Essays On The Morphology Of Palms

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VI. THE PALM STEM

In woody dicotyledons, represented by our hardwood trees, increase in thickness of the stem is a result of cell division in a cylinder of actively dividing or meristematic cells, the cambium, situated between the hard wood, or xylem, of the stem and the softer part of the bark, or phloem. This cambium originates early in young seedlings and is continually developed in all new shoots. Since it also remains active throughout the life of the plant, the slender sapling is able to develop into a tree with a wide massive bole. Consequently, although the crown of the tree continually increases in size through branching, it is always supported effectively by an ever-widening trunk (Fig. 58A-C). Monocotyledons, on the other hand, with few exceptions have no cambium and so are not capable of gradual development into trees. Palms, however, are rather exceptionable amongst monocotyledons in that woody trunks, often over 100 feet high are typically developed. Even so, palms have no permanently active thickening meristem. How then, does the palm develop its erect solid trunk? Before this question can be answered, we must understand the construction of the mature palm stem. A brief outline of the anatomy of the palm stem will therefore serve as an introduction to the mechanism of its growth.

The Anatomy of the Palm Stem

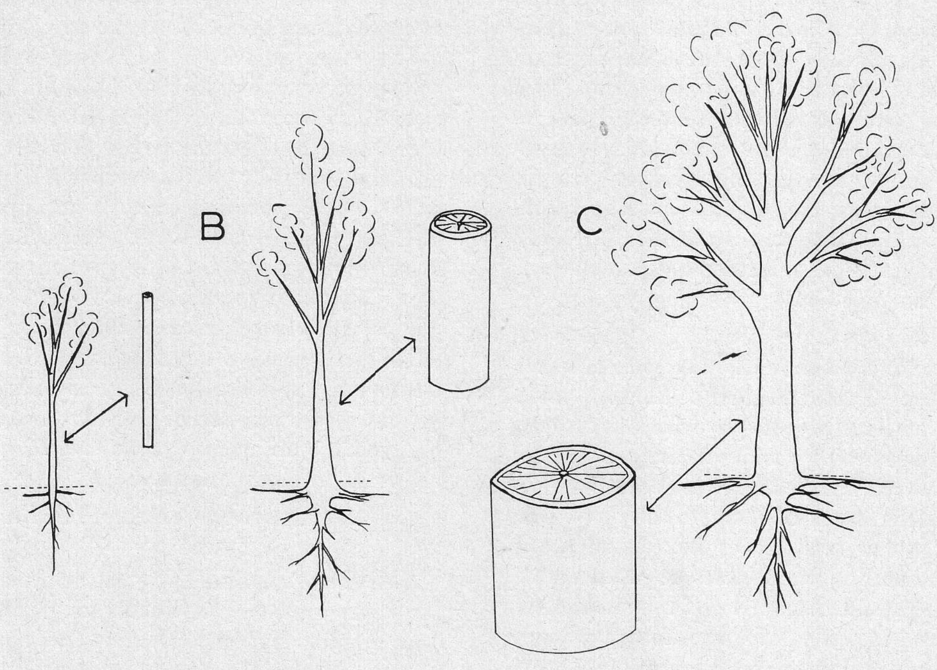
Botanists have been interested in the internal structure of palm stems for many years and although a generalized picture of their construction is now available, a surprising amount of fundamental detail is still obscure. The reason for this dearth of information is largely technological and not difficult to understand. The palm stem is a massive organ, not homogeneous, and, to the anatomist, very complex. The mature parts are often hard and brittle, so that it is difficult to cut sections of them thin enough to be studied under the microscope. One small area of the palm stem does not give a true picture of the whole. The wood of a dicotyledonous tree is, on the other hand, usually easy to section and is comparatively homogeneous so that a good knowledge of the anatomy of the whole stem can be gained by studying a small block of wood. One other great difficulty is that no botanist working in a temperate climate has access to unlimited palm material. Palms only appear in abundance in the tropics and even in regions to which palms are native the anatomist can rarely collect freely because his methods are essentially destructive and palms are large and valuable plants.

It is therefore not surprising to learn that most of our information about the anatomy of the palm stem is based on observations made over 100 years ago. Although various peculiarities of the palm stem, more particularly the ways in which it differs from the woody trunk of a dicotyledon, had been established by the earliest botanists and were even known to Greek writers of classical times, the most fundamental studies were made by Hugo von Mohl. His account was first published, in Latin, in Martius's monumental work *Historia Naturalis Palmarum* (1831). It is characteristic of the quality of this work that the anatomical illustrations it contains have never been bettered. Translations of this account exist in German and English, but without the illustrations.

