Phloem Structure and Function

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The phloem collects photoassimilates in green leaves and supplies the heterotrophic plant organs (e.g. fruits, buds and roots). Phloem structure is specialized for loading, long-distance transport and unloading of assimilates.

Introduction

The development of vascular tissues was prerequisite to the evolution of land plants, allowing for the division of labour between different organs. Instead of the entire plant body, the roots alone became specialized for the uptake of water and nutrients. The aerial organs diversified into stems, leaves and flowers. Photosynthesis shifted increasingly into leaves, expanding the light-exposed area with large two-dimensional blades. The shoot axis served not only as mechanical support for the aerial organs, but also provided functional links between the organs by vascular tissues: the xylem supplied the surface parts of the plant with water and nutrients, and the phloem supplied the heterotrophic organs – roots, flowers, fruits and buds – with photo-assimilates. Both vascular tissues are continuous into the farthest ends of the organs. The internal structure of the conducting cells within the vascular bundles is optimized for low-resistance transport. Low resistance is achieved by apoptosis and total autophagy in the case of xylem elements, and by only selective autophagy in the case of phloem elements that are living when functional.

Phloem Structure and Structure-deduced Function

Since their discovery in the nineteenth century, the sieve elements of the phloem have fascinated plant biologists because of their conspicuous sieve-like cell contacts (**Figure 1**). However, it took a century to demonstrate that these elements form the long-distance conduit for assimilate transport. Comparative studies of phloem physiology, molecular biology and structure of flowering plants have recently uncovered the degree of interaction that occurs between sieve elements and their ontogenetically related companion cells that is unique in plants.

After introducing the phloem structure, this article describes different models of phloem loading. Loading is the active step driving assimilates from photosynthetically active green leaves to organs for utilization in growth and storage. It will be pointed out that phloem translocation is linked with symplasmic and apoplastic pre- and post-phloem transport processes. Finally, several examples with transgenic plants show that phloem transport depends upon a finely balanced equilibrium between photosynthesis in source leaves and growth-related assimilate consumption in sink organs. Disturbance of this regulation hints at the possibility of feedback mechanism and signalling along the phloem pathway.

Implications of the phloem structure

Phloem development and architecture

Protophloem sieve elements are the first cells of vascular bundles to differentiate and become functional in young organs. Arranged in-line, these phloem elements differentiate at a distance of less than 1 mm from the apical meristem. This close relationship emphasizes the fact that unloading of assimilates from the phloem nourishes mitotic activity and cell growth. From the beginning of seedling growth, elongation of mature phloem keeps pace with the growth of the stems and organs and is guided by the orientation of procambial strands so that phloem continuity throughout the plant is guaranteed up to the farthest ends (**Figure 2a**).

