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Hydraulic architecture of palms

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ABSTRACT. — The water transport and storage system of palms is adapted to maintain the primary stem xylem functional over the life of the shoot, and in spite of severe drought. However, our structural information far exceeds our knowledge of vascular function, and these functional considerations bring more questions than answers. The tendency to generalize from limited data on a few species begs the question of how the hydraulic parameters discussed vary between palms with different growth forms and ecologies.

Key words: vascular function, cavitation, segmentation.

One of the most unique and interesting aspects of palm biology is their acheivement of arboreal size and longevity while possessing only primary growth. This constraint is most pronounced in the palm stem, as opposed to roots or leaves, because the stem alone must live as long as the plant and support its full size. The lack of secondary growth in the palm stem has important implications for how this organ performs one of its main functions: water transport.

Two questions make the topic of water transport especially interesting in palms. The first is the structural riddle of how the thousands of scattered vascular bundles of a palm stem are organized to supply a crown of leaves that is continuously adding new leaves as old ones are shed. In a plant with secondary growth, the vascular organization of the stem is relatively simple because the secondary xylem provides a solid matrix of conduits that is not committed to any particular set of leaves. As new leaves are added, new xylem is added to the matrix by the vascular cambium.

The second question is how this single set of vascular bundles can continue to perform the inherently vulnerable process of water transport throughout the potentially long life of the palm. The water is transported under negative pressure and is susceptable to vaporizing (cavitation); especially during periods of water stress or freezing temperatures. Xylem conduits in temperate trees with secondary growth often only function for as little as one season and are replaced by new ones. In no case do they function for the 100 years or more that a palm stem can live.

The answers to these questions involve an interesting interplay between development, structure, biophysics, and physiology; a blend of disciplines called "hydraulic architecture" by one of its earliest investigators, M.H. ZIMMERMANN. While the issue of vascular organization has been considered in some detail for a number of palms through the efforts of ZIMMERMANN and P. B. TOMLINSON, our understanding of functional aspects of water transport is imperfect. The discussion of these issues will be speculative, and perhaps inspiring of more experimental work on these fascinating plants.

VASCULAR ORGANIZATION: THE "*RHAPIS* PRINCIPLE"

A transverse or longitudinal section of a palm stem reveals a network of vascular bundles so complex as to appear chaotic. Through the heroic efforts of Tomlinson and Zimmermann in the 1960's and 1970's, the underlying organization of this system was deduced, and revealed to be rather simple in principle. They developed a cine method of viewing the palm stem by photographing serial transverse sections and tracing the course of the vascular bundles through many internodes in a film. For much of this work, they

focussed on the tractably small palm *Rhapis excelsa* having "only" 1000 vascular bundles in transverse section rather than several times more in the larger palms. The organizing principle of the vascular system in this palm has been called the "*Rhapis* principle" and applies to all other palms examined. Their findings have been published in several papers (e.g., see ZIMMERMANN & TOMLINSON, 1972), and it is only necessary here to review the main points.

The fact that each vascular bundle follows essentially the same pathway greatly simplifies the apparent complexity. This path is best described as if viewing the films of serial sections from the *Rhapis* stem. Starting with a vascular bundle near the stem periphery and moving distally, the bundle gradually follows a helical path towards the stem center. At its most central position, the bundle divides once, and both branches move abruptly back toward the stem periphery at a node. One, the leaf trace, departs at the node. The other is the continuing stem, or "axial," bundle. As it moves to the periphery, it forms several short branches called "bridge" bundles that connect with neighboring axial bundles. Once at the periphery, the axial bundle repeats the process of moving back towards the stem center. Developmentally, it is the leaf trace that branches to form the axial continuation rather than vice-versa; thus, the stem bundles are sympodia formed from multiple leaf traces. The recurring pattern of an upwardly-branching leaf trace restoring axial continuity along the stem is the *Rhapis* principle. While different species are known to vary in a number of details (ZIMMERMANN & TOMLINSON, 1974), the organizing principle is the same.

The axial bundles differ in the number of nodes between leaf traces: minor bundles supply leaves at relatively short intervals and also penetrate less deeply into the stem, major bundles supply leaves at greater intervals and penetrate to the center of the stem. As a result, a given leaf is supplied by more minor bundles than major ones. In addition to this "inner" system of continuous axial bundles, there is also an "outer" system of cortical bundles that, in *Rhapis* at least, consist only of dense fiber caps. These are discontinuous bundles that appear in the cortex and depart into the leaf; they function in mechanical support and protection of the palm stem. Leaf traces of the various types of bundles depart at various angles from the stem and there is no nodal plexus.

