

## XYLEM EMBOLISM IN THE PALM RHAPIS EXCELSA

by

John S. Sperry

Harvard Forest, Harvard University, Petersham, Massachusetts 01366, U.S.A.

**Summary**

Xylem failure via gas embolism (cavitation) was investigated in *Rhapis excelsa* (Palmae). Embolism was detected using measurements of xylem flow resistance in excised stems and petioles: a decrease in resistance after the removal of flow-impeding embolisms by a pressure treatment indicated their previous presence in the axis. Results suggested that *Rhapis* avoids serious damage from embolism in at least four ways. 1) Xylem pressure potentials reached embolism-inducing levels (c. -2.90 MPa) only during prolonged drought. 2) When embolism did occur, it was confined to leaf xylem; stem xylem, most critical to shoot survival, remained fully functional. This is due in part to hydraulic architecture: 70 to 85% of shoot xylem resistance is in the leaf, and thus xylem pressures are much lower in leaves than stems. 3) Even during prolonged drought, the amount of embolism is probably limited by complete stomatal closure, which occurred at xylem pressure potentials of  $-3.20 \pm 0.18$  MPa. 4) Embolism is potentially reversible during prolonged rains, since embolism dissolved within 5 h at zero pressure (atmospheric), and xylem pressure potential can reach zero during extended rain. **Key words:** *Rhapis*, xylem embolism, xylem transport, cavitation, water relations, water stress, xylem pressure potential, hydraulic architecture.

**Introduction**

Embolism in the xylem of plants refers to gas-filled tracheids or vessels. It occurs as a result of the negative pressure potential of xylem water falling below the cohesive capacity of water-filled tracheary elements. At the limiting negative pressure potential for a given vessel, xylem water undergoes a rapid transition to the equilibrium vapour phase, termed 'cavitation'. The resulting embolised vessel is initially vapour-filled, but air soon enters by diffusion. Embolism restricts the conducting system of plants because an embolised vessel cannot conduct water.

Embolism is potentially a serious problem for plants, and is known to occur routinely in

several species (Zimmermann & Milburn, 1982; Tyree et al., 1984a & b). However, there is little information about its distribution within a plant, at what pressure potentials it occurs, to what extent it affects xylem transport, and whether it is reversible. This investigation considered these fundamental questions by asking the more specific question: how does embolism affect the water transport system in a palm, which has a fixed vascular capacity? In dicotyledonous trees and other plants with secondary growth, embolised vessels can be replaced with new functional vessels as new wood is produced. In palms, however, the problem of embolism is especially severe because they lack the ability to renew vascular tissues by secondary growth.

According to a hypothesis advanced by Zimmermann and Sperry (1983; see also Zimmermann, 1983), *Rhapis* and other palms suffer embolism only in their leaves, which can be readily replaced, whereas the stem xylem remains fully functional, insuring the continued growth of the plant. The exclusive occurrence of embolism in leaf xylem is a consequence of an observed hydraulic constriction in the xylem of the stem-to-leaf connection (Fig. 1); this constriction is constituted primarily by the protoxylem connection between the discrete metaxylem systems of stem and leaf (between B' and D, Fig. 1). Xylem pressure potential is always much lower in leaves than stems because of the high resistance to water flow in the constriction. In times of water stress, pressure potentials in the leaf xylem reach embolism-inducing levels while the stem xylem remains at a safe value. Of course, palms may avoid excessive damage from embolism simply because embolism does not occur over the normal range of xylem pressure potentials; or, if it does occur, the gas-filled vessels may refill readily with water, restoring their conductivity.

The first part of this study determined the importance of the constriction in the stem-to-leaf connection in confining low xylem pressure potentials to leaves. This involved describing the 'hydraulic architecture' of the *Rhapis* shoot; that is, the relationship between shoot

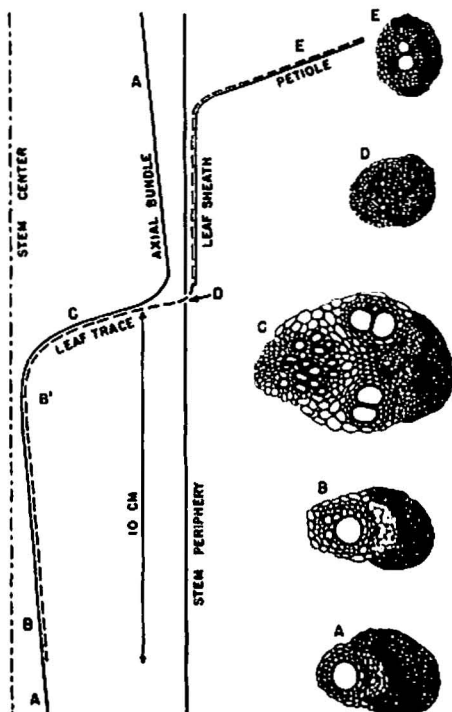


Fig. 1. Diagrammatic representation of departure of single leaf-trace bundle in *Rhaps excelsa* (c. 100 leaf-trace bundles per leaf). Solid curves A-B-C-A and D-E indicate metaxylem (mx) vessels; dashed lines, narrow protoxylem (px) tracheids. Transverse sections of vascular bundles (A-E, right) correspond to positions A-E in curves on left. Structure shown in diagram repeats itself axially, as indicated by 2 positions marked A. B-B' is where water flows from the stem mx into px which enters the leaf at D. The high resistance of the px tracheids connecting the discrete mx systems of stem and leaf indicate a hydraulic constriction (modified from Zimmermann & Sperry, 1983).

