Phloem

The original version of this chapter was revised. The correction to this chapter can be found at https://doi.org/10.1007/978-3-319-77315-5_20

R. Crang et al., *Plant Anatomy*, https://doi.org/10.1007/978-3-319-77315-5_8

Introduction

Phloem is plant vascular tissue that transports sugars made by photosynthesis from green tissues, where they are manufactured, to parts of the plant where they are needed. That process is called translocation and is described by the Münch pressure flow hypothesis in which osmotically active sugars are loaded at the source and unloaded at the sink. Phloem also plays a role in while-plant communication by being a conduit for plant growth regulators. Pathogenic viruses can also move through the phloem and are the cause of many devastating crop diseases. Phloem has four cell types. Sieve tube elements (STEs) perform the actual translocation of sugars. Companion cells load and unload the sugars into the STEs. Parenchyma cells move water radially and store water. Fibers protect the delicate phloem STEs. The origin, function, and interaction of those cell types are discussed in this chapter.

8.1 Phloem Is a Complex Tissue Containing Multiple Cell Types, Each with a Specific Structure and Function

Angiosperm phloem tissue has four distinct cell types while gymnosperm has two (◘ Table 8.1, ◘ Fig. 8.1a). In angiosperms, the long-distance transport of phloem sap takes place via the **sieve tube elements** (STE, also known as **sieve tube members**). Individual STEs are joined end-to-end to form a **sieve tube**, and sieve tubes travel the length of the plant, from shoot tip to root tip. **Companion cells** (CC) and **phloem parenchyma** (PP) provide metabolic support for the STE and are involved in the loading and unloading of the molecules to be translocated. STEs, CCs, and PP cells are all parenchyma, with thin primary cell walls. Protection is provided by stout phloem fibers usually positioned to the abaxis (outside) of the other phloem cell types. The four types of cells in the phloem tissue work together to load, transport, and unload molecules while being shielded from damage from the exterior. There can be considerable diversity in the detailed phloem characters such as STE length and width, sieve plate type, and number and arrangement of parenchyma and companion cells (Pace et al. 2015).

Gymnosperm phloem tissue has **sieve cells** and phloem parenchyma, but lacks companion cells and phloem fibers (◘ Table 8.1). The term "sieve cell" is used instead of "sieve tube element" because the sieve cells are connected side-to-side and do not form a sieve tube, as the angiosperm STEs do. In other words, because gymnosperms do not form sieve tubes they, by reasoning, cannot have sieve tube elements. Phloem loading/unloading, which is the responsibility of the angiosperm companion cell (► Sect. 8.4), is accomplished by **albuminous cells** in the gymnosperms (a.k.a. **Strasburger cells**, ► Sect. 8.8). They were named for rich deposits of protein that stain similar to egg albumin (albuminous) and after Eduard Strasburger, a nineteenth-century botanist who first described the cells. Finally, gymnosperms do not make fibers, so they obviously cannot have phloem fibers.

Table 8.1 Phloem cell types and their functions in angiosperms and gymnosperms

Phloem cell type	Function	Angiosperm	Gymnosperm
Sieve tube elements	Translocation of sugars, amino acids and hormones	Yes	Yes
Companion cells	Metabolic support, phloem loading/unloading	Yes	No, but contain albuminous cells
Fibers	Support/protection	Yes	No
Parenchyma	Storage/synthesis	Yes	Yes

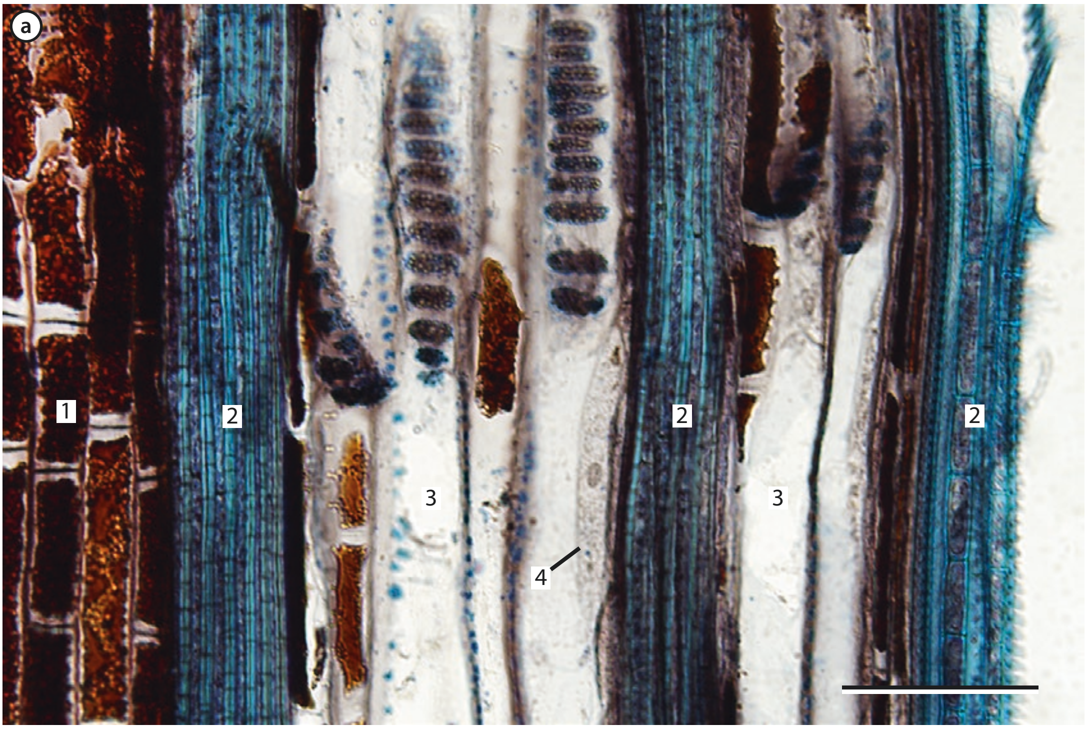
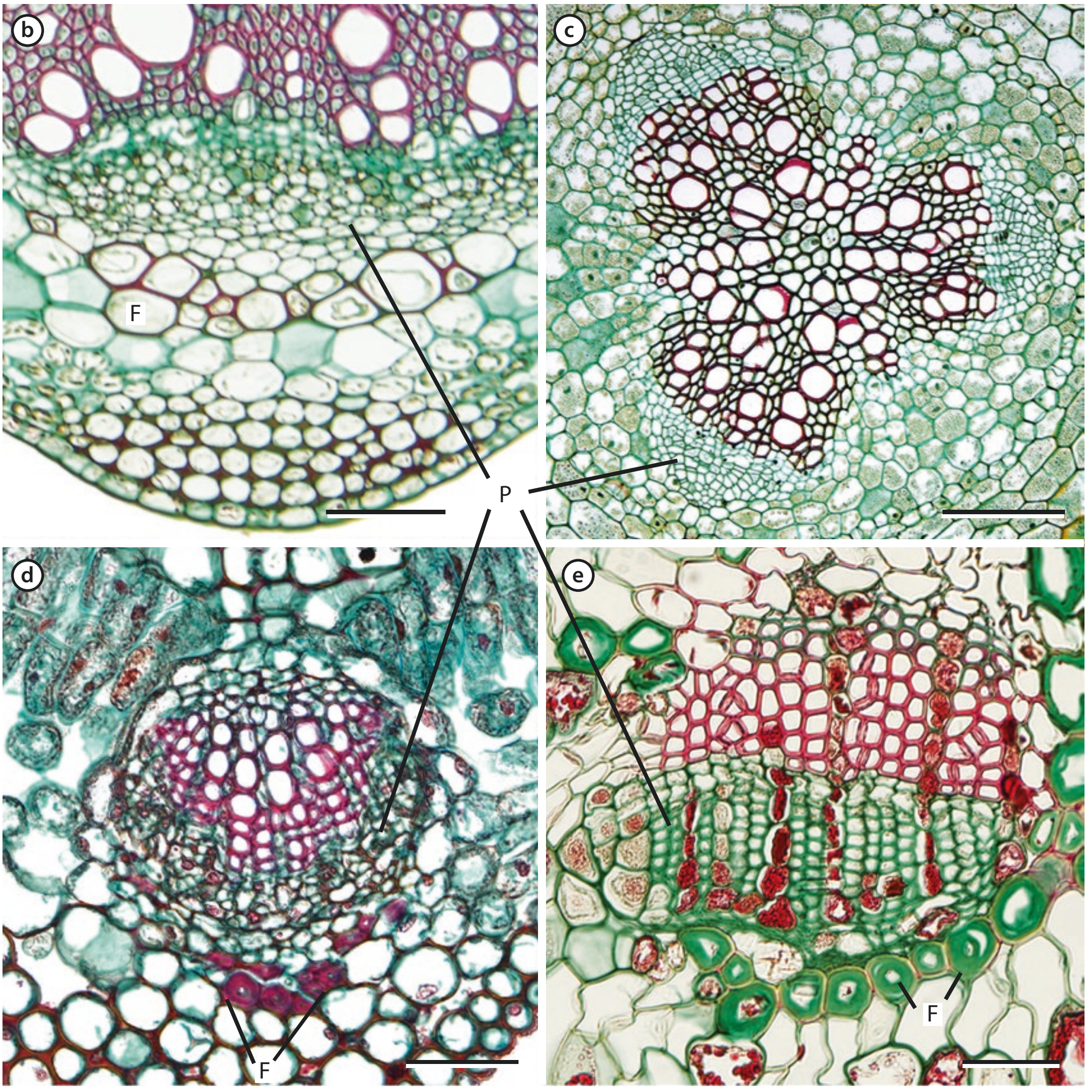


Fig. 8.1 **a** Phloem tissue in a grape (*Vitis* sp.) stem showing the relationship of the four cell types; the stem abaxis is to the left. Phloem parenchyma (1) are darkly stained due to the presence of tannins, fibers (2) are blue, sieve tube elements (3) have slanted **compound sieve plates**, and companion cells (4) have a nucleus and dense cytoplasm. Note that the companion cell shown is shorter than the sieve tube element it serves. Scale bar = 50 µm. (RR Wise)

Plant organs are arranged along an axial (up and down) direction and a radial (from the interior to the exterior) direction, and water and nutrients must flow along both axes. Sieve tube elements and companion cells only run in the axial direction. Radial translocation, which can be significant in a tree trunk with actively growing periderm (refer to ► Chap. 16), occurs exclusively via phloem ray parenchyma (refer to ► Sect. 8.5).

Phloem and xylem tissues are almost always found together because they are derived from the same bifacial meristematic tissue,



◘ **Fig. 8.1** **b**–**e** Abaxial phloem in **b** beet (*Beta vulgaris*) stem, **c** baneberry (*Actaea alba*) root, **d** lilac (*Syringa* sp.) leaf, and **e** pine (*Pinus* sp.) leaf. The abaxial direction for **b, d,** and **e** is toward the bottom of the page. In **c** the abaxial direction is any centripetal direction, because the vasculature is in the center of the root. Phloem (P) is indicated. Xylem conducting cells are the dark red cells to the adaxis of the phloem. Fibers (F) are indicated in **b, d,** and **e**. Scale bars = 50 µm in **b**, 100 µm in **c**, and 25 µm in **d** and **e.** (**b**–**e** RR Wise)

the vascular cambium. Therefore, their elements run parallel to each other in vascular bundles. Phloem is usually positioned abaxial to the xylem in leaves, stems, and roots (◘ Fig. 8.1b–e), although other, more complicated arrangements may be found (refer to ► Sect. 11.6—Stems). ◘ Figure 8.1b shows a typical arrangement found in stems in which a vascular bundle contains xylem to the interior and conducting phloem to the exterior, with a cap of phloem fibers external (abaxial) to the conducting phloem.

Roots (◘ Fig. 8.1c) also have abaxial phloem, even though root vasculature architecture (refer to ► Chap. 10—Roots) is distinctly different from that of the stem vasculature (refer to ► Chap. 11—Stems).

Leaves maintain the abaxial phloem position of the stem vasculature, resulting in phloem being positioned toward the "bottom" side of the leaf (◘ Fig. 8.1d, e). Not all phloem tissue produces fibers, but when it does, the fibers are either abaxial to the conducting phloem or intermixed with it (refer to ► Chap. 16—Periderm). Phloem may be the location of secretory ducts (◘ Fig. 13.3c) and laticifers. Phloem, especially the fibers and dead conducting cells, is also a major component of bark, as is described in ► Chap. 16—Periderm.