At this level of description, the functional implications of this vascular pattern for water (and phloem) transport are straightforward. The branching of the leaf trace provides an axial pathway for water movement along the stem, and insures that the number of stem bundles remains approximately constant. Flexibility exists in the number of axial branches formed, from none to three or four. Presumably this is a response of the apical meristem to environmental conditions and allows adjustments in the numbers of axial bundles along the stem. The presence of bridge bundles linking different axial bundles is very important functionally, because it provides redundancy to axial transport pathways. If an axial bundle is damaged, transport through its entire length is not interrupted, because the bridge bundles allow a path for water to "detour" around the obstruction. Dye and isotope labelling studies have confirmed extensive lateral connections between the individual stem bundles.

There are also important functional implications of the distribution of protoxylem and metaxylem within the vascular bundle network. The branching of the leaf trace occurs as the leaf is being displaced from the meristematic "cap" at the palm apex. This late development is followed by similarly late maturation of the xylem above the branch point with the result that the axial bundle at the stem periphery generally consists of only metaxylem; often just a single vessel. Acropetal differentiation of this branch rapidly penetrates the meristematic cap as it joins the base of a distal leaf primordia. This development is reflected in the appearance of protoxylem in the mature axial bundle as it moves towards the stem center. The amount of protoxylem increases distally and departs to the leaf, while the metaxylem continues axially.

As a result of this anatomy, the stem bundles have continuous large-diameter

metaxylem vessels that have a correspondingly high hydraulic conductance while the leaf is supplied solely by narrow and relatively short protoxylem vessels and tracheids forming a hydraulic bottleneck. Metaxylem reappears in the leaf bundles in the sheath and petiole distal to the leaf-base meristem. This protoxylem link between metaxylem vessels of stem and leaf has the advantage of preventing embolism within the axial bundles of the stem when a leaf is abscissed: only the short protoxylem elements become air-filled after abscission rather than much longer metaxylem vessels that would reduce hydraulic conductance in the stem. This bottleneck is also important in protecting the stem from cavitation resulting from water stress, and in buffering stem water storage from depletion under favorable conditions, as discussed in the next section.

VASCULAR FUNCTION: FOUR DEFENSES AGAINST XYLEM CAVITATION

Although the vascular pathway in palms provides redundancy in the event of physical damage, protects the stem from embolism during leaf abscission, and has some capacity for adjustment during development in the apex, the fundamental constraint of primary growth remains: there is no mechanism for adjusting the transport capacity of the mature axis. The fixed transport capacity of the stem is reflected in the general absence of vegetative branching in the aerial shoot, and the relative constancy of crown size with age. It must also be reflected in adaptations that minimize or mitigate the occurrence of xylem dysfunction by cavitation: the vaporizing of water held under negative pressure.

A few comments on water transport will be useful for understanding the specific situation in palms. According to the cohesion-tension theory, water is lifted to the leaves by capillary forces in the cell walls at the site of evaporation. This places the water in the plant under sub-atmospheric and sub-vapor (negative) pressure. In this condition, the liquid water is metastable and becomes vulnerable to vaporizing (cavitation). The reason negative pressures can exist is because nucleating sites for the vapor phase change are minimal in the xylem.

Beginning with the work of MILBURN (1966) and M.H. ZIMMERMANN (e.g., 1983), attention has been focussed on the limits to negative pressures in plants. The reasoning was that because water is transported in a metastable state, cavitation could be an important limiting factor for tolerance of water stress. Over the last decade, we have learned a considerable amount about the causes and consequences of cavitation in plants, and the magnitude and distribution of pressure gradients in the xylem. This body of knowledge, together with the vascular anatomy constitutes what can be called "hydraulic architecture."

While cavitation and the resulting loss of transport capacity is theoretically a problem for all plants, it is especially so for palms which lack any means for regenerating new xylem conduits to replace ones lost to cavitation. This reasoning inspired M.H. Zimmermann and colleagues to make some of their initial inquiries into water transport and cavitation in palms. Once again, owing to its convenient size, *Rhapis excelsa* was the subject of most experiments. Most of what we know about cavitation in palms concerns this species (ZIMMERMANN, 1983; SPERRY,1985, 1986). Generalizing to other palms of different growth forms and habitats can only be tentative.

