1 Conducting Units: Tracheids and Vessels

1.1 Evolutionary Specialization

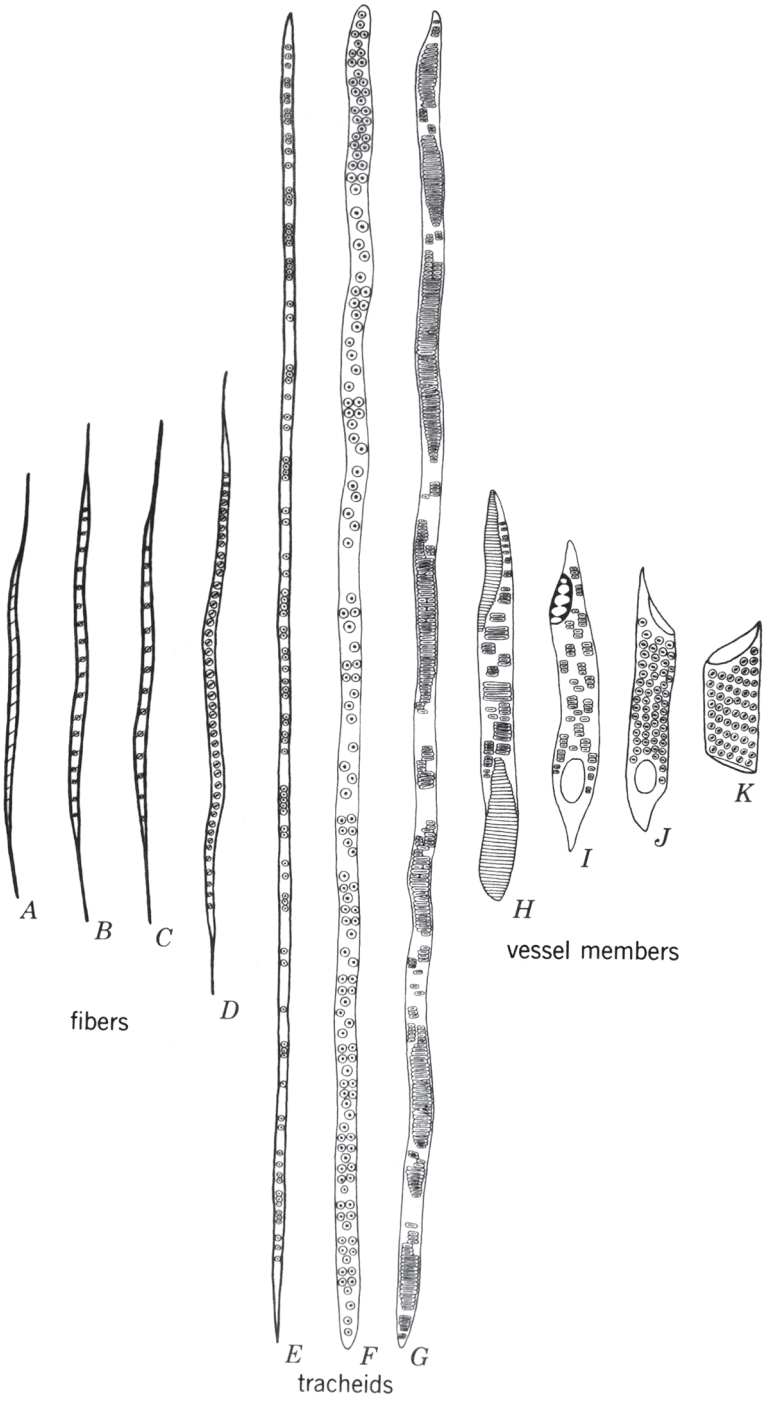
The development of upright land plants depended on the development of a water-conducting system. Many of the earliest land plants, e.g., species of *Rhynia* and *Cooksonia*, had little woody stem, depending mostly on turgor pressure of soft tissues for support (Niklas 1993a,b). As plants evolved to taller sizes, water conduction and mechanical support were more closely linked; in fact, this still is the case in many present-day plants that have no vessels, like the conifers. Both water conduction and rigidity depend largely upon cell-wall lignification, and it is thought that it was the evolution of the biochemical synthesis of lignin that made upright land plants possible (Barghoorn 1964).

