

Xylem cavitation in roots and stems of Douglas-fir and white fir

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Summary Roots of hardwoods have been shown to be more vulnerable to xylem cavitation than stems. This study examined whether this pattern is also observed in a conifer species. Vulnerability to cavitation was determined from the pressure required to inject air into the vascular system of hydrated roots and stems, and reduce hydraulic conductance of the xylem. According to the air-seeding hypothesis for the cavitation mechanism, these air pressures predict the negative xylem pressure causing cavitation in dehydrating stems. This was evaluated for stems of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and white fir (*Abies concolor* (Gord. & Glend.) Lindl.). The air-injection method was applied to roots and stems of different sizes and positions in Douglas-fir trees. Roots, especially smaller roots with a xylem diameter < 5 mm, were more vulnerable to cavitation than stems. Mean cavitation pressure for smaller roots was -2.09 ± 0.42 versus -3.80 ± 0.19 MPa for larger roots (> 8 mm diameter). Within the shoot system, smaller stems (< 5 mm diameter) were most vulnerable to cavitation, having a mean cavitation pressure of -4.23 ± 0.565 versus -5.27 ± 0.513 MPa for large stems (> 8 mm diameter). There was no correlation between tracheid diameter and mean cavitation pressure within root or stem systems, despite larger tracheid diameters in roots ($23.3 \pm 3.9 \mu\text{m}$) than in stems ($9.2 \pm 1.6 \mu\text{m}$). Smaller safety margins from cavitation in roots may be beneficial in limiting water use during mild drought, and in protecting the stem from low xylem pressures during extreme drought.

Keywords: drought stress, water transport, xylem physiology.

Introduction

Recent studies of xylem cavitation in hardwoods have shown that roots are more susceptible to cavitation than stems (Sperry and Saliendra 1994, Alder et al. 1996, Hacke and Sauter 1996). Studies have demonstrated the importance of stomatal regulation in avoiding excessive stem cavitation (Tyree and Sperry 1988, Cochard et al. 1992, Neufeld et al. 1992); however, cavitation in roots may be a more important factor in limiting gas exchange. Published data on root cavitation are limited to four hardwood species (*Betula occidentalis* Hook., *Acer grandidentatum* Nutt., *Alnus glutinosa* (L.) Gaertn., *Populus balsamifera* L.), and to roots of a limited diameter range. Our main study objective was to extend comparisons of root and

stem cavitation to a conifer species, and to characterize more thoroughly cavitation variation within root and shoot systems.

A second objective was to validate for conifer xylem the method applied for studying root cavitation in hardwoods. Normally, susceptibility of xylem to cavitation is determined from “vulnerability curves” which show the relationship between hydraulic conductance of xylem and xylem pressure (Tyree and Sperry 1988). As xylem pressures decrease and cavitation is nucleated, hydraulic conductance decreases. Xylem more vulnerable to cavitation shows a decrease in conductance at less negative pressures than more resistant xylem. This method, although easily applied to stems, is difficult to apply to roots.

Root vulnerability curves for hardwoods were determined from an “air-injection” method that has also been applied to stems (Sperry and Saliendra 1994, Alder et al. 1996, Hacke and Sauter 1996). This technique measures the hydraulic conductance of hydrated stems or roots (whose xylem pressure approximates atmospheric) as a function of air pressure surrounding the xylem. When air pressure is high enough, injected air fills the xylem conduits and hydraulic conductance through the xylem decreases. The air pressure causing loss of hydraulic conductance in hydrated material estimates the negative xylem pressure causing an equivalent conductance loss through air entry and subsequent cavitation in dehydrated material. The only difference is that air is being *pulled* into the dehydrated conduit by negative xylem pressure rather than being *pushed* into the hydrated conduit by increased air pressure.

The air-injection method only estimates cavitation pressure that is caused by aspiration of air into xylem conduits (i.e., the “air seeding” hypothesis; Zimmermann 1983). The close correspondence between vulnerability curves obtained by air-injection versus dehydration methods strongly supports this hypothesis (summarized by Sperry et al. 1996). The site of air-seeding appears to be the inter-conduit pits between embolized (gas-filled) and water-filled conduits (Crombie et al. 1985, Sperry and Tyree 1990, Jarbeau et al. 1995).

Most studies comparing the air-injection and dehydration methods have been done on species having vessels and a uniformly porous interconduit pit membrane. The different torus-margo structure of the inter-tracheid pit membrane in conifers versus angiosperms could influence air seeding dynamics, and affect the accuracy of the air-injection technique.

