

Water stress induced cavitation and embolism in some woody plants

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A comparison was made of the relative vulnerability of xylem conduits to cavitation and embolism in three species [*Thuja occidentalis* L., *Tsuga canadensis* (L.) Carr. and *Acer saccharum* Marsh.]. Waterlogged samples of wood were air dehydrated while measuring relative water loss, loss of hydraulic conductance, cumulative acoustic emissions (= cavitations) and xylem water potential. Most cavitation events and loss of hydraulic conductance occurred while water potential declined from -1 to -6 MPa. There were differences in vulnerability between species. Other people have hypothesized that large xylem conduits (e.g. vessels) should be more vulnerable to cavitations than small conduits (e.g. tracheids). Our findings are contrary to this hypothesis. Under water stress, the vessel bearing wood retained water better than tracheid bearing wood. However, within a species large conduits were more prone to cavitation than small conduits.

Additional key words – *Acer saccharum*, acoustic emission, hydraulic conductance, stem psychrometer, *Thuja occidentalis*, *Tsuga canadensis*.

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Introduction

Ever since the introduction of the cohesion theory of sap ascent in plants (Dixon 1914), it has been recognized that xylem conduits can be under tension (= minus the xylem pressure potential). Xylem has been aptly termed "the vulnerable pipeline", because as a water conducting system, it operates at the edge of physical possibility. Under normal circumstances xylem functions at pressures below vacuum (typically -1 to -2 MPa and, rarely, down to -10 MPa). Because the vapor pressure of water is slightly above vacuum, liquid water in the xylem at sub-vacuum (< 0.1013 MPa) is in a metastable state (Zimmermann 1983).

This instability of xylem water poses a direct threat to the survival and photosynthetic productivity of plants. The degree of tension that can exist in the xylem before water makes a violent transition to the equilibrium vapor phase is limited. This explosive phase change is

termed cavitation, and it occurs in plants subject to even moderately low negative pressures associated with mild water stress (Zimmermann and Milburn 1982, Tyree and Dixon 1983, Tyree et al. 1984a,b). Immediately after a cavitation the xylem conduit begins to embolize, i.e. fill with air as gases come out of solution in surrounding tissue to fill the void left by the cavitation event. The danger of emboli for plants is that emboli impair water conduction, the overall conducting capacity of the xylem is reduced and mid-day water stress in leaves increases. Leaf water stress is a major factor limiting terrestrial plant productivity on a worldwide basis (Fischer and Turner 1978, Turner and Kramer 1980, Boyer 1982, Hanson and Hitz 1982). A wide variety of growth-related processes are affected by water deficits, with cell expansion being one of the most sensitive (Hsiao et al. 1976, Bradford and Hsiao 1982, Tyree and Jarvis 1982).

Although it is recognized that cavitations could ad-

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versely affect the water economy of plants, little is known about the water potentials at which cavitations begin to have a significant impact on water conduction in xylem. Also little is known about how xylem structure relates to the ability of plants to avoid cavitations. However, a common presumption is that large xylem conduits (e.g. vessels) are more prone to cavitations than small conduits (e.g. tracheids), see Pickard (1981), Baas (1976, 1982), Zimmermann and Milburn (1982) and Zimmermann (1983). Within the xylem of any one species there is a range of sizes of xylem conduits. If large conduits are more vulnerable to cavitations than small conduits within a species, then we would expect to find a larger net water loss per cavitation event at the beginning of a dehydration period than at the end. Also if cavitated conduits rapidly embolize, then we would expect a disproportionately large drop in hydraulic conductance for the first few cavitations than for the later cavitations. This follows because the hydraulic conductance of pipes increases with the fourth power of the pipe radius according to the Hagen-Poiseuille Law (Zimmermann 1983). If we compare woody species then we would expect to find a larger percentage of cavitated conduits in hardwoods (bearing vessels) than in softwoods (bearing tracheids) at any given xylem pressure potential (Carlquist, 1975). The purpose of the present paper is to test this hypothesis of the relative vulnerability of the xylem of woody species to cavitation and embolism by determining the relationship between cumulative cavitation events in sapwood samples and (a) water loss, (b) loss of hydraulic conductance and (c) xylem water potential.

Abbreviation – AE, acoustic emission.

