COMMENTARY

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Going with the flow: Structural determinants of vascular tissue transport efficiency and safety

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1 | INTRODUCTION

The woody tissue of flowering plants contains many vessels, which interconnect to form a vascular network responsible for the bulk transport of water through the plant. The structure of individual vessels, combined with network traits, such as the connections between vessels and the distribution of vessels of differing structural properties, determines the hydraulic efficiency and safety of the xylem tissue. In this issue, Mrad, Domec, Huang, Frederic, and Katul (2018) present a new model of xylem tissue function developed by combining information across multiple structural scales, including intervessel pit membrane and pore structure, vessel structure, and vessel network traits. This model was able to predict xylem hydraulic function in *Acer* and provides a new framework in which to evaluate the impact of vessel structural and network trait variation on hydraulic function and resistance to dehydration induced water transport failure (embolism).

Declines in xylem conductivity during water deficit are often plotted as "vulnerability curves," which depict hydraulic transport losses due to embolism formation in response to negative pressures in the xylem. The role of individual vessel structural traits, such as vessel diameter, on xylem tissue vulnerability to cavitation has been the focus of many studies, but few studies have combined traits across multiple scales (i.e., pits, vessels, and networks; Figure 1). In particular, understanding the role of network properties on hydraulic function has been rarely examined. The combination of modeling with plant anatomical and functional studies has potential to greatly advance understanding of these complex multiscale networks (Venturas et al., 2016).

Mrad et al. discussed the implications of their results in the context of vessel connectivity and the scaling between pit and vessel structures. They identify the scaling between vessel and pit traits and how these determine the likelihood of embolism propagation

through the xylem as a particularly important and understudied topic for future research. Here, we draw attention to novel avenues of future research that derive from their study and discuss some of the broader implications of their new xylem model.

2 | ESTIMATING HYDRAULIC FLOW THROUGH AN EMBOLIZED NETWORK

Understanding how conductivity declines as vessels in a network become embolized is important for biological and methodological reasons. Some methods rely on evaluation of visual data (e.g., microCT and optical methods), and image-based estimates of hydraulic function have assumed that water-filled vessels maintain optimum values of hydraulic conductivity with dehydration. Thus, image-based studies have used Hagen–Poiseuille based flow estimates for xylem vessel conductivity across all water potentials and levels of network embolism (e.g., Choat et al., 2016). This assumption has not been carefully tested, and the model by Mrad et al. suggests that there is potential for considerable divergence between visual estimates of conductivity and the actual conductivity of a tissue. Data from visual methods that assume maintenance of optimal flow would not be expected to agree with methods that directly measure hydraulic conductivity.

