Mortality Rates of Some Rain Forest Palms in Panama

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Palms are good subjects for the study of tropical plant population dynamics because their growth pattern of continuous leaf production allows approximate determination of the ages of individuals (cf. Sarukhan 1978). Growth from a single terminal meristem renders palms especially susceptible to mortality, since generally no resprouting capability exists if the meristem is destroyed. While mortality is an important parameter in the study of the dynamics of populations, there are few published data on the incidence or extent of mortality in natural palm populations with the exception of studies on seed and seedling losses (e.g., Bannister 1970, Janzen 1971, Vandermeer 1977, Bullock 1980). We here report notes on palm mortality obtained during a study of the phenology of an assemblage of palm species in the rain forest of Barro Colorado Island, Panama. We first describe observations of animals as a source of terminal meristem damage and potential plant death. We then report some general mortality rates in different palm species which allow assessment of the relative susceptibility of different species to mortality and comparison with mortality rates of woody dicotyledonous plants in the same community.

Animal-caused Mortality

The climate of the tropical moist forest on Barro Colorado Island is strongly seasonal, with a dry season lasting from late December through early April. The plant and animal communities also show seasonal behavior, and, in particular, there is a period of sparse fruiting from November through February that results in a seasonal food shortage for frugivorous mammals (Foster 1982). The frugivores seek a wider range of foods at this time, and palms, especially the understory species, frequently suffer their apices being torn apart by animals feeding on the succulent developing terminal bud. From various observations, it appears that the major agent responsible for this damage is the white-faced monkey, Cebus capuchinus (Oppenheimer 1982; de Leon, pers. obs.), but collared pecaries, Tayassu tajacu, have been observed to push over small palms and feed on the terminal buds as well (Putz, pers. obs.). Foster (1982) noted that this damage to palms was especially prevalent in a year that was extremely poor in fruit availability for animals. In the course of a monthly phenology census of 13 palm species, we recorded the incidence of damage by animals to permanently-marked individuals. Other researchers have identified such bud feeding by animals as a cause of mortality in palms (Bullock 1980, Foster 1982). We noticed, however, that despite the destruction of a large proportion of the bud, the apical meristem itself was often left intact and the palm would subsequently continue to produce new leaves, some of which show signs of having been partially chewed off while still in the bud. We also therefore recorded the incidence of recovery of damaged palms.

	# Plants/4	Mean %	Mean % Re-		
Species	1981	1982	1983	Damaged	covered
*Bactris barronis	9/6/5	10/4/3	23/3/1	40	64
*Bactris coloniata	29/23/21	30/11/11	32/1/1	40	97
*Bactris major	36/1/1	36/0/-	36/0/-	1	100
Chamaedorea wendlandiana	11/0/-	11/0/-	12/0/-	0	
Geonoma cuneata	22/17/13	16/6/3	11/6/5	56	70
Geonoma interrupta	10/0/-	5/1/1	9/0/-	7	100
Geonoma procumbens	3/3/1	n.d.	n.d.	100	33
Synechanthus warscewiczianus	3/0/	6/2/1	13/0/-	11	50

Table 1. Animal-caused damage to crowns of understory palms.

* For clonal species, # plants = # stems, n.d. = no data available.

During a three-year observation period, nearly all of the damage to immature and adult understory palms took place between the months of November and February, the usual season of food shortage. It is clear that some species are damaged more frequently and more severely than others (Table 1). It is surprising that the small Bactris species are heavily utilized despite the presence of sharp spines on the leaves and stems. Whether the differences among species represent true preferences is unclear. Apart from Geonoma procumbens, for which the data are scant, the palms most frequently damaged are clonal (Bactris) or occur in dense patches (Geonoma cuneata); in both cases, stem densities are locally high and this apparently increases their conspicuousness to animals in contrast to the more scattered solitary species. The higher incidence of attacks on clustering species may also be because these species are particularly palatable. Most striking is the fact that one species, Chamaedorea wendlandiana, was never damaged at all and we never encountered such damage to this species anywhere in the forest. This may indicate that the terminal shoot of this species possesses some repellent characteristics.