Radial development of the phloem leads to the addition of parallel strands of sieve elements (metaphloem and, in perennial plants, the secondary phloem), increasing the cross-sectional area of assimilate-conducting elements. In addition to the conducting cells, the phloem is comprised of parenchyma cells and, depending upon the species, crystal cells and fibres. During primary growth of shoot organs (i.e. in the shoot axis, the petioles and the main leaf veins), the phloem runs parallel to the water-conducting xylem in a variable number of collateral or bicollateral vascular bundles (**Figure 1a**). In roots, phloem and xylem are combined in the central cylinder stele. During secondary growth, the vascular cambia continuously add phloem elements to the outside and xylem elements to the inside, thus ensuring the existence of functional phloem elements in trees that are less than 1 year old.
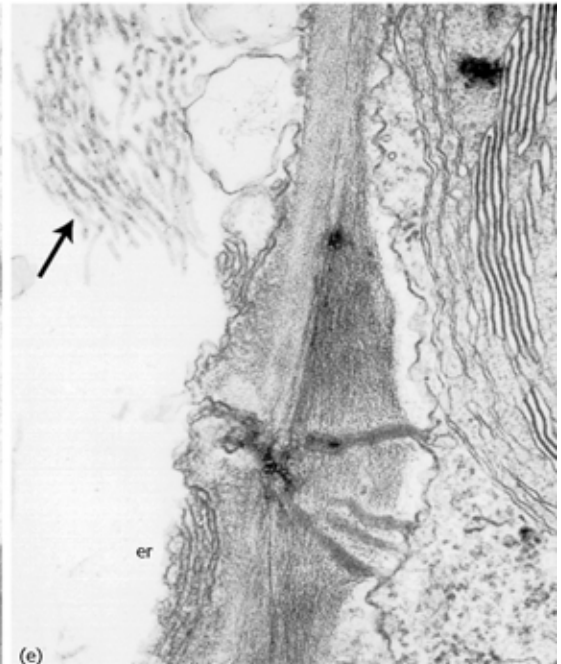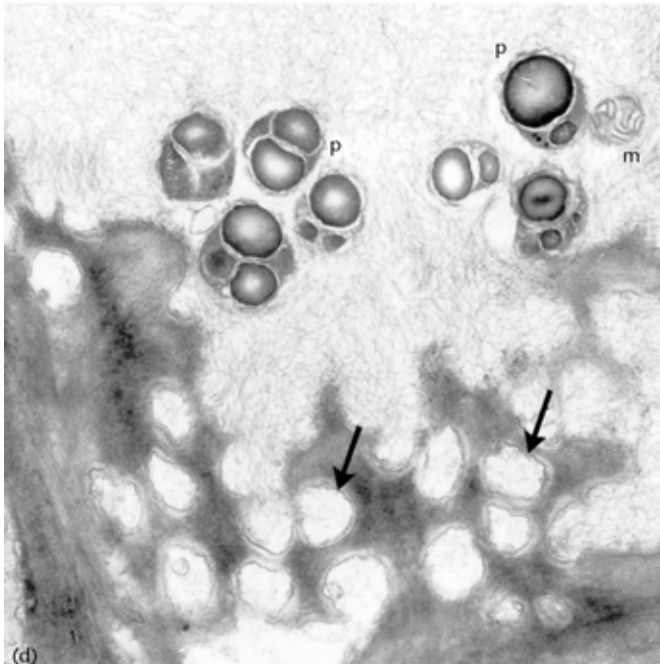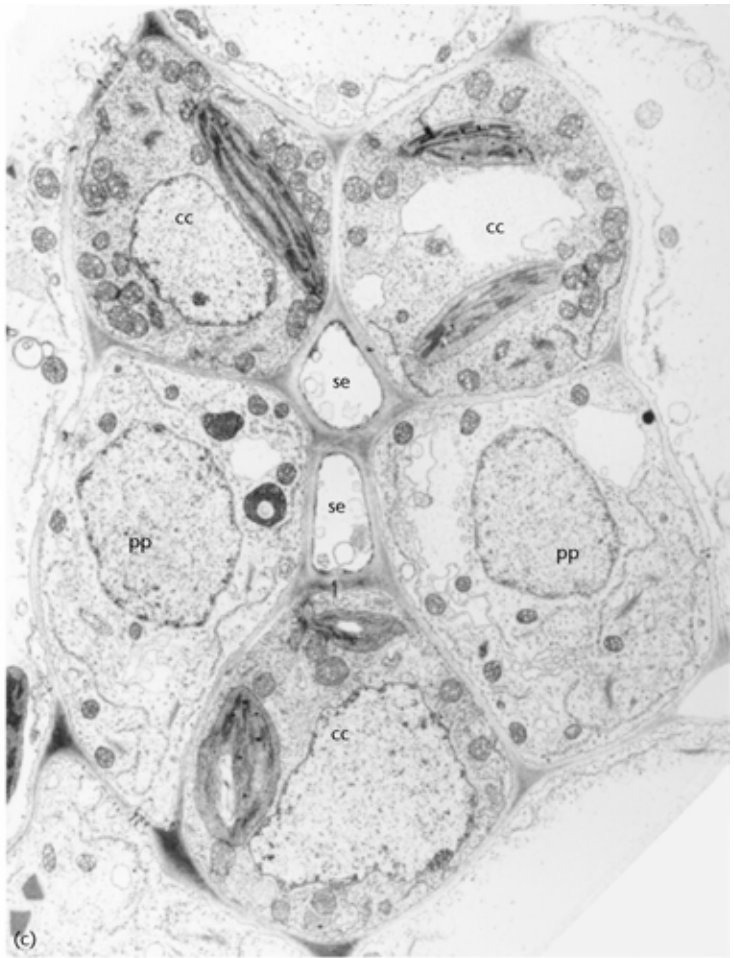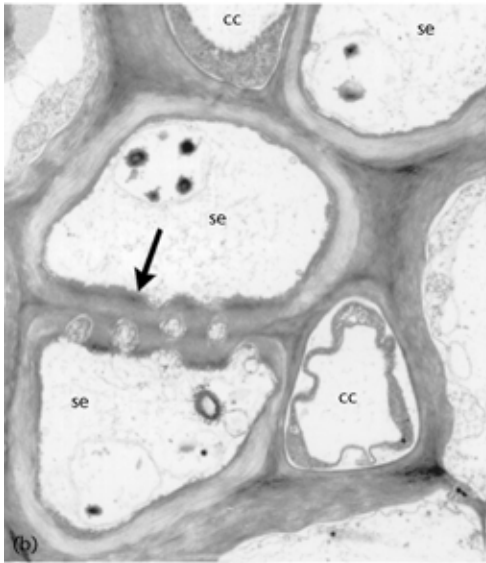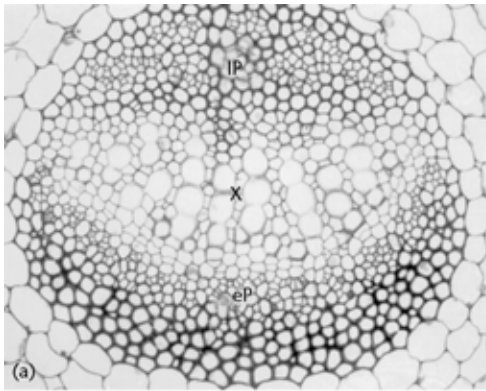
Sieve element structure and association with companion cells or Strasburger cells

The assimilate-conducting sieve elements of the phloem are the most highly specialized cell type in plants. During development, flow resistance in these cells is reduced by changes in the protoplast. In addition, a functional conduit becomes established across the end walls when the cell-to-cell connections (plasmodesmata) linking two sieve elements widen by a factor of 10 to 100, forming sieve pores (**Figures 1d**, **2b**). In the protoplast the nucleus disintegrates, as do the Golgi apparatus and ribosomes, before sieve elements become functional. While it is undisputed that the vacuole disappears during maturation, the fate of the tonoplast membrane is unclear. The smooth endoplasmic reticulum (ER), free of ribosomes, changes its conformation and ultimately forms stacks or a single, fenestrated cisterna overlying the plasma membrane (**Figure 1e**). It is quite possible that this ER sheet plays an essential role in maintaining the parietal cytoplasm, preventing the enzymes, metabolites and proteins necessary for sieve element function from being swept away in the assimilate stream. The remaining organelles – plastids and mitochondria – become spherical and part of the parietal cytoplasm (**Figures 1d**, **2b**). They seem to be anchored at the ER and/or plasma membrane. Depending on the species, the sieve-element plastids acquire protein filaments or crystals and/or amylopectin-rich starch grains. In angiosperms, the only structures within the lumen of a sieve element are the phloem-specific proteins arranged as filaments, tubules and/or crystalline bodies (**Figures 1d, e**). It is possible that these structures are homogeneously dispersed over the sieve element so that the flow of assimilates is not inhibited.