A priori, palms should either exhibit adaptations that minimize the effects of cavitation on water transport, or alternatively, be limited to regions where the threat of cavitation is minimal. Based on their ecological distribution alone, the former alternative applies. Palms occur in desert situations where they can develop very low xylem pressures (e.g., to -3.5 MPa in *Washingtonia filifera* of Baja peninsula; SCHMITT *et al.*, 1993), in mangrove swamps where they are subject to salinity stress (*Nypa* spp.), and in seasonally dry tropical forests. Their generally shallow root systems also imply exposure to at least seasonally low water availability and xylem pressures. Although they may drop several leaves under water stressed conditions, they appear capable of continuing

transpiration and carbon dioxide uptake under arid conditions. These observations indicate that palms are not restricted to mesic or hydric sites where conditions alone would minimize the threat of cavitation.

What little we know of the hydraulic architecture of palms suggests that it contributes significantly to their ability for tolerating water stress while protecting the integrity of the stem xylem necessary for survival of water stress. Altogether, there are four "lines of defense" that allow growth and/or survival under varying degrees of stress. Although none of the features are unique to palms, their occurrence together in this group of plants is exceptional.

VULNERABILITY TO CAVITATION AND STOMATAL BEHAVIOUR

It is becoming increasingly obvious that one adaptive reason for the stomatal regulation of transpiration is the avoidance of excessive cavitation in xylem (e.g., TYREE & SPERRY, 1988). Some of the first evidence for this was from observations on the palm *Rhapis excelsa*.

Figure 1 shows the loss of hydraulic conductance from cavitation in petiole xylem as a function of negative xylem pressure. This relationship has become known as a "vulnerability curve." It is measured by comparing the hydraulic conductance of the xylem before and after exposure to a known negative pressure. It indicates the minimum pressure possible without causing cavitation, as well as the pressure causing complete cavitation. In the *Rhapis* petiole, cavitation occurs between ca. -2.5 and -6.0 MPa. A number of studies have shown that the mechanism of this cavitation is the aspiration of air into functional xylem conduits through inter-conduit pits; this is the "air-seeding" hypothesis proposed by ZIMMERMANN (1983).

How does the vulnerability curve for *Rhapis* compare with other plants? What kind of safety margin exists between actual xylem pressures and those inducing cavitation in this palm? These questions are addressed in Figure 2 which shows the range of pressures required to cause complete cavitation vs. the minimum recorded negative pressure in the field for plants of diverse affinity and habitat.

There is a wide range of vulnerabilities to cavitation: plants lose xylem transport at pressures anywhere from -2 to less than -10 MPa. *Rhapis*, (solid symbol) the only palm studied so far, is among the moderately resistant species. Safety margins from complete cavitation are indicated by the vertical distance between the data and the 1:1 line (dashed line). They range from a few tenths of a megapascal in more vulnerable species, to several megapascals in more resistant plants. In *Rhapis*, this maximum safety margin is ca. 3.5 MPa based on a minimum field xylem pressure of -2.5 MPa (Fig. 1, single arrow) and complete cavitation occurring at -6.0 MPa. Although this safety margin may be reduced during extreme drought, these data suggest that this particular palm, anyway, is well-buffered against complete cavitation.

Interestingly, stem xylem of bamboo (*Rhipidocladum racemoflorum*) has a vulnerability curve nearly identical to that in *Rhapis*, and it maintains a similarly large safety margin from complete cavitation (2.25 MPa; COCHARD *et al.*, 1994). Like palms, bamboo lacks secondary growth and must avoid cavitation in its stem xylem.

In addition to maintaining a large safety margin from cavitation, plants can minimize cavitation by preventing low xylem pressures via stomatal control of transpiration. *Rhapis* also exhibits this behaviour because complete stomatal closure was induced at an average pressure of -3.2 ± 0.18 MPa (double arrow, Fig. 1). Although this is within the cavitation range, it is still well above the pressure causing complete cavitation.