A typical palm stem (Fig. 59A), exemplified by that of the coconut (*Cocos nucifera*), unlike the homogeneous woody cylinder of a hardwood tree (Fig. 59B), contains a system of many hundreds of separate conducting strands, or vascular bundles scattered in softer ground tissue. Each vascular bundle consists of a rigid fibrous sheath, wholly or partly enclosing the conducting tissues proper. These tissues consist of a strand of phloem elements, which conduct organic food material, and xylem elements, which largely conduct water against gravity. The fibrous part of the bundle is always most conspicuous adjacent to the phloem, it is commonly absent adjacent to the xylem. The bundles towards the periphery of the stem are very congested and since they possess very well developed fibrous sheaths they together form a much denser tissue than the softer central portions. In fact, most palm stems have such a soft central region that they split and collapse on drying and so have little use as constructional timber. In the living palm, however, such a distribution of supporting tissues permits the maximum amount of strength and stability with the most economic use of strengthening tissue. In fact the palm is constructed according to the best principles of engineering.

The palm stem, as seen in transverse section, is divided into two very unequal regions (Fig. 59B). The central region, described above, is known as the central cylinder. This is surrounded by a very narrow cortex which includes only a few narrow vascular bundles and frequent strands composed wholly of fibres. Sometimes the ground tissue of the central cylinder also includes scattered narrow fibrous strands.

In a longitudinally split palm stem it can be seen that individual vascular bundles are very long, but their length is not indefinite. Nor are the bundles distributed entirely at random as seems possible from a superficial examination of a transversely cut face. Von Mohl was able to dissect out some of the individual bundles from partially rotted pieces of palm stem. He found that each vascular strand eventually extends into a leaf. Such vascular bundles are known as leaf traces and all vascular bundles in a palm stem appear to be leaf traces. In an old palm stem, of course, only the more distal bundles extend into an attached leaf. The leaves with which lower traces are connected have fallen so that the lower vascular bundles terminate blindly at a leaf scar. There are, however, frequent fusions between bundles in various parts of the stem which maintain vascular continuity between the leafy crown and the base of the stem. If a single leaf trace is followed downwards from a leaf into the stem (Fig. 60B), it passes through the dense peripheral tissue into the centre of the stem at a fairly sharp angle. On reaching the centre of the stem, the trace turns downwards. Its subsequent course is not exactly vertical because, as it passes through many internodes on its downwards course, it gradually re-approaches the periphery of the stem and re-enters the region of congested bundles. Here it may either end blindly or, more often, it fuses with adjacent vascular bundles. In palms with very short internodes in which the leaves are crowded together on the stem, recently entered leaf traces are very conspicuous because they enter the stem almost horizontally. Even in palms with long internodes, recently entered traces can usually be recognized in the polished longitudinal face of a sawn palm stem since they run at a distinct angle to the remaining, more or less vertical bundles. The congestion of the vascular bundles at the periphery of the central cylinder is thus seen to be a result of the overall course of each bundle, each bundle passing in and out of the central region over a short dis-



58. The palm and the hardwood tree compared. A, B, and C. Diagrammatic representation of a dicotyledonous tree at three successive ages. The insets are representations of lengths of the main trunk at the same height, from individuals of the three different ages. D, E, F. Diagrammatic representation of a single-stemmed palm at three successive ages. Inset a length of the aerial trunk, only developed at the oldest stage.

tance, but remaining in the peripheral region for a greater distance. However, the arrangement is probably much more complex than the simple scheme outlined above. Each leaf contributes many hundreds of traces to the stem and all bundles do not behave alike. There is a tendency for them to corkscrew irregularly and there may be fusion between different bundles in any part of their course, as well as at their lowest extremities. Most differences are found between leaf traces from median and lateral parts of a single leaf.

