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Xylem

7

Introduction

Land plants have two primary conducting systems, designated as xylem and phloem. Xylem is a conductor of water and dissolved substances mostly from the soil through the roots, stems, and leaves. Phloem transports the sugars made by photosynthesis from green tissues where they are manufactured to other parts of the plant, as well as moving a variety of growth regulators. Fossil studies have indicated that water-conducting cells, termed tracheary elements, evolved first in primitive root systems of early land plants, providing both transport of water and support. Subsequent evolutionary development of tracheary elements occurred throughout progressively higher stem and leaf structures. In a similar fashion, phloem elements have developed along with vascular cambium in land plants. Phloem will be covered in ► Chap. 8, and the vascular cambium, which gives rise to both xylem and phloem, is discussed in ► Chap. 14.

7.1   Xylem Is a Complex Tissue Containing Multiple Cell Types, Each with a Specific Structure and Function

Xylem is responsible for the transpiration of water from the soil to the leaves (ascending transport, refer to ► Sect. 7.2), while phloem translocates the products of photosynthesis from leaves to the rest of the plant (ascending and descending transport, refer to ► Sect. 8.2). Both xylem and phloem are complex tissues containing multiple cell types, and being the main highway for transport throughout the plant, they play multiple roles in whole-plant transport, communication, and coordination. The structure and function of xylem will be considered in this chapter. Phloem is discussed in ► Chap. 8.

The evolution of vasculature was a major and necessary advancement for the colonization of land by plants. Indeed, lacking vasculature, bryophytes are limited to short stature and moist environments. As noted above, xylem is a tissue with multiple types of cells. The cell types will be briefly introduced in ► Box 7.1 and ◙ Fig. 7.1a, b and then treated in more detail in ► Sects. 7.3–7.8. It is common in many botany texts to distinguish only two types of tracheary elements—tracheids and vessel elements—and then proceed to state that gymnosperms have tracheids, whereas angiosperms have tracheids and vessel elements. To be more precise, the sclerified xylem cells (which excludes xylem parenchyma, which have primary cell walls) can be divided into two groups—**imperforate** (refer to ► Sect. 7.3) and **perforate** (refer to ► Sect. 7.5). The angiosperm tracheid, fiber tracheid, and libriform fiber are all imperforate xylem cells, meaning they lack perforations in the side walls and end walls. Perforate cells possess perforation plates at both ends of the cell and, in some instances, on the side wall (refer to ► Sect. 7.5). The angiosperm vessel element is the only perforate cell type, although there is considerable variation in length, width, side wall (refer to ► Sect. 7.6), and end-wall (refer to ► Sect. 7.7) design. The distinction between imperforate and perforate sclerified xylem cells is very useful for plant anatomists and is supported by numerous

Box 7.1   Xylem Cell Types

Gymnosperm
1. Tracheid: function in conduction of water and minerals, densely covered with circular bordered pits, lack a perforation plate (therefore, imperforate)
2. Parenchyma: alive at maturity, function in storage/synthesis/cavitation recovery

Angiosperm
1. Imperforate tracheary elements: long, narrow, tapered at ends, lack a perforation plate
    1. Tracheid: function in conduction of water and minerals, densely covered with circular bordered pits, usually found adjacent to vessels.
    2. Fiber-tracheid: function in support, largely non-conductive, fewer and smaller bordered pits than found in tracheids
    3. Libriform fiber: function in support, largely nonconductive, may be alive at maturity, containing a few simple pits, pits often slit-shaped
2. Perforate tracheary elements: possess a perforation plate, short, wide, connected end-to-end to form a vessel
    1. Vessel elements: function in conduction of water and minerals, large diversity in size and shape, side walls thickenings may be annular, helical, reticulate or pitted, perforation plates may be simple or compound
3. Parenchyma: storage/synthesis/cavitation recovery
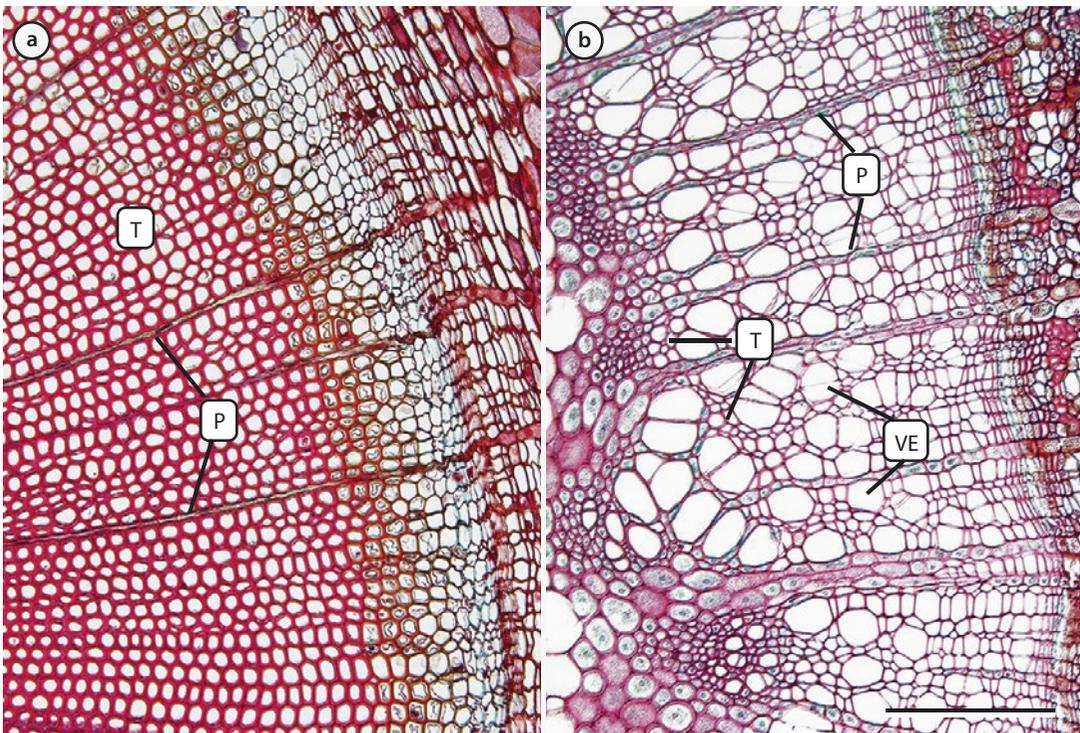
◲ **Fig. 7.1**   Representative cell types in cross sections of young stems of **a** Canadian yew (*Taxus canadensis*, a gymnosperm) xylem has parenchyma (P) in the xylem rays against a field of axial tracheids (T, imperforate tracheary elements). **b** Tulip tree (*Liriodendron tulipifera*, a woody eudicot) has ray parenchyma and tracheids intermixed with the much larger axial vessel elements (VE, perforate tracheary elements). Both of the images are from one-year-old stems. Scale bar in **b** = 100 μm and applies to both panels. (**a**, **b** RR Wise)

anatomical, physiological, and evolutionary studies. Finally, parenchyma cells are found in the xylem of both gymnosperms and angiosperms (refer to ▶ Sect. 7.8). They function in storage, synthesis, and recovery from cavitation (the deleterious formation of gas bubbles in the transpiration stream).

7.2   The Primary Functions of Xylem Are Water Conduction, Mineral Transport, and Support

Transpiration is the movement of water from the soil, through the xylem tracheary elements (vessel elements and/or tracheids), and finally to the atmosphere through the stomata. Like every process that involves movement, there has to be an energy source to drive transpiration; transport moves from an area of high energy to an area of less energy. In the case of transpiration, the driving force is the difference in the free energy of the water at the beginning of the transpirational stream (the H_2O in the soil) and the energy of the water at the end of the stream (the H_2O in the air). With very few exceptions, air water has significantly less energy than soil water, although either can vary tremendously depending on rainfall, soil type, relative humidity, and climate. The energy differential between the water in the soil and the water in the air is sufficient to draw water to the top of a 100 meter tree. Minerals dissolved in the soil water are passively carried with the transpiration stream. They likewise enter the root and are pulled upward with the cohesive transpirational water.

The movement of water is described by the **cohesion-adhesion-tension model**. Water is very polar; it sticks to itself (cohesion) and any other molecule with a polar group (adhesion). Water is drawn through the xylem by its evaporation at the stomatal pore (stomata are discussed in ▶ Sect. 9.2). The water lost to the atmosphere is replaced, in turn, by water from the leaf mesophyll cells, the leaf xylem, the stem xylem, the root xylem, and ultimately, the soil water (◘ Fig. 7.2a). Being pulled by the atmosphere, transpirational water is always under tension [in contrast, phloem sap is under pressure and is pushed through the sieve tube (▶ Sect. 8.2)]. At night, when stomata close and water is no longer evaporating to the atmosphere, the water is held in the plant by adhesive and cohesive forces and does not run back down to the roots.

The constant tension applied to the water in the transpiration stream has a direct impact on xylem functioning and architecture. If the water column is pulled too hard because the air (large driving force) or the soil (limited supply) are too dry, the water column will break, or **cavitate**, and produce a bubble of gas in the form of water vapor that blocks any further transpiration in that vessel element or tracheid (Tyree and Sperry 1989). Recovery from cavitation is possible with the adjacent living xylem parenchyma cells providing the water needed to refill the tracheary element (Brodersen et al. 2010).

The relationship between tracheary element diameter and water conductance is illustrated in ◘ Fig. 7.2b. Water is a highly polar molecule with an asymmetric distribution of positive and negative charges. As such, it will stick to itself (cohere) and stick to other
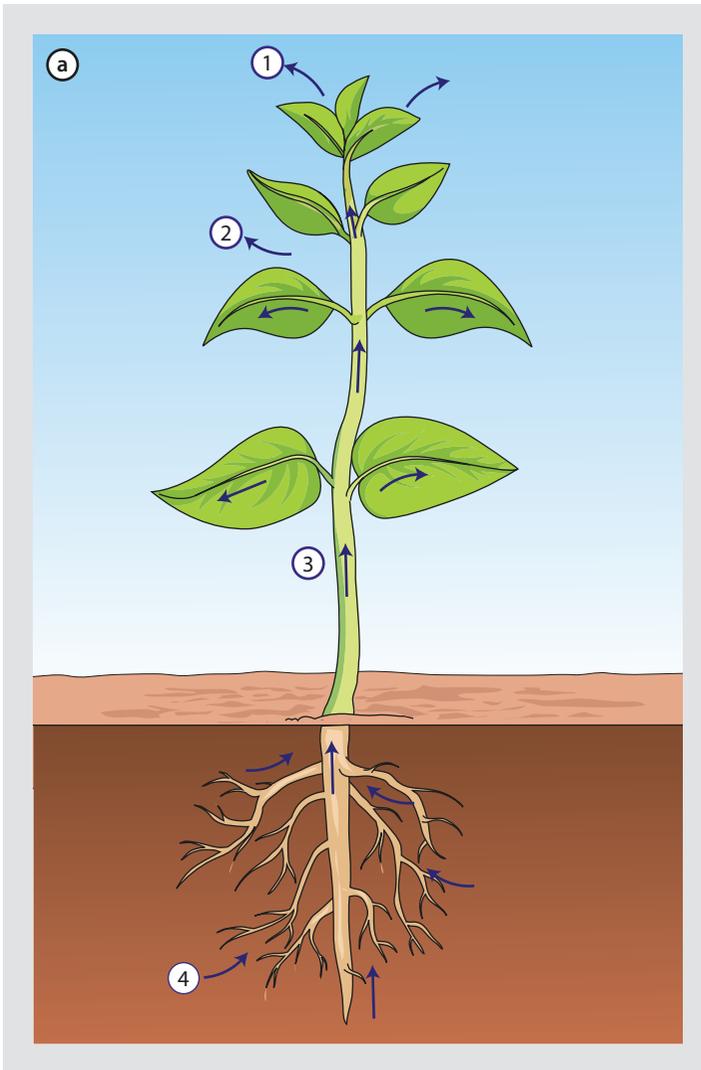
◘ Fig. 7.2 **a** A schematic drawing of the path of transpirational water from the soil to the atmosphere. (**1**) The process starts with the evaporation of water from stomata on the leaf epidermis. (**2**) That water is replaced by water in the leaf, which is supplied by xylem of the leaf vasculature. (**3**) That creates a tension in the water column and draws water through the stem and (**4**) ultimately from the soil. (Redrawn from Crang and Vassilyev 2003)
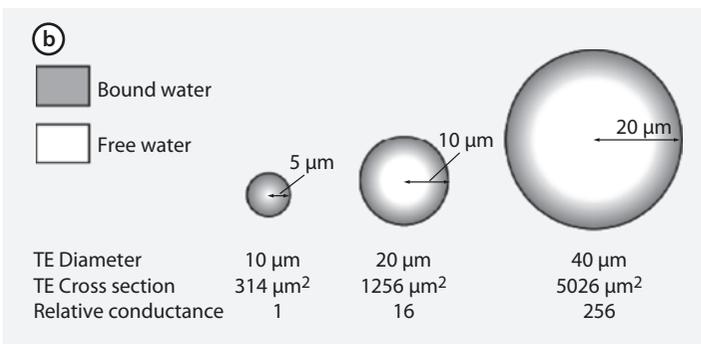
◘ Fig. 7.2 **b** The relationship between tracheary element (TE) diameter and relative water conductance. (Redrawn from Mauseth (1988), with permission)