Based on this information from one species, we can hypothesize that the first line of defense from cavitation is xylem that is relatively resistant to cavitation, and a stomatal control mechanism that minimizes the occurrence of cavitation-inducing pressures.
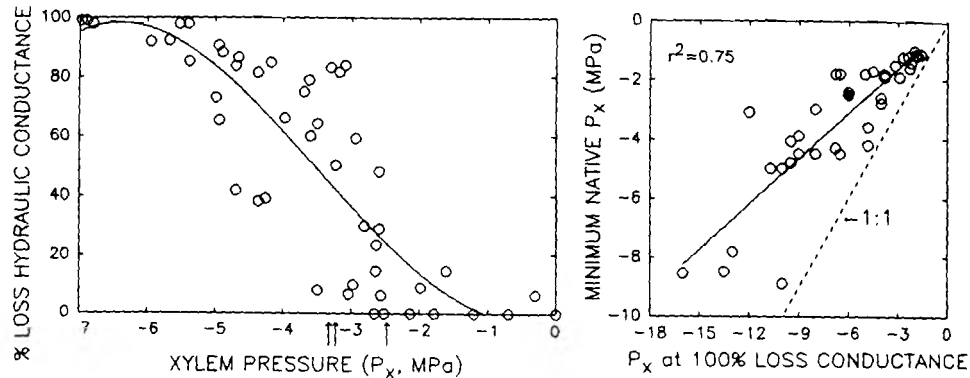
XYLEM PRESSURE (P_x, MPa)

P_x at 100% LOSS CONDUCTANCE

Fig. 1 (left) — "Vulnerability curve" for petiole xylem of *Rhapis excelsa*.
Fig. 2 (right) — Minimum negative xylem pressure (P) vs. xylem pressure causing 100% loss of hydraulic conductance. Solid symbol is *Rhapis excelsa*.

SEGMENTATION

A second line of defense involves a more detailed consideration of vascular structure and function. Figure 3 shows a typical pressure drop in the xylem of the shoot of *Rhapis excelsa*. At night, when flow is minimal, the pressure drops an even 0.01 MPa/m to counteract the force of gravity on the water column (Fig. 3, line 1). The intercept at the base of the shoot is the soil water potential. During the day, the gradient steepens as water is flowing through the xylem and overcoming its frictional resistance (Fig. 3, line 2). The important observation here is that this frictional gradient is not constant, but increases considerably in two parts of the shoot: the stem-leaf junction ("S" for sheath, in Fig. 3), and the leaf blade ("B" in Fig. 3). Anatomically, this corresponds to the protoxylem bottleneck at the leaf insertion, and to smaller vessel diameters in the lamina vascular tissue. The result of this is that the xylem pressure in the leaf is significantly lower than the stem, by a range of 0.7 to 1.5 MPa.

These areas of localized pressure drops effectively segment the plant in terms of the range of pressures experienced. M. H. Zimmermann hypothesized that this "hydraulic segmentation" was adaptive in localizing cavitation to the leaves, thereby protecting the hydraulic integrity of the stem (ZIMMERMANN, 1983). For example, the horozontal dashed-dotted line in Figure 3 represents the onset of cavitation at ca. -2.5 MPa for *Rhapis* petioles (Fig. 1). As soil drought progresses, the intercept of the pressure profile becomes increasingly negative, and pressures in the leaves will reach cavitation-inducing levels while the stem maintains a greater safety margin (Fig. 3, line 3). Although stomatal closure will tend to flatten this profile, closure may not be complete, especially in older leaves with poorer stomatal control. The result will be cavitation occurring in the leaves and not the stems. The same result would in theory occur without hydraulic segmentation, but the segmentation favors this outcome.

What is the evidence for this "segmentation" hypothesis? Cavitation in *Rhapis* after a dry season in Miami, Florida (USA) caused as much as 64% loss of hydraulic conductance in petioles while stem xylem suffered less than 11% loss of conductance (Fig. 4). This preferential accumulation of cavitation in leaves may trigger premature leaf senescence and accelerated leaf shedding that is characteristic of palms during dry seasons. This loss of leaves further favors the water balance of the stem by reducing surface area and transpiration while at the same time increasing the hydraulic conductance

