

## Torus-Margo Pits Help Conifers Compete with Angiosperms

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Efficient water transport in plants allows for increased photosynthetic uptake of CO<sub>2</sub> for a given vascular investment and should improve fitness through enhanced growth and reproduction. The evolution of long, multicellular xylem vessels from short, unicellular tracheids reduces the number of times water must flow through high-resistance pits that link conduits end-to-end. Accordingly, the tracheid-based wood of conifers should have much higher flow resistance per length (resistivity) than the vesseled wood of angiosperms. However, despite the presumed tracheid handicap, conifers dominate many of the world's ecosystems and include the tallest plants (*Sequoia sempervirens*) and the oldest living organisms (*Pinus longaeva*). Just how handicapped is conifer xylem transport relative to that of angiosperms?

We found that conifers had lower sapwood-area resistivity than did angiosperms for the same average conduit diameter (Fig. 1A) (1). Even on the basis of an individual conduit, conifer tracheids averaged only 1.2 times the resistivity of vessels for the same diameter (Fig. 1B). Although vessels achieve a greater maximum diameter, in many species they are as narrow as tracheids (Fig. 1A). The similarity in resistivity is striking because the conifer tracheids were >10 times shorter than vessels of similar diameter (Fig. 1B). Compared with vessels, conifer tracheids must have low flow resistance through their end-walls, be-

cause these are encountered much more frequently as water ascends the tree.

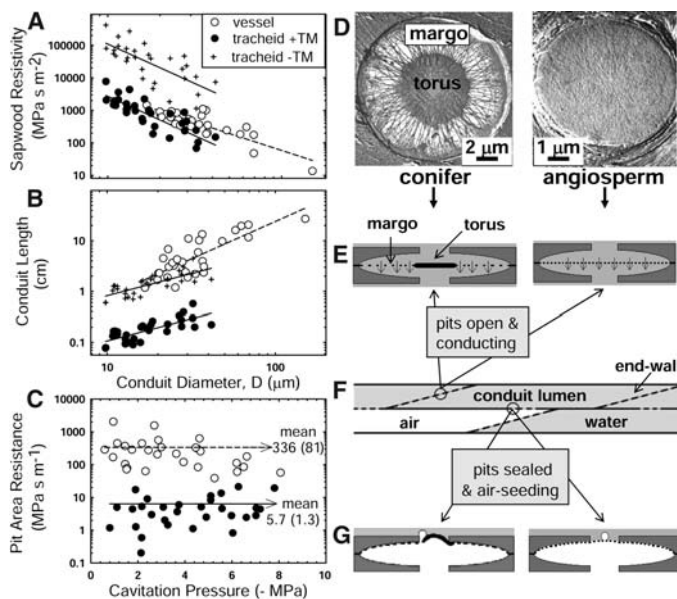
Tracheid end-walls must have either a large area of connecting pits or have pits with a low flow resistance for their area (pit-area resistance). Total pit area was actually much lower in tracheids (0.016 ± 0.003 mm<sup>2</sup>) than in vessels (0.95 ± 0.51 mm<sup>2</sup>) (1, 2). Instead, the pit-area resistance of conifers was 59 times lower than the angiosperm average (Fig. 1C) (2). This compensates for short tracheid length and low pit area and results in comparable resistivities of conifer tracheids and angiosperm vessels.

These findings indicate a function—minimal hydraulic resistance—for the unique torus-margo anatomy of the conifer pit membrane (Fig. 1, D and E). The large 0.1-μm-scale

pores in the margo (Fig. 1D) are responsible for the reduced flow resistance. Low margo resistance more than compensates for the impermeable torus, which blocks much of the membrane. The torus is required for sealing the pit against the air seeding of cavitation (Fig. 1, F and G). In contrast, the angiosperm pit membrane is uniformly microporous (Fig. 1D). The narrow, nm-scale pores create high resistance to flow when the pit is conducting, but are required to seal the pit effectively by capillary force because there is no torus (Fig. 1, F and G). We found no difference in the range of cavitation pressure between conifer tracheids and angiosperm vessels (Fig. 1C) (1, 2). The torus-margo pit not only has less flow resistance, but it is just as safe from air seeding as the angiosperm pit.

The superior hydraulics of the conifer pit are crucial for minimizing sapwood resistivity. If conifer tracheids had the pit resistance of angiosperms, their sapwood resistivity would increase by 38-fold (Fig. 1A, crosses) (1). This, added to the narrow diameter range of tracheids, would make it much more difficult for conifers to compete effectively with angiosperms.

The reduction in resistivity achieved by the torus-margo pit membrane is equivalent to a 7.7-fold increase in conduit length. This would require a tracheid to be as long as a vessel of equal diameter (Fig. 1B, crosses) (1). We conclude that the evolution of the torus-margo membrane within the gymnosperm lineage from homogenous pits was equivalent to the evolution of vessels within the angiosperms. The towering redwoods and the sweep of the boreal coniferous forest exist in no small part because of this clever microscopic valve.



**Fig. 1.** (A) Sapwood-area resistivity versus average conduit diameter for conifer tracheids with torus-margo (+TM) pit membranes and for angiosperm vessels with homogenous pit membranes. Crosses are tracheids substituted with angiosperm pit resistance (–TM). (B) Average conduit length versus diameter. Crosses show the tracheid length required to compensate for the substitution of angiosperm pits. (C) Flow resistance through pits on a membrane-area basis versus cavitation pressure. (D) Scanning electron microscope image of pit membranes with secondary wall removed. (Left) Torus-margo membrane of conifer tracheids; (right) homogenous pit membrane of angiosperm vessels (3). (E) Schematic side view of conducting pits. (F) Conduit network with pits conducting water and sealed against air entry. (G) Side view of pits in sealed and air-seeding position. Air leakage nucleates cavitation in the xylem sap.

### References and Notes

1. Materials and methods available as supporting material on Science Online.
2. U. G. Hacke, J. S. Sperry, J. K. Wheeler, L. Castro, *Tree Physiol.*, in press.
3. J. F. Siau, *Transport Processes in Wood* (Springer, Berlin, 1984), pp. 49 and 59.
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### Supporting Online Material

www.sciencemag.org/cgi/content/full/310/5756/1924/DC1

Materials and Methods

Table S1

References

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