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Relationship of Xylem Embolism to Xylem Pressure Potential, Stomatal Closure, and Shoot Morphology in the Palm *Rhapis excelsa*[1]

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ABSTRACT

Xylem failure via gas embolism (cavitation) induced by water stress was investigated in the palm *Rhapis excelsa* (Thunb.) Henry. Xylem embolism in excised stems and petioles was detected using measurements of xylem flow resistance: a decrease in resistance after the removal of flow-impeding embolisms by a pressure treatment indicated their previous presence in the axis. Results supported the validity of the method because increased resistance in an axis corresponded with: (a) induction of embolism by dehydration, (b) increased numbers of cavitations as detected by acoustic means, (c) presence of bubbles in xylem vessels. The method was used to determine how *Rhapis* accommodates embolism; results suggested four ways. (a) Embolism was relatively rare because pressure potentials reach the embolism-inducing value of about −2.90 megapascals only during prolonged drought. (b) When embolism did occur in nature, it was confined to the relatively expendable leaf xylem; the stem xylem, which is critical for shoot survival, remained fully functional. (c) Even during prolonged drought, the extent of embolism is limited by complete stomatal closure, which occurred at the xylem pressure potential of −3.20 ± 0.18 megapascals. (d) Embolism is potentially reversible during prolonged rains, since embolisms dissolved within 5 h at a pressure potential of 0.00 megapascals (atmospheric), and xylem sap can approach this pressure during rain.

Embolized (gas-filled) vessels or tracheids arise from excessively negative xylem sap pressure potentials accompanying water stress, and result in impaired water conduction (10, 13, 14, 18). The way in which plants avoid significant disruption of xylem transport via embolism is poorly understood. The present paper investigates this question in the palm *Rhapis excelsa*; embolism is potentially very serious for palms, which lack secondary growth and cannot continually produce new functional xylem, but must rely on the primary xylem of their stems for water transport throughout their life.

Embolism was detected using measurements of xylem flow resistance in excised petioles and stems. A series of experiments were conducted to evaluate the method, and it was used to determine: (a) if embolism in the aerial shoot is confined to the relatively expendable leaf xylem, thereby preserving the water transport capacity of the stem as predicted from previous studies of the xylem anatomy and hydraulic architecture of *Rhapis* (11, 19); (b) the potential reversibility of embolism; (c) the xylem pressure potential required to induce embolism. This pressure potential was compared to the value that induced complete stomatal closure, and to the range known to occur in nature (11). This comparison indicated the likelihood of embolism in nature, and the role of stomata in limiting its occurrence.

In addition, the pattern of flow in axes with embolized vessels was analyzed using dye infusions to understand further the flow resistance method used to detect embolism, and the anatomical distribution of embolism.

MATERIALS AND METHODS

Experiments were conducted at Fairchild Tropical Garden in Miami, FL, using erect shoots from clumps of *Rhapis excelsa* (Thunb.) Henry, a rhizomatous coryphoid palm native to eastern Asia. Shoots were 2 to 3 m tall, each with roughly 10 to 15 expanded leaves. Leaves were numbered beginning with the youngest-expanded one. Additional work was done at the Harvard Forest, Harvard University, using greenhouse-grown plants.

Detection of Embolism. Embolism was indicated in excised axes by the presence of xylem flow resistance (R) above the minimum, or base resistance (R_B), of the axis. Base resistance of an axis represented its embolism-free condition; resistance above base level was caused by embolisms which impeded flow in the xylem. The amount of resistance above base level ($R - R_B$) gave a measure of the amount of embolism in the axis.

Xylem flow resistance is defined as,

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

where ΔP is the pressure difference, J_v is the volume flow rate,[2] and l is axis length. Resistance was measured on stem and petiole segments (about 70 and 45 cm long, respectively), with volume flow rate measured in a pipette attached to one end under a pressure gradient induced by a vacuum pump attached to the other end. A filtered (GF/F Whatman; retention to 0.7 μm) 5 mM KCl solution was used in the measurements (16). Pressures were chosen that induced easily measurable volume flow rates because preliminary experiments confirmed the independence of resistance and pressure gradient for gradients used. Measurements were made under steady state conditions, so it was unimportant whether flow rate was measured at the influx or efflux end of the axis. Between each resistance measurement for an axis, about 5 mm was trimmed off either end to prevent increases in resistance; increases without this trimming procedure were presumably caused by debris gradually clogging the vessels. In fresh transverse sections of the axis, this debris was seen trapped in scalariform perforation plates near the influx end of the axis.

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[2] In reporting volume flow rates, the mass unit kg is used rather than the unwieldy SI volume unit m^3. The volume term is retained for clarity.

Resistance was not affected by changes in axis length, because it was defined on a unit length basis, and was similar throughout a given stem or petiole segment.

Resistance was measured in axes after excision from the shoot or dehydration in the laboratory. Before measurement, the axis was submerged in water and both ends trimmed in order to remove superficial air blockage. Trimming was completed within 10 min of submersion, and resistance was measured immediately, because the procedure brought xylem pressures to zero (atmospheric) allowing the gradual dissolution of embolisms (Fig. 3)

Base resistance was measured after treating the axis to remove any embolisms. The axis was submerged in a container of water and pressurized at 0.35 MPa for at least 20 min in a pressure bomb. The pressure treatment was repeated until resistance reached a stable and minimum value, the base resistance. Depending on experimental design, base resistance was measured either before or after resistance.