The first more-or-less continuous record of upright land plants dates back to the upper Silurian era, about 400 million years ago (Andrews 1961; Banks 1964), although there are sporadic earlier records. Tracheids appear to have been the only highly specialized water-conducting elements in existence for some 300 million years. At the end of this time, when the flowering plants arose, xylem became more specialized by a separation of water conduction from mechanical support. This can perhaps best be shown by the imaginative illustration of Bailey and Tupper (1918; Fig. 1.1). This figure suggests how, during evolution, cells became specialized as support cells on the one hand (the fibers) and water-conducting cells on the other (the vessel elements). In 1953, Bailey published a paper in which he discussed various aspects of the evolution of tracheary tissue.

Figure 1.1 also illustrates the significance of cell length. Tracheids in vessel-less woods are generally not only much longer than vessel elements in vessel-containing woods, but also longer than fibers. The fibers serve a primarily mechanical function; this tells us that the great length attained by some tracheids before the evolution of vessels served a hydraulic rather than a mechanical purpose. In the flowering plants, where long-distance water conduction is mostly via vessels, the bulk of the water flows through cell series, namely, the vessels, rather than through individual cells.

Sediments of the lower Cretaceous (ca. 125 million years ago) contain fossil wood that looks quite like modern dicotyledonous wood (Andrews 1961, p. 181; Kramer 1974). How long such vessel-containing wood had been in existence prior to that time is by no means certain.

The construction of a vessel is shown in Fig. 7.5 (left), which illustrates three successive vessel elements of which the middle one is entire and the two outer ones are cut open. These vessel elements (of red maple) have simple perforation plates, i.e., their end walls are completely dissolved. Figure 7.5 (lower right) shows


A
B
C
D
fibers
E
F
G
tracheids
H
I
J
K
vessel members

an example of a scalariform perforation plate in birch wood. End walls are not completely hydrolyzed during the final stages of development in this species. The stages in vessel development, e.g., the degradation of the perforation plate (end wall pairs), have been reviewed by Butterfield and Meylan (1982). The cytochemical studies of Benayoun et al. (1981) are also of interest.

Vessels show a great variety of structural features. Some are wide, others narrow, their perforation plates are of many forms, some occur in clusters, others more or less solitary, etc. This is not the place to describe this diversity in detail; there are books that illustrate it beautifully (e.g., Meylan and Butterfield 1972, 1978a). However, during the course of discussion of hydraulic properties we shall have to explore the possible functional significance of some of these features in more detail.

1.2 Vessel-Length Distributions

The overall dimensions of tracheids, their length and width, can be grasped relatively easily by looking at macerated xylem. Some tracheids are quite long, but those of most of our present-day conifers can at least still be shown on a single page without distortion of the proportion, by diagrammatically "folding" them (e.g., Fig. 11.6 in Esau 1965). However, others are rather too long for convenient illustration. In *Agathis cunninghamii*, lengths up to 10.9 mm have been reported; a 6-mm length is even exceeded occasionally in several pine species (Bailey and Tupper 1918). In a (carboniferous) *Sphenophyllum* species, lengths range up to 3 cm (Cichan and Taylor 1982)! It would be rather difficult to illustrate these to scale.

Vessels are almost impossible to illustrate on a printed page; in fact, their extent and shape was poorly known until recently. Inside vessel diameter is hydraulically an extremely important parameter; this will be discussed in the next section. Vessel diameter has been measured many times in the past. It is somewhat variable and depends, for example, upon age of tree and location within the tree (leaves, branches, trunk, etc.), a feature that will be discussed in Chapter 7.2.