It is also interesting that many plants do not necessarily die after animals feed on their buds, indicating that the meristem itself often escapes destruction (Table 1). Even plants damaged repeatedly may recover, provided that the destruction is limited each time. Of 15 individuals of three species (*B. barronis*, *B. coloniata*, and *G. cuneata*) that were damaged in two or three successive years, 14 (93%) recovered subsequently as shown by expansion of new leaves.

Levels of damage do vary from year to year. For the susceptible species, rates were higher in 1981, which appeared from other evidence to be a year of low food availability for frugivorous mammals (pers. obs.). Thus the pressure placed on palm populations by animals is in part determined by other events in the community as a whole.

Adult and immature individuals of canopy palm species appear immune to damage from animals presumably because their crowns are too large and the ensheathed terminal buds too massive to be easily torn apart. The one understory species not included in Table 1, Elaeis oleifera, also has a massive crown of 20 or more leaves that would be difficult for an animal the size of a white-faced monkey or peccary to damage. Orangutans and wild pigs, however, are known to damage equally massive palms in Southeast Asia (Dransfield pers. comm.). We collected no data on juvenile (rosette-stage) individuals of either canopy or understory species, but it seems likely that animals could tear open the leaf sheaths of canopy as well as understory species because of the less

	# Pl	Mean Death Rate per		
Species	1981	1982	1983	Year (%)
Understory		-		
*Bactris barronis	36/0	37/0	39/3	2.6
*Bactris coloniata	41/2	45/1	52/0	2.4
*Bactris major	59/5	53/0	56/2	4.0
Chamaedorea wendlandiana	11/0	13/0	12/0	0
Flagis algifera	13/(1)**	12/0	12/0	(2.6)**
Coopoma cupeata	19/0	15/1	13/2	7.4
Coopoma interrupta	10/1	13/1	13/0	5.9
Synechanthus warscewiczianus	7/0	16/2	13/2	9.3
Canopy/Subcanopy				
Astrocaryum standlevanum	19/0	20/0	21/0	0
Crysophila warscewiczii	10/0	13/0	14/0	0
Oenocarpus mapora	298/8	83/0	85/4	2.5
Schooleg zonensis	19/0	19/0	19/0	0
Socratea durissima	12/0	12/0	12/0	0

Table 2. Mortality of immature and adult palms on Barro Colorado Island.

* For clonal species, # plants = # stems; no clones died during the study.

** Death of individual not certain; treefall obliterated site.

massive proportions of juveniles. One of us (DD) has found this to be the case for small *Oenocarpus* individuals. It should be pointed out, however, that where large mammals such as elephant and rhinoceros occur, even large palm species may suffer from shoot tip feeding.

Other Causes of Mortality

From the permanently marked census plants, we were able to estimate the mortality of adult and immature individuals of all the palm species from factors such as tree falls, drought stress, or unknown causes. For each year, we calculated mortality as the number of individuals dying. Such data are useful as baseline information on turnover rates of individuals in palm populations and they allow comparison of mortality among different species in the same community. The results in Table 2 suggest that, not surprisingly, large canopy palms suffer lower mortality than small understory palms. The one exception would seem to be Oenocarpus, but in this clonal species the mortality figure rep-

resents stem (ramet) losses, not clone death. In comparison with clonal species with widely separated ramets, clonal species with a tightly clustered growth habit are more likely to be killed by treefalls and other intense localized perturbations. However, the death of entire clones is rare, as we observed no deaths of whole clones in any of the clonal species during the entire three-year study period. The mortality of some species appears especially high, for example, that of Synechanthus. The reasons are unclear but may indicate that populations of this species are particularly stressed in the community at this time. Chamaedorea individuals are not immune to treefall damage, but prostrate stems have a well developed capacity to re-root and to redirect crown growth upward; no deaths of this species were observed although several fell over or were pulled down by vines.

Conclusion

Published mortality rates of dicot trees on Barro Colorado Island range between 1-3% (Putz and Milton 1982). The mortality rates of some of the palms are within this range, but some appear to suffer much higher mortality. This may reflect the extreme susceptibility of palms to death as a result of their growth form; loss of their single terminal meristems will result in death, whereas damage to dicot trees and shrubs, whether it be from treefalls or herbivory, is not fatal due to their capacity for resprouting and for aboveground branching.

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