Seed Predation of *Attalea dubia* (Arecaceae) in an Island in the Atlantic Rainforest of Brazil

CARLA ELISABETE STEFFLER[1]

CAMILA IOTTE DONATTI[2]

AND

MAURO GALETTI[1]

[1]*Laboratório de Biologia da Conservação, Grupo de Fenologia e Dispersão de Sementes, Departamento de Ecologia, Universidade Estadual Paulista (UNESP), C.P. 199, 13506-900 Rio Claro, SP, Brasil, carlafrugi@yahoo.com.br*

[2]*Department of Biological Sciences, Stanford University, Stanford, California 94305 USA*

The palm *indaiá* (*Attalea dubia*) is endemic to the Atlantic rainforest of Brazil, and is important as a food source for the local fauna. This paper investigates aspects of seed predation and seed dispersal on a 15,100 ha island in southeastern Brazil.

The post-dispersal seed predation of arboreal tropical species is very high, varying from 75 to 90 percent (Howe et al. 1985, Schupp 1988a, b) and it is even higher close to mother trees (Janzen 1971, 1972). Seed predation depends on seed size, seed nutritional compounds (Osunkoya 1994, Fox & Mousseau 1995, Campbell 2002, Scherer & Romanowski 2005) and on the combined effects of density and distance from the mother plant (Janzen 1970, Burkey 1994, von Allmen et al. 2004). These are the main factors that determine the recruitment of new individuals (Janzen 1971) and contribute to the maintenance of plant diversity (Janzen 1970, Connell 1971, Augspurger 1983).

Rodents and insects that specialize in seed predation usually forage closer to mother plants (Janzen 1970, 1972, Howe et al. 1985, Traveset 1990, Peres et al. 1997). Rodents often remove and scatter-hoard seeds for later consumption (Forget 1990, Donatti 2004) and, as a result, some seeds can germinate if the rodent forgets the seeds it caches. This behavior makes the rodents important seed dispersers (van der Wall 1992); the scatter-hoarded seeds show a higher survival and germination rate in comparison to seeds left in the soil (Smythe 1989, Forget 1990, Forget & Milleron 1991, Asquith et al. 1999, Silva & Tabarelli 2001).

Forest fragmentation, poaching and palm harvesting are the main factors that negatively affect fruit-eating mammals (Johns 1988, 1991, 1992, Peres 2000). In impoverished (defaunated) areas that completely or partially lose their herbivores, seed dispersers or seed predators, there is a decrease in seed removal (Asquith et al. 1999, Guariguata et al. 2000, Wright et al. 2000, Forget et al. 2001, Galetti et al. 2006), as well as a decrease in seed dispersal and predation by vertebrates (Wright et al. 2000, Bleher & Bohning-Gaese 2001). The consequences of defaunation then, are increases in the seedling density and survival below the parent tree, resulting in decreases of plant diversity in the long term (De Steven & Putz 1984, Dirzo & Miranda 1991, Wright & Duber 2001, Wright 2003, but see Asquith et al. 1997, Róldan & Simonetti 2000 for different results).

The Atlantic rainforest of Brazil is considered a very highly endangered biome and the areas in southeastern Brazil are the most disturbed (Dean 1996). The vertebrate-dispersed plant species (representing 86% of trees in the Atlantic forest, Campassi 2006), such as palms, can suffer in the absence of herbivores, seed predators and dispersers (Donatti 2004, Galetti et al. 2006). According to Galetti et al. (2006), 45% of all palm species dispersed by scatter-hoarding rodents in the Atlantic rainforest may face problems in population recruitment due to defaunation effects, i.e. the loss of seed dispersers. The population crash of palms may have strong cascading effects on the whole community (Peres 2000).

Palms are important because they present a low fruiting synchrony, unlike other vertebrate-dispersed plants (Terborgh 1986, Peres 1994, Galetti 1996), and also because of the high energy value of their fruits (Zona & Henderson 1989). Bruchid beetles depend on palm seeds because they thrive on the nourishment of the seeds during a large part of their life cycle (Johnson & Romero 2004). These beetles may use 60 to 90 percent of all fruits found beneath the mother plant, mainly in the beginning of the fruiting season (Forget et al. 1994, von Allmen et al. 2004).

We investigated the seed dispersal and predation of the Atlantic forest endemic palm, the indaiá *Attalea dubia*: (1) the importance of seed predators; (2) the selection of bruchid beetles *Pachymerus* sp. and rodents on the pyrene size; (3) the proportion of seed predation by beetles in the pyrenes with one or two seeds; (4) the variables that affect seed predation and (5) the seed dispersal of scatter-hoarding rodents. The pyrenes are structures that comprise the endocarp and the seeds in palm fruits.

Materials and Methods

Study site. The study was carried out at Ilha do Cardoso (25º03'S; 47º53'W), Cananéia, São Paulo, Brazil. Observations on seed predation were made in May 2003 and on seed removal in September 2003. The climate is subtropical and the annual rainfall can exceed 3,000 mm. The area is 15,100 ha and has many forest formations, from beaches to highland forests (Noffs & Baptista-Noffs 1982). The diversity of mammals and birds in the Ilha do Cardoso is high, including important seed dispersers of palm trees, e.g. *Attalea dubia*, such as squirrels (*Sciurus ingrami*) and agoutis (*Dasyprocta leporina*) (Bernardo & Galetti 2004). However, the island suffered intense poaching that resulted in the extinction of the jaguar (*Panthera onca*) and the tapir (*Tapirus terrestris*) in the past and nowadays is threatened by Mbya Indians (Olmos et al. 2004).