Comparisons of resistance above base level ($R - R_B$) were made when the base resistances involved were similar. This was naturally the case for a given axis, as well as for different axes within each of the petiole, or stem catagories. Quantitative comparisons between petioles and stems were complicated by their different base resistances, and comparisons were limited to the presence or absence of resistance above base levels.

Evaluation of Resistance Method. If the flow resistance of an axis is a good indicator of embolism, it should increase when embolism is present, and decrease in its absence. The influence of embolism on resistance above base level was determined in stems and petioles in which embolism had been induced by air dehydration and removed by pressurizing or soaking in water.

Increased resistance as an indicator of cavitation was compared with the acoustic method pioneered by Milburn (7, 8), and recently refined by Tyree and colleagues (1, 12–15). Vibrations, or acoustic emissions, in the xylem are detectable with amplification at both audible and ultrasonic frequencies, and appear to correspond with cavitation in tracheids or vessels. They occur in association with water loss (14) and decreasing xylem density (1), and are induced by a threshold water potential (*e.g.* −1.00 MPa in *Thuja occidentalis*; 12). They occur only when xylem water is under tension, and not when xylem tissue is independently stressed (13). Furthermore, the number of acoustic emissions agree very closely with the number of tracheids in small sapwood samples (14).

Experiments compared resistance above base level with production of ultrasonic acoustic emissions in petioles, and were conducted at the University of Toronto in the laboratory of Dr. M. T. Tyree. The equipment and procedure for detecting ultrasonic acoustic emissions from excised plant axes has been described previously (14). Petioles at base resistance were attached at their midpoint to the acoustic transducer (Bruel and Kjear, model 8312) with a standard contact force, and supplied with water while the background level of acoustic noise was determined. The water supply was removed, and the number of acoustic emissions above the background level monitored as the petiole dehydrated. Petioles were allowed to produce between 10 and 5000 acoustic emissions before resistance above base level was determined.

Anatomical studies were made in an attempt to confirm the presence of embolism in petioles with resistance exceeding base value. The central portion (about 5 cm) of a segment was excised and sectioned longitudinally on a sliding microtome at 100 to 150 μm thickness. The central portion was used to avoid including any vessels which communicated with air at the cut ends of the axis. The widest vessels in the petiole are less than 60 μm, so some sections included portions of vessels with longitudinal walls intact. Sections were mounted in water and examined for the presence of gas bubbles in intact vessel portions. Bubbles were not likely to be induced by the sectioning procedure, because the xylem was at zero pressure; thus, any bubbles present would be embolisms. Control petioles were sectioned while at their base resistance.

Sections with bubbles in xylem vessels were pressurized or soaked in water in order to directly observe effect of these treatments on the dissolution of bubbles.

Distribution of Resistance above Base Level in Shoots. Resistance relative to base value was measured in stem and petiole segments taken directly from shoots in the field in order to determine its distribution in leaves *versus* stems.

Resistance above Base Level *versus* Xylem Pressure Potential. Stem and petiole segments at base resistance were dehydrated to xylem pressure potentials between −0.30 and −7.00 MPa. Xylem 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 entire leaves. Resistance above base level was determined following the pressure measurement, and plotted *versus* xylem pressure potential for each axis type.

Dye Experiments. Immediately following the final resistance measurement in petioles treated as above, the end of the petiole attached to the pipette was transferred to a vial of filtered 0.5% aqueous basic fuchsin, and dye pulled into the axis by the vacuum pump at a uniform pressure gradient. The velocity of complete dye staining in controls at base resistance determined the time the dye was pulled through a given petiole, regardless of its resistance (velocity of the dye front is proportional to the pressure gradient, and is independent of resistance; 17, p. 191).

The stained petiole was sectioned transversely every 1, 2, or 3 cm by hand, the sections air-dried, and permanently mounted on slides. The section-series was analyzed, and a plot of the dye penetration in the xylem of the vascular bundles was constructed (Fig. 9).

Xylem Pressure Potential at Stomatal Closure. Stomatal closure was induced by excising healthy, mature leaves (No. 3, 4, 5) and allowing them to dehydrate in sun and shade conditions. Stomatal resistance (porometric method, LI CORR 1600) of the abaxial surface of median blade segments (*Rhapis* leaves are effectively hypostomatous,and palmately compound), was monitored *versus* time after excision (Fig. 10). Stomata were assumed to be completely shut when: (a) stomatal resistance showed a rapid increase to effectively infinite values (*e.g.* Fig. 10A, 'excised' curves, open symbols), (b) stomatal resistance became high (>100 s cm^{-1}), and rather erratic (Fig. 10A, excised curve, solid symbols); a characteristic of measurements made on the adaxial surface, and which was presumably due to the difficulty of accurately measuring high diffusive resistances. Xylem pressure potential of laminae at stomatal closure was measured in the pressure bomb. Preliminary experiments indicated that the stomata on all blade segments closed at roughly the same time. To assess the effect of the cuvette itself on stomatal resistance over time, controls were done by clamping the cuvette on an attached leaf and monitoring stomatal resistance for the same time period as the measurements on excised leaves (Fig. 10, attached leaves).