polar molecules or groups (adhere). The cellulosic plant cell wall has numerous polar groups with which water can adhere; therefore, the water in a tracheary element closest to the cell wall is adhered to the cell wall. This is called bound water. The water that is one H_2O molecule away is cohered to the water bound to the wall; other water molecules are cohered to those and so on with progressive distance from the cell wall. The energy of the water-to-wall adhesion is higher than that of water-to-water cohesion. Therefore, as the distance from the cell wall increases, the water becomes less bound and freer. As the conducting cell diameter increases arithmetically, the cell cross-sectional area and the conductance to water flow increase geometrically.

It can be seen that a larger tracheary element (either tracheid or vessel element) will offer less resistance to water flow because the water is bound with less energy, requiring less energy for transport. However, it also takes less energy for a cavitation event to occur and therein lies the conflict in tracheary element design. When water is freely available, as in the spring, larger diameter tracheary elements allow for a large flux of water at a time when the risk of cavitation is low. Later in the growing season, or higher up in the plant, the transpirational water is under greater tension and the risk of cavitation is higher. Gymnosperms and angiosperms respond to this seasonal variation in water supply and cavitation risk by varying the diameter of tracheids and vessel elements produced throughout the growing season.

Note that the unit of conduction for gymnosperm tracheids is the tracheid itself. Water, and cavitation events, must pass through pits to move from one tracheid to another. However, the unit of conduction for angiosperm vessel elements is the vessel, which is series of dozens or even hundreds of individual vessel elements connected end-to-end. With large perforations at the end of each cell, water and cavitation events can pass easily through the vessel. This distinction, and the presence, size, and mixture of tracheids and vessel elements between angiosperms and gymnosperms as well as across a growing season, has allowed vascular plants to adapt to a wide variety of ecological niches.

Box 7.2   Phloem to the Rescue: Symplastic Transport of Water

Daily cycles of transpiration and water supply can impose undue tension on the xylem water column and cause cavitation. Pfautsch and colleagues injected a fluorescent dye into the phloem and were able to visualize water movement between the phloem and xylem. They demonstrated that under conditions of high transpiration demand, water moved from the phloem parenchyma cells into the xylem tracheary elements. Thus, it is apparent that phloem tissue can serve as a water reservoir for, and relieve, xylem tension when xylem tissue is at risk for cavitation.

Reference: Pfautsch et al. (2015)

7.3   Tracheids Are Imperforate Tracheary Elements and the Sole Water Conductors in Gymnosperms

With few exceptions, gymnosperms only have tracheids (imperforate tracheary elements), whereas angiosperms contain both tracheids and vessel elements (perforate tracheary elements) (▶ Box 7.1). The exceptions are the advanced, vessel-containing gymnosperms of the Gnetophyta and the primitive, vessel-less angiosperms in the Winteraceae family. Both of those groups are discussed in more detail in ▶ Chap. 15—Wood.

Gymnosperm tracheids can be quite flexible in both structure and function with the key to the specific function due to the lignified and sculptured cell walls. Tracheids are produced by the vascular cambium. Environmental conditions during development are sensed by the developing cells, in a manner that is not well understood, and result in cell morphologies that are suited to the particular water status at the time of development. Therefore, at maturity, tracheids may differ significantly in their proportion, size, shape, and cell wall thickness. Basic tracheid anatomy is discussed below.

Tracheids are long and narrow, with tapered ends. The tapering is gradual, such that tracheids lack an obvious end wall and terminate in a point (◘ Fig. 7.3a, b); hence, they are imperforate. Water movement from one tracheid to its neighbor is through the numerous pit
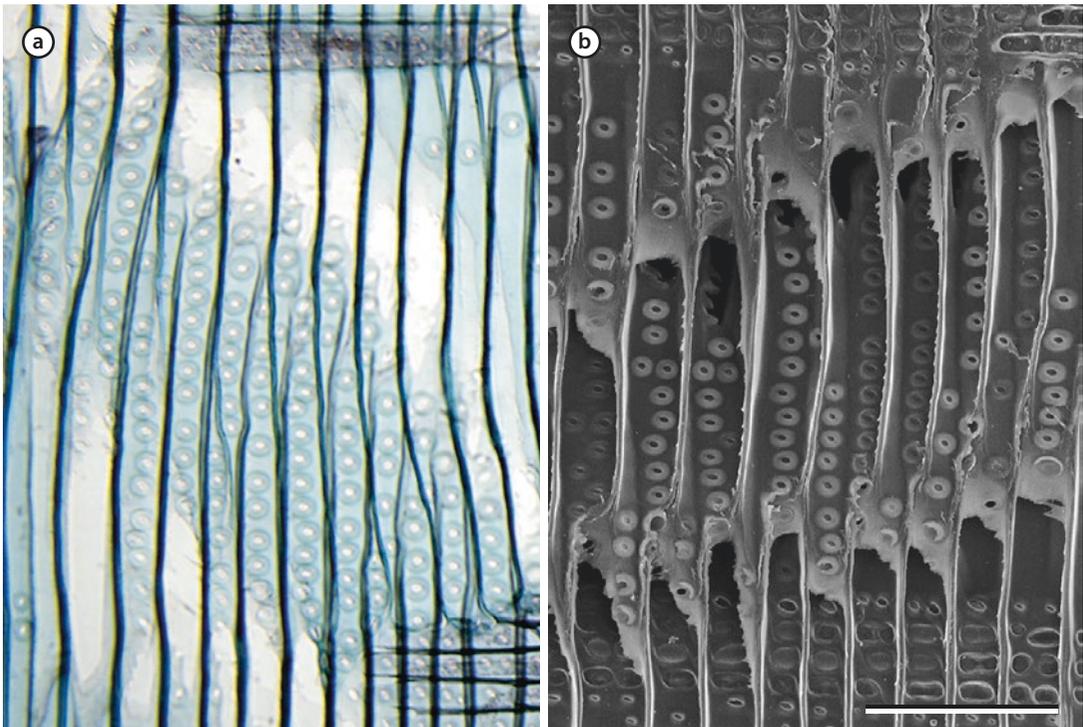
◘ **Fig. 7.3   a, b** Tapered ends of tracheids in radial sections of coast redwood (*Sequoia sempervirens*) and pine (*Pinus* sp.). Note the numerous circular bordered pits in the radial walls. Scale bar in **b** = 100 μm and applies to both panels. (**a** RR Wise)
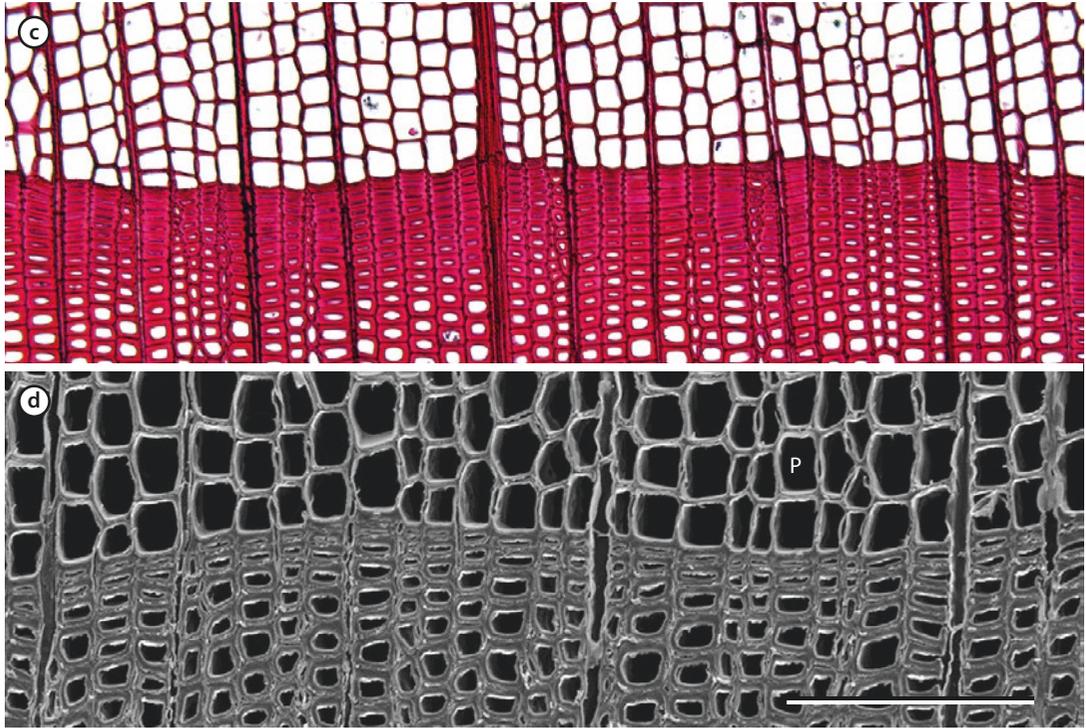
▣ Fig. 7.3   **c**, **d** Seasonal growth ring boundaries in **c** Norway spruce (*Picea abies*) and **d** pine (*Pinus* sp.) stems in cross-section. **Early wood** tracheids (toward the top in each panel) have a large diameter and thin walls, while **late wood** tracheids (toward the bottom) are narrow with thick walls. Note several bordered pits surrounding the letter P in **b**. Scale bar in **b** = 200 μm and applies to both panels. (**c**, **d** RR Wise)

pairs in the radial walls. Tracheids are packed tightly in the xylem tissue with little to no air space between adjacent cells, giving them an angular, often square cross-section (▣ Fig. 7.3c, d). Gymnosperm tracheids range from 100 to 6000 μm in length and 10 to 70 μm in width, with root tracheids being longer and wider than shoot tracheids (data reported in Sperry et al. 2006). While there is significant resistance to water flow from cell-to-cell through the pits and across the pit membrane, resistance within any one tracheid is much less. Thus, tracheids allow for efficient water movement while minimizing the risk of cavitation, and the tight packing of cells provides support.