Study species. The indaiá palm *Attalea dubia* occurs in secondary forests and in open and disturbed areas (Henderson et al. 1995). The individuals have one stem from 15 to 25 meters high and a diameter of 20 to 30 cm. The fruits are fleshy, with a fibrous mesocarp and a hard endocarp, and generally contain only one seed (Reitz 1974). The pyrenes are 23.0 ± 2.5 mm in diameter and 38.4 ± 3.5 mm in length (n= 307). Lorenzi (1996) indicated that this species can bear fruits all year round, yet predominately during spring and summer.

Seed predation. We evaluated the importance of the seed predation by bruchid beetles and rodents by collecting all the pyrenes found within a 3 m radius from the mother palm beneath nine *Attalea dubia* palms. The pyrenes were visually classified as: **intact**, when there were no signs of seed predation; **preyed on by beetles**, when entry or exit holes of larva or adults were present (the entrance hole is much smaller than the exit hole, but can still be easily identified), **preyed on by rodents** when we found teeth marks in the endocarp (Cintra 1997, Wright et al. 2000, Wright & Duber 2001); and **germinated**, when the root in the germinative hole was present. To verify the effect of the density of pyrenes beneath the mother palm on the proportion of seed predation, we used a Spearman correlation test.

All pyrenes collected were opened for an examination of the seed condition and were classified in the same four categories: intact, for no sign of predation; preyed on by beetles, when the pyrenes presented a larva or an adult inside them; preyed on by rodents; and germinated, when no seeds were found inside the pyrenes and these did not present entry or exit holes. The difference between the apparent evaluation of the pyrenes (visual) and their real state (when we opened them) was analyzed using a Chi-square test.

In order to test if the predators selected the pyrenes for size, we measured the diameter and the length of all pyrenes that we collected. We compared the measurements between predated pyrenes by rodents and beetles using an ANOVA (one factor) and Multiple Comparisions (Tukey).

The following variables were examined around the mother palm from which we collected the pyrenes, because they could have some effects in the proportion of seed predation. We then used a Multiple Regression Analysis (Stepwise) to relate these variables with the proportion of seeds preyed on by rodents and beetles:

Number of adult palms of *A. dubia* within a 10 m radius of the mother plant;

Distance from the closest adult of *A. dubia* (maximum distance: 20 m);

Average canopy cover (percent) at four points (N, S, E, W), 3 m distance of the mother palm;

Average leaf litter depth at four points (N, S, E, W), 3 m distance of the mother palm;

Number of fallen trunks with a breast high diameter of more than 5 cm., within a 5 m radius of the mother plant;

Number of juveniles of *A. dubia* with a breast high diameter of more than 10 cm., within a 10 m radius of the mother palm;

Distance from the closest treefall gap (maximum distance: 20 m.).

Seed removal and fate experiment.

Fruits of *A. dubia* were collected from ten individuals, the pulp was removed manually and the seeds were inspected for insect infestations. Only the uninfested seeds were exposed to the animals. Pulp consumers are not likely to remove seeds without pulp; therefore, only the interactions between the rodents and the seeds were investigated to measure the seed removal, dispersal and predation of *A. dubia*. All seeds received an individual code for identification.

We observed the fate of the seeds through this system of marking: by attaching threads to the seeds we observed their fate by using a modified version of the spool and line method (Donatti 2004). Each seed was threaded with a line spool that was placed inside a small box, allowing the line to unroll easily when the seed was removed. Ten of these boxes (each one with one seed attached) were fixed in one palm stem that represented one experimental station. Each experimental station was located beneath a randomly selected fruiting palm. We worked with 10 experimental stations. Palms closer than 50 m of other selected palms or within 10 m of other conspecific adults were not selected for the experiment. Due to the fast removal of seeds during the pilot study using other species of palm trees (Donatti 2004), we searched the area and followed the threads to locate the seeds after seven days. The seeds were placed on the forest floor, just after the period of fruit fall (December 2002 to February 2003).

Each spool line was 35 m long; this length was based on previous work, which showed this distance to be the maximum that rodents usually disperse seeds (Forget 1990, Peres et al. 1997, Forget et al. 2000, Pimentel & Tabarelli 2004, but see Hallwachs 1986). Intact seeds were defined to be seeds not removed from the experimental stations. Removed seeds were categorized as either dispersed or preyed upon. Dispersed seeds were separated into two subgroups: seeds dispersed in the litter (seeds removed but left in the litter) or scatter-hoarded seeds (buried or found beneath the leaf litter). Seeds totally or partially destroyed were considered preyed upon by rodents.

Results

Seed predation. We collected 900 pyrenes beneath nine individuals of *A. dubia*, with the follow apparent (visual) predation: 41.9% were intact, 48.9% showed signs of predation by beetles, and 3.2% were empty and did not present any sign of predation. Rodents preyed on only 5.9% of the pyrenes. However, these animals may carry seeds far from the mother plant (Forget 1990, Forget & Milleron 1991), suggesting that this data might be an underestimate.

We found a positive correlation between the number of pyrenes collected and the number of pyrenes preyed upon (rs=0.883; p=0.002), which means that we found more seed predation in palms that presented a high availability of seeds. We also compared the apparent (visual) evaluation of pyrenes with the true evaluation (actual state when we opened the pyrenes): