

XYLEM OF RATTANS: VESSEL DIMENSIONS IN CLIMBING PALMS¹

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We examined 11 species in four genera of rattans (*Calamus*, *Daemonorops*, *Korthalsia*, *Plectocomia*) growing in their native rainforest habitat in Singapore. Using aqueous safranin dye, we found that >95% of all vascular bundles at the base of a mature stem were functioning to transport water. We determined the frequency of vessel lengths in the long stems of these climbing palms by infiltration with dilute latex paint. Separate length distributions were made for metaxylem and protoxylem vessels; in both, there were many short and a few long vessels. The longest protoxylem vessels ranged from 7.5 to 62 cm in length, but one stem had an exceptional protoxylem vessel measuring 3.0 m. Maximum metaxylem vessel diameters were positively correlated to maximum vessel lengths in these species. The longest metaxylem vessel was found in *K. rigida* and was 3.96 m in length and was constructed from ~1200 vessel elements (cells). The widest vessel in that same stem was 532 μm in diameter. Long, wide vessels decrease resistance and increase water transport efficiency. In addition, we suggest that wide metaxylem vessels may have an important function in water storage.

Key words: Areaceae; Calamoideae; *Calamus*; *Daemonorops*; *Korthalsia*; Palmae; *Plectocomia*; vessels; xylem.

Rattans (climbing palms) have the longest stems of any vascular plant, with some reported to be well over 100 m long (Dransfield, 1979; Tomlinson, 1990). These climbing species also have the widest xylem vessels among palms (Klotz, 1978a) and thus follow the widespread trend of climbers in having wider vessels than do related nonclimbing species (Ewers and Fisher, 1989b; Ewers, Fisher, and Chiu, 1990; Gartner, 1995). Although rattan stems are often coiled on the forest floor or loop through the rain forest canopy, they rarely root and thus represent a very long pathway for water transport from roots to the leaf crown. In addition, all vascular tissues are primary and thus must function for the entire life of the stem. To better relate and understand these unique structural and physiological attributes, we determined the size and structure of the vessels in a variety of rattan palms growing under natural conditions.

Vascular features and details of vascular architecture were described in qualitative and quantitative terms for the first time by Tomlinson and Fisher (2000) and Tomlinson et al. (2001). The present study extends these descriptions and further supports the original conclusions about the special vascular arrangement in rattans relative to other palms.

MATERIALS AND METHODS

Techniques were initially perfected on the following cultivated plants in the Fairchild Tropical Garden, Miami, Florida, USA: *Calamus longipinna* Lauterb. & K. Schum. (=specimen FTG87268) and *C. palustris* Griff. (=specimen FTG64129). Plants growing naturally were used from the Bukit Timah Nature Reserve, Singapore and the Central Catchment Nature Reserve, Singapore by kind permission of the National Parks Board of Singapore (Re-

search Pass Number 99/NR/DC-27). These wild-collected species are listed (Table 1) with complete botanical names following Dransfield (1979). Herbarium vouchers are deposited in FTG (Fairchild Tropical Garden herbarium) and SINGU (National University of Singapore herbarium).

To measure vessel lengths, latex paint was diluted to 1% (v/v) with tap water and filtered through filter paper (Whatman No. 1) to obtain a 5 μm maximum paint particle size, which is small enough to pass through the narrowest vessels (Ewers and Fisher, 1989a). We used two methodologies for paint infusion into large stems. In method 1, stems were cut (with a long-handled pruner) underwater at their bases (water was taken from either a clear stream or a tap) in a plastic basin and then recut several times underwater. The surface was then carefully shaved with a razor blade. The stem was transferred to a container of the diluted latex paint, keeping the cut surface flooded at all times to prevent introduction of air into the xylem. Paint uptake was driven by transpiration of the attached leaves. After there was no observable uptake of paint (usually a few days, depending upon weather conditions), the shoot was pulled from its supporting trees and transported to the laboratory.

