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Crown Relationships in Two Samoan Palms

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Abstract

Dissection of crowns in *Balaka* aff. *rechingerana* and *Clinostigma onchorhynchum* in Western Samoa reveal that Corner's postulate of equal numbers of exposed and unexposed leaves in palms holds for the *Balaka* but not for the *Clinostigma* in which there are more than twice as many developing as exposed leaves.

In his book *The Natural History of Palms*, Corner makes the interesting conjecture that "the palm crown should have as many developing leaves as it has open leaves" (1966), a suggestion that has been repeated in more recent texts (Hallé et al. 1978). This statement appears to be related to his postulation of equal rates of leaf initiation and abscission in a steady-state crown. He uses both assumptions to derive formulas of an essentially demographic nature that can be used to determine the age of individual leaves. Corner provides evidence of a somewhat anecdotal nature for his assumption by describing the results of complete dissections of the crowns of six species of palms. For two specimens of *Cocos nucifera*, one specimen of *Elaeis guineensis* (in which "the bud snapped in dissection and damaged the soft apex"), and an unspecified number of specimens of *Ptychosperma macarthurii*, *Pinanga simplicifrons*, *Pinanga furfuracea*, and *Pinanga kuhlii*, Corner found essentially equal numbers of open and developing leaves.

I became interested in Corner's conjecture and decided to test it on two Samoan species of palm, *Balaka* aff. *rechingerana* Burret and *Clinostigma onchorhynchum* Beccari.

Materials and Methods

In July and August, 1979, ten specimens of *Balaka* aff. *rechingerana* (*maniuniu* in Samoan) were collected from an area soon to be cleared for agricultural purposes near Falemauga, on the island of Upolu, Western Samoa. Five specimens of *Clinostigma onchorhynchum* (*niu vao* in Samoan) were collected on land to be cleared for agricultural purposes near Tiavi on the island of Upolu. Each specimen was completely dissected after recording the stem length and diameter immediately beneath the crown. The number of developing (unexposed) and the number of exposed leaves were counted. A chi-square test was made on the number of unexposed and exposed leaves in each crown. Measurements of sheath, petiole, and lamina lengths were recorded for each leaf in all of the crowns. Voucher specimens for each species (*Cox 221* for *Balaka* aff. *rechingerana*, and *Cox 162* for *Clinostigma onchorhynchum*) were made and deposited with the Gray Herbarium.

Illustrations of the natural logarithms

Results

Balaka aff. *rechingerana*

Specimen	Stem length	Diameter	No. unexposed leaves	No. exposed leaves	χ^2	p
1	74 cm	2 cm	7	5	0.3	NS
2	257	3	8	7	0.7	NS
3	251	4	7	7	0	NS
4	177	3	8	7	0.7	NS
5	87	2	8	6	0.3	NS
6	285	4	8	6	0.3	NS
7	217	5	7	7	0	NS
8	179	3	8	7	0.7	NS
9	148	3	8	8	0	NS
10	61	3	7	7	0	NS

Clinostigma onchorhynchum

Specimen	Stem length	Diameter	No. unexposed leaves	No. exposed leaves	χ^2	p
1	342 cm	11 cm	22	10	4.5	0.05
2	795	18	27	13	4.9	0.05
3	394	14	21	9	4.8	0.05
4	270	14	21	8	5.8	0.025
5	*	*	32	12	9.0	0.001