Materials and methods

Materials

Experiments were conducted on two softwood species and one hardwood. Cedar (*Thuja occidentalis* L.) and hemlock [*Tsuga canadensis* (L.) Carr.] were chosen because the wood of these softwoods is free of resin which would otherwise plug the tracheids of excised wood samples and make measurements of hydraulic conductance difficult. Maple (*Acer saccharum* Marsh.) was chosen because it is representative of many diffuse porous hardwoods but the vessels are relatively short, i.e. mostly < 10 cm (Zimmermann and Jeje 1981). Vessel endings contribute significantly to the hydraulic resistance of woody species (Zimmermann and Brown 1971), and vessel endings prevent the passage of emboli to adjacent vessels (Zimmermann 1983). Consequently it is important that the stem segments used be significantly longer than the longest vessel. With maple samples this could be achieved with stem segments of a manageable length (40 to 60 cm).

Experiments were conducted from January 1984 to February 1985. Stem segments were collected from the forest on Snake Island, Lake Simcoe 90 km north of Toronto, Canada. The segments were stripped of leaves and minor branches and floated in a basin of water until they sank, i.e. until waterlogged which usually happened in 12 to 24 h. This procedure should have removed most emboli (J. S. Sperry, 1985. Ph. D. Thesis, Harvard University, Cambridge, MA, USA). During experiments, waterlogged segments were progressively air dehydrated while measuring two or more of the following parameters: (1) relative water loss, (2) percentage loss of initial hydraulic conductance, (3) cumulative acoustic emissions (= cavitations) and (4) xylem water potential. Stem segments were 1 to 2 cm in diameter and 40 to 60 cm long in all experiments except for measurements of water loss versus cumulative acoustic emissions (or versus loss of hydraulic conductance) in which cedar and hemlock segments were 0.5 to 0.8 cm in diameter and 3 to 6 cm long. Cedar segments were rapidly growing terminal shoots of 2 to 4 years of age collected from saplings. Hemlock segments were secondary or tertiary horizontal branches 8 to 15 years old collected from young trees. Maple segments were the main stems from saplings that were 5 to 10 years old.

Acoustic emissions

Cavitation events were counted during air dehydration of stem segments by the ultrasonic acoustic emission (AE) method (Tyree et al. 1984a) using a Bruel and Kjaer model 8312 broad band ultrasonic transducer and preamplifier. Ultrasonic AE signals were further amplified and conditioned through a 100 kHz high pass filter by a Bruel and Kjaer model 2638 amplifier or an equivalent amplifier built in our laboratory. The AEs were counted by the electronic methods described by Tyree et al. (1984a,b). The AE transducer was clamped to the sapwood stripped of bark. In large stem segments a strip of bark 4 mm by 30 mm was removed near the center of the segment and exposed sapwood was covered with grease to reduce local evaporation.

Relative water loss

During air dehydration stem segments were sometimes removed and weighed. At the end of the experiment the samples were oven dried at 70°C and again weighed. Relative water loss, R, was calculated from

$$R = 100\%(W_0 - W)/(W_0 - W_d), \quad (1)$$

where W_0 is the waterlogged weight, W is the current fresh weight and W_d is the oven dry weight. To accelerate dehydration of large stem segments bark was removed for a distance of 10 to 15 cm from each cut end. In small samples (3 to 6 cm) all bark was removed.

Hydraulic conductance

Waterlogged stem segments were stripped of bark and the maximum hydraulic conductance, L_0 , was measured using a pipette, a stop watch and a gravitational pressure head of about 30 cm water. The hydraulic conductance, L , is defined as

$$L = \Delta V \Delta P / (\rho g h \Delta t), \quad (2)$$

where ΔV is the volume flow increment measured on the pipette in time Δt , ΔP is the pressure head calculated from $\rho g h$ (= water density times acceleration due to gravity times water column height) and l is the length of the stem segment. To minimize artifacts that are presumably caused by swelling of pit membranes when conductances are measured with distilled water (Zimmermann 1978), flow rates were measured with 10 mM NaCl solutions. After measurement of the initial hydraulic conductance, the sample was weighed and then air dehydrated a desired amount. After the dehydration period the sample was weighed again and then submerged under water. Sufficient wood was trimmed off each end to remove surface emboli that were sucked into the severed xylem conduits at the cut ends of the segment during dehydration. For cedar and hemlock 2 to 3 mm was removed from each end and for maple 10 to 15 cm was removed. The hydraulic conductance, L_d , was again measured to determine the effect of internal emboli on the conductance. The sample was subsequently oven dried. Plots were constructed of relative water loss, R , versus the percentage loss of initial conductance [100% $(L_0 - L_d)/L_0$].