One study shows the method to be valid for conifers (Sperry and Tyree 1990), but the protocol differed significantly from that of the present study.

In this paper, the air-injection and dehydration methods were compared in two conifers, white fir (*Abies concolor* (Gord. & Glend.) Lindl.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco.). Comparisons of root versus stem cavitation in Douglas-fir were then made with the air-injection method.

Materials and methods

Plant material

All material was collected from the Wasatch Mountains west of Salt Lake City, UT, USA. White fir branches were collected in midwinter in Red Butte Canyon (40°48' N; 111°46' W, elevation 1915 m). Douglas-fir was collected in fall, primarily near Parley's summit (40°45' N; 111°36' W, elevation 2133 m). Some collections were also made from Big Cottonwood Canyon (elevation 2100 m). Material was sealed in plastic bags to minimize dehydration during transport to the laboratory.

Douglas-fir trees at Parley's summit were widely scattered in an otherwise low (1–2 m) scrub oak (*Quercus gambelii* Nutt.) community. Sampling was concentrated on a single Douglas-fir tree of about 6 m in height growing on an open, north-facing 20° slope. Roots were collected from the top 300 mm of soil in both down- and up-slope directions, and stems were collected from the lower 3 m of its well-developed crown.

Air-injection experiments

The air injection protocol described by Sperry and Saliendra (1994) was followed to determine vulnerability curves. Branch (Douglas-fir, white fir) or root segments (Douglas-fir) (0.10–0.20 m in length and with xylem diameters of 2–12 mm) were placed, both ends protruding, in a double-ended pressure chamber. Two shallow (0.5 mm deep) notches were cut into opposite sides of the xylem about 0.05 m apart in the center of the segment. These cuts insured entry of air into the xylem inside the pressure chamber. One end of the segment was attached to tubing filled with filtered (0.22 µm) water adjusted with HCl to pH 2 to prevent microbial growth. The hydraulic pressure difference across the segment was controlled by raising or lowering the tubing.

Initial hydraulic conductance was measured at a pressure difference of about 0.01 MPa, with air pressure inside the chamber held at about 0.1 MPa to prevent leakage of solution from the notches. Effluent from the free end of the segment was collected over one-minute intervals in tared vials filled with dry cotton wool. Hydraulic conductance was calculated as the mass flow rate divided by the pressure difference. One-minute measurements were continued until flow rate remained constant. Hydraulic conductance was the average of at least three one-minute readings during steady flow.

After this initial measurement, flow through the segment was reduced by lowering the tubing, and air pressure inside the

chamber was increased to a prescribed value and held for 10 minutes. Air pressure was then lowered back to 0.1 MPa for 3 minutes and the hydraulic conductance remeasured. Exposure of the segment to progressively higher air pressures continued until hydraulic conductance measurements were at least 95% below the initial value. A vulnerability curve was later constructed for each segment showing cumulative percentage decrease in hydraulic conductance versus the negative of air-injection pressure (see Figure 1). To determine mean cavitation pressure, we replotted vulnerability curves as the loss of hydraulic conductance per unit pressure change (rather than plotting cumulative loss of conductance), and took the mean of this distribution based on the mid-point of each pressure change (Sperry and Saliendra 1994).

Dehydration experiments

We compared vulnerability curves obtained by the air-injection method with those obtained by dehydration for stems of Douglas-fir and white fir. Intact branch ends (i.e., only cut at one end) were selected that were free of side branches for at least 90 mm. Two 40-mm long segments separated by 10 mm were located in this region. The proximal and distal segments were labeled "a" and "b," respectively. The "a" segment was cut from the branch underwater (to avoid air blockage of severed tracheids) and its hydraulic conductance measured (Sperry et al. 1988). The "b" segment, now located 10 mm from the proximal end, was then dehydrated along with the rest of the branch. The 10 mm distance from the cut end insured that no air-blocked tracheids extended into the "b" segment. Following dehydration, xylem pressure was measured with a pressure chamber, the "b" segment was cut from the branch underwater, and hydraulic conductance of the "b" segment was measured. The percentage that the hydraulic conductance of "b" (post-stress) was below "a" (pre-stress) gave the percentage loss of conductance resulting from dehydration.