RESULTS

Evaluation of Resistance Method. Resistance above base value was induced in stem and petiole segments by dehydration. Stem and petiole segments taken directly from shoots in the field during relatively wet weather (Fig. 1, shoot 1) were consistently at base resistance, whereas considerably increased values were present in segments from shoots which had been cut at the base and allowed to dry in the sun for a few hours (Fig. 1, shoot 2). Petioles initially at base resistance showed increased values after dehydration (Fig. 2); a single pressure treatment caused these petioles to return to their former base level. Prolonged soaking

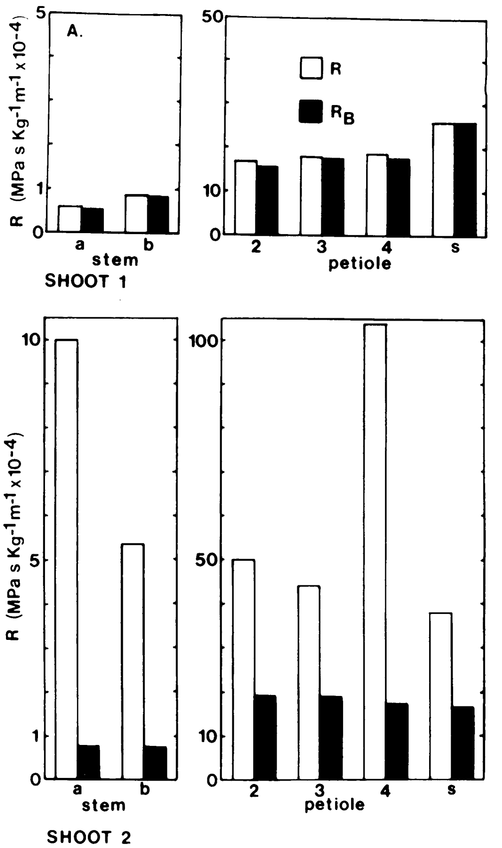

Fig. 1. Resistance (R, open histograms) and base resistance (R_B, shaded histograms) for stem and petiole segments of shoot 1 measured directly after harvesting, and shoot 2 measured after 3 h of drying in the sun. Stem segments are arbitrarily lettered; petioles are numbered beginning with the youngest expanded leaf, s is a senescing leaf. Note 10-fold scale difference between stem and petiole.

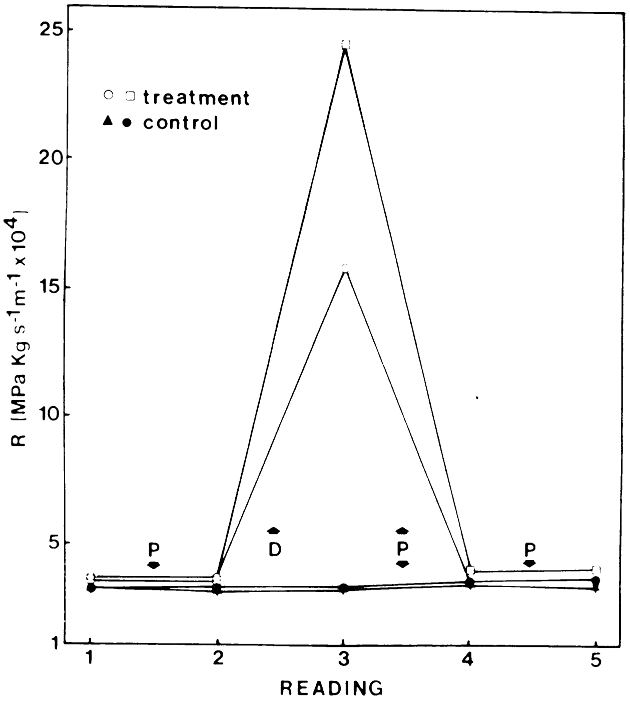

Fig. 2. Resistance (R), petioles. R readings 1 and 2 are unchanged by the intervening pressure treatment (P) indicating all petioles are at their base resistance. Two of these petioles (treatments) were then dried for about 35 min in the laboratory (D), while the other two soaked in water (controls).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

in water at zero pressure produced the same effect as a pressure treatment: in Figure 3, resistance in petioles gradually approached base values within 5 h of soaking. Controls of Figures 2 and 3 indicated base resistance was relatively stable despite continued pressure treatments, or prolonged soaking.

Resistance above base level in petioles increased with increasing numbers of acoustic emissions (Fig. 4). 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.

Anatomical observations revealed that petioles at base resistance possessed no bubbles in intact vessel portions, whereas petioles with increased resistance had many bubbles. These bubbles appeared in series, one in each vessel member (Fig. 5). The vessel, which would have been entirely gas filled at the xylem pressure potential that induced the embolism, partially refilled by meniscus formation at scalariform perforation plates as xylem pressure potential approached zero prior to the resistance measurement and sectioning procedure. When sections with bubble-containing vessels were subjected to the same pressure or soak treatment used to eliminate increased resistance in entire axes, the bubbles disappeared.

Distribution of Resistance above Base Level in Shoots. Resistance in excess of base levels was present only during dry periods, and only in petiole segments, never in the stem (Fig. 6, A and B). It was not determined if the high initial resistance in Figure 6A was due to greater water stress in the shoot prior to measurement.

Resistance above Base Level *versus* Xylem Pressure Potential. Figure 7 summarizes results for petioles. Xylem pressure potential in the graph was measured at maximum dehydration; all resistance measurements were made while xylem pressures were near zero. Resistance above base level was induced by pressure potentials below about −2.90 MPa. Results were similar for stems.