The drier maple samples tended to absorb water for 2 to 6 min following recutting under water. This transient absorption was permitted to diminish before the reduced conductance L_d was measured.

All cuts to cedar and hemlock stems were made with new razor blades; maple segments were cut with a recently sharpened pruning shear (secateur). Cuts made with dull implements or hand saws caused enough surface blockage to substantially reduce the hydraulic conductance of the stem segments.

Xylem water potential

A strip of bark about 4 mm by 3 cm was removed near the center of the segments. A stem hygrometer was mounted on the strip. Exposed sapwood of the strip was covered with silicone grease to reduce local evaporation. When AEs were measured simultaneously a second strip of bark was removed on the same side of the stem 5 to 6 cm above the hygrometer strip to mount the AE transducer. The central portion of the segments containing the hygrometer and AE transducer was usually enclosed in a constant temperature chamber which was maintained at $25 \pm 0.5^\circ\text{C}$. About 15 cm of each end of the stem segments protruded out of the upper and

lower ends of the constant temperature chamber. Initially the base of the stem segment was kept in water to allow thermal and water vapor equilibrium in the stem hygrometer chamber. After the equilibration period, the water was removed from the stem and the bark stripped away for a distance of 10 to 15 cm from each end to increase the rate of dehydration. Apparent stem water potentials were corrected for the temperature gradient between the stem surface and psychrometer thermocouple by the method in Dixon and Tyree (1984).

In some instances stem segments were allowed to dehydrate a known amount (as measured by weight loss) before mounting the stem psychrometer. After mounting the psychrometer the whole stem and psychrometer was wrapped in plastic film (Saran wrap) to prevent further dehydration. After 30 to 40 min to permit vapor equilibration and partial thermal equilibrium, the xylem water potential was determined. Over the next 8 to 16 h, additional measurements of stem water potential were made to determine the magnitude of change with time. In some instances the hydraulic conductance of the stem segments were measured just prior to air dehydration and again after the determination of the stem water potential using the methods described above.

Results

Plots of percentage water loss versus a measure of cumulative acoustic emissions (AEs) for cedar, hemlock and maple are shown in Fig. 1. It can be seen that waterlogged samples of all species lost 10 to 12% of their initial water content before a significant number of AEs were recorded. This confirms earlier measurements (Tyree et al. 1984b). Tissue shrinkage was negligible during the loss of more than half of the initial water in cedar and hemlock (Tyree et al. 1984b) and also in maple (results not shown).

Once AEs began in all three species (Fig. 1) the amount of water lost per AE was relatively larger at the beginning of the dehydration than towards the end. The large springwood tracheids cavitated first as confirmed by dye ascent experiments performed by Dr V. A. Seymour Berg (personal communication) during a brief visit to our laboratory. Waterlogged hemlock stems stained uniformly when dye was drawn through them, but the staining was confined to summerwood annuli when dye was drawn through partially dehydrated samples. Note also that in hemlock the plot of percentage water loss versus percentage cumulative AEs is more curved than in cedar. This suggests that the size distribution of cedar tracheids was more uniform in our samples than the size distribution of hemlock tracheids. Cross sections of our samples revealed that the percentage of large springwood cells in cedar ($75 \pm 4\%$) was larger than in the hemlock samples ($47 \pm 8\%$).

Plots of relative water loss versus percentage loss of initial hydraulic conductance for the three species are

