

Xylem Hydraulics: Rising Up and Higher!

Dilip Amritphale and Santosh K Sharma

This article attempts to examine how xylem hydraulic function is related to the size and redundancy of conduits and whether xylem hydraulic constraint limits tree height.

Introduction

Most studies on ‘rocks and clocks’ (i.e., fossils and DNA sequences) suggest that land plants appeared some 450 million years ago. Early land plants displayed poikilohydry (i.e., little or no capacity to restrict water loss). The development of vascular tissue and stomata propelled land plants to homoiohydric (i.e., capacity to maintain an equitable water balance under changing environmental conditions). However, it was the evolution of xylem, which is designed hydraulically for transport efficiency, safety and mechanical strength, that allowed plants to grow upright and taller. Similar to the hydraulics that relates to the flow of liquids in pipes along a gradient, xylem hydraulics deals with the flow of water in xylem conduits and their hydraulic properties such as conductivity, cavitation resistance, refilling capacity, vessel networking etc. Among the three basic functions of xylem: transport of water and minerals, mechanical support, and storage (*Figure 1*), the transport function of xylem, which allows water to scale tree heights of 100 meters or more, has continued to attract the attention of the scientists and laymen alike for long.

Xylem Conduits: Is Bigger the Better?

Water (technically speaking, about 10 mol m^{-3} aqueous solution of mineral nutrients and some other solutes) moves through the xylem hydraulic network because it provides the path of lowest resistance in higher plants. The network consists of two types of conduits: tracheids and vessels (*Figure 2*). Tracheids are about 5 mm long, spindle-shaped cells arranged in overlapping vertical



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Keywords

Cavitation and embolism, conduit size, tree height, xylem redundancy.



Figure 1. Relationship between xylem structure and function. Transport: vessels and tracheids (heteroxylous wood) in angiosperms and tracheids (homoxylous wood) in conifers; Mechanical support: fibers and tracheids; Storage: parenchyma.

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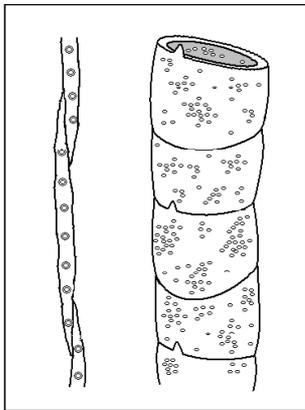
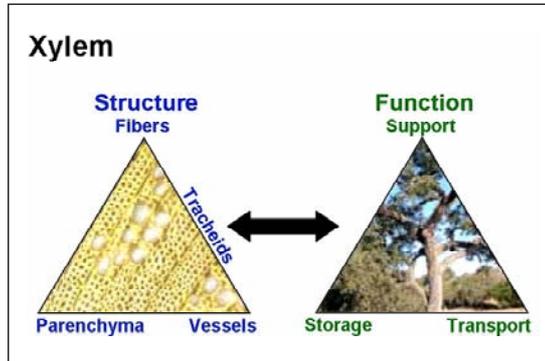


Figure 2. Xylem conduits: (a) tracheids and (b) vessel.

files. Water flows between the tracheids by means of numerous pits in their lateral walls. In contrast to the tracheids, which are relatively small hydraulic compartments, the vessels are relatively long continuous structures formed by the stacking of individual cells known as vessel elements (note that vessel ends are not necessarily aligned, as erroneously given in some books). Vessel elements, which form vessels, are shorter than the tracheids and have perforated end walls that form a perforation plate at each of the end of the cell. They also have pits like tracheids on their lateral walls. Conduit diameters span two orders of magnitude from below 5 μm in diffuse porous angiosperms to over 500 μm in vines – the mechanical parasites (Table 1). The conduits cover an even greater range in length from a few millimeters as in tracheids to over 10 meters as in vessels of vines and ring porous trees.

Table 1. Xylem conduits: Size, flow rate, and conductive efficiency in different plant groups.

(With permission: E D Schulze, Max Planck Institute for Biogeochemistry, Germany.)