Tracheids are considered to be more primitive in design and derivation than vessel elements (Friedman and Cook 2000). Lacking vessel elements, gymnosperm tracheids are more varied in size and shape than angiosperm tracheids and vessel elements, as xylem development responds to seasonal changes in water supply and demand. Diameter is larger in the spring and narrower later in the season as soil water is depleted (▣ Fig. 7.3c, d). The wood of conifers and angiosperms not only transports water but also provides support for freestanding plants. In the wood of conifers, the tracheid must be strong enough to hold open the water column and hold up the tree at the same time. In angiosperm wood, xylary fibers take on much of the plant support task, reducing this demand on vessel element strength. Thus, any mechanical constraint on conduit size is more limiting for conifer tracheids than individual angiosperm vessel elements.
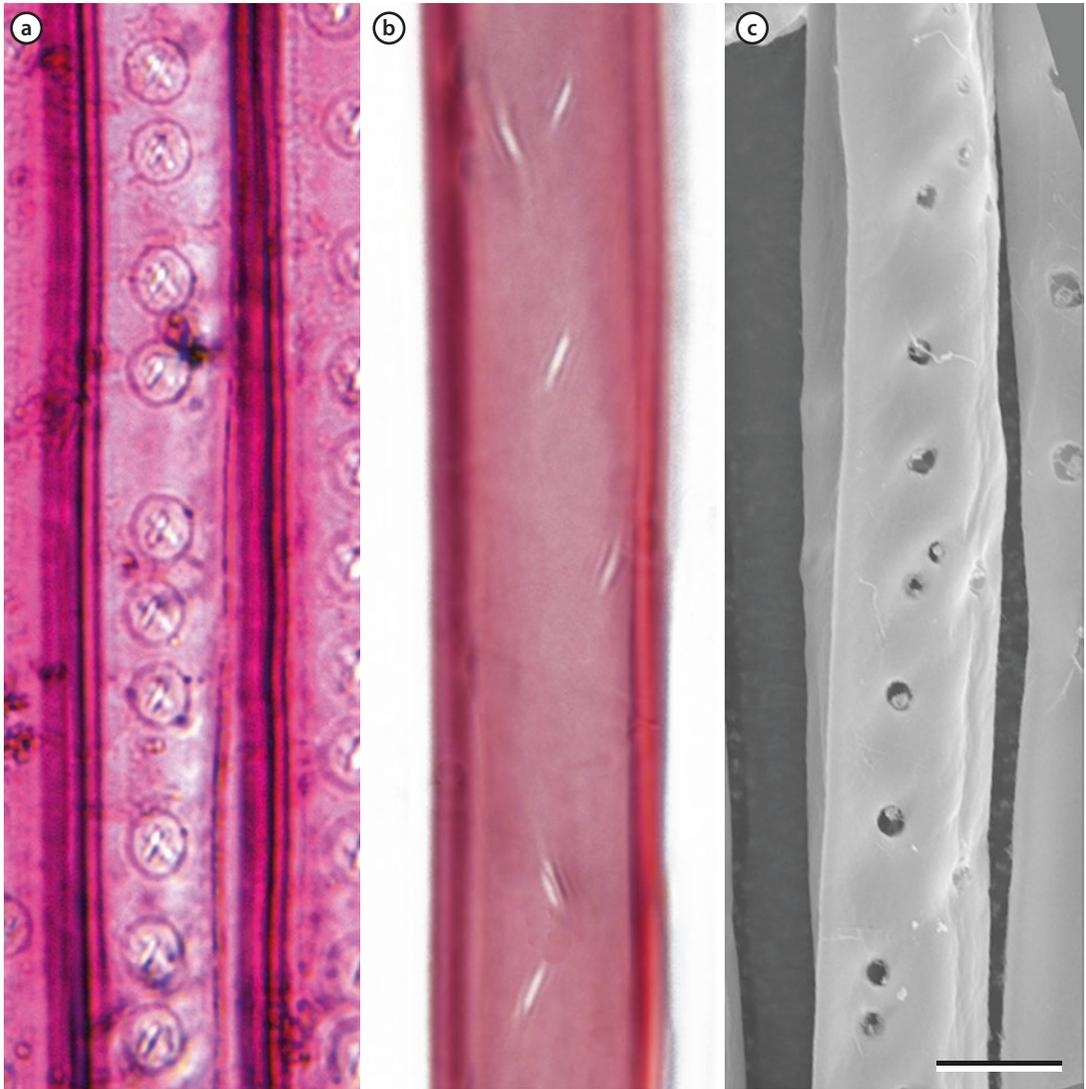
7.4 Angiosperm Tracheids, Fiber Tracheids, and Libriform Fibers Represent a Continuum of Imperforate Tracheary Element Design and Function

As noted in ► Box 7.1, angiosperm xylem contains three forms of imperforate tracheary elements—the tracheid, the fiber-tracheid, and the libriform fiber (Carlquist 2001). All three share the common features of 1) the presence of a secondary cell wall, 2) the absence of a perforation plate (i.e., all three are imperforate), and 3) all are derived from the vascular cambium. Their general shape is long and narrow with thick, pitted walls and tapered ends. Angiosperms have tracheids, fiber tracheids, and libriform fibers in addition to vessel elements (refer to ► Sects. 7.5, 7.6, and 7.7). Gymnosperm wood is composed almost exclusively of tracheids with fiber tracheids in only a few, advanced groups such as the Gnetales.

The main differences between the three cell types are in the number and shape of pits in the walls. Angiosperm tracheids, like gymnosperm tracheids, are covered with a dense covering of **circular bordered pits** (◘ Fig. 7.4a). Fiber tracheids are similar except they have fewer pits and those pits have lenticular to slit-like pit apertures (◘ Fig. 7.4b). Libriform fibers have the fewest pits and those pits are simple (◘ Fig. 7.4c) (IAWA 1964). The libriform fiber is the most abundant imperforate tracheary element type in most hardwoods. In addition to their anatomical differences, libriform fibers and fiber tracheids may be distinguished by differential staining based on cell wall lignin content, with libriform fibers containing less lignin than fiber tracheids (Vazquez-Cooz and Meyer 2002).

Tracheids, fiber tracheids, and libriform fibers are located in the angiosperm wood and are therefore called **xylary fibers**, due to their location and not necessarily their **ontogenetic** origin. **Extraxylary fibers** (those not found in the wood) include phloem or bast fibers. Intermediate forms exist, making a positive identification difficult in many instances (Carlquist 2001). Nonetheless, the morphologies do have distinct differences. The evolutionary sequence was from tracheids to fiber tracheids, libriform fibers, and ultimately vessel elements. Angiosperm tracheids, especially those found adjacent to a vessel (called vasicentric tracheids), are involved in water transport, whereas fiber tracheids and libriform fibers have lost that function and serve mainly in support (Sano et al. 2011).

Angiosperm imperforate tracheary elements tend to be shorter and make up a smaller proportion of the wood than gymnosperm tracheids, as is to be expected given that gymnosperm wood is almost 100% tracheids, and angiosperm wood has a diversity of cell types. Bailey and Tupper (1918) measured tracheid length in 152 gymnosperm species and 275 angiosperm species. They reported that the average gymnosperm tracheid length was 3530 μm, and that for angiosperms, the value was 1200 μm, with large variation around both means. That comparison is useful in terms of comparative xylem anatomy, and for taxonomic applications, but it is not particularly suitable in comparative xylem phys-

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◘ **Fig. 7.4   a–c** Pitting patterns of imperforate tracheary element side walls. **a** Tracheids from *Drimys*, a primitive vessel-less angiosperm, have side walls with numerous circular bordered pits. **b** Fiber tracheids from red maple (*Acer rubrum*) have fewer pits, with slit-like apertures. **c** Libriform fibers from grape (*Vitis* sp.) have simple pits. Scale bar in **c** = 10 μm and applies to all panels. (**a–c** RR Wise)

iology. As pointed out above, the tracheid is the conducting unit for gymnosperms; however, the vessel, which is composed of may interconnected vessel elements, is the main conducting unit for angiosperms, not the tracheid. That is why studies comparing xylem transport in gymnosperms and angiosperms compare size and function of gymnosperm tracheids to angiosperm vessels (e.g., Sperry et al. 2006).

Paper is manufactured by chipping and then delignifying gymnosperm and angiosperm wood. This process releases the individual imperforate and perforate tracheary elements, which in the paper industry are collectively called "fibers." The fibers are suspended in water, sprayed onto a screen, flattened, and dried into a sheet of paper. Unbleached fibers are brown from residual lignin,
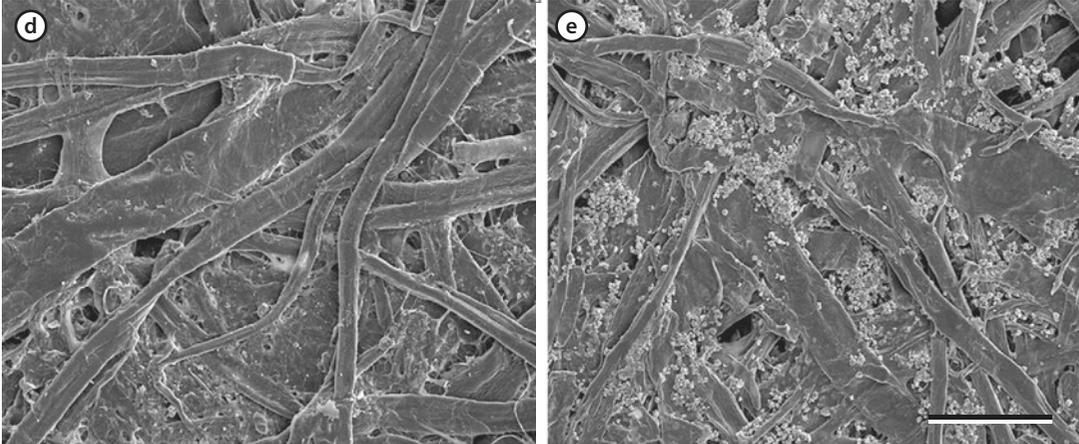
Fig. 7.4 d, e High-magnification view of **d** a brown paper bag and **e** white copier paper. Note the different size and texture of the fibers that make up each paper. The granular material in the copier paper is clay and other materials added during the paper making process to control the color, sheen, and printing qualities. Scale bar in **e** = 100 μm and applies to both panels. (**d, e** RR Wise)

whereas bleaching will remove the color. Softwood (i.e., gymnosperm) fibers are long and coarse, and produce a strong paper with large pores (■ Fig. 7.4d), suitable for paper bags and cardboard, but not for printing. Hardwood (i.e., angiosperm) fibers are shorter and finer, thus capable of producing a paper that interacts well with wet and dry inks (■ Fig. 7.4e). Paper qualities such as strength, thickness, density, color, and porosity are controlled by specifying the types and percentages of wood and fibers used in the paper making process.

7.5 Vessel Elements Are Perforate Cells and the Main Water Conductors in Angiosperms

While gymnosperms are clearly a successful group of plants, the evolution of vessel elements in angiosperms gave them greater flexibility and adaptive capacity (Pitterman 2010). The lineage was from tracheids, to fiber tracheids, to libriform fibers, and to vessel elements. Vessel element evolution had four major stages as shown in ■ Fig. 7.5a, which is an oft-reproduced diagram from Bailey and Tupper's seminal 1918 paper on size variation in tracheary cells: (1) decrease in length and increase in width of the vessel element, (2) decrease in the angle of inclination of the end wall and perforation plate, (3) a transition from scalariform to simple perforation plates, and (4) a transition from scalariform vessel-to-vessel, lateral pits in the side walls to an alternate arrangement of pits in the side walls.

