THE PHLOEM

The phloem, although correctly called the principal food-conducting tissue of vascular plants, plays a much greater role than that in the life of the plant. A wide range of substances are transported in the phloem. Among those substances are sugars, amino acids, micronutrients, lipids, hormones, the floral stimulus (florigen), and numerous proteins and RNAs, some of which, in addition to the hormones, floral stimulus, and sucrose serve as informational or signaling molecules As a rule, the phloem is spatially associated with the xylem in the vascular system and, like the xylem, may be classified as primary or secondary on the basis of its time of appearance.

The **primary phloem** is initiated in the embryo or young seedling, which originates **from the procambium**, is constantly added to during the development of the primary plant body, and completes its differentiation when the primary plant body is fully formed. The **secondary phloem** originates from the **vascular cambium** and reflects the organization of this meristem in its possession of axial and radial systems. The phloem rays are continuous through the cambium with those of the xylem, providing a pathway for radial transport of substances between the two vascular tissues.

CELL TYPES OF THE PHLOEM

Primary and secondary phloem tissues contain the same categories of cells. The primary phloem, however, is not organized into two systems, the axial and the radial; it has no rays.

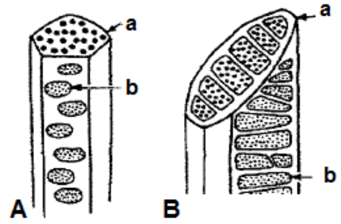
■ Cell Types of the Secondary Phloem ■

Cell Types	Principal Functions
Axial system	
Sieve elements	
Sieve cells (in gymnosperms); Sieve-tube elements, with companion cells (in angiosperms)	Long-distance conduction of food materials; long-distance signaling
Sclerenchyma cells	
Fibers; Sclereids	Support; sometimes storage of food materials
Parenchyma cells	Storage and radial translocation of food substances
Radial (ray) system	
Parenchyma	Storage and radial translocation of food substances

The basic components of the phloem are the sieve elements and various kinds of parenchyma cells. Fibers and sclereids are common phloem components. Laticifers, resin ducts, and various idioblasts, specialized morphologically and physiologically, may also be present in the phloem. The principal conducting cells of the phloem are the **sieve elements**, so called because of the presence in their walls of areas (sieve areas) penetrated by pores. Among seed plants the sieve elements may be segregated into the less specialized **sieve cells** (Fig. 13.4A) and the more specialized **sieve-tube elements**, or sieve-tube members (Fig. 13.4B–H). The term sieve tube designates a longitudinal series of sieve-tube elements, just as the term vessel denotes a longitudinal series of vessel elements.

SIEVE TUBE ELEMENTS

Sieve tube elements are slightly elongate cells whose walls bear differentiated regions occupied by numerous narrow sieve pores filled with protoplasmic connecting strands that link them to adjacent sieve elements. *[Young sieve elements contain all of the cellular components characteristic of young plant cells but at maturity the sieve element protoplast retains a plasma membrane, endoplasmic reticulum, plastids, and mitochondria, all of which occupy a parietal position (along the wall) within the cell.]* Each of the

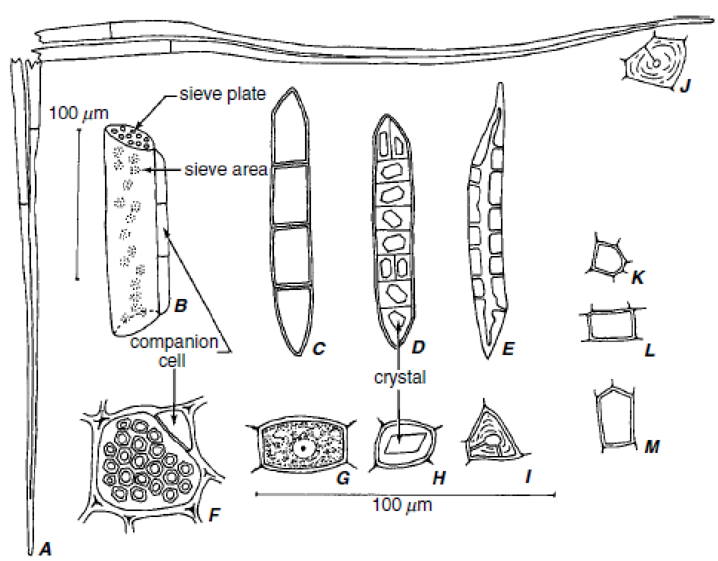


Parts of sieve elements. (A) Sieve tube element with simple transverse sieve plate (a) and lateral **sieve areas** (b). (B) Sieve tube element with compound **inclined sieve** plate (a) and lateral **sieve areas** (b).

numerous recessed areas on the wall containing grouped sieve pores is called a **sieve area**. In sieve cells the wall pores are the same diameter (usually less than 1 µm) on both end walls and lateral walls. The specialized end wall of a sieve tube element is termed a **sieve plate** and is composed of one or more sieve areas with large pores. These are often wider than 5 µm. Through enlarged pores in the opposing walls of sieve plates, the protoplasts of two contiguous and functional sieve elements are interconnected by means of continuous cytoplasmic bridges that resemble enlarged plasmodesmata. Each plasmodesmatally derived interconnecting strand is usually seen to be encased in callose, a carbohydrate (β-l,3-glucan). Another unique feature of the sieve tube elements of dicotyledons and some monocotyledons is the presence of proteinaceous substances of as yet unknown function called phloem protein bodies (P-protein).

COMPANION CELLS

Sieve-tube elements of flowering plants are characteristically associated with (present laterally) densely cytoplasmic nucleated specialized parenchyma cells called **companion cells**. Typically, companion cells are derived from the same mother cell as their associated sieve-tube elements by unequal cell division, so that the two kinds of cells are closely related ontogenetically.



Cell types in the secondary phloem of a eudicot, *Robinia pseudoacacia*. **A–E**, longitudinal views; **F–J**, transverse sections. **A**, **J**, fi ber. **B**, sieve-tube element and companion cells. **F**, sieve-tube element in plane of sieve plate and companion cell. **C**, **G**, phloem parenchyma cells (parenchyma strand in **C**). **D**, **H**, crystal containing parenchyma cells. **E**, **I**, sclereids. **K–M**, ray cells in tangential (**K**), radial (**L**), and transverse (**M**) sections of phloem.

STRASBURGER CELLS

The counterpart of the companion cell in gymnosperm phloem is the **Strasburger cell**, named after Eduard Strasburger who gave it the name "Eiweisszellen," or ***albuminous cell***. The principal feature distinguishing the Strasburger cell from other parenchymatous elements of the phloem is its symplastic connections with the sieve cells. These connections are reminiscent of the connections between sieve-tube elements and companion cells: pores on the sieve-cell side and branched plasmodesmata on the Strasburger-cell side.