Letter to the Editor

Vessel ends and the disruption of water flow in plants.

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Vessels are indeed of limited length as Beckman and Keller (2) pointed out in their recent Letter to the Editor. However, their description of vessel ends is incomplete and could be interpreted as supporting the common misconception of continuous capillaries with occasional transverse septa (i.e., undissolved end walls of vessel elements). Resistance to flow would be extremely high in such a system. Ironically, I may be partly responsible for this misconception by having used Scholander's figure (9, Fig. IV-1) which implies such a structure. However, this figure is not intended to show how vessels end or how water flows from one vessel to the next on its way up the plant. Precise information is given in another figure (9, Fig. IV-6) as an actual plot of all vessels contained in a piece of wood, $2 \times 3 \times 43$ mm. This shows six ending vessels and the legend points out that "vessel-to-vessel movement of water must be visualized through pits in areas where vessels run in pairs or groups."

It is impossible to obtain a clear concept of vessels and their ends from single microtome sections as Beckman and Keller (2) point out, despite some reports to the contrary (e.g., 4). Indeed, the principle that Beckman and Keller (2) employed had been used by Skene and Balodis (6) for a complete quantitative account of the distribution of vessel lengths in *Eucalyptus obliqua* [cited and illustrated also in (9) as Fig. IV-2 and IV-3].

The best methods to show vessels and their endings clearly and unambiguously is with motion picture film, assembled from images of serial transverse sections. We developed such methods about 1963 and since then have used them extensively, primarily to study vascular development in palms (8, 11). With these methods, it is possible to plot distribution and length of all vessels in a plant organ (a single *Ricinus* petiole, for example, contains several hundred vessels). When such a film is projected, one sees successive transverse images on the screen and by substitution of the axial dimension by time, one obtains a very accurate concept of even the most complex three-dimensional structures. Such a film, showing the three-dimensional structure of wood over long axial distances (not merely three-dimensional in the sense of SEM pictures with a great depth of field) has been published and is available for rental or purchase (7).

We are presently in the concluding stages of writing a chapter, entitled "The effect of disease on the flow of food" for Vol. III of J. G. Horsfall and E. B. Cowling's "Plant Pathology - An Advanced Treatise" (10). The editors have given me permission to use here one of my illustrations before the publication of Vol. III. Figure 1-A

shows in a very diagrammatic way how vessels are arranged in the xylem. Vessels always end in close contact with one or more continuing vessel(s). Ends are always many, perhaps 20-50 individual elements long and often taper out. Wherever vessels run parallel in pairs or groups, their common walls are entirely occupied by bordered pit pairs. The fact that these pits are bordered is crucial for the movement of water from one vessel to the next (1). Most of this area, perhaps as much as 80% consists of primary wall (the pit membrane) which is very permeable to water and can be reached via the pit aperture (Fig. 1-B, C). The mechanical support (i.e., the secondary wall) arches over most of the pit membrane and touches it only on a small total area, shown in Fig. 1-C as a black hexagonal pattern. The reasons why the conductivity of vessels is not much lower than that of endless capillaries of equal diameter are the large area of overlapping vessel ends and the large percentage of primary wall area exposed as pit membrane.

Limited vessel length gives the plant the benefit of safety. Xylem water is usually under tension. If embolism occurs through an accident, it remains confined within the vessel in which it occurs, because the air-water interface cannot penetrate the pit membrane [for a discussion of quantitative aspects of this, see (9), p. 207]. Assume, for example, that a fungal hypha dissolves a spot of the short vessel shown at the far left of Fig. 1. Air then will be sucked into the vessel because ambient air is at a pressure of +1 atm, whereas vessel water is at a pressure below zero. Water will retreat from the injured vessel via intervessel pits into the neighboring intact xylem which is still under tension. Such an air embolism puts the vessel permanently out of function. It may later be plugged by gums, tyloses, or fungal hyphae. But the initial, and probably only cause of disruption of water conduction is embolism, not plugging. Diseases like chestnut blight, Dutch elm disease, and oak wilt are so deadly because the affected trees are ring-porous. Ring-porous trees have a water conduction "strategy" of high efficiency and high risk. Vessels are wide and long and develop emboli every winter. A new set is formed in the spring before leaves emerge (hence their ring-porousness). Because of their efficiency the new vessels are sufficient to supply the crown of the tree with water, but their large size, comparatively small number, and superficial location make them extremely vulnerable (5, 9). As Beckman and coworkers (3) described, spores sucked into an injured vessel cannot travel further than to the vessel ends, but in ring-porous trees this may involve considerable distances.