The reduction in cytoplasmic contents leads to an important problem in the physiological maintenance of sieve elements. How is vitality maintained when the replacement of enzymes, membrane proteins and metabolites is not guaranteed, and when aggressive radicals are not inactivated by continuously replaced molecular scavengers? This problem becomes even more significant when the longevity of sieve elements is considered. While the first-formed protophloem sieve elements have a longevity in the range of hours to days, metaphloem and secondary sieve elements can live for weeks and months. Indeed, the sieve elements in certain palms seem to remain functional for decades. This is in contrast to the comparably enucleate erythrocytes of mammals, which on average live for only 4–6 weeks.

A growing body of evidence indicates that the vitality of enucleate sieve elements is maintained through intimate associations with ontogenetically related companion cells in angiosperms (**Figure 2c**) and Strasburger (albuminous) cells in gymnosperms. In stark contrast to mature sieve elements, these cells have a conspicuously dense cytoplasm with numerous mitochondria and ribosomes indicative of high metabolic activity (**Figures 1b**, **2a**). Moreover, specialized symplasmic contacts, called pore–plasmodesma contacts, link these cells with the sieve elements. Pore–plasmodesma contacts consist of a single sieve pore on the sieve element side extending into a median cavity that branches into numerous plasmodesmata on the companion (or Strasburger) cell side (**Figure 1e**). These contacts are numerous and often grouped as pit fields along the common wall. Thus, the cytoplasm of sieve elements is well connected to that of its associated cell type. In comparison with ordinary plasmodesmata, the pore–plasmodesma contacts are distinguished by an increased size-exclusion limit, the full extent of which has not been determined. Studies with selective fluorochromes, fluorescently tagged viruses and endogenous phloem proteins also confirm that macromolecules are transported between companion cells and sieve elements via pore–plasmodesmata contacts. Most recently, several studies suggest that plant mRNA as well as proteins traffic from companion cells into sieve elements. Experimental evidence illustrating the dependence of sieve elements on their companion cells to provide essential macromolecules is rapidly accumulating.

Different Pathways and Mechanisms of Translocation

General mechanism of phloem translocation

Current theories explaining the mechanisms of assimilate translocation are based on the pressure-flow hypothesis first proposed by Ernst Münch in 1927. Münch designed a very simple model for the 'mass' or 'bulk' flow of assimilates based on the differential concentration of osmotically active solutes at separate locations in a continuous transport system. Water crossing a semipermeable membrane into a region of high solute concentration and out of a connected region of low solute concentration creates a turgor pressure gradient in the pathway that passively transports solutes until equilibrium is achieved.