Dye Experiments. Data points lettered a to h in Figure 7 indicate petioles used in the dye studies summarized in Figure 9, A to H. Typically, xylem of a bundle in transverse section was either completely stained, or not stained at all. Occasionally, protoxylem (Fig. 8, px) alone was stained; rarely was staining confined to metaxylem (Fig. 8, mx). In either case, the vascular bundle was indicated as conducting dye in Figure 9. Longitudinal discontinuity in the staining of a vascular bundle occurred, as indicated by discontinuous black lines. This resulted from dye being conducted around a blocked portion of the bundle via small transverse veins which cross-link the otherwise discrete bundles.

Petioles showed a broad correlation between resistance above base level (Fig. 7, a–h) and the extent of nonstained bundles (Fig. 9, blank areas in plots A–H). Dye failed to pass through petioles with resistances greater than 200 × 10^4 MPa s kg^{-1} m^{-1} (petioles, G, H), so resistances above this value were considered effectively infinite.

Two lines of evidence indicate that embolized vessels conducted to a limited extent at the near-zero pressures used in the resistance measurements. (a) Resistance was measurable, though very high and variable, in petioles where dye failed to pass completely through (Fig. 9, G, H). (b) Embolism is likely to be a random process and should occur throughout the petiole. However, nonstained vessels were always localized at the petiole

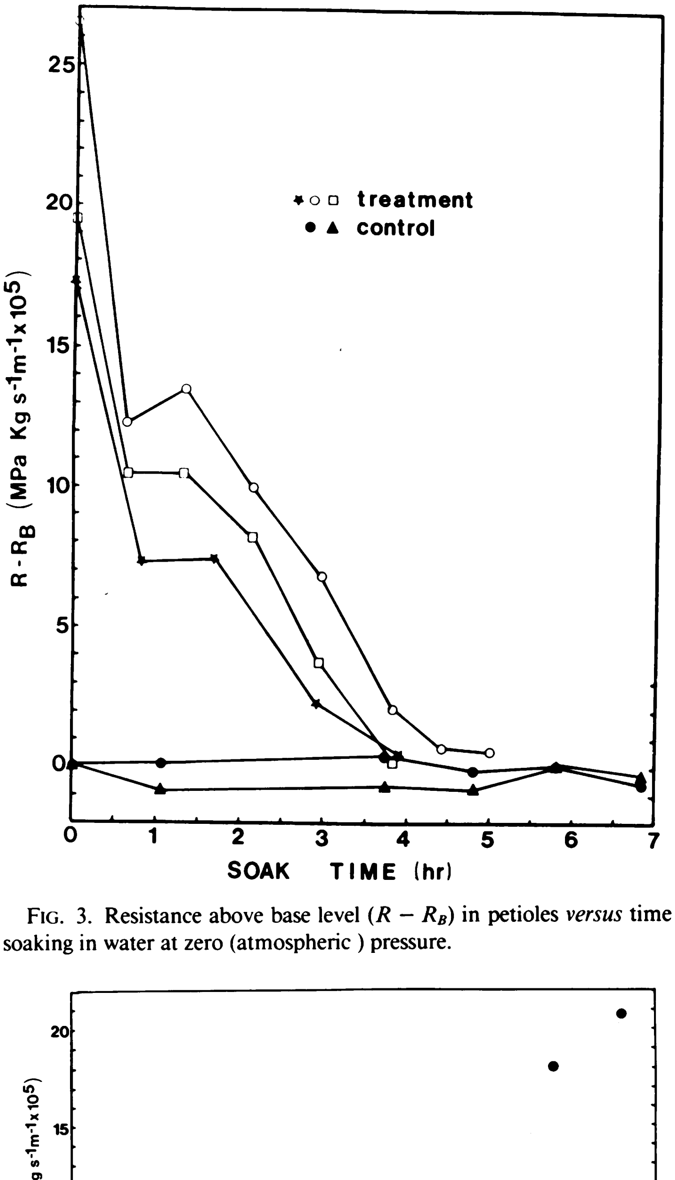

FIG. 3. Resistance above base level ($R - R_B$) in petioles *versus* time soaking in water at zero (atmospheric) pressure.

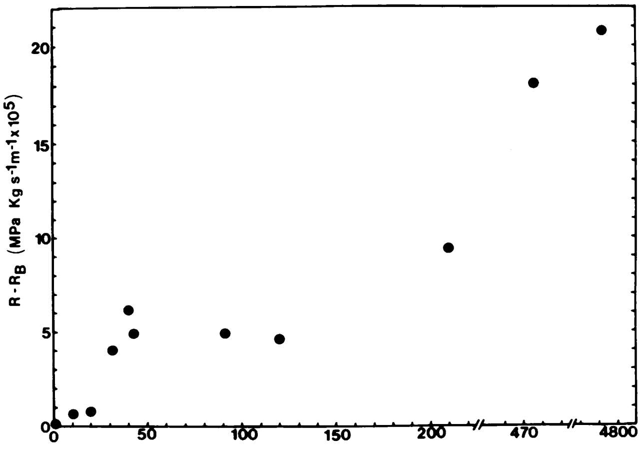

FIG. 4. Resistance above base level ($R - R_B$) in petioles *versus* cumulative acoustic emissions (AE).

end remote from the dye source (to the right in each plot in Fig. 9). This suggests that embolized vessels near the dye source were conducting and thus became stained.

Although the dye-staining did not discriminate precisely between embolized and functional vessels, it appears that embolism was not located preferentially in any region of the petiole; central, adaxial, and abaxial bundles (Fig. 8) all suffered impeded flow.

