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Vessel Elements in Roots of Young Palms

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Abstract

Perforation plate type, end wall slope, and length to width ratio are described in wide vessel elements from roots of seedlings of 17 species of palms. Vessel elements with two different (i.e., "mixed") perforation plate types or end wall slopes occur in many of the specimens. The data contain correlations between the end wall characters and the length to width ratio of vessel elements. There is little resemblance between the sequence of the species according to Moore's (1973) systematic classification of palms, and the sequence according to the length to width ratio of vessel elements. The wide vessel elements from roots of young palms are usually more variable than those from roots of adult palms of the same species.

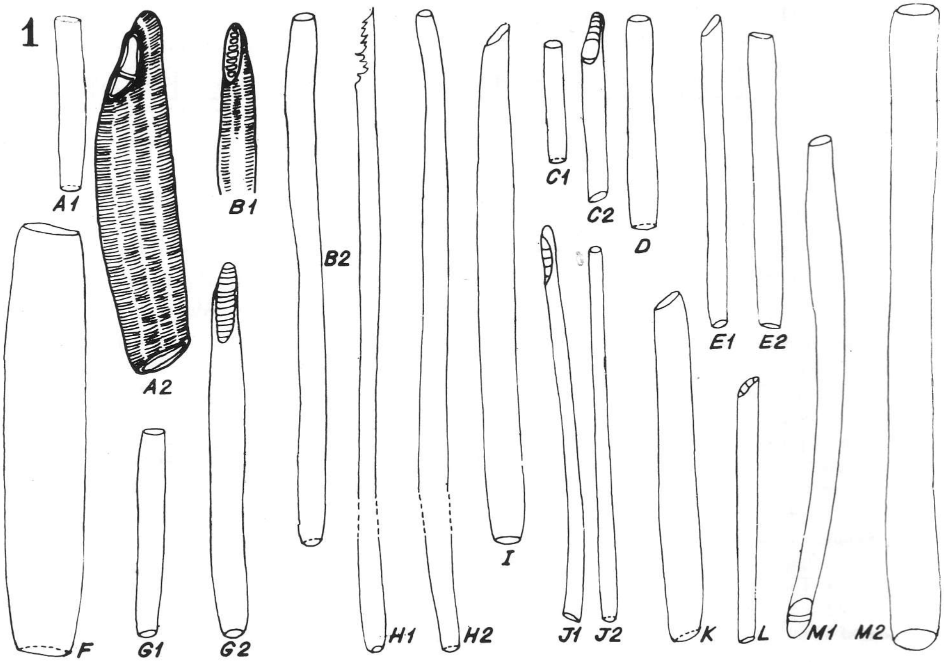
Data have been published on tracheary elements in the organs of adult palms (Bierhorst and Zamora 1965; Cheadle 1942, 1943*a*, 1943*b*; Klotz 1978*a*, 1978*b*, 1978*c*; Parthasarathy and Klotz 1976; Tomlinson 1961; Tomlinson and Zimmermann 1967). In seedling palms, no comparable work appears to have been done so far. The present study describes perforation plates, end wall slopes, lengths, widths, and length-width ratios of vessel elements in roots of seedling palms. The objectives are (1) to compare the data from young palms with those presented by Tomlinson (1961) and Klotz (1977) from adult palms, (2) to determine the degree to which end wall characteristics are correlated with length to width ratios, and (3) to observe whether the arrangement of species according to length to width ratios of vessel members resembles the systematic sequence of taxa in Moore's (1973) classification of palms.

The form of tracheary elements and the correlations among their features have supplied evidence for hypothetical evolutionary pathways (Carlquist 1975; Dickison 1975). Recently, Aldridge (1978) used a method of statistical correlation between features of tracheary elements in studying evolution within the genus *Sonchus*. The present analysis is based on her hypothesis about the evolution of tracheary elements. She used the length to width ratio of vessel elements as a tool to determine the phylogenetic relationship among species. A higher ratio indicates primitiveness while a lower ratio is more advanced (Aldridge 1978). According to Cheadle (1943*a*), primitive vessel elements have long, extremely oblique or very oblique end walls in which the perforation plates have many bars that are closely spaced while advanced vessel elements have slightly oblique to transverse end walls on which the bars are few or absent.

