

Xylem dysfunction in *Quercus*: vessel sizes, tyloses, cavitation and seasonal changes in embolism

HERVÉ COCHARD¹ and MELVIN T. TYREE²

¹ *Station de Sylviculture et de Production, INRA, Centre de Recherches Forestières de Nancy, Champenoux 54280 Seichamps, France*

² *Northeastern Forest Experiment Station, P.O. Box 968, Burlington, Vermont 05402, USA*

Received January 16, 1990

Summary

The seasonal progression of xylem dysfunction from tyloses and embolism induced both by cavitation and frost was studied in *Quercus rubra* L. and *Quercus alba* L. branches. Vessel lengths and diameters were measured in current-year rings of branches of various ages. Vessels in current-year shoots are about the same size as those in many diffuse porous trees, but vessels in older branches are two to six times larger in diameter and typically more than 10 times longer. Large *Quercus* vessels were more vulnerable to cavitation than small vessels. The small vessels in current-year shoots were more vulnerable to cavitation than vessels of comparable size in diffuse porous species. Earlywood vessels are completely blocked by tyloses within a year of their formation. Tylose growth starts in winter, but the vessels are not fully blocked until the next summer. Many latewood vessels, by contrast, remain free of complete blockage for several years. In *Q. rubra*, loss of hydraulic conductivity in current-year shoots due to cavitation reaches 20% by August and >90% after the first hard frost. Both laboratory and field observations confirm that the role of frost in causing loss of hydraulic conduction by embolism is much more dramatic in *Quercus* than in conifers and diffuse porous hardwoods.

Introduction

Interest has been renewed in the vulnerability of xylem to stress-induced dysfunction (Tyree and Sperry 1989). The most common kind of xylem dysfunction is an air embolism that interrupts water transport in xylem conduits (i.e., vessels or tracheids). Embolism can be induced by winter desiccation (Sperry et al. 1988*b*) or cavitation events. Cavitations have been a recognized cause of xylem dysfunction ever since the introduction of the cohesion theory of sap ascent ascribed to H.H. Dixon (1914). According to the cohesion theory, water is conducted in xylem in a metastable state, because water pressure is subatmospheric. Cavitations are now thought to occur by an air-seeding mechanism; whenever the xylem pressure potential, Ψ_{xp} , becomes too low, an air bubble is sucked into the xylem conduit through a pore in the conduit wall or through a pit membrane adjacent to an already embolized conduit (Crombie et al. 1985, Sperry et al. 1987*b*, Sperry and Tyree 1988).

Before methods were developed to measure the vulnerability of xylem conduits to cavitation, it was suggested frequently that there must be a trade-off between efficiency and vulnerability based on conduit size. Big conduits (large diameter and long) were viewed as being efficient for hydraulic conduction but highly vulnerable to cavitation compared to small conduits (e.g., Carlquist 1977, Baas 1982 and

Zimmermann 1983). There is evidence that these concepts apply when comparing large to small conduits in a stem (Tyree and Sperry 1989). Unfortunately, these ideas have no support in fact when making interspecific comparisons. Vulnerability curves have been measured in four conifers and three dicotyledonous species to date. Three of the conifers that have conduits (tracheids) much smaller than the dicotyledonous conduits (vessels) are *more* vulnerable to cavitation events than the conduits of dicotyledonous species (Tyree and Sperry 1989). The vessel-bearing species observed so far have been diffuse porous species that are known to have smaller vessels than many species. Ring porous species are known to have the largest and most hydraulically efficient vessels in woody species. The possibility still remains that these very large vessels could be more vulnerable to cavitation events than all other conduits.

The purpose of this study was to correlate vessel size with vulnerability in *Quercus*, one of the most common ring porous genera. Because xylem dysfunction in ring porous trees can be caused by tylose formation as well as by embolism, we have developed techniques to address both mechanisms. Ellmore and Ewers (1986) report that long vessels of ring porous trees become nonconductive after the first growing season; and the role of frost in causing this dysfunction has been suggested (Zimmermann 1983, Ellmore and Ewers 1986). In this study we examined the role of freezing on embolism formation and on the contribution of large earlywood vessels to hydraulic conduction.

Materials and methods

Most observations were conducted on *Quercus rubra* L. and some were repeated on *Q. alba* L. Samples were collected from University of Vermont land, Burlington, or from Camp Johnson, Winooski, Vermont.

Vessel lengths were measured by Zimmermann's method (Zimmermann and Jeje 1981). A solution of blue pigment (a suspension of mineral crystals used to color Benjamin Moore³ latex paint) was diluted 100:1 in water and passed through a 5- μ m filter. The solution was perfused through stem segments from the apical end at a pressure of 2 to 2.5 MPa for 0.5 h (occasionally at 0.2 MPa for 2 h). The branches were dried overnight and then sectioned into segments of equal length (4 to 40 cm long depending on the experiment). The number of vessels filled with pigment was counted under a dissecting microscope for each ring in vessels > 20 μ m diameter.