A representative sample of vessel elements is shown in ■ Fig. 7.5b–e. They are characterized by being short and wide. Indeed, with a width of ~380 μm and a height of ~100 μm, the example from honey locust (■ Fig. 7.5c) is more drum-shaped than
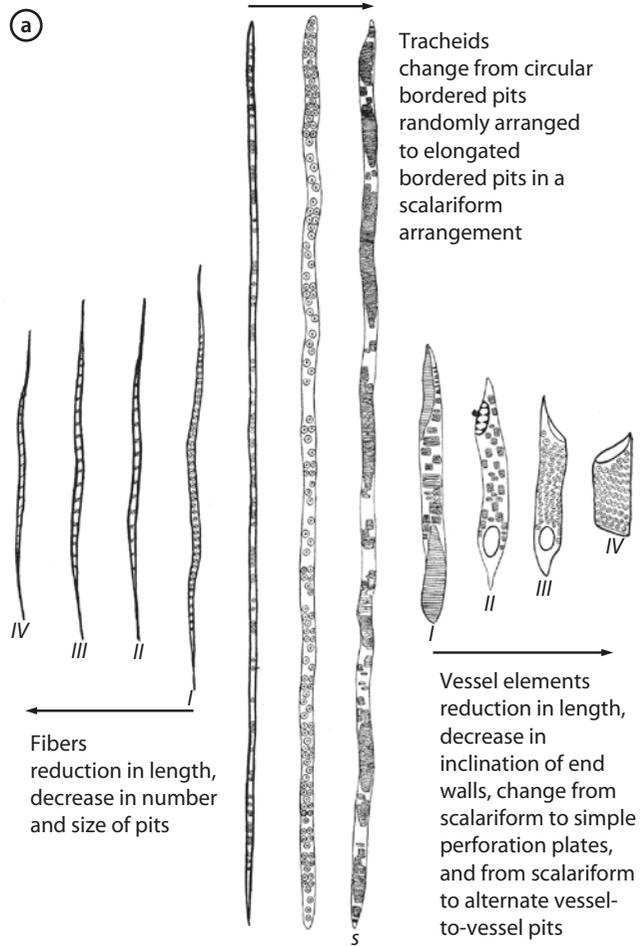
◘ Fig. 7.5   a Drawings indicating the evolution of eudicot fibers (left), tracheids (middle), and vessel elements (right). All cells are drawn to scale with the exception of the tracheid labeled with an "S," which is shorter than the others. For the vessel elements, I = scalariform, II = intermediate between scalariform and porous, III and IV = porous. Arrows indicate the direction of the adaptive changes over evolutionary time. (From Bailey and Tupper (1918), public domain)

tubular. Vessel element side walls contain numerous pits that allow for the lateral, vessel-to-vessel exchange of water. A curious feature of vessel elements is the presence of a tail (sometimes called a beak) at either end (◘ Fig. 7.5b), the function of which is unknown.

During development, the cells enlarge and lay down the requisite pattern of secondary cell wall on the sides and at the perforation plate. At maturity, the remaining pit membrane (the original primary cell wall) in the perforation is degraded, opening the perforation to the adjacent vessel element in the vessel. The cell protoplasm is lost and degraded, via a process called programmed cell death (Fukuda 2000), and the resulting mature tracheary element is dead. That does not, however, mean the cell is totally unresponsive to environmental conditions. See the side box on how cations can alter xylem function.
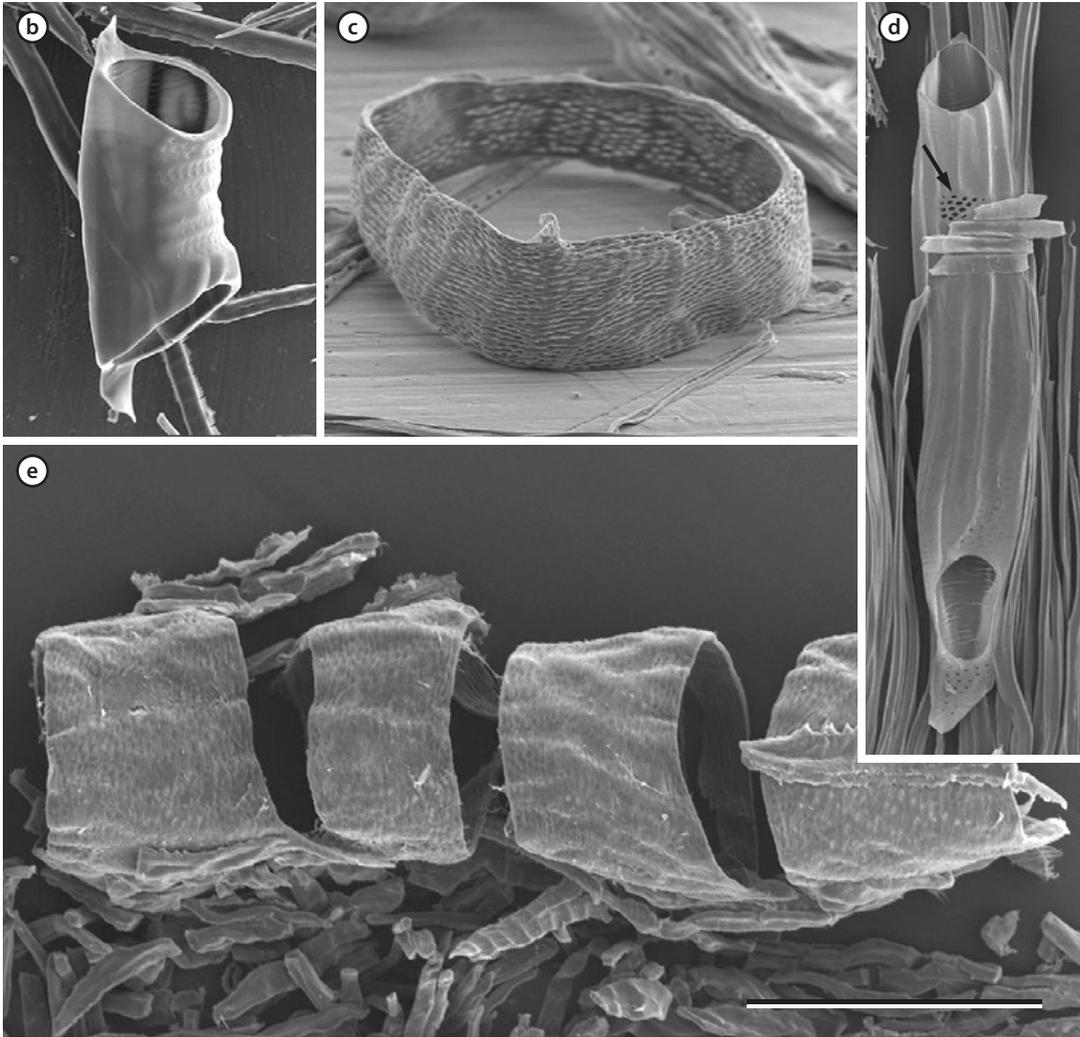
◧ **Fig. 7.5   b**–**e** Representative vessel elements. **b** This vessel element from red oak (*Quercus rubra*) has large, prominent tails at both ends. **c** A honey locust (*Gleditsia triacanthos*) vessel element is larger in diameter than height. A small tail is present in the middle of the figure. The side walls contain numerous scalariform pits. **d** and **e** Red maple (*Acer rubrum*) vessel elements. Note the lateral pit field and associated ray parenchyma at the top of the vessel element in **d** (arrow). The four vessel elements in **e** were once interconnected to form part of a vessel. All of these vessel elements shown here have simple perforation plates. Scale bar in **e** = 200 µm and applies to all panels. (**b**–**e** RR Wise)

Box 7.3   Xylem: More Active than You Thought
The cohesion-adhesion-tension model of transpiration only requires that xylem tracheary elements have a continuous water column from soil to atmosphere. The resistance to flow (or its inverse, conductance) under different conditions, therefore, should remain constant, in the absence of cavitation. However, recent evidence has accumulated indicating that xylem hydraulic conductance varies over the short term as a consequence of the concentrations of cations in the xylem sap. The working hypothesis is that the ions are affecting the hydrogel properties of the pit membrane,

allowing more water to flow from element to element when cations are present. The source of the cations may be the adjacent, living phloem, in which case, the phloem is mediating a direct control over xylem hydraulic properties. This would increase xylem-phloem coordination and may be an adaptive advantage under rapidly changing environmental conditions of water and light.

Reference: Nardini et al. (2011)

## 7.6   Vessel Element Side Walls Are Patterned for Strength and Water Movement

Unlike tracheids (which are imperforate), vessel elements have perforations in their end walls and, less commonly, side walls (are perforate). The side walls are optimized for lateral or radial water flow, which tends to be minimal, and strength. Vessel elements must allow for the free movement of water, but not collapse under the negative pressures generated during active transpiration. Vessel element end walls are optimized for axial water flow (the direction of the majority of the water follows). Patterns of side wall secondary wall deposition will be discussed in this section; end wall perforations are covered in ► Sect. 7.7.

There are five basic patterns of vessel element side wall thickenings, (1) annular, (2) helical or spiral, (3) scalariform, (4) reticulate, and (5) an almost continuous wall pierced by bordered pits (◻ Fig. 7.6a). With few exceptions, this sequence of cell wall patterns, which is arranged in order of complexity, is also ordered in terms of evolutionary advancement (Esau 1953).

A vessel element with **annular** secondary thickenings has individual rings of lignified secondary cell wall. This is the simplest and most economical form of vessel element wall patterning (◻ Fig. 7.6b). The remainder, and majority, of the vessel wall is composed of primary cell wall which, although fairly weak, represents a low resistance of vessel-to-vessel water movement. The primary cell wall is also extensible, allowing the annular vessel element to stretch a certain amount in an axial dimension. With this combination of low cost and extensibility, annular vessel elements are frequently found in young, expanding stems, roots, and leaves and represent a common form found in protoxylem (refer to ► Sect. 11.6 for details of protoxylem development). Ultimately, the weak primary cell walls will be stretched and broken, and the vessel will be replaced by metaxylem.

A **helical** or **spiral** vessel element wall pattern is one in which secondary wall thickenings wrap around the cell (◻ Fig. 7.6a, b). The vast majority of the cell wall is primary, with only the thickened rings made of secondary wall. A vessel element with a helical pattern has the same strength, water flow, and extensibility characteristics as found in annular patterns and would be found in young, expanding tissues.
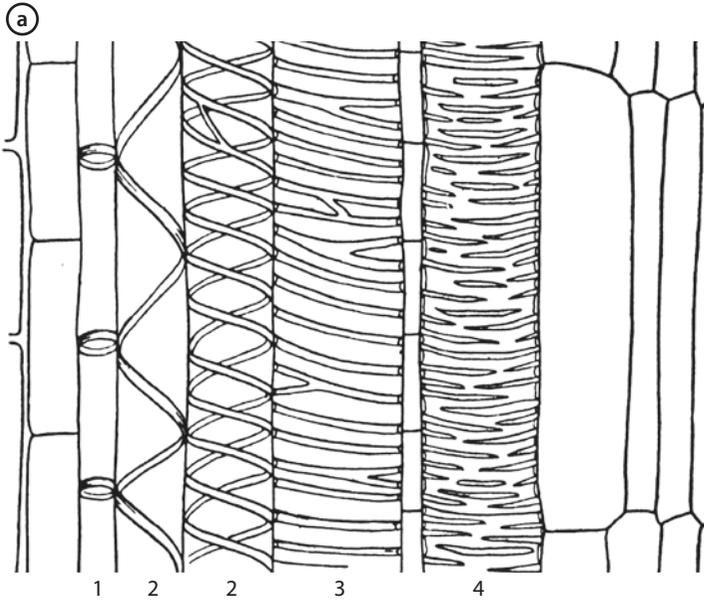
□ Fig. 7.6   a Patterns of secondary cell wall deposition in vessel elements. 1 = annular, 2 = spiral or helical, 3 = scalariform, 4 = reticulate. (From Coulter et al. (1910), public domain)
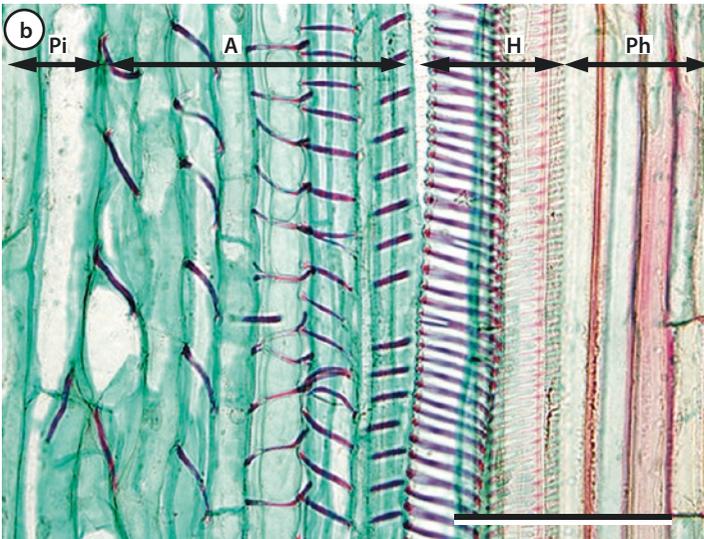
□ Fig. 7.6   b Annular and helical (or spiral) wall patterns in a single longitudinal section of a hemp (*Cannabis sativa*) stem. The stem shows primary growth of pith (Pi) to the left, five xylem vessels made of vessel elements with annular wall thickenings (A), two with helical thickenings (H), and phloem (Ph) to the right. The vessels to the far left, adjacent to the pith, were laid down first (protoxylem) and have been stretched in an axial direction as the stem elongated. Scale bar = 50 μm. (RR Wise)