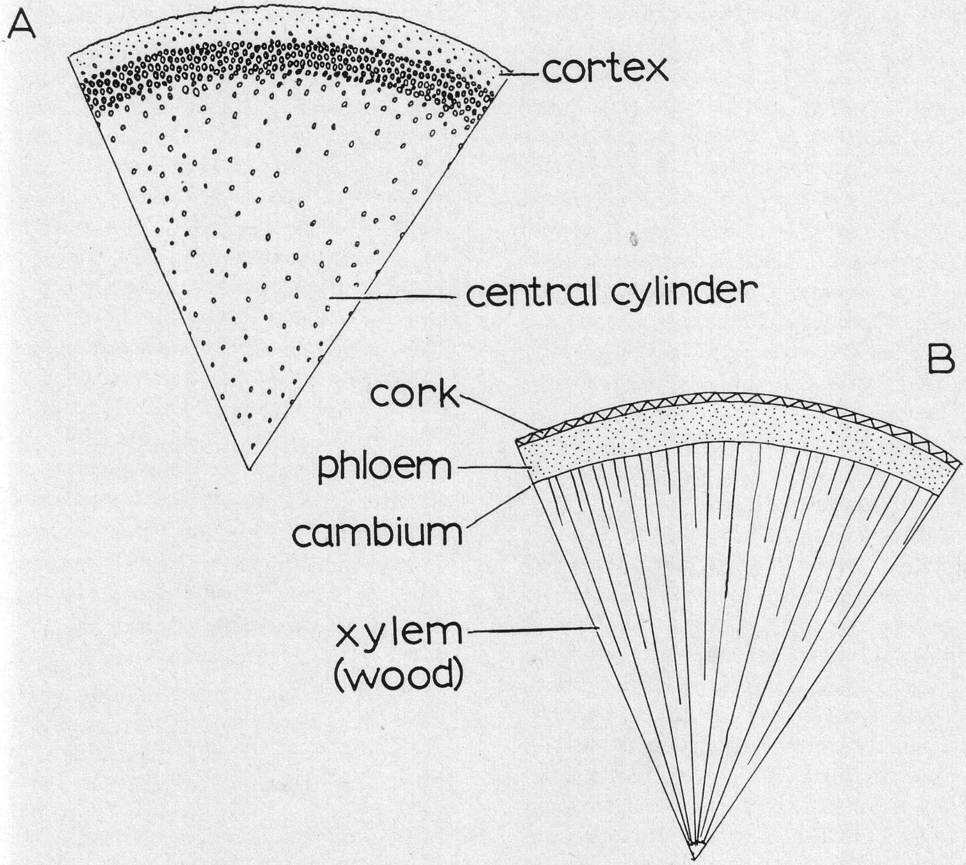
The structure of a single trace is not the same at all levels. Consequently, microscopic examination of the transversely cut face of a single palm stem reveals a bewildering variety in the structure of vascular bundles. This is because the cut will have passed through the distal part of some leaf traces but through the middle and basal parts of other traces. Von Mohl demonstrated that in the upper part of each trace there are many xylem elements and the fibrous sheath around the phloem is not well developed. Towards the base of the same trace both xylem and phloem are much reduced and the bundle is made up mainly of fibres and commonly ends blindly as a purely fibrous strand. However, over a large part of its middle course the bundle is fairly uniform; it commonly contains either one or two wide vessels and since this part is most commonly observed in a transverse section which includes the centre of the stem, its appearance is of some diagnostic value.

One further conspicuous difference between the palm stem and the trunk of a woody dicotyledon is that the latter develops a protective bark, arising from a specialized layer of meristematic cells, the cork cambium. Palms do not develop so specialized a protective tissue, one reason being that the surface of the trunk does not undergo continual expansion. In many instances the persistent leaf bases may afford some protection. Otherwise in many palms the surface layers of cells become thick-walled and sclerotic owing to the deposition of hard cell-wall substances known as lignin. These thick-walled cells gradually erode from exposed surfaces, but they are replaced by gradual modification of deeper-seated cells. In some palms, cell division does take place in the outer cortex, producing protective cork cells, but a specialized, single-layered cork meristem, like that of a dicotyledonous tree, can never be recognized. Aerating organs, comparable to the lenticels of dicotyledons, only arise passively as the result of irregular vertical splits, presumably as a result of slight internal expansion.

The Anatomy of Specialized Palm Stems

The above remarks apply to the aerial stems of single-stemmed or tufted palms (see Tomlinson, 1961a). Where the palm has a stem which differs markedly from this type, as in scandent or in creeping palms, the anatomy is considerably modified, although the fundamental plan of construction remains the same. Climbing palms, as exemplified by the rattans of the Eastern tropics, have narrow stems with exceedingly long internodes. The surface remains smooth and often becomes heavily silicified. The cortex is very narrow. The texture of the stem is relatively homogeneous because the vascular bundles are uniformly crowded and mechanical fibrous tissues are not strongly developed. The conducting tissues are well developed and the stem as a whole is very porous because the xylem vessels are very wide. Such stems are remarkable, more for their elasticity than their rigidity.