Tylose blockage was measured in samples collected at weekly intervals from mid-March to late May 1989. Branches, 4 or more years old, were cut with pole pruners from *Q. rubra* and *Q. alba* trees and transported immediately to the laboratory where they were immersed in water. Internodal segments, each 22 cm in length,

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were cut from internodes ranging in age from 1 to 6 years. To determine if vessels were embolized, the segments were perfused from the base with Congo red (1 kg m^{-3}) at a pressure of 2 kPa (20 cm water head). Previous experiments demonstrated that this pressure was not enough to blow air bubbles out of "open" vessels, i.e., vessels free of vessel ends and tyloses, so only water-filled vessels should stain with dye. Congo red was chosen because preliminary experiments indicated that it stained only pit fields of vessels, leaving most of the wood fibers and tracheids unstained, thereby making the counting of stained vessels easier.

A perfusion time of 1 h should have been adequate for Congo red to travel more than 1 m in vessels $> 20 \mu\text{m}$ diameter (Zimmermann 1983 p. 63) at the applied pressure gradient. After staining, the last 2 cm of segment farthest from the site of dye application was excised and the presence of dye was checked under a dissecting microscope at $50\times$ magnification. The remaining 20-cm-long segment was then perfused with water at 0.1 MPa for 0.5 h; this is enough pressure to blow air bubbles out of open vessels and to dissolve air bubbles in most closed vessels. The segments were then perfused with Congo red for 1 h at 2 kPa to stain vessels without tylose blockage. The stained segments were dried overnight and sectioned in the middle (10 cm from the site of dye application), and the number of stained vessels was counted in each ring under a dissecting microscope. Counts were made of earlywood vessels (mostly $>60 \mu\text{m}$ diameter) and latewood vessels (mostly $<30 \mu\text{m}$ diameter).

Dye uptake by the transpiration stream was measured using Congo red and safranin (both at 1 kg m^{-3}) in leaf-bearing stems during the day. Stems were cut in one of three separate ways: (1) stems cut while immersed in dye; (2) stems cut in air and allowed to transpire for 5 to 10 minutes and then the basal end recut under dye about 1–2 cm from the end; and (3) stems cut in air and allowed to transpire in air and then placed in dye solution without recutting. The movement of dye in the stems was observed by sectioning stems at appropriate locations.

Seasonal changes in embolism were measured on stems collected at approximately weekly intervals from early August until mid-November 1989. Tylose studies in early 1989 indicated that vessels formed and functional in 1988 were embolized by March 1989; so, these measurements were undertaken to determine when current-year vessels embolize.

Branches 3 to 5 years old (at the base) were cut with pole pruners from the crown of dominant *Q. alba* and *Q. rubra* trees growing at Camp Johnson. The branches were immediately recut under water and after a few minutes all the current-year shoots were recut under water. The current-year shoots were immersed in water and transported to the laboratory. While immersed in water, short pieces of the shoot (usually 4 to 6 cm long) were taken from the upper 1/2 or 1/3 of the shoot. The cut surfaces of the segments were shaved with a new razor blade, and leaf blades were excised leaving the petiole and half of the midrib vein attached. This both reduced transpiration and reduced leaks in subsequent steps.

The level of embolism was measured by its effect on the percentage loss of hydraulic conductivity using a Sperry conductivity system (Sperry et al. 1987a). Conductivities were measured using 0.9 kg m^{-3} oxalic acid solution degassed under

vacuum for 45–60 min and filtered through a 0.22 μm inline filter. Resaturation of the solution with air was reduced by storing it in a commercial “captive air” tank. The tank holds water in a plastic bag, which can be filled without air bubbles through a connecting pipe, and the bag is inside a metal pressure vessel that can be pressurized to about 0.4 MPa. The solution can be delivered under constant pressure by use of a compressed air tank and a pressure regulator. The source reservoir in the Sperry apparatus was changed to a beach ball filled with a solution free of air bubbles. The initial conductivity, k_i , of the stem segments was measured at a pressure difference of about 6 kPa (not enough to blow air bubbles out of open vessels in current-year shoots, although enough to blow bubbles out of older shoots). The maximum conductivity, k_m , was measured by flushing the segments for 20 to 30 min at a pressure of 170 kPa. Maximum conductivity was usually achieved with one flush and was confirmed by repeated flushes until the maximum had been reached. Percentage loss of hydraulic conductivity, which is a measure of the embolism level, was calculated from $100(k_m - k_i)/k_m$. See Sperry et al. (1987a) for other details.