Scalariform, thickenings run in a transverse direction, like the rungs of a ladder, and cover large portions of the vessel element side wall (□ Fig. 7.6c, d). Because the ends of the "rungs" are attached to vertical portions of the wall, a scalariform vessel element cannot
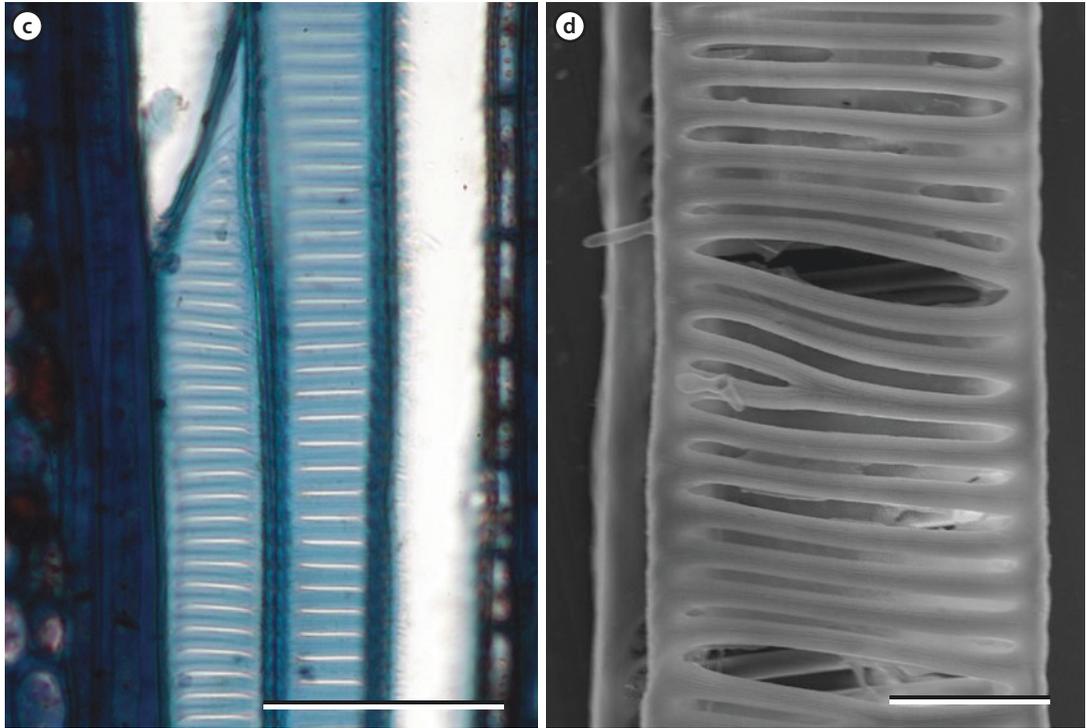
◼ Fig. 7.6   c, **d** Scalariform wall patterning as seen in vessel elements from grape (*Vitis* sp.) stem as visualized with **c** light microscopy and **d** scanning electron microscopy. Scale bars = 50 μm in **c**, and 10 μm in **d**. (**c**, **d** RR Wise)

stretch in an axial direction; therefore, scalariform vessel elements are found in tissues that have ceased elongation.

The **reticulate**, vessel element wall pattern is an irregular, net-like combination of different secondary cell layers of slightly different orientations (◼ Fig. 7.6e, f). The majority of the cell surface is covered by wall material, leaving less area for vessel-to-vessel water movement but providing for greater strength in both the radial and axial dimensions. Vessel elements with a reticulate wall pattern are not capable of axial extension.

The secondary lateral walls of tracheary elements may be more or less continuous, interrupted only by pits, which were introduced in ► Sect. 5.5. Because pits allow for cell-to-cell water movement, and each cell has a cell wall, pits almost always exist as a pit pair, with the pit in one secondary cell wall aligned with a pit in the secondary cell wall of an adjacent cell. In walls shared between a vessel element and a parenchyma cell (which lacks a secondary wall), **half-bordered** pits are found. Several examples of bordered pit pairs are given in ◼ Fig. 7.6g–i. Simple pits are the least common (◼ Fig. 7.6j) and composed of a hole in the secondary cell walls of two adjacent cells; the opening is spanned by the pit membrane. The pit membrane is made of the remnants of the primary cell walls of the adjacent tracheary elements. As such, the pit membrane is not lignified and is relatively porous to water, but will block an air embolism. It is, however, weak and can rupture if stretched too far.

The bordered pit pair is common in gymnosperms, but less so in angiosperms. It represents a means to maximize water flow while
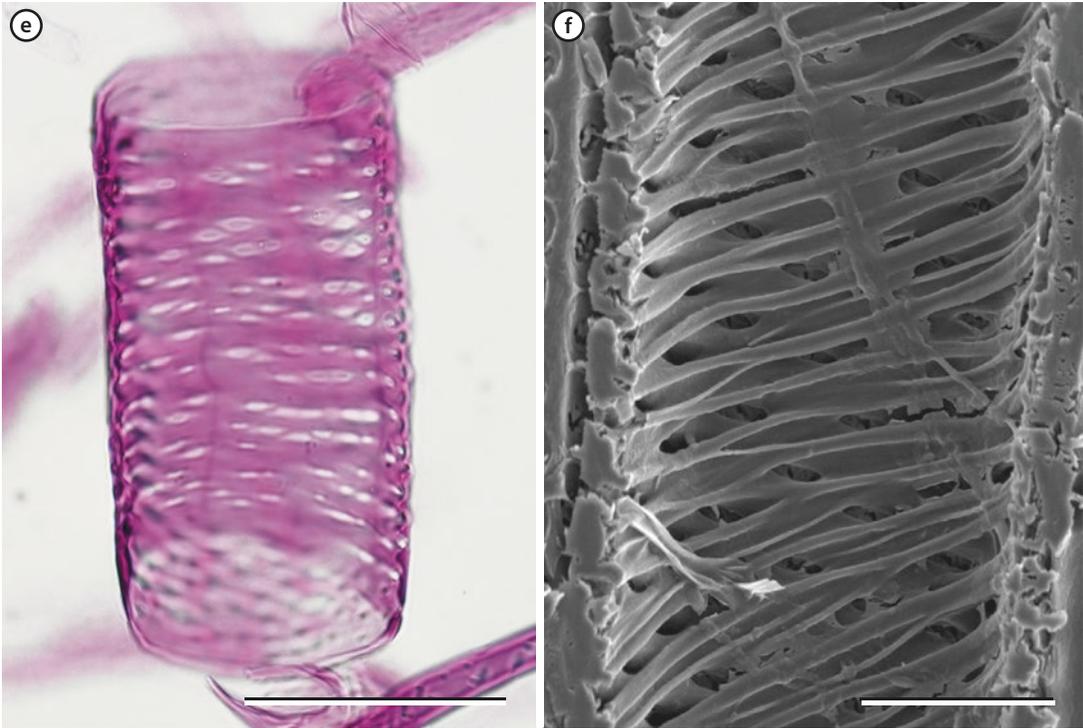
◨ **Fig. 7.6** **e**, **f** Reticulate wall patterning in isolated vessel elements from **e** Dutchman's pipe (*Aristolochia* sp.) and **f** honey locust (*Gleditsia triacanthos*) vessel elements. Note the multiple layers of secondary wall thickenings in the honey locust vessel element as seen in the scanning electron microscope. Scale bars = 50 μm in **e** and 20 μm in **f**. (**e**, **f** RR Wise)
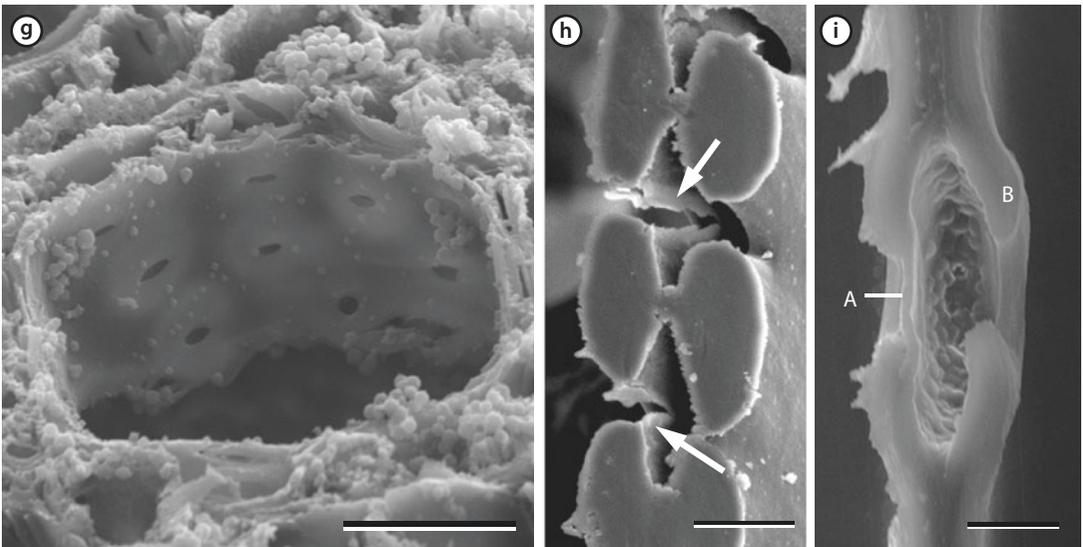
◨ **Fig. 7.6** **g** Oak (*Quercus* sp.) vessel element with circular bordered pits. **h** section of two adjoining vessel element walls from black walnut (*Juglans nigra*) showing pit pairs. Remnants of the broken pit membrane can be seen (arrows). **i** A bordered pit pair from pine (*Pinus* sp.) wood. The pit membrane has been lost during specimen preparation, but the apertures (A) and borders (B) are clearly evident. Scale bars = 10 μm in **g** and 5 μm in **h** and **i**. (**g**–**i** RR Wise)
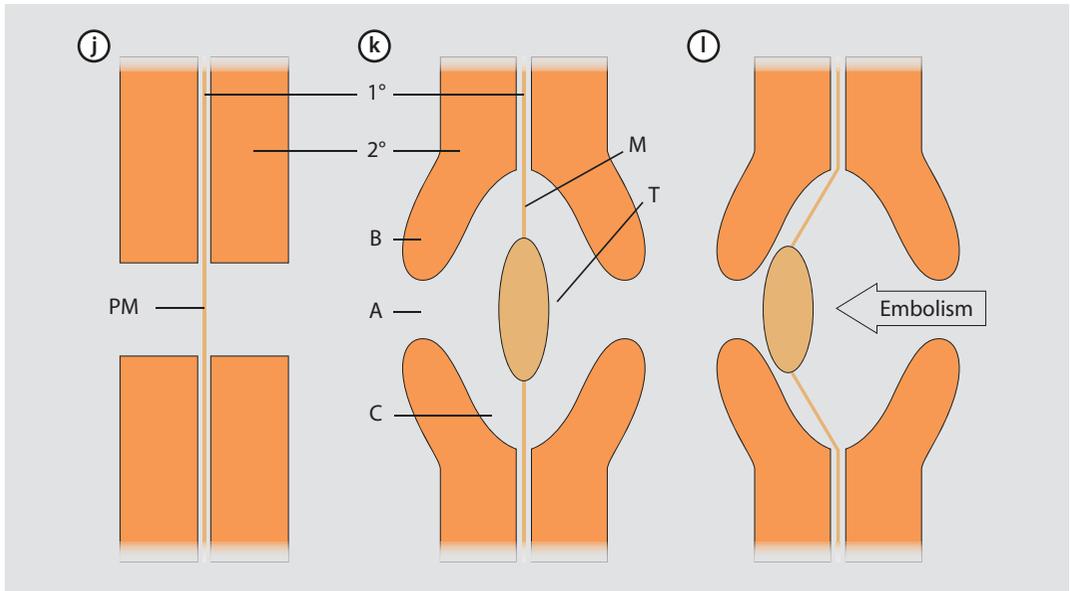
■ **Fig. 7.6**   **j–l** Cross-sectional views of pit pairs. **j** A simple pit is a pair of gaps in the secondary cell walls (2°) of adjacent cells. It has a pit membrane (PM), which is derived from the primary cell walls (1°) and the middle lamella of the two cells. Water movement is across the entire pit membrane, which is somewhat effective at blocking embolisms. **k** In a bordered (B) pit pair, water flows through the pit aperture (A), enters the pit chamber (C), and crosses the permeable margo (M) to the opposite pit chamber. **l** If an embolism forms, it pushes the torus (T) against the pit aperture and blocks water flow and the propagation of the embolism. In this condition, the pit is said to be **aspirated**. (**j–l** RR Wise)