* not recorded

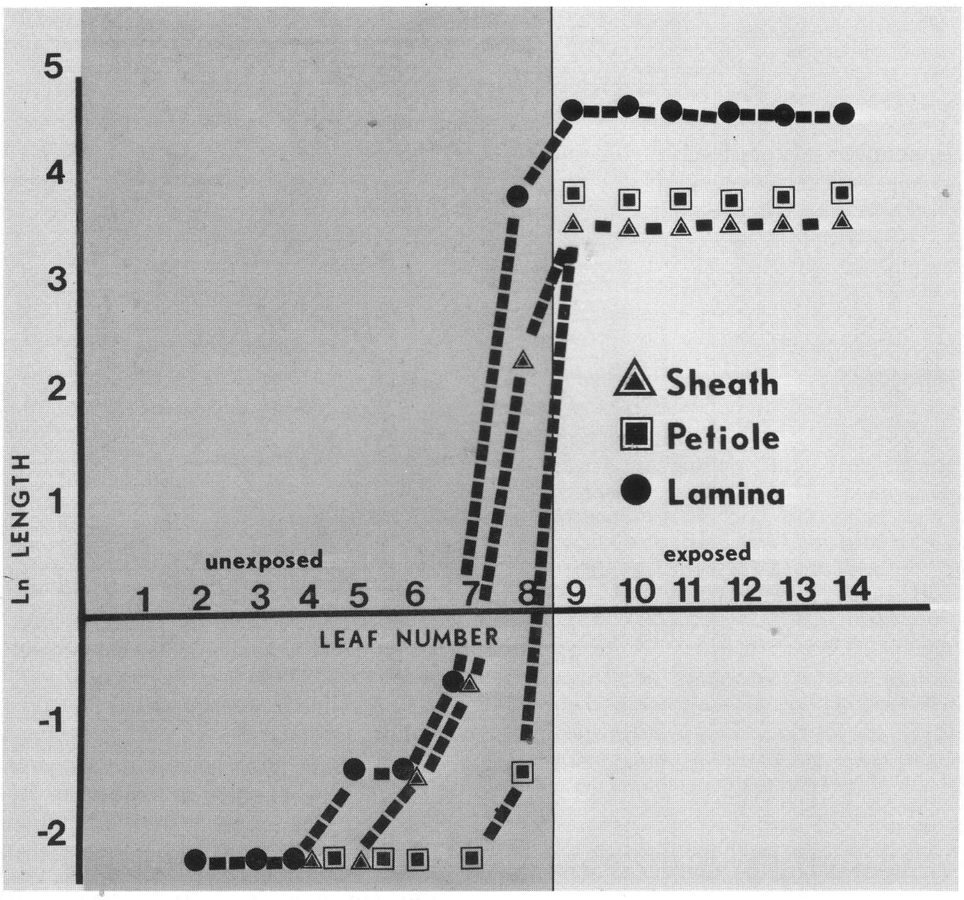
of the leaf lengths plotted against the leaf order are shown for a typical crown of *Balaka* aff. *rechingerana* and a crown of *Clinostigma onchorhynchum* in Figures 1 and 2.[1]

Discussion

The crowns of *Balaka* aff. *rechingerana* seem to have roughly the same number of expanded and unexpanded leaves and therefore fit Corner's hypothesis well. Although there were slight differences between the numbers of expanded and unexpanded leaves in the sample of ten crowns, none of these differences were statistically significant.

The crowns of *Clinostigma onchorhynchum*, however, do not fit Corner's hypothesis. All of the crowns in the sample had more than twice as many unexpanded as expanded leaves, and all of the differences between numbers of developing and exposed leaves were statistically significant. The great deviation of the crowns of *C. onchorhynchum* from Corner's hypothesis raises questions concerning the cause of this deviation and its effect upon the validity of the demographic formulas derived by Corner.

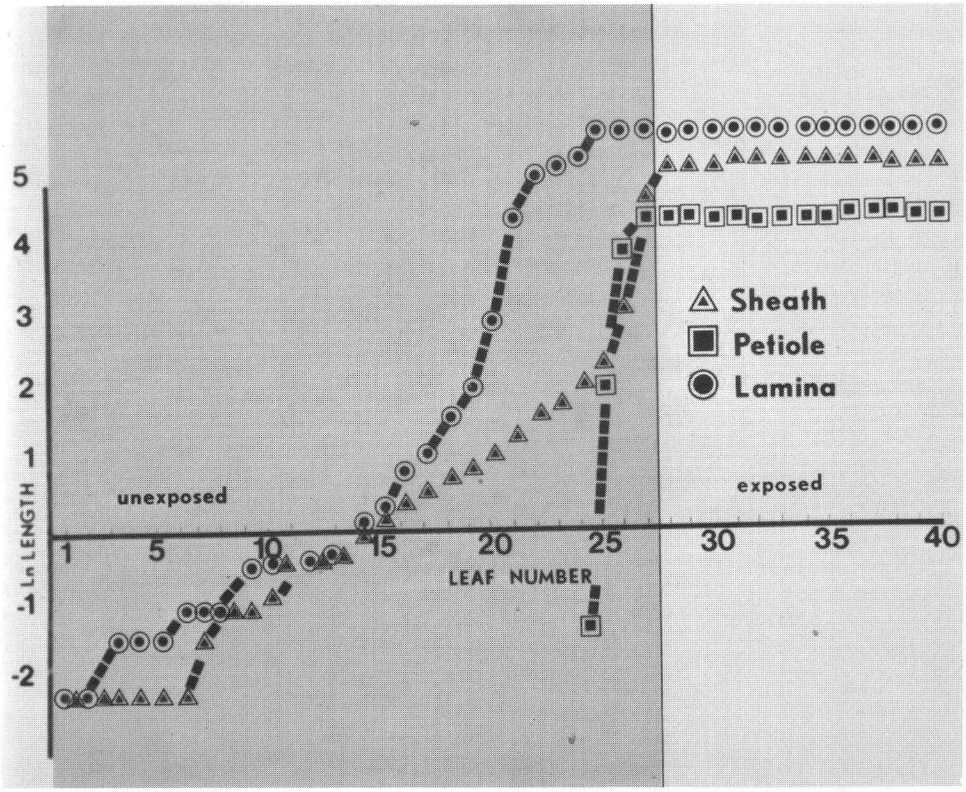
[1] Figure 1 shows the plot for specimen #6 of *B.* aff. *rechingerana*; Figure 2 gives the graph for specimen #1 of *C. onchorhynchum*. The data for the other specimens are available on request.