Vulnerability to cavitation is represented by a graph of percentage loss of hydraulic conductivity *versus* xylem water potential. Vulnerability was determined on current-year shoots and on leaf petioles of *Q. rubra*. Shoots 3 to 5 years old were cut from large trees with pole pruners and then immediately recut under water to remove the lower 10 to 20 cm of stem. Shoots were immediately transported to the laboratory and allowed to rehydrate. Usually 1 h was sufficient to raise xylem pressure potential, Ψ_{xp} , to > -0.1 MPa. The shoot was then removed from the water and allowed to dehydrate. Shoot xylem pressure potential was estimated by the pressure bomb technique on randomly chosen leaves. In most experiments, ultrasonic acoustic emissions (AEs) were also monitored as an indication of cavitation events using a model 4615 drought stress monitor (Physical Acoustics Corp., Lawrenceville, NJ). The ultrasonic transducer was attached to the stem (bark removed) with a spring-loaded clamp with a force of 30 Newtons applied to I15I transducer (PAC, Lawrenceville, NJ). Different branches were dehydrated to Ψ_{xp} values ranging from -1.5 to -4.5 MPa; once the desired Ψ_{xp} had been achieved, the shoot was wrapped in a black plastic bag to reduce transpiration and hold Ψ_{xp} at a fixed value for at least 12 h, to allow air to diffuse into recently cavitated vessels. At the end of the holding period, Ψ_{xp} was remeasured. Current-year shoots were cut at the base under water and left to rehydrate for about 0.5 h. A short segment (4 to 6 cm long) was excised from the upper 1/2 or 1/3 of the shoot, and the cut surface recut with a new razor blade. In other instances, entire petioles, which are 2 to 2.5 cm long in *Q. rubra*, were excised with a fresh razor blade. Percentage loss of conductivity was then measured on shoot segments and petioles as described above.

Freezing-induced embolism was measured after it had been observed that frost seemed to induce a large increase in embolism in vessels under field conditions. *Quercus rubra* shoots were collected and rehydrated as above. Shoot segments about 60 cm long, including the current-year shoots, were excised under water. The shoots were placed in an insulated, refrigerated box so that the apical 5 cm and the basal 30 cm of each shoot remained outside the box and approximately 25 cm of the

current-year shoot remained in the box. The apical and basal ends were fitted with water-filled tubing and source and sink reservoirs used for continuous perfusion of water. The temperature of the box was controlled by circulating cold ethanol through a heat exchanger inside the box. The temperature of the ethanol and thus of the box were set by a model RTE-110 bath circulator (Neslab, Newington, NH). Water flowed continuously through the branch under a slight tension achieved by placing the sink reservoir about 0.7 m below the source. The temperature in the box was measured by an LM335 temperature sensor attached to the stem surface and interfaced to a computer that also measured the water flow rate through the stem and stem hydraulic conductivity as described by Sperry et al. (1987a). The shoot sections inside the box were taken through freezing and thawing cycles while continuously measuring flow rate and conductivity.

Results

Vessel lengths and diameters

Vessels measured in current-year shoots were much shorter than in other parts of *Q. rubra* and *Q. alba* trees. When current-year shoots were cut less than a third of the way back from the apex and perfused with pigment, over 70% of the vessels were less than 4 cm long. Generally less than 10% of the vessels were more than 20 cm long. If more than half of the current-year shoot was excised before perfusion, then some vessels that extend for more than 50 cm were cut open. Representative data for *Q. rubra* are shown in Figure 1; length distributions for *Q. alba* were comparable and

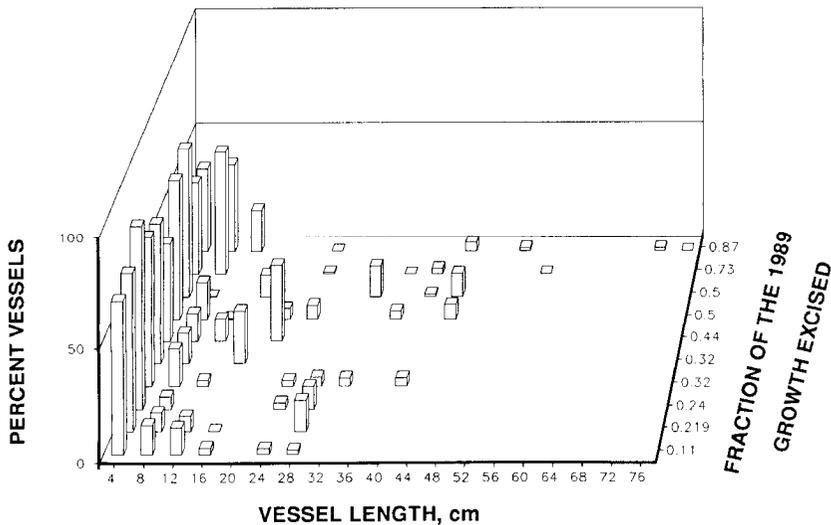


Figure 1. Vessel length distribution in current-year shoots (leaf-bearing shoots grown in 1989). The y-axis for vertical bars is percent of vessels in a size class (multiples of 4 cm) given on the x-axis. The z-axis is used to separate different shoots on the basis of the fraction of the current-year growth excised prior to pigment infusion from the apex.

are, therefore, not shown. When 2-year-old shoots were perfused with pigment, some vessels extended for more than 1 m in the 1989 ring. Vessels in the 1988 ring were plugged with tyloses so pigment penetrated less than 5 cm in over 75% of the vessels (Figure 2). In larger stems, some vessels were often several meters long (data not shown, cf. Zimmermann and Brown 1971). Latewood vessels, which were included in Figures 1 and 2, made up the majority of the vessels less than 4 cm long. Mean vessel diameters are shown in Table 1. In current-year shoots, there was no clear difference between earlywood and latewood vessels. The first-formed vessels nearest the pith were as small as the latewood vessels; vessels near the middle of the wood ring were largest. In all other rings, earlywood and latewood vessels were clearly distinguishable. Vessels in current-year shoots of *Q. alba* and *Q. rubra* were about the same, or up to 30% larger in diameter than vessels found in the third to fifth annual rings of *Acer saccharum*, *Rhizophora mangle* and *Cassipourea elliptica* (Sperry et al. 1988a, 1988b, Sperry and Tyree 1988, and unpublished results). But vessels in second-year rings of *Q. alba* and *Q. rubra* were two to three times larger in diameter.

