A Note on the Abscission of Spiny Leaves of Palms

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Spines on palms function presumably to preclude or to decrease the damage done by herbivores (Tomlinson, 1962b, and Uhl and Moore, 1973). Whereas old leaves are dropped from most plants, some plants with leaf spines appear to droop, not drop, their dead foliage, thereby providing their stems with a protective mesh of spines. Such a mesh would serve to protect the stem tissues as well as to hinder climbing herbivores such as squirrels and coatis bent on reaching the apical bud. Thus, there is some ecological importance to the persistence or abscission of old leaves (Tomlinson, 1962a) in that there may be a close association between the presence of spines and the process of abscission (Tomlinson, 1962b). A particularly striking example is the genus *Washingtonia* whose trunks are unarmed, yet well protected by skirts of dead leaves whose petioles have spines (McCurrach, 1960).

In this study, in order to test the association between abscission and spines, a number of common palm species were observed to determine if the percentage of leaves which are dead (but still attached to the trunk) is higher for species with spiny leaves.

Methods

In several locations in Costa Rica the more common palm species were studied to determine if the lack of abscission of old leaves was associated with the presence of spines on the leaves. The numbers of green leaves and dead leaves still attached to the trunk were recorded for six to nine individuals of each of nine palm species. Old leaves were often in various states of decay, so only those with the petiole and rachis still prominent were counted. Only those individuals whose trunks were longer than their leaves were studied, so the force of gravity would have been operating uniformly to assist abscission; thus, young and small individuals whose dying leaves drooped onto the ground were not studied.

Nine Costa Rican palm species were studied, five near Puerto Viejo on Río Sarapiquí, one in Santa Rosa National Park, and three on the Osa Peninsula near the Agua Buena. The palms from the Osa and the Sarapiquí areas are wet lowland forest species, but the one from Santa Rosa occurs in old pastureland.

Results

The results of the counts of green and dead leaves are presented in Table 1 for the nine species. The only two species with spines on the leaves are *Acrocomia vinifera* and *Astrocaryum alatum*. These two species exhibited the highest percentages of leaves that are dead, 74% and 33%, respectively. (Statistically, the data totals of green leaves and dead leaves were analyzed with chi-square tests of independence for pairwise comparisons for each of the spiny-leaf species against each of the unarmed-leaf species. With a one-tailed hypothesis

Table 1. The numbers of green leaves and dead leaves on individual palms and summary data

Individual Number	*Acrocomia vinifera*	*Astrocaryum alatum*	*Socratea durissima*	*Geonoma congesta*	*Cryosophila albida*	*Prestoea decurrens*	*Asterogyne martiana*	*Cryosophila guagara*	*Synechanthus warscewiczianus*
1.	15–31	19–20	5–0	9–0	13–5	6–2	21–0	11–0	4–2
2.	15–44	23–9	6–0	11–0	17–5	16–1	23–0	25–5	5–2
3.	22–52	12–9	7–0	7–0	17–3	7–1	17–3	11–3	6–2
4.	15–35	14–9	8–1	10–0	16–3	7–1	19–3	9–2	7–2
5.	19–50	16–7	7–0	9–2	11–2	7–0	21–5	21–0	6–0
6.	17–57	19–3	5–0	7–0	17–5	10–0	17–1	19–2	7–1
7.	17–75	23–8		13–2			20–0	18–2	
8.	20–60	10–1						13–1	
9.								18–4	
Total	140–404	136–66	38–1	66–4	91–23	53–5	138–12	165–24	35–9
% Dead Leaves	74%	33%	3%	6%	20%	9%	8%	13%	20%
Mean # of Dead Leaves	51	8	0	1	4	1	2	2	2

that the greater proportion of dead leaves is associated with the spiny-leaf species, the tests revealed statistical significance with $p < 0.01$ in all cases except the comparison of *Astrocaryum alatum* and *Synechanthus warscewiczianus* where $0.05 < p < 0.10$.)

Perhaps more important than percentages are the actual numbers of dead leaves drooped about the palm trunks potentially to provide protection. Again, *Acrocomia vinifera* and *Astrocaryum alatum* exhibited the highest mean numbers, 51 and 8 dead leaves, respectively. Thus, the two species with spiny leaves apparently retain their old leaves more than the other seven species.

Discussion

The drooping of spiny fronds suggests that protection may be essential against herbivores which climb palm trunks. While spines on the living leaves may give protection against herbivory on the fronds, the function of drooping of the dead, spiny fronds must be related to trunk-climbing animals if the drooping has some adaptive value. Climbing herbivores such as coatis, squirrels, and monkeys could easily be deterred by spines, either on the trunk or on drooping, dead fronds. Of course, monkeys can drop from adjacent trees into the palm crown and thereby avoid the trunk armature; however, the drop involves

some risk in falling, and many palms grow in the open or in forest openings where monkeys cannot drop into them. Furthermore, it has been suggested by Uhl and Moore (1973) that one purpose of spines is to protect pollen and ovules. Many of the shade-tolerant palms may produce large flower and fruit crops only when they are exposed to full sunlight—a situation which arises through release after the fall of a tree which previously shaded a palm. Thus, maximum reproduction would occur at a time when monkeys would be unable to drop into the palm crowns.

If there is a relation between frond abscission and the occurrence of spines, it is likely to be more complex than that suggested by the data presented here. Palms without trunk spines and without frond spines should drop their dead fronds if a smooth trunk is any deterrent at all against climbing herbivores; this pattern is evident in the majority of species in this study (*Socratea durissima*, *Geonoma congesta*, *Prestoea decurrens*, *Asterogyne martiana*, and *Synechanthus warscewiczianus*). Palms without trunk spines and with spines on the fronds should retain their dead fronds, drooped about the trunk as in *Acrocomia vinifera* and *Astrocaryum alatum*. Palms with spines on the trunk but with unarmed fronds should drop their dead fronds because the presence of a skirt of dead fronds would facilitate climbing herbivores trying to avoid the trunk armature; this case may be represented by *Cryosophila albida*, which has spines along the trunk. Finally, palms with trunk spines and frond spines both should drop their dead leaves because again the skirt of dead fronds would tend to negate the effect of trunk armature; unfortunately, there are no examples of this case in the present study although an example is *Astrocaryum standleyanum*.

It is noteworthy that the phenomenon of drooping spiny leaves in lieu of abscission—illustrated here for some palm species—occurs in other taxonomic groups such as thistles (Compositae: *Carduus* and *Cirsium*).

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