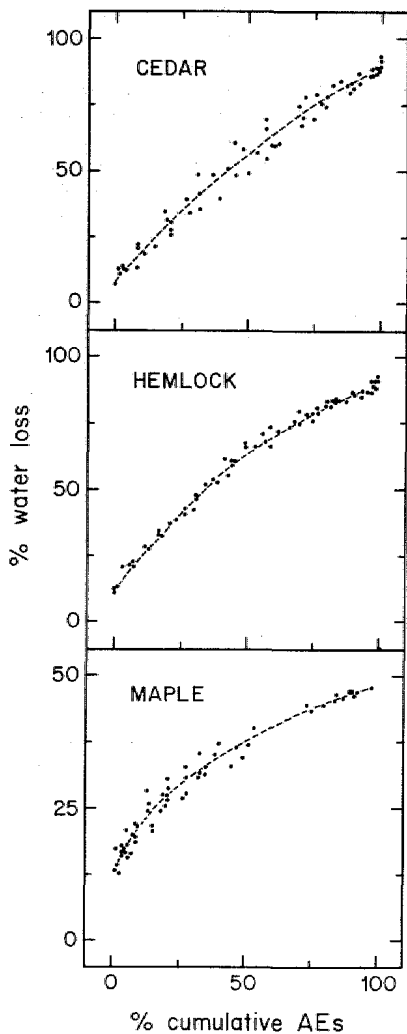


Fig. 1. Percentage water loss versus percentage cumulative acoustic emissions measured during the air dehydration of sapwood samples initially waterlogged. The graphs consist of the combined data of 5, 5 and 11 stem segments for cedar, hemlock and maple, respectively.

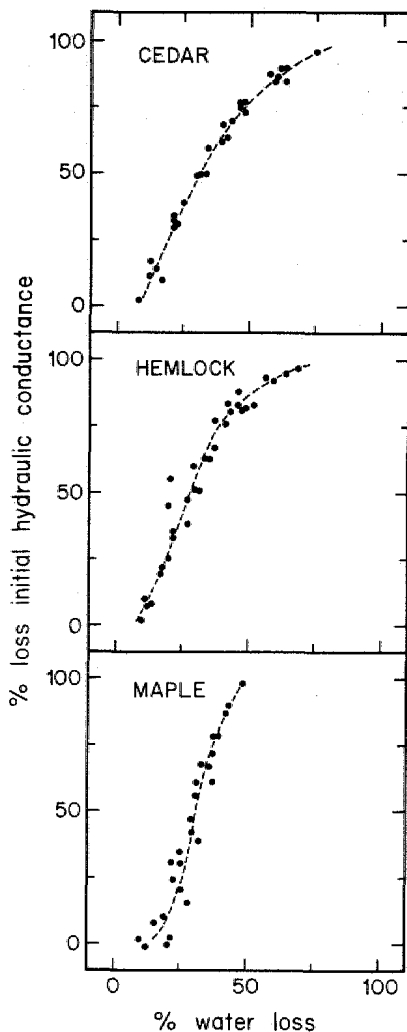


Fig. 2. Percentage loss of initial hydraulic conductance versus percentage water loss. The initial hydraulic conductance was measured in waterlogged stem segments. Each point represents the dehydration of one stem segment.

shown in Fig. 2. A 10 to 15% decline of water content occurred before the hydraulic conductance declined significantly. Maple sapwood showed a precipitous fall in conductance over a narrow range of water content (from 15 to 50% relative water loss) whereas the conductance dropped more gradually for the conifers (from 12 to 80% relative water loss). This suggests that maple vessels embolized well before much water was lost from wood fiber lumina, living cells and cell walls.

In Fig. 3 are plots of the percentage cumulative AEs

versus the xylem water potential measured during the dehydration of stems of cedar and hemlock. (See details for maple in the next paragraph.) In most instances the water potential fell below measurable values (< -10 MPa) within 24 to 48 h. In conifer stems AE measurements were continued for 3 to 5 days until AE activity ceased. Acoustic activity persisted in maple stems for more than 2 weeks so measurements were usually terminated once the stem water potential fell below -10 MPa, i.e. after 24 to 48 h.