Materials and Methods

Small pieces of mature roots of average diameter were studied in seedlings of 17 species of palms (Table 1). Most of the seedlings were raised at the Crop Garden of the Indian Statistical Institute, Calcutta, from seeds collected from the Indian Botanic Garden, Howrah. The seeds of *Veitchia* and *Phoenix rupicola* were collected in Australia. Seeds were sown at different times according to their availability. The ages of the seedlings ranged from 8 to 30 months.

One piece of a root was sampled for each species. The roots were cut into small pieces and fixed in formalin-acetic acid-alcohol (FAA) for 48 hours or more. They were then boiled in 10% potassium



1. Camera lucida drawings of wide vessel elements of roots. Lateral-wall pits are represented as short, horizontal lines in A_2 and B_1. Magnification is 107 × in A_2 and B_1, 43 × in all the others. A_1, A_2. *Areca catechu.* A_1. Simple perforation plates, transverse end walls. A_2. Mixed perforation plates and end wall slopes. B_1, B_2. *Chrysalidocarpus lutescens.* B_1. Details of scalariform perforation plate. B_2. Simple perforation plates, transverse end walls. C_1, C_2. *Livistona rotundifolia.* C_1. Simple perforation plates, transverse end walls. C_2. Mixed end wall characters. D. *Arenge pinnata.* Simple perforation plates, transverse end walls. E_1, E_2. *Borassus flabellifer.* E_1. Simple perforation plates, end wall slopes mixed. E_2. Simple perforation plates, transverse end walls. F. *Cocos nucifera.* Simple perforation plates, transverse end walls. G_1, G_2. *Areca triandra.* G_1. Simple perforation plates, transverse end walls. G_2. Mixed end wall characters. H_1, H_2. *Veitchia merrillii.* H_1. Mixed end wall characters. H_2. Simple perforation plates, transverse end walls. I. *Phoenix rupicola.* Simple perforation plates, mixed end wall slopes. J_1, J_2. *P. reclinata.* J_1. Mixed end wall characters. J_2. Simple perforation plates, transverse end walls. K. *Salacca zalacca,* mixed end wall slopes, simple perforation plates. L. *Elaeis guineensis,* mixed end wall characters. M_1, M_2. *Hyphaene dichotoma.* M_1. Mixed end wall characters. M_2. Simple perforation plates and transverse end walls.

hydroxide (10 minutes), washed in water, soaked in 25% chromic acid (15 minutes), and washed again. The macerated material was teased apart and mounted on slides in phenol-glycerine. Some specimens fixed in FAA were sectioned transversely with a microtome and stained with safranin and fast-green. Camera lucida drawings and photomicrographs were made.

An ocular micrometer in a compound microscope was used to measure the length and width of 10 intact wide (or sometimes semi-wide) vessel elements in each species (Fig. 3). Slopes of end walls and types of perforation plates were also recorded. The mean and standard error of the measurements were computed. Spearman's rank correlation coefficient was employed to demonstrate the correlation between the end wall characteristics and length to width ratios.

Categories of Perforation Plates and End Wall Slopes

The terminology for perforation plates (except "mixed") is taken from Esau (1958), and the vessel elements are cat-

Table 1. Perforation plate types, end wall slopes, and dimensions of wide metaxylem vessel elements in roots of young palms.[1]