to the remaining leaves. In this way, cavitation in the leaves favors the preservation of stem water transport capacity. Once the drought is finished, the stem can readily produce new leaves. It would require much more energy for the plant to replace the whole shoot.
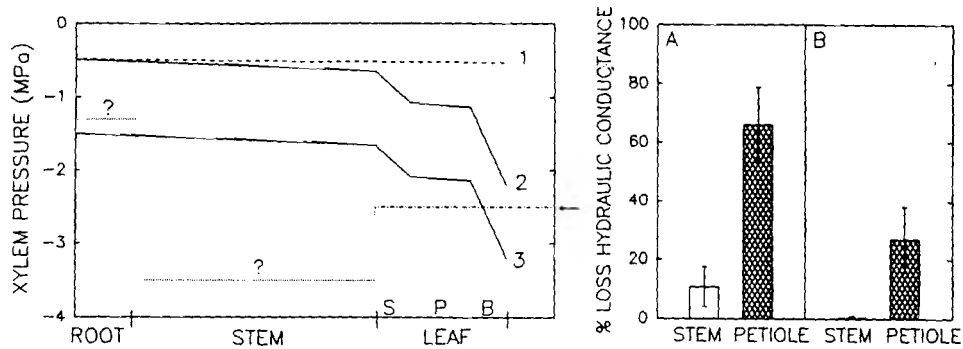

Fig. 3 (left) — Xylem pressure vs. distance from ground in *Rhapis excelsa.*. Line 1: no transpiration with soil water potential of -0.5 MPa. Line 2: transpiration at same soil water potential as line 1. Line 3: transpiration at soil water potential of -1.5 MPa. Horozontal dash-dotted line (arrow) shows pressure initiating cavitation in petiole xylem from Fig. 1. Horozontal dotted lines are hypothetical cavitation thresholds for stem and root xylem if the palm exhibited vulnerability segmentation.

Fig. 4 (right) — Loss of xylem conductance from cavitation in stems vs. petioles of two shoots of *Rhapis excelsa* (A&B).

Recently, evidence from other plants has uncovered another aspect of plant segmentation. Rachises of walnut leaves (*Juglans regia*) have been found to be more vulnerable to cavitation than the subtending stem (TYREE *et al.*, 1992). The leaves not only experience significantly more negative pressures than the stem, but the onset of cavitation occurs at higher pressures than the stem. This is interpreted as giving added insurance that leaves will cavitate and be shed before stems approach cavitation pressures. In terms of the pressure profile in Figure 4, this "vulnerability segmentation" means the cavitation pressure is not equal between stems and leaves, but that stems are more resistant to cavitation than leaves (Fig. 3, dotted line [?]).

The same phenomenon seems to characterize the peripheral parts of the other end of the plant, the roots. In all plants studied so far, roots are more vulnerable to cavitation than stems: especially the smaller roots (e.g., SPERRY & SALIENDRA, 1994). This aspect of vulnerability segmentation would drastically reduce hydraulic contact with the soil during a drought. This may be beneficial by reducing water use, and also in extreme drought, protecting the stem from being dried out by the soil. This is known to occur in cacti, which can maintain high shoot water potentials despite being rooted in much drier soil (NOBEL & NORTH, 1993). It is illustrated in Figure 3 by the dotted line showing a hypothetical cavitation pressure for the palm root.

Do palms exhibit these types of vulnerability segmentation? The data is limited but suggestive. Unpublished observations from *Rhapis* support the hypothesis that the stem is more resistant to cavitation than the leaves. However, confirmation of this awaits further experimentation. While there is no data at all for roots of any palm, generalizing from other plants it seems likely that palm roots would also be more vulnerable than the stem.

The hydraulic- and possible vulnerability-segmentation in palms appears to constitute a second line of defense that specifically protects the hydraulic integrity of the palm stem

by selective sacrifice of peripheral organs during stress.

RE-FILLING OF CAVITATED XYLEM CONDUITS

The third line of defense in the water supply system of palms is relatively straightforward. In the event that cavitation does occur, even within the stem, vessels are apparently capable of re-filling after a drought. Once again, the evidence comes from limited studies of *Rhapis excelsa*.. Xylem pressures approach atmospheric during rain storms, and laboratory studies showed that 5 hours of exposure to atmospheric pressure was sufficient for the air to dissolve in embolized vessels (SPERRY, 1986).

It is possible that the presence of scalariform perforation plates in the xylem of many palm species assists in embolism reversal. These create a meniscus within embolized vessels as xylem pressures approach atmospheric (i.e., at night or during rain). Increasing the surface-area to volume ratio of air-water contact in this way may increase the rate of bubble dissolution.

