

Seed Dispersal and Predation of the Palm *Acrocomia aculeata*

ALDICIR SCARIOT

CENARGEN/EMBRAPA, C.P. 02372, 70.770-900 Brasília, DF, Brazil

Dispersal can increase the probability that a seed will find an adequate site in which to establish, thus reducing the level of seed predation and introducing the plant to another still unoccupied habitat. The seed stage represents one of the periods of highest mortality in the life cycle of many plant species and substantial reduction of seed crop due to predation may affect the distribution and abundance of plants. Mammals can be quite effective at transporting seeds and increasing the probability that a seed will find an adequate site. In disperser-free habitats, seeds may lie under parent tree and rot (e.g., *Acrocomia*, Janzen 1983a). However, seed dispersers may also act as seed predators or increase the risk of predation by attracting predators.

This study addresses three issues: the possible role of wild and domestic animals as seed consumers and dispersers, their possible effect on seed predation, and the rates of seed predation by bruchid beetles on the palm *Acrocomia aculeata* (Jacq.) Lodd. ex Mart. in Central Brazil. It complements other studies on pollination, phenology, and fruit set (Scariot et al. 1991, 1995).

Methods

The study was conducted on a privately owned farm, Fazenda Taboca, located 45 km (15°35'S, 47°45'W) from Brasília, Brazil. The elevation at this farm is 1,000 m. Mean annual rainfall is 1,566 mm and the temperature ranges from 19° (June) to 23° C (September). *A. aculeata* is an arborescent spiny palm reaching up to 16 m in height and occurring as the dominant tree species in pastures of the grass *Hyparrhenia rufa*. Flowering occurs from August to December, with the peak of open inflorescence (>50%) occurring from mid-October to mid-November (Scariot 1987, Scariot et al. 1991, 1995). The

fruits are globose-spheric, weighing 20–64 g, and measuring 28–49 × 26–49 mm. Generally, there is one seed per fruit, but sometimes two and even three seeds occur. Several aspects of the reproductive biology have been discussed elsewhere by Scariot (1987) and Scariot et al. (1991, 1995).

“Tomahawk” traps (490 × 170 × 160 mm), with fruits of *Acrocomia aculeata* as bait, were used to capture possible dispersers. One hundred forty-three traps per night were used in the pasture and 454 traps per night in the gallery forest. Success was the number of animals captured divided by the total number of traps used per night. Captured animals were released after identification. Adjacent gallery forest was included in the study because there were few wild animals in this region due to deforested areas, and some plants of *A. aculeata* may occur in forest edges. The role of domestic animals in dispersal was observed using binoculars, during the day and by naked eye at night.

The rate and intensity of predation were determined using 14 boxes. A box consisted of a wood frame (400 × 200 × 150 mm) covered with wire mesh. The mesh size (15–20 mm) allowed insects access to the inside of the box, while impeding the entrance of larger animals. The boxes were placed in the pasture on 13 October 1985, under the crowns of individuals of *Acrocomia aculeata*. The boxes, each with 20 fruits, were paired, one with intact fruits and the other with fruits from which pulp was partially removed to mimic fruits chewed by cattle. The boxes were placed approximately 0.5 m from the trunk at an angle of 180° to each other. All the previously fallen fruits under the canopy were collected and removed on the day that the boxes were placed in the field. No oviposition was ever observed on the fruits while they were still attached to the in-

fructescences. On each of the first five days after placing these boxes, and later at irregular intervals, I recorded the number of fruits in which beetles had oviposited and the number of eggs per fruit. When oviposition on the fruits was finished, I collected the fruits and opened them to check the seeds and identify the predators.

Results

Only a few species of animals were captured and not all of them may consume the fruits of *A. aculeata*. The species of vertebrates captured were *Didelphis albiventris* (opposum, 31), *Nectomys squamipes* (water rat, 8); *Cebus apella* (capuchin monkey, 1), and *Turdus* sp. (thrush, 2). Overall capture success rate was 7.0%, being higher in the gallery forest (8.3%) than in the pasture (2.8%). Of the domestic animals that fed on fruits of *Acrocomia aculeata*, only adult cattle ingested them, while horses, pigs, and young cattle only chewed the fruits, removing the epicarp and mesocarp. Fruits ingested by adult cattle were regurgitated at night in piles of up to 85 fruits. Cattle regurgitated seeds mixed with residues of grasses, and the seeds usually had either portions of the epicarp and/or mesocarp attached, or only the endocarp.