Figure 1 Micrographs of transverse sections through phloem tissue. (a) A collateral vascular bundle in the petiole of *Plantago major* has internal (iP) and external phloem (eP) on either side of the xylem (X) enclosed by several phloem fibre layers with dark appearing cell walls. (b) Sieve elements (se) are linked by a sieve plate (arrow) and intimately associated with companion cells (cc). (c) The abaxial phloem of a seventh-order minor vein in a potato leaf is composed of two sieve elements, associated companion cells (cc) and two phloem parenchyma cells (pp), all surrounded by the bundle sheath. (d) A glancing section through a sieve plate in a developing cotyledon of castor bean shows large sieve pores (arrows), sieve-element plastids (p), one mitochondrion (m) and filamentous P protein. (e) Pore–plasmodesma contacts symplasmically join a sieve element (containing tubular P protein; arrow) and its companion cell in a potato leaf. Note that the sieve element plasma membrane is covered by smooth ER cisternae (er).
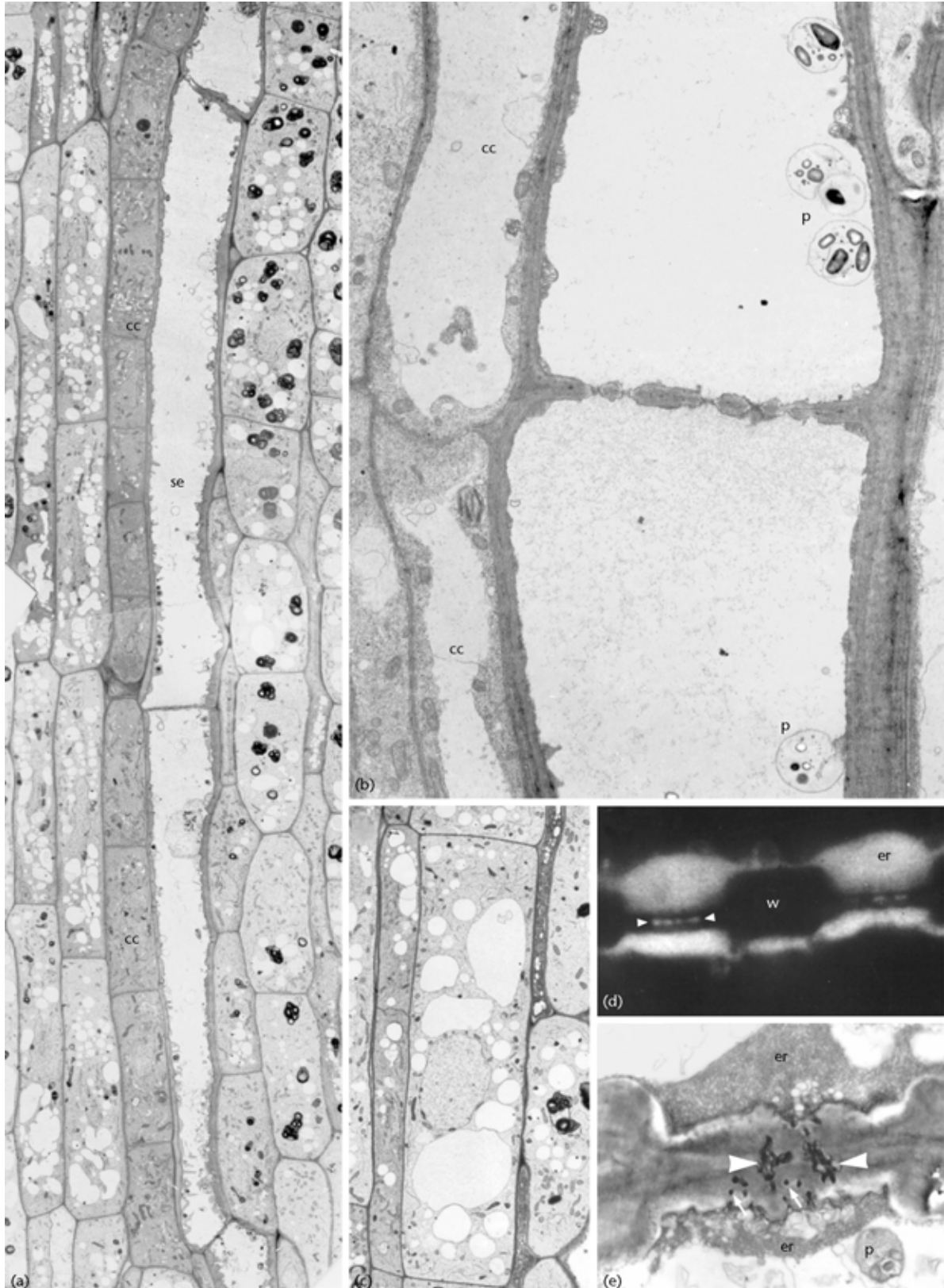
In terms of phloem transport, the osmotic differential is maintained as assimilates (sugars) are 'loaded' into sieve elements in source tissues (location of photosynthate production or remobilization) and 'unloaded' from sieve elements in sink tissues (location of photosynthate consumption or storage). The uptake of sugar leads to an osmotic pressure difference across the plasma membrane that stimulates the influx of water and the development of a high turgor pressure in sieve elements of source tissues. The removal or unloading of sugars (and water) from sieve elements lowers the turgor pressure in the sink tissues. The pressure differential between source and sink drives sucrose and water transport in the phloem (see **Figure 3**).

Development and maintenance of the phloem architecture guarantees that sieve elements are continuous from source to sink. Because of this functional divergence it is sensible to divide the phloem in three parts: the collection phloem, the transport phloem and the release phloem. In angiosperms the minor veins in green leaves form the collection phloem. Spacing of minor veins ensures that a short distance is maintained between photosynthetically active mesophyll cells and assimilate-exporting sieve elements. An interesting structural feature of collection phloem, as compared with transport and release phloem, is that the relative sizes of the sieve elements and companion cells are inverted, with companion cells being much larger than the sieve elements (**Figure 1c**). The same applies to the relationship between Strasburger cells and sieve cells in gymnosperm needles. The collection phloem is specialized for loading and well equipped with membrane transporters or distinguished by other features that allow for assimilate loading against a concentration gradient. Analysis of the phloem exudate after cutting stems or exudate from stylectomized aphids revealed that sieve elements contain an extremely high concentration of sugars. In the case of sucrose-translocating plants, the exudate was found to be composed of up to 30% sucrose, equalling nearly $1 \, mol \, L^{-1}$ sucrose. However, it is clear that the transport phloem also has the ability to take up assimilates actively. This ability serves either for a retrieval of assimilates leaking out of the phloem continuum or for the uptake of a surplus of assimilates along the phloem pathway. The latter situation can be found in higher-order veins of the leaf (midrib up to third-order veins) and in plants with photosynthetic stems. This reinforces the idea that different types of phloem are adapted to serve different functions, but their basic properties remain qualitatively the same.