morphology, xylem anatomy, and hydraulic resistance of the xylem. The second part developed and evaluated a method for detecting embolism using xylem flow resistance measurements in petiole and stem segments. The study concluded by using this method to evaluate how *Rhaps* copes with embolism. The hypotheses in the previous paragraph were investigated by determining: 1) if, in fact, embolism is confined to the leaves as predicted by Zimmermann and Sperry; 2) the potential reversibility of em-

bolism; 3) the relationship of the xylem pressure potential required to induce embolism to the range in nature, and to the value inducing complete stomatal closure. This indicated the likelihood of embolism in nature, and the role of stomata in limiting its occurrence.

## Materials and Methods

### Plant material

*Rhaps excelsa* (Thunb.) Henry is a rhizomatous coryphoid palm native to eastern Asia. Palms used in the study grew in the Fairchild Tropical Garden in Miami, Florida; erect shoots were 2 to 3 m tall, each with roughly 10 to 15 expanded leaves. For comparative purposes, leaves were numbered beginning with the youngest-expanded one. Measurements of xylem sap pressures and xylem flow resistance described below concerned the four youngest-expanded leaves (nos. 1-4), and a senescing leaf.

### Hydraulic architecture

The Scholander pressure bomb (Scholander et al., 1965) was used to measure the difference in xylem pressure potential between stem and leaf. On a given palm, pressure potential of lamina xylem at mid-day was measured in the conventional fashion, and compared with nearly simultaneous estimates of pressure potential in stem xylem. These estimates were pressure bomb measurements of leaves that had been enclosed in plastic bags and foil-wrapped while attached to the shoot. Enclosing the leaves stopped transpiration and allowed lamina and stem pressure potentials to equilibrate (Begg & Turner, 1970).

The difference in pressure potential ( $\Delta P$ ) measured in this way can be accounted for by resistance to flow ( $R$ ) in the xylem between the stem and the lamina according to the equation derived by analogy with Ohm's law (Pickard, 1981):  $\Delta P = R J_v$ , where  $J_v$  is the volume flow rate of water in the xylem. Thus, at a given volume flow rate, the relative values of xylem resistance in the stem, stem-to-leaf connection, petiole, and lamina xylem approximate their relative contribution to the overall pressure potential difference between lamina and stem measured with the pressure bomb. By measuring these resistances, the importance of the constriction at the leaf insertion in generating low xylem pressure potentials in the leaf relative to the stem was estimated.

Flow resistance ( $R$ ) was defined as:

$$R = \frac{\Delta P}{J_v l}$$

where  $\Delta P$  is the pressure difference,  $J_v$  is volume flow rate, and  $l$  is axis length. Although this definition gives a unit length measure, in some cases, resistance was expressed by incorporating axis length (e.g. Fig. 3). Shoots were divided into lamina, petiole, leaf insertion (leaf sheath and portion of subtending stem; this segment included the constriction in the stem-to-leaf connection; Fig. 1), and stem segments. Resistance in all but lamina segments was determined by measuring volume flow rate in a pipette attached to one end of the axis under a pressure gradient induced by a vacuum pump attached to the other end (Sperry, 1985). Lamina xylem resistance was measured using the pressure bomb (Tyree & Cheung, 1977).

#### Detection of embolism

Embolism was indicated in petiole and stem segments by the presence of xylem flow resistance ( $R$ ) above the minimum, or 'base' resistance ( $R_B$ ) of the segment. The base resistance of an axis represented its embolism-free condition; resistance above the base level ( $R - R_B$ ) was caused by embolisms which impeded flow in the xylem. This method, and its application in *Rhapis*, has been fully explained elsewhere (Sperry, in press), and will be described in brief.

The resistance ( $R$ ) measurement was made in axes directly after excision from the shoot, or after they were dehydrated in the lab. Before measurement, the axis was submerged in water and both ends trimmed in order to remove superficial air blockage. Trimming was completed within 10 minutes of submersion, and resistance was measured immediately, because the procedure brought xylem pressures to zero allowing the gradual dissolution of embolisms (Fig. 5). After the resistance ( $R$ ) was measured, base resistance ( $R_B$ ) was determined. Embolisms in the axis were removed by submerging the axis in a container of water and pressurising it at 0.35 MPa for at least 20 minutes inside the pressure bomb, and resistance was measured. The pressure treatment was repeated until resistance reached a stable and minimum value, the base resistance.