In method 2, shoots were first pulled from the supporting trees. If the stem was undamaged, its base was cut (with a long-handled pruner) underwater as in method 1, and a container of water was taped to the stem to keep the cut end submerged in the water while the shoot was transported to the laboratory. All lower leaves were cut off to leave a small crown of ~6–10 terminal leaves. In the laboratory, the stem was recut, shaved with a razor blade, and a plastic tube was tightly fitted over the cut end while it remained underwater. Diluted latex paint was fed into the stem through the plastic tube with a 2.5-m column of paint (pressure = 25 kPa). Paint uptake was driven by the pressure applied by the paint column and transpiration of the few attached leaves. Some stems were similarly supplied with diluted latex paint via plastic tubing in the field immediately after pulling the stem from its supporting tree. After paint flow stopped (usually after a few days), the stem was harvested. For both methods, stems were cut longer than 10 m, which was longer than the longest vessels, as indicated in preliminary studies.

Harvested stems treated by either method were cut into uniform lengths, carefully labelled, and the basal end of each segment was observed under a stereozoom microscope. The number of paint-filled (or paint-lined) vessels were counted as described in Ewers and Fisher (1989a). The raw counts of paint-filled vessels were used for calculating the frequency distributions of different vessel lengths according to the procedures of Ewers and Fisher (1989a) and Zimmermann (1983).

General histological observations were made on hand sections of stem

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TABLE 1. Rattan palms examined and typical sizes of their internodes.

Species	Collection number	Internode length (cm)	Internode diameter (cm)
<i>Calamus</i> sp.	VR11	19	0.58
<i>Calamus insignis</i> Griff. var. <i>insignis</i>	VR2, 10, 16	22.6, 21, 30	0.57, 0.45, 0.67
<i>Calamus javensis</i> Blume	VR32	15	0.55
<i>Calamus laevigatus</i> Mart. var. <i>laevigatus</i>	VR31	27	1.44
<i>Calamus oxleyanus</i> T. & B. ex Miq.	VR23, 24, 33	19, 23, 18	—, —, 1.31
<i>Daemonorops grandis</i> (Griff.) Mart.	VR13, 15, 35	18.5, 14.7, 29	1.36, 1.82, 1.4
<i>Daemonorops hystrix</i> (Griff.) Mart.	VR12, 14, 18, 25, 26, 36	9.9, 10.5, 17, 11	1.92, 1.33, 1.60, 1.74, 1.14, 1.38
<i>Korthalsia echinometra</i> Becc.	VR8	20	1.20
<i>Korthalsia rigida</i> Blume	VR9	42	2.20
<i>Korthalsia rostrata</i> Blume (= <i>K. scaphigera</i> Mart. ex Griff.)	VR5, 7	24, 24	0.51, 0.62
<i>Plectocomia elongata</i> Mart. ex Blume	VR1, 27, 28	26.4, 31, 27.7	2.19, 2.05, 3.0

stained with aqueous toluidine blue O. Slivers of stem were macerated in Jeffrey's solution (chromic acid + nitric acid) for several days (Ruzin, 1999), washed, stained with safranin, and mounted on slides in corn syrup or glycerine beneath a cover glass for light microscope observations. Photomicrographs were made of cut surfaces and hand sections of stems. Vessel diameter was measured directly with the ocular scale of a compound light microscope.

RESULTS

Summary of the general vascular anatomy—In transverse section, the stems contained bundles of various sizes with the largest in the central region (Fig. 1). The largest bundles usually had one wide metaxylem vessel element, several narrow metaxylem vessel elements and one or more protoxylem vessel elements (Figs. 2–5). Phloem was usually divided into two separate areas in each bundle. Narrow bundles in the stem periphery had one to several small metaxylem cells with two phloem areas (but only one in the smallest bundles that grades into fiber bundles adjacent to the epidermis). Occasional small transverse commissural bundles irregularly anastomosed and joined the larger longitudinal bundles. The general three-dimensional architecture of the vascular system was similar to the description of Tomlinson et al. (2001). Within one transverse section, all the variations in the anatomy of a single large vascular bundle (as illustrated in Tomlinson et al., 2001) could be observed in different bundles. The structure of a large vascular bundle changes from its origin until it departs the stem as a leaf trace. This change has the following three phases: (a) the basal end is narrow with little to no protoxylem; (b) along most of the length is wide, with one large metaxylem vessel and two regions of phloem (Fig. 2, right side with one phloem area only partially seen, and Fig. 5); and (c) the distal region where the bundle migrates to the stem periphery to become a leaf trace and has narrow metaxylem vessels and an increased area of protoxylem (Fig. 2, left side, and Fig. 3, upper side).