Xylem Pressure Potential at Stomatal Closure. There was no effect of the porometer cuvette on stomatal resistance in attached leaves in direct sunlight (Fig. 10A, attached leaves); in shade conditions, however, there was a gradual increase in stomatal resistance (Fig. 10B, attached leaves), perhaps because of an increase in CO_2 concentration in the cuvette. Detached leaves showed a transient opening of stomata following excision. This 'Ivanov effect' (9, pp. 132–133) was less noticeable in direct sunlight where water loss was more rapid. Xylem pressure potential of laminae at complete stomatal closure averaged −3.20 ± 0.18 MPa (n = 14). The relationship between stomatal closure, resistance above base level, and xylem pressure potential is indicated in Figure 7.

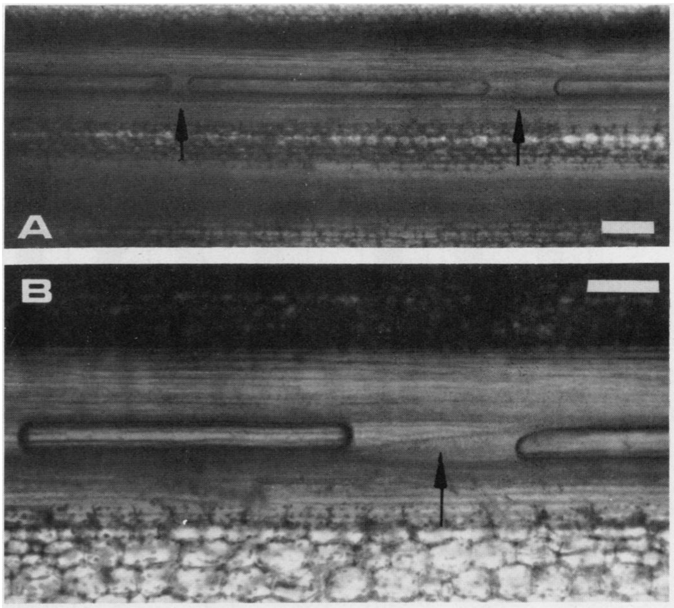

FIG. 5. Longitudinal sections (100–150 μm in thickness) of petioles previously showing resistance above base level. A, Intact length of vessel with bubbles arranged in series, one in each vessel member (scalariform perforation plates marked by arrows; bar, 200 μm). B, Meniscus at scalariform perforation plate (bar, 100 μm).

DISCUSSION

Although changes in xylem flow resistance in a given axis have been noted previously and attributed to the removal of gas from embolized vessels (3–6), with the exception of recent work by Edwards and Jarvis (2), resistance has not been used to study embolism. Results of the present investigation demonstrated that resistance above base level was a valid indication of embolism. Base resistance as an embolism-free reference was supported by: (a) its stability with soaking or pressure treatments which act to dissolve bubbles (Figs. 2, 3; controls); (b) the absence of bubbles in vessels in the anatomical preparations; (c) its conformation to anatomical expectations: base resistance in stem segments was approximately 20 times less than in petioles (*e.g.* Fig. 1, shoot 2, note scale difference between stem and petiole) which agrees with the ratio of resistance in stem *versus* petiole calculated from measurements of vessel diameter using the Hagen-Poiseuille equation (11). In addition, base resistances within either the stem or petiole category were similar to one another reflecting the similar anatomical construction of a given axis type (Figs. 1, 6). Embolism as the cause of resistances above the base level was suggested by: (a) induction of higher resistances by dehydration (Figs. 1, 2); (b) increase of resistance with increasing numbers of acoustic emissions (Fig. 4) which have independently been shown to correspond with cavitation events (*e.g.* 13, 14); (c) elimination of high resistance by the soaking or pressure treatment (Figs. 2, 3); (d) presence of bubbles in anatomical preparations of petioles with resistance above base level (Fig. 5). Concurrent work has shown that changes in xylem flow resistance can be used to detect