Comparisons of resistance above base level ( $R - R_B$ ) were made then the base resistances involved were similar. This was naturally the case for a given axis, as well as for all petioles, or all stems. Quantitative comparisons between petioles and stems were limited to the presence or absence of resistance above base levels.

Experiments were conducted to evaluate the method. The first set determined how soaking or pressurising axes in water affected flow resistance, and indicated the relationship between dehydration, and thus induction of embolism,

and increased resistance in axes. A second experiment compared flow resistance as an indicator of embolism with the more established acoustic method pioneered by Milburn (1973a, b), and recently refined by Tyree and colleagues (Tyree & Dixon, 1983; Tyree et al., 1984a, b; Dixon et al., 1984). This latter method is based on considerable evidence that ultrasonic vibrations produced by a dehydrating axis correspond to cavitation events. Experiments were conducted in the laboratory of Dr. Tyree at the University of Toronto. Finally, anatomical studies were made in an attempt to confirm the presence of embolism in vessels of axes with resistance above the base level, and to determine if in fact the soaking or pressure treatments dissolve these embolisms.

#### Application of resistance method

Resistance above the base level was assessed in stem and petiole segments excised directly from palms in the field in order to determine the distribution of embolism in leaves versus stems.

The xylem pressure potential required to induce embolism in stem and petiole segments was determined by dehydrating axes initially at base resistance to pressure potentials between -0.30 and -7.00 MPa. Pressure potential was measured by sealing the axis in a pressure bomb with one end protruding and determining the balance pressure in the same manner used for

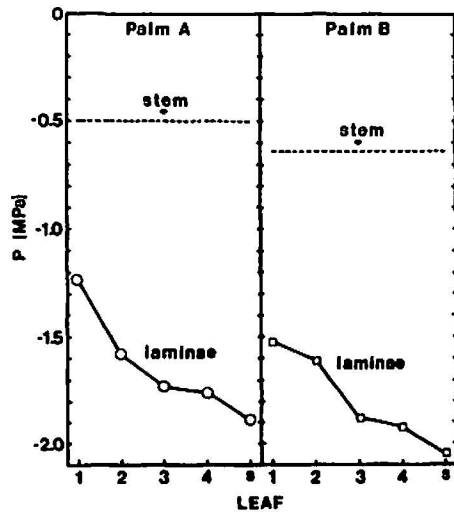


Fig. 2. Xylem pressure potentials ( $P$ ) of laminae and stem at mid-day.

entire leaves. Resistance relative to the base value was determined following the pressure potential measurement.

#### *Xylem pressure potential at stomatal closure*

Stomatal closure was induced by excising healthy, mature leaves (nos. 3, 4, 5), and allowing them to dehydrate. Complete closure was assumed to occur when stomatal resistance (porometric method, LI-Corr 1600) showed a rapid increase to effectively infinite values ( $> 100 \text{ s cm}^{-1}$ ; Sperry, in press). Immediately following closure, xylem pressure potential of the lamina was measured in the pressure bomb.

### Results and Discussion

#### *Hydraulic architecture*

Figure 2 indicates that the mid-day pressure potential of laminae during the 'rainy season' (roughly June to January in Miami) decreased with leaf number, and that there was a pressure potential difference between stem and lamina of 0.70 to 1.50 MPa. This difference accounted for at least 60 to 75% of the total drop in pressure potential from soil to lamina if soil had a water potential of zero (atmospheric); the percentage would be greater if the soil was at lower water potentials.

Similar results were obtained during the dry season, although lamina pressure potentials were lower (typically between -2.00 and -3.00 MPa), and the stem-to-lamina difference less (0.10 to 0.60 MPa).

The large difference between stem and lamina pressure potentials is explained by Figure 3, which shows resistance (incorporating axis length) from shoot base to lamina tip for leaves 1 to 4, and a senescing leaf (s): an overwhelming 70 to 80% of the total resistance in the shoot occurred in the leaf xylem. Stem resistance (estimated leaf-specific values, see Sperry, 1985) was at most 31% of the total. In leaf 1, the insertion segment which includes the constriction in the stem-to-leaf connection (Fig. 1), accounted for 57% of the total resistance. In progressively older leaves, however, the insertion resistance drops to a minimum of 13% in leaf 4, and lamina resistance increases dramatically from 25% in leaf 1 to 63% in the senescing leaf. Thus, although the pressure difference measured between stem and lamina is primarily due to the insertion and its included constriction in leaf 1, as the leaf ages, most of the pressure difference must occur in the lamina xylem.