Given the other defenses against the disruption of stem water transport in palms, it is surprising that there are few reports of strong root pressures. On a number of occasions I have looked carefully for root pressures during the night or during rain storms in *Rhapis* and *Desmoncus* sp. and have found none. Reports of root pressures in the literature are often from excised roots, rather than from the stems of intact palms. In contrast to palms, the bamboo mentioned previously (*Rhipidocladum racemifolorum*) shows strong root pressures (to 120 kPa) during the rainy season; these were effective in reversing the limited embolism occurring in the stem during the previous dry season (COCHARD *et al.*, .1994).

STORAGE

A last defense against water stress and disruption of stem xylem transport is the tremendous water-storage capacity of the palm stem. The vascular bundles of the palm stem are dispersed in ground tissue which in the center of the stem is chiefly composed of thin-walled parenchyma. This parenchyma constitutes a large symplastic reservoir for stored water that is spatially integrated with the vascular system. According to Holbrook and colleagues, a 4 m *Sabal palmetto* stem contains 100 kg of water. In a series of studies on this large arboreal palm, they determined the importance of these reserves in its water economy (HOLBROOK & SINCLAIR, 1992a,b). Their results revealed an added benefit of the segmentation described above.

Although the stem contains large amounts of stored water compared to leaves, the withdrawal of this water requires significant decreases in stem xylem pressure. Under transpirational conditions, hydraulic segmentation buffers the stem xylem from large changes in xylem pressure while it causes leaf xylem pressures to change more dramatically (Fig. 3, changes from line 1 to line 2). Consistent with this, under normal conditions, relatively little stored stem water was lost to the transpiration stream in *S. palmetto*. Indeed, if stem water alone was supplying the water for normal transpiration rates, a 4 m tree would run out of water after only 6 days. Thus, the hydraulic segmentation of the palm assists in preventing the unnecessary depletion of stored water in the stem during favorable conditions. However, as soil drought increased and stomata began to limit transpiration (possibly in conjuction with cavitation in leaf xylem) stem xylem pressures dropped and an increasing amount of the reduced transpiration was supplied by stem water stores. Under extreme conditions when stomata were completely closed and leaves began to abscise, the very low epidermal transpiration rates could be sustained by stem water stores for an estimated 158 days in a 4 m tree. This survival of extreme drought would be enhanced if cavitation of root xylem minimized backflow of water from the stem to the soil.

Thus, segmentation coupled with a large capacity for water storage provides the stem

with a final defense from critically low xylem pressures in the event that water stress has become extreme enough to close stomata, cavitate leaf xylem, and perhaps also cavitate stem xylem. This emergency supply of water can allow the stem to survive extreme drought in a semi-dormant state for long periods of time. Survival time may be enhanced by very low epidermal transpiration rates associated with thick cuticles and sunken stomata.

FREEZING AND CAVITATION

While palms are capable of thriving in arid habitats, their distribution is sharply limited by cold and freezing temperatures. Cavitation can be a limiting factor for freezing tolerance as well as drought tolerance. When xylem sap freezes, bubbles form in the ice and can nucleate cavitation when negative pressures are restored after thawing. Susceptability to this form of cavitation increases with increasing conduit size (ZIMMERMANN, 1983). Whereas tracheids are largely resistant to cavitation by freezing and thawing, large vessels are extremely susceptable.

Nothing is known of the relative susceptability of palm vessels to freeze-thaw induced cavitation beyond the observation of Scholander and colleagues of complete cavitation in rattan (*Calamus* sp) from localized freezing of the stem (SCHOLANDER *et al.,* 1961). It seems likely, based on the lengths and diameters of typical palm vessels that cavitation by this mechanism in most palms would be extensive. Palms are especially susceptable to ground frost (SAKAI & LARCHER, 1987), and it is interesting that the largest diameter vessels in the palm occur in the roots. Although damage to living tissue by freezing is known to limit palm distributions (SAKAI & LARCHER, 1987), it is not known whether cavitation is an additional factor.

CONCLUSIONS

Even with the limited information in hand, we can begin to appreciate how the water transport and storage system of palms is adapted to maintain the primary stem xylem functional over the life of the shoot, and in spite of severe drought. However, our structural information far exceeds our knowledge of vascular function, and these functional considerations bring more questions than answers. The tendency to generalize from limited data on a few species begs the question of how the hydraulic parameters discussed vary between palms with different growth forms and ecologies. We still have much to learn.

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