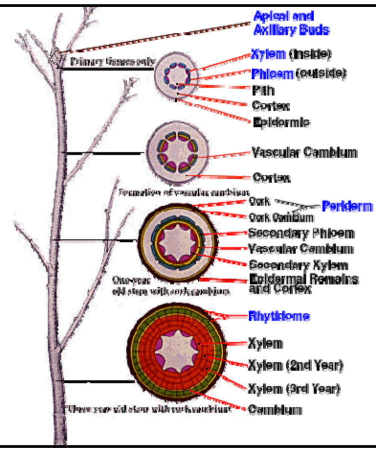
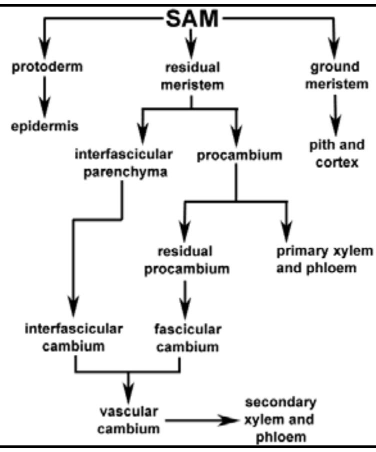
Lecture 19

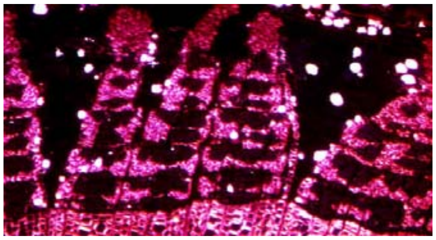
Secondary phloem (cont'd)





Secondary Phloem in *Tilia americana*
(American Basswood)

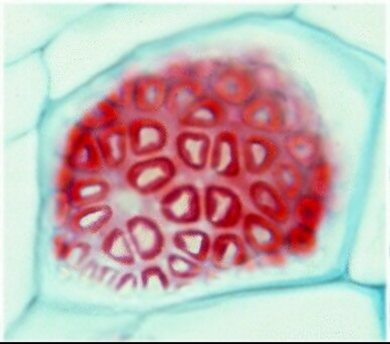
- **Secondary Phloem of *Tilia* Stained with Toluidine Blue & viewed with Crossed Polarizers.**



Secondary Phloem

- Secondary Phloem is produced by the Vascular Cambium and can form a continuous cylinder of tissue opposite secondary xylem in woody plants.
- It is a complex tissue which contains Sieve Elements.
  - **Sieve Cells (SC)** are characteristic for Gymnosperms,
  - while Angiosperms produce **Sieve Tube Members (STM)**. The latter form Sieve Tubes when joined end to end.
    - Sieve Tube Members have Sieve Plates on their end walls. These contain large Sieve Pores.
    - Sieve Pores are also present on the lateral walls of Sieve Tube Members.
  - **Sieve Cells** do not have Sieve Plates but only have Sieve Pores. These may be more concentrated where they overlap with other Sieve Cells but they do not have Sieve Plates.
  - **Sieve Cells** are generally longer than STM and are generally smaller in diameter.

A Sieve Plate with large Sieve Pores



Companion vs. Albuminous Cells

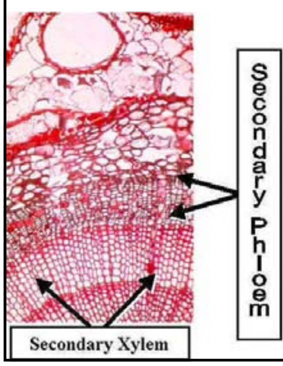
- **Companion Cells** are derived from the same cell which forms a **Sieve Tube Member**. They control the physiological processes involved in phloem transport.
- **Albuminous Cells** perform a similar function for **Sieve Cells**. However, they are not a direct descendent of the cell which produces the Sieve Cell.
- **Companion Cells** and **Albuminous Cells** resemble Parenchyma cells. Furthermore, Parenchyma cells are also present in Secondary Phloem. Consequently, it is sometimes difficult to distinguish Companion Cells and Albuminous Cells from Phloem Parenchyma.

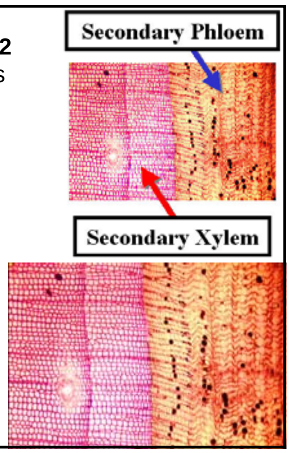
Secondary Phloem may contain Fibers

- Fibers may occur as individual cells scattered in the Phloem,
- or they may occur in clusters or layers.
- Function: Fibers help to strengthen the Phloem and can protect its thin-walled cells from the pressure which develops from secondary growth.