Plant groups	Conduit diameter (μm)	Conduit length (m)	Maximum rate (m h^{-1})	Conductive efficiency ($\text{m}^2 \text{s}^{-1} \text{MPa}^{-1}$)
Conifers	10–40	0.002–0.005	1–2	$5\text{--}10 \times 10^4$
Diffuse porous angiosperms	5–150	1–2	1–6	$5\text{--}50 \times 10^4$
Ring porous angiosperms	10–600	10	4–44	$50\text{--}300 \times 10^4$
Herbaceous plants	10–500	1–2	10–60	$30\text{--}60 \times 10^4$
Vines and lianas	600	Ca. 10	150	$300\text{--}500 \times 10^4$



Box 1. Glossary

Air seeding: Entry of air in the conduits through the pores in the pit membrane.

Cavitation: Phase change of liquid water to water vapour that results into a vapour-filled conduit.

Conduit: A water-transporting element in a plant; a xylem vessel or a tracheid.

Embolism: Air-filling of the conduit leading to breakage of hydraulic continuity.

Homoiohydric: Capacity of organisms to maintain an equitable water balance under changing environmental conditions.

Integrated redundancy: A high degree of interconnectedness through conduit networking.

Modular redundancy: Division of whole plant into independent hydraulic units.

Munch water: Sap flowing between phloem and xylem.

Pit membrane: The porous layer between two adjacent pits, consisting of two thin primary walls and a middle lamella.

Pit: A circular area in the conduit wall where a pit membrane separates two adjacent conduits.

Poikilohydric: Little or no capacity of organisms to restrict water loss.

Tracheid: Spindle-shaped, nonliving water-conducting cells with tapered ends and pitted walls without perforations found in the xylem of both angiosperms and gymnosperms.

Vessel elements: Nonliving water conducting cells with perforated end walls found in angiosperms and a small group of gymnosperms.

(a) Conduit Diameter

As you might have already noticed in *Table 1*, the wider the conduits are the higher is their hydraulic conductivity (or the lower their resistance to water flow). According to the Hagen–Poiseuille equation, the lumen conductivity increases with the fourth power of the lumen diameter (i.e., $k \propto d^4$ where k = hydraulic conductivity and d = conduit diameter). Thus, if the relative diameters of three conduits are 1, 2, and 4, the relative volume of water flowing through them under similar conditions would be 1, 16, and 256, respectively. What is not emphasized in the literature is that an increase in lumen conductivity does not necessarily increase the total conduit conductivity. This is because water does not only flow through the lumen, but also through the narrow pits of the conduit end-walls. Therefore, if an

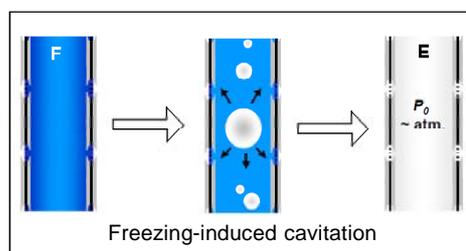


increase in conduit diameter is to cause a fourth-power increase in total conduit conductivity, the end-wall conductivity must increase in concert. Otherwise, an increase in diameter brings diminishing returns.

Although increased conduit diameter increases efficiency of water conduction, at the same time it decreases safety. The conductive efficiency versus hydraulic safety dilemma exists because water in xylem conduits is under negative pressure due to transpiration pull and thus vulnerable to cavitation. Cavitation is an extremely rapid invasion of a xylem conduit mainly by water vapor. A slower entrance of air, which corresponds to embolism, follows cavitation. A negative-pressure flow hydraulic system such as plant xylem is prone to fail because air bubbles (emboli) can lead to breakage of hydraulic continuity. Embolism need not be permanent though, since a number of repair mechanisms such as root pressure, stem pressure or, as recently envisaged, flow of sap between phloem and xylem (Munch water) may operate in plants. But again, cycles of embolism and repair cannot go indefinitely because refilling process may slow down as well as cavitation fatigue may reduce cavitation resistance.

Figure 3. Mechanism of freezing-induced cavitation: When xylem sap in a functional conduit (F) freezes, dissolved gases come out of solution and form bubbles. On the melting of ice, these bubbles nucleate cavitation and with increase in negative pressure the conduit becomes fully embolized (E).

(With permission: J S Sperry, Department of Biology, Utah University, USA.)