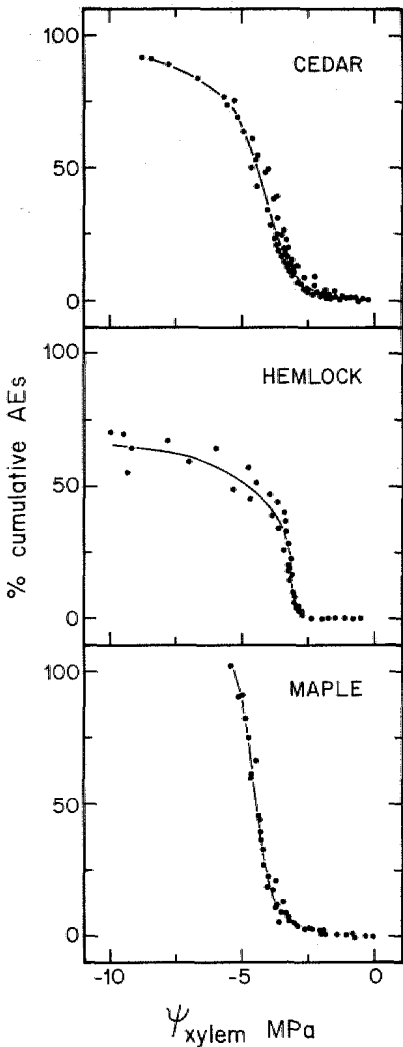


Fig. 3. Percentage cumulative acoustic emissions (= cavitations) versus xylem water potential measured during the dehydration of stem segments. The graphs consist of the combined data of 5, 3 and 3 stems for cedar, hemlock and maple, respectively. For maple 100% cumulative AEs corresponds to the point where the hydraulic conductance of the xylem has fallen to 2% of its initial value (= 48% relative water loss or -5.3 MPa xylem water potential).

Xylem water potential was plotted versus a measure of cumulative AEs. In small cedar and hemlock samples the number of AEs correspond closely to the number of tracheids in the samples (Tyree et al. 1984b). In the present study the hydraulic conductance of the xylem did not fall below 2% of the maximum conductance until >80% of the AEs had occurred in cedar or until

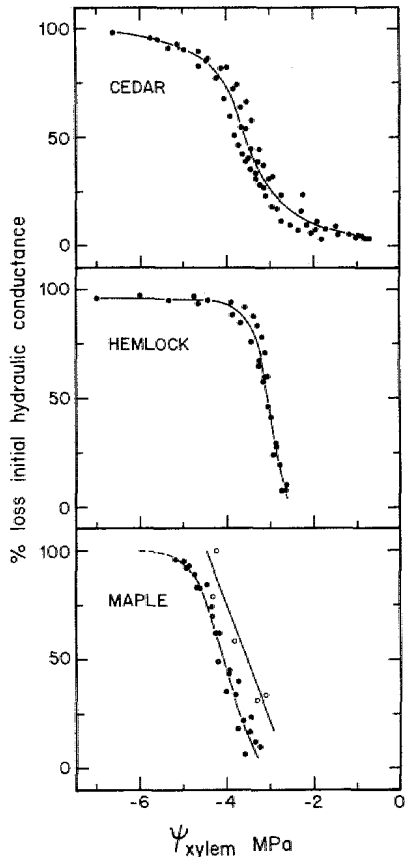


Fig. 4. Percentage loss of initial hydraulic conductance versus stem water potential measured during the dehydration of stem segments. The open circles represent direct measurements. The solid points were obtained by combining data in Fig. 3 with Fig. 5. Ordinate values of percentage cumulative AEs for points in Fig. 3 were converted to percentage loss of initial hydraulic conductance read from the curved line in Fig. 5.

> 75% of the AEs had occurred in hemlock. In order to compare relative xylem vulnerabilities to cavitation, plots were made of stem water potential versus the percentage maximum cumulative AEs for cedar and hemlock. Maple stem hydraulic conductance fell below 2% of the maximum value when fewer than 20% of the maximum AEs had occurred; this corresponded to a stem water potential of about -5.3 MPa and a relative water loss of 48%. Presumably most of the AEs occurring below -5.3 MPa were associated with cavitation events in wood fiber lumina and the lumina of living cells. For maple stems, water potential was plotted versus a "cavitation index" in which 100% corresponded to a stem water potential of -5.3 MPa or a relative water