Loading of assimilates

It is generally accepted that phloem translocation is driven by an active accumulation of photoassimilates against the concentration gradient in source organs. In most plants, active accumulation occurs across the cell walls surrounding a sieve element–companion cell complex and is defined as phloem loading. It is preceded by the prephloem transport of assimilates, which starts in the photosynthetically active palisade or spongy parenchyma cells, proceeds in connecting mesophyll cells, and eventually ends up in the bundle-sheath and phloem parenchyma cells of the veins that contact a sieve element–companion cell complex. Assimilates continue to move into the sieve element–companion cell complex symplasmically or are released into the apoplast and must be actively loaded into the conducting elements. Within the last decade different modes of phloem loading – apoplastic, symplasmic and alternate – have been revealed in different plant families.
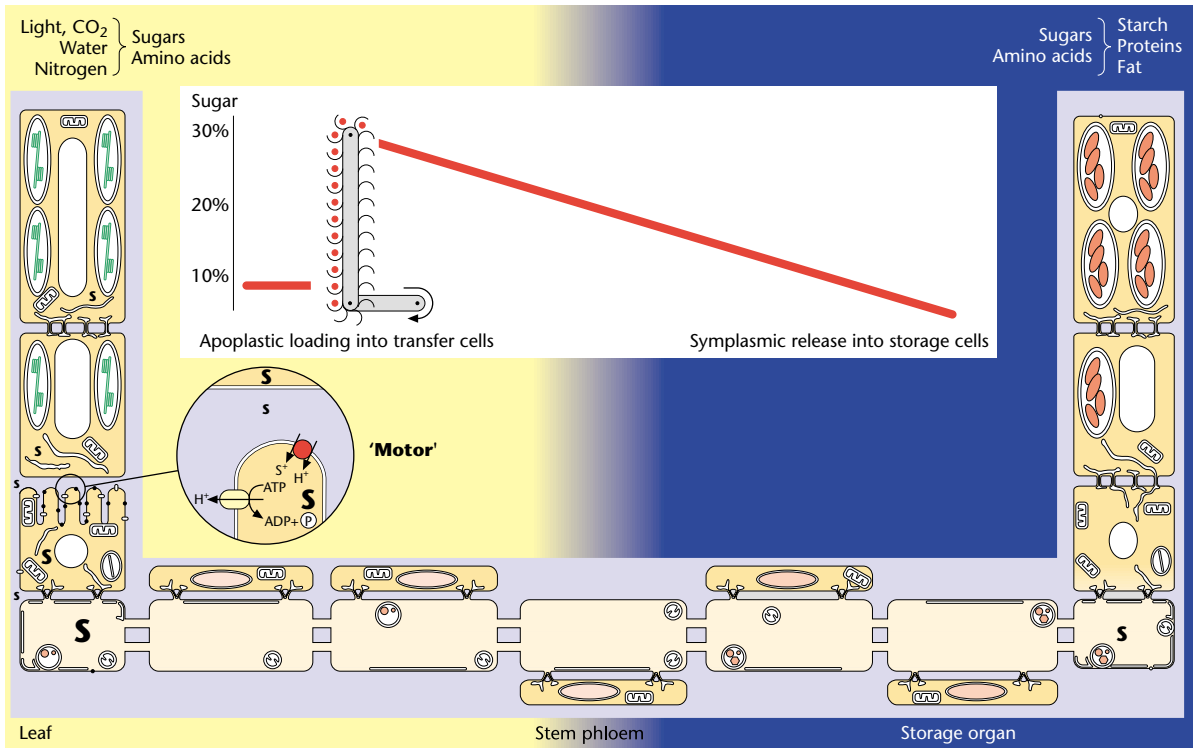
The term apoplast applies to the entity of extracellular space in the plant body, including the cell wall and the lumen of dead cells but excluding the air-filled intercellular spaces. Within the present context, an apoplastic step in transport refers to the release of a transport sugar and/or an amino acid across the plasma membrane into the water-filled space of the cell wall, diffusion through the wall and the reuptake into the neighbouring cell. In contrast, the term symplasm applies to the entity of living protoplasts in the plant body linked by plasmodesmata or sieve pores spanning the cell walls. The intercellular route through plasmodesmata is formed by the continuous cytoplasmic sleeve between the plasma membrane and the desmotubule.

Apoplastic loading of sucrose

In some plant families an apoplastic mode of phloem loading is structurally evident. In these species, virtually no plasmodesmata connect the sieve element–companion cell complexes to the surrounding tissue, resulting in symplasmic isolation of the conducting elements. All translocated compounds require an apoplastic step at this border to enter the long-distance translocation system. An addi-
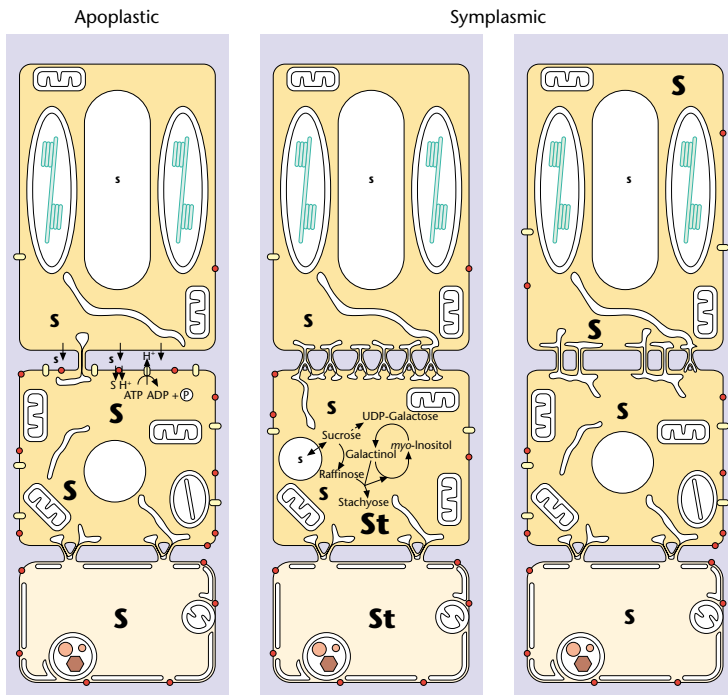
Figure 2 Micrographs of longitudinal sections through phloem tissue. (a) Four sieve elements of a sieve tube in the developing hypocotyl of castor bean *Ricinus communis* are each associated with several cytoplasmically dense companion cells (cc). (b) Two sieve elements of *Cheiranthus cheiry* containing parietal sieve-element plastids (arrows) are connected by a sieve plate. Owing to their identical ontogenetic origin, the ends of the associated companion cells (cc) are in-line with their sieve elements at the sieve plate (by courtesy of H.-D. Behnke, Heidelberg, Germany). (c) A young sieve element–companion cell complex of castor bean shortly after the unequal division of the mother cell. The sieve element still contains a nucleus, vacuoles and all organelles. Note the thin transverse end walls that mark the site of future sieve plates. (d) Sieve areas of living stem phloem in spruce as visualized with confocal laser scanning microscopy; (e) after preparation for electron microscopy. Complexes of smooth ER are covering the sieve area on either side. The pores (small arrows) are connected via cavities (arrowheads) in the cell wall (w).

