

THE QUESTION OF DIFFUSE SECONDARY GROWTH OF PALM TREES*

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ABSTRACT. ^{14}C activity measurements were used to investigate the growth pattern of the stem of a palm tree (*Cocos nucifera*) which does not form annual rings. The results reveal that there was no diffuse secondary growth (thickening of the stem) over the entire mature stem during the last 25 years of growth, with the exception of a restricted zone in the center at medium height.

INTRODUCTION

Knowledge concerning the anatomy and physiology of adult palm trees is still limited, and issues remain in dispute. One of these issues is the occurrence of so-called diffuse secondary growth, the existence of which is favored by some botanists (Tomlinson, 1961) and opposed by others (Pigott, 1964; Child, 1964; Tomlinson, pers commun). Comparing palms with other trees of the gymnosperm group or the dicotyledonous group, a fundamental difference is evident. Palms are thick at an early age and grow cylindrically in a vertical manner, whereas other (non-monocotyledonous) trees thicken with age, forming new tissue in the form of tree rings. This is why the former are thought to lack a secondary growth. However, it is questionable whether the thickening growth in the former ceases totally or continues in a manner that may be designated as "diffuse secondary growth." In this work, ^{14}C measurements made on a coconut palm that grew in Brazil were used to study the possibility of this secondary, thickening growth.

BOTANICAL DISCUSSION

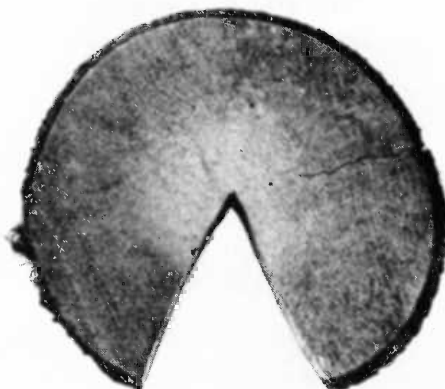
The following is a survey of the specialized literature on palm anatomy and growth (Tomlinson, 1961; Tomlinson and Zimmermann, 1967). Palms, which are monocotyledons, are easily distinguished from most other woody plants by their typical leafy crowns, their unbranched stems, and leaf scars on the stem. The wood is also very different from that of gymnospermous or dicotyledonous trees, as can be seen from a transverse section of the stem (pl 1A): vascular bundles are dispersed all over the stem and are embedded in a more or less uniform parenchyma. Usually, the wood

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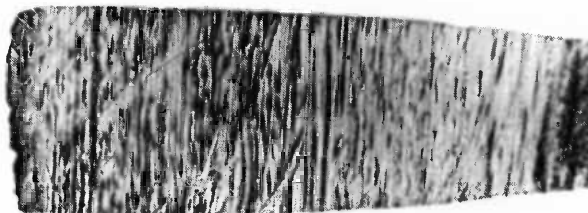
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PLATE 1A



Transverse section of stem at 3.5m height above ground

PLATE 1B



Longitudinal section of stem at 5.5m height above ground. Note the dark, congested bundles in the cortical zone and the appearance of some inclined bundles passing to the surface of the stem.

is soft and succulent in the center, containing widely scattered vascular bundles, whereas the peripheral zone is much denser with congested bundles (pl 1B). This explains the enormous mechanical strength of palm stems. Palm wood of the cortical zone is one of the hardest tissues known in the plant kingdom. In the material studied here, bundles were dense in the cortical zone within the lower part of the stem and less dense elsewhere; no literature was found that accounts for this observation. The longitudinal course of single vascular bundles is more difficult to examine. Single leaf traces were followed through the stem (fig 1) and revealed:

- 1) Leaf traces that enter the stem at the leaf base pass across the cortex more or less horizontally towards the center of the stem.
- 2) The vascular bundles do not remain in the center, but rather pass gradually to the periphery.
- 3) The variability in the structure of vascular bundles seen at a single level is due to the systematic variation along the course of one individual leaf trace.
- 4) At their lower ends, the bundles probably end blindly.
- 5) The continuity of phloem and xylem is maintained by anastomosis, that is, by fusion with lower bundles.

6) The number of vascular bundles is about the same at any given height of the stem.

7) New vascular bundles do not arise in the center of a mature stem.

8) Old vascular bundles are not compressed at the stem periphery by new bundles growing in the center.

