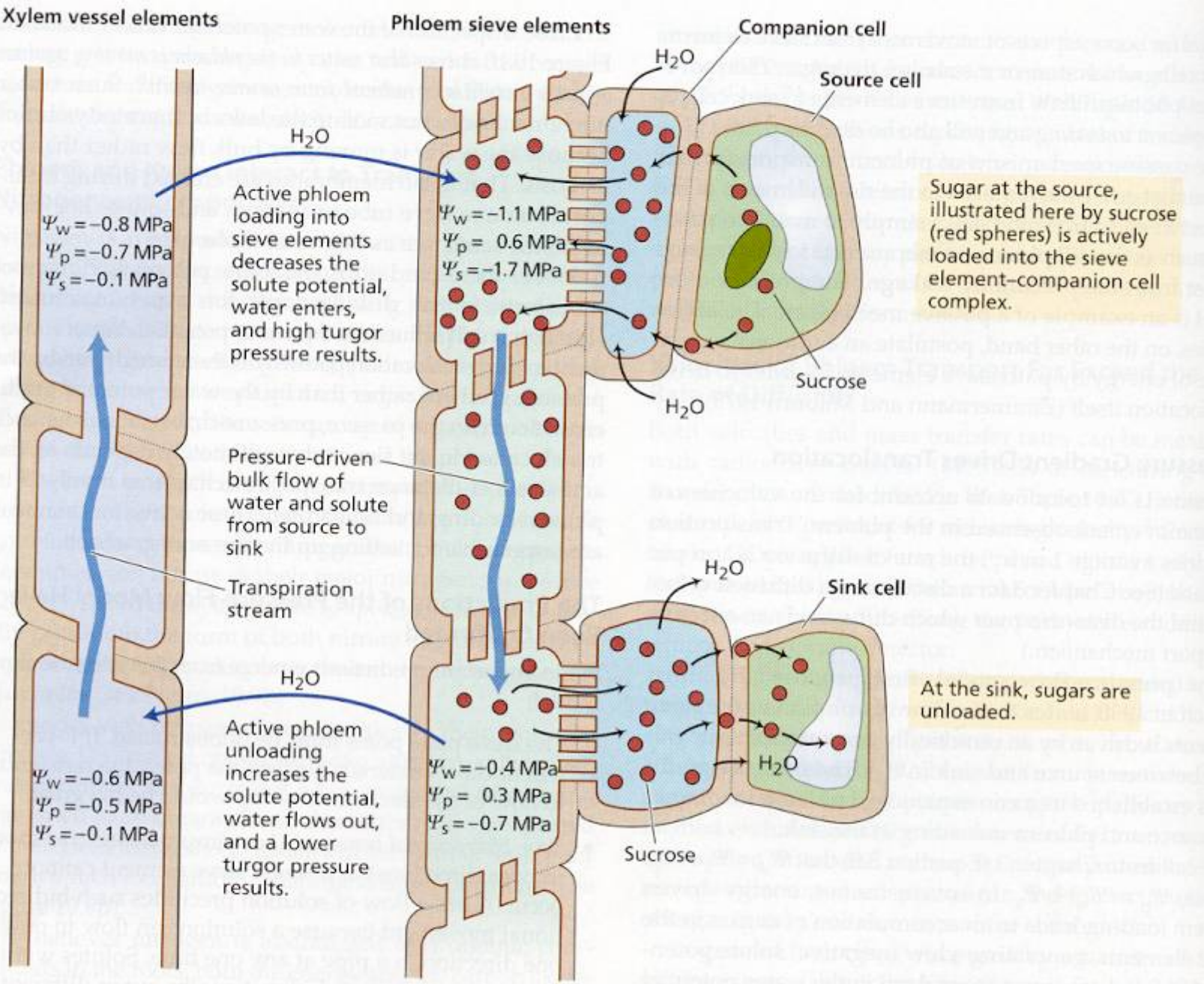


FIGURE 10.10 Pressure-flow model of translocation in the phloem. Possible values for Ψ_w, Ψ_p, and Ψ_s in the xylem and phloem are illustrated. (After Nobel 1991.)