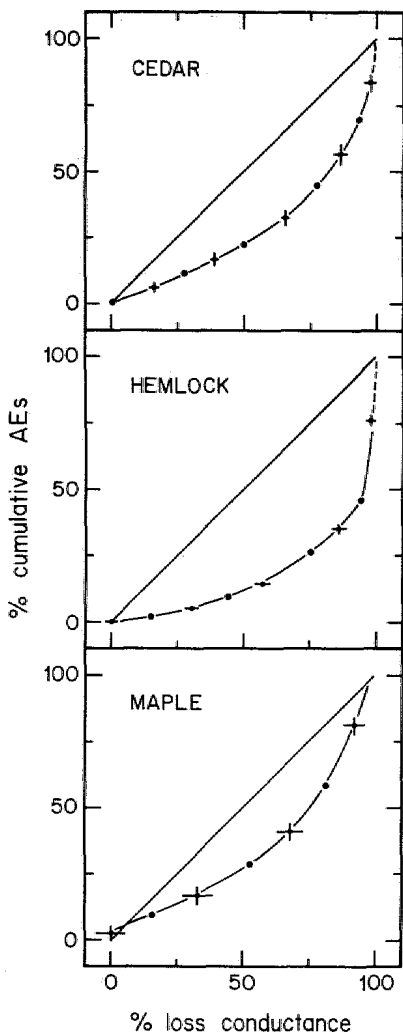


Fig. 5. Percentage cumulative acoustic emissions versus loss of initial hydraulic conductance during the dehydration of stem segments. These data were derived from data in Figs 1, 2. The horizontal and vertical bars represent estimates of the SD of some of the plotted points.

loss of 48% (= the point at which the hydraulic conductance had fallen to about 2% of its maximum value).

In the experiments in Fig. 3, the AE transducer and stem hygrometer were mounted near the center of a 40 to 60 cm stem segment. But most of the evaporation occurred from the ends of the segments where bark had been removed over a distance of 10 to 15 cm. Consequently, considerable water potential gradients might have existed in the samples due to longitudinal and/or radial resistances to water flow. The magnitude of these

resistances and the resultant disequilibria would increase as the dehydration proceeded. To assess the magnitude of any disequilibria, we dehydrated similar branches, attached a stem hygrometer, and then wrapped the whole stem in plastic film to prevent subsequent evaporation. We then measured stem water potential over the next few hours. The water potentials were either constant over a period of 8 to 16 h or grew less negative with time by at most 0.05 MPa in maple and 0.2 MPa in cedar. If the extreme ends of the segments were at a lower water potential than the central bark-covered section, then the apparent stem water potential should have declined with time. The increase in water potential may have been brought about by a few additional cavitation events which have released additional water from the cavitated conduits and partly rehydrated surrounding tissue. There appears to be no evidence of substantial disequilibrium in xylem water potential during the time course of the dehydrations shown in Fig. 3.

In Fig. 4 are a few direct measurements of loss of hydraulic conductance in maple that were made during the course of measurement of water loss versus xylem water potential. The other data points plotted were derived from data in the previous three graphs as explained below.

Discussion

Acoustic emissions began in cedar when the xylem pressure potential fell below -1 MPa (Dixon et al. 1984, Tyree et al. 1984a). Before the xylem pressure potential can fall very low, water must first evaporate from severed tracheids (or vessels) at the cut ends of the stem segments. In similar cedar and hemlock samples the tracheids were about 1 mm long. So water held in severed tracheids at the ends of 5 cm long samples could contain only about 2% of the initial water content. It can be seen from Fig. 1 that samples lost 10 to 12% of their water before AEs began. Similar conclusions can be drawn for maple when vessel lengths and the number of vessels are taken into account.

It would appear that 8 to 10% of the water contained in cedar and hemlock is so-called 'capillary water' (Zimmermann 1983). This would suggest that 8 to 10% of the lumina still contain at least small emboli after waterlogging or that substantial holes exist in the walls surrounding these lumina. In either case water would drain out of such lumina at pressure potentials well above -1 MPa (Zimmermann 1983). An alternative interpretation is that non-violent cavitation events, which do not produce ultrasonic AEs, are occurring at pressure potentials higher than -1 MPa. However, the distinction between this possibility and Zimmermann's concept of capillary water becomes confused and reduces to a question of semantics. Two of the mechanisms proposed whereby a cavitation event is 'seeded' are: (1) when the pressure potential drops low enough to either draw in air through tiny 'pin holes' in the walls of xylem condu-

its or (2) when the pressure is low enough to cause the explosive expansion of tiny air bubbles embedded in the walls (Dixon 1914, Pickard 1981, Zimmermann 1983). With these considerations in mind, it is easy to concede that capillary water is water held in xylem lumina in which cavitations are seeded by large 'pin holes' or large emboli.