minimizing the structural weakness caused by having a hole in the wall that supports the cell. It also protects the pit membrane from rupturing. ■ Figure 7.6k shows the structure of a bordered pit pair. The pit apertures are small openings in the secondary cell walls, one each per cell. The areas of the pit apertures are small, but unobstructed, and therefore resistance to water flow is low. The pit apertures open in the pit chamber, a much larger area. The two pit chambers are separated by the pit membrane. The pit membrane of a bordered pit pair has two components, a central, impermeable **torus** and a peripheral, permeable region called the **margo** (■ Fig. 7.6k, l, m). The bordered pit pair, with its margo and torus, is an engineering marvel. Each is a little valve that allows cell-to-cell water flow, but seals shut when an embolism caused by a cavitation event occurs in one of the cells.

Vestured pits are bordered pits containing tiny outgrowths that project into the pit cavity from the secondary wall that surrounds the pit (■ Fig. 7.6n, o). They are found in *Eucalyptus* and related species of the Myrtaceae as well as legumes (Fabaceae), members of the Malpighiaceae, and the gymnosperm order Gentianales. Vestures may also be found in the inner walls of some vessel elements as well as the rim of perforation plates. Vestured pits are more common in tropical plants and may be of an advantage in managing the lateral stresses on the pit membranes caused by repeated or continuous drought conditions (Jansen et al. 2004). In short, they provide even more protection to the delicate pit membrane in those plants that experience repeated cavitation.
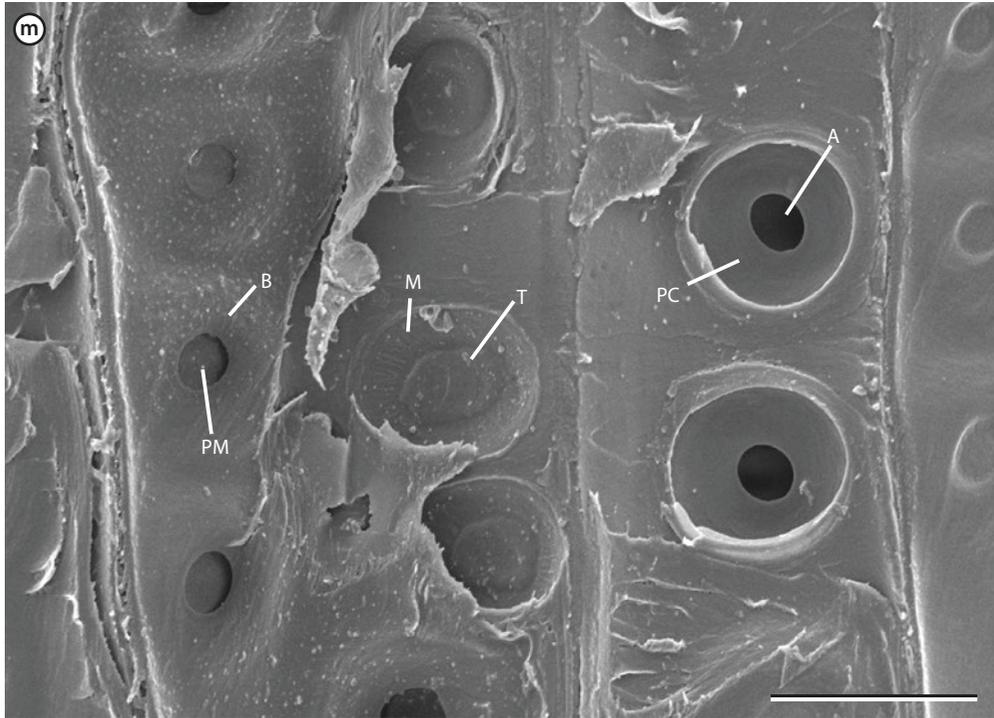
◘ **Fig. 7.6   m** Face view of a fortuitous section through three columns of pit pairs in pine (*Pinus* sp.) wood. The three pits to the left are viewed from the interior of a tracheid and have a prominent pit border (B) and pit membrane (PM) viewed through the pit aperture. The three pits in the middle have been sectioned to show the margo (M) and torus (T) in the center of the pit pair. The two pits to the right have been sectioned to show the pit chamber (PC) and the aperture (A) leading to the adjacent cell. Scale bar = 20 μm. (RR Wise)
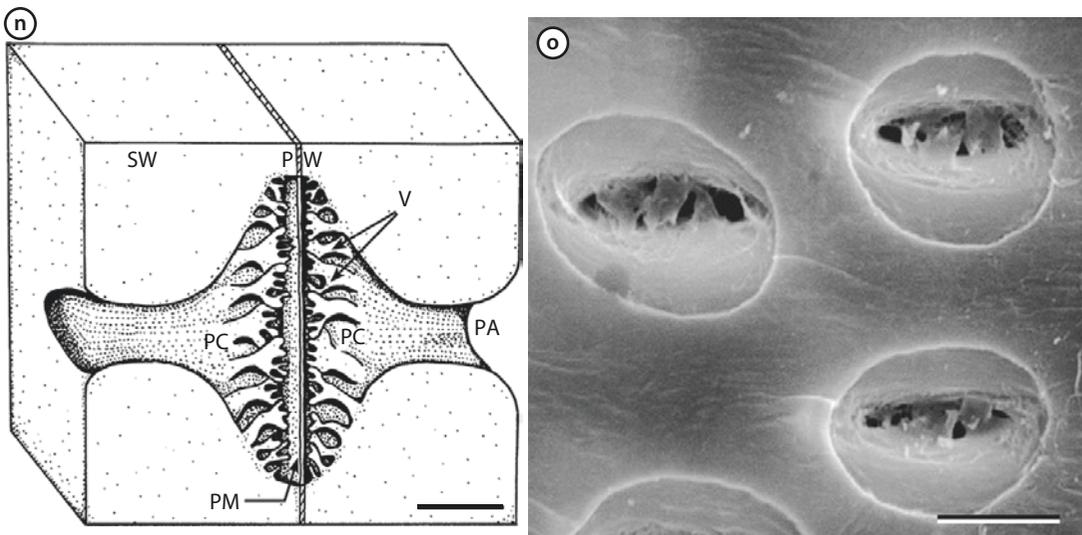
◘ **Fig. 7.6   n** Side view of a vestured pit pair in *Flabellaria paniculata* (no common name, Malpighiaceae) with overarching secondary cell wall (SW), vestures (V), pit chamber (PC), pit aperture (PA), pit membrane (PM), and primary cell wall + middle lamella (PW). Bar = 2μm. From Jansen et al. 2004, with permission. Copyright (2004) National Academy of Sciences, USA **o** Face view of vestured pits from the wood of honey locust (*Gleditsia triacanthos*, Fabaceae). The vestures can be seen through the pit aperture. Scale bars = 2 μm. (**n** Jansen et al. 2004; **o** RR Wise)
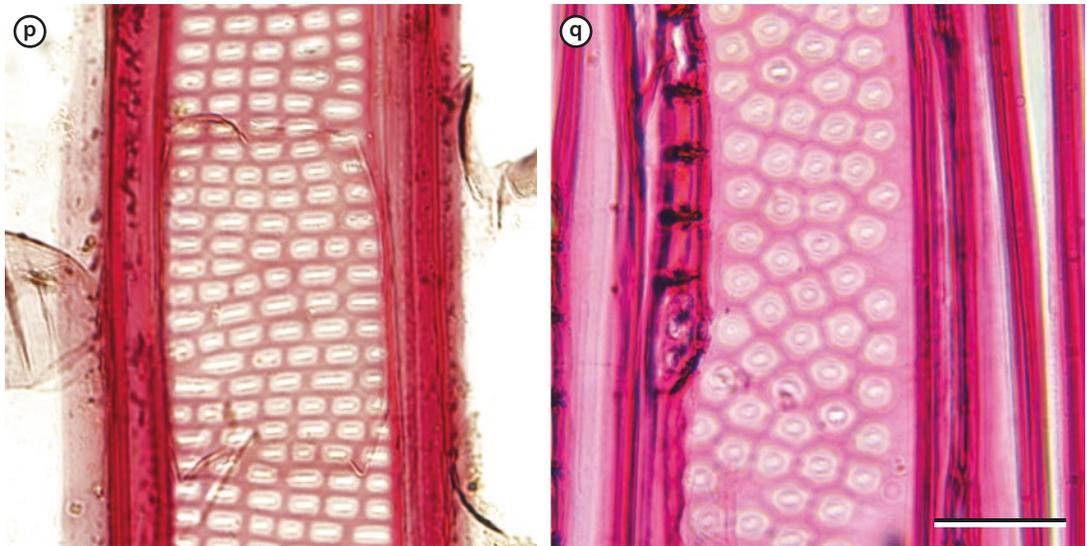
◘ Fig. 7.6   p Opposite pitting in a tulip tree (*Liriodendron tulipifera*) vessel element with elongate bordered pits. **q** Alternate pitting in a large-tooth aspen (*Populus grandidentata*) vessel element with circular bordered pits. Scale bar in **q** = 25 μm and applies to both panels. (**p, q** RR Wise)

Pit pairs are rarely found singly and usually occur as large fields of pits packed into tight, coordinated arrangements. An opposite arrangement shows linear rows of pits (◘ Fig. 7.6p), while in an alternate arrangement, the pits are staggered in distribution (◘ Fig. 7.6q). Both patterns maximize the amount of cell wall and therefore strength while still providing for significant lateral, vessel-to-vessel, or vessel-to-parenchyma water movement. In evolutionary terms, the alternate pattern is considered to be more advanced than the opposite (see ◘ Fig. 7.5a).

7.7   Most Vessel Elements End in a Perforation Plate and Are Connected to Another Vessel Element

The two adjacent end walls of vessel members may be partially or wholly degraded during development, which opens perforations. Through these perforations, water moves by bulk flow along a continuing series of end-to-end cells that form the multicellular tubelike vessel. Perforation plates may be simple as seen in ◘ Fig. 7.7a–c or complex. Complex perforation plates are referred to as scalariform (◘ Fig. 7.7d, e), reticulate (◘ Fig. 7.7f), or ephedroid (◘ Fig. 7.7g). Simple perforation plates can also be seen in ◘ Fig. 7.5b–e.