The decrease in leaf insertion resistance from leaf 1 to 4 is explained by Zimmermann and Sperry's (1983) observation that the basipetal

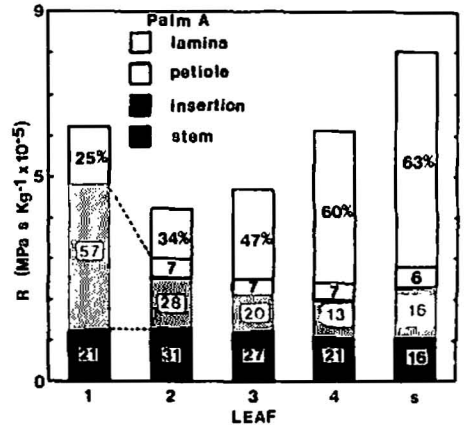


Fig. 3. Resistance to flow (incorporating axis-length) in the xylem from shoot base to lamina tip vs. leaf number (numbered from the youngest-expanded leaf; 's' is a senescing leaf). Palm was of average height (stem 2.5 m long). Total value for each leaf is divided into stem, leaf insertion, petiole, and lamina portions, and the percentage of the total indicated for each portion. The constriction (Fig. 1) is included in the leaf-insertion portion. Insertion and petiole resistance were combined in leaf 1.

maturation of metaxylem vessels in the vascular bundles of the leaf axis (Fig. 1 from E to D) is not complete until leaf 4. This retarded maturation is due to the prolonged activity of the meristem at the leaf base. When metaxylem maturation is still very incomplete as in leaf 1, insertion resistance is exceptionally high because water must flow in long stretches of narrow protoxylem tracheids with high resistance (Sperry, 1985). The simplest explanation for the large increase in lamina resistance with leaf number, as well as for the small increases in petiole and insertion resistances in the senescing leaf, is that with time, xylem conduits become irreparably damaged. This is obvious in laminae, where even the relatively young expanded leaves (no. 3, 4) can have blade segments that are torn and tattered.

The decrease in xylem pressure potential of laminae from leaves 1 to 4 (Fig. 2) was a fairly consistent pattern; the relative value for the senescing leaf was variable. This decrease has been explained by the average transpiration rates in the different leaves (Sperry, 1985): although there is an approximate inverse relationship between the resistance supplying the first four laminae and their transpiration rates,

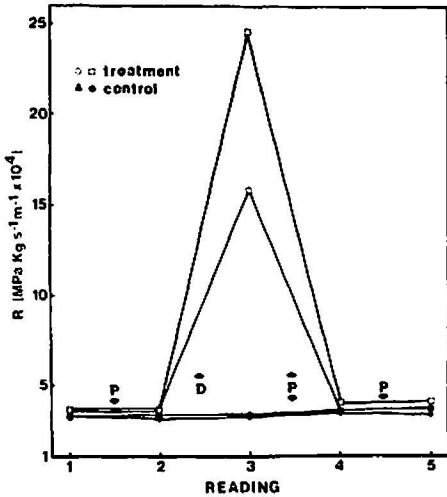


Fig. 4. Resistance (R) in petioles. R readings 1 and 2 were unchanged by the intervening pressure treatment (P) indicating all petioles were at their base resistance. Two of these petioles (treatments) were dried for c. 35 min. in the lab (D), and the others soaked in water (controls). Dehydration induced considerable resistance above the base level (reading 3); this original base level was restored by pressure treatments (readings 4 and 5; from Sperry, in press).

transpiration is high enough in leaves 2, 3, and 4, to produce the low xylem pressure potentials in these leaves.

*Detection of embolism*

Preliminary experiments conducted to evaluate the resistance method indicated its validity for detecting embolism. Embolism as the cause of resistances above the base value was suggested by the following four results:

1) Resistance above the base level was induced in stem and petiole segments by dehydration, which was accompanied by embolisation. For instance, in Figure 4, petioles initially at base resistance (as indicated by no change in resistance before and after a pressure treatment: P), showed increased resistance following dehydration (D).

2) Pressure or soak treatments which act to dissolve embolisms eliminated resistance above the base level in axes. In Figure 4, resistance dropped to base values after a single pressure treatment. In Figure 5, resistance in petioles gradually approached base levels within 5 hours of soaking in water at zero pressure.

3) Resistance relative to the base level increased with increasing numbers of acoustic emissions (Fig. 6) which have been independently shown to correspond to cavitation events (e.g., Tyree et al., 1984a, b). Variation in this relationship was probably because the influence of a cavitation event on resistance depended entirely on its location in the vascular system i.e., cavitation in a large diameter vessel would decrease conductivity more than in a small diameter vessel, or tracheid.

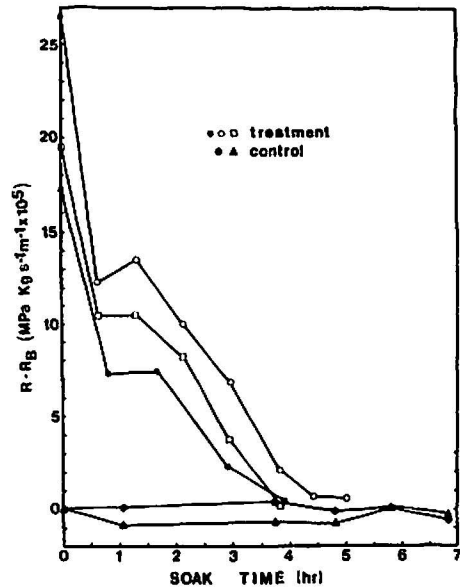


Fig. 5. Resistance above base level ( $R - R_B$ ) in petioles vs. time soaking in water at zero (atmospheric) pressure (from Sperry, in press).