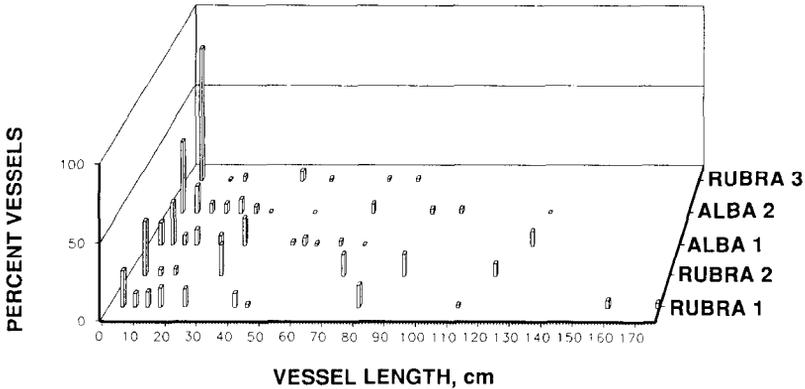


Figure 2. Similar to Figure 1 except pigment perfusions were done on 2-year-old shoots. Rubra 1 and 2 are vessel-length distributions for two *Q. rubra* shoots measured in 1989 rings. Alba 1 and 2 are vessel-length distributions for two *Q. alba* shoots measured in 1989 rings. Rubra 3 is representative data measured in the 1988 ring on 3-year-old shoots. These vessels are blocked with tyloses.

Table 1. Vessel diameter (μm) in young stems of *Quercus alba* and *Q. rubra*. Values are means \pm standard deviation with number of measurements given in brackets. First rings refer to vessels measured in current-year shoots and second rings refer to vessels measured in the outermost ring of 2-year-old shoots.

Species	First rings		Second rings	
	Earlywood + Latewood		Earlywood	Latewood
<i>Quercus alba</i>	35.8 \pm 10.6 (100)		79.9 \pm 15.4 (50)	22.0 \pm 4.7 (50)
<i>Quercus rubra</i>	29.1 \pm 6.8 (100)		79.7 \pm 21.5 (50)	29.1 \pm 6.8 (50)

Tylose formation

We found no evidence of progressive tylose formation in our weekly sample collections from mid-March to mid-May. Although intensive sampling was not continued into the 1989 growth season, it was clear that 1988 earlywood vessels formed tyloses in the 1989 growth season. During the weekly collections, virtually all 1988 earlywood vessels were found to be embolized (based on the first low pressure dye perfusion results). Subsequent high pressure perfusions demonstrated that few 1988 vessels were blocked by tyloses, whereas most vessels more than 1 year old were closed by tyloses. In Figure 3, we plot the percentage of dyed earlywood vessels (vessels free of tyloses) on the *y*-axis. The years of growth of the rings are indicated by different symbols and the age of the internodes (i.e., number of rings) are plotted on the *x*-axis. Lines connect rings of the same age between internodes of different ages. With the exception of vessels in 1-year-old internodes (i.e., shoots grown in 1988), few of the vessels formed in 1988 were blocked with tyloses. But > 85% of the earlywood vessels in the 1987 rings were blocked by tyloses. The vessels in current-year shoots may have been blocked by emboli rather than tylose; the emboli may have been trapped in vessels that are typically less than 4 cm long in current-year shoots. The stems were perfused with water at 0.1 MPa for 0.5 h, which should have eliminated emboli. To confirm this we perfused current-year (1989) shoots at 0.1 MPa for 0.5 h while measuring the gradual increase in hydraulic conductivity and confirmed that our treatment did eliminate emboli in December. So we concluded that tylose blockage is completed in current-year shoots by mid-winter. Tyloses were frequently visible under the microscope in nonstained vessels, but as tyloses generally do not fill the entire length of the vessel, microscopic observations proved less

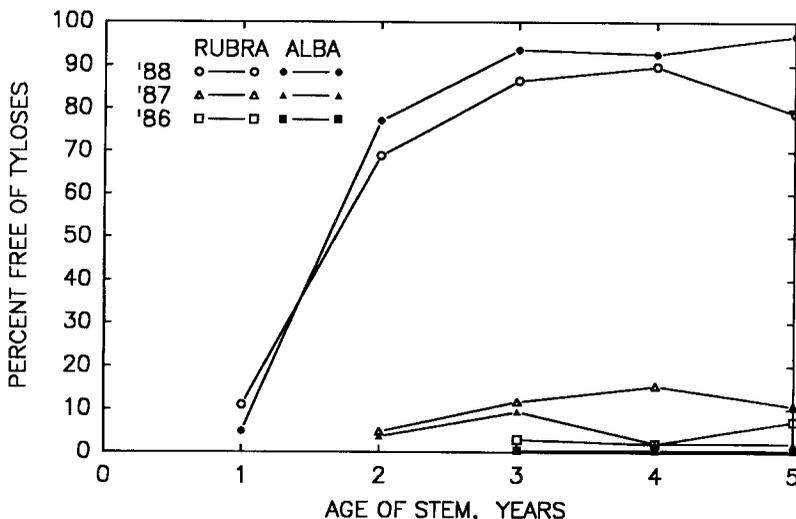


Figure 3. Percentage of earlywood vessels free of tyloses in 20 cm segment lengths (*y*-axis) versus segment age (*x*-axis). Lines connect rings formed in the same growth season. Rubra (open symbols) and alba (closed symbols) refer to *Q. rubra* and *Q. alba*, respectively.