Major groups and species	% of vessel elements with perforation plates			% of vessel elements with end walls				Dimension of vessel elements		
	Both scalariform	Mixed	Both simple	Both oblique	Both slightly oblique	Mixed	Both transverse	Length (mm) Mean ± std. error	Width (mm) Mean ± std. error	Length : width rate Mean ± std. error
Coryphoid										
Livistona rotundifolia (Lam.) Mart. (10)	—	20	80	—	—	30	70	0.62 ± 0.04	0.062 ± 0.006	11.9 ± 2.1
Phoenicoid										
Phoenix reclinata Jacq. (8)	10	20	70	10	10	50	30	1.12 ± 0.07	0.042 ± 0.005	28.5 ± 3.8
P. rupicola Anders. (10)	10	10	80	10	40	—	50	2.05 ± 0.13	0.090 ± 0.004	23.5 ± 2.0
P. sylvestris (L.) Roxb. (16)	—	—	100	—	—	—	100	1.84 ± 0.10	0.091 ± 0.002	20.5 ± 1.1
P. pusilla Gaertn. (16)	—	20	80	10	40	10	40	1.07 ± 0.08	0.079 ± 0.010	14.9 ± 1.7
Borassoid										
Borassus flabellifer L. (8)	—	10	90	20	10	30	40	1.40 ± 0.15	0.064 ± 0.002	22.6 ± 3.0
Hyphaene dichotoma (White) Furtado (15)	10	10	80	10	—	20	70	2.16 ± 0.16	0.104 ± 0.009	23.3 ± 4.0
Lepidocaryoid										
Salacca zalacca (Gaertn.) Yoss (12)	—	20	80	—	—	20	80	1.52 ± 0.11	0.090 ± 0.005	18.8 ± 3.6
Caryotoid										
Arenga pinnata (Wurmb.) Merr. (30)	—	—	100	—	—	—	100	1.02 ± 0.06	0.091 ± 0.009	11.3 ± 0.9
Caryota urens L. (12)	—	—	100	—	—	—	100	2.39 ± 0.24	0.189 ± 0.023	15.0 ± 3.4
Arecoid										
Areca catechu L. (24)	10	10	80	—	10	10	80	0.88 ± 0.10	0.077 ± 0.005	12.3 ± 2.1
A. triandra Roxb. (19)	—	40	60	—	—	40	60	1.02 ± 0.12	0.068 ± 0.004	16.8 ± 3.9
Chrysalidocarpus lutescens H. A. Wendl. (16)	—	10	90	10	—	—	90	1.90 ± 0.16	0.084 ± 0.003	22.9 ± 2.2
Roystonea regia (H.B.K.) Cook. (11)	—	—	100	10	—	—	90	1.18 ± 0.09	0.111 ± 0.004	10.7 ± 0.9
Veitchia merrillii (Becc.) Moore (10)	—	20	80	—	—	40	60	2.15 ± 0.14	0.064 ± 0.003	33.7 ± 2.2
Cocosoid										
Cocos nucifera L. (12)	—	—	100	—	—	—	100	1.86 ± 0.18	0.200 ± 0.017	10.4 ± 1.8
Elaeis guineensis Jacq. (12)[2]	30	40	30	15	40	30	15	1.03 ± 0.07	0.043 ± 0.003	24.7 ± 1.8
Total of species	5	12	17	8	6	10	17	— —	— —	— —

[1] The classification is that of Moore (1973). The age of the plant in months is given in parentheses after the binomial.

[2] Only 7 vessel elements were examined in *Elaeis guineensis*.

egorized as follows: both perforation plates scalariform; "mixed" perforation plates, i.e., one plate simple and the other scalariform or reticulate (Fig. $1A_2$, C_2, G_2, H_1, J_1, L, M_1); both perforation plates simple (Fig. $1A_1$, B_2, C_1, D, etc.). Similarly, Cheadle's (1943*a*) classification of end wall slopes is employed, and the vessel elements are categorized as follows: both end walls oblique; both end walls slightly oblique; "mixed" end wall slope, i.e., one end wall transverse, and the other either oblique or slightly oblique (Fig. $1A_2$, C_2, E_1, G_2, H_1, I, L, etc.); both end walls transverse (Fig. $1A_1$, B_2, C_1, D, E_2, F, G_1, etc.).