The dehydration method differed between species. In white fir, minimum xylem pressures were measured on three shoots cut from branches that were air-dried and bagged for several hours to promote pressure equilibration. Douglas-fir branches were dehydrated in a large pressure chamber by sealing in all but the proximal cut end (Cochard et al. 1992). The balance pressure of the entire branch was periodically determined. Once the desired target pressure had been achieved, pressure was lowered, and the branch was bagged for 2 hours to allow diffusion of air into cavitated (and initially vapor-filled) tracheids. This drying method permitted reproducibility of particular degrees of stress during one- or two-hour periods, whereas targeting particular pressures by air drying was more difficult, and lower pressures required two days or more to attain. The chamber method only tested whether dehydration caused more loss of conductance than air injection because of the exposure of the stems to elevated air pressure in the chamber.

Anatomical measurements

Tracheid diameters in a subset of Douglas-fir root and branch segments used in air-injection experiments were measured to

determine any correlation with cavitation pressure. A free-hand transverse section was cut through the middle of the segment. We measured a minimum of 50 tracheids in radial sectors spaced at 90° intervals around the section, giving a minimum of 200 tracheids measured per segment. Measurements were made with a drawing tube and a bit pad (Donsanto Microplan II, Natuck, MA). The percentage of tracheids in 5 µm diameter classes was calculated, as well as the percentage of estimated hydraulic conductance contributed by tracheids in each diameter class. Tracheid hydraulic conductance was assumed proportional to diameter raised to the fourth power as predicted by the Hagen-Poiseuille equation (Zimmermann 1983). A "hydraulic mean" tracheid diameter was calculated from this latter distribution; it equals the sum of all diameters to the fifth power divided by the sum of all diameters to the fourth power.

We also observed the structure of the intertracheid pit membranes in selected root and stem segments by scanning electron microscopy (SEM; S-450, Hitachi, Tokyo, Japan). Radial and tangential longitudinal sections of the segment were made, dehydrated in an alcohol series, dried at the critical point, and sputter-coated with gold-palladium.

Results

Stems of white fir (Figure 1a) and Douglas-fir (Figure 1b) had similar vulnerability curves regardless of whether the air-injection or dehydration method was applied. At more extreme pressures (higher air pressure and lower xylem pressure), both dehydration methods tended to cause a greater loss of hydraulic conductance than air injection. However, for comparative purposes, air pressure causing loss of hydraulic conductance was a useful proxy for the negative pressure causing cavitation.

Extensive sampling of the Douglas-fir tree revealed differences in vulnerability to cavitation within and between the root and shoot systems. Variation was correlated with root and stem size (Figures 2 and 3).

Roots had mean cavitation pressures approximately 2 MPa less negative than stems of equal xylem diameter (Figure 2). Within the root system, smaller roots (< 5 mm xylem diameter) were most vulnerable (Figure 3) with a mean cavitation pressure of -2.09 ± 0.42 MPa (mean \pm standard deviation; $n = 7$) versus -3.80 ± 0.19 MPa ($n = 6$) for larger roots (> 8 mm xylem diameter) (Figure 3). Smaller roots also had a differently shaped vulnerability curve that predicted more cavitation at modest negative pressures than either larger roots or stems (Figure 3). There was a tendency for roots growing up-slope to be more resistant to cavitation than roots growing down-slope (Figure 2).

Although stems were more resistant to cavitation than roots, there was also significant variation within stems that was correlated with xylem diameter (Figure 2). As with roots, smaller stems (< 5 mm xylem diameter) were most vulnerable (Figure 2) with a mean cavitation pressure of -4.23 ± 0.57 MPa ($n = 5$) versus -5.27 ± 0.51 MPa ($n = 5$) for larger stems (> 8 mm xylem diameter; Figure 2).