reliable than staining methods. The pattern of tylose formation in latewood vessels is different (Figure 4). More than 50% of the 1988 latewood vessels were plugged by May 1989, but tylose plugging increased slowly in older rings. Some conduction was still evident even in 6-year-old rings.

Seasonal changes in embolism formation

Seasonal changes in embolism formation were followed in the 1989 growth season to determine when embolisms occur. The percentage loss of hydraulic conductance was stable around 20% during August and September 1989 (Figure 5), but a significant increase to 60 or 70% occurred after the first hard frost, and a subsequent increase to > 95% loss of conductance occurred after the second hard frost. Dates of subzero temperatures at the Burlington International Airport (about 1 km from the collection site) are indicated on Figure 5 by arrows together with the minimum temperatures reached. During these frost events, leaves were still on the trees so the xylem pressure may have been subatmospheric. It is well known that air bubbles come out of solution during freezing of xylem water (Ewers 1985); so, if the water was under tension, a large drop in conductance might have occurred.

Freezing-induced embolism was confirmed under laboratory conditions in a few experiments. The results of one representative experiment are shown in Figure 6. At time zero, the bath circulator was set at -30°C and the temperature measured on the surface of the stem began to fall. At the point marked "E," the brief temperature increase marks the onset of the freezing exotherm and the stem conductivity fell to nearly zero. Because the xylem pressure potential was controlled in the unfrozen stem apex and base at approximately -10 to -17 kPa during the entire experiment, the air bubbles formed on freezing expanded when the box was again warmed. The start of the warming phase is marked "W" in Figure 6. The stem never returned to

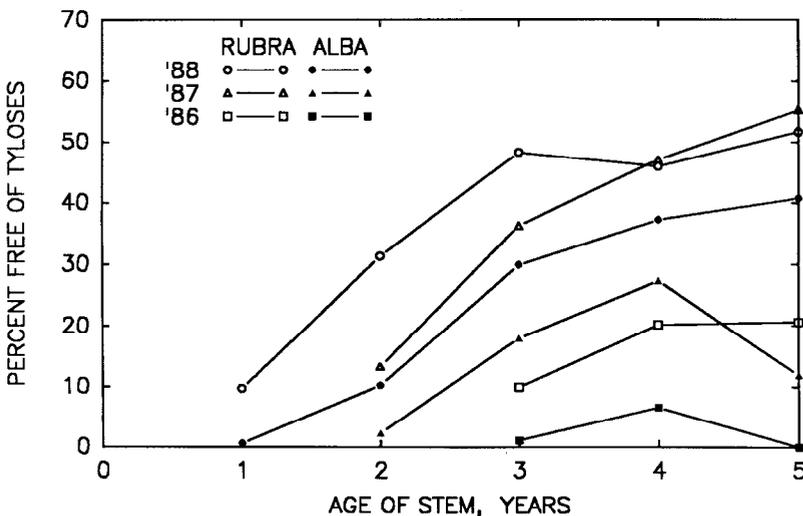


Figure 4. Similar to Figure 3 but for latewood vessels.

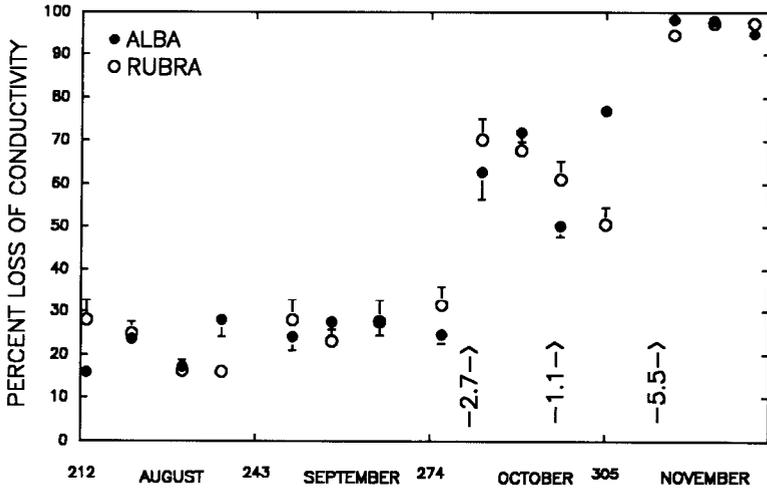


Figure 5. Seasonal change in percentage loss of hydraulic conductance due to embolism in *Q. rubra* (open symbols) and *Q. alba* (closed symbols). Numbers on x-axis refer to Julian day of year. Arrows indicate the approximate date of subzero minimum temperatures and the numbers next to the arrows indicate temperature.

