

The ascent of water

Melvin T. Tyree

The transport system that drives sap ascent from soil to leaves is extraordinary and controversial. Like their animal counterparts, large multicellular plants need to supply all their cells with fuel and water. For animals, the solution was the evolution of a vascular system, with a pump to circulate an isotonic blood plasma that prevented cell rupture through the osmotic inflow of water. Plants took a different route to solve the problem of osmoregulation, encasing each cell in a rigid exoskeleton, the cell wall. But this rigidity brought with it a lack of mobility — for whole organisms and also for tissues and cells. Plant tissues were too rigid to evolve a pump mechanism for long-distance transport. So what force is responsible for the ascent of water in plants?

More than a century ago, H. H. Dixon (1896) proposed that a pulling force was generated at the evaporative surface of leaves and that this force was transmitted downward through water columns under tension to lift water much like a rope under tension can lift a weight. The cohesion–tension theory (C–T theory), as it is known, supposes both adhesion of water to conduit walls and cohesion of water molecules to each other.

Francis Darwin, when commenting on Dixon's proposed theory, said: "To believe that columns of water should hang in the tracheals like solid bodies, and should, like them, transmit downwards the pull exerted on them at their upper ends by the transpiring leaves, is to some of us equivalent to believing in ropes of sand."

Dixon proposed that plants transport nearly pure water in the xylem conduits — the woody channels that run from soil to leaves — at negative fluid pressures. Plants seem to retain and transport water in conduits while under pressures as negative as -1 to -10 megapascals (MPa) — that is, pressures 10 to 100 times more negative relative to atmospheric pressure than a perfect vacuum. I can think of no other botanical theory that has engendered more incredulity among physical scientists and animal physiologists than the C–T theory, because it requires us to suppose that water is transported in a metastable state. If an air-bubble or vapour-void of sufficient diameter were to arise in a xylem conduit under negative pressure, the water column would cavitate and the void would expand to displace the water, making the conduit dysfunctional. Direct measurements of negative pressure in xylem made with a cell pressure-probe 5–15 years ago failed to confirm the C–T theory. But an improved pressure-probe technique has now proved that the mechanism functions as supposed. How do plants do it, and what other limitations on plant performance result?

Negative pressure is generated by surface tension (capillarity) that arises at the air–water interfaces (menisci) at the cell-wall surfaces of leaves, where a system of pores about 20 nm in diameter can, theoretically, sustain negative pressures down to about -15 MPa before a meniscus is sucked through the cell wall to seed embolisms in adjacent xylem conduits. Water in conduits under negative pressure is metastable and hence should cavitate. The propensity of metastable water to cavitate is indeed the principle argument that many have used to reject the C–T theory. But cavitations frequently occur, and it is this exception that proves the rule. Cavitation events can be detected acoustically, and the overall impact of cavitations can be measured by loss of hydraulic conductance, which in different species can be reduced to half at negative pressures from -0.5 to -9 MPa. Cavitations are confined to single conduits. The C–T mechanism works in spite of the high probability of millions of cavitations in conduits, because there are billions to trillions of conduits in a tree and because adjacent conduits are isolated from each other by primary cell

Plant hydraulics

When you're a large organism and made of wood, you can't have a heart or other contractile organs, but you still need to move fluids to live. How is this done?

walls in pits. Conduits are interconnected by multiple adjacent conduits, providing redundancy in multiple pathways for water movement should one conduit cavitate. The pore diameter in primary cell walls determines how negative the pressure can be in a water-filled conduit before cavitations are seeded from an adjacent, embolized conduit.

Using a large number of small-diameter conduits increases redundancy and stability in the transport of metastable water — but there are trade-offs. The Hagen–Poiseuille law tells us that the hydraulic conductivity of a conduit should be proportional to the fourth power of the lumen diameter. Hence, as conduit diameter drops, the pressure difference from root to leaf required to maintain an adequate water flow rate increases, and this sets a practical limit of minimum conduit diameter between 5 and 10 μm . At the other extreme, the upper limit of conduit diameter obtained by natural selection seems to be about 500 μm . There seems to be a trade-off between large, efficient conduits and increased vulnerability to cavitation in plants. There is also growing evidence that the hydraulic conductivity of plants limits the maximum rate of gas exchange and carbon gain, so the typical conduit diameter of a species can limit the maximum height the species can reach. Fast-growing species have large, efficient conduits that are highly vulnerable to embolism; such plants perform poorly in drought. Slow-growing species have small, inefficient conduits that are very resistant to cavitation.

Other trade-offs that have driven the evolution of diversity in land plants were unexpected — trees with dense wood are strong but hydraulically inefficient. An understanding of this legacy of natural selection should allow us to breed or engineer improved drought-resistant or fast-growing trees. ■

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FURTHER READING

Tyree, M. T. & Zimmermann, M. H. *Xylem Structure and the Ascent of Sap* (Springer, Berlin, 2002).
Wei, C., Tyree, M. T. & Steudle, E. *Plant Physiol.* **121**, 1191–1205 (1999).
Tyree, M. T. *Trees* **17**, 95–100 (2003).



Trees transport metastable water by a mechanism unparalleled in engineering science.

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