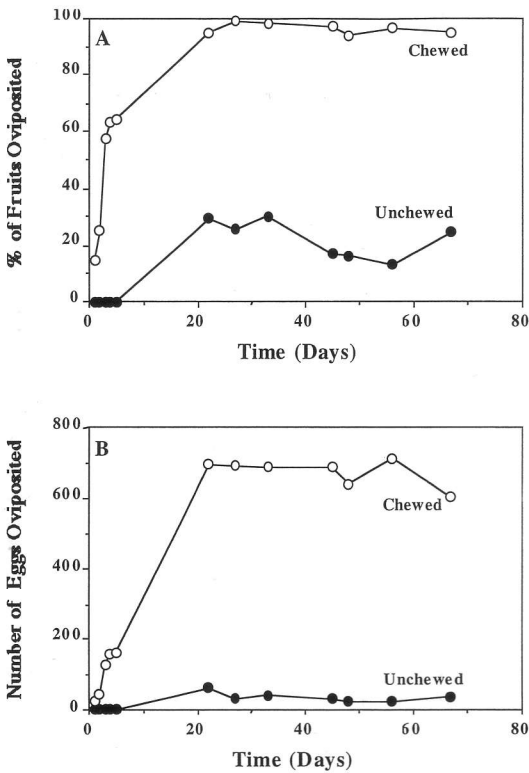
The bruchid beetles *Pachymerus* sp. and *Caryobruchus acrocomiae* (Pachimerinae, Pachimerinii) preyed on seeds of *A. aculeata*. The adult *C. acrocomiae* feeds on pollen, remaining during the day under dead leaf sheaths and in the leaf sheath of *A. aculeata*. At night they oviposit on fallen fruits. After oviposition the larvae perforate the exocarp and mesocarp (if present), and finally the endocarp, reaching the seed. More than one larva can reach the seed, but only one reaches the adult stage, which suggests that the first larva reaching the seed cannibalizes the others. By the final instar, the larva consumes almost all (*Pachymerus* sp.) or all (*C. acrocomiae*) of the seed. An operculum, visible from outside the fruit, protects the insect from contact with the external environment and opens when the adult bruchid emerges. In the experimental seeds *Pachymerus* sp. (13 individuals) was more abundant than *C. acrocomiae* (6 individuals).

After three days on the ground >50% of the chewed fruits in boxes had at least one bruchid egg, and after 27 days, 99% had eggs deposited on them, suggesting that chewed fruits had a higher level of oviposition than unchewed fruits

(Fig. 1A). The high number of eggs per fruit (up to 15) suggests that female bruchid beetles do not discriminate among fruits with or without eggs during oviposition (Fig. 1B). Cattle destroyed some boxes and removed the fruits, reducing the final number of fruits in boxes to 97 chewed and 75 nonchewed. Of 101 seeds in 97 chewed fruits, 76.2% were preyed by insects, 19.8% were intact, and 4% were nonviable (absent, rotten, etc.). Of 75 seeds in 75 nonchewed fruits only 10.6% were preyed by insects and 89.4% were intact. Thus, chewed fruits had a significantly higher predation level than nonchewed fruits ($\chi^2 = 77.17$, $df = 1$; $P < 0.001$). Eggs of bruchids may be washed away by the rain. This may account for the observed decreased percentage of fruits oviposited (Fig. 1A) and number of eggs layed (Fig. 1B), which after some time increases again as the layed eggs accumulate.

Discussion

An advantage of seed dispersal by several species is an increase in the number of possible habitats and the number of seeds dispersed (Gautier-Hion et al. 1985, Howe and Primack 1975). However, due to their small size and feeding behavior, the wild animal species captured in this study can be considered only as possible dispersers. As a result of environmental disturbance and hunting, the number of species and the abundance of wild fauna have been drastically reduced in the study area. In fact, in this area the wild fauna were represented only by small animals that are not important for the dispersal of *Acrocomia aculeata*. In the Pantanal (a wetland area in Mato Grosso and Mato Grosso do Sul states, Brazil), where fruits of *A. aculeata* are smaller than in my study sites (personal observation), endocarps were found to constitute 63% of the volume of 69 fecal samples of *Cerdocyon thous* (crab-eating wolf, J. C. Dalponte, personal communication). Schaller (1983) also found endocarps in 22% of 36 fecal samples of *C. thous* in the same area. These observations implicate *C. thous* as a disperser of *A. aculeata* in the Pantanal, and perhaps in other areas where fruits are smaller than in my study area. In the Pantanal region, the macaws *Anodorhincus hyacinthinus* and *Ara chloroptera* feed on seeds and transport rachillae of *A. aculeata* with fruits attached, which eventually fall during the flight (*C. Yamashita*, personal communication). However, in



1. Oviposition by bruchid beetles on fruits of *Acrocomia aculeata* either chewed or not chewed by cattle. (A) Percentage of fruits oviposited. (B) Number of eggs per fruit.

my study area these species do not occur. Bates (1944) reported the vulture *Cathartes* sp. eating *Acrocomia* fruits, although nothing else is known about this species as a potential disperser.