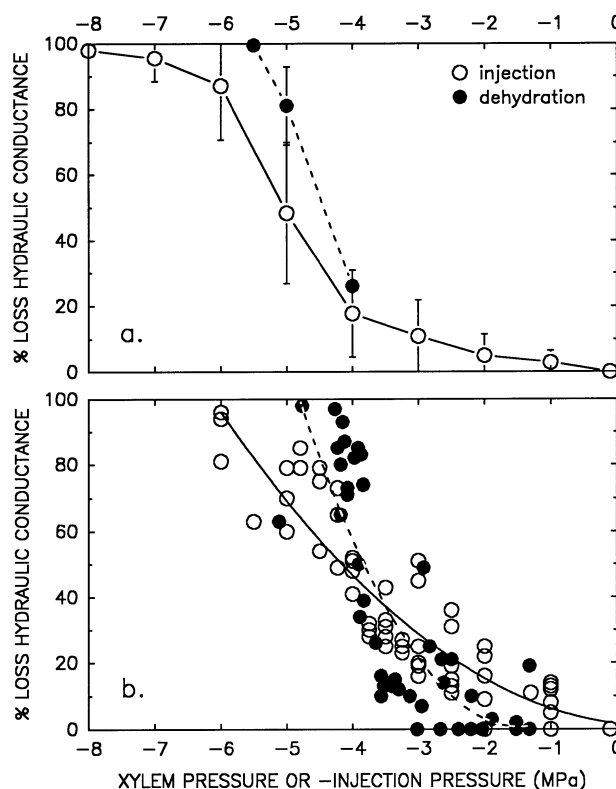


Figure 1. Vulnerability curves showing percentage loss of hydraulic conductance in xylem versus: (1) the negative of air pressure used in air-injection experiments (○), and (2) the minimum xylem pressure during dehydration experiments (●). Correspondence of the two techniques in Douglas-fir (a; $n = 16$ for each injection mean, $n = 3$ for each dehydration mean; error bars are standard deviations) and white fir (b; $n = 55$ for injection curve, $n = 43$ for dehydration curve) shows that negative air pressure was an approximate predictor of cavitation pressure.

Tracheids in roots had much larger diameters (23.32 ± 3.92 µm, $n = 7$) than in stems (9.22 ± 1.61 µm, $n = 6$; Figure 4); when both root and stem data were considered, and increasing cavitation vulnerability was correlated ($P < 0.01$) with increas-

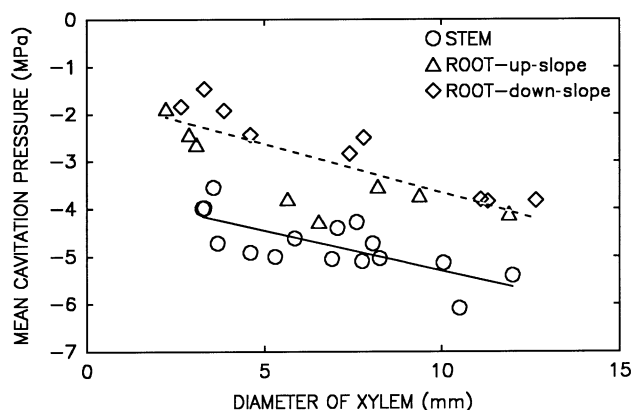


Figure 2. Mean cavitation pressure versus xylem diameter for stems (○) and roots (up-slope, △; down-slope, ◇). Both correlations are significant ($P < 0.01$).

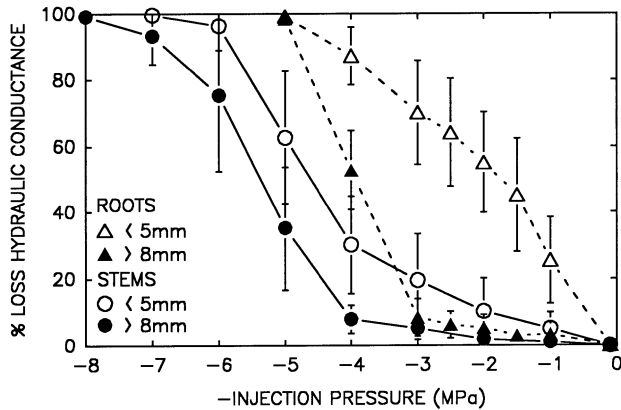


Figure 3. Vulnerability curves for a Douglas-fir tree from an air-injection experiment. Within the root system, small roots (< 5 mm xylem diameter, Δ , $n = 7$) were more vulnerable to cavitation than large roots (> 8 mm, \blacktriangle , $n = 6$). In the shoot system, small branches (< 5 mm, \circ , $n = 5$) were more vulnerable to cavitation than large stems (> 8 mm, \bullet , $n = 5$). Error bars are standard deviations.