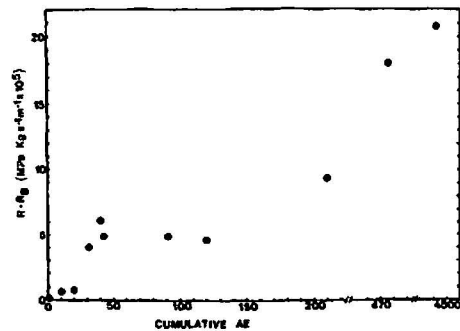


Fig. 6. Resistance above base level ( $R - R_B$ ) in petioles vs. cumulative acoustic emissions (AE; from Sperry, in press).

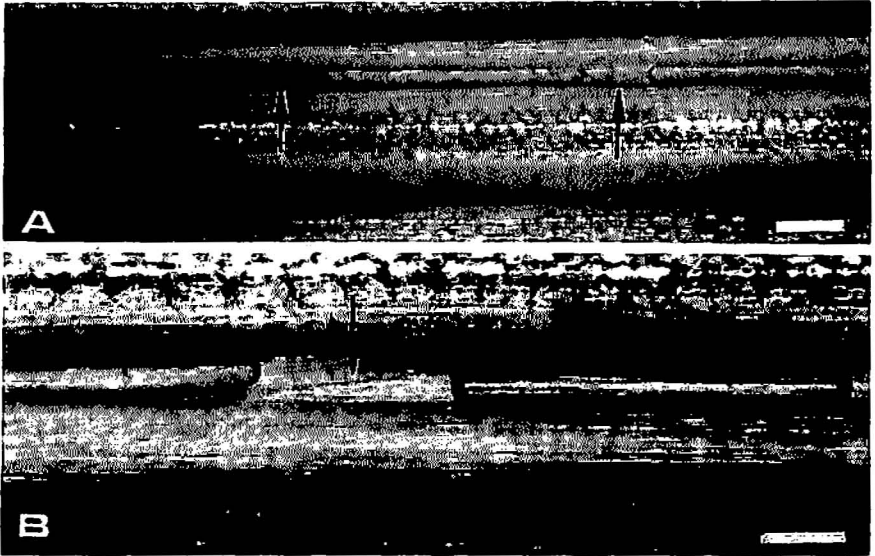


Fig. 7. Longitudinal sections (100–150  $\mu\text{m}$  in thickness) of petioles previously showing resistance above base level. – A. Intact length of vessel with bubbles arranged in series, one in each vessel member (scalariform perforation plates marked by arrows; bar: 200  $\mu\text{m}$ ). – B. Meniscus at scalariform perforation plate (bar: 100  $\mu\text{m}$ ; from Sperry, in press).

4) Anatomical observations revealed that vessels in petioles with resistance above base value contained many bubbles. Bubbles appeared in series, one in each vessel member (Fig. 7); the vessel, which would have been entirely gas-filled at the pressure potential inducing the embolism, partially re-filled by meniscus formation at scalariform perforation plates as xylem pressure potentials approached zero. When sections with bubble-containing vessels were subjected to the same pressure or soak treatment used to eliminate increased resistance in entire axes, bubbles disappeared.

Base resistance as an embolism-free reference was supported by: 1) its stability with soak or pressure treatments which act to dissolve bubbles (Figs. 4, 5; controls), 2) the absence of air bubbles in vessels of petioles sectioned at their base resistance, 3) its conformation to anatomical expectations: base resistance in stem segments was approximately 20 times less than in petioles (e.g., see Fig. 8B; Sperry, in press), which agrees with the ratio of resistance in stem vs. petiole calculated from measurements of vessel diameter using the Hagen-Poiseuille equation (Sperry, 1985). In addition, base resistances within either the stem or petiole cate-

gory were similar to one another, reflecting the similar anatomical construction of a given axis type (see Fig. 8A, B, C).

Although decreases in xylem flow resistance in a given axis have been noted previously and attributed to the removal of gas from embolised vessels (Hansen, 1886; Janse, 1887; MacDougal, 1925; MacDougal et al., 1929), with the exception of recent work by Edwards and Jarvis (1982), resistance has not been used to study embolism. Concurrent work has shown that changes in xylem flow resistance can be used to detect embolism in plants besides *Rhapis* (e.g., *Thuja*, *Tsuga*, *Acer saccharum*, Tyree & Dixon, 1986), and as a new technique it shows promise because of its simplicity, and because it detects embolism by directly assessing its most important physiological consequence: its effect on the transport capacity of the xylem.