In the early development of angiosperms, primary phloem is first formed as a growth from procambium parenchyma cells from the apical meristem in what will become the midvein site through extension. These are termed **protophloem** cells and are narrow, enucleate, and mostly without companion cells. As growth of a eudicot embryo takes place, phloem development separately occurs in the root and the cotyledons (a.k.a. seed leaves). Protophloem is formed during cell expansion which also eventually stretches and tears apart the cells. The sieve tube elements are typically narrow and elongated and rarely possess companion cells. Once cell elongation ceases, phloem cells that are formed are termed **metaphloem**, and the cells are wide and long but are not stretched longer with additional cell growth. These cells include sieve tube cells, companion cells, phloem parenchyma as well as phloem fibers.

As secondary growth occurs, **secondary phloem** is derived from the vascular cambium (► Chap. 14) and there is no distinction between protophloem and metaphloem. Sieve tube cells are wide and relatively short, and both phloem parenchyma and phloem fibers are typically found. Parenchyma cells may be companion cells, which are much smaller than the sieve tube cells, densely cytoplasmic and connected to the sieve tube cells via plasmodesmata. However, there are also companion cells that are virtually lacking plasmodesmata, and transfer cells that have greatly irregularly thickened primary walls that move solutes to other sites or for storage.

8.2 Phloem's Main Function Is Photosynthate Translocation

Phloem's main function is the long-distance transport of sugars and other **photosynthates** from the source (mature leaves), or reserves (the cotyledons of germinating seedlings) toward the sinks, e.g., roots, developing reproductive structures (flowers, fruits, and seeds), meristems, and young leaves. The process is called **translocation,** and the aqueous solution being translocated is called **phloem sap** consisting of carbohydrates, minerals, and soluble ions. The distance between source and sink can be significant, and phloem makes a continuous connection between those organs. Consider the distance between the leaves of the tallest tree and its roots. Phloem is also the primary pathway in vascular plants for the movement of amino acids, plant growth regulators, and other compounds that signal and direct responses at sites remote from their origin.

Box 8.1 Plants Fight Back—Defenses Against Phloem-Feeding Insects

Some insects indiscriminately feed on plants, while others are much more specific. Aphids are specialists in that the feed specifically on the phloem, termed phloem feeding insects (PFI). They use their piercing stylet to penetrate phloem sieve tube elements in the stem or leaf and feed off the phloem sap. Plants are not without their defenses. Infestation by PFIs induces the expression of a number of biotic stress defense genes. The activation of cell wall proteins and calcium signally proteins are some of the first responses with the plant hormones ethylene, jasmonic acid, and salicylic acid playing signaling roles in mounting the defense response. The combined effect of the defense responses is to inhibit, or at least reduce, the aphid's ability to successfully feed from the phloem strand. Successful PFIs, on the other hand, have evolved mechanisms to overcome the plant molecular defenses.

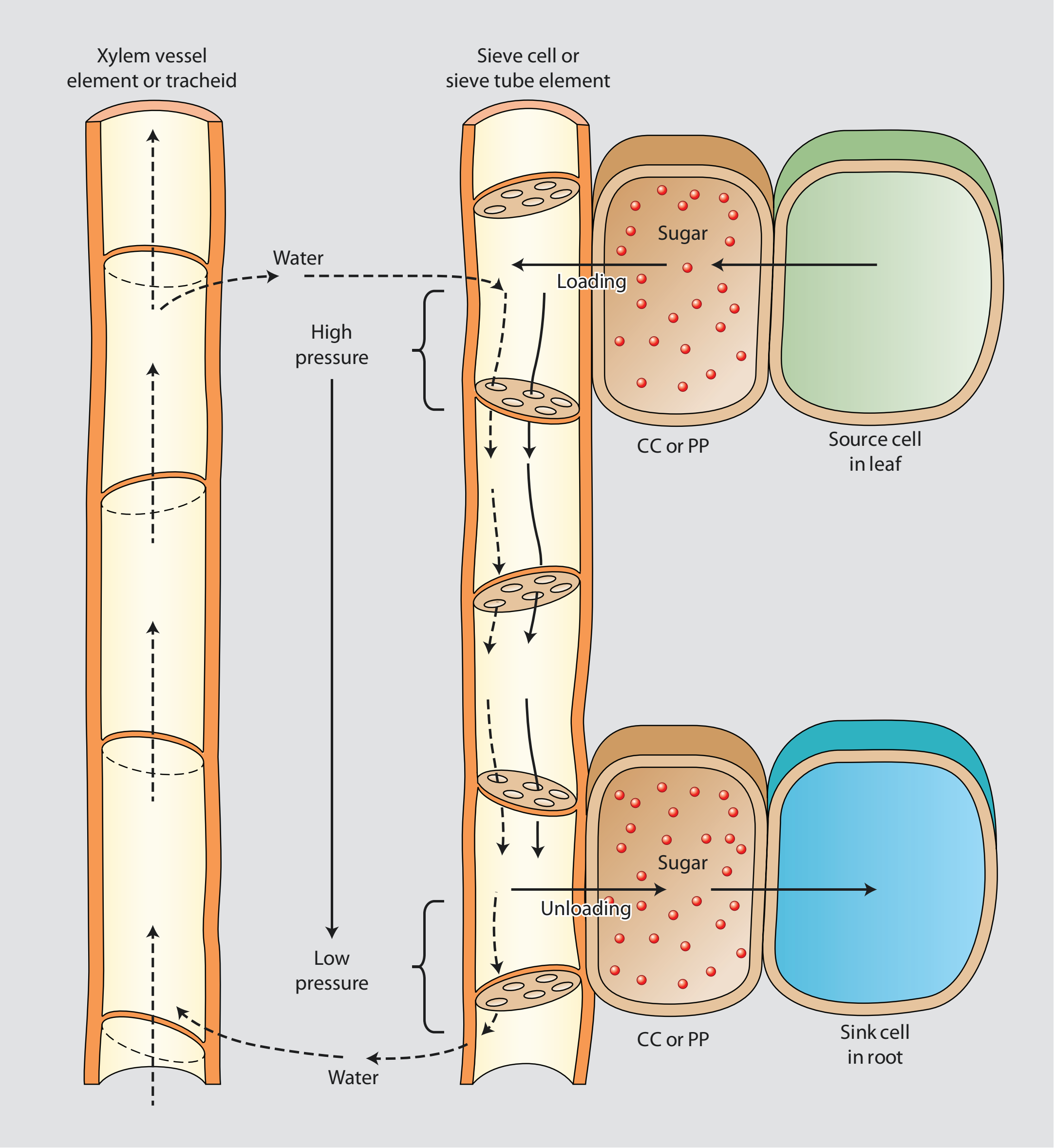
Reference: Foyer et al. (2015)

The mechanism of phloem translocation was first described by the German botanist Ernst Münch in 1926. Those early ideas (now called the Münch pressure flow hypothesis) remain at the core of our modern understanding of the relationship between phloem structure and function. In brief, sugars made by photosynthesis are loaded into the phloem at the source tissues, usually leaves. The sugar is commonly sucrose (a disaccharide), but raffinose (trisaccharide) or stachyose (tetrasaccharide) may also be translocated, depending on the plant species.

The sugars are not only a translocatable form of reduced carbon, but they are also osmolytes, meaning as they go into solution, they lower the osmolarity of the phloem sap. Osmosis then draws water from the adjacent xylem tissues into the phloem, increasing the pressure inside the phloem sieve cell (gymnosperms) or sieve tube element (angiosperms). The pressurized phloem sap is forced toward the sink tissues (which may be tens of meters distant) where the osmotically active sugars are removed and respired or stored in the form of starch in amyloplasts. Removing the sugars causes water to leave the phloem via osmosis and the pressure drops. Therefore, the sugars being translocated are responsible for the pressure gradient between the source and sink tissues which drive the movement of those same sugars (◘ Fig. 8.2).

8.3 Sieve Tube Elements Are Living Cells Responsible for Translocation

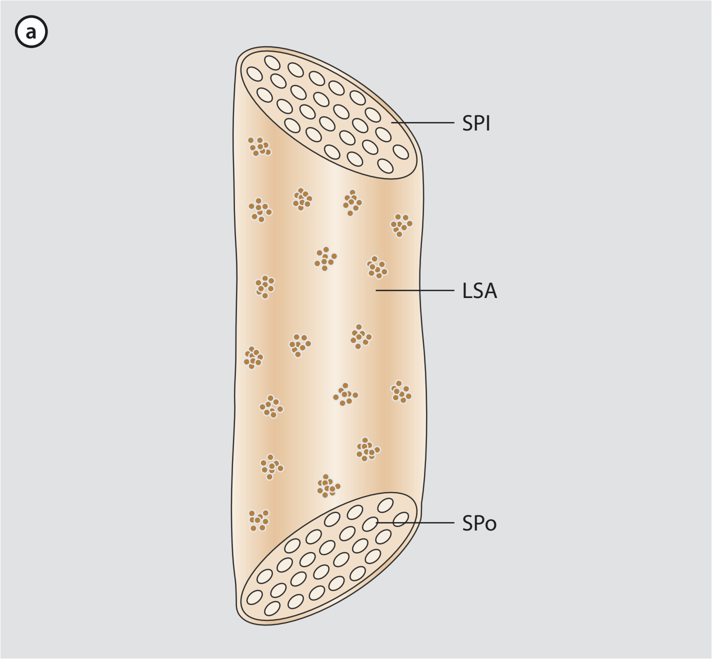
Sieve tube elements (STE), in flowering plants, and sieve cells (SC), in gymnosperms (► Sect. 8.2), are the functional components of phloem tissue by which photosynthates and other molecules are distributed around the plant. The angiosperm sieve tube, formed by the end-to-end connection of STEs, is analogous to a vessel in the xylem. Unlike the dead tracheary elements of xylem, however, sieve



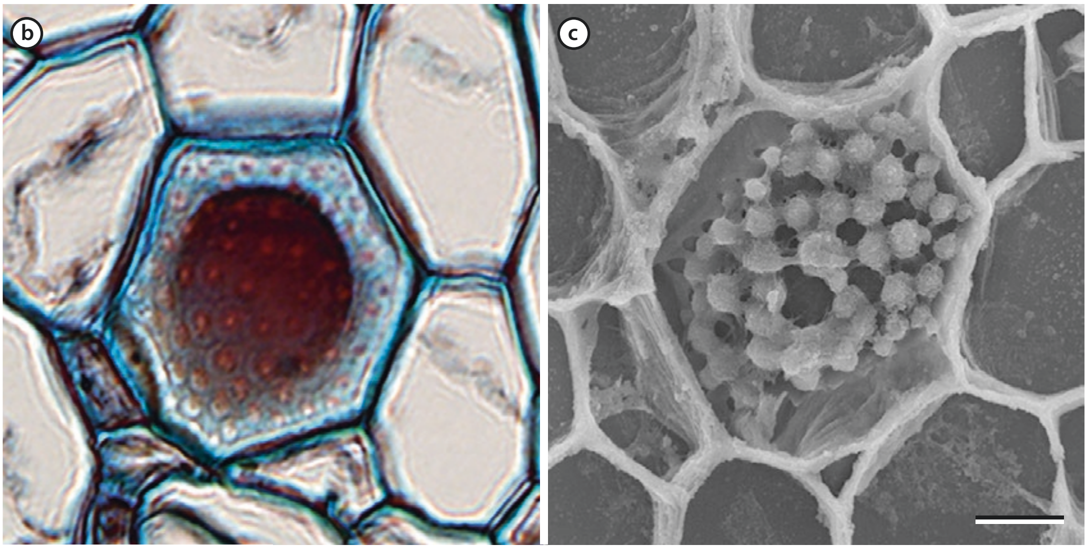
◘ **Fig. 8.2** Anatomy and physiology of the Münch pressure flow hypothesis. Sugar loading (top right of figure) from a source cell to a phloem sieve tube element (STE) occurs via either companion cells (CC) or phloem parenchyma (PP), depending on the species. This lowers the water potential of the STE which draws water via osmosis from the neighboring xylem tracheary element and pressurizes the STE. Phloem sap is therefore pushed to the sink tissues, where the sugar is unloaded (by either a CC or PP) (Redrawn from Crang and Vassilyev 2003)

tube elements are living cells with an intact, osmotically active plasmalemma, a few mitochondria, modified plastids, and an endoplasmic reticulum. In the mature, conducting state, STEs lack cytosol, ribosomes, Golgi apparatus, a nucleus, and the central vacuole with its tonoplast. Thus, the cell lumen is mostly free for phloem sap movement. By contrast, companion cells are rich in cytoplasm and contain a nucleus and other organelles (▶ Sect. 8.4).