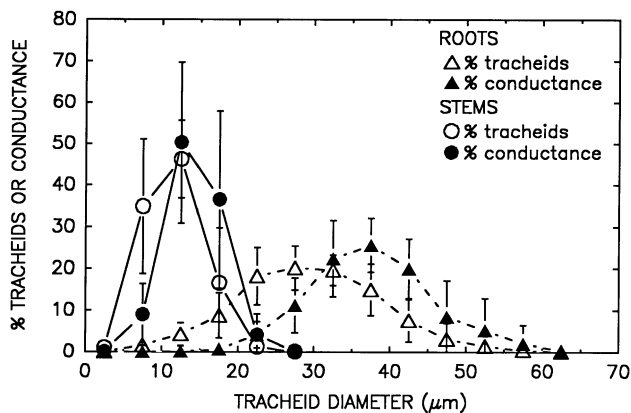


Figure 4. Percentage tracheids (open symbols) or percentage hydraulic conductance (solid symbols) versus $5 \mu\text{m}$ tracheid diameter class for roots (Δ , \blacktriangle , $n = 6$) and stems (\circ , \bullet , $n = 7$). Error bars are standard deviations.

ing tracheid diameter (Figure 5). Differences in cavitation vulnerability within stems or roots were not correlated with differences in mean tracheid diameter.

The SEM observations revealed no obvious qualitative differences between the inter-tracheid pit membrane structure of roots and stems. In both cases, the torus and margo were clearly differentiated, with similar microfibril orientation in the margo region. Cursory examination, however, showed that pit membranes of roots often had larger diameters (to $15.2 \mu\text{m}$) than those of stems (to $9.7 \mu\text{m}$), because of differences in tracheid diameters between the two organs.

Discussion

The general correspondence between the air-injection and dehydration experiments (Figure 1) in both species is consistent

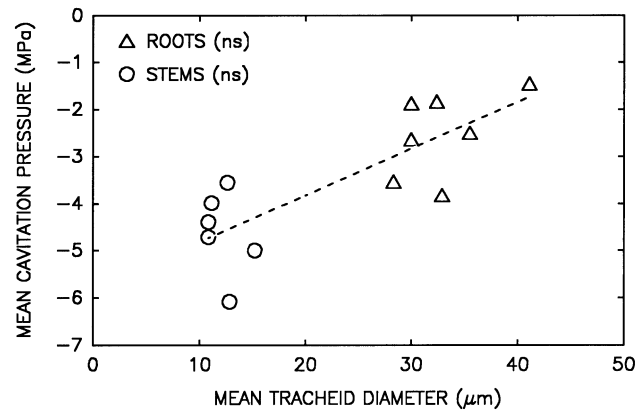


Figure 5. Mean cavitation pressure versus hydraulic mean tracheid diameter for roots (Δ) and stems (\circ). The correlation is significant ($P < 0.01$) only for collective root and stem data.

with previous results for conifers (Sperry and Tyree 1990) and hardwood species (Sperry et al. 1996), thus further supporting the "air seeding" hypothesis and justifying use of the air-injection method for estimating conifer cavitation pressures. The previous comparison of conifers showed that air seeding occurred by slippage of the torus from its sealing position over the pit aperture. Once the torus was displaced, air could pass across the relatively large margo pores into the next conduit. In support of this explanation, conifer species with xylem more resistant to cavitation were shown to have stronger pit membranes that were presumably capable of holding the torus in place against higher pressure differences (Sperry and Tyree 1990).

The tendency for dehydration to cause more cavitation at extreme pressures than air injection (Figure 1) was also seen in two species of the previous study (*Abies balsamea* (L.) Mill. and *Picea rubra* Sarg., Sperry and Tyree 1990), possibly resulting from different stress application dynamics on the pit membranes in the two species. During air injection, stress is applied for only 10 min (20–30 min in Sperry and Tyree 1990), whereas during dehydration, stress is applied over two to several hours. If there is any hysteresis between stress application and pit membrane slippage, a longer dehydration treatment would result in more cavitation for a given pressure than a shorter air-injection treatment.

Our results predict that Douglas-fir roots are more vulnerable to cavitation than stems (Figures 2 and 3), as was shown previously for four hardwood species (Sperry and Saliendra 1994, Alder et al. 1996, Hacke and Sauter 1996), and also *Quercus petraea* (Matt.) Liebl. (H. Cochard, unpublished data). Our results further show that smaller roots are most vulnerable to cavitation. The vulnerability curve for small Douglas-fir roots (Figure 3) is similar to the curve for *Acer grandidentatum* roots growing in a non-riparian, oak-scrub habitat in the same mountain range (Alder et al. 1996). There was also a trend for up-slope roots to be more resistant to cavitation than down-slope roots (Figure 2). Alder et al. (1996) observed that *A. grandidentatum* roots growing at a dry site

were significantly more resistant to cavitation than roots growing at a wet site. Perhaps such adjustments in cavitation resistance can occur within a single root system if up-slope soil conditions are drier on average than down-slope conditions.