The chief limitation of the method is the necessity of having to measure resistances at near-zero pressures. When embolisms are present in the axis, resistance is time-dependent (Fig. 5), and can show fluctuations which are not fully accounted for, but may be caused by changes in bubble configuration and/or ground tissue hydration. Bubble size may be dependent on

the time lapse between cavitation and the resistance measurement since bubbles are probably air which has diffused into the originally vapour-filled vessel (Tyree & Dixon, 1986). In addition, dye experiments indicated that embolised vessels in *Rhapis* at zero pressure are capable of conducting to a limited extent (Sperry, in press); this conduction probably occurs around the small bubbles occupying each vessel element (Fig. 7). Thus, resistance measurements in the presence of embolisms may under-estimate the value in the intact plant where pressures are negative and vessels are entirely gas-filled and non-conducting.

*Embolism in Rhapis*

Despite limitations, the resistance method has provided answers for how *Rhapis*, and perhaps other palms, accommodates xylem failure via embolism. The distribution of resistance above base level in shoots, summarised in Figure 8, indicates embolism is confined to leaves. Resistance in shoots taken directly from the field was above base levels only during dry periods, and only in petiole segments, never in the stem. The shoot in Figure 8A was harvested during a relatively wet period, and was at base resistance, as indicated by the similarity between resistance in stem and petiole segments measured directly after excision (open histograms), and base resistance (solid histograms). Shoots in Figure 8B, and C, however, which were measured during dryer weather, possessed significant resistance above base value in petiole segments, particularly in Figure 8C; stem segments were at base resistance.

The localisation of embolism to the leaves agrees with the prediction of Zimmermann and Sperry (1983), and is doubtless due to the consistent presence of low xylem pressure potentials in the leaves relative to the stem (Fig. 2). Zimmermann and Sperry emphasised the importance of the constriction at the leaf insertion in generating this pressure difference; however, it is clear from results summarised in Figure 3, that over leaf development, resistance in the lamina xylem also plays an important role. The distribution of xylem pressure potentials in the *Rhapis* shoot is a good example of Zimmermann's principle of 'plant segmentation' (Zimmermann, 1983: 80-82): peripheral parts of plants (leaves in this case) are subject to low xylem pressures with concomitant risk of xylem embolism, while proximal parts (stems) function at considerably more moderate pressures. This segmentation is advantageous because peripheral organs are more readily replaced than main axes.

The relationship between resistance above

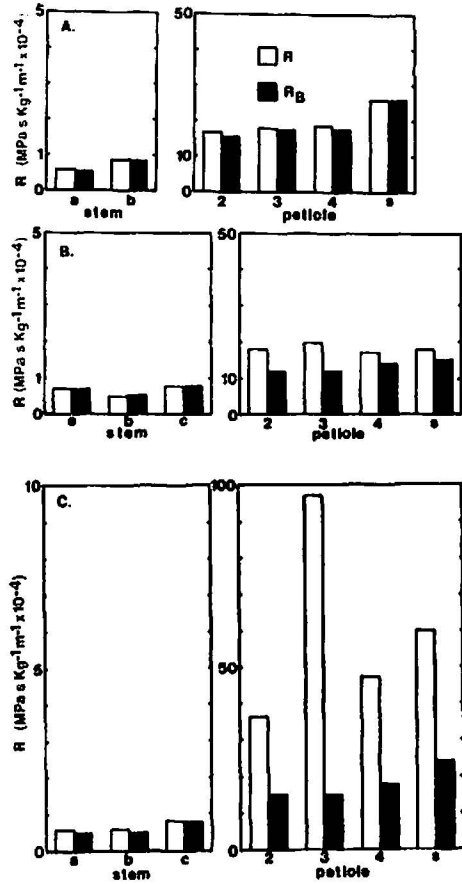


Fig. 8. Resistance (R, open histograms) and base resistance (R<sub>B</sub>, shaded histograms) for stem and petiole segments measured directly after excision from three shoots (A, B, C). Stem segments were arbitrarily lettered; petioles were numbered beginning with the youngest-expanded leaf, 's' was a senescing leaf. Note 10-fold scale difference between stem and petiole. Shoot A, measured during relatively wet weather, was at base resistance (i.e., R = R<sub>B</sub>); shoots B and C, measured during dry spells, showed resistance above base level, but only in petioles (modified from Sperry, in press).

base level and xylem pressure potential shown for petioles in Figure 9 indicates that embolism was induced by xylem pressure potentials below c. -2.90 MPa. Pressure potential in the graph refers to values at maximum dehydration; all resistance measurements were made while