Sieve tube elements (◘ Fig. 8.3a) have two types of specialized intercellular communications, **sieve plates** in their end walls

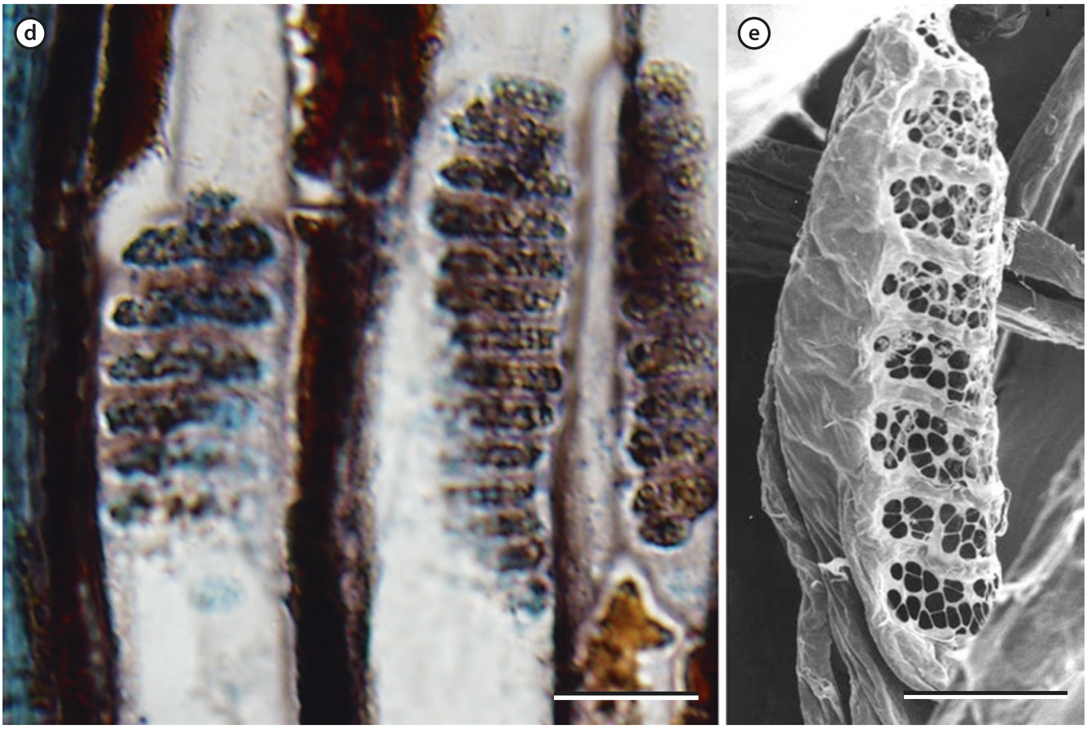


◘ **Fig. 8.3** **a** Drawing of a sieve tube element showing the terminal sieve plates (SPl) with sieve pores (SPo) and lateral sieve areas (LSA) (Redrawn from Crang and Vassilyev 2003)



◘ **Fig. 8.3** **b**, **c** Simple sieve plates in squash (*Cucurbita pepo*) seen face-on. **b** The primary cell wall stains blue in this LM section while the P-protein stains red. Compare this image to the longitudinal section in **g**. **c** Scanning electron micrograph of a sample that was prepared the same as in **b**. Note the companion cells in the 8 o'clock position next to both sieve plates. Scale bar in **d** = 10 µm and applies to both panels. (**b**, **c** RR Wise)

(◘ Fig. 8.3b–f) and **sieve areas** in their lateral walls (◘ Fig. 8.3g). Both contain numerous **sieve pores**. Sieve pores are modified, enlarged plasmodesmata (see below), and, like plasmodesmata, they interconnect sieve tube elements at both the ends and sides.

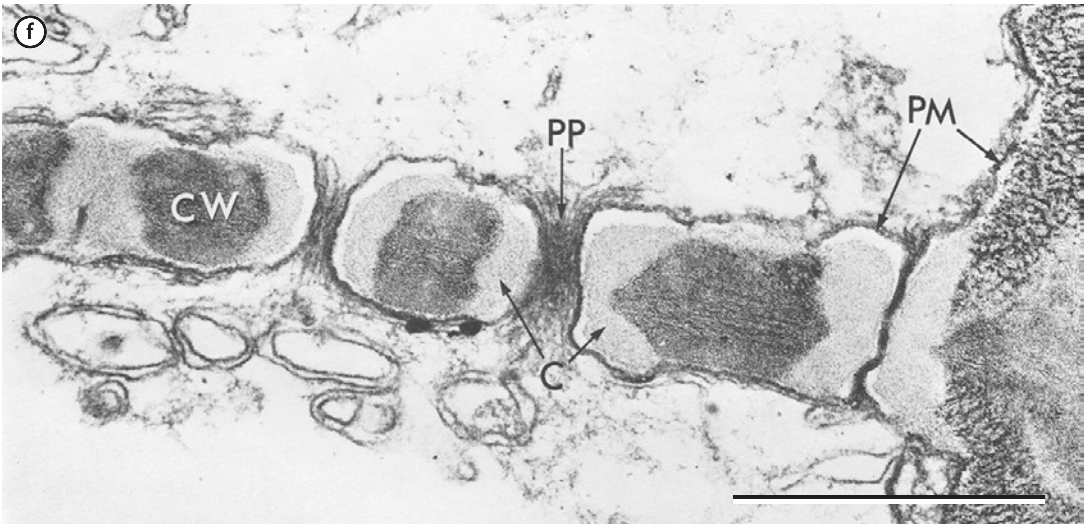


■ **Fig. 8.3** **d**, **e** Compound sieve plates in grape (*Vitis* sp.). **e** Light micrograph of three sieve plates. **f** Scanning electron micrograph of an isolated grape STE from a stem maceration. The specimen experienced some shrinkage during preparation for microscopy. Scale bars = 20 μm in both panels. (**d** RR Wise; Image **e** courtesy of J. D. Curtis)

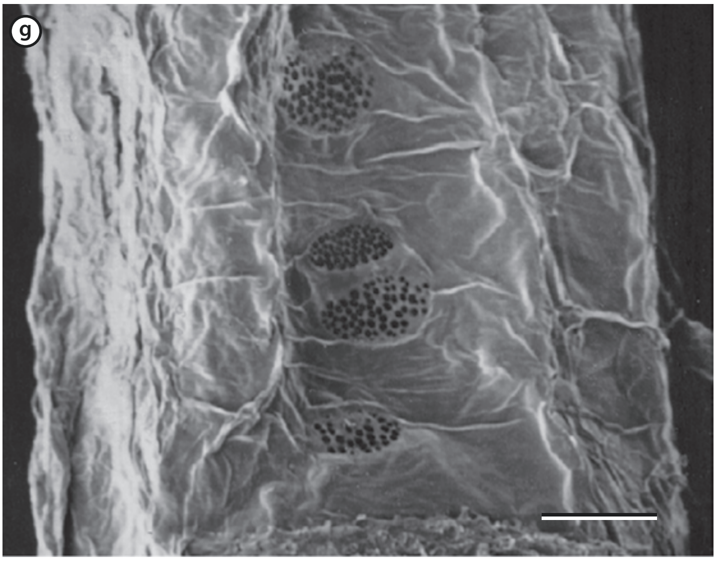
Sieve plates may be simple, with the entire end wall modified into a sieve area (■ Fig. 8.3b, c), or compound, consisting of several sieve areas interrupted by intact end wall areas (■ Figs. 8.3d, e and 8.4e). Non-inclined, simple sieve plates are considered most derived and are adapted for intercellular flow, like straight perforation plates in xylem vessels. On the other hand, inclined compound scalariform sieve plates are considered ancestral, like inclined perforation plates in xylem vessels.

The development of simple sieve plates has been studied in more detail than inclined sieve plate development. During phloem development, plasmodesmata in the walls between future sieve elements are converted into sieve pores usually 0.2–0.4 μm in diameter (but up to 1 μm in some cucurbits). This facilitates the unimpeded flow of the translocation stream between adjacent sieve elements. Like plasmodesmata, the sieve pores are delimited from the cell wall by a plasmalemma membrane which is continuous between the adjacent sieve elements and continuous throughout the length of the sieve tube (■ Fig. 8.3f). This, in effect, makes the sieve tube a continuous pathway. Development of sieve pores involves the deposition of an amorphous polysaccharide callose in the cell wall around each plasmodesmata that displaces cellulose microfibrils. Due to the subsequent enzymatic digestion of the centers of these cylinders of callose, sieve pores will replace the callose depositions.

A unique filamentous protein termed **P-protein** (“P” derived from “phloem”) is formed in the sieve elements of many plants



◘ Fig. 8.3 **f** Transmission electron micrograph of a portion of a sieve plate in Arabidopsis showing details of the sieve pores. Seen in cross-section, the areas of cell wall (CW) between the pores appear as isolated islands. Callose (C) lines the pores, while the plasma membrane (PM) surrounds the cells and extends through the sieve pores. Strands of P-protein (PP) are indicated. Scale bar = 1 μm. (Image from Ledbetter and Porter (1970), with permission)



◘ Fig. 8.3 **g** Sieve areas in a grape (*Vitis* sp.) sieve tube element isolated from a stem maceration. STEs are parenchyma cells, and this one shriveled somewhat during specimen preparation, but the sieve areas are clearly visible. Scale bar = 10 μm. (Image courtesy of J. D. Curtis, UW Stevens Point)

during differentiation. It has filaments which are anchored to the periphery of the mature cell and which permeate the sieve element lumen (◘ Fig. 8.3h). After injury to the phloem, P-protein is released from its anchoring sites and accumulates at sieve pores by hydrostatic pressure of the sieve tube sap, blocks the pores, and prevents assimilate loss at the injury site (◘ Figs. 8.3i, j). Such aggregations of P-protein, sometimes also called **slime plugs**, are usually formed during the processing of phloem for light microscopy.

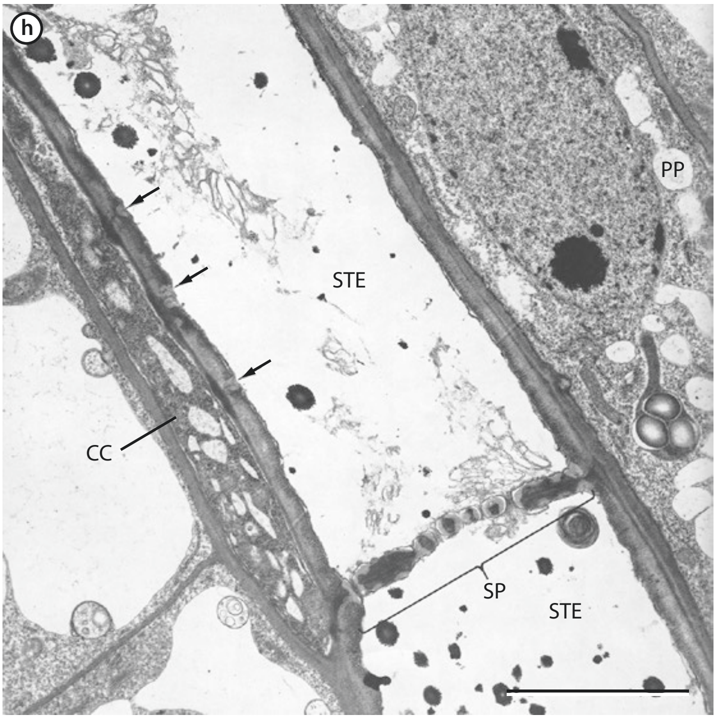


Fig. 8.3 **h** Transmission electron micrograph of portions of two sieve tube elements in an *Arabidopsis* stem. A sieve plate (SP) separates the two sieve tube elements. Plasmodesmata connecting the companion cell (CC) and sieve tube element (STE) are indicated with arrows. The wispy material in the STE lumen is P-protein. A phloem parenchyma (PP) cell lies to the top right. Scale bar = 5 µm. (Image from: Ledbetter and Porter (1970), with permission)

Box 8.2 Dangerous Hitchhikers—Viruses Use Phloem to Spread Throughout a Plant

Phloem is a continuous, living transportation network of vascular tissue that spreads throughout the plant. Viruses enter a plant through damage such as insect bites and make their way, via plasmodesmata, to the phloem sieve tube elements. Plants have numerous defense mechanisms to keep viruses out of sieve tube elements. Once in the phloem, the viruses may spread either as virions in which the viral genome is protected by virus capsid proteins, or as ribonucleoprotein (RNP) complexes in which the viral genome is protected by either viral proteins or host proteins. Susceptible plants are not able to prevent the long-distance viral spread. Resistant plants have molecular mechanisms to block viral passage in the phloem and survive. The fascinating molecular details of this viral-plant arms race are beginning to be elucidated.