Mechanism of phloem transport

Light, CO$_2$
Water
Nitrogen } Sugars
Amino acids

Sugars
Amino acids } Starch
Proteins
Fat

Sugar
30%
20%
10%

Apoplastic loading into transfer cells

Symplasmic release into storage cells

'Motor'

S$^+$ H$^+$
ATP
H$^+$
ADP+ P
S

Leaf

Stem phloem

Storage organ

(a)

Modes of phloem loading

Apoplastic

Symplasmic

Unloading

S H$^+$
ATP ADP + P

UDP-Galactose
Sucrose
Galactinol myo-Inositol
Raffinose
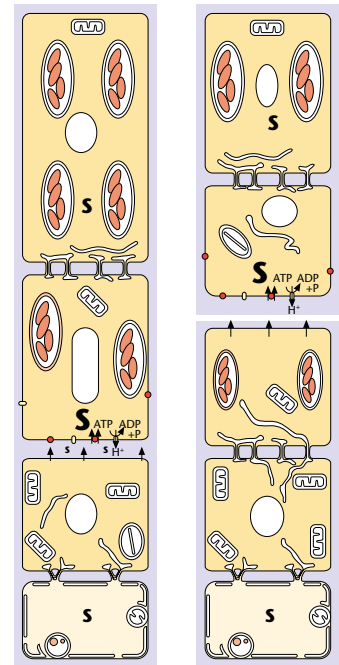Stachyose
St

St

S
ATP ADP
+P
H$^+$

S ATP ADP
s S H$^+$ +P

Active membrane transport

Oligomer trap

Alternate

Release into the apoplast

(b)

(c)

tional structural feature of plants that utilize apoplastic loading are numerous plasma membrane invaginations forming a wall labyrinth in the companion cells. The wall labyrinth increases the surface area of the plasma membrane adjacent to the bundle sheath and phloem parenchyma cells. Companion cells having this wall labyrinth are termed transfer-type companion cells (**Figure 3a**).

Activity of membrane transporter proteins is required for apoplastic loading. The sucrose/proton cotransporter is the best characterized example of transporters involved in phloem loading. Much less is known about transporters involved in amino acid uptake and other compounds actively loaded into phloem sieve elements. Apoplastic loading is energized by plasma membrane-bound ATPases that hydrolyse ATP to pump protons from the cytoplasm into the apoplast. The sucrose/proton cotransporter has a 1:1 stoichiometry transporting one proton with one sucrose molecule from the apoplast into the cytoplasm. In intact leaves, differences in solute potential and indirect measurements indicate a 2- to 3-fold higher concentration of sucrose in the sieve element–companion cell complexes compared with mesophyll cells. However, considering the lower concentration of sugars in the apoplast, the capacity of sucrose transporters must be higher and the real accumulation factor should be in the range of 3 to 30. The latter value resulted from experiments where labelled sucrose was applied with an apoplast medium.

The maximal values of sucrose transmembrane fluxes were reported to be 3×10^{-6} mol m^{-2} s^{-1} on the plasma membrane of the sieve element–transfer cell complexes of minor veins of pea leaves. ATPase as well as sucrose transporters were immunolocalized to the transfer cell membranes. However, apoplastic loading of sucrose is not restricted to plants with a symplasmic isolation of the collection phloem and transfer cell-type companion cells. In members of the Solanaceae, a sucrose transporter was localized to the sieve element plasma membrane (**Figure 3b**). Its inhibition in antisense transgenic plants led to an accumulation of photoassimilates in source leaves and a strong reduction in phloem export. The role of plasmodesmata in apoplastically loading plants linking the sieve element–companion cell complexes with the surrounding tissue is undetermined. Detailed investigations of sucrose uptake in castor bean (*Ricinus communis*) cotyledons indicated that some sucrose is taken up already in cells of the prephloem pathway, possibly approaching the phloem symplasmically, and is also loaded directly into sieve element–companion cell complexes.

Symplasmic loading of raffinose and higher sugars

Plants translocating raffinose or higher polymers of sucrose–galactosyl sugars (stachyose, verbascose) appear to load assimilates symplasmically into the collection phloem of mature leaves. In contrast to the paucity of plasmodesmal connections in apoplasmically loading species, a prerequisite for symplasmic loading is the presence of a sufficiently high number of plasmodesmata linking the sieve element with the rest of the leaf symplasm. These plants have structurally distinctive intermediary-type companion cells with many small vacuoles and numerous plasmodesmata linking them to bundle-sheath cells. The plasmodesmata are predominantly branched on the companion cell side where the orifices appear very small. In developing leaves, plasmodesmatal branching occurs concomitantly with the sink–source transition, i.e. the stage when a leaf starts to export photoassimilates (**Figure 3b**).