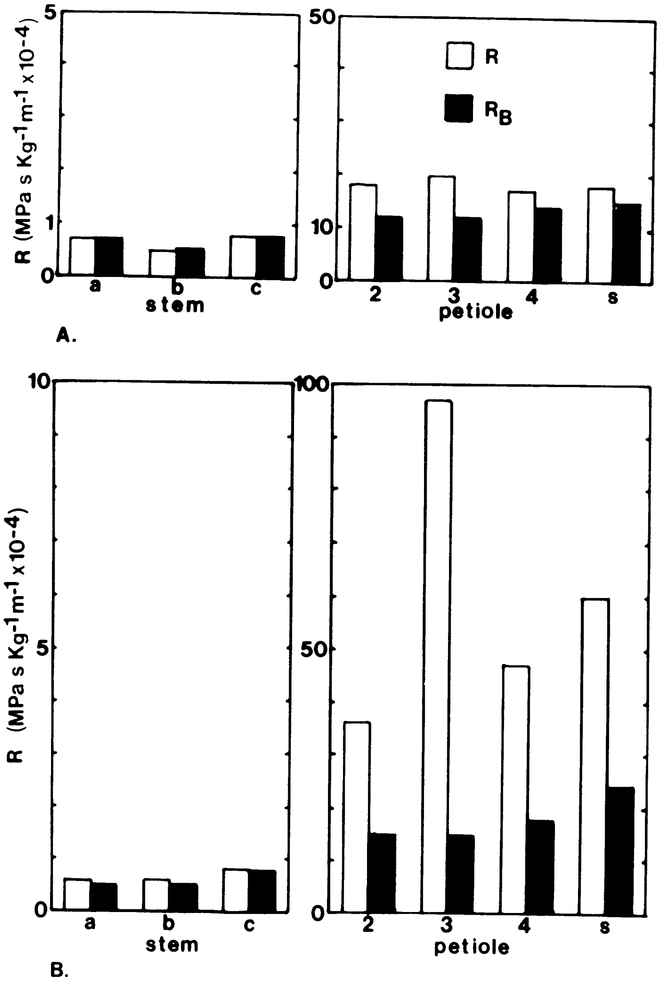

FIG. 6. Resistance (R, open histograms) and base resistance (R_B, shaded histograms) for stem and petiole segments of two shoots (A, B) measured directly after harvesting. Stem segments were arbitrarily lettered; petioles were numbered beginning with the youngest expanded leaf, *s* was a senescing leaf. Note 10-fold scale difference between stem and petiole.

embolism in plants besides *Rhapis* (*e.g.* cedar, hemlock, sugar maple; 15), and as a new technique it shows promise because of its simplicity, and because it detects embolism by directly assessing its effect on the transport capability of the xylem.

A limitation of the method is the necessity of measuring resistance at xylem pressure potentials near zero. Dye studies indicated that embolized vessels conducted to a limited extent at these pressures; flow probably occurred around the small bubbles within each vessel element (Fig. 5). As a result, measured resistance above base level may have underestimated the actual value in the intact plant where pressure potentials are negative and embolized vessels are entirely gas filled and nonconducting. The somewhat variable relationship between resistance above base level and xylem pressure potential in Figure 7 may be due to variation in the size and configuration of the small bubbles in embolized vessels. Bubble size could depend on the time lapse between cavitation and the resistance measurement since bubbles are probably air which has diffused into the originally vapor-filled vessel (15).

Results of the resistance method indicated that *Rhapis* has several means of avoiding the damaging effects of embolism. The exclusive presence of resistance above base level in petioles of shoots taken directly from the field (Fig. 6) suggests that embolism under natural conditions occurs only in the leaf, not in the

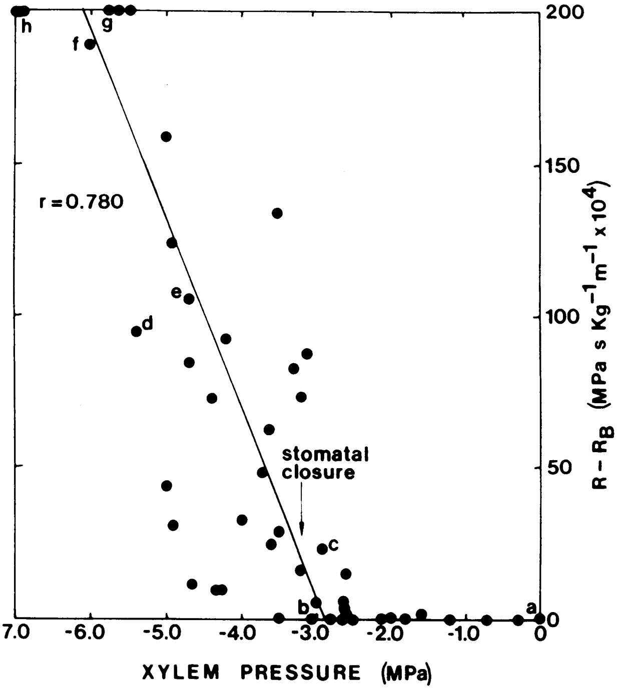

FIG. 7. Xylem pressure potential at maximum dehydration *versus* resistance above base level ($R - R_B$) for petioles. Each point represents a single petiole. Linear regression of data at pressure potentials below −2.60 MPa indicated increased resistance was induced by pressure potentials below approximately −2.90 MPa. Petioles labeled a to h were used in dye studies summarized in Figure 9. Xylem pressure potential of laminae at stomatal closure (3.20 ± 0.18 MPa) is indicated (lamina and petiole pressure potentials are likely to be similar under conditions of high stomatal resistance).

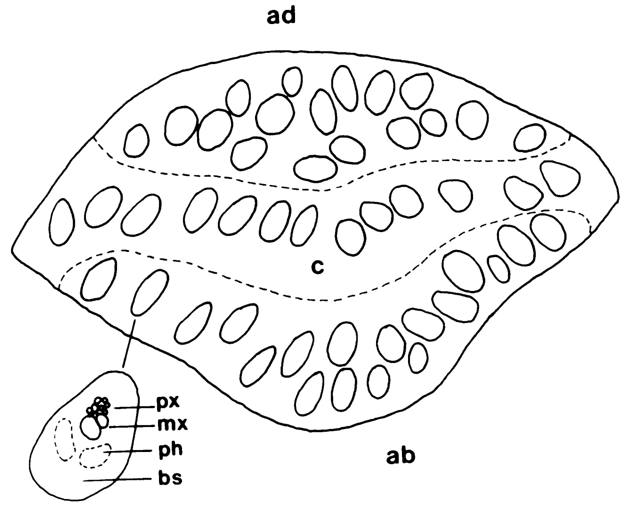

FIG. 8. Drawing of transverse section of petiole showing adaxial (ad), central (c), and abaxial (ab) vascular bundles (circles) referred to in the dye studies summarized in Figure 9. Small vascular bundles in adaxial and abaxial regions are not shown. Inset shows gross vascular-bundle structure; px, protoxylem; mx, metaxylem; ph, phloem; bs, bundle sheath. Vascular bundles pictured maintain the same position relative to one another throughout the petiole and do not anastomose. Cross-linking occurs via small transverse veins not pictured.