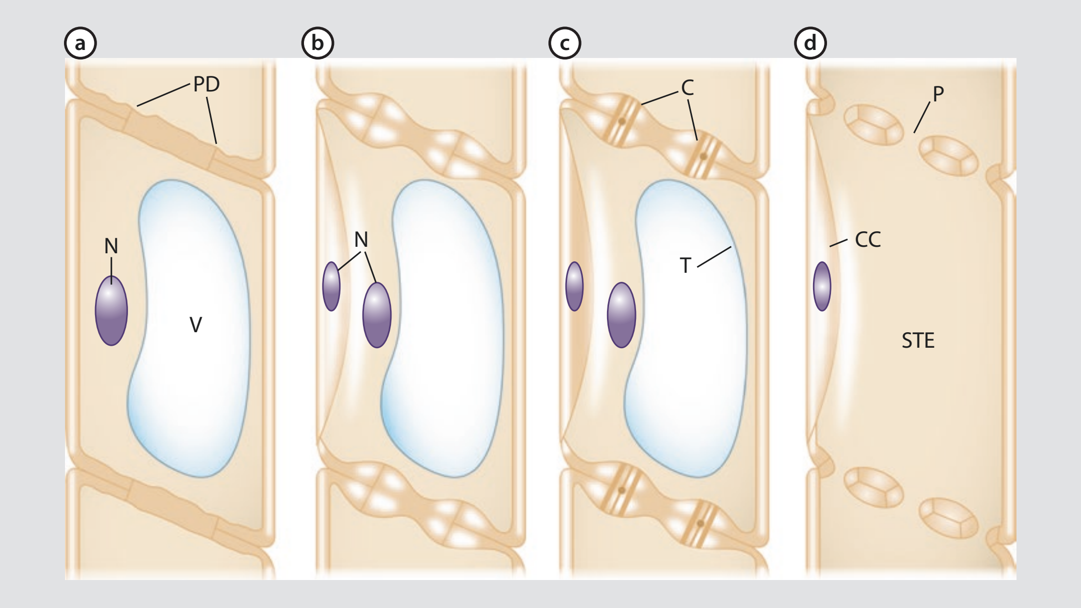
Reference: Hipper et al. (2013)

Fig. 8.3 **i**, **j** Longitudinal section of a squash (*Cucurbita pepo*) stem showing P-protein details. **i** Every sieve tube element in the field of view has an accumulation of red-staining P-protein at the lower end of the cell as an artifact of tissue preparation. Phloem sap is under pressure, and the direction of flow was toward the bottom of the image when these samples were collected. Two files of phloem parenchyma (PP) are labeled. **j** A higher magnification view of several sieve tube elements. P-protein has accumulated at the lower end of each STE. Note also the companion cell (*) to the left of the STE in the middle of image **j**. Scale bars = 50 μm in **i** and 20 μm in **j**. (**i**, **j** RR Wise)

8.4 Companion Cells Support the Sieve Tube Element and Are Involved in Phloem Loading and Unloading in Angiosperms

Each sieve tube element in angiosperms is accompanied by a single cytoplasmically dense cell called a companion cell. **Companion cells** lie along the sieve element, and, in fact, the two cells together are considered to be a single functional unit called an STE-CC complex. The two cells are the product of longitudinal division from a common phloem mother cell (Fig. 8.4a–d). Phloem mother cells are found in both the procambium (generating primary phloem) and the vascular cambium (generating secondary phloem).

Companion cells have been studied intensively for decades and appear to have a variety of roles depending on species, organ, and developmental stage (Otero and Helariutta 2017), with two basic roles being the most important. First, companion cells provide metabolic support for the sieve tube element. Upon maturation, phloem sieve tube elements undergo partial apoptosis (i.e., programmed cell death). They have a degenerate cytoplasm with minimal organelles and lack a nucleus and ribosomes. In spite of this, phloem STEs can remain alive for decades. The companion



◘ **Fig. 8.4** **a**–**d** Development of a sieve tube element (STE) and its companion cell (CC) from a single phloem mother cell. **a** The phloem mother cell has a single nucleus (N), a large vacuole (V) and plasmodesmata (PD). **b** Mitosis generates two cells, each with its own nucleus. **c** The STE nucleus and tonoplast (T) break down. Callose (C) accumulates at the developing sieve pores. **d** In the mature state, sieve tube elements each have an accompanying companion cell and are connected via a sieve plate (SP) containing large sieve pores (P). The CC retains its nucleus and the common wall between the CC and STE has numerous plasmodesmata (not shown). The CC is often shorter than the STE (Redrawn from Crang and Vassilyev 2003)

cell serves to provide the STE with all the necessary biochemical requirements for it to survive. The STE-CC complex represents the ultimate stage in eukaryotic cell compartmentation in that one cell, the STE, relies almost completely on another, the CC, for its basic metabolic needs.

Companion cells also play an important part in loading sieve tubes with photosynthates and other molecules at source tissues and unloading from sink tissues. These are the sugars that drive translocation (refer to ► Sect. 8.2, above). Loading/unloading can have two pathways, depending on the plant and the organ. In **symplastic loading** small monomeric sugars diffuse from a companion cell into a sieve tube element via plasmodesmata in their common wall. Once in the STE, the monomers are polymerized to larger sugars that are too large to diffuse back through the plasmodesmata to the companion cell. This physiological process is called polymer trapping. The polymers are subsequently carried in the phloem sap to a source tissue where they are depolymerized and unloaded. In **apoplastic loading**, **transport proteins** in the CC plasma membrane facilitate unidirectional movement of sugar monomers from the CC cytoplasm into the apoplastic space between the CC and an adjacent STE. Other transport proteins in the STE plasma membrane facilitate unidirectional uptake of the apoplastic sugars into the STE cytoplasm for long-distance translocation.

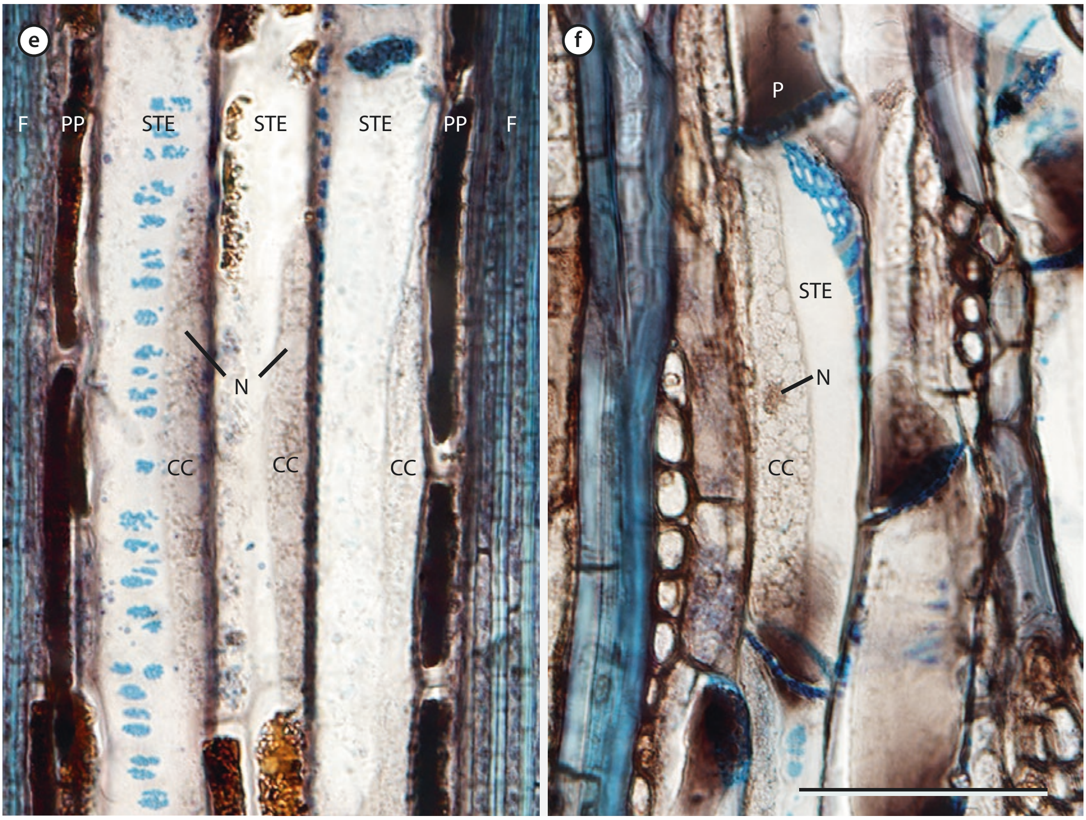
Gymnosperms lack angiosperm-like companion cells and have, instead, specialized cells called **albuminous cells** that are thought to play the same role in phloem loading and unloading (► Sect. 8.8). Seedless vascular plants have sieve tube elements, but lack specialized companion cells. Instead, the adjacent phloem parenchymas have numerous plasmodesmata and pores on the STE common walls, indicating that they function in a role similar to the angiosperm companion cell and the gymnosperm albuminous cell (Evert 1990a).

8.5 Phloem Parenchyma Cells Are Involved in Radial Translocation, Xylem/Phloem Coordination, and Storage

Companion cells (► Sect. 8.4) and albuminous cells (► Sect. 8.8) are parenchyma cells. Indeed, even sieve tube elements qualify as parenchyma cells, although they are highly modified via partial apoptosis. However, phloem tissue contains other parenchyma cells that do not fit into any of the previous categories. Such phloem parenchyma cells play multiple roles in radial translocation, coordination of adjacent xylem and phloem tissues, and storage.

As noted previously, sieve tube elements, companion cells, and phloem fibers run in the axial direction. Phloem parenchyma in secondary tissues, on the other hand, occurs in two orientations or systems. (Tissues in the primary state may have little need for radial transport, due to their small size.) **Axial phloem parenchyma** cells (◘ Fig. 8.4e, f) run up and down the axis of the plant and are part of the vascular bundle containing sieve tube elements, companion cells, and phloem fibers, as well as the adjacent tissues of the xylem. **Ray parenchyma** cells run in a radial direction forming xylem rays to the interior (► Chap. 7) and **phloem rays** to the exterior (◘ Fig. 8.5a), meaning that an individual ray is both a xylem ray and a phloem ray, depending on the tissue it penetrates. Ray parenchyma are formed in the vascular cambium by the division of ray initials (► Sect. 14.3). Those toward the xylem side are usually short lived, while the phloem ray parenchyma may last considerably longer. Transpirational water moves up the axial xylem from the roots, enters the parenchyma of the xylem ray, and moves in a radial direction into the phloem ray and then to the periderm (◘ Figs. 8.5b, c). Photosynthate is translocated from the source (usually a leaf), through phloem sieve tube elements in the axial phloem, enters the ray parenchyma, and moves in a radial direction out to the living tissues of the periderm (► Chap. 16). There are no sieve tube elements in the radial system—all translocation is via the symplasm of the phloem ray parenchyma. In a mature tree, the flux of phloem sap in the radial direction may be significant because it is usually the sole source of water and nutrients for the physiologically active periderm.

Phloem ray parenchyma cells may be elongated in the radial direction, termed **procumbent cells**, or elongated in the axial direction, called **upright** or **erect cells** (◘ Fig. 8.5d, e). Upright cells are usually at the upper and lower margins of the ray.