The anatomy of vascular bundles may be generally understood by examining their development near the apical meristem. The primary thickening near the apex accounts for the wide stem, with no secondary growth as in gymnospermous and dicotyledonous trees. However, some factors suggest a diffuse secondary growth. If expansion occurs, it is not due to any increase in the total number of vascular bundles, but it may be explained by enlargement of the fibrous bundle-sheaths and by expansion of ground tissue, with a possible longitudinal division of the expanding cells. In *Caryota* and in *Roystonea* (*Oreodoxa*) where a pronounced expansion was reported, the late separation of cell walls results in a lacunous, spongy ground tissue. Therefore, in one group of palms, the primary thickening growth may cease early, resulting in a cylindrical stem, and in another group, the thickening growth may be more continuous, producing a more conical stem. Some tissues, *ie*, the cortical fibrous bundles, the conducting tissues, and the bundle sheaths close to the phloem, do not contribute to diffuse secondary growth, but rather maintain their early-reached size.

Experimental methods to investigate the hypothesized diffuse secondary growth include the following:

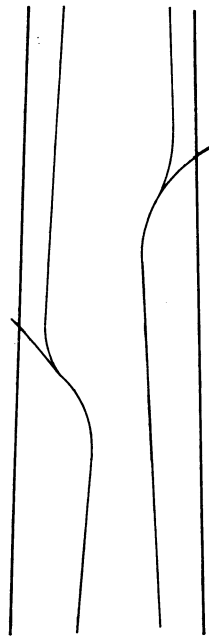


Fig 1. Course of single leaf traces in a palm stem

- 1) Direct measurements of the diameter of a single stem at a given height over a long period of time.
- 2) Measurements of the diameter of a single stem at different heights.
- 3) Comparison of cell dimensions of a single stem at different heights.
- 4) Comparison of the diameters of young and old palms at constant heights.
- 5) Comparison of cell dimensions of young and old palms at constant heights.
- 6) Measurements of the ^{14}C activity at different heights. (Parts of the stem that contain the natural pre-bomb ^{14}C levels have not incorporated the more recent nuclear bomb-produced ^{14}C .)

Methods 2 and 4 are not very reliable because of systematic errors, but they are useful in obtaining a rough idea about diffuse secondary growth. For example, an ideally cylindrical growth is almost proof of the absence of secondary growth; unfortunately, the opposite does not hold true. Methods 3 and 5, although somewhat more reliable, are not totally faultless either. The problem with method 1 is obvious. Method 6 is used in this study.

RADIOCARBON ANALYSIS

^{14}C levels are presented here as $\Delta^{14}\text{C}$, the deviation in per mil (parts per thousand) of sample activity from the activity of the accepted 95% NBS oxalic acid standard. Results are isotopically normalized to a $\delta^{13}\text{C}$ of -25‰ (PDB).

From 1860 (approximately when the palm used in this study started growing) to 1910, the natural tropospheric $\Delta^{14}\text{C}$ (*uncorrected* for radioactive decay to AD 1950) was $-12 \pm 3\text{‰}$ (Stuiver, 1982). Because of man's addition to the atmosphere of ^{14}C -free CO_2 from the combustion of fossil fuels, $\Delta^{14}\text{C}$ decreased from that value to $-25 \pm 5\text{‰}$ during the period from 1910 to 1950. More recently, a drastic increase in ^{14}C levels took place due to the atmospheric nuclear weapons tests. Since 1953, atmospheric ^{14}C levels have been substantially higher than natural levels because of this input of bomb-produced ^{14}C . An excess of 900% above the natural level was reached in the troposphere at mid-latitudes of the northern hemisphere in 1963, and an excess of 650% was reached in the troposphere at mid-latitudes of the southern hemisphere in 1965 (Nydal, Lövseth, and Gulliksen, 1979). This artificial ^{14}C opened up the possibility of testing if carbon-containing material forms a closed system or not: If the material maintains the natural ^{14}C level, then there was no incorporation of new CO_2 . The actual conditions are unique in the earth's history and probably will never be repeated in such an ideal manner.

The specimen investigated was a coconut palm (*Cocos nucifera*) found near Aracaju, Sergipe state, NE Brazil (ca $11^\circ 00' \text{S}$, $37^\circ 01' \text{W}$). The palm had grown at this near-sea-level location for 110 to 120 years. The stem was not cylindrical (fig 2), suggesting a marked diffuse secondary growth. Slices were cut from the stem at 1m intervals up the tree, but only selected sections were analyzed in this study. From each slice to be analyzed, samples were taken from the center (0 to 3 or 4cm from the center) and

from the periphery (ca 0.5 to 2cm from the bark). At the Mt Soledad Radiocarbon Laboratory, the process went as follows: The wood was cut into matchstick-sized pieces and underwent the usual chemical pretreatment, consisting of extraction of mobile organic fractions by acetone followed by hot alkali and acid treatments. After rinses with distilled water, the wood was dried at 110°C and then combusted in an oxygen atmosphere on a high vacuum line. The resulting CO₂ was converted to acetylene via lithium carbide. The ¹⁴C activity was determined by measuring decays for 2 days in each of 2 gas proportional counters. No decay correction from the year of growth to AD 1950 could be made, since palm trees do not form annual rings. A rough age correction could be made in the Δ¹⁴C values if a constant rate of vertical tree growth were assumed: +11‰ would be added to the Δ¹⁴C value at a height of 0m, with the prescribed correction being decreased by 0.8‰ per meter up the tree.