Developing visual methods that can account for the importance of network properties in determining tissue function, especially in the context of networks that contain emboli, is an important research priority. For hydrated xylem tissue samples, theoretical conductivity (K_t) estimates based only on Hagen–Poiseuille calculations overestimate conductivity. This is because vessels are not perfect cylinders and also vary in diameter longitudinally (Tyree & Ewers, 1991), and neither perforation plate resistance (Ellerby & Ennos, 1998) nor pit membrane resistance (Sperry, Hacke, & Wheeler, 2005) is accounted for
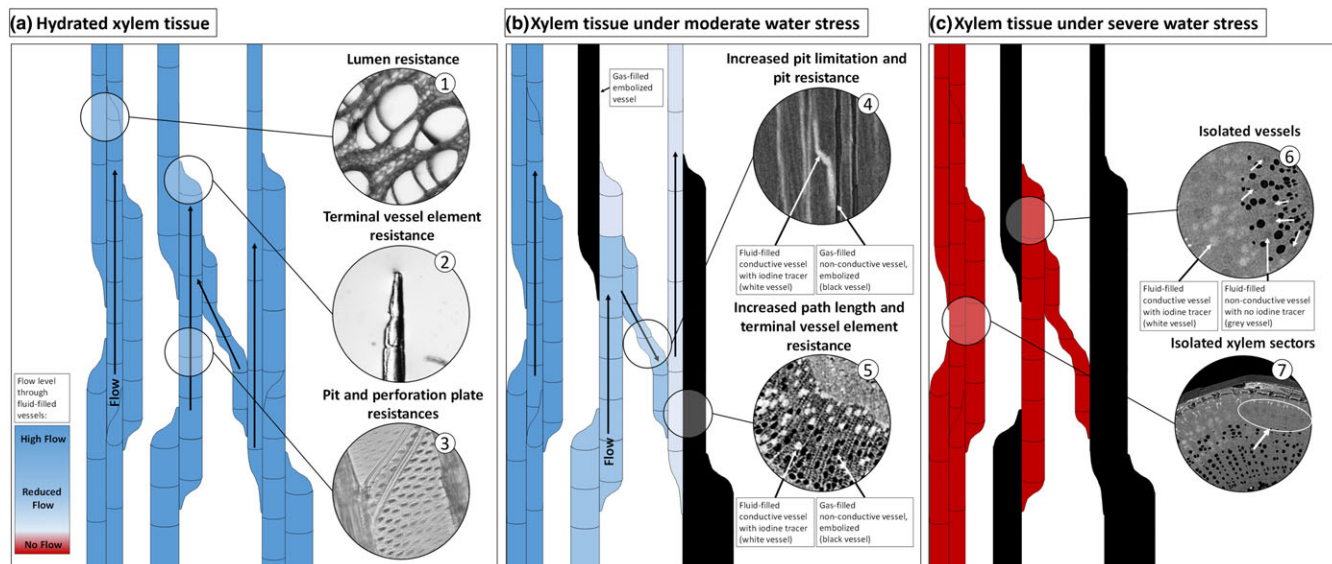
FIGURE 1 Estimating the hydraulic flow through vessels within the xylem tissue relies on knowledge of the resistances impacting flow. These resistances vary depending on the proportion of embolism within the vessel network. For hydrated xylem tissue (a), flow through the tissue is determined by the lumen resistance of individual vessels (based on the Hagen–Poiseuille equation), resistance linked to vessel endings (terminal vessel element resistance) that require that flow be diverted to other conduits, pit and pit membrane resistances, and perforation plate resistances. As vessels within the network start to embolize (b), flow is further reduced by increased pit limitation and path length. Embolism in a vessel reduces the flow through all vessels connected to it, because the number of pits that are available for water to flow into or out of a water-filled vessel is reduced (pit limitation). Additionally, fluid must flow through increasingly tortuous pathways of vessels, which increases the transport path length of fluid; in some cases, flow may even reverse direction within vessels in embolized networks (Lee et al., 2013). At more extreme water potentials (c), propagation of embolism through the network results in vessels and xylem sectors becoming isolated leading to a conductivity of zero through these vessels, even though they remain water-filled. Inset photos: (1) vessel lumens from a xylem cross-section, (2) silicone cast of a terminal vessel element, (3) connections between vessel elements, including a perforation plate and many visible pits, (4) longitudinal section showing conductive vessels (white), with flow diverting around an embolized vessel (black) creating a very short and limited connection between two vessels, (5) cross section showing many embolized vessels (black) with dispersed conductive vessels (white), with flow likely having to considerably divert from the shorter pathways that would have connected vessels when most were fluid-filled, (6) several nonconductive fluid-filled vessels (grey; image modified from Pratt & Jacobsen, 2018), and (7) a sector of xylem containing many nonconductive fluid-filled vessels (image modified from Pratt & Jacobsen, 2018). Images 4–7 are high resolution computed tomography scans (microCT, photos 4 and 5 Pratt unpublished data) of xylem that has been feed iodine tracer to identify conductive fluid-filled vessels (see Pratt & Jacobsen, 2018, for information on this method)