Interruption of water conduction also can be caused by embolism in the absence of injury. Excessive stress caused by drought or by opening of stomata by a "hormonal" stimulus, produced by certain wilt diseases and swept to the leaves with the transpiration stream, can break water
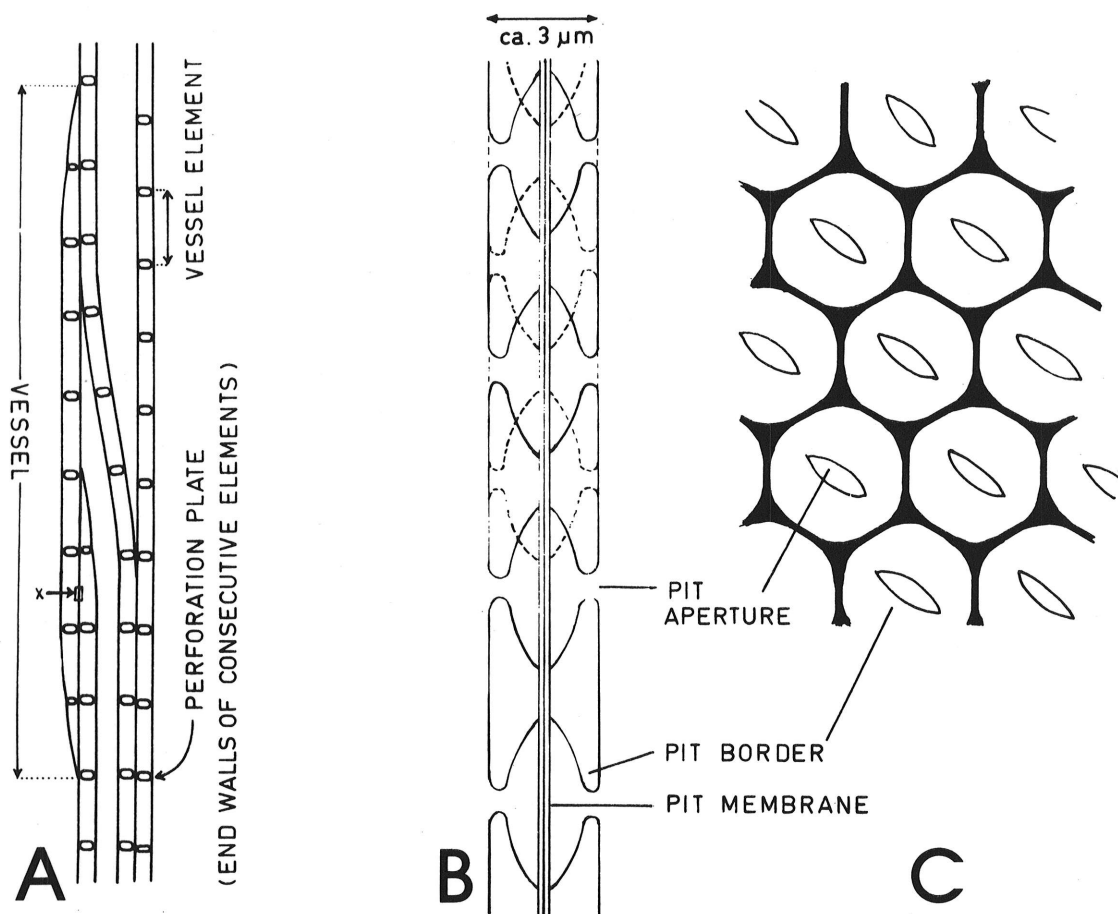
Fig. 1-(A to C). A) Diagrammatic view of vessel network. The functional unit of water conduction is the vessel, not the vessel element. Water moves freely in the vessel, but must pass from one vessel to the next on its way up to leaves. Overlapping vessel ends are dozens of elements long, not merely three or four as shown here. In case of injury, the whole vessel is embolized. From Zimmermann, 1976. Pages 221-235 *in* I. F. Wardlaw and J. B. Passioura, eds. Transport and transfer processes in plants. Academic Press, New York. **B)** A diagrammatic section through the wall between two adjacent vessels as, for example, in the boxed area at X in the left-hand drawing. Passage of water from vessel to vessel is through the pit membranes of the bordered pit pairs. If an embolus forms in one of the vessels, the gas-water interface cannot enter the neighboring vessel. The dashed lines in the upper part of the drawing shows the section at another level. **C)** Vessel-to-vessel pits in surface view to show how they are often arranged in honeycomb fashion. Pit apertures are usually slit-like because cellulose microfibrils in the secondary wall have a high degree of parallel orientation. The secondary wall which gives the vessel elements strength, touches the primary wall (i.e., the pit membrane) only in a limited area, indicated here as a black hexagonal pattern. A very large percentage of the primary walls of the two adjacent vessel elements is exposed and thus available for water movement from vessel to vessel. [By permission of the editors (J. G. Horsfall and E. B. Cowling) of the forthcoming Vol. III, Plant Pathology - An Advanced Treatise, Academic Press, New York.]

columns, in this case by the formation of water vapor emboli. The question of vapor blocks in xylem vessels has received little attention in plant pathology, but it is an interesting area of research.

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