Figure 3 shows the results of the ¹⁴C activity measurements for the palm, most of which are listed in Linick (1980). It is evident that only the uppermost, *ie*, youngest, parts of the stem have incorporated significant amounts of bomb ¹⁴C. Despite the fact that the stem was not cylindrical, there was no pronounced secondary growth over most parts of the stem. It was to be expected that incorporation of man-made ¹⁴C due to diffuse secondary growth would be most pronounced in the wood newly grown just before the beginning of the nuclear weapons tests in 1955, but high activity was restricted to the uppermost part of the stem, with a rather distinct delimitation. Although any ¹⁴C level of > -30‰ could be

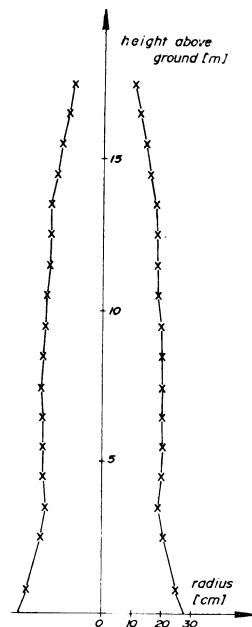


Fig 2. Dimensions of the palm stem investigated

the result of a mixture of carbon from years of different ^{14}C levels, the degree of incorporation of bomb ^{14}C below 15m height could generally have only been very small. The high activity in the center of the stem at a height of 9.4m is surprising and needs more investigation for proper interpretation. Two center samples from 9.4m height were measured, and they gave quite different $\Delta^{14}\text{C}$ values ($+87 \pm 8$ and $+13 \pm 4$), both of which are significantly higher than the ^{14}C levels in the other center and outside samples from 8.4 to 10.4m height. The high activity may be due to late growth to give the stem additional strength. Both center results at 9.4m may be valid, since an active vascular bundle might have been present in one part of the center of that disk of wood but not another part. It is worth noting that the high activity is coincident with the upper limit of the cylindrical part of the stem and the bottom of the conical part. Thus, it may be that the stem undergoes at a certain age a distinct modification in the center, only then assuming its final state. This zone may be correlated with the formation of the hard peripheral sclerotic zone composed of congested, dark vascular bundles and ground parenchymatic tissue (see pl 1B). The difference in ^{14}C activity between the periphery and the center at 12.4 to 16.4m heights is also significant; this observation indicates that cells in the center remain active for a longer period than do the cells near the cortex.

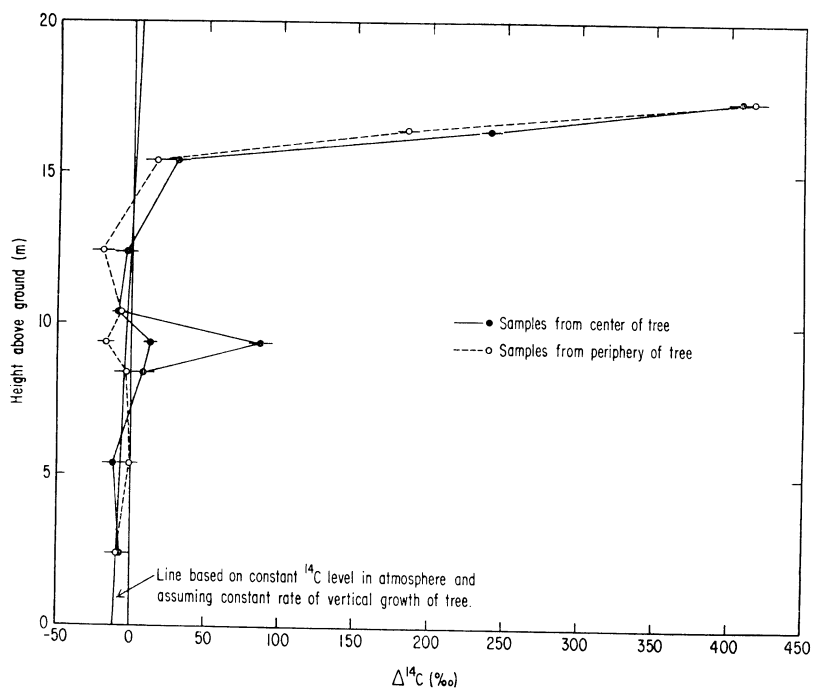


Fig. 3. ^{14}C activity at different heights in stem of palm tree; samples from center and periphery of stem.

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