(Figure 1a). As vessels embolize, the conductivity of a water-filled vessel that is connected to embolized vessels will decline further relative to Hagen–Poiseuille based K_t estimates as pit resistance and flow into and out of the vessel become increasingly limiting. Within the tissue, path length increases as flow diverts around blocked conduits (Figure 1b). Additionally, according to the air-seeding model of cavitation, the most vulnerable conduits with the most conductive pit membranes (larger diameter pores) will be the first to embolize, limiting transport to more resistant and less conductive vessels within the tissue. At more extreme water potentials, propagation of embolism through the network results in vessels and xylem sectors becoming isolated leading to a conductivity of zero through these vessels, even though they remain sap-filled (Figure 1c). The degree of vessel isolation is affected by vessel connectivity and the distribution of vessels of differing vulnerabilities within the network (Mrad et al., 2018; Venturas et al., 2016). Thus, K_t estimates solely based on Hagen–Poiseuille based calculations become increasingly susceptible to overestimation errors as samples dehydrate and embolize. Information on xylem anatomy and network structure could be used to hone conductivity estimates from visual methods using Mrad et al.'s model.

3 | EVOLUTION OF VESSEL NETWORKS TO MINIMIZE REMAINING VESSEL WATER

Mrad et al. modeled hydraulic flow through xylem networks to generate vulnerability to cavitation curves. They found that approximately 50% of vessel water (the proportion of water in vessels relative to the amount of water that all vessels could contain) remained within modeled networks with 100% loss of conductivity (their figure 4). This was primarily due to the isolation of vessels and xylem sectors as embolism progressed (pink vessels shown in their figure 2). Vessel isolation was previously suggested in a prior xylem model (Loepfe, Martinez-Vilalta, Piñol, & Mencuccini, 2007), and there is some evidence to support this within plants (Figure 1c; Pratt & Jacobsen, 2018), although further experimental validation of this model prediction is required.

Although the current model was developed for a diffuse porous vessel network composed of predominantly short vessels, it is clear from the model of Mrad et al. that vessel networks with different vessel structure and network topology would likely yield different outputs. At the dry end of the vulnerability curve, this may be particularly important. Leaving 40–60% of vessel water "behind" may

be an outcome of certain vessel network structures and topologies, but where embolism is common, there may be selection for networks that can continue to function in spite of considerable embolism. Studies combining both microCT, to visualize embolism quantity and patterns, and hydraulic conductivity measurements should yield new insights in this context.

It is intriguing to think about xylem traits that minimize vessel isolation in embolized networks, particularly in the context of the trade-off of safety and efficiency. Networks with increased connectivity and pit area may leave fewer vessels and xylem sectors isolated, but such a network would have high connectivity and pit area, which would increase the potential for embolism spread. In contrast, networks with lower connectivity and pit area may be more likely to have vessels and sectors become isolated, but they would be less vulnerable to widespread network embolism, that is, they would be more sectored. In the context of efficiency, a less connected network could have greater numbers of wide and long vessels that minimize the number of pits that must be traversed, thus increasing efficiency.

One way to increase connectivity of a network is by having many small conduits. The presence of tracheids, along with vessels, is an oft overlooked anatomical adaptation in angiosperms, which are particularly well represented in angiosperm species from water limited environments (Carlquist & Hoekman, 1985; Pratt, Percolla, & Jacobsen, 2015). The model by Mrad et al. highlights that vasicentric tracheids (those that surround vessels) within these plants could be important in increasing the connectivity of the network and minimizing the number of isolated vessels when embolism levels are high. As such, tracheids allow for the xylem to maintain function when there are high levels of vessel embolism. The hydraulic role of tracheids in vessel-bearing plants is a fascinating topic of research, and Mrad et al.'s model suggests consideration of anatomical features, such as tracheids, are likely important to minimize vessel isolation.

4 | FUTURE RESEARCH DIRECTIONS

In summary, much of how the vessel network responds to water stress remains little understood. With greater use of new technologies that permit the identification of individual vessels as they embolize, as well as determination of their position within vessel networks, there will be many opportunities to evaluate and fine tune the model presented by Mrad et al. and to develop similarly detailed models for species that exhibit other types of vessel network topologies. This is a necessary step in our evolving understanding of how xylem vessel networks respond to water stress and the traits that are critical in determining plant hydraulic transport strategies and different plant responses to water stress.

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