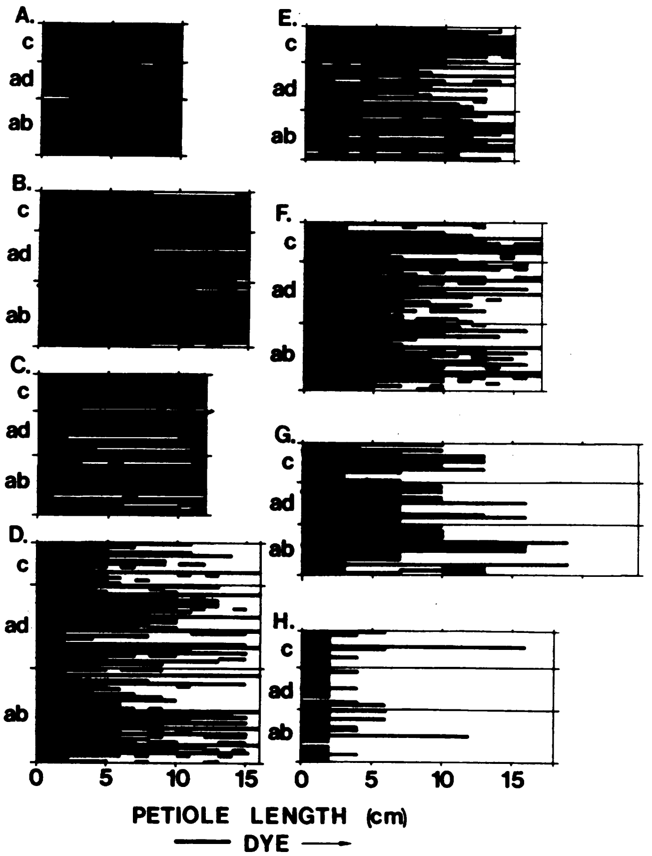

FIG. 9. Penetration of dye in vascular bundles (black lines) of petioles A to H from Figure 1. Dye movement was from left to right. For each plot, c, ad, ab, refer to central, adaxial, and abaxial vascular bundles, respectively (see Fig. 8). Resistance above base level increased from 0 in A and B, to more than 200 × 10^4 MPa s kg^{-1} m^{-1} in G and H (see Fig. 7 for differential resistance values). There is a broad correlation between incomplete dye penetration and resistance above base level.

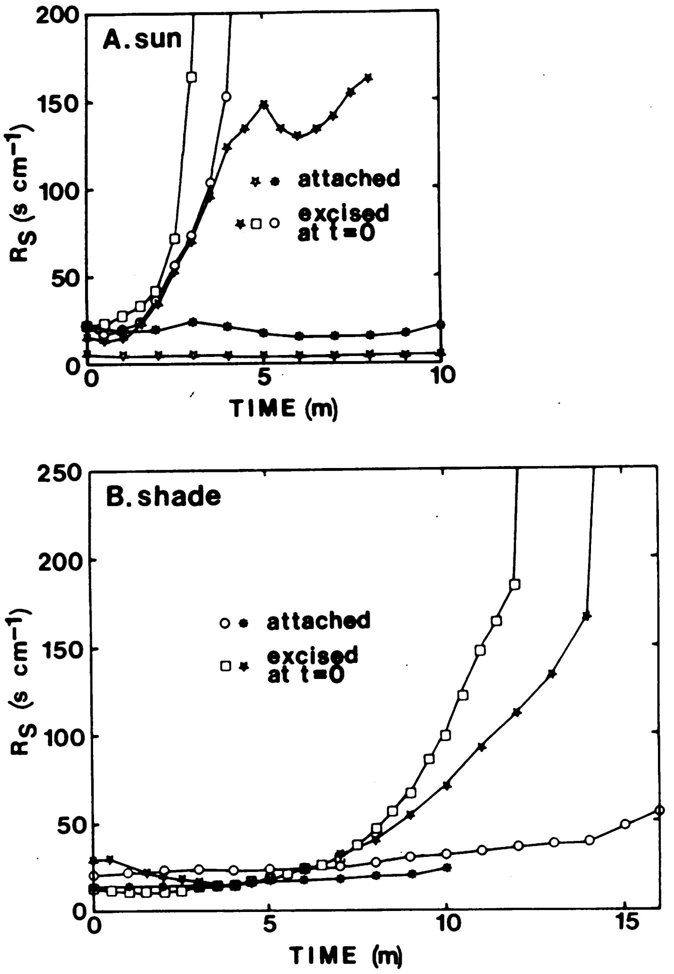

FIG. 10. Stomatal resistance (R_S) *versus* time for attached and excised leaves in sun (A), and shade (B) conditions. Each curve represents one leaf. Excision curves show the response of the stomata to dehydration. Curves for attached leaves showed the cuvette itself either had no effect on stomatal resistance (A), or caused a gradual increase (B).

stem. This would have the important advantage of xylem failure always occurring in leaves, which can be readily regenerated. Water flow in the stem, which is critical for the survival of the shoot, would remain undiminished. The localization of embolism to the leaves would presumably be due to the distribution of xylem pressure potentials, which have previously been shown in *Rhapis* to be much lower in leaves than stems (by as much as 1.5 MPa, [11]). In turn, this distribution of pressure potentials is due to quantitative differences in xylem construction between stem and leaf, and to a hydraulic constriction in the stem-to-leaf connection (11, 19).