1. Leaf number (a rough determination of leaf age) plotted against the natural logarithms of leaf sheath, petiole, and lamina lengths for an individual of *Balaka* aff. *rechingerana*. The shaded area indicates leaves that are unexposed; i.e. those that are still developing and have not yet opened.

The significance of the first question can be discussed at two levels. At a more general level, Corner's initial generalization was based on observations of only six species of arecoid and cocosoid palms; three of the species were in the same genus. The two species here (both arecoid) show that further studies are needed to determine the strength of Corner's generalization. It might be that the relationship found in the crown of *Clinostigma onchorhynchum*, where the numbers of developing and exposed leaves are very different, occurs in many different species; conversely, this relationship might prove to be very rare among the palms. Only further observations of palm crowns of different species can resolve this question.

At a more specific level, we may ask why the crown of *Clinostigma onchorhynchum* should be different in the number of expanded and unexpanded leaves than the crown of *Balaka* aff. *rechingerana*. There are several possible explanations, but since so little is known about these species and palm



2. Same as for Figure 1 for an individual of *Clinostigma onchorhynchum*.

crowns in general, it would be premature to assign any more than a speculative status to these alternatives. First of all, there may be a historical explanation in that some external trauma, such as a large wind, disturbed the crowns of *Clinostigma onchorhynchum* in Samoa, removing part of the crown, but did not affect the crowns of *Balaka* aff. *rechingerana*. Although this is a possibility because *C. onchorhynchum* is a tall palm, which often exceeds the canopy of the surrounding forest, while *B.* aff. *rechingerana* is a small understory palm, I consider this to be highly unlikely because Samoa has not experienced any large hurricanes or other large physical traumas since 1966. Also, if this explanation were true, one would expect to find a relationship with height so that tall individuals would have more of their crown missing than small individuals. This, as shown by the data, is not the case.

Secondly, there may be an evolutionary explanation in that there has been natural selection for equivalent numbers of exposed and unexposed leaves in *B.* aff. *rechingerana* and against equivalent numbers of exposed and unexposed leaves in *C. onchorhynchum*. Greatly different selective forces operating on the two species, however, are difficult to imagine as both species have similar habi-

3. An individual of *Clinostigma onchorhynchum* near Tiavi, Upolu, W. Samoa.

tats and similar ecologies. The species are sympatric in several areas; they grow together on the slopes of Mt. Fia Moe, Upolu, although *C. onchorhynchum* seems to occur more frequently in open habitats such as the edges of clearings or on the edges of gorges while *B.* aff. *rechingerana* appears to

4. An individual of *Balaka* aff. *rechingerana* near Falemauga, Upolu.

be mostly confined to the interiors of undisturbed rainforest. Mature individuals of *C. onchorhynchum* (Fig. 3) are much larger than mature individuals of *B.* aff. *rechingerana* (Fig. 4), the former often reaching into the canopy of the mature forest, while the latter is strictly a small understory palm.

It is possible, then, that a selective force involved with different positions and light environments could play a role; in this regard it is of interest that the genera *Pinanga* and *Ptychosperma* which Corner studied tend to consist of understory palms (McCurrach 1960, Essig 1978).