Among domestic animals, only adult cattle that ingest the seeds and disperse them by regurgitation have importance as dispersers. This observation differs from Janzen's (1983a) observations in Costa Rica where he reported that the seeds were dispersed in the feces of cattle. The fact that horses, pigs, and young cattle partially remove the pulp without ingesting the seeds reduces the potential of additional dispersal because these fruits attract less or no attention from potential dispersers.

Long-distance dispersal or the wide distribution of this palm in the Neotropics are not explained by wild or domestic animals except for the adult cattle cited here. However, *Acrocomia aculeata* occurs only in disturbed habitats and it is possible that cattle herds moving along roads, in pasture lands and between farms are the major

contemporary seed dispersers. It is also possible that the wide geographic distribution results in part from use by Amerindians (Kozak et al. 1979, Hill et al. 1984, Baleé 1989), as South American Indians used seeds of *A. aculeata* (Levi-Strauss 1963), and the Chaco Indians used seeds of *A. totai* (Métraux 1963) as food. Also, Turner and Miksicek (1984) found a mineralized seed of *Acrocomia* in Maya sites in Guatemala, which suggests possible ancient use of the species by these people in Central America. Lentz (1990) suggested that it was introduced in some sites in Mexico and Central America by the Maya. It is also possible that *Acrocomia* is one of the large-seeded plant species whose fruits were consumed and dispersed by large Pleistocene mammals (Janzen and Martin 1982). According to this hypothesis, cattle are now an ecological analogue of these Pleistocene dispersers.

The strong odor from recently chewed fruits may serve as a cue for oviposition. The high rate of oviposition on individual fruits may be due to low fruit abundance in comparison to the female bruchid population. Indeed, a bruchid female can lay 50–100 eggs, serving an equal number of fruits (Janzen 1980). Oviposition on recently fallen fruits increases the probability that the first larva to reach the seed may have a competitive advantage over subsequent larvae. However, female bruchids that lay eggs on intact fruits are still available for fruit eaters that could destroy the eggs and young larvae. Thus, early oviposition can be advantageous for the insect in areas with either no or low density of fruit eaters. Conversely, regurgitated seeds may attract fewer consumers; in this way there is less risk for oviposited eggs or young larvae, but larvae have to face strong competition to reach the seed because oviposition is significantly higher.

The seeds of *A. aculeata* are poorly defended chemically (Janzen 1983b). However, they can escape predation in space via dispersal, and via morphology. Escape via dispersal may be affected in populations that have high levels of cattle chewing on fruits. However, fruits falling on the small, dispersed shrub patches occurring in the pasture may not suffer high bruchid oviposition as they cannot be reached by cattle (personal observation). Escape via fruit morphology arises due to the hard endocarps, which eliminate a large number of generalists (Janzen 1971), but

do not impede predation by specialized bruchids such as *Caryobruchus acrocomiae* and *Pachymerus* sp.

Acknowledgments

I am very grateful to Mr. Wantuil L. Werneck for his help in the field, to Dr. J. M. Kingsolver and the late Dr. Pedrito Silva for the identification of the bruchids. A. Henderson, G. R. Colli, and R. P. B. Henriques criticized the manuscript. Field support was received from US-AID (Grant PDC-5542-G-SS-5034-00) and from EMBRAPA (Grant PNPE 036.83.040/4). The author received financial support from CNPq through a fellowship.

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Amazon Palm Safari—August 4–15, 1997

In mid-August, 14 members of the International Palm Society, led by Dr. Andrew Henderson, Associate Curator of the New York Botanical Garden, participated in a palm-searching excursion along the Rio Negro in Brazil. Taking advantage of the Amazon dry season, the group arrived in Manaus after a five-hour flight from Miami where we were met and transported to a double-decked river boat, the "Harpy Eagle," our home base for the next ten days. Complete with air-conditioned, double cabins, this all-wood, typical Amazonian river boat, measuring 22 m long with a draft of 1.2 m, was constructed in local Amazonian shipyards.

Our modus operandi while on the river was to cruise upstream by night, anchor in the morning, and begin palm excursions in two motorized launches for hiking ashore or for taking trips up the multitude of streams and tributaries.