Palms with short, mostly subterranean or creeping stems have very congested



59. The stem of the tree and the palm. A. Diagrammatic cross-section of a sector of the stem in a palm. B. Diagrammatic cross-section of a sector of the stem in a tree.

internodes. The cortex is wide and often not well demarcated from the central cylinder, since the vascular bundles are uniformly scattered and not specially congested at the periphery of the central cylinder. The course of the vascular bundles is very irregular. Mechanical tissues are usually reduced and as a consequence, the texture of the stem is rather soft.

On the basis of these anatomical notes it should now be possible to understand as much as is known about the development of this peculiar axis.

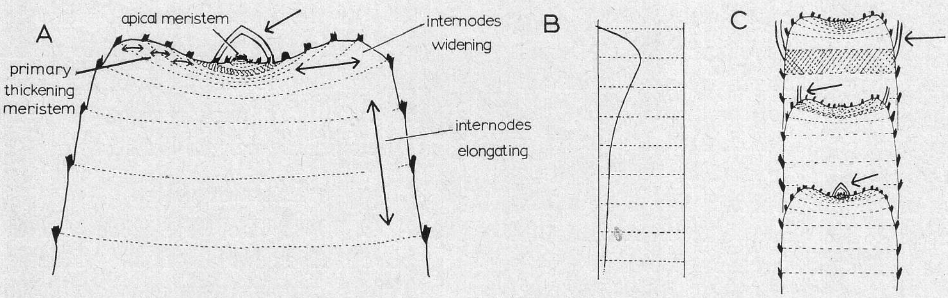
The Growth of the Palm Stem

Botanists familiar with the development of the palm from the seedling stage know that its stem first grows considerably in girth and develops a broad woody foundation before the leafy crown is visibly raised above the soil surface and the aerial stem is developed (Fig. 58 D-F) (see Tomlinson, 1960). In this predominance of thickening growth over extensive growth, the palm contrasts remarkably with dicotyledons. In the dicotyledons, primary (elongation) growth always precedes secondary (thickening) growth so that tall but slender saplings are characteristic of early stages in the life of hardwood trees (Fig. 58A). Thus we measure the age of a dicotyledonous tree by the thickness of its bole, but the age of a palm is indicated only by its height. Even then the tallest palm is not necessarily the oldest because different species grow at different rates.

The reason for the fundamental difference between a palm and a dicotyledonous tree is that the former has no permanently active cambium by which its stem thickens and can become consolidated. Consequently, all the tissues of the palm stem are developed within the terminal bud. Each internode therefore must grow to something approaching its maximum thickness before it can grow in length. One most obvious result of this failure of the internodes to elongate as soon as they appear is that the leaves are congested in a terminal crown. The peculiarities of stem development in palms can be most clearly revealed if successively younger leaves, of decreasingly smaller size, are carefully dissected away from the terminal rosette. Then it is found that the unexpanded leaves are not arranged on the sides of a long tapering cone, as in a dicotyledon, but that they are situated on the surface of a shallow, basin-like depression at the apex of the stem (Fig. 60A).

The microscopic apical meristem is situated at the centre of the depression and on this minute papilla, the leaf primordia originate. It is evident that as each leaf primordium grows in size, its circular insertion widens, but not as a result of activity of the apical meristem proper, this being solely the leaf-initiating meristem, but by the activity of a somewhat hemispherical thickening meristem which forms the "bowl." Only when the leaf bases have been carried to the rim of the basin do their associated internodes extend and bring about increase in length of the stem (Fig. 60C). Because this bowl-shaped meristem functions in widening the internodes before they are elongated, it is called a primary thickening meristem. Its behaviour has been described most recently by Helm (1936) and Ball (1941). This part of the palm, together with the younger leaves is often edible and highly nutritious. It is protected by the woody leaf bases of the outermost leaves at the crown and often also by additional spines of various kinds. This is necessary because the palm bud is attractive to some of the larger forest mammals as the owner of a large oil palm plantation is likely to discover.