◘ **Fig. 8.4** **e**, **f** STE-CC complexes. **e** Three sieve tube elements from grape (*Vitis* sp.) are bordered by phloem parenchyma (PP) and fibers (F) to either side. Blue-stained callose marks locations of portions of two sieve plates at the top of the figure and lateral sieve areas in the leftmost STE. Three companion cells (CC) are indicated as two CC nuclei (N). Note that the STEs are considerably longer than the CCs. **f** A single STE-CC complex in elm (*Ulmus americana*) in which the STE and CC have the same length. The brown areas are sieve plate slime plugs made of P-protein (P). Note the CC nucleus (N). Scale bar in **e** = 50 µm and applies to both panels. (**e**, **f** RR Wise)

Phloem parenchymas store starches, tannins, oils, other secondary compounds, and water in both the axial and ray systems. Given their intimate association within the phloem tissue, and that sieve tube elements, companion cells, and phloem fibers have specific and defined roles to play, phloem parenchyma may be seen as the most metabolically flexible of the four phloem cell types. This versatility fits with their multiple roles in storage. Starch storage increases in the autumn, and those carbohydrates are subsequently remobilized to support cambial activity upon the reactivation of the vascular cambium during spring growth in conifers (◘ Fig. 8.5f, Rahman et al. 2016) and ginkgo (Cui et al. 2016). Tannins are well-known **antiherbivory** compounds, and phloem is an attractive target for insect attack. Therefore, many species fill phloem parenchyma cells with tannin deposits (◘ Fig. 8.5g) to deter herbivory. Finally, water from phloem parenchyma may be used to supplement xylem water at times of high transpirational demand (Pfautsch et al. 2015).

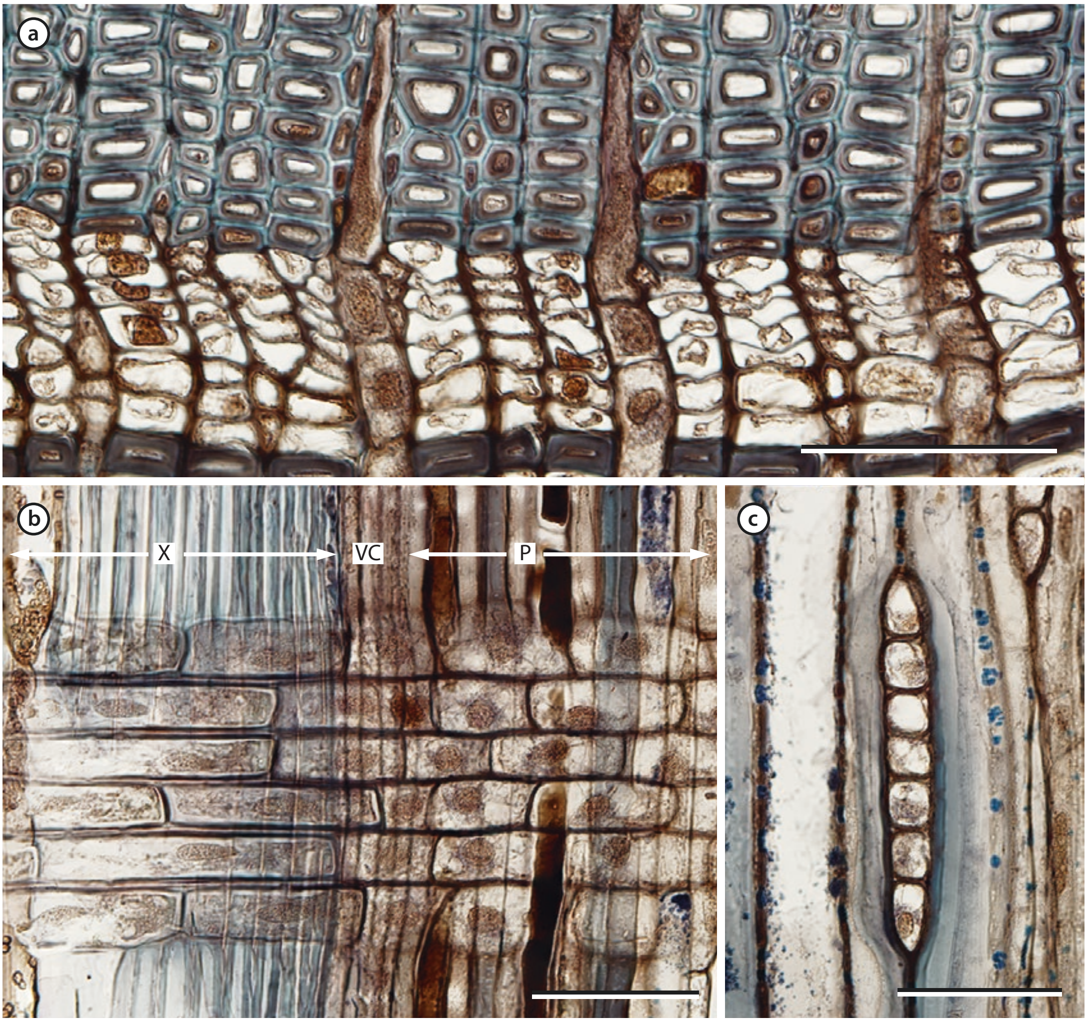


Fig. 8.5 **a** Phloem rays in a coast redwood (*Sequoia sempervirens*) stem. **a** Cross-sectional view showing xylem to the top, phloem to the bottom, and three rays that originate in the xylem and continue through the phloem. The thick-walled cells in the xylem are tracheids and the source of transpirational water. **b** Radial view of a single ray, extending from the xylem (X) into the phloem (P). The vascular cambium (VC) lies between the xylem and phloem, and the periderm would be to the right in the figure. The ray is six cells tall. **c** Tangential view of a single phloem ray which is seven cells tall and one cell layer wide. This is a **uniseriate ray**. The blue dots to the right of the ray are lateral sieve areas in the phloem sieve cells. Scale bars = 50 μm in all three panels. (**a**–**c** RR Wise)

The vascular system may be thought of as having five components: (1) axial xylem, (2) xylem rays, (3) axial phloem, (4) phloem rays, and (5) a mesh of xylem and phloem parenchyma (both derived from the vascular cambium) that integrates and interconnects the other four components. It has recently been proposed that this network of parenchyma plays critical roles in whole-plant coordination of resource transport and, more importantly, resource allocation (Spicer 2014). Anatomical details such as taxon-specific variations in size, shape, and location of parenchyma as well as pits and plasmodesmatal connections to adjacent tissues suggest that the vascular parenchyma is a highly evolved tissue that plays a crucial role in both long-distance and short-distance transport of transpirational

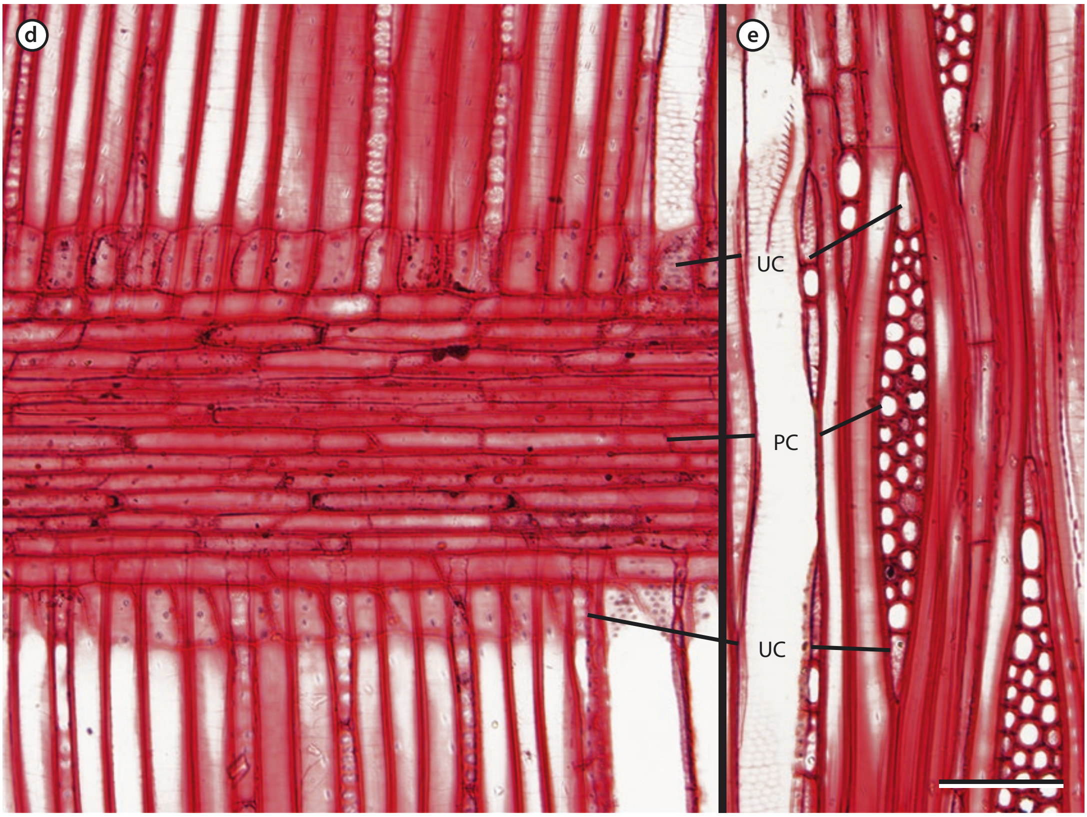


Fig. 8.5 **d**, **e** Procumbent (PC) and upright cells (UC) in xylem rays from holly (*Ilex opaca*) wood. **d** is a **radial section**, and **e** is a **tangential section**. Xylem tissue is shown because the ray cells are more easily seen than in phloem tissues. However, the arrangement is the same in phloem. Scale bar in **e** = 50 μm and applies to both panels. (**d**, **e** RR Wise)

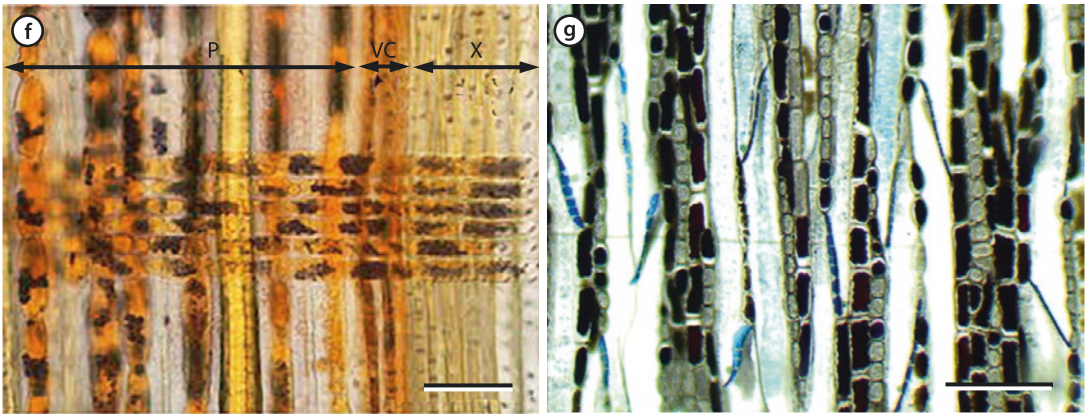
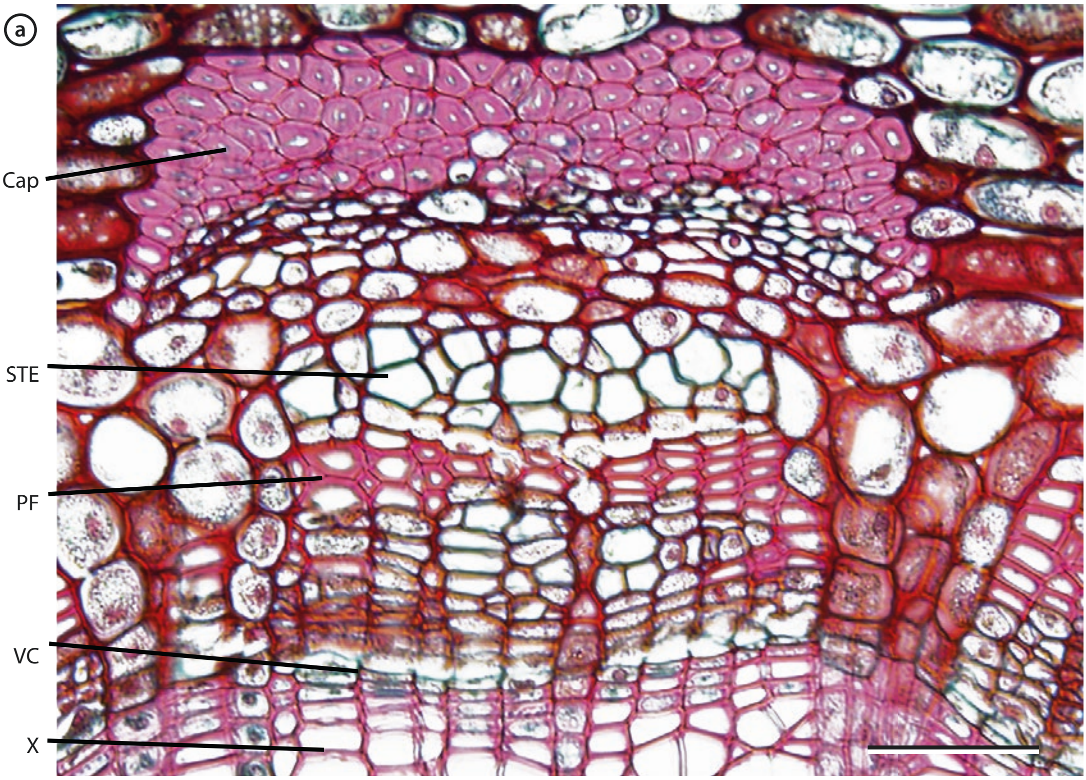