It is rarely possible to see vessels throughout their entire length because they consist of small cells which need a microscope for observation, and at the same time they are so long that a microscope is far too myopic to grasp their extent. They can never be seen on single sections or even on short series of transverse or longitudinal sections. To observe them in their entirety, we need to apply the technique of cinematographic analysis: we look at long series of wood transverse sec-

Fig. 1.1. Diagrammatic illustration of average size and structure of tracheary elements in the mature wood of some conifers and dicotyledons. **E–G** Long tracheids from primitive woods (**G** showing *Trochodendron* or *Dioon*, axially foreshortened). **D–A** Evolution of fibers showing decrease in length and reduction in size of pit borders. **H–K** Evolution of vessel elements, decrease in length, reduction in inclination of end walls, change from scalariform to simple perforation plates, and from scalariform to alternate vessel-to-vessel pits. (Bailey and Tupper 1918)

tions, recorded on film, with a special movie projector, a so-called analyzer. By running the film forward or backward, we can move up or down the stem in axial direction at any speed, go frame by frame, or stand still at any one point. The intractable axial dimension, otherwise inaccessible to the microscope, is thus translated into time, and we can move from one end of a vessel to the other end by observing a "moving" transverse stem section on the projection screen. Vessel ends thus become visible, the course of vessels can be plotted and the vessel network can be reconstructed. Cinematographic analysis will be discussed briefly in the next chapter in connection with vessel network reconstructions. Let us now look at vessel length in another way.

Vessels consist of series of individual cells, the vessel elements, whose end walls are partly or completely dissolved during late stages of cell maturation, thus forming together long capillaries. The ends usually taper out; it is very important for the understanding of water conduction to realize that the water does not leave a vessel in axial direction through the very end, but *laterally* along a relatively long stretch where the two vessels, the ending and the continuing one, run side by side. The principle is shown in Fig. 1.2. A vessel consisting of nine elements is shown on the left in its entirety. Parts of three others are shown. The illustration is rather diagrammatic, because vessels consist in reality of a far greater number of elements and lengths of overlap can be very much longer. The overlap area between two vessels is of a peculiar structure, shown on the right of Fig. 1.2; this will be discussed later (Sect. 1.5).

The older literature contains only information on maximum vessel length (e.g., Greenidge 1952) and "average" vessel length (Scholander 1958). The concept of vessel-length distribution has been introduced by Skene and Balodis (1968). The only accurate way to obtain information on vessel-length distribution is to use the cinematographic technique, which is far too labor intensive to be practical for routine studies. One way to obtain a qualitative impression of vessel-length distribution is to perfuse cut stems with a dilute latex paint. Suitable paint mixes have pigment particles that are small enough to pass through all vessel lumina and large enough to be stopped by the pit membranes. Ideal particle sizes are between 0.2 and 2 μm in diameter. At the cut surface of the stem, all vessels are cut open so paint particles can freely enter when perfused under pressure. Particles presumably travel the full length of the vessels and accumulate along the walls of the vessel wherever water flows through a pit to an adjacent vessel. The stem is then cut into segments of equal length (e.g., 2-cm length) and the number of paint-filled vessels observed under a microscope in each 2-cm segment. A plot of the number of paint-filled vessels versus distance from the point of infusion gives a length distribution for the length of vessels from the infusion surface to the end of the vessel. Without further analysis, these data cannot yield information on vessel-length distribution because it cannot be determined whether the infusion surface was near the distal, basal or median portion of any particular vessel.