Only one attempt has been made to relate the developmental changes taking place at the apex of the palm stem with the structural arrangements seen in the mature stem. This was done by an American geologist, J. C. Branner (1883) as a result of observations on many Brazilian palms studied at first hand. Unfortunately his analyses were never published in detail and, although his conclusions seem very reasonable, they have never found their way into botanical textbooks. Branner showed, with considerable conviction, that the course of each vascular bundle in the stem was the result of the peculiar configuration of tissues at the apex of the stem. Since we have already seen that the distribution of vascular bundles in the stem accounts for its overall construction, Branner offered an explanation of the peculiarities of the palm stem based on simple mechanical laws. It is not possible to interpret this complex analysis in this present brief article, although I have attempted to do this elsewhere in summarizing the whole of our knowledge of the palm stem (Tomlinson, 1961b). However, anybody wishing to



60. Development of the palm stem. A. Diagrammatic vertical section of the bud of a palm. B. Course of a single leaf trace in the stem represented diagrammatically. C. Increase in height of the palm stem, represented by a diagrammatic vertical section of the bud at 3 successive ages. (Nodes are represented by dotted lines. Only the insertions of leaf bases are shown, in solid black.)

In A and C a single leaf is shown (see single-headed arrow), its outline not blacked out. The development of its associated internode, which is cross-hatched, is represented by the three successive drawings of C. Diagram A may be regarded as an enlargement of the lowest bud of C.

understand the nature of the palm stem should be familiar with Branner's ideas.

Secondary Thickening in the Palm Stem

The above account indicates that the tissues of the palm stem originate entirely in primary meristems and that no permanent, long-lived secondary meristem exists which can add tissues to the mature stem, as does the cambium in all woody dicotyledons. Nevertheless, close examination of growing palms suggests that secondary thickening of their stems does occur. This is most obvious in *Roystonea* in which the trunk tapers considerably from below upwards in young plants, but is uniformly cylindrical in the tall stems of old plants. Careful measurements by a number of workers during the last century and subsequently has confirmed this superficial observation and shown that over a period of years the stem in many palms, as well as in *Roystonea,* does increase appreciably in girth. The most extensive observations are those of Schoute (1912) who, in addition to summarizing early observations, was able to work on the large living collection of palms in the botanic gardens at Bogor (then Buitenzorg). Although none of the palms he examined had a secondary meristem, secondary growth in girth could be measured in many of them. This was a result largely of expansion and division of the ground tissue cells, together with expansion of the fibres which form the vascular bundle sheaths. Because this expansion is not restricted to any one region of the palm stem, it can be called diffuse secondary growth. In most palms this secondary expansion is restricted to the terminal region of the stem, still enclosed by leaf bases. In other palms, of which *Roystonea* is perhaps the extreme example, expansion of the ground tissue continues well below the leafy crown and it may be detected even at the base of quite old palms. The most noticeable result of this process is that the ground tissue cells become lobed or stellate and wide intercellular spaces are produced. As a result the central tissues are very soft and spongy. To accommodate the expansion of the central regions, tangential expansion of the cortical cells is very marked. In the same way development of superficial protective tissues may be stimulated by expansion of the surface.

Ventricose Palm Stems

Palm stems frequently bear distinct ventricose swellings. These are most conspicuous in the so-called "belly" or "bottle" palms which include species of *Acrocomia, Colpothrinax* and *Iriartea,* in which the swelling may have a diameter as much as two to three times that of the non-swollen stem. The tallest individuals of the West African *Borassus aethiopum* are very distinctive because they may bear two or even three successive dilations. No adequate explanation for the origin of these swellings has been made, although it has been suggested that they are regions in which food and water reserves may be stored. From my own observations on *Borassus* in West Africa, it seems that they are not localized areas of diffuse secondary growth but rather that the whole stem apex is enlarged during their production. This suggests that they result from enhanced vegetative vigour of the primary thickening meristem.

The reverse of this situation is known to occur. Harshberger (1905) has recorded in *Sabal* that reduction of vegetative vigour in unfavourable seasons causes localized constrictions of the aerial stem, a phenomenon which produces "hour-glass" stems. That decrease in overall stem diameter is the result of the onset of reproductive activity is known for *Pseudophoenix vinifera,* in which the stem has the shape of an attenuated wine-bottle, the long "neck" being developed when the palm starts to flower (Read, 1961).

It is hoped that these notes on the palm stem will be understood by palm-growers and help to eliminate some of the misconception which exists over this subject. I have summarized all the available literature elsewhere (Tomlinson, 1961) and in doing so have been convinced of the need for much more detailed work. Our comprehension of the structure and development of the palm stem is still so sketchy that its study can be said scarcely to have begun.

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