Fig. 8.5 **f**, **g** Phloem storage compounds. **f** Starch has been stained dark brown in phloem parenchyma cells as shown in this radial section of sawara cypress (*Chamaecyparis pisifera*) stem. Axial parenchymas are to the left in the image, and radial parenchyma runs across the image. Both contain starch. **g** Tannin-filled parenchyma cells are dark brown and interspersed among sieve tube elements in this black willow (*Salix nigra*) stem. Scale bars = 100 μm in both panels. (**f** from Rahman et al. (2016), with permission; **g** RR Wise)

water and phloem sap. The interconnected parenchymas of xylem and phloem rays therefore take on an important role in whole plant physiology.

8.6 Phloem Fibers Protect the Delicate Sieve Tubes

Technically speaking, all phloem STEs, CCs, and phloem parenchyma are products of the procambium (primary phloem) or the vascular cambium (secondary phloem). However, not all cells termed phloem fibers fit that tight definition. Fibers are sclerenchyma cells found throughout the stems, leaves, and other organs of angiosperms and gymnosperms, and they may have a variety of origins (◘ Fig. 8.1b, d, e and 8.4e). While some fibers are produced by the vascular cambium (◘ Fig. 8.6a), all fibers found within or adjacent to the phloem are often termed phloem fibers based on their location, and not necessarily their origin.



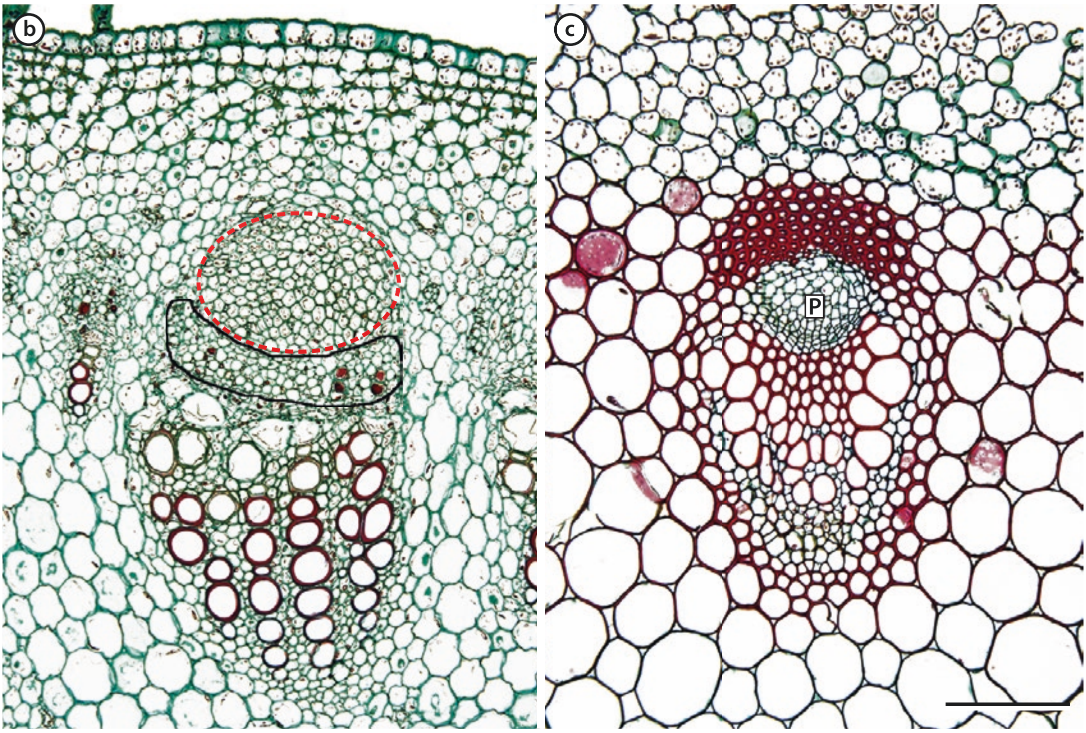
◘ **Fig. 8.6** **a** Tulip tree (*Liriodendron tulipifera*) vascular bundle. *Liriodendron* has a cap of fibers to the exterior of the sieve tube elements. Other phloem fibers (PF) to the interior of the sieve tube elements (STE) were derived from the vascular cambium (VC) and will probably become part of the periderm with time. Their alignment with cells and derivatives of the vascular cambium reveals their origin from the vascular cambium. (X = xylem. Scale bar = 25 μm) (RR Wise)

Regardless of their ontogenetic origin, all phloem fibers are responsible for support and protection. Sieve tube elements are relatively thin-walled parenchyma cells with a function for which no other cell type can substitute. Therefore, they must be protected from wounding, damage caused by bending, and attack by insects. STEs also provide little in the way of support for the stem in either primary or secondary tissues.

Not all phloem tissues have associated fibers; those in the primary state may lack them entirely (◘ Fig. 8.6b). In tissues that do have phloem fibers, it is common for them to form "caps" to the abaxial side of vascular bundles (◘ Fig. 8.6c). Phloem in secondary tissues is protected by the periderm, which is a mixture of phloem fibers, phelloderm, and phellem (refer to ► Chap. 16—Periderm).

8.7 Secondary Phloem Typically Only Functions for One Growing Season

In the elongating stem region, the first nutrient conducting tissues (protophloem) are formed from the procambial strands which are initiated in the apical meristems. The phloem cells lengthen very rapidly to form conducting strands. At about the same time, the first



◘ **Fig. 8.6** **b** A vascular bundle from a cosmos (*Cosmos* sp.) stem showing a lack of fibers in or around the phloem (inside black bounding area), although there is a large cushion of densely packed parenchyma cells to the abaxial side (inside red-encircled bounding area). **c** This vascular bundle from a meadow buttercup (*Ranunculus acris*) stem has a large cap of red-stained fibers to the abaxis of the phloem (P). Scale bar in **c** = 50 µm and applies to both panels. (**b**, **c** RR Wise) strengthening tissues (sclerenchyma fibers) develop on the outside of the phloem. The procambial strand continues to produce vascular tissue beyond the elongating region until only a narrow band of cambium remains. Protophloem sieve tube elements may mature into metaphloem sieve tube elements of the primary phloem, or they may be abandoned and destroyed. The origin and development of proto-/metaphloem and proto-/metaxylem are described together in ► Chap. 11—Stems.

In tissues with only primary growth, the primary phloem serves for the life of that organ, and in woody eudicots, most of the phloem is functional for only a single growing season. However, several reports exist of sieve tube elements functioning for 5 or even 10 years (Evert 1990b, and references therein).

Secondary thickening occurs to some degree in most eudicotyledons and is especially notable in those with perennial (or persistent) aerial parts (i.e., woody plants). ► Chapter 15—Wood—discusses secondary thickening in detail. Secondary thickening involves the laying down of extravascular and strengthening tissue necessitated by the increased size of the plant (◘ Fig. 8.6d, e). Some of the cells of the medullary rays become active and join with the cambium of the vascular bundles to form a meristematic ring. Secondary phloem (along with xylem) tissues are then formed. The xylem tissues build up inside the cambium and force it and the phloem further from the center. Thus, a tree trunk consists mainly of xylem tissue, with a thin layer of phloem near the outside. In most temperate ecosystems, the xylem shows **annual rings**. In the spring, when the sap is rising, the xylem consists mainly of large vessels, but in autumn there is a high proportion of fibers and smaller vessels.

In cross-sectional view, spring and autumn woods are distinctively different, producing a ringed effect. Secondary phloem does not build up a thick layer because the cells do not have thickened walls and, being outside of the trunk, become crushed by the pressure of the expanding xylem tissue and must be replaced each growing season. These forces usually break down the epidermis also, and its protective function is assumed by the phellem (protective nonliving cells). That corky tissue is formed from a layer of cortex which became meristematic. The phellem is a dead tissue and cuts off food from all tissues outside of it forming dead bark (refer to ► Chap. 16—Periderm). ◘ Figure 8.7 illustrates the progress of the phloem development over the course of progressive seasonal growth stages.

8.8 Gymnosperm Phloem Is Simpler Than Angiosperm Phloem

The anatomy of gymnosperm phloem is simpler with fewer cell types than that found in angiosperms (◘ Table 8.1), with gymnosperms only having two or three (depending on how one chooses to count them) cell types. Angiosperm phloem has sieve tube elements, companion cells, phloem parenchyma, and phloem