Secondary Phloem - 2

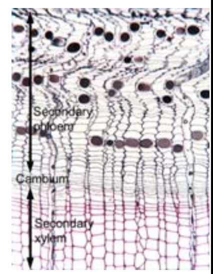
Gymnosperms - Pinus



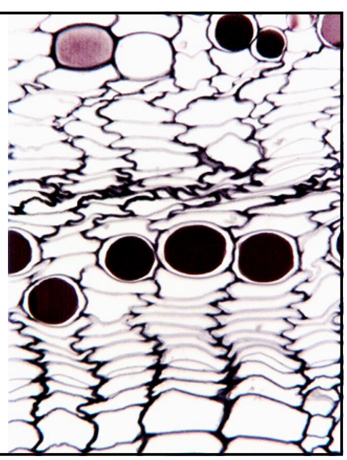


Transverse section of pine (Pinus).

- Bottom - Wood (secondary xylem)
- Center - the cambial zone
- Above - the secondary phloem
- Fusiform initials that produce rows of tracheids in the secondary xylem also produce sieve cells in the secondary phloem (the cambium is bidirectional)
- Ray initials produce rays in phloem as well as xylem. The cells with darkly stained contents in the phloem are tannin cells.
- **Although sieve cells are abundant here, they are virtually impossible to identify in transverse section** – the sieve areas cannot be seen in this micrograph.
- Albuminous cells occur in the rays; they are not sister cells to the sieve cells and are not even produced by the fusiform initials.
- Much of the outer part of the phloem rows are undulate: as the sieve cells stop functioning and collapse, axial tissue contracts into this irregular pattern. Because most ray cells do not collapse, rays retain their size and consequently are forced into folds by the collapsing sieve cells.

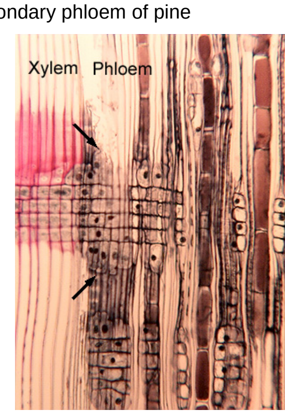


High magnification of transverse section of secondary phloem in pine



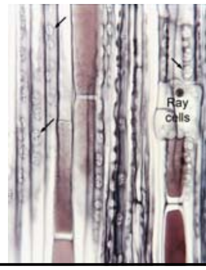
Radial section of secondary phloem of pine

- Left – xylem
- Right – phloem
- Between - the two labels is the vascular cambium.
- **Examine the ray between the two arrows.** In the vascular cambium at this point is a set of ray initials that has produced the xylem ray as well as the phloem ray.



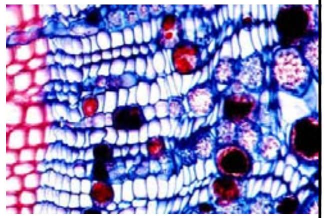
Radial section of pine bark

- **Simple nature of secondary phloem in conifers**.
- The tall cells with dark contents are tannin cells, all the other tall cells are sieve cells (the arrows indicate a few sieve areas, which are shown in higher magnification in the small micrograph).
- Each white dot in the sieve areas is an individual sieve pore.
- Pine wood is similarly simple, having just tracheids and a few resin canals.



Cross-Section of Secondary Xylem & Phloem of *Pinus*

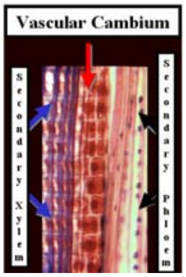
- **The Secondary Phloem in *Pinus* lacks fibers and is composed of Sieve Cells, Albuminous Cells & Parenchyma. The Parenchyma cells have dark contents. Otherwise it is impossible to discern the other cell types.**
- **Secondary Phloem in *Pinus*. The Phloem Parenchyma contain Druse Crystals and darkly stained deposits. It is hard to distinguish other cell types in Cross-section.**



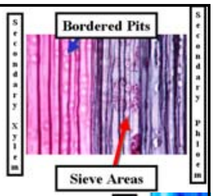
Note the collapsed Secondary Phloem on the far right side of the image

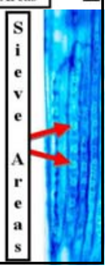
Secondary Phloem in *Pinus*

Longitudinal section of *Pinus* at the interface of secondary Xylem (Blue) and Secondary Phloem.