Initially, symplasmic loading via plasmodesmata appears to contradict mechanistically the concept that sugars must accumulate to higher concentrations within the sieve elements than in the surrounding cells for osmotically driven translocation. The 'polymer trap hypothesis', illustrated in *Coleus blumei* and members of the *Cucurbitaceae*, proposes an elegant solution for the problem of loading sugars through plasmodesmata to obtain higher sugar concentrations in sieve elements than in the cells of the prephloem pathway. According to this hypothesis, sucrose diffuses symplasmically through the prephloem pathway into the intermediary cells. Enzymes involved in raffinose and stachyose synthesis from sucrose and galactose have been localized to the intermediary cells. Synthesis of sucrose–galactosyl polymers (raffinose and stachyose) in intermediary cells result in sugar molecules that are too large to diffuse back through the narrow orifices of the branched plasmodesmata into the prephloem pathway. Indeed, the highest carbohydrate concentration in mature leaves was shown in the sieve element–intermediary cell complexes of microdissected tissue.

Figure 3 Illustrations of the general mechanism of phloem transport and different models of phloem loading and unloading.
(a) This simplified drawing shows the generally accepted mechanism of phloem transport where the sieve element–transfer cell complex is symplasmically isolated from the surrounding cells in source leaves. Sucrose (S) produced by photosynthesis in the mesophyll cells moves cell-to-cell (symplasmically) through the bundle sheath and phloem parenchyma, where it is released into the apoplast. Apoplastic phloem loading is driven by sucrose/proton cotransporters in the plasma membrane of transfer cells and energized by ATPase activity (see 'Motor' inset). Active loading of sucrose into the sieve element–transfer cell complex results in the high concentration of sugars required for turgor-driven transport (see the graph inset). After loading, sucrose is passively transported down the concentration gradient in sieve elements and unloaded from the phloem symplasmically towards the assimilate-consuming parenchyma cells in storage organs or towards growing tissue in roots or shoots.

Alternate modes of symplasmic phloem loading

The phloem in a number of woody plant families have numerous plasmodesmal connections between sieve elements and the mesophyll tissue, but neither translocate sucrose–galactosyl polymers nor have intermediary-type companion cells. In conifers, the symplasmic pathway is continuous from mesophyll via transfusion parenchyma and Strasburger cells flanking the sieve cells of the central vascular bundle in needles. Specific, dome-shaped wall portions provide numerous branched plasmodesmata between the Strasburger cells. These regions are covered by extended ER complexes. Although the elaborate symplasmic connections point to a putative function in assimilate transfer, the physiology of phloem loading in conifers remains to be determined.

In *Salix*, the collection phloem is well linked symplasmically with the surrounding tissue and the highest sucrose concentration is in the mesophyll cytosol, not in the sieve elements. It is postulated that photoassimilates are transferred from mesophyll into the sieve elements by diffusion along the concentration gradient, rather than against the concentration gradient observed in most species. Since the gradient extends from the assimilate-producing mesophyll cells to the sink tissues, the term 'phloem loading' does not apply. The only membrane step, the exchange of triose phosphate against orthophosphate across the chloroplast envelope, could, in *Salix*, be considered the 'motor' of phloem transport, possibly modulated by the interchange of sucrose across the tonoplast along the pre- and postphloem transport pathway. As with the other modes of phloem loading, partitioning of sucrose between the vacuole and cytoplasm in source and sink tissues contributes to the regulation of phloem transport (**Figure 3b**).

Undisturbed transport

P-protein in angiosperms

As previously described, the ultrastructure of the conducting elements of the phloem is optimized for a low-resistance pathway. However, sieve elements of most angiosperms contain highly polymerized aggregations of phloem proteins (P-proteins) that, if present throughout the lumen of a sieve element, would inhibit the flow of sugars. In light and electron microscopy, P-proteins are most often found accumulating at the sieve plates (**Figure 1d**). Preparation of plant material for microscopic analysis typically includes disruption of the phloem resulting in a sudden pressure release shifting cellular contents to the sieve plate. Recent investigations using confocal laser scanning microscopy of intact sieve elements support earlier observations that P-proteins are involved in wound responses, either to maintain turgor pressure within damaged sieve elements or to protect the valuable contents of sieve elements from leakage.

The P-proteins of cucurbits have been intensively investigated since the 1970s. Two major structural proteins, the phloem filament protein and phloem lectin, appear to be the primary components of highly polymerized aggregates and filaments in sieve elements of these species. Crosslinking of evenly dispersed polymerized filament protein with the carbohydrate-binding lectin has been hypothesized as a mechanism to anchor the protein polymers to membrane glycoconjugates, allowing the assimilate stream to remain undisturbed. Recent studies have shown that the subunits of both P-proteins are also freely mobile in the assimilate stream, demonstrating that the phloem does not only translocate the nonreducing sugars (sucrose, raffinose, stachyose and verbascose) and certain amino acids, but also polypeptides. Localization studies indicate that P-protein synthesis occurs primarily, if not exclusively, in the companion cells. Therefore, macromolecular trafficking of P-protein subunits from companion cells to sieve elements must occur through the sieve pore–plasmodesma contacts. The equilibrium between polymerized P-protein filaments and the surplus of subunits might be critical for the physiological function of these proteins within the phloem.