Perforation plates—Wide vessel elements had simple perforation plates as reported by Klotz (1978b) and often long narrow tails extending beyond the transverse perforation (Fig. 6). The wide metaxylem vessel elements of *Korthalsia rigida* ranged in cell length from 2.65 to 4.55 mm. Narrow metaxylem vessel elements have either scalariform (Fig. 7) or simple (Fig. 8) perforation plates. In *K. rigida*, intervascular pitting is alternate. Short vessel elements that form the connection between longitudinal bundles via transverse commissural bundles were very irregular in outline, often many armed, and with more than two simple or scalariform perforations. In one

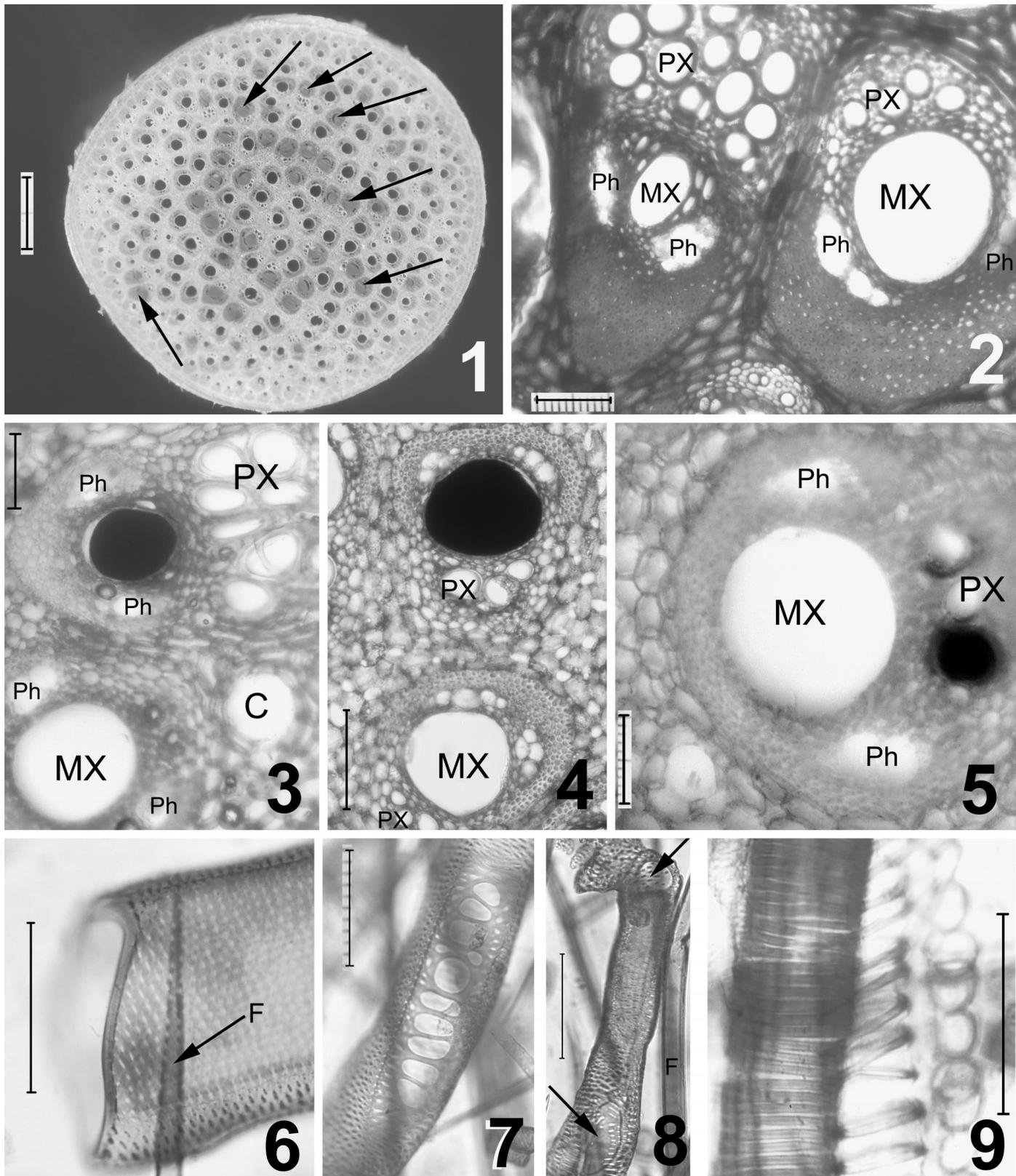
irregular element, up to five separate scalariform perforation plates were observed.

Protoxylem elements rarely had intact cell ends due to ripping of the thin primary wall during maceration and processing. Early-formed elements had annular thickenings and late-formed elements had helical wall thickenings with progressively tighter coils of wall thickening (Fig. 9). A few helical elements with tight coils were nearly entire, and most had long tapered ends, although two were observed with simple perforations in *K. rigida* (collection VR9) on their tapering ends.

Functional vessels and vascular bundles per stem stained with dye—The majority of vascular bundles in stems that were cut and supplied with paint had at least one element filled with paint at the cut end. This was evident when the cut end was viewed after the painted surface was shaved with a razor thus removing 1–2 mm from the original proximal end, the point of paint introduction (Fig. 1). In large stems, painted bundles numbered ~270 (*C. insignis*, collection VR2), 500 (*D. hystrix*, collection VR12), and 430 (*P. elongata*, collection VR27).

Two stems were cut underwater and placed in aqueous safranin stain while still attached to their supporting trees. Essentially all vascular bundles were colored and assumed to be functional in these transpiring plants. At 5 mm from the cut surface of *D. hystrix* (collection VR36), 1194 bundles were stained, and 44 bundles (8 wide bundles and 36 narrow bundles or leaf traces) were unstained (3.6% of the total number). These unstained bundles were presumably nonfunctional in water transport. In *D. grandis* (collection VR35), there were a total of 815 bundles, and of these, 2.0% were unstained at 5 mm from the cut surface.

Frequency distribution of vessel lengths—The calculated distributions of vessel lengths by the latex paint method showed many short vessels and a decreasing percentage of long vessels (Figs. 10 and 11). In a few stems (Figs. 12–14), additional counts were made to distinguish between paint-filled metaxylem (Figs. 3 and 4) and protoxylem vessels (Fig. 5). The paint-filled protoxylem elements were clearly defined by their position within the vascular bundle. In a few leaf traces, protoxylem is particularly obvious since the large metaxylem vessel(s) became progressively smaller and the protoxylem vessels increased in number and size. The absence of metaxylem vessels between 0.8 and 1.8 m long (Fig. 12) was an artifact of the technique. Many vessels that were between 0.6 and 2.0 m in length had only traces of paint lining the vessel lumen. Presumably, these long vessels were completely



Figs. 1-9. Vascular tissues of rattans. 1. Internode of *Calamus insignis* (VR16), transverse surface with paint-filled vessels in many vascular bundles (arrows) at a distance of 1.4 m from paint introduction. 2. Two wide bundles of *Calamus palustris* (87268), one to left is a leaf trace with narrow metaxylem vessels and much protoxylem, section stained with toluidine blue. 3. Paint-filled metaxylem vessel in a leaf trace bundle near stem periphery of *Calamus longipinna*, section unstained. 4. Paint-filled vessel in a wide bundle in center of stem of *Daemonorops hystrix* (VR18), metaxylem vessel in upper bundle filled with paint, section unstained. 5. Paint-filled protoxylem vessel in wide bundle of *Calamus longipinna*, section unstained. 6. Simple perforation plate in late metaxylem

filled with paint at their distal ends and basal ends but not in their central regions. Thus, many vessels were not counted at these intermediate lengths and consequently distorted the frequency calculations. Protoxylem vessels (Figs. 13 and 14) followed a similar frequency distribution as metaxylem (Fig. 12) and all vessels (Figs. 10 and 11), but protoxylem vessels were shorter.