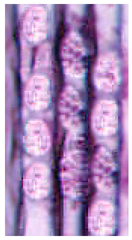


The Vascular Cambium can be seen between the two Vascular Tissues





- **It is easy to distinguish Secondary Phloem and Xylem in a longitudinal section. The Xylem has stained positively for Lignin (Red). The Phloem has stained Blue. The freckled areas along the radial walls of the Sieve Cells contain Sieve Pores. Sieve Areas contain numerous Sieve Pores in small, discrete areas. Note the elongated shape of the Sieve Cells.**



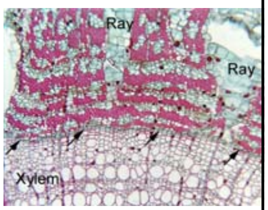
Sieve Areas

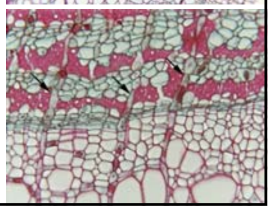
Transverse section of bark of ash (Fraxinus).

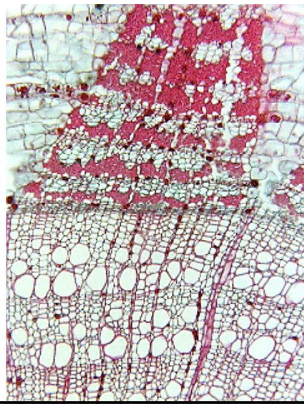
- Secondary phloem of ash also has alternating bands of conducting cells (lightly stained here) and fibers (darkly stained).
- The arrows on the left indicate some of the many narrow rays; notice that one ray is greatly enlarged (upper arrow).
- Also, the axial bands of sieve tube members and fibers are distorted near the top of the micrograph: cell division and enlargement of at least some of the parenchyma cells has pushed the axial masses apart.

Transverse section of linden (Tilia).

- General orientation, with secondary xylem at the bottom, phloem at the top, and the vascular cambium running horizontally across the center (indicated by arrows).
- **This secondary phloem is more complex than that of pine.**
- The bands that are stained dark red consist of secondary phloem fibers, seen more clearly in the high power view. Alternating with the bands of fibers are bands consisting predominantly of sieve tube members and companion cells. It is tempting to assume that these phloem bands correspond to the annual rings in xylem, but typically they are not annual: several sets can be produced per year.
- **Two rays are visible in the phloem,** and are a bit unusual in being narrower near the cambium (where they are young) and wider away from the cambium (where they are older; remember that phloem is pushed outward by formation of new phloem interior to pre-existing phloem). The width of the rays results because ray cells themselves divide (a process called dilatation and illustrated in micrographs below).

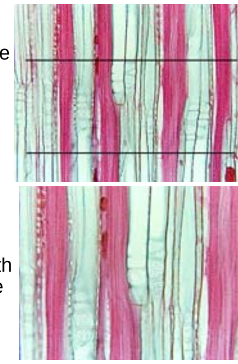


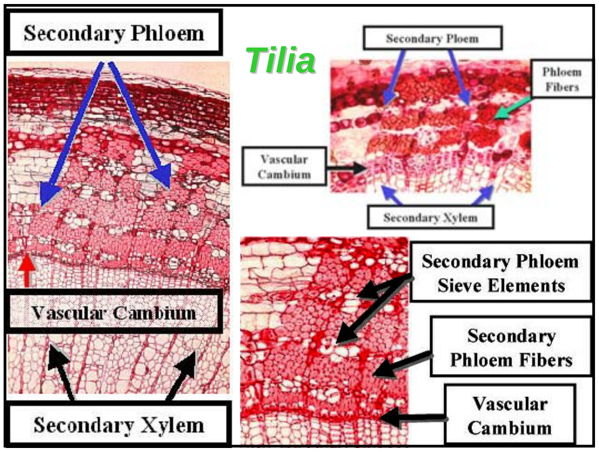


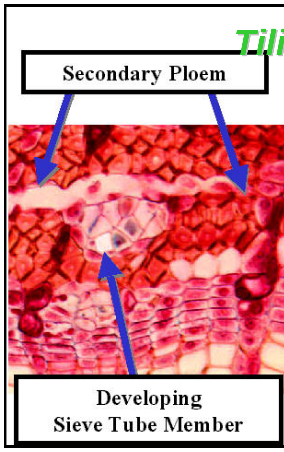


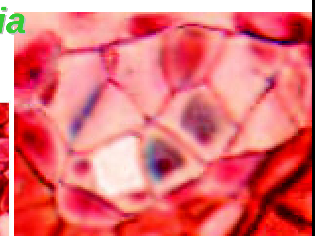
Radial longitudinal section of linden (Tilia).