Quantitative information on the probable vessel-length distribution can be derived if we assume that vessel ends occur randomly over the length of a stem segment. Vessel ends are randomly distributed if successive stem segments of the same length, dL, are likely to contain the same number of vessel ends. Skene and Balodis (1968) provide a rigorous statistical analysis to deduce vessel-length distributions from a paint-infusion experiment by use of a double-difference (DD)

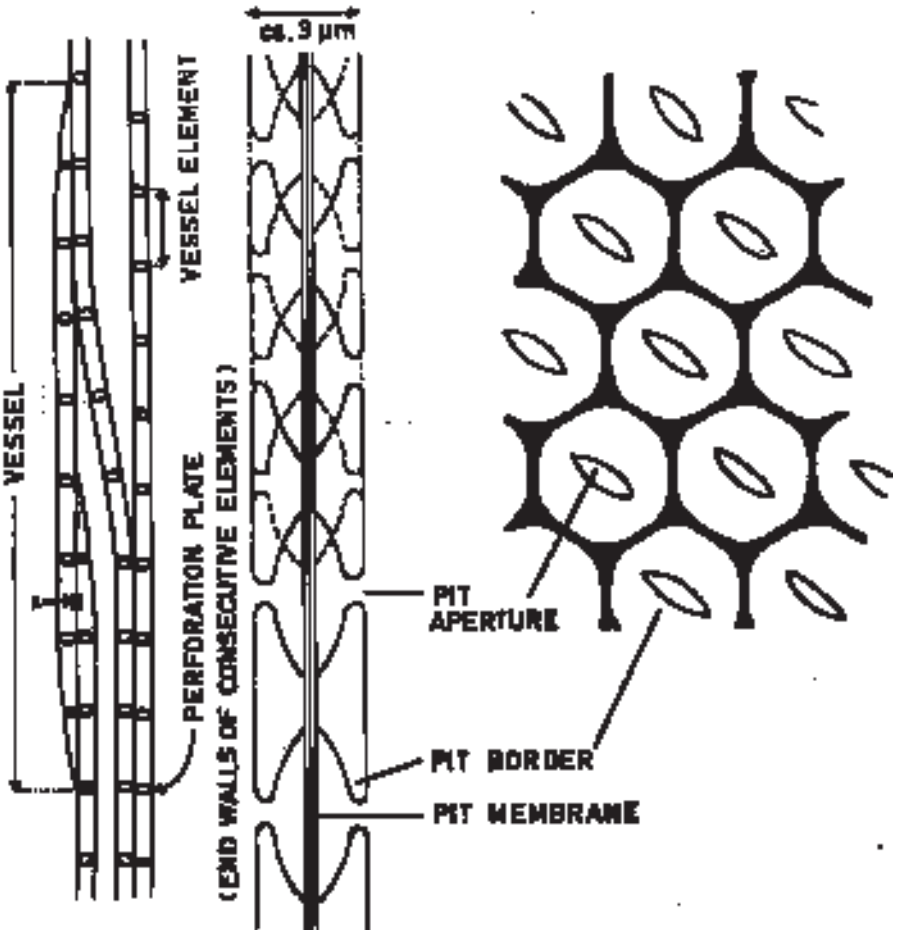


Fig. 1.2. *Left* Diagrammatic representation of a vessel network. Vessels are of finite length, their ends are overlapping. Water moves from one vessel to the next laterally through bordered pits. *Center* Diagrammatic section through a bordered pit field as we would see it at higher magnification in the *boxed area at X* of the left-hand drawing. The secondary walls arch over the primary wall pair, the pit membranes, providing mechanical strength with minimal obstruction of the membrane area. *Right* Vessel-to-vessel pit membrane in surface view. *Black hexagonal pattern* is the area where the secondary wall is attached to the primary wall, thus leaving much of the membrane accessible to water flow. (Zimmermann and McDonough 1978)

algorithm. The DD algorithm is used to convert the counts of paint-filled vessels into a frequency distribution of the number or percentage of vessels in size classes of length *L*. To illustrate the DD algorithm, let us consider a stem containing vessels of equal length but with randomly located vessel ends. Figure 1.3 A is a two-dimensional representation of a stem containing 10 vessels in a cross section. The stem is 40 cm long and contains 50 open or closed vessels. (An open vessel is a ves-