Observations

Simple perforation plates and transverse slopes are the most frequent end wall characters in the vessel elements examined in this survey. Mixed perforation plates and mixed end wall slopes are the next most frequent. Table 1 shows that 17 species have vessel elements with two simple perforation plates; 12 species, mixed perforation plates; and five species, two scalariform perforation plates. *Elaeis* shows the highest percentage (30%) of scalariform perforation plates. The highest percentages of vessel elements with mixed perforation plates occur in *Elaeis* (40%) and *Areca triandra* (40%). The percentage of vessel elements with two simple perforation plates is highest in all of the species except *Elaeis.*

Vessel elements with both end walls oblique occur in eight species, both slightly oblique in six species, and both transverse in all the species. Vessel elements with mixed slopes occur in 10 species. The highest frequencies of vessel elements with both end walls slightly oblique occur in *Elaeis, Phoenix rupicola* and *P. pusilla. Areca triandra* (40%), *Phoenix reclinata* (50%), and *Veitchia* (40%) show the highest percentages of vessel elements with mixed slopes. The percentage of vessel elements with two transverse end walls is highest in all of the species except *Elaeis* and *Phoenix reclinata.* The highest numbers of vessel elements with both perforation plates simple and both end walls transverse occur in *Arenga, Caryota, Cocos, Phoenix sylvestris* and *Roystonea.*

The dimensions and length to width ratios of the vessel elements are also given in Table 1. The longest is found in *Caryota,* the shortest in *Livistona.* On the other hand, the widest is in *Cocos* and the narrowest are in *Elaeis* and *Phoenix reclinata.* The highest mean ratio occurs in *Veitchia* and the lowest in *Cocos.*

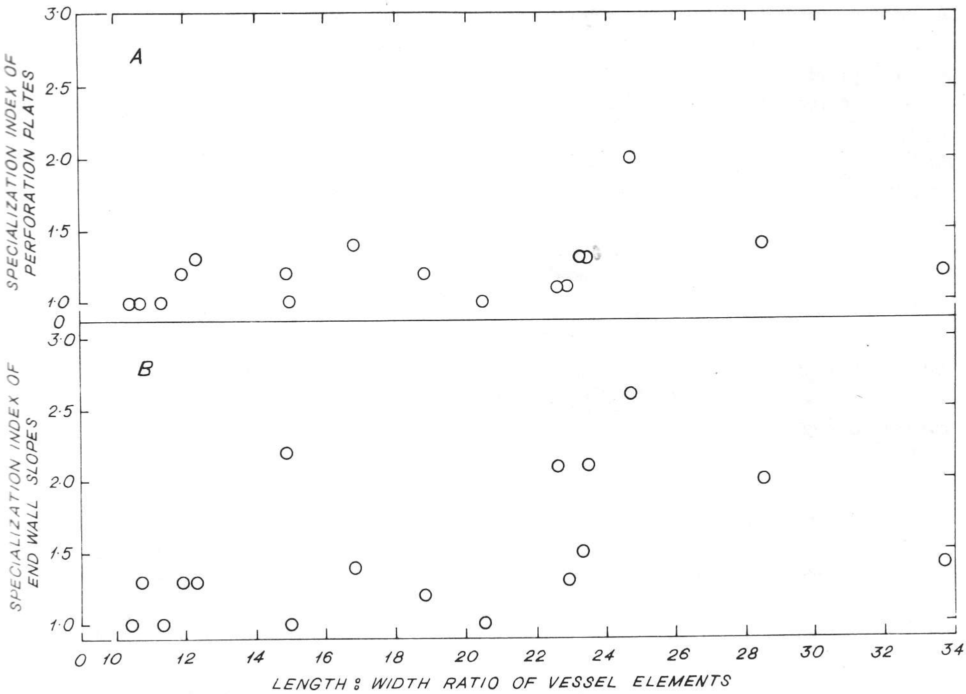
Spearman's coefficient of rank correlation (Steel and Torrie 1960) was employed to demonstrate correlations between the length to width ratio and the end wall characters. The data for these calculations are displayed graphically in Figure 2. The 17 species were ranked in increasing order of the average length to width ratio, and in a specialization index (adapted from Klotz 1978) based on end wall slopes (Fig. 2B):

> Specialization index of end wall slopes × 100 = 1 (% of both end walls transverse) + 2 (% of mixed end walls) + 3 (% of both end walls slightly oblique) + 4 (% of both end walls oblique).