A vessel may extend great distances but it will eventually terminate. In leaves, the distal end of the terminal vessel element is blind and does not contain a perforation plate. Refer to ► Fig. 12.2h for an example of a terminal vessel element in a leaf.
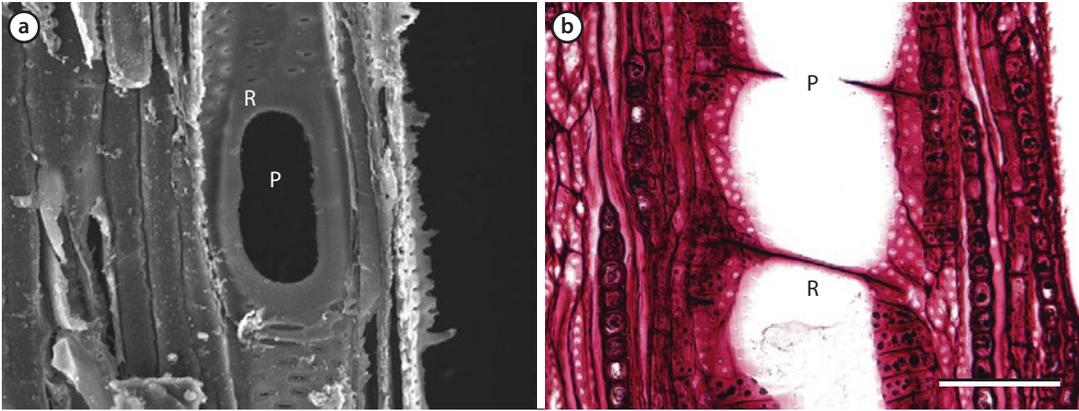
◘ Fig. 7.7 **a**, **b** Oak (*Quercus* sp.) simple perforation plates with large rims. **a** In this view, the plate is inclined and seen end-on. **b** In this view, two *Quercus* perforation plates are seen in side view, one showing the entire rim and the other showing the rim and perforation. P = perforation, R = rim. Scale bar in **b** = 50 μm and applies to both panels. (**a**, **b** RR Wise)
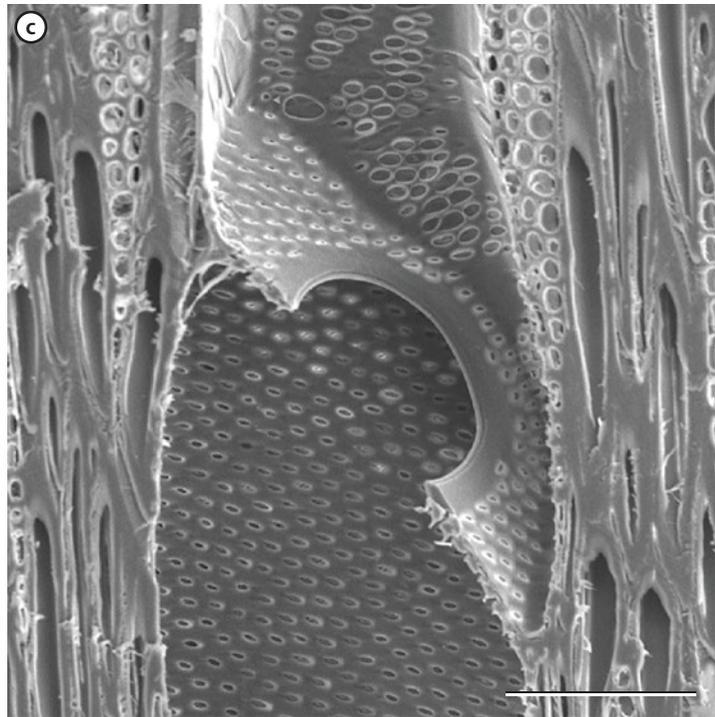
◘ Fig. 7.7 **c** Simple perforation plate in a black walnut (*Juglans nigra*) connecting two vessel elements. In this example, the perforation plate is a combination of a simple pore with a large rim containing numerous pits. Scale bar = 100 μm. (RR Wise)

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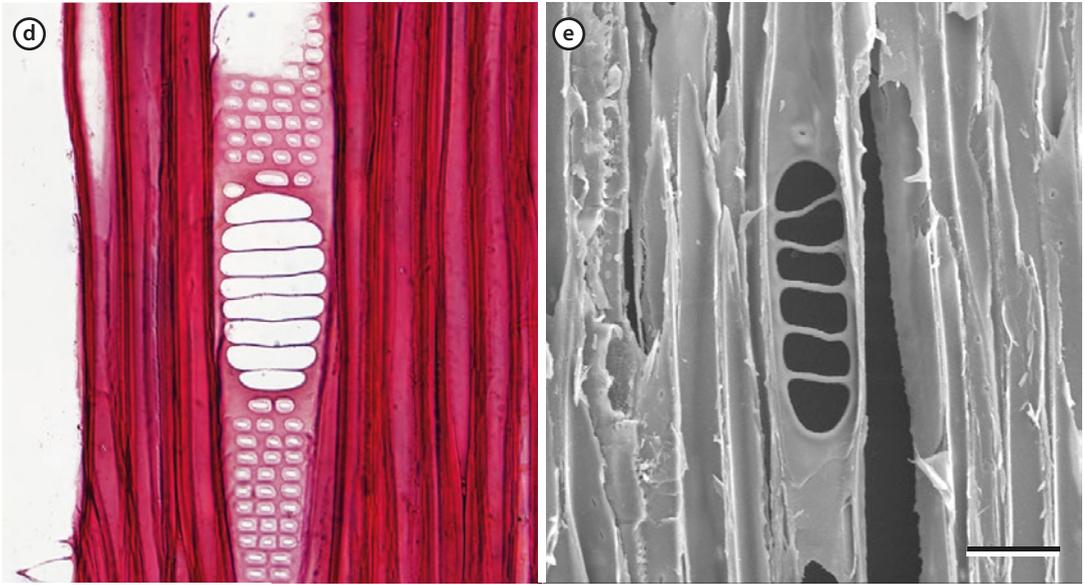
□ **Fig. 7.7   d**, **e** Scalariform perforation plates in tulip tree (*Liriodendron tulipifera*) vessel elements. Scale bar in **e** = 25 µm and applies to both panels. (**d**, **e** RR Wise)
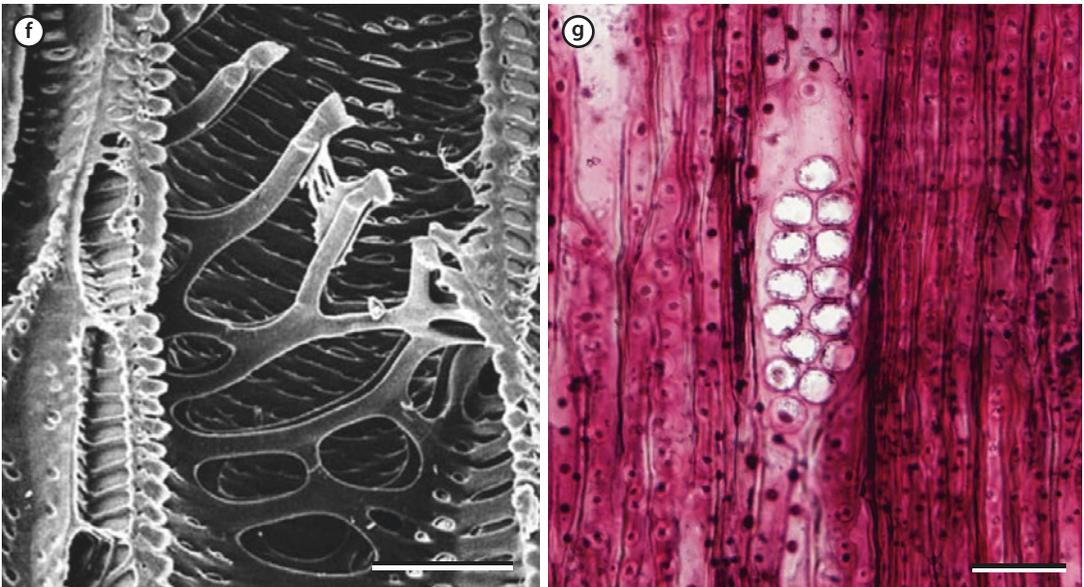
□ **Fig. 7.7   f** Reticulate perforation plate from the feather duster palm (*Rhopalostylis sapida*). **g** Ephedroid perforation plate from longleaf joint fir (*Ephedra trifurca*) = 10 µm in **f** and 25 µm in **g**. (**f** from Crang and Vassilyev 2003; **g** RR Wise)

## 7.8 Xylem Parenchyma Are Living Cells Involved in Xylem Metabolism and Protection

Xylem vessel elements, tracheids, and fibers are dead at maturity. However, xylem parenchyma cells are living. Some of the functions of xylem parenchyma will be discussed in this section. Other aspects are addressed in ► Chap. 15—Wood.

Maple syrup is a well-known product of xylem parenchyma starch storage. Parenchyma starch content increases in the late summer to early fall and that carbohydrate reserve is remobilized in the spring, loaded into the xylem water, and used to support the early heterotrophic growth of leaves. Lacking transpiration (the leaves have not yet expanded), the mechanism of water movement relies on nighttime freezing and daytime thawing, conditions commonly found in the spring. Apoplastic water freezes before symplastic water. The apoplastic ice crystals draw water out of the parenchyma cells during the night. Upon warming, the apoplastic ice thaws and enters the adjacent xylem vessel element or tracheid, thus pressurizing the xylem water and forcing it toward the expanding leaf buds (or the sap spigot, if the tree has been tapped). Stored starches are hydrolyzed to sucrose and loaded into the xylem. This is one of the few instances in which sugars are transported in the xylem and not the phloem.

Xylem parenchyma are also the living cells responsible for response to pathogens and wood repair. The CODIT model (Compartmentalization of Decay in Trees, Morris et al. 2016) postulates that upon attack, trees seal off the damaged areas by the activation of parenchyma cells that divide and differentiate into sclereids (◘ Fig. 7.8a, b). Absent such a repair, pathogens (mainly wood-rotting fungi) and air (which would cause cavitation) could enter and spread through the xylem conducting tissues.

Axial parenchyma cells are oriented parallel along the axis of elongation. Ray parenchyma cells are oriented along the radial axis. Both can be observed in the transverse (cross-sectional) plane. There is considerable variation of parenchyma cellular orientation and shape. Some are square, some are elongated but upright, some are procumbent (longest axis radially oriented), and some are perforated (e.g., *Bathysa meridionalis*, a tropical tree). Perforated ray cells larger than other ray and vessel elements are typically found in uniseriate rays and may be important in horizontal water transport. Most commonly, scalariform perforations in the side walls of ray cells are found and are similar to the end walls of vessel elements.
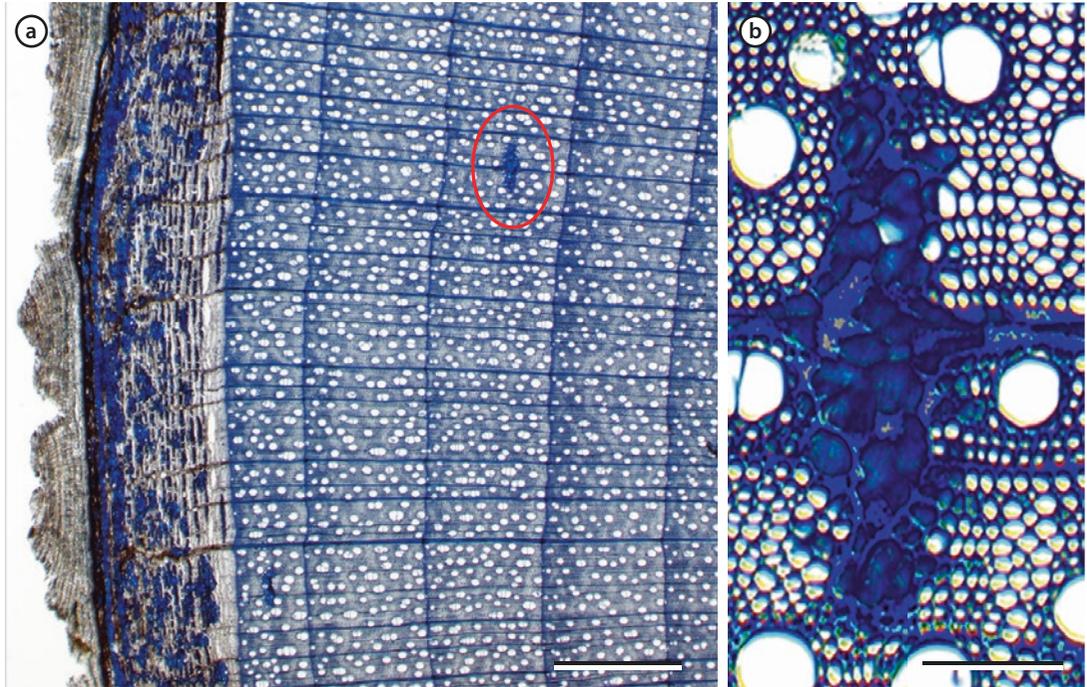
◘ Fig. 7.8   a, b Wound repair in sugar maple (*Acer saccharum*) xylem. **a** Low-magnification image showing area of wound repair (red ellipse). **b** Higher-magnification view of repaired area. Note thick-walled sclereids. Scale bars = 500 μm in **a** and 100 μm in **b**. (**a**, **b** RR Wise)