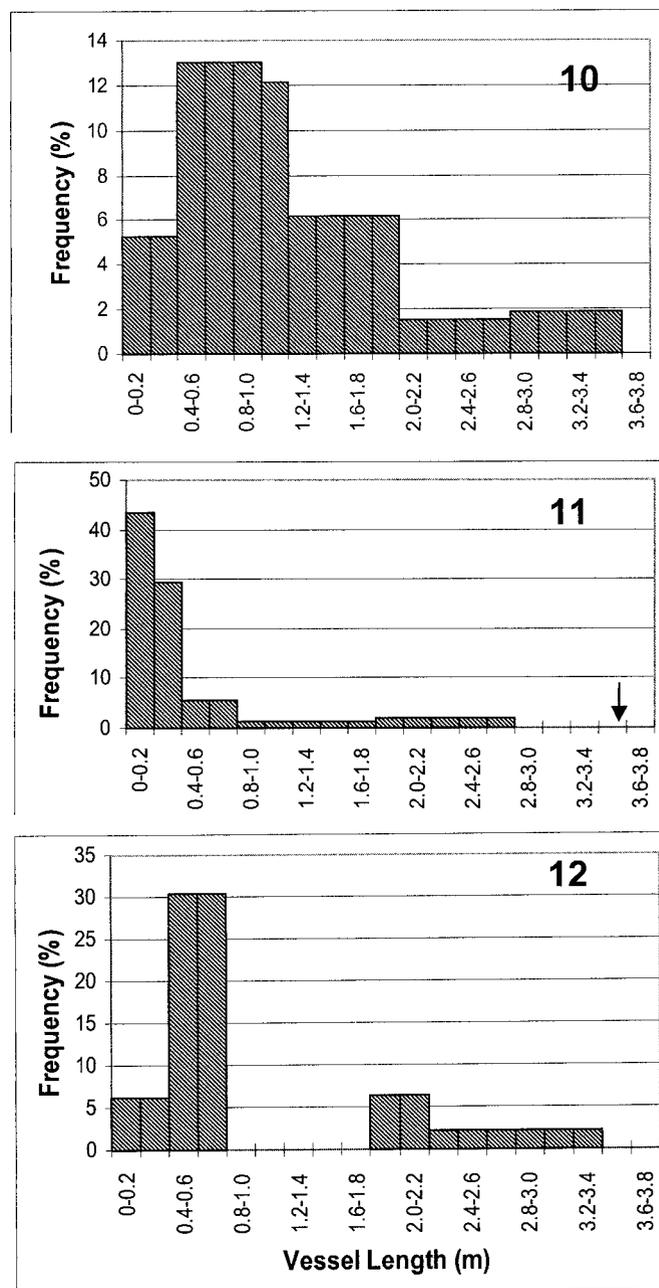
Maximum vessel lengths—The maximum lengths of metaxylem and protoxylem vessels are presented for different species (Table 2). There was considerable variability among stems of the same species. *Calamus insignis*, *Daemonorops hystrix*, and *Korthalsia rostrata* had longest vessels that were twice or nearly so in length in different stems. In *D. hystrix*, protoxylem length ranged widely among stems. In all cases, the longest protoxylem vessels ended distally in a peripheral bundle that had the structure of a leaf trace (Fig. 2, right side).

The longest vessels in all stems were in the metaxylem. Each long vessel could be followed from the basal cut end (paint entrance), which has the single wide vessel of a bundle (Figs. 3 and 4), to the distal end of the vessel. The metaxylem vessel became more narrow, often with metaxylem overlap (several adjacent vessels in transverse section), and the number of vessels (and maybe tracheids) in the protoxylem area of the bundle greatly increased. Therefore, the longest vessels were the widest vessels of the stem for most of their length, but these same vessels became narrow at their distal ends when their longitudinal vascular bundles were recognizable as leaf traces near the periphery of the stem. These same leaf trace bundles lack metaxylem when they enter the leaf base (as illustrated in Tomlinson et al. [2001]). There was a general linear relationship between the length of the longest vessel of a stem and the widest vessel in that same stem (Fig. 15); however, the correlation was not very strong ($R^2 = 0.416$, $N = 17$). When a similar data set was plotted (data not shown) using the diameter of the longest vessels measured when their bundles were still in the central region of the stem and therefore with a wide metaxylem vessel, diameter and length had a weaker correlation ($R^2 = 0.316$, $N = 32$).

To estimate the number of cells that form a single long vessel, we examined two species (one stem each) and used macerations to measure length of the wide metaxylem vessel elements. In *K. rigida* (collection VR9), the maximum vessel length was 3.96 m and its wide vessel element length was ~ 3.276 mm (mean for $N = 10$). Thus, this longest vessel is constructed of ~ 1208 cells. In *D. grandis* (collection VR13), the maximum vessel length was 2.7 m, vessel element length was 2.236 mm (mean for $N = 10$), and therefore, the longest vessel was 1207 vessel elements.