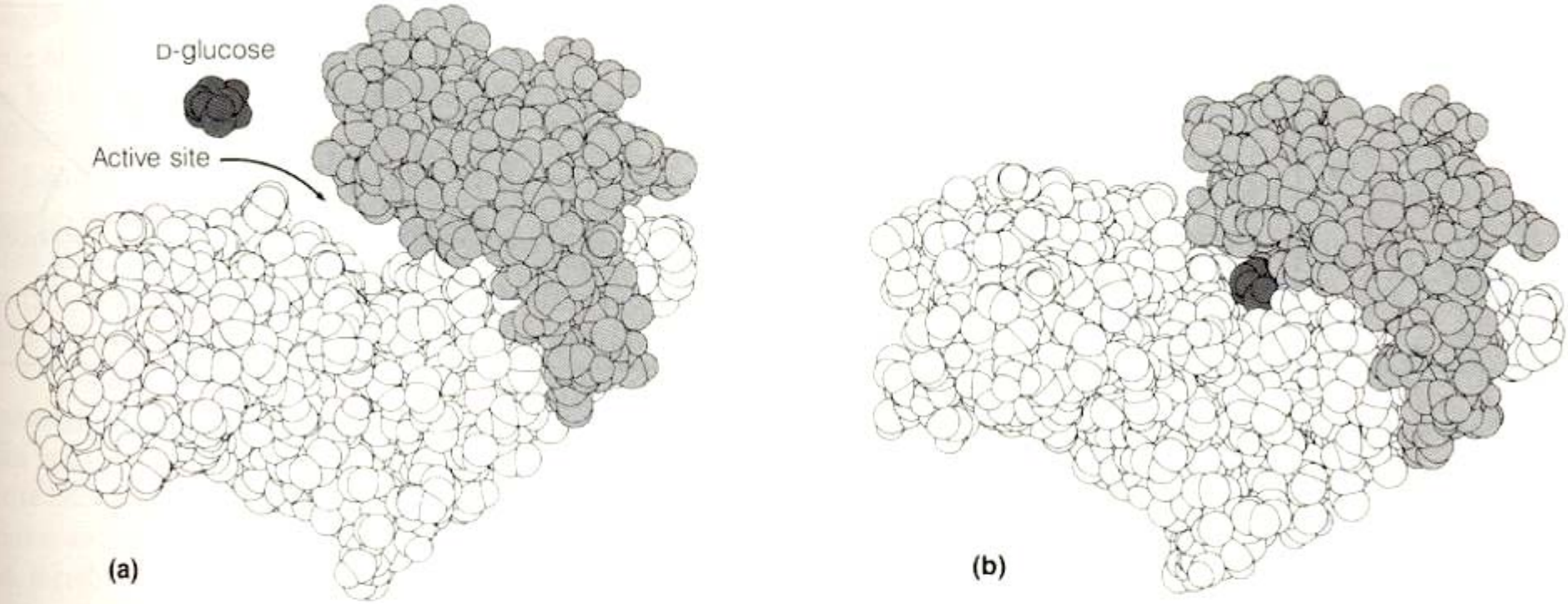


FIGURE 2.12. Hexokinase conformational change induced by its first substrate, D-glucose. (a) Before glucose binding. (b) After glucose binding. The binding of glucose to hexokinase induces a conformational change in which the two major domains come together to close the cleft containing the active site. This change sets up the binding site for the second substrate, ATP. In this manner the enzyme prevents unproductive hydrolysis of ATP by shielding the substrates from the aqueous solvent. The overall reaction is the phosphorylation of glucose and formation of ADP.

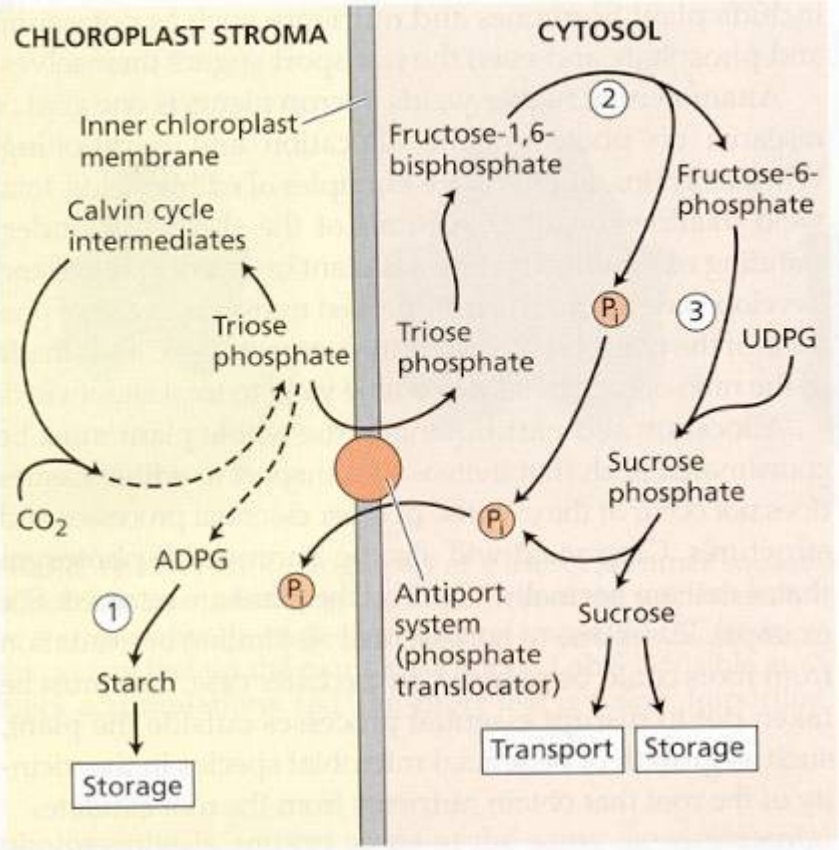


FIGURE 10.20 A simplified scheme for starch and sucrose synthesis during the day. Triose phosphate, formed in the Calvin cycle, can either be utilized in starch formation in the chloroplast or transported into the cytosol in exchange for inorganic phosphate (P_i) via the phosphate translocator in the inner chloroplast membrane. The outer chloroplast membrane is porous to small molecules and is omitted here for clarity. In the cytosol, triose phosphate can be converted to sucrose for either storage in the vacuole or transport. Key enzymes involved are starch synthetase (1), fructose-1,6-bisphosphatase (2), and sucrose phosphate synthase (3). The second and third enzymes, along with ADP-glucose pyrophosphorylase, which forms adenosine diphosphate glucose (ADPG), are regulated enzymes in sucrose and starch synthesis (see Chapter 8). UDPG, uridine diphosphate glucose. (After Preiss 1982.)