Besides mechanical injury, herbivory and pathogen attack, two phenomena – freezing and drought – are largely responsible for cavitation events. Freezing and drought induce cavitation by two separate mechanisms. When xylem sap in the conduit freezes, dissolved gases come out of solution and form bubbles. These bubbles nucleate cavitation when the ice melts and the xylem water is under negative pressure. When the pressure becomes more negative, the bubbles expand fully embolizing the conduit

(Figure 3). Cavitation is less likely to occur as conduit diameter decreases (Figure 4). In addition, narrow short conduits refill more efficiently following cavitation because gas emboli therein have larger surface to volume ratio. This might explain why conifers are much more abundant than broad-leaved trees in many temperate climatic zones. In contrast to

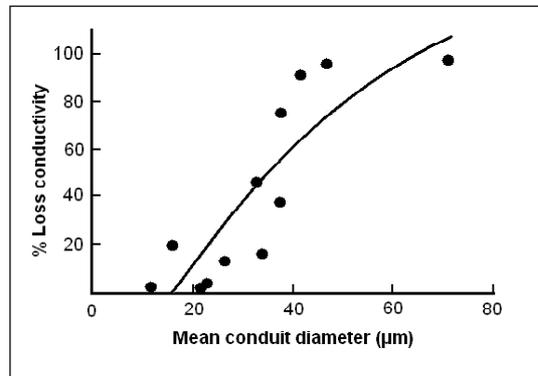


Figure 4. Percent loss conductivity with freeze-thaw as a function of mean conduit diameter.

(Adapted from P Bass and associates in: *The Evolution of Plant Physiology*, A R Hemsley and I Poole (eds.) *Linn. Soc. London*, 2004)

freezing, drought-induced cavitation is more a function of inter-conduit pits and pit membrane porosity than the conduit diameter. The pits are circular areas in the conduit wall where a pit membrane separates two adjacent conduits. The pits are termed as bordered pits when the secondary wall of the conduit arches over the pit cavity (*Figure 5*), and simple pits in which it does not. The pit membrane is not a lipid bilayer, but a layer of degraded primary cell wall and middle lamella located between the pits of two adjacent xylem conduits (*Figure 6*) allowing free movement of water and solutes while restricting air bubbles. The drought-induced cavitation occurs under negative pressure, when air is pulled into a water-filled conduit from an adjacent air-filled

Figure 5 (left). A typical bordered pit: (a) SEM and (b) outline diagram.

(5a) Adapted from www.steve.gb.com

Figure 6 (right). SEM of a bordered pit showing (a) pit membrane (PM) and pit border (PB) and (b) closer view of pit membrane composed of cellulose microfibrils in a matrix of hemicellulose and pectin polysaccharides.

(With permission: B Choat, Research School of Biology, Australian National University, Australia.)

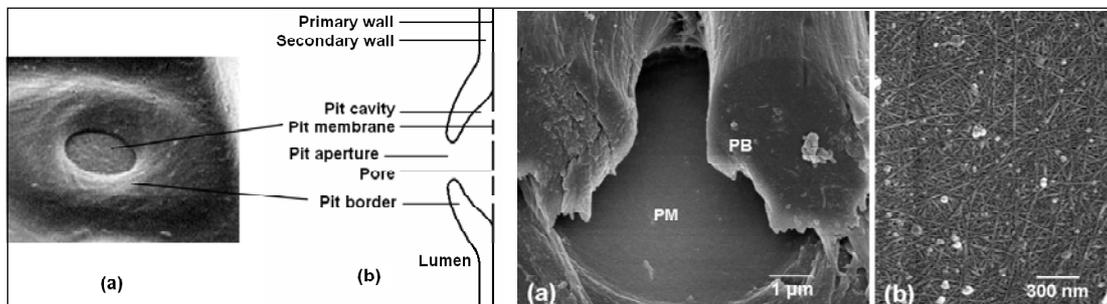
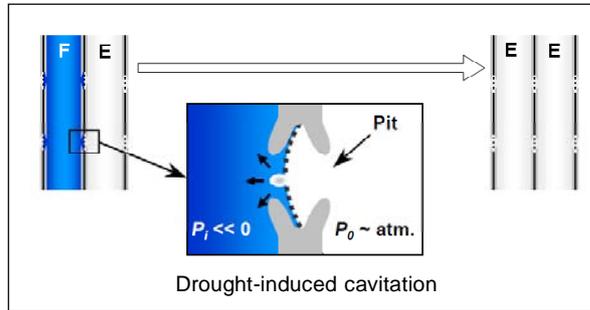


Figure 7. Mechanism of drought-induced cavitation (air seeding): Two adjacent xylem conduits are shown. The left-hand one is filled with xylem fluid, i.e., functional (F). The right-hand one is embolized (E). When the pressure difference between the two conduits exceeds a critical threshold, an air bubble is pulled in through the pit membrane pores consequently embolizing the functional conduit.