DISCUSSION

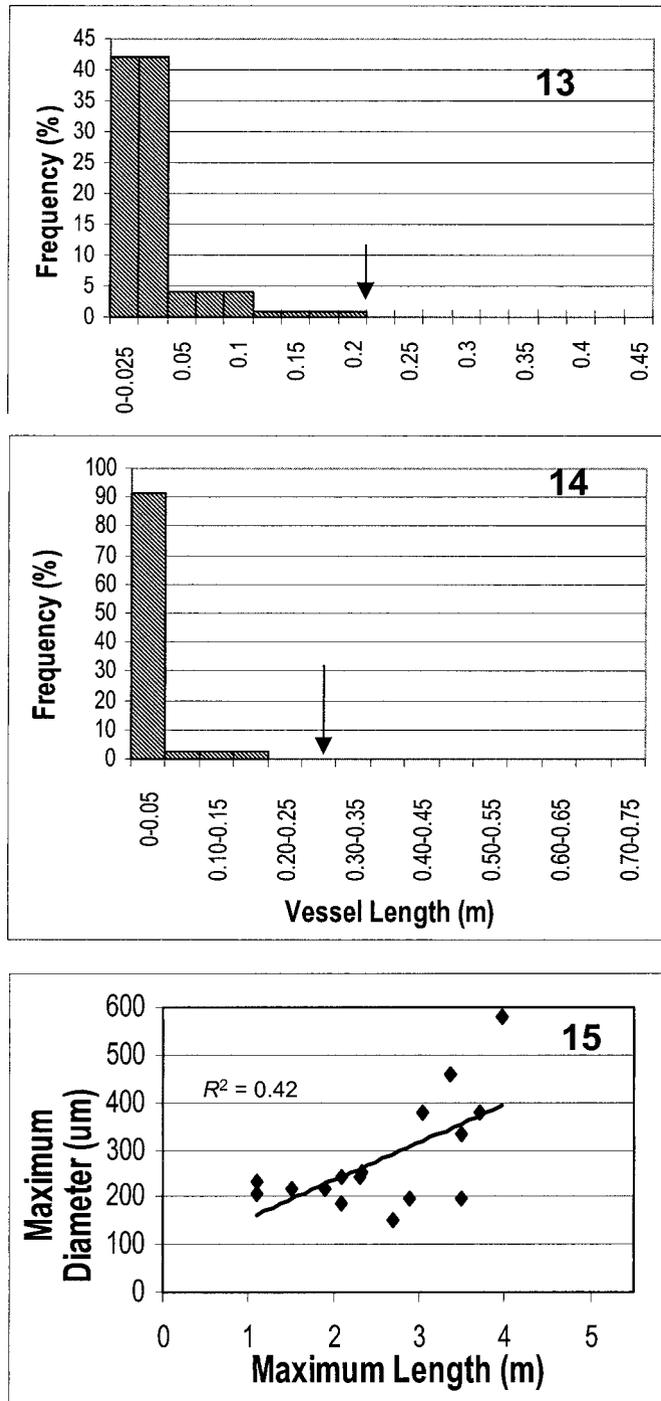
The general structure of xylem anatomy is similar in all species. One large metaxylem vessel predominates along most of the length of each large vascular bundle. Protoxylem consists of a few narrow elements, some of which are demonstra-



Figs. 10–12. Frequency of vessel length size classes. **10.** Meta- and protoxylem combined, for *Korthalsia echinometra* (VR8). **11.** Meta- and protoxylem combined, for *Plectocomia elongata* (VR27); arrow denotes longest vessel. **12.** Metaxylem only, for *Calamus insignis* (VR16).

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element of *Korthalsia rigida* (RV9), safranin stained. **7.** Scalariform perforation plate in late metaxylem element of *Korthalsia rigida* (RV9), safranin stained. **8.** Simple perforation plates (arrows) in metaxylem element from a commissural bundle of *Korthalsia rigida* (RV9), safranin stained. **9.** Series of protoxylem elements in a single wide bundle of *Korthalsia rigida* (RV9), safranin stained. Scale bars = 1.0 mm in Fig. 1, 100 μ m in Figs. 2–9. C, mucilage cell; F, fiber; MX, metaxylem; Ph, phloem; PX, protoxylem.



Figs. 13–15. 13, 14. Frequency of vessel length size classes; arrow denotes longest vessel. 13. Protoxylem only, for *Calamus insignis* (VR16). 14. Protoxylem only, for *Daemonorops hystrix* (VR14). 15. Linear regression of the distribution of maximum vessel length and widest vessel in the same stem, as determined in 13 different rattan species. Data taken from Table 2.

bly constituents of vessels up to 40–60 cm long by the paint method. However, fully intact protoxylem elements were not observed. Metaxylem vessel diameter decreased dramatically, and the vessel disappeared as its vascular bundle departed the stem as a major leaf trace. At the same position the number of protoxylem elements increased in both number and diam-

eter (compare these two xylem arrangements in Fig. 2). We did not attempt to follow individual vascular bundles along the length of a stem as was done for *Calamus* by Tomlinson et al. (2001).