- Notice that all the sieve plates visible here are located at about the same level, between the two lines. Just as a radial section of wood shows vessel element perforation plates aligned, a radial section of secondary phloem shows aligned sieve plates for the same reason – these sieve tube members were produced by one set of fusiform initials, and the ends of the sieve tube members here are aligned with the ends of the initials that produce them.









- **Mitotic Cells from the adjacent Photo which shows the early differentiation of a Sieve Tube Member and associated cells.**

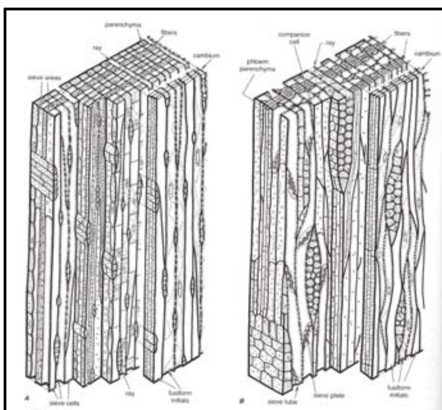


FIGURE 14.1

Block diagrams of secondary phloem and vascular cambium of A. *Thuja occidentalis* (white cedar), a conifer, and of B. *Liriodendron tulipifera* (tulip tree), a hardwood. (Courtesy of I. W. Bailey; drawn by Mrs. J. P. Rogerson under the supervision of L. G. Livingston. Redrawn.)

Secondary Phloem – Conifers vs Angiosperms

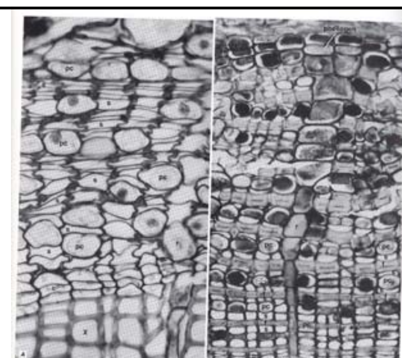


FIGURE 14.5

Transverse sections of secondary phloem. A, from a twig of *Ginkgo biloba*. Sieve cells (s) and axial parenchyma cells (pc) in layers. Sieve cells partly collapsed, particularly in older phloem. Parenchyma cells turgid. In older stems the layers, or bands, of sieve cells and axial parenchyma are more obvious than here. B, from stem of *Taxodium distichum*. Cells alternate radially in sequence of fiber (f), sieve cell (s), parenchyma cell (pc), sieve cell (s), fiber (f), and so on. In nonconducting phloem (above) sieve cells are crushed by enlarged parenchyma cells. Other details: c, cambium; r, ray; x, xylem. (A, ×600; B, ×400. From Esau, 1969 www.schweizerbart.de)

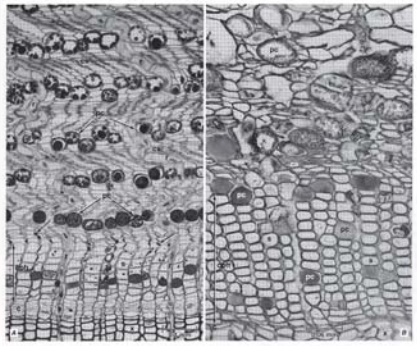


FIGURE 14.3

Transverse sections of secondary phloem of *Pinus*. Conducting phloem (cph) much smaller in amount than the nonconducting phloem (only partly shown in these figures), in which all sieve cells are crushed (cs) and only axial parenchyma cells (pc) and ray parenchyma cells (r) are intact. In **A** (*Pinus strobus*), the axial parenchyma cells are arranged in tangential bands and separate early phloem from late phloem in each increment. Portions of 7 growth increments can be seen here. In **B** (*Pinus* sp.), the axial parenchyma cells are scattered. Other details: c, cambium; s, sieve cell; x, xylem; in **A**, unlabeled arrows point to definitive callose. (**A**, from Esau, 1977; **B**, from Esau, 1969. www.schweizerbart.de)

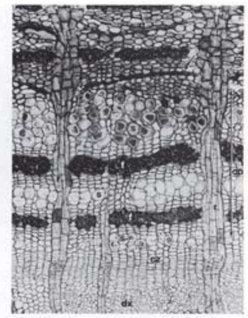


FIGURE 14.12

Transverse section of secondary phloem of black locust (*Robinia pseudoacacia*) showing mostly conducting phloem (cp). Cambial activity has resulted thus far in the production of three new bands of sieve tubes (s) and two of fibers (f). Sieve tubes of the nonconducting phloem (indicated by arrows) have collapsed. Other details: cz, cambial zone; dx, differentiating xylem; r, ray. (×150.)