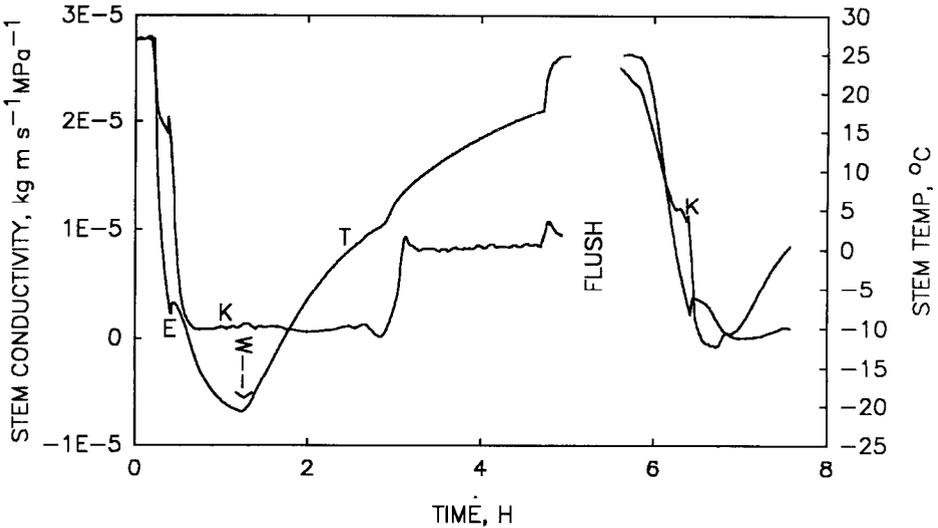


Figure 6. Change of hydraulic conductivity of stems (*Q. rubra*) versus time during a freeze-thaw cycle. "K" indicates the conductivity (left y-axis) and "T" indicates the stem temperature (right y-axis). On the temperature plot, "E" marks the freezing exotherm and "W" the beginning of the rewarming. "FLUSH" indicates the 0.5-h period when air bubbles were dissolved by flushing the stem with degassed water at 170 kPa pressure head.

the original conductivity until after a positive pressure flush.

Vulnerability to cavitation

Vulnerability to cavitation of current-year shoots and petioles is shown in Figure 7. The minimum percentage loss of conductivity averaged about 20%. Higher losses did not occur until Ψ_{xp} fell below -2 MPa. This is probably because shoot Ψ_{xp} typically reached minimum values of -2 MPa during the summer. Vulnerability curves for petiole and current-year shoots were similar, except for the petioles that had been exposed to the first frost on October 10, 1989 (solid squares), which all had higher embolism values. Vulnerabilities could not be measured in older stems because stems had to be cut longer than the longest vessel, and in older stems this meant that we would have to dehydrate stems several meters in length. The vulnerability curve shows a 50% loss of hydraulic conductivity at $\Psi_{xp} = -2.5$ MPa indicating that *Q. rubra* is more vulnerable than *Acer saccharum*, which does not reach 50% loss of conductivity until $\Psi_{xp} = -3.8$ MPa. The vulnerability of *Q. rubra* is about the same or less than that of two conifers, *Abies balsamea* and *Tsuga canadensis* (Tyree and Sperry 1989).

Loss of hydraulic conductivity and the onset of ultrasonic AEs is not correlated in *Q. rubra*. Figure 8 is representative of many replicate experiments. It was common to find many ultrasonic AEs as excised branches 1.5 to 2.5 m long were dehydrated from 0 to -2 MPa, but the percentage loss of conductivity stayed at 20% whether the shoots were rehydrated overnight to $\Psi_{xp} = 0$ MPa and sampled or dehydrated to

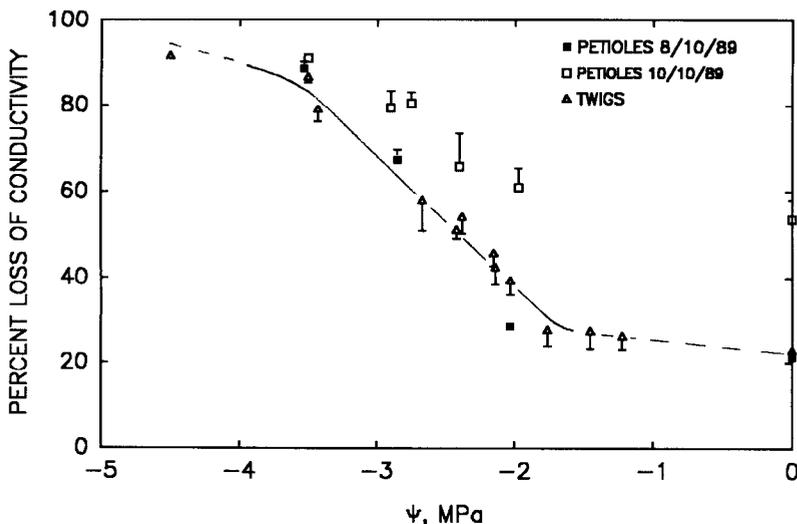


Figure 7. Vulnerability of *Q. rubra* stems and petioles to loss of hydraulic conductivity due to embolism. The y-axis is the percentage loss of conductivity versus the water potential (on the x-axis) to which excised shoots were dehydrated. Petioles collected after October 10, 1989 (\square) had a higher level of embolism due to the frost event of the night preceding the collection date compared with petioles collected two days earlier before the frost (\blacksquare).