Narrow commissural bundles form transverse connections between large longitudinal vascular bundles. The narrow and highly contorted metaxylem elements of commissural bundles are clearly vessel elements, as shown in macerations (Fig. 8). We did not observe whether perforations were present at the connection of commissural elements with wide vessel elements of the large vascular bundles. Furthermore, as we did not observe paint-filled commissural bundles, such perforations are unlikely.

Dye ascents demonstrated that >95% of vascular bundles are functional in water transport in long mature stems. Functional vessels were similarly demonstrated by paint movement both under pressure and tension using paint columns or paint uptake by intact shoots, respectively. Many short and a few long vessels occur in metaxylem and protoxylem. Although the technique may not be precise (i.e., when vessels fail to fill completely with latex particles), paint did travel the length of the longest vessels into the leaf traces.

Long vessels are correlated with wide vessels, a trend found in other climbers (Ewers and Fisher, 1989a, b; Ewers, Fisher, and Chiu, 1990; Fisher and Ewers, 1995). Vessel element diameter is correlated to vessel element length and to the climbing (or scandent) habit in palms (Klotz, 1978a, b). Thus, the generalization that climbing plants (e.g., dicots, monocots, and *Gnetum*) have wider vessels than related nonclimbing species continues to be supported. The longest metaxylem vessels (four species with a vessel longer than 3 m) can be compared to the length of internodes in these species. When the maximum length for each species (Table 2) is divided by the internode length for that same stem (Table 1), we find that the mean number of internodes included by this longest vessel was 13.25 ($N = 8$, range = 8–18). While there is considerable quantitative variation among stems of the same species and replicate sizes are small, there appears to be a general range in the absolute maximum length possible for a wide vessel, namely the total length of a large vascular bundle. This upper limit to vessel length equals the maximum length of a single large vascular bundle. This finding is in accord with the those of Tomlinson et al. (2001) who determined that large vascular bundles were continuous through ~3 m or 15 internodes of *Calamus longipinna*.

Protoxylem vessels attained maximum lengths of 20–60 cm and were frequently observed in many individual vascular bundles. Yet the observed lengths of 2 and 3 m in *Korthalsia rigida* were unexpected and far greater than other maximum protoxylem vessel lengths (Table 2). This species should be reexamined to confirm this extraordinary finding and eliminate the possibility of some artifact of the technique. There is little or no published information on the lengths of vessels in other palms, so we cannot contrast vessel lengths in palms with different growth forms.

In functional terms, we conclude that xylem water in rattan stems has the following potential pathway. Water enters the stem base from connections between adventitious roots and longitudinal stem vascular bundles. Details of initiation and structure of these root/stem vascular connections are poorly described for palms (Tomlinson, 1990). Water travels along both wide and narrow wide vascular bundles located both in the stem center and periphery, respectively. At least 95% of

TABLE 2. Longest measured vessels in the metaxylem and protoxylem of selected rattan palms.

Species and stem number (collection number)	Diameter of widest metaxylem vessel in stem (μm)	Longest metaxylem vessel length (m)	Longest protoxylem vessel vessel length (m)
<i>Calamus</i> sp. VR11	114	1.3	—
<i>Calamus insignis</i> var. <i>insignis</i> VR2, 10, 16	190, 190, 213	2.1, 1.9, 3.3	—, —, 0.21
<i>Daemonorops grandis</i> VR13, 15	152, 152	2.7, 2.5	0.62, —
<i>Daemonorops hystrix</i> VR12, 14, 18, 25, 26	182, 152, 243, —, —	1.1, 1.9, 2.3, 1.9, 1.7	0.27, 0.42, 0.075, —, —
<i>Korthalsia echinometra</i> VR8	380	3.5	—
<i>Korthalsia rigida</i> VR9	532	3.96	Observed at 2.0 and 3.0
<i>Korthalsia rostrata</i> VR5, 6, 7	205, 137, 198	1.9, 1.3, 0.9	—, —, —
<i>Plectocomia elongata</i> VR1, 27, 28	380, 334, 458	3.05, 3.5, 3.36	—, —, —

all bundles in the base of a mature stem are functional in transport of aqueous dye solution. In many of these bundles, both proto- and metaxylem elements are functional. In fact, surveys of old stems of climbing palms (Fisher and Ewers, 1991) found little evidence of tyloses or deposits (gums or mucilage) within vessels, which would be expected in non-functional vessels.