ER in gymnosperms

The sieve pores of gymnosperms are much smaller than those in angiosperms and traversed by ER membranes. Confocal laser scanning microscopy has shown that they are grouped in areas that are themselves covered by extensive complexes of smooth ER (**Figure 2d**). The position and density of the ER at the sieve areas seems to exclude a strictly passive translocation in gymnosperms down a concentration gradient. It was postulated that the ER complexes might serve as 'relay stations' for assimilates and, by actively taking up and releasing sucrose, might steepen the sucrose gradient in a sieve cells wherever necessary.

Phloem-feeding Insects

Aphids and other phloem-feeding insects of the taxon Sternorryncha have evolved elaborate strategies to use nitrogenous compounds out of translocated assimilates for their nutritional requirements. Aphids insert specialized mouthparts, called stylets, between plant mesophyll cells and penetrate sieve elements to feed on phloem sap. The high hydrostatic pressures in sieve elements, combined with the high carbon (sugar) and low nitrogen (amino acids and proteins) content of the phloem sap, result in copious excretion of a 'sugary' honeydew from the aphids. Aphids feeding from sieve elements can create sinks by removing assimilates, altering normal source-to-sink relations and carbohydrate partitioning in host plants. In addition, aphids damage plants by transmitting pathogenic viruses

and, in some plant species, inducing phytotoxic responses ranging from localized cell browning to systemic tissue damage. Aphids and other phloem-feeding insects are important experimental tools for translocation studies. An actively feeding insect is cut away from its stylet, and the cut stylet, still inserted in the phloem, used to record turgor pressure or sample the contents of sieve elements.

Phloem Unloading and Postphloem Transport

In contrast to phloem loading, the mechanisms involved in the removal or 'unloading' of assimilates from the phloem are less well defined. In part, this is due to the complexity created by different types of sink tissues, their function and developmental stage. In most cases, unloading of assimilates from the phloem is essentially a passive process. It follows the assimilate gradient, which is steepest toward an active sink tissue. In this context, phloem unloading refers only to the first step in the release of assimilates from phloem elements and the following steps belong to postphloem transport in sink tissues. Utilization sinks, such as root and shoot apices, are regions involved in mitotic activity and extension growth. Storage sinks, such as tubers, fruits and seeds, accumulate sucrose, lipids and/ or starch. Sucrose leakage and carrier-mediated retrieval also occurs in sieve element–companion cell complexes along the axial pathway during long-distance transport.

Phloem unloading in utilization and storage sinks is primarily a symplasmic process where assimilates are removed from sieve elements into the postphloem pathway via plasmodesmata (**Figure 3a**). Changes in plasmodesmal conductivity determined by their overall length or relative diameter could regulate the rate of unloading. Apoplastic unloading occurs in specific situations where sieve element–companion cell complexes are symplasmically isolated or the number of plasmodesmata is insufficient to allow symplastic transport. Meristematic cells and the vascular tissue in utilization sinks are typically well connected by plasmodesmata; only in exceptional cases are low plasmodesmatal frequencies observed. Considerably more variation in unloading mechanisms are found in storage sinks. Studies of phloem unloading in potato tubers indicate that both symplasmic and apoplastic pathways may be functioning during postphloem transport. In fruits, sucrose is symplasmically unloaded from sieve elements into phloem parenchyma, and an apoplastic step often occurs during postphloem transport. For example, during tomato fruit development the symplasmic to apoplastic transition in the postphloem pathway involves the hydrolysis of sucrose into hexoses; subsequent uptake by the storage parenchyma requires activity of H^+ ATPase and a hexose/proton symporter. Physical separation between cells in the postphloem pathway of developing seeds results in an apoplastic step requiring facilitated transport of sucrose or hexoses at the interface of maternal and filial tissues (**Figure 3c**).

Altering Transport in Transgenic Plants

The ability to modify phloem function by expressing foreign genes in transgenic plants or altering existing gene expression in the transport or pre- and postphloem pathways provide new insights into our understanding of phloem physiology. Several studies have already shown the negative effects of inhibiting phloem transport on plant growth. For example, the essential role of the sucrose/ proton cotransporter in apoplastic phloem loading was demonstrated directly in transgenic potato by decreasing its expression in antisense plants. Inhibiting carrier-mediated phloem loading resulted in carbohydrate accumulation in source leaves and stunted plants. Similar results were observed by expressing yeast invertase in the apoplast of several species that utilize apoplastic phloem loading. Presumably invertase hydrolysed apoplastic sucrose into hexoses, preventing sucrose loading into the sieve element–companion cell complex. The importance of the sucrose metabolism in source organs is also emphasized by transgenic plants expressing cytosolic invertase in companion cells. Coexpression of the *Escherichia coli* gene encoding pyrophosphatase functionally complemented inorganic pyrophosphate-dependent sucrose synthase conversion of sucrose to hexoses. In addition, phloem unloading and the postphloem pathway can be significantly affected by sink-specific expression of transgenic invertases or overexpression of pyrophosphatases. In potato, the effects ranged from changes in number, growth and development of the tubers to the accumulation of certain sugar metabolites at the expense of others. While the mechanisms effecting these physiological changes are not clearly defined, their influences on plant development are conspicuous. It appears that any changes in the metabolite levels of source or sink organs by overexpression or antisense inhibition decisively interferes with assimilate partitioning at the whole-plant level. Thus, results obtained by transgenic plants point to the importance of certain metabolic pathways and demonstrate the capability of plants to adjust readily to severe metabolic changes.

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