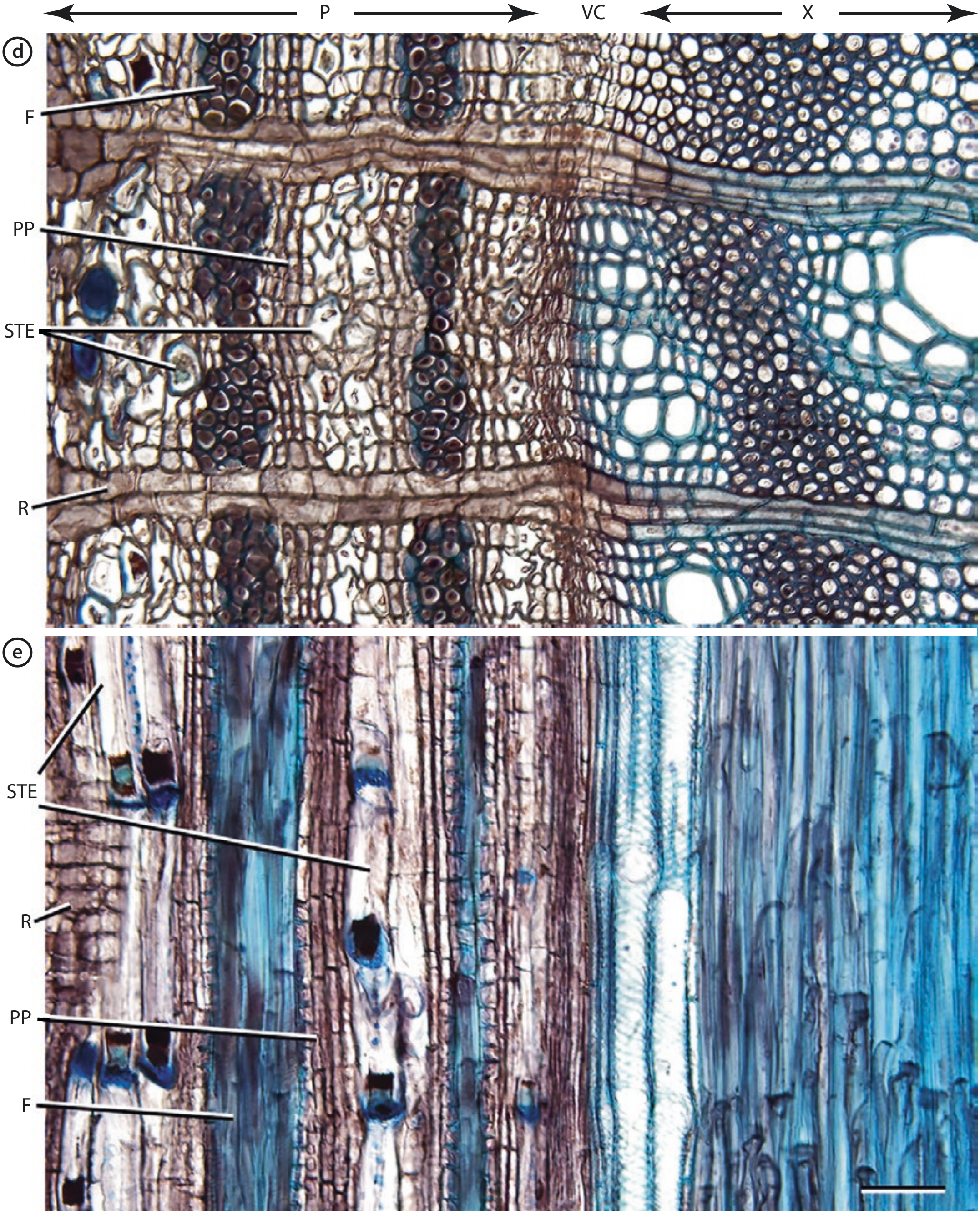
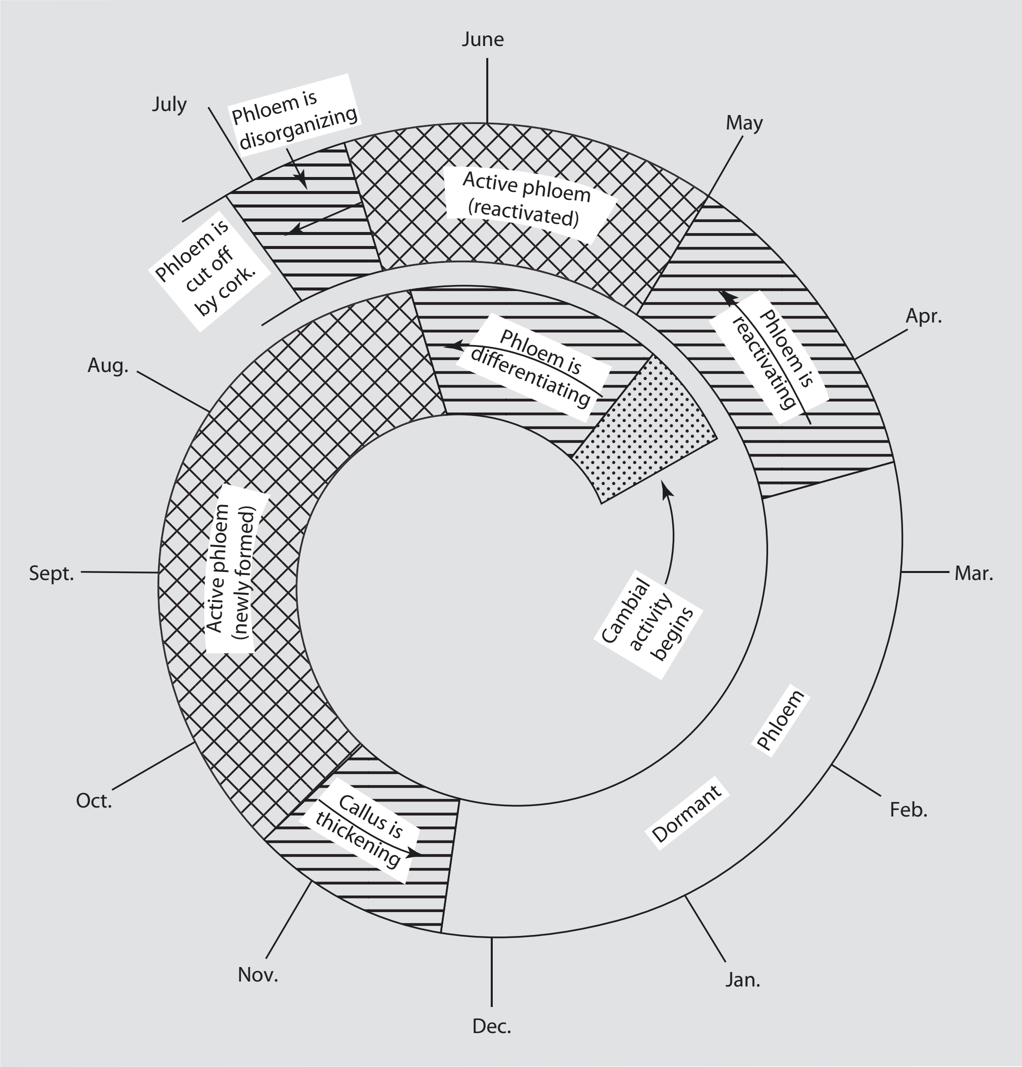


Fig. 8.6 **d**, **e** Secondary phloem in the stem of black locust (*Robinia pseudoacacia*) in **d** cross-section and **e** radial section. Phloem (P) is to the left and xylem (X) is to the right in both panels. The two images are of separate sections and are aligned to show correspondence between the two sectional views. Fibers (F), phloem parenchyma (PP), sieve tube elements (STE), and rays (R) are indicated in both panels. Scale bar in **e** = 25 μm and applies to both panels. (**d**, **e** RR Wise)

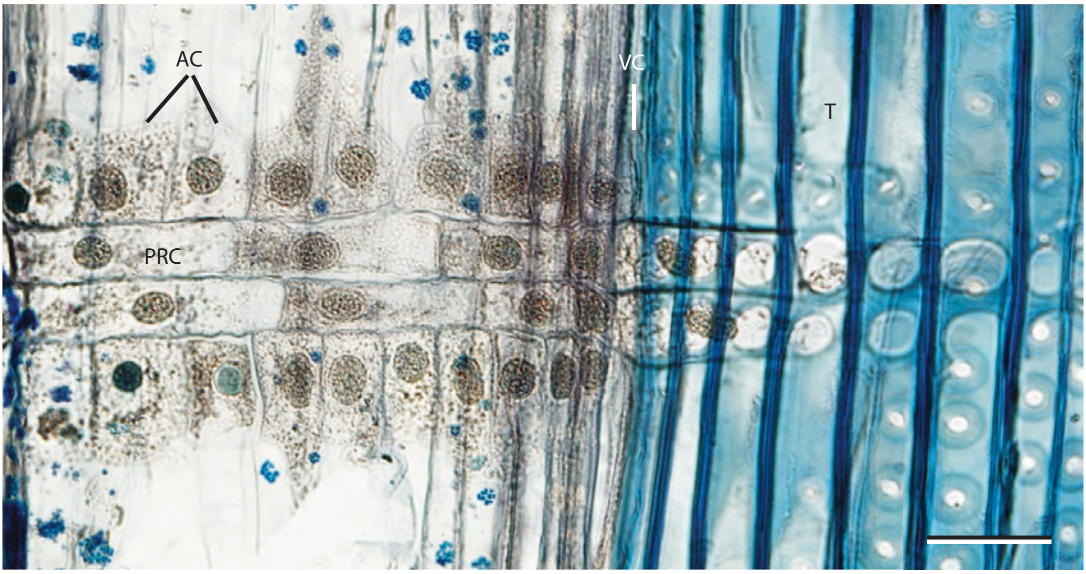


■ **Fig. 8.7** An annual cycle of phloem activity as found in seed plants from a temperate climate zone. Begin in the center with spring cambial activity and follow the spiral to a second year of growth. After that, succeeding year's growth will be similar. (Designed by Dr. L.K. Mann and redrawn from Esau (1948) Hilgardia 18:217–296)

fibers. Gymnosperms have sieve cells and phloem parenchyma. Gymnosperms lack fibers, and albuminous cells (a.k.a. Strasburger cells) (Sauter 1980) take the place of companion cells. Albuminous cells are most commonly found along phloem rays (■ Fig. 8.8).

Gymnosperm sieve cells have tapering ends, and phloem sap transport is through sieve areas in overlapping side walls. Thus, a sieve tube (the end-to-end connection of the angiosperm sieve tube elements) cannot be formed, and phloem translocation typically has a higher resistance to flow (Liesche et al. 2015). Gymnosperm sieve cells are also usually narrower and longer than angiosperm sieve tube elements.

The angiosperm companion cell is a sister cell to the sieve tube element. The two start out as a single cell, and then later in development, they divide into two, connected cells (► Sect. 8.4).



◘ Fig. 8.8 Albuminous cells (AC) line the top and bottom of a phloem ray made of procumbent ray cells (PRC). The vascular cambium (VC) separates the phloem to the left from the xylem tracheids (T) to the right. Scale bar = 50 µm. (RR Wise)

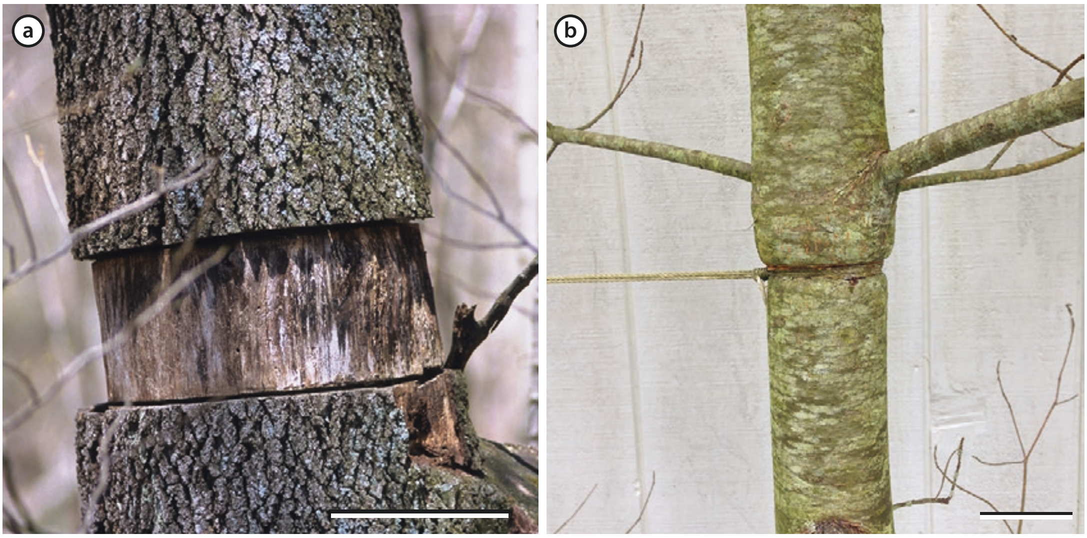
Gymnosperm albuminous cells, on the other hand, are not derived from the same mother cell as the sieve cell; they are derived from separate cells. Albuminous cells do, however, perform many of the same functions for a sieve cell as a companion cell performs for a sieve tube element—phloem loading/unloading and metabolic support.

Gymnosperm phloem parenchyma is similar in structure and function as the angiosperm analog.

The simpler nature of the gymnosperm vascular tissues, as compared to that found in angiosperms, does not mean that gymnosperms are not as successful at moving water and photosynthate throughout the plant. Indeed, the tallest trees are gymnosperms, so they must be pretty good at hydraulics. However, limits to their phloem (and xylem) versatility have restricted the ecological range and potential habitats of gymnosperms.

8.9 Girdling Inhibits Phloem Translocation and Can Kill a Tree

Girdling involves the removal of a ring of bark around the entire circumference of a stem or tree trunk (◘ Fig. 8.9a). The removal includes the cork cambium, bark, secondary phloem, and possibly portions of the secondary xylem. When this takes place around a tree trunk, the entire tree will die. Girdling can be performed on stems as well as the tree trunk and can be done below the soil surface or around the root. It may be caused by animals or insects in the process of herbivory, or by foresters to thin forests. However, horticulturists may utilize girdling in order to obtain a larger yield of cer-



■ **Fig. 8.9** **a** Girdling of this tree trunk involved removing the bark, cambium, and likely the sapwood in a ring around the trunk. This will kill the tree due to cutting off the flow of sap and nutrients. **b** If not removed, the string tied around this white pine (*Pinus strobus*) stem will eventually girdle and kill the tree. Note the swollen stem diameter above the girdle. Sugars accumulate above the girdle and cause the stem to swell. Scale bars = 10 cm in **a** and 5 cm in **b**. (**a** Image courtesy of the Wisconsin Department of Natural Resources, CC BY ND-2.0; **b** RR Wise)

tain fruits. This is commonly utilized with grapes, apple, avocado, and citrus trees. In these cases, more careful girdling is employed not to kill the plant but to remove bark from a branch in which all the carbohydrates and minerals produced by the leaves are unable to be transported down to the root system, but rather are taken up by the fruit which may become larger and sweeter than usual.