7.9   Chapter Review

■   **Concept Review**

7.1 *Xylem is a complex tissue containing multiple cell types, each with a specific structure and function.* Xylem cell types include tracheary elements (tracheids and vessel elements which are dead at maturity) and parenchyma (which are alive at maturity). With their thick secondary cell walls, tracheary elements conduct water and provide support. Tracheary elements are divided into two classes. Imperforate tracheary elements are long, narrow, and tapered at the ends. As their name suggests, they lack a perforation. They include tracheids in gymnosperms and tracheids, fiber tracheids, and libriform fibers in angiosperms. Perforate tracheary elements are short and wide and are connected end-to-end via perforations (large holes at the ends of the cell) to form a vessel.

7.2 *The primary functions of xylem are water, mineral conduction, and support.* Transpirational water moves from the soil to the atmosphere via the xylem and is driven by difference in energy between the water in the soil and the water in the atmosphere as described in the cohesion-adhesion-tension model. Xylem water is pulled through the plant and is therefore under tension. As a result cavitation—the formation of a gas bubble that blocks water flow—is a constant threat. The need to minimize cavitation while maximizing water flow has driven almost every aspect of tracheid and vessel element evolution.

7.3 *Tracheids are imperforate tracheary elements and the sole water conductors in gymnosperms.* Gymnosperms tracheids serve the dual role of water conduction and support. Their tapered ends overlap and water movement between tracheids is via pits in the side walls.

7.4 *Angiosperm tracheids, fiber tracheids, and libriform fibers represent a continuum of imperforate tracheid design and function.* Angiosperm imperforate tracheary elements serve mostly for support, although water-conducting tracheids are not uncommon. The three imperforate cell types differ in the number and shape of side wall pits. Tracheids have circular bordered pits. Fiber tracheids have fewer and slit-like pits. Libriform fibers have the least pitting, and those pits are simple. Numerous examples exist of intermediate morphologies. All three cell types are collectively called xylary fibers. Angiosperm wood has a lower percentage of imperforate tracheary elements than gymnosperm wood. To manufacture paper, xylary fibers are digested from angiosperm and gymnosperm wood and formed into thin sheets.

7.5 *Vessel elements are perforate cells and the main water conductors in angiosperms.* The evolution of vessel elements was a major advancement for angiosperms and followed from tracheids, to fiber tracheids, to libriform fibers, to vessel elements. Over evolutionary time, vessel elements evolved to be short and wide with large openings at the ends (perforations).

7.6 *Vessel element side walls are patterned for strength and water movement.* Vessel element side walls have distinct patterns that reflect the balance between the age of the tissue (developing or developed), the need for strength, and the need for the free movement of water. In order of complexity, the five basic patterns are annular, helical (spiral), scalariform, reticulate, and pitted. Pits are holes in the secondary cell wall and may be simple, half-bordered, or bordered. The pit aperture is covered by the pit membrane, which is the remnant of the original primary cell wall. Bordered pits often have a cavitation-limiting valve composed of a margo and torus. Vestured pits have numerous cell wall projections into the pit cavity. Pits may be arranged in an opposite pattern or an alternate pattern.

7.7 *Most vessel elements end in a perforation plate and are connected to another vessel element.* The vessel element end wall is called a perforation. Simple perforation plates have no obstructions. Complex perforation plates have obstructions in a scalariform, reticulate, or ephedroid pattern. The last vessel element in a vessel typically does not have a perforation in its distal end.

7.8 *Xylem parenchyma are living cells involved in xylem metabolism and protection.* Xylem parenchyma cells are the living cells of the tissue and play a variety of roles including storage, pathogen defense, wound repair, and the maintenance of water balance. There are axial parenchyma and ray paren-

chyma. Parenchyma may have perforations that allow rapid exchange of water with adjacent vessel elements.

■ **Concept Connections**

1. Complete the concept map using the following terms: ephedroid, imperforate tracheary element (x2), libriform fiber, perforate tracheary elements, reticulate, simple, tracheid, fiber tracheid, and vessel elements.
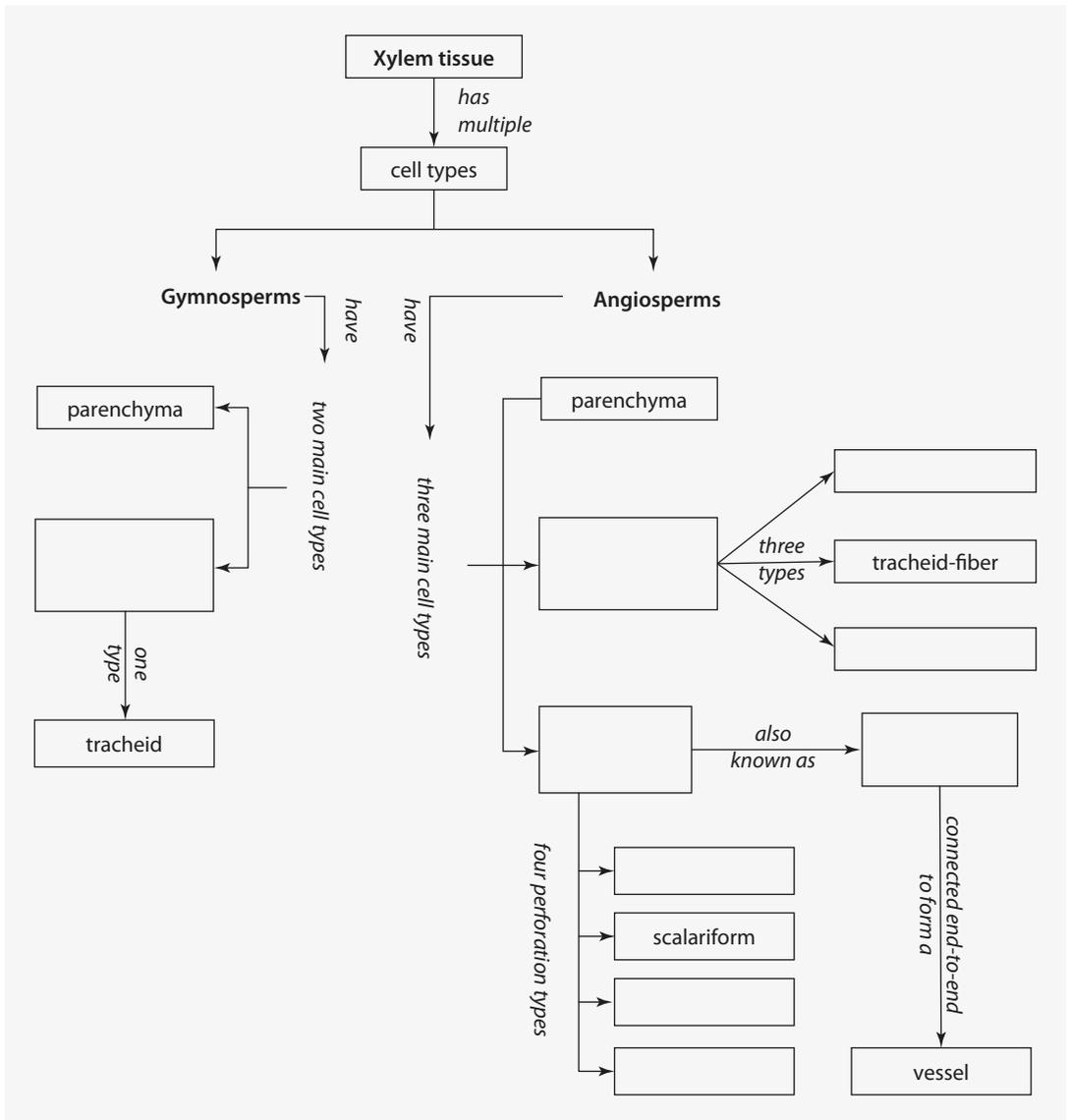
■ **Concept Assessment**

❓ 2. After primary growth is complete, elements of the protoxylem are
   a. recognized by circular or spiral secondary wall thickenings.
   b. transformed into metaxylem.
   c. active in water conduction.
   d. differentiated into tracheids.
   e. stretched, broken and replaced by metaxylem.

❓ 3. The most "derived" perforation plates are considered to be
   a. scalariform.
   b. simple.
   c. oblique and foraminate.
   d. foraminate.
   e. with beaks.

❓ 4. Crassulae are represented by
   a. thickened end walls of tracheids.
   b. pitting in vessel members.
   c. primary wall thickenings between bordered pits.
   d. the secondary wall covering a margo and torus.
   e. ray tracheids.

❓ 5. Which sequence of progression of secondary cell wall complexity is correct?
   a. scalariform pitting-alternate pitting-opposite pitting-annular thickening-helical thickening.
   b. helical thickening-alternate pitting-annular pitting-reticulate pitting-scalariform pitting.
   c. annular thickening-scalariform pitting-reticulate pitting-alternate pitting-opposite pitting.
   d. helical thickening-reticulate pitting-scalariform pitting-opposite pitting-alternate pitting.
   e. annular thickening-alternate pitting-opposite pitting-scalariform pitting-reticulate pitting.

❓ 6. Which is not found in a monocot (e.g., corn) vascular bundle?
   a. metaxylem.
   b. scalarified bundle sheath.
   c. protoxylem lacuna.
   d. metaphloem.
   e. cambium.

❓ 7. A bicollateral vascular bundle
   a. has phloem on both sides of the xylem.
   b. has xylem on both sides of the phloem.
   c. is represented by the fusion of two vascular bundles.
   d. possesses no vascular cambium.
   e. has only one layer of xylem and of phloem.

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❓ 8. Half-bordered pits are found between
   a. ray and axial tracheids.
   b. tracheid and parenchyma cell.
   c. two vessel members.
   d. two tracheids.
   e. two parenchyma cells.

❓ 9. Closed vascular bundles are the only form of bundle
   found in
   a. ferns and other lower plants.
   b. gymnosperms.
   c. eudicots.
   d. monocots.
   e. all plants.

❓ 10. In ferns, scalariform thickenings of tracheary elements
   a. do not allow the plant cell to elongate.
   b. are transformed into reticulate thickenings.
   c. form simple pits.
   d. are deposited during the early growth and elongation.
   e. cannot be seen in macerated preparations.

❓ 11. What are the most advanced features of derived vessel
   members?
   a. long, inclined perforation plates, simple openings, no pits.
   b. short, wide cells, simple openings, pits.
   c. long, tapered end walls, pits, reticulate openings.
   d. short, narrow cells, reticulate openings, no pits.
   e. long, scalariform perforation plates, pits, straight end walls.

▪ **Concept Applications**

❓ 12. List the cell types in angiosperm secondary xylem 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 cohesion-adhesion-tension model.
   Include in your answer an explanation of cavitation.

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