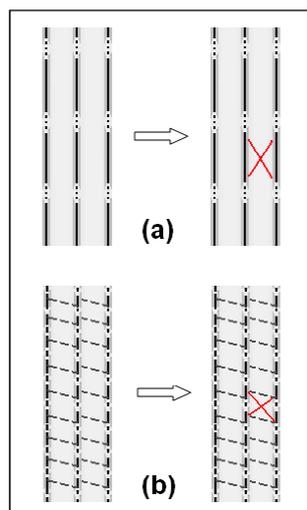


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conduit through the pores in the pit membrane, a process known as air seeding (Figure 7).

(b) Conduit Length

Figure 8. (a) Out of a single set of two conduits traversing the entire path, one conduit was point-injured and (b) out of a single set of two conduits each consisting of ten conduit tiers, one conduit received point injury to only one of the ten tiers.



Another feature of conduits affecting xylem transport efficiency is length (Table 1). This is because end-walls contribute about 50% to total xylem resistance in both conduit types. Obviously therefore, increased conduit length would reduce the number of wall-crossings and the hydraulic resistance to flow within the xylem by decreasing the sequential number of separate conduits needed to traverse the entire pathway. However, similar to width, the efficiency versus safety dilemma sets upper limits on conduit length also. For example, consider the extreme situation where a single set of conduits traverses the entire flow path in a plant. If 50% of the conduits become dysfunctional at one point in the flow path due to drought stress or a mechanical injury for instance, then the whole-plant conductance would be reduced by 50% (Figure 8). In contrast, if the flow path consists of ten conduit lengths, then the same point injury of 50% would cause only about 9% loss of whole-plant conductance. This is because when resistance in one of the ten tiers has doubled due to point injury compared to the others, the total path resistance would increase by a factor of 1.1 given to the fact that resistances are additive in series. Or, the conductance would decrease by a factor of 0.91 (you may recall that conductance is the inverse of resistance) corresponding to a loss of about 9%.



Xylem Redundancy: Are Two Heads Better Than One?

The simplest case for redundancy is having two conduits for one. So, if one is embolized, the other one remains available for conduction. Xylem redundancy, however, does not pertain to conduit number only. Rather, it can vary from a high degree of inter-connectedness through conduit networking (i.e., integrated redundancy) to the division of whole plant into independent hydraulic units (i.e., modular redundancy) (Figure 9).

Integrated redundancy of conduits can protect the hydraulic transport stream against failure by offering alternative transport routes when some conduits become inoperative due to air embolism. But, it may also render the transport system more vulnerable to runaway embolism (i.e., occurrence of further cavitation events due to embolism-induced increase in resistance to water flow). Modular redundancy, on the other hand, can restrict embolisms to a single conduit or group of conduits and also allow independent stomatal regulation of water use in hydraulic modules. But at the same time, it may not allow water and nutrient sharing and re-routing of water flow around blocked pathways. From an ecological perspective, hydraulic integration could be advantageous to plants growing in humid environments, whereas modular redun-

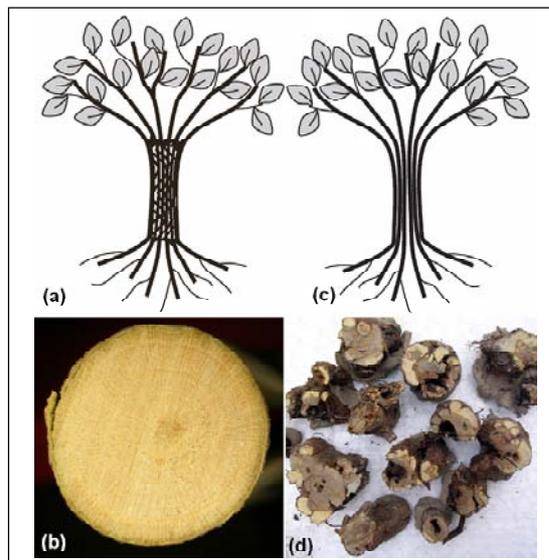


Figure 9. Integrated hydraulic redundancy: (a) schematic and (b) e.g., *Rhus glabra*; Modular hydraulic redundancy: (c) schematic and (d) e.g., *Junellia aspera*. (With permission: H J Schenk, Department of Biological Science, California State University, USA.)

dancy might be beneficial to plants that face increased risk of hydraulic failure caused by drought.