Thirdly, the different number of open and developing leaves in *C. onchorhynchum* might be a product of allometry in the sense that selection has not favored different numbers of open and developing leaves directly, but rather has favored some other trait, which of necessity, has involved the relative proportion of open and developing leaves. For example, the massive leaf sheaths of the entire Clinostigma alliance may function to protect developing inflorescences (Uhl and Moore 1973), and selection might have favored numerous layers in the crown shaft to increase this protective function. The inflorescence in *C. onchorhynchum* is very fleshy and succulent at the time the first flowers open, in contrast to the more "woody" inflorescence of *B.* aff. *rechingerana*; possibly the inflorescence of *C. onchorhynchum* needs additional protection from physical and biological hazards. In both species, however, the leaf sheaths serve to push the leaves up into the crown as shown by their exponential growth in older developing leaves (see Figs. 1, 2).

The demographic formulas developed by Corner for determining the ages of individual leaves merely by counting their order in the crown and by knowing the rate of abscission might be applicable in *B.* aff. *rechingerana* if Corner's postulate of uniform and equal rates of initiation and abscission of leaves in palm crowns is correct, but will yield incorrect determinations if applied to *C. onchorhynchum*, and any other palm in which the number of developing leaves is not equal to the number of exposed leaves. Corner states that if the number of days between successive leaf yellowings is p days and the number of leaves in the crown is n, that the "working life" of the leaf will be np days, its period of development will be also np days, and that the total age of the leaf will be 2np days. If we assumed equal rates of abscission and initiation, and that these rates were uniform through time, np days would be a good estimate of the number of days a leaf is exposed in the crown, but would be a great underestimate of its period of development. The total age of the leaf derived from 2np would also be a gross underestimate of the total age of the leaf. Similarly, deriving the age of the palm by adding 2np to the trunk age, as Corner suggests, would also lead to a great underestimation of the age. Unfortunately, since there is no strict ratio between number of exposed and unexposed leaves in crowns of *C. onchorhynchum*, any attempt to accurately estimate the number of developing leaves within the crown by using only rate of abscission and the total number of exposed leaves as parameters will fail.

It is clear that more studies are needed to develop a comprehensive theory of crown relationships and their possible functions. Since such studies are of necessity destructive, it is hoped that any work done in crown dissection will be confined to cultivated material, or wild material from "doomed" sites such as areas of road construction or agricultural expansion.

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PALM QUESTIONS AND ANSWERS

Q. What are the quarantines concerning lethal yellowing?

A. I am listing the following regulations:

Quarantine Area—entire counties of Broward, Dade, Hendry, Martin, and Palm Beach; and that portion of Monroe County not considered to be mainland.

Suppressive Area—Collier County. This county has been engaged in an intensive injection and tree removal project on all hosts exhibiting lethal yellowing symptoms for the purpose of achieving complete eradication. Therefore, all host material moving into Collier County from the Quarantine Area must be accompanied by a special permit.

Florida Requirements—a special permit is required for movement of all hosts outside both the Quarantine and Suppressive areas. If anyone is interested in obtaining a permit, contact your local Division of Plant Industry Agricultural Products Specialist.

California Requirements—California will not accept any host material originating in the lethal yellowing regulated areas. Any such material arriving there from these areas will be destroyed or returned to the shipper.

Hawaii Requirements—all host plants and parts thereof, including seeds, from Florida are prohibited; all palms of any species, parts and seeds, from the regulated area are also prohibited. Phytosanitary export certificates showing origin must accompany certifiable shipments of plants.

Louisiana Requirements—all palm trees which originate in a lethal-yellowing infested county or 25 miles from a known infection (whichever is the farthest) are refused entry. Nonhost palms may be moved from a noninfested county but must be accompanied by a certificate of origin stating the palms originated in an area free of lethal yellowing.

Mississippi Requirements—host plants from regulated areas prohibited entry. Host plants from outside of regulated areas prohibited unless accompanied by a Florida certificate stating the origin of the shipment.

Puerto Rico Requirements—the introduction of all varieties of palms, products of palm, and palm seeds into the Commonwealth of Puerto Rico, from any place outside thereof, is prohibited.

Texas Requirements—all host plants listed above, *Arecastrum romanzoffianum* and *Phoenix roebelenii* are refused entry into Texas if plants originated in the regulated area of Florida.

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