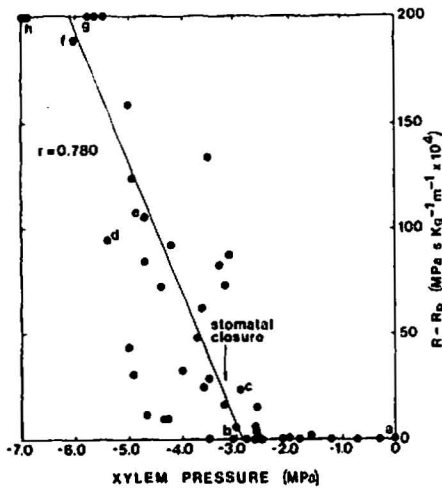


Fig. 9. Xylem pressure at maximum dehydration vs. resistance above base level ( $R - R_B$ ) for petioles. Each point represents a single petiole. Regression of data at pressures below  $-2.60$  MPa indicates increased resistance was induced by dehydration pressures below c.  $-2.90$  MPa. Pressure potential of lamina xylem at stomatal closure ( $3.20 \pm 0.18$  MPa) is indicated (from Sperry, in press).

xylem pressures were near zero. Results were similar for stems, although fewer experiments were made. The embolism-inducing pressure is low relative to the normal range of lamina xylem pressures in Miami (e.g., see Fig. 2), indicating that embolism in *Rhapis* is probably a rare event, occurring only once or twice a year during a prolonged drought (most likely during the dry season, February to May). The occurrence of embolism at xylem pressure potentials only slightly lower than normal has been observed in other plants (Zimmermann & Milburn, 1982), and may be a general phenomenon.

In the rare event of prolonged drought, stomatal closure may protect shoots from excessive embolism. Complete stomatal closure in *Rhapis* leaves occurred at xylem pressure potentials only slightly below the embolism-inducing value ( $-3.20$  MPa, Fig. 9). In the intact shoot, this would have the obvious advantage of preventing pressure potentials from dropping further and inducing massive xylem failure in the leaf, and the possible spread of embolism into the stem. The same relationship between embolism and stomatal closure was observed in

*Thuja* (Dixon et al., 1984), and may apply to plants generally. In addition, the study of *Thuja* indicated that after stomatal closure, water displaced from embolising tracheary elements was sufficient to significantly re-hydrate portions of detached shoots. Thus, following stomatal closure, the xylem may become more important as a water storage tissue than as a water conducting one.

In addition to being confined to leaves, and of rare occurrence, results indicate embolism in *Rhapis* is potentially reversible. Embolisms in petiole xylem dissolved within 5 hours at zero pressure (Fig. 5); during prolonged rain, xylem pressure potentials in *Rhapis* shoots can equal zero (Sperry, 1985). Thus, extended rain may allow reversal of embolism in the field. Positive xylem pressures which have been implicated in the re-filling of embolised vessels in other plants (i.e., root pressures, Milburn & McLaughlin, 1974; Zimmermann, 1983; Tyree, pers. comm.), were never observed in *Rhapis*. Reversibility in *Rhapis* may be enhanced by the division of the gas in an embolised vessel into a series of small bubbles with meniscus formation at scalariform perforation plates when xylem pressures are near zero (Fig. 7). In plants with simple perforation plates, gas bubbles tend to be longer than the individual vessel members (e.g., *Acer saccharum*, Sperry, unpubl.); embolism may be more difficult to reverse in these plants because the longer bubbles may take much more time to dissolve due to lower surface area to volume ratio, and lower surface tension.

#### Concluding remarks

The results of this investigation together with the related studies cited above, indicate that *Rhapis* and other plants are protected from the danger of xylem embolism by a number of mechanisms. This protection involves features of the xylem itself, such as hydraulic architecture, and embolism-inducing pressure; as well as stomatal mechanics, and an ability to achieve positive or near-positive xylem pressure potentials enabling the re-filling of embolised conducting units.

In addition to discovering how plants cope with embolism, the study of embolism is changing the way we think about xylem structure and function. With an embolism-inducing pressure near  $-2.90$  MPa, *Rhapis* is among the more embolism-resistant plants thus far studied. The lowest embolism-inducing pressure previously determined was  $-3.00$  MPa for *Fraxinus* (Crombie & Milburn, unpubl., cited in Zimmermann & Milburn, 1982); recent work indicates a similar value for *Acer saccharum* (Tyree &



Dixon, 1986). In contrast, *Thuja* and *Tsuga* have embolism pressures of c. -1.50 and -2.50 MPa, respectively (Tyree & Dixon, 1986). These findings contradict the common impression that tracheids are more resistant to embolism than vessels; *Thuja* and *Tsuga* with tracheids are clearly not more resistant to embolism than the other taxa which have vessels. Although within a plant there appears to be a correlation between the volume of the conducting unit and its susceptibility to embolism (Tyree & Dixon, 1986; Lewis & Tyree, 1985), this relationship does not hold between taxa. Until the mechanism of embolism is determined, we can only continue to speculate what features of the xylem confer resistance to embolism (e.g., pore size in tracheary element walls; cf. Zimmermann, 1983).

With current techniques, the potential exists to quantify xylem vulnerability in taxa with diverse xylem structure and ecological habitat. The concept of xylem vulnerability should include the relationship between embolism, conductivity, and xylem pressure potential; the more vulnerable the xylem, the less negative the pressure potential at which embolism occurs, and conductivity is impaired. Such studies will lead to a better understanding of the functional significance of certain features of xylem structure, and may eventually shed light on what actually triggers embolism. Not in the least, they may provide a better understanding of drought tolerance in plants.