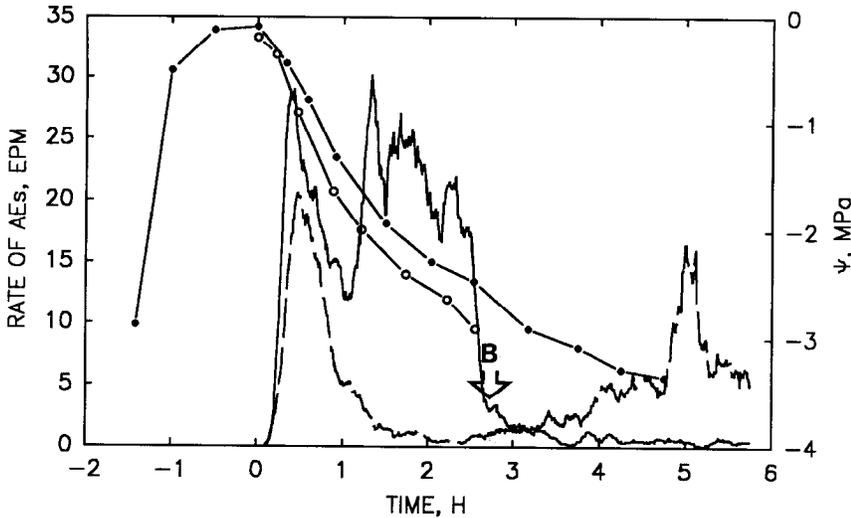


Figure 8. Effect of repeated dehydration on acoustic emissions (AEs). Positive times on the x -axis give the time since the beginning of the dehydration period for both dehydration events; negative times indicate rehydration after the first dehydration. The rate of AEs (10 min running means) are indicated by solid and dashed lines without symbols for the first and second dehydration, respectively. Water potentials, Ψ_{xp} , are indicated by solid lines with open and closed circles for the first and second dehydration, respectively. After 2.8 h of the first dehydration, Ψ_{xp} had reached -3 MPa; the shoot was covered in a plastic bag to reduce transpiration and the rate of AEs declined. After 20 h, the water potential had changed little as indicated by the reading at -1.5 h (closed circle). The negative times (closed circle) indicate a 1.5-h period of rehydration after the base of the shoot was placed in water (without recutting the stem). At time zero the second dehydration began. Fewer AEs were found on the second dehydration but once Ψ_{xp} had fallen below the previous low (-3 MPa at 3.2 h during the second dehydration) more AEs were observed.

-2 MPa before sampling of current-year shoots. In the first dehydration in Figure 8, the shoot was dehydrated to $\Psi_{xp} = -2.8$ MPa and then placed in a black plastic bag at the time marked "B." The rate of AEs recorded fell to nearly background levels soon after the shoot was placed in the bag and Ψ_{xp} remained at -2.8 MPa for 20 h. The shoot was then recut under water (removing only 2 cm of the base of the stem) and the leaf Ψ_{xp} recovered to nearly 0 MPa within 1 h (see closed circles on the negative part of the time scale). On the second dehydration there was still significant AE activity (but less than before) as Ψ_{xp} fell from 0 to -2 MPa. The rate of AEs fell to a low value for Ψ_{xp} between -2 and -2.8 MPa then resumed again at lower water potentials. If the AEs between 0 and -2 MPa indicated cavitation, this may have been confined to wood fibers or the smallest latewood vessels and wood tracheids. In any case, cavitation, if it occurred was evidently insufficient to cause a measurable decline in hydraulic conductivity.

Although individual xylem tracheids do not contribute much to water conduction, collectively the vast number of these small tracheids and vessels may have an important influence on the water balance of *Quercus* species. This idea is supported by the results of some preliminary experiments which were as follows. Several 2- to