An important caveat to our results is that, unlike stems, air-injection results for root xylem have not been compared with dehydration data, therefore, confirmation of air-injection predictions for roots is desirable. Results we are obtaining currently with a centrifuge technique (Pockman et al. 1995), seem to show that air-injection results are valid for roots (N.N. Alder and J.S. Sperry, unpublished data). Greater cavitation vulnerability in roots versus stems may be a general pattern in woody plants.

Within the shoot system of Douglas-fir, we found that smaller branches were more vulnerable to cavitation than larger branches (Figure 3), but this result appears not to be a general phenomenon. In a study of stem cavitation in eight conifers, Cochard (1992) found that half showed no difference between large and small stems, whereas in the other half (including Douglas-fir) smaller stems were less vulnerable than larger stems. More resistant small branches were also seen in *Betula occidentalis* (Sperry and Saliendra 1994). However, Cochard's trees were growing under well-watered conditions and were substantially more vulnerable than our material (i.e., about 80% loss of conductance at -4 MPa versus 18% in Figure 1a).

The variation in Douglas-fir vulnerability to cavitation was correlated with tracheid diameters when both root and stem data were considered (Figure 5). However, there was no correlation within root or stem data (Figure 5). Vulnerability to cavitation and tracheid diameter were also correlated in *Betula occidentalis* (Sperry and Saliendra 1994) and *Populus balsamifera* (Hacke and Sauter 1996). On the other hand, no simple relationship between conduit diameter and vulnerability to cavitation was seen for *Acer grandidentatum* (Alder et al. 1996) or *Alnus glutinosa* (Hacke and Sauter 1996) or across hardwood and conifer species (Sperry et al. 1994).

The ambiguous relationship between conduit size and vulnerability to cavitation is consistent with the lack of a necessary causal link between them. The relevant structural correlate with cavitation vulnerability is the permeability of the inter-conduit pit membranes to air (Sperry et al. 1996). Although root and stem pit membranes of Douglas-fir appeared qualitatively similar under SEM, the greater area of pit membranes in roots may have reduced the pressure necessary to displace the torus from its sealing position over the pit aperture, making roots more vulnerable to cavitation than stems.

The concept of "vulnerability segmentation," advanced by Tyree et al. (1993), considers the significance of variation in cavitation vulnerability. This concept suggests that designed failure of water transport in minor twigs and leaf xylem can play an adaptive role in preserving stem xylem from failure during drought, as observed in the rachis xylem of walnut (*Juglans regia* L.) which was more vulnerable to cavitation than that of the subtending stem. Cavitation in the rachis during drought led to leaf shedding, which in turn prevented further water loss that could have ultimately cavitated the stem

(Tyree et al. 1993). Similarly, more vulnerable small twigs of Douglas-fir may cavitate during severe drought to protect larger stems from further water loss and cavitation.

Vulnerability segmentation and cavitation in roots may benefit woody plants during soil drought. During extreme drought, complete cavitation in the smallest roots would hydraulically isolate the plant from continually drying soil. As long as stomata remained closed, this could buffer the stem from experiencing pressures low enough to cause complete cavitation. Cavitation in cactus roots has been shown to play this role (North et al. 1992). During modest drought, partial root cavitation would reduce transpiration rates through a reduction in hydraulic conductance and a consequent decrease in stomatal conductance, allowing more soil water to be taken up over a longer interval. These two benefits of root cavitation would be renewed after a drought by new root growth, or refilling of cavitated conduits in the roots, or both.

Although the greater cavitation vulnerability of roots versus stems could help protect the stem and its meristems from drought, trade-offs may be associated with resistance to cavitation that have driven the evolution of narrow safety margins in relatively expendable organs such as small roots. Trade-offs could include the energy cost of a more cavitation-resistant pit membrane, and also the reduced hydraulic conductance through such a membrane. However, the correlation between cavitation resistance and hydraulic efficiency is weak or absent (Cochard 1992, Sperry et al. 1994, Tyree et al. 1994) probably because any effect of pit membranes on hydraulic conductance can be countered by changes in conduit length or diameter, or both.

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