Girdling was used by Marcello Malpighi in 1686 to demonstrate that sugars moved through the phloem and water through the xylem.

In some cases, merely tying a string about a tree will eventually cause girdling as secondary growth increases the trunk diameter (■ Fig. 8.9b). Indeed, even other plants, primarily vines (English ivy, wisteria, etc.), may climb and encircle the stem and cause a disruption of the bark sufficient to girdle and kill the tree.

8.10 Chapter Review

■ Concept Review

8.1. *Phloem is a complex tissue with multiple cell types, each with a specific structure and function.* Primary phloem develops from the procambium; secondary phloem develops from the vascular cambium. Angiosperm phloem consists of sieve tube elements, companion cells, fibers, and parenchyma. Gymnosperm phloem only has sieve cells and phloem parenchyma. In almost every instance, phloem and xylem always occur together, because they are derived from the same, bifacial meristems. Phloem is to the outside, abaxial to the xylem.

8.2. *Phloem's main function is photosynthate translocation.* Photosynthate (the product of photosynthesis) is translocated via the phloem from autotrophic tissues (called "sources," typically leaves) to heterotrophic tissues (called "sinks," typically roots and developing fruit) via the sieve cells and sieve tube elements of the phloem via a mechanism described by the Münch pressure flow hypothesis. Sugars are actively loaded at the source and actively unloaded at the sink. Water follows the sugars via osmosis, which pressurizes the sieve tube and drives the system.

8.3. *Sieve tube elements are living cells responsible for translocation.* Sieve tube elements contain a living plasmalemma and minimal internal organelles. They are connected at the ends via sieve plates (simple or inclined) and at the sides via sieve areas. Both contain sieve pores. Sieve pores develop from enlarged plasmodesmata and the deposition of callose. The callose is degraded to enlarge the pore. P-protein filaments are loosely attached to the interior of the sieve tube element. They are released upon damage to the sieve tube and plug the sieve pores (forming a slime plug), thus isolating the injury.

8.4. *Companion cells support the sieve tube element and are responsible for phloem loading and unloading in angiosperms.* Companion cells (CC) develop from the same phloem mother cell as the sieve tube element (STE). Together they form the STE-CC complex. Companion cells provide metabolic support to the minimally alive STE, and they are the site of phloem loading and unloading. Loading/unloading may be symplastic (via plasmodesmata) or apoplastic (across the plasmalemma).

8.5. *Phloem parenchyma cells are involved in radial translocation, xylem/phloem coordination, and storage.* Ray parenchyma is the conduit for the movement of water and photosynthate from the stem or root interior to the living periderm at the stem or root exterior. Procumbent phloem ray parenchyma cells are elongated in the radial direction. Upright cells are elongated in the axial direction. Phloem parenchyma may store starches, tannins, oils, and water. The axial and radial xylem and phloem cells work together as a complex tissue that is integrated and interconnected by the xylem and phloem parenchyma cells.

8.6. *Phloem fibers protect the delicate sieve tubes in primary tissues.* Phloem STE, CC, and parenchyma are defined as having arisen from the vascular cambium. However, phloem fibers are defined as fibers in or near the phloem, regardless of their ontogenetic origin. Phloem fibers serve to protect and support the fragile STE-CC complexes.

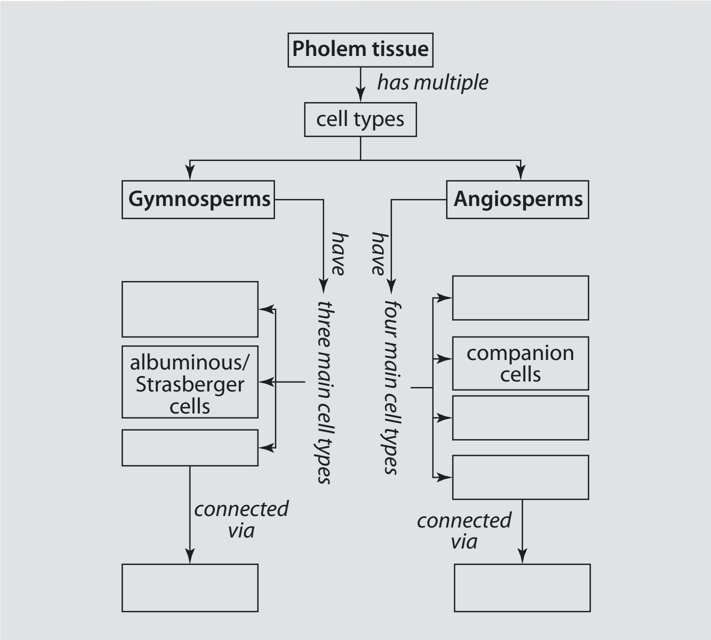
8.7. *Secondary phloem only functions for one growing season.* Secondary phloem is generated by the vascular cambium. Because the phloem lies to the exterior of the xylem, it is forced outward and crushed by the growing xylem tissue to the interior. The crushed phloem becomes incorporated into the phellem, or bark, of the stem and root.

8.8. *Gymnosperm phloem is simpler than angiosperm phloem.* Although gymnosperm phloem has fewer cell types than angiosperm phloem, all of the major phloem functions are present. However, this limitation restricts the ecological niches available to gymnosperms.

8.9. *Girdling inhibits phloem translocation and can kill a tree.* Girdling is the stripping away of all tissues from the outer bark of a tree down to the xylem, or applying a tourniquet around the stem. Because phloem is the only route for photosynthate translocation from the shoot downward, girdling will usually starve the roots and eventually kill the tree.

Concept Connections

1. Complete the concept map using the following terms: phloem fibers, phloem parenchyma (x2), sieve areas (lateral), sieve cells, sieve tube elements, and sieve plates (terminal).



Concept Assessment

2. In most angiosperms, primary phloem
   a. is organized into annual rings.
   b. replaces secondary phloem.
   c. possesses axial rays.
   d. is derived from the vascular cambium.
   e. is eventually torn apart.

3. In gymnosperms, ______________ serve the same role as the angiosperm companion cells.
   a. sieve tube elements.
   b. sieve cell.s

   c. albuminous cells.
   d. parenchyma.
   e. phloem fibers.

4. P-protein appears to function in
   a. the movement of assimilates (sugars) throughout the sieve tube.
   b. conveying information from the companion cell to the sieve element.
   c. providing a site for the accumulation of callose.
   d. plugging sieve plates upon mechanical damage.
   e. enzymatic activities.

5. Upon maturity, sieve tube elements are missing
   a. nuclei.
   b. cytoplasm.
   c. p-protein.
   d. callose.
   e. sieve pores.

6. Phloem parenchyma include
   a. companion cells.
   b. sieve tube elements.
   c. axial parenchyma.
   d. ray parenchyma.
   e. all of the above.

7. Phloem fibers are so designated based on
   a. their derivation from the procambium.
   b. their derivation from the vascular cambium.
   c. their location in or near the phloem.
   d. the organ in which they are found (leaf, stem, or root).
   e. the structure of their secondary cell walls.

8. Angiosperm phloem cell types include
   a. sieve tube elements, collenchyma cells, and fibers.
   b. companion cells, collenchyma cells, fibers, and parenchyma cells.
   c. sieve tube elements, albuminous cells, and parenchyma cells.
   d. sieve tube elements, companion cells, parenchyma cells, and fibers.
   e. sieve tube elements and parenchyma.

9. Sieve pores originate from
   a. callose deposits.
   b. plasmodesmata.
   c. microtubules.
   d. sieve plates.
   e. companion cells.

10. Secondary phloem lives an average of
    a. 1 month.
    b. 1 year.
    c. 2 years.
    d. variable, depending on rainfall.
    e. one growing season.

11. The main function of phloem is to
    a. translocate photosynthate.
    b. provide water for transpiration.
    c. store carbohydrates for use during the winter.
    d. store water for use during arid periods.
    e. provide a means to transport carbohydrates from roots to leaves.

- **Concept Applications**

12. List the cell types in angiosperm secondary phloem and give the function of each. Compare the structure and function of angiosperm cell types to those found in gymnosperms.

13. Explain the basics of the Münch pressure flow hypothesis. Include in your answer the difference between symplastic loading and apoplastic loading.

References and Additional Readings

Crang RFE, Vassilyev A (2003) Electronic plant anatomy. McGraw-Hill, New York

Cui J, Zhao J, Xu H, Wang L, Jin B (2016) Cytological and miRNA expression changes during the vascular cambial transition from the dormant stage to the active stage in *Ginkgo biloba* L. Trees 30:2177–2188

Cutler DF, Botha T, Stevenson D (2008) Plant anatomy: an applied approach. Blackwell Publishing, Malden

Dickinson WC (2000) Integrative plant anatomy. Hardcourt, Inc., Orlando

Esau K (1948) Phloem structure in the grapevine, and its seasonal changes. Hilgardia 18:217–296

Esau K (1953) Plant Anatomy. Wiley, New York

Esau K (1977) Anatomy of seed plants. Wiley, New York

Evert RF (1990a) Seedless vascular plants. In: Behnke H-D, Sjolund RD (eds) Sieve elements: comparative structure, induction and development. Springer-Verlag, Berlin, pp 35–62

Evert RF (1990b) Dicotyledons. In: Behnke H-D, Sjolund RD (eds) Sieve elements: comparative structure, induction and development. Springer-Verlag, Berlin, pp 103–137

Evert RF (2006) Esau's plant anatomy: meristems, cells and tissues of the plant body - their structure, function and development, 3rd edn. Wiley, Hoboken

Fahn A (1990) Plant Anatomy, 4th edn. Pergamon Press, New York

Foyer CH, Verrall SR, Hancock RD (2015) Systematic analysis of phloem-feeding insect-induced transcriptional reprogramming in *Arabidopsis* highlights common features and reveals distinct responses to specialist and generalist insects. J Exptl Bot 66:495–512

Hipper C, Brault V, Ziegler-Graff V, Revers F (2013) Viral and cellular factors involved in phloem transport of plant viruses. Front Plant Sci 4:154. https://doi.org/10.3389/fpls.2013.00154

Ledbetter MC, Porter KR (1970) Introduction to the fine structure of plant cells. Springer-Verlag, Berlin

Liesche J, Windt C, Bohr T, Schulz A, Jensen KH (2015) Slower phloem transport in gymnosperm trees can be attributed to higher sieve element resistance. Tree Physiol 35:376–386

Mauseth JD (1988) Plant Anatomy. Benjamin/Cummings, Menlo Park

Metcalfe CR, Chalk L (1979) Anatomy of the Dicotyledons: Vol 1, systematic anatomy of the leaf and stem, 2nd edn. Oxford Univ Press, New York

Metcalfe CR, Chalk L (1983) Anatomy of the Dicotyledons: Vol 2, wood structure and conclusion of the general introduction, 2nd edn. Oxford University Press, New York

Otero S, Helariutta Y (2017) Companion cells: a diamond in the rough. J Exptl Bot 68:71–78

Pace MR, Alcantata S, Lohmann LG, Angyalossy V (2015) Secondary phloem diversity and evolution in Bignonieae (Bignoniaceae). Ann Bot 116:333–358

Pfautsch S, Renard J, Tjoelker MG, Salih A (2015) Phloem as capacitor: radial transfer of water into xylem of tree stems occurs *via* symplastic transport in ray parenchyma. Plant Physiol 167:963–971

Rahman MH, Begum S, Nakaba S, Yamagishi Y, Kudo K, Nabeshima E, Nugroho WD, Oribe Y, Funada R (2016) Relationship between the earlywood-to-latewood transition and changes in levels of stored starch around the cambium in locally heated stems of the evergreen conifer *Chamaecyparis pisifera*. Trees-Struc Func 30:1619–1631

Sauter JJ (1980) The Strasburger cells - equivalents of companion cells. Plant Biol 93:29–42

Solereder H (1908a) Systematic anatomy of the Dicotyledons: a handbook for laboratories of pure and applied botany, vol 1. Clarendon Press, Oxford

Solereder H (1908b) Systematic anatomy of the Dicotyledons: a handbook for laboratories of pure and applied botany. Vol. 2, Monochlamydea, addenda, and concluding remarks. Clarendon Press, Oxford

Spicer R (2014) Symplasmic networks in secondary vascular tissues: parenchyma distribution and activity supporting long-distance transport. J Exp Bot 65:1829–1848