5-year-old *Q. rubra* branches were cut by pole pruner during bright sunny days and allowed to dehydrate in the air for 5 to 15 minutes. The lower 1 to 2 cm of wood was then recut under water and the branches left to transpire for 2 to 12 h in direct sunlight. Branches were placed in either Congo red (which primarily stains early-wood vessels) or safranin (a general stain) for most of the transpiration period. In some instances, the ultrasonic AE detector was attached during the transpiration period. Near the end of the transpiration period, leaf water potentials were measured and the stems were cut into sections to determine the movement of dye and some were cut under water to check for air bubbles in the larger vessels. Our observations were as follows. (1) Large vessels were filled with air and Congo red traveled in earlywood vessels only a few cm consistent with capillary rise. (2) Leaf water potentials remained between -0.1 and -0.2 MPa. (3) AEs did not exceed background rates. (4) Safranin traveled throughout the small vessels and tracheids of the 1989 ring and through much of the latewood vessels of the 1988 ring. (5) High rates of transpiration (1.2 to 2.5×10^{-4} kg s $^{-1}$ m $^{-2}$) were measured by rate of water uptake and from some occasional measurements made with a Li-Cor steady state porometer. Because earlywood vessels were quite long and probably embolized over their entire length, and because the leaf water potentials and transpiration were high, this indicates that the smallest vessels and tracheids were quite efficient conductors of water over distances of 1 m or more. Successive dehydration experiments like those of which results are shown in Figure 8 also demonstrated that substantial water uptake could occur when stems are returned to water without recutting them under water (data similar to those in Figure 8). Although the dehydrations were performed under low-light laboratory conditions, water uptake was always sufficient to return leaf Ψ_{xp} to > -0.1 MPa within 1 h. Before rehydration, leaf Ψ_{xp} was always < -2 MPa and therefore all cut vessels must have been fully embolized. To account for the observed rehydration, we conclude that numerous short tracheids at the cut base of the stem must rapidly refill with water and become functional again. Water transport in minor vessels and tracheids of *Quercus* species clearly deserves further study.

Discussion

Vessel diameter in 1- to 2-year-old stems of *Q. rubra* and *Q. alba* was only a half or a third the diameter of vessels in main stems, which are typically 200 to 300 μ m in diameter based on our observations (unpublished) and previous observations (Zimmermann and Brown 1971 p. 195, Akachuku 1987). Fortunately vessel lengths in current-year shoots were < 20 cm, allowing us to impose negative xylem Ψ_{xp} by dehydrating excised shoots. If vessels had extended from the boles throughout the current-year shoots, it would have been necessary to dehydrate whole trees to establish vulnerability curves.

Tyloses begin to form in many trees at the end of the growing season (Zimmermann 1979) and can begin to form within a day in *Q. alba* in response to wounding (Meyer 1967). Our results show that tylose growth is not enough to block earlywood vessels completely in undamaged wood until the next growth season; although others

report tylose growth is complete by December (Fujita et al. 1978, Zimmermann 1983). Our results suggest that the life history of *Quercus* vessels can be summarized by the following sequence: growth in early spring; functional water conduction until early fall with a loss of perhaps 20% of water transport capacity by August; irreversible embolism of vessel by the first hard frost in fall; and gradual growth of tyloses until the vessels are completely blocked by the following summer. The presence of air embolism before tylose growth seems to be an absolute requirement (Klein 1923).

We were surprised to find a 50% loss of hydraulic conductivity in current-year shoots at a Ψ_{xp} of -2.5 MPa. We did not observe such negative values of Ψ_{xp} under field conditions (unpublished), but our measurements were not very extensive. Others have reported Ψ_{xp} values reaching -3 MPa in *Q. alba* (Hinckley and Bruckerhoff 1975, Hinckley et al. 1979) and predawn values of -2.8 MPa for *Q. rubra* and *Q. alba* (Parker et al. 1982). This seems to indicate that there is little margin of safety against catastrophic loss of hydraulic conductivity in these species. Two alternative possibilities must be considered. (1) The Missouri provenances studied in the above papers may have been less vulnerable to cavitation than Vermont provenances, which are rarely exposed to the drought common in Missouri. (2) Our samples may have been made more vulnerable as a result of excision. Normally, in intact trees, air emboli would be sucked in through vessels opened in recently damaged leaves and twigs, e.g., damaged by insects, wind, hail, etc. If the pit membranes at the apical extremities have smaller pores than the pit membranes exposed by excising branches, then (according to the air-seeding hypothesis) intact trees would be more able to withstand drought-induced embolism than would excised branches. These possibilities deserve more study. It should be emphasized, however, that the small earlywood vessels in current-year wood of 1- to 2-year-old twigs of *Q. rubra* are no more vulnerable to water stress-induced embolism than the tracheids of two species of conifers (Tyree and Sperry 1989), so the vulnerability cannot be attributed to the diameter of the vessel lumina.

The role of frost in causing embolism in *Quercus* is unusually significant. The onset of frost does not cause much embolism in *Acer saccharum* (Sperry et al. 1988b), or in several other conifers and northeastern hardwoods (Sperry, personal communication). Embolism becomes quite extensive during prolonged periods of subzero temperatures because of winter desiccation, but this is the first time we have seen extensive embolism resulting from a relatively brief frost. This may be due to a combination of factors. Some stems undergo pressurization during freeze-thaw cycles (Hammel 1967, Sucoff 1969, Tyree 1983, Johnson et al. 1987) and this could prevent bubble formation or the growth of bubbles. An alternative explanation is that the size of bubbles formed during a freeze depends on the diameter of the conduit and that large bubbles take a long time to dissolve and thus are more likely to be enlarged by tensions induced by transpiration after the thaw (Ewers 1985). This would make many ring-porous trees particularly vulnerable to frost-induced embolism.

Acknowledgments

The senior author thanks the Institut National de la Recherche Agronomique, Station de Sylviculture et de Production, Nancy, France, for salary and travel funds to conduct this research. Other research costs were provided by the US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station and by grant number USDA 88-33520-4073. We thank Maj. Alan L. Nye of the Vermont National Guard for permission to collect oak samples at Camp Johnson.

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