Xylem Hydraulic Limitation: Why Trees Don't Grow up to the Heaven

'Why don't trees grow up to the heaven?' was the theme of a heated debate held sometime ago in front of the Physical-Medical Society at Würzburg, Germany on the pros and cons of the cohesion tension mechanism for the ascent of sap in plants. Trees seem to have mechanisms that slow their growth as they age and prevent them from growing beyond a certain height. For example, a young mountain ash (*Eucalyptus regnans*) may grow 2–3 m per year in height. By 90 years of age, height growth would slow down to 50 cm per year. By 150 years, height growth might virtually cease, although the tree may live for another century or more. A number of explanations, viz., respiration hypothesis, nutrient limitation hypothesis and maturation hypothesis have been offered from time to time to explain the decline in tree growth with age, but none is widely accepted.

Figure 10. *Eucalyptus* sp.: Hydraulic resistance increases as trees grow taller because water must travel a longer path against gravity.



In the late 1990s, the US forest scientists MG Ryan and BJ Yoder proposed the hydraulic limitation hypothesis to explain what limits tree height. According to them, hydraulic resistance increases as trees grow taller because water must travel a longer path against gravity (*Figure 10*). To move the same amount of water through a path with higher resistance would require lower, i.e., more negative leaf water potential. But, as one might recall, lowering of leaf water potential may cause a reduction in stomatal aperture. This, in turn, may reduce photosynthesis by limiting CO₂ uptake thus reducing carbon availability for further height growth. In addition, reduced water potential may also cause a decline in turgor of living cells necessary for cell growth and leaf expansion. Indeed, given the role of turgor in leaf expansion, its reduction with height may underlie the distinct vertical gradient in leaf size and shape observed in some redwoods (*Figure 11*). Of course, the hydraulic limitation hypothesis is on a probation period still. However, if xylem hydraulic limitation does play



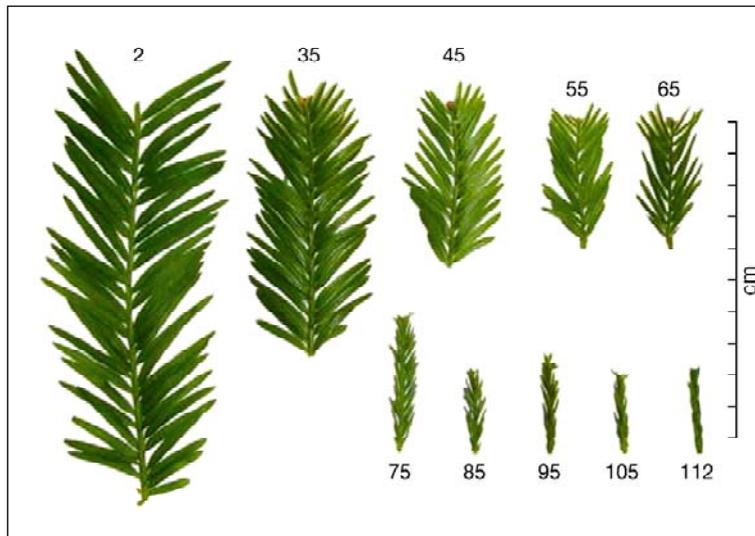


Figure 11. Variation in leaf structure with height in *Sequoia sempervirens*. Leaf length and the angle between the long axis of the leaf and supporting stem segment both decrease with height. Numbers denote the height (in metres) from which leaf samples were collected.

(With permission: G W Koch, Department of Biological Sciences, Northern Arizona University, USA.)

some role in limiting tree height, and if global warming is a real threat causing temperatures to shoot and precipitation to drop so drastically as to more than counter-balance the effect of elevated carbon dioxide concentration, we may predictably soon witness stunted forests in an era of stunted human values.

Suggested Reading

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