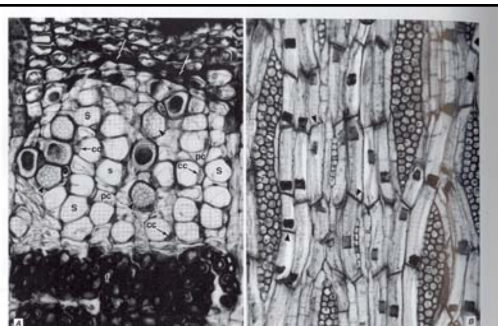


FIGURE 14.8

Secondary phloem of black locust (*Robinia pseudoacacia*). **A**, transverse section showing part of a band of functional sieve tubes. Many of the sieve-tube elements (s) have been sectioned near the plane of their end walls, revealing their simple sieve plates (darts). The sieve-tube elements of the previous year's phloem increment (above) have been crushed and obliterated (arrows); below is a band of fibers (f). **B**, tangential section, revealing the storied nature of the phloem. Darts point to the sieve plates. The dark bodies in the sieve-tube elements are nondispersive P-protein bodies. Other details: cc, companion cell; pc, parenchyma cell; r, ray. (A, ×370; B, ×180. **A**, from Evert, 1990b, Fig. 6.1. © 1990, Springer-Verlag; **B**, courtesy William F. Derr.)

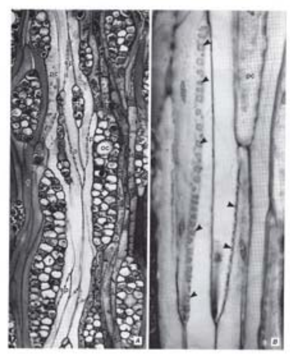


FIGURE 14.7

Tangential sections of nonstoried secondary phloem of *Liriodendron tulipifera* (**A**) and *Austrobaileya scandens* (**B**), both of which have sieve-tube elements with compound sieve plates (sp) on inclined end walls. Several sieve plates can be seen in **A**, a single sieve plate in **B**. The greatly inclined sieve plates of *Austrobaileya* have numerous sieve areas (darts). Other details: f, fiber; pc, axial parenchyma cell; oc, oil cell in ray; r, ray. (A, ×100; B, ×413. **B**, Plate 5D from Esau, 1979. *Anatomy of the Dicotyledons*, 2nd ed., vol. I, C. R. Metcalfe and L. Chalk, eds., by permission of Oxford University Press.)

FIGURE 14.2

Transverse section of the bark from an 18-year-old stem of *Liriodendron tulipifera*. Except for the cortex (co) and remnants of primary phloem, as evidenced by the presence of primary phloem fibers (f), this bark—all tissues outside the vascular cambium—consists almost entirely of secondary phloem; the original periderm is still present outside the cortex. Only a very narrow portion (0.1 mm wide) of the phloem next to the cambium (c) contains mature, living sieve tubes, that is, is conducting phloem (cph); the rest of the phloem is nonconducting. Some rays (r) are dilated. Other detail: x, xylem. (×37. Reproduced by permission University of California Press: Cheadle and Esau, 1964. *Univ. Calif. Publ. Bot.* © 1964, The Regents of the University of California.)

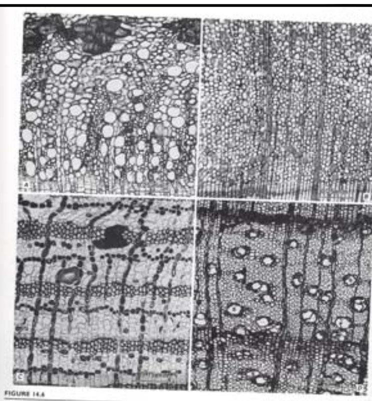


FIGURE 14.4

Secondary phloem of woody angiosperms in transverse sections. **A**, *Drimys winteri*, which lacks fibers. The large cells are secretory cells. **B**, *Carpinus*, fibers (f) scattered single. **C**, *Castanea*, fibers (f) in parallel tangential bands. **D**, *Carya*, fibers (f) surround groups of sieve elements (s) and parenchymatous cells.