Since both ends of the samples were immersed during the measurements of hydraulic conductance (Fig. 2), the xylem pressure potential of these samples was returned to zero (atmospheric). During the course of measurement at near zero pressure potential, air emboli might be dissolving. Consequently, the reported decline in hydraulic conductance must be viewed as an underestimate of the true magnitude of the decline. It should also be remembered that cavitated conduits filled only with water vapor (no air) would refill almost instantly during the measurement of hydraulic conductance. Since the period of dehydration of most of these samples was 1 to 6 h, it is likely that the transition from the water vapor filled (cavitated) to the partially air filled (embolized) states must occur over a period of minutes to hours.

Our results on loss of initial conductance versus relative water loss (Fig. 2) are in marked contrast to those reported for *Pinus contorta*. Edwards and Jarvis (1982) reported that the hydraulic conductance of *P. contorta* began to decline after a relative water loss of 3% compared to 10 to 15% in cedar and hemlock. Furthermore, after an additional water loss of 7% the conductance of *P. contorta* had fallen 70 to 90% compared in our case to about 18% loss of conductance in cedar and hemlock for the first 7% of water loss after conductance began to decline (Fig. 2). At this time we do not know whether these differences have an anatomical basis or whether they reflect differences in methodology. Edwards and Jarvis (1982) used polyethylene glycol (20 kdalton) to impose negative pressure potential on excised stems of *P. contorta*. The authors state that "the solutions were kept separate from the wood by a necol collodion, semi-permeable membrane which was cast directly onto the wood faces after first filling the tracheid ends and resin canals with a thin slurry of plaster-of-Paris". It is possible that cavitations occurred preferentially at the interface between the collodion membrane and the plaster-of-Paris or between the plaster and the water in the tracheid ends. This would have caused an overestimate in the loss of hydraulic conductance in *P. contorta*. In our experiments, however, we could have underestimated the loss of conductance because of dissolution of emboli after the segments were placed in water. However, we think this is unlikely because we observed little rise in conductance in the course of the conductance measurements; any dissolution of emboli would have had to have occurred in the short time (1 min) required to trim the ends of our samples and to mount them in the apparatus for measuring conductance.

According to the Hagen-Poiseuille law, the flow rate

through a cylindrical pipe increases with the fourth power of its radius. Xylem vessels and tracheids are not cylindrical and significant resistances to water flow reside at the vessel or tracheid ends. Nevertheless it is reasonable to assume that the largest xylem conduits in a stem will make a disproportionate contribution to hydraulic conductance of a stem segment. If the larger conduits are more prone to embolism then there ought to be a larger decline in stem conductance per AE at the beginning of a dehydration than at the end. By combining the data in Figs 1 and 2 it is possible to make a plot of percentage loss of initial conductance versus the cumulative AE (Fig. 5). If large and small conduits cavitated with equal probability at any given water loss, then data points should have followed the straight line relationships in Fig. 5. It can be seen that there is a 50% loss of conductance after only 28, 22 and 13% of the AEs in maple, cedar and hemlock, respectively. Large conduits appear to cavitate first. This is further confirmed by Fig. 1 and the dye ascent experiments.

From the data in Figs 1 and 5 it would appear that within a species the large xylem conduits are more prone to cavitation than small conduits. But this relationship appears not to hold when maple is compared to conifers. The large vessels of maple appear to be less vulnerable to cavitations than the much smaller tracheids of cedar and hemlock. By combining the data in Fig. 3 with those in Fig. 5, a plot can be constructed of xylem water potential versus the percentage loss of initial conductance during the dehydration of maple, cedar and hemlock. These data are shown in Fig. 4 (solid dots). There are dramatic differences between the three species. A 50% reduction of initial conductance occurs at xylem water potentials of -4.1 , -3.4 and -3.1 MPa for maple, cedar and hemlock, respectively (Fig. 4). Although cedar and hemlock tracheids are all about the same length (1.0 to 1.5 mm) and diameter (15 to 20 μm), significant numbers of emboli begin to appear at -1 MPa in cedar whereas hemlock appears to hold on to most of its water down to -2.5 MPa. However, cedar appears to be better able than hemlock to maintain a residual conductance at very low water potentials, e.g. compare the curves from -3.5 to -5.0 MPa. At a water potential of -3.5 MPa, hemlock has lost 84% of its transport capacity whereas cedar has lost only 48%. Maple, which has vessels much larger (10 to 100 μm long and 20 to 50 μm diameter) than the tracheids of cedar and hemlock, is more successful at holding on to its water. Substantial emboli with concomitant reduction in hydraulic conductance do not start until the xylem water potential reaches -3.2 MPa. At the same water potential cedar has lost 30% of its original conductance and hemlock has lost 65% of its capacity to transport water.