#### Acknowledgements

Funding for this research came from the Atkins, Anderson, and Cabot funds of Harvard University, NSF Doctoral Dissertation Improvement Grant BSR-84-01216, and Sigma Xi grant-in-aid. A. Smith graciously loaned me the LI CORR porometer. The late Martin Zimmermann, along with P.B. Tomlinson, M.T. Tyree, M.A. Dixon, F.W. Ewers, and J.B. Fisher had a hand in guiding the research. The staffs of the Harvard Forest, and of the Fairchild Tropical Garden assisted in its execution. Monica Mattmuller of the Harvard Forest, and Jim Watson of the Fairchild Garden, were of particular help.

#### References

- Begg, J. E. & N. C. Turner. 1970. Water potential gradients in field tobacco. *Plant Physiol.* 46: 343-346.
- Dixon, M. A., J. Grace & M. T. Tyree. 1984. Concurrent measurements of stem density, leaf and stem water potential, stomatal conductance, and cavitation on a sapling of *Thuja occidentalis* L. *Plant Cell Environ.* 7: 615-618.
- Edwards, W. R. N. & P. G. Jarvis. 1982. Relations between water content, potential, and permeability in stems of conifers. *Plant Cell Environ.* 5: 271-277.
- Hansen, A. 1886. Ein Beitrag zur Kenntnis des Transpirationsstromes. *Arb. Bot. Inst. Würzburg* 3: 305-314.
- Janse, J. M. 1887. Die Mitwirkung der Markstrahlen bei der Wasserbewegung im Holze. *Jahrb. Wiss. Bot.* 18: 1-69.
- Lewis, A. M. & M. T. Tyree. 1985. The relative susceptibility to embolism of larger vs. smaller tracheids in *Thuja occidentalis*. *IAWA Bull. n.s.* 6: 93 (abstract).
- MacDougal, D. T. 1925. Reversible variations in volume, pressure, and movements of sap in trees. *Carnegie Inst. Washington Publ.* 365.
- , J. B. Overton & G. M. Smith. 1929. The hydrostatic-pneumatic system of certain trees: movement of liquids and gases. *Carnegie Inst. Washington Publ.* 397.
- Milburn, J. A. 1973a. Cavitation in *Ricinus* by acoustic detection: induction by various factors. *Planta* 110: 253-265.
- 1973b. Cavitation studies on whole *Ricinus* plants by acoustic detection. *Plant* 112: 333-342.
- & M. E. McLaughlin. 1974. Studies of cavitation in isolated vascular bundles and whole leaves of *Plantago major* L. *New Phytol.* 73: 861-871.
- Pickard, W. F. 1981. The ascent of sap in plants. *Progr. Biophys. Molec. Biol.* 37: 181-229.
- Scholander, P. F., H. T. Hamel, E. D. Bradstreet & E. A. Hemmingsen. 1965. Sap pressure in vascular plants. *Science* 148: 339-346.
- Sperry, J. S. 1985. Hydraulic architecture and xylem embolism in the palm *Rhapis excelsa*. Ph.D. Thesis, Harvard Univ.
- In press. Relationship of xylem embolism to xylem pressure potential, stomatal closure, and shoot morphology in the palm *Rhapis excelsa*. *Plant Physiol.*
- Tyree, M. T. & Y. N. S. Cheung. 1977. Resistance to water flow in *Fagus grandifolia* leaves. *Canad. J. Bot.* 55: 2591-2599.
- & M. A. Dixon. 1983. Cavitation events in *Thuja occidentalis* L.? Ultrasonic acoustic emissions from the sapwood can be measured. *Plant Physiol.* 72: 1094-1099.
- & — 1986. Water stress induced cavitation and embolism in some woody plants. *Physiol. Plant.* In press.
- , — & R. G. Thompson. 1984a. Ultrasonic acoustic emissions from the sapwood of

- Thuja occidentalis* measured inside a pressure bomb. *Plant Physiol.* 74: 1046–1049.
- , —, E.L. Tyree & R. Johnson. 1984b. Ultrasonic acoustic emissions from the sapwood of cedar and hemlock. *Plant Physiol.* 75: 988–992.
- Zimmermann, M.H. 1983. Xylem structure and the ascent of sap. Springer, New York, Heidelberg, Berlin.
- & J.A. Milburn. 1982. Transport and storage of water. In: *Physiological plant ecology II* (eds. O.L. Lange, P.S. Nobel, C.B. Osmond & H. Zeigler): 135–151. *Encycl. Pl. Physiol.* n.s. Vol. 12B. Springer, New York, Heidelberg, Berlin.
- & J.S. Sperry. 1983. Anatomy of the palm *Rhapis excelsa*. IX. Xylem structure of the leaf insertion. *J. Arn. Arbor.* 64: 599–609.