In addition to being confined to leaves, results indicate embolism is potentially reversible. Embolisms in petiole xylem dissolved within 5 h at xylem pressure potentials of zero (Fig. 3); during prolonged rain, xylem pressures in *Rhapis* shoots can equal zero (11). Thus, extended rain may enable the reversal of embolism. Positive xylem pressure potentials (e.g. root pressure), which have been implicated in the refilling of embolized vessels in other plants (10), were never observed in *Rhapis*.

Resistance above base value, and thus embolism, was induced by xylem pressure potentials below about −2.90 MPa; most vessels were apparently embolized at −6.00 MPa (Fig. 7). Since normal midday lamina xylem pressures in *Rhapis* range roughly between −1.50 and −2.50 MPa in Miami (11), xylem pressure potentials probably reach embolism-inducing levels only during prolonged drought, which may occur once or twice a year during the dry season (February to May). In the rare event that this occurs, complete stomatal closure would prevent xylem pressure potentials from dropping much below −3.20 MPa (Fig. 7). Thus, massive xylem failure in the leaf, and the possible spread of embolism into the stem would be avoided. The same relationship between embolism and stomatal closure was observed in *Thuja* (1), and may apply to plants generally. In *Thuja*, stomatal closure in detached shoots coincided with partial rehydration; this was accounted for by water released from embolizing tracheids. Thus, after stomatal closure, xylem may become important as water storage tissue, rather than as a water conducting one.

With an embolism-inducing pressure potential near −2.90 MPa, *Rhapis* is among the more embolism-resistant plants currently known. The lowest embolism-inducing pressure previously determined was −3.00 MPa for *Fraxinus* (18), and recent work indicates a similar value for *Acer saccharum* (15). In contrast, *Thuja* and *Tsuga* have embolism pressures of about −1.50 and −2.50 MPa, respectively (15). 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 (15), this relationship does not hold between taxa. It remains to be seen what features of the xylem confer resistance to embolism.

Although comparative data on embolism in a variety of plants is presently scarce, with current techniques the potential exists to determine the role of xylem embolism in the physiology of plants with a variety of ecological and morphological characteristics. Such studies may uncover the mechanism that actually triggers embolism, and the extent to which the mechanisms of embolism tolerance found in *Rhapis* apply to plants in general.

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LITERATURE CITED

1. Dixon MA, J Grace, MT 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
2. Edwards WRN, PG Jarvis 1982 Relations between water content, potential, and permeability in stems of conifers. Plant Cell Environ 5: 271–277
3. Hansen A 1886 Ein Beitrag zur Kenntniss des Transpirationsstomes. Arb Bot Inst Wurzburg 3: 305–314
4. Janse JM 1997 Die Mitwirkung der Markstrahlen bei der Wasserbewegung im Holze. Jahrb Wiss Bot 18: 1–69
5. MacDougal DT 1925 Reversible variations in volume, pressure, and movements of sap in trees. Carnegie Inst Wash Publ 365
6. MacDougal DT, JB Overton, GM Smith 1929 The hydrostatic-pneumatic system of certain trees: movement of liquids and gases. Carnegie Inst Wash Publ 397
7. Milburn JA 1973a Cavitation in *Ricinus* by acoustic detection: induction by various factors. Planta 110: 253–265
8. Milburn JA 1973b Cavitation studies on whole *Ricinus* plants by acoustic detection. Planta 112: 333–342
9. Milburn JA 1979 Water Flow in Plants. Longman, London, 225 pp
10. Milburn JA, ME McLaughlan 1974 Studies of cavitation in isolated vascular bundles and whole leaves of *Plantago major* L. New Phytol 73: 861–871
11. Sperry JS 1985 Hydraulic architecture and xylem embolism in the palm *Rhapis excelsa*. PhD dissertation. Harvard University
12. Tyree MT, MA Dixon 1983 Cavitation events in *Thuja occidentalis* L.? ultrasonic acoustic emissions from the sapwood can be measured. Plant Physiol 72: 1094–1099
13. Tyree MT, MA Dixon, RG Thompson 1984 Ultrasonic acoustic emissions from the sapwood of *Thuja occidentalis* measured inside a pressure bomb. Plant Physiol 74: 1046–1049
14. Tyree MT, MA Dixon, EL Tyree, R Johnson 1984 Ultrasonic acoustic emissions from the sapwood of cedar and hemlock. Plant Physiol 75: 988–992
15. Tyree MT, MA Dixon 1985 Water stress induced cavitation and embolism in some woody plants. Physiol Plant. In press
16. Zimmermann MH 1978 Hydraulic architecture of some diffuse-porous trees. Can J Bot 56: 2286–2295
17. Zimmermann MH, CL Brown 1977 Trees: Structure and Function. Springer, New York
18. Zimmermann MH, JA Milburn 1982 Transport and storage of water. *In* OL Lange, PS Nobel, CB Osmond, H Ziegler, eds, Physiological Plant Ecology II. Encyclopedia of Plant Physiology New Ser Vol 12B. Springer, New York, pp 135–151
19. Zimmermann MH, JS Sperry 1983 Anatomy of the palm *Rhapis excelsa*. IX. Xylem structure of the leaf insertion. J Arnold Arbor Harv Univ 64: 599–609