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Little Things Reveal the Big Picture

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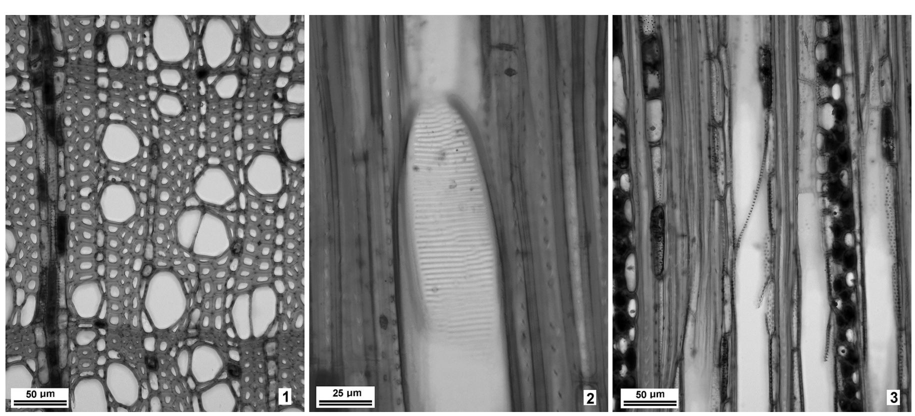
As enthusiasts who enjoy native plants in natural habitats, we tend to focus on gross morphology—aspects of plant form that can be readily observed with the naked eye or with a hand lens. And there is plenty to see at the gross level. The *Flora of Virginia* contains 1,269 pages of keys and descriptions devoted to gross morphology of the commonwealth's botanical treasures. Morphological diversity, however, does not stop at the magnification limit of a hand lens. Light and electron microscopes open up whole new worlds of intricate structure for appreciation and study. And tiny structural details can illuminate and provide insight at much larger scales, such as whole-plant biology or ecology.

This article contemplates a single aspect of the internal microscopic structure of our VNPS Wildflower of the Year, *Clethra alnifolia*, also known as Sweet Pepperbush. Our focus will be vessel elements, cells that function like water pipes in xylem tissue. These cells move water from roots to above-ground organs. It may be a surprise for some to learn that vessel-element cells are dead at functional maturity—they consist of nothing more than their tough cell walls that stack together, end to end, forming minuscule pipes (technically, vessels). The large, empty-looking cells in Figures 1–3 are vessel elements viewed in wood, each sectioned in a unique orientation. A critical step in the conversion of a living cell to a vessel element (cell resembling a short length of pipe) is the dissolution of its end walls. Imagine a process analogous to using a can opener to remove the ends of soup cans and then stacking the cans together to make a long conduit for water. Vessel elements stack end to end, forming the water-conducting vessels found in xylem.

Many plants have vessel elements for which the soup-can analogy, minus tops and bottoms and stacked together, requires little additional explanation. Vessel elements of oak and ash trees are good examples. The situation in *Clethra,* though, is a little more complex. First, the end walls are not perpendicular; instead, they are inclined so that in profile view the end of the cell takes the form of a wedge (Figure 3). Nevertheless, each wedgelike, low-angle end wall in the vessel elements of *Clethra* overlaps with that of the next vessel element above and below, so these cells also form pipelike vessels. But there is one more difference; instead of a single hole in the end wall (as would be made by a can opener), the vessel elements of *Clethra* have multiple slitlike openings, each separated from the next by a slender bar of cell wall material (Figure 2). The openings do, of course, align with each other, and water passes from one cell to the next by passing between the bars. For *Clethra*, the topless, bottomless soup-can analogy is just too simple.

Plant anatomists refer to the openings in the end walls of vessel elements as perforations. Perforations in oak and ash are simple, while those of *Clethra* are scalariform (ladder-like). Among flowering plants at large, simple perforations are more common than scalariform perforations. Can we find any meaning in this information about the details of the water-conducting system of *Clethra*? As mindful readers of this year's Wildflower of the Year articles will remember, *Clethra* and *Cyrilla* are widely acknowledged to be early offshoots of the lineage leading to Ericaceae. As it turns out, scalariform perforations are frequent throughout all three of these families, supporting evidence for their close relationship. Notably, however, some Ericaceae (*Arbutus, Arctostaphylos)* have simple perforations.

It is widely thought that water moves more efficiently through vessels with simple perforations than those with scalariform perforations; all those little bars of wall material must impede water flow to some extent. Ecological data support this idea. As noted by Sherwin Carlquist (1976),



WOOD OF *CLETHRA ALNIFOLIA.* 1. Cross section; large open cells are vessels seen in cross section. 2. Radial section; scalariform perforation from the shared end wall of two overlapping vessel elements. 3. Transverse section; the steeply inclined end walls of two overlapping vessel elements.

the flora of Southern California is dominated by plants with simple perforations. Southern California, of course, is an arid land that imposes harsh demands for efficient conduction during those brief occasions when water is available. Of all the plants in this habitat, only five species possess scalariform perforations, and all of those occur in canyons, near watercourses, or where the water table is relatively shallow. Many related ecological observations support the general conclusion that, because scalariform perforation plates are inherently inefficient, plants with scalariform perforations conduct adequately only in environments with plentiful soil moisture. And where does *Clethra* grow? Though sometimes found in dry conditions, it is much more frequently a denizen of moist forests, swamps, seeps, and ditches.

Whereas conductive inefficiency may well be an impediment that limits the ability of *Clethra* and plants with similar plumbing to colonize dry habitats, students of xylem structure and function have identified a potential adaptive value for scalariform perforation plates. Xylem conducts water and, in temperate regions, water freezes in winter. As water freezes, it loses its capacity to hold atmospheric gases in solution. In winter, when water freezes inside vessel elements, inevitably, little bubbles form. Problems arise when the ice melts because these bubbles rise as far as they can go inside the xylem vessel. In plants with simple perforations, this means that bubbles can accumulate from the ice of many individual vessel elements, ultimately coalescing as a large air bubble (embolism) somewhere in the upper reaches of the vessel. This is a problem because a large air bubble completely shuts down the flow of water; the mechanism of water flow in plants requires continuity of the water column. In plants with scalariform perforations, however, air bubbles from melting ice will be caught by the bars of perforation plates at the upper end of each vessel element. There is no chance for multiple bubbles from long stretches of the water column to coalesce; consequently, continuity of the water column and therefore the capacity to conduct water from root to shoot is maintained. Birch trees, for example, are also thought to benefit in this way from their scalariform perforations. Of course, most species of *Clethra* are found in the tropics, where freezing is not an issue. Nevertheless, scalariform perforations in the xylem of *Clethra alnifolia* (or its ancestor) may well have functioned as an adaptation, allowing it to maintain water columns in the conduction system as this once tropical plant expanded its range into temperate regions to the downright frigid conditions that it must endure at its northern limits, in Nova Scotia.

Bottom line: everything in biology is connected; even tiny microscopic details can illuminate ecology and systematic relationships!

Literature Cited

Carlquist, S. 1976 Ecological Strategies of Xylem Evolution. University of California Press, Berkeley.