The Spearman's coefficient of rank correlation between these two features is 0.650, which is significant at the 1% level. Similarly, the following specialization index was assigned for perforation plates (Fig. 2A):

> Specialization index of perforation plates × 100 = 1 (% of both plates simple) + 2 (% of mixed plates) + 3 (% of both plates scalariform).

The Spearman's coefficient of rank correlation (with length to width ratio) is 0.525, which is significant at the 5% level. In summary, the species with the lower length to width ratios tend to possess the



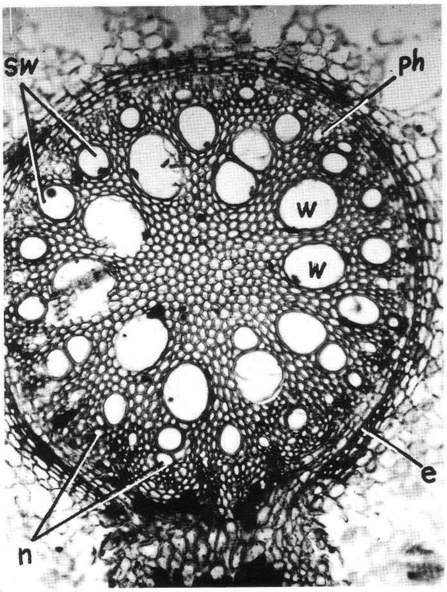
2. Correlation of length to width ratios with end wall features. A. Specialization indices of perforation plates plotted against length to width ratios. B. Specialization indices of end wall slopes plotted against length to width ratios.

higher percentages of simple perforation plates and transverse end walls. In contrast, the higher length to width ratios tend to occur in the species with the higher percentages of mixed end wall characters. A few species are exceptions to these trends (e.g., *Livistona*, *Phoenix sylvestris*, and *P. pusilla*).

Table 2 shows the differences in wide vessel element dimensions and end wall characteristics between young and adult palms. The young plants possess various types of perforation plates, the simple type predominating, whereas adult plants possess only the simple type. Again, various types of end wall slopes occur in young plants, but only transverse or sometimes slightly oblique occur in adults. The range of lengths of vessel elements is generally larger in the young plants than in the adults. The upper limit of length of vessel elements in young plants exceeds that in adult plants except in *Elaeis* and *Phoenix*. In contrast, the widths of the vessel elements are mostly greater in the adult plants.

Discussion

The data in the present study differ from the comparable observations by Tomlinson (1961) and Klotz (1977) in adult palms of the same species. The comparisons between young and adult palms reveal a general trend of shortening and widening of the wide vessel elements in the roots. Also, the end wall characters of these vessel elements are more variable in the young palms than in the adult palms. Thus, the pattern of differentiation of these cells apparently undergoes a transformation during the development of an individ-



3. Transverse section of root of *Phoenix pusilla.* ×100. e, endodermis; n, narrow tracheary elements; ph, phloem; sw, semi-wide vessels of metaxylem; w, wide vessels of metaxylem.

ual palm from the seedling stage to the adult. In the above features, the wide vessel elements from seedling roots resemble the narrow, early-maturing vessel elements from roots of adult palms (described by Cheadle 1942; Klotz 1977, 1978*a*; Parthasarathy and Klotz 1976).

Tomlinson (1961), Cheadle (1942, 1943*a*, 1973*b*) and Klotz (1978*a*) did not mention any mixed end wall characters in vessel elements from the species of adult palms that they studied. Apparently, such vessel elements either are absent in adult palms or have not been reported by the previous authors. However, Tomlinson and Zimmermann (1976) depicted mixed end wall characters in vessel elements from the lower part of the stem of *Sabal palmetto*; and Klotz (pers. comm.) observed but did not describe such vessel elements in the vegetative organs of various palms.

