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DISCUSSION

THE QUESTION OF DIFFUSE SECONDARY GROWTH OF PALM TREES: A COMMENT

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In a recent paper (Wiesberg & Linick, 1983), the authors investigated the $\Delta^{14}C$ levels in the stem of a coconut palm (*Cocos nucifera* L) to determine whether diffuse secondary growth occurred. The authors concluded that "there was no diffuse secondary growth 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," though they did not define what they meant by a "mature" stem.

The palm was apparently planted ca 1860, and had developed a conical basal part up to ca 2m height, a virtually cylindrical part up to ca 13m, and a conical part above this. The authors assumed a constant rate of height growth, though this was not critical for their analysis. Samples were taken from the center and the periphery of the stem at various heights between 2.5m and 17.5m, from which the "wood" fraction was extracted for $\Delta^{14}C$ determination. Up to a height of 12.4m the $\Delta^{14}C$ levels were fairly constant, mostly between -20 and $+20$ $\Delta^{14}C‰$, and the levels then rose sharply, reaching $+420$ $\Delta^{14}C‰$. in the top sample. The $\Delta^{14}C$ levels were slightly higher in the samples from the center of the stem, at least in the upper parts of the stem. The pattern of $\Delta^{14}C$ levels up the stem was interpreted as showing a gradual rise in $\Delta^{14}C$, in accordance with the prevailing atmospheric $\Delta^{14}C$ levels since 1860, up to a height of ca 15m, above which the rise in $\Delta^{14}C$ was attributed to the bomb effect following nuclear weapons testing since 1955.

Unfortunately, the authors did not attempt to obtain precise dates for the formation of the stem at various heights, though it has been observed that coconut stems can be dated reasonably accurately from the number of leaf scars and by applying a growth rate of ca 12 leaves y^{-1} (Corner, 1966; Child, 1974). The height growth of stems changes markedly during the life of the palm (Child, 1974).

It is, therefore, uncertain whether the observed dramatic rise in $\Delta^{14}C$ levels above 15m height is simply recording the contemporary changes in atmospheric $\Delta^{14}C$, or whether there has been transport of more recent carbon to lower parts of the stem which may have undergone secondary thickening. Without accurate dating at particular heights, the results of this study are ambiguous and cannot be taken as a refutation of the hypothesis that secondary thickening is occurring in the upper part of the stem.

In their introduction (p 806), the authors state "an ideally cylindrical growth is almost proof of the absence of secondary growth; unfortunately, the opposite does not hold true." It is not clear from the description of the coconut stem whether this was entirely conical or partly cylindrical and, therefore, where secondary growth might be present. In one place (p 807) the authors state that "Despite the fact that the stem was *not cylindrical,* there was no pronounced secondary growth over most parts of the stem," while they later state that (p 808) "It is worth noticing that the high activity is coincident with the upper limit of the *cylindrical* part of the stem and the bottom of the conical part." It seems probable that if there was any secondary growth, this should cease at the transition from the conical to the cylindrical part of the stem.

The conical base of the stem was not investigated though this is evidently a possible zone for secondary growth. Waterhouse and Quinn (1978) showed that the basal cone of the stem of *Archontophoenix cunninghamiana* (Wendl) Wendl et Drude underwent sustained diameter growth.

While it is clear that ^{14}C determinations may help to solve such problems as secondary growth in palms, it is apparent that in this study there was insufficient information to reject the hypothesis.

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REPLY

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It is difficult to understand the criticism expressed by Julian Ash because our findings do not depend so much on precise dates for the formation of the stem. He gives no argument why our statement that "there was no diffuse secondary growth 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" may be wrong.

The rise in ^{14}C above 15m and the almost complete absence of excess ^{14}C below that height are so drastic that it seems justified to maintain our original conclusion.

Ash questions "whether the observed dramatic rise in $\Delta^{14}C$ levels above 15m height is simply recording the contemporary changes in atmospheric $\Delta^{14}C$, or whether there has been transport of more recent carbon to lower parts of the stem which may have undergone secondary thickening."

The main problem seems to be the term "secondary thickening" which should not be applied to growth of cells which originate from the primary apical meristem.

Surely, the formation of new wood in palms may last some years until it becomes mature. The terms "mature" and "immature" are open for discussion, but may be defined easily by means of the incorporation or not of recent photosynthetic products as traced, eg, by radiocarbon. As we found a sharp limit of enhanced ^{14}C activity, which proves the viability of this definition, all growth of the stem has to be considered primary in nature. In a group of palms the maturation is a long-lasting process; according to Waterhouse and Quinn (1978) it should be termed, "sustained primary growth."

It is unrealistic and contradictory to experience to paint a picture in which the palm ceased to grow in height, say 20 years before it was cut, but continued to grow in width. A palm that stops growing taller is already dying—the normal flowering and fructification implies the formation of new axillary buds and, thus, new leaves and wood.

We have no clear indication of the time span of formation of the wood in *Cocos nucifera,* but we expect a figure of about five years, coinciding more or less with the mean life of an individual leaf (Child, 1974); the bulk of the tissue should form, however, in a much shorter interval.

The main doubt about diffuse secondary growth still originates from the high ^{14}C activity found at 9.4m which shows that there is the possibility of incorporation of new photosynthates into old tissue. We suggested that "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." If so, then the old trunk at any height may be a mixture of photosynthates of different ages. But we want to point out that there is another possibility to explain the high activity at 9.4m. Higher up in the trunk there were injuries caused by insects and the high ^{14}C level may be due to a response of the plant in order to re-establish the continuity of the bundles. This would also explain why the high $\Delta^{14}C$ value was found only in a very restricted zone.

We agree with Ash that the base of the stem is evidently a zone for (diffuse) secondary growth because adventitious roots are continually produced from the base of the stem (Child, 1974). However, the criticism by Ash about the description of the trunk does not hold because he gives an exact figure of the stem, apparently derived from our Figure 2, which shows the dimensions of the stem. Thus, the stem was not totally cylindrical; only the main part was almost cylindrical.

We agree that there are still many questions that could well be investigated by means of ^{14}C measurements, taking advantage of the unique radiocarbon situation due to atmospheric nuclear weapon tests.