Water can pass from one wide vascular bundle to another by the interconnecting vessels of commissural bundles. These commissural bundles are scattered irregularly along the length of the stem (Tomlinson et al., 2001). There is no pattern of vascular connections or plexi associated with the nodes. However, the structural changes in the xylem of leaf traces means that water must move increasingly through the protoxylem since the metaxylem of each vascular bundle decreases as the bundle approaches the stem periphery. At nodes with attached live leaves, all water enters the leaf base via the protoxylem of the major leaf traces. The peripheral small bundles that lack protoxylem also enter the leaf sheath and may contribute to water flow as a result of commissural interconnections, but we did not study this. Presumably, the protoxylem should experience the extreme in low water potentials. Thus, the protoxylem of leaf traces in the leaf sheath should cavitate before the metaxylem of the leaf trace in the stem.

Within the stem, proto- and metaxylem vessels are separated by at least one layer of live parenchyma cells, which form a living barrier to possible transfer of gas bubbles between proto- and metaxylem vessels (Tomlinson et al., 2001). In other palms, the vessels of these two xylem regions may touch directly, presumably offering less resistance to gas movement via pit membranes or pores (Tomlinson and Fisher, 2000).

Water loss by foliar transpiration in palms appears to be similar to other plants and under expected stomatal control (Zobel and Liu, 1980; Sperry, 1986; Holbrook and Sinclair, 1992a, b), although we have no information for rattans. The large-trunked palm tree, *Sabal palmetto*, was shown to be capable of stopping essentially all transpiration when water stress occurred after digging it from the ground (Holbrook and Sinclair, 1992a, b). In this palm, water stored in the trunk (in cells of living tissues and in free space within vessels) was critical to survival during prolonged water stress. It may be possible that the volume of water stored in wide and long vessels of rattans may have a similar function, in addition to efficient water transport, as suggested in other lianas (Ewers, Fisher, and Chiu, 1990). Like other lianas of tropical rainforests, the leafy crown of a rattan is eventually exposed to full sun conditions when it reaches the top of the forest canopy. When rattans grow above the forest canopy, they produce shorter internodes (Putz, 1990), a possible indication of reduced growth rate caused by increase light, transpiration, and other

environmental factors. During periods of limited rainfall, rattans and other lianas can experience severe water stress. At such times, both stomatal closure and stem water storage would aid survival. In other lianas, water-storing tubers or succulence of stems and leaves are common (Fisher and Ewers, 1991). Rattans lack tuberous roots and their narrow stems have a small proportion of parenchyma that could function in water storage. However, their long stems with a relatively large volume of water in wide vessels represent a significant water reservoir that would become available if cavitation of vessels occurred during periods of extreme water stress (Holbrook, 1995). If cavitation of wide vessels does play a role in water supply during draught periods, then the question of vessel refilling must be addressed. Further studies should also focus on the water capacity of rattan stems compared to nearby non-climbing palms, as well as their relative degrees of stomatal control.

At present, we have no information on production of embolisms in rattan xylem. Yet the low percentage of nonfunctional vascular bundles in old stems suggests either a lack of vessel cavitation or a mechanism for refilling vessels (and tracheids). Other lianas have root pressure that is sufficient to refill air-filled xylem, as in *Vitis* (Sperry et al., 1987), or to decrease xylem tension and thus assist in removal of embolisms (Fisher et al., 1997). In a nonclimbing palm, Sperry (1986) found that embolisms were dissolved when xylem pressure potential approached that of the atmosphere during periods of rain. When stem bases of cultivated species of *Calamus*, *Daemonorops*, and *Desmoncus* (a climbing nonrattan palm) were cut at dawn during rainy periods, no exudation appeared, thus indicating no root pressure (Fisher et al., 1997); however, there was an indication of root pressure in one species of *Calamus* cultivated in a mountainous rainforest. We suggest that future measurements for possible root pressure are needed to better understand water conduction for rattans growing in natural environments.

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