Klotz (1977, 1978*a*) observed reticulate and/or scalariform-reticulate perforation plates in wide vessel elements from

Table 2. Comparison of wide vessel elements from roots of young and adult palms.

Species	Author's data (young plants)		Tomlinson's (1961) data (adult plants)		Klotz's (1977) data (adult plants)	
	Dimensions (µm)	End wall*	Dimensions (µm)	End wall*	Dimensions (µm)	End wall*
Phoenix reclinata	900–1,500 × 30–60	sc, si/o, s, t	—	—	1,000–1,900 × 140–260	si/t
Salacca zalacca (*S. edulis*)	1,000–2,200 × 40–100	sc, si/s, t	1,000–1,400 × 180–260	si/t	—	—
Areca catechu	600–1,600 × 60–100	sc, si/s, t	840–1,210 × 115–190	si/t	—	—
Chrysalidocarpus lutescens	1,400–2,800 × 60–90	sc, si/o, t	1,400–1,800 × 95–210	si/t	—	—
Cocos nucifera	900–3,100 × 130–270	si/t	1,740–2,740 × 200–315	si/t	1,100–2,500 × 200–230	si/s, t
Elaeis guineensis	700–1,300 × 30–50	sc, si/o, s, t	1,210–1,500 × 270–340	si/t	—	—

* End wall characters: sc = scalariform perforation plates; si = simple perforation plates; o = oblique end walls; s = slightly oblique end walls; t = transverse end wall slopes.

roots of some species of adult palms. Such perforation plates were not observed in the present study.

Vessel elements from roots of young palms exhibit positive correlations between the length to width ratio of the cell and the degree of primitiveness of the perforation plates. This finding supports the conclusions of Aldridge (1978) and Cheadle (1943*a*) that were summarized in the introduction of this paper.

The sequence of mean length to width ratios in Table 1 can be compared with the sequence of species according to Moore's (1973) classification of palms. The lowest ratios occur in species of cocosoid, arecoid, and lepidocaryoid groups, while the highest ratios occur in species of arecoid and coryphoid groups. There is little resemblance between Moore's (1973) systematic sequence of the evolutionary lines and major groups and the sequence of species based on length to width ratio of vessel elements. For example, *Livistona* and *Phoenix pusilla* show advanced ratios although they belong to primitive coryphoid and phoenicoid groups, respectively. Similarly, *Veitchia* and *Chrysalidocarpus* of the advanced arecoid group and *Elaeis* of the advanced cocosoid group show a high ratio, which is a primitive character.

There is considerable variation among the species of individual major groups in characters of the vessel elements. For example, within the cocosoid major group, *Cocos nucifera* shows relatively advanced characters and *Elaeis guineensis*, more primitive characters. Similarly, within the arecoid major group, more advanced xylem occurs in *Roystonea regia* and more primitive in *Veitchia merrillii.* In phoenicoid major group, more advanced xylem occurs in *Phoenix pusilla* and more primitive in *P. reclinata*. Such differences among the members of individual major groups may be explained by Klotz's (1978*a*) conclusion that "evolution in the xylem appears to have progressed independently in the various taxonomic groups of palms."

Acknowledgments

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I thank Mr. S. K. De, Artist and Dr. A. Dasgupta, Senior Research Fellow, Indian Statistical Institue, for drawings and statistical calculations, respectively.

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PALM LITERATURE

A BIBLIOGRAPHY OF GRADUATE THESES ON PALMS, PART II

An initial compilation of 101 titles appeared in a previous issue of this journal (Vol. 27(2), 1983, pp. 85–88). The results of continued research into this primary source of information on palms, following the same criteria, now justifies a second installment.

This listing consists of 57 additional doctoral and master's theses. More than one-half of the total were completed in three countries: United States (14), The Philippines (12) and France (10). As before, the major economic palms dominate the subject matter: coconut (23), oil palm (11) and date palm (8). Although most of the studies were completed within the past 15 years, a few older titles were found, such as the dissertation by Gatin dated 1906. Once again I must acknowledge the assistance of numerous individuals who provided me with thesis titles.

Doctoral Theses

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