The difference between the direct measurements (open circles) and the values derived from Figs 3 and 5 (closed circles) is the amount of time that has elapsed between the dehydration period and the measurement of the hydraulic conductance. In the former case, after

the dehydration period the stems were wrapped in plastic film to prevent evaporation while the xylem water potential was measured over a period of several hours. In the latter case, the hydraulic conductances were measured immediately after the dehydration period. The open circle values are shifted up from (or to the right of) the closed circle values in Fig. 4. The increase in water potential observed over the period of measurements was less than 0.2 MPa for cedar and 0.05 MPa for maple. The displacement of values defined by the open circles is more than can be accounted for by the observed rise in water potential. The additional displacement might be explained if we assume that a few hours are required for emboli to fully develop in recently cavitated conduits. It is not unreasonable to expect it to take several hours for gases to reach atmospheric pressure in cavitated lumina. The mechanism of embolism formation must involve diffusion of air through the xylem water to the surface of the cavitated lumina; the gases must then come out of solution into the cavitated vessels. Conduits that are not fully embolized could refill with water in the course of the hydraulic conductance measurement.

Readers are referred to Pickard (1981) for an excellent and thought-provoking discussion of surface tension and of the possible mechanisms of nucleation and cavitation events in plants. These considerations are central to the interpretation of the relation between xylem conduit size and type (vessel versus tracheid) and the vulnerability of conduits to cavitation. Pickard discussed a number of mechanisms that pertain to bodies of water at pressure potentials below -5 MPa. These mechanisms can clearly be eliminated from consideration. The mechanisms that could apply to xylem pressures in the range of -1 to -5 MPa are (1) air-seeding, (2) nucleation at bubbles embedded in hydrophobic cracks in conduit walls and (3) nucleation at flat hydrophobic surfaces.

The air-seeding hypothesis has most recently been advanced by Zimmermann (1983) although similar ideas have been advanced by Oertli (1971) and Renner (1925). This mechanism involves meniscal failure at the site of water-filled holes that pass through conduit walls to air spaces outside. Air is sucked through such holes when the xylem tension exceeds the yield stress of the solid-gas-liquid interface and the meniscus retreats abruptly into the conduit lumen. Zimmermann (1983) has even suggested that conduits have "designed leaks", i.e. holes of specific sizes to cause meniscal failure at "designed" xylem pressure potentials. Holes designed to cause cavitation at -1 and -3 MPa would have to be about 300 or 100 nm in diameter, respectively.

Within hydrophobic cracks a tiny air bubble could remain stable with an inward bending meniscus. A mathematical relationship describing the criterion for stability versus meniscus diameter has been worked out for conical hydrophobic cracks (Pickard 1981). The xylem tension required to suck such a bubble out depends on the

diameter of the base of the cone. Pickard calculated that a hydrophobic crack 280 nm in diameter would cavitate at -3 MPa, i.e. at about the same diameter as a hole in the air-seeding hypothesis.

The third potential site for nucleation, a more or less flat hydrophobic surface, does not lend itself to easy quantitative consideration. The pressure at which cavitations occur on such surfaces seems to decline with the time period it has been wet (see Pickard 1981 p. 204). But in our view this hypothesis should not be ignored.

Pickard (1981), after a lengthy discussion, rejected all of the above mechanisms for nucleation of cavitation events. However, cavitations do clearly occur at pressures from -1 to -5 MPa and no alternative mechanisms are apparent. Obtaining experimental evidence for or against all these mechanisms deserves renewed effort. We can only speculate about why some conduits are more likely to cavitate than others. The differences between species could be explained by supposing that the walls of maple vessels have smaller holes or crevices or fewer and smaller hydrophobic regions than do cedar and hemlock. Within a species we might suggest that such wall imperfections (holes, crevices or hydrophobic regions) occur at random over wall surfaces. So large conduits (with more wall area) are more likely to have wall imperfections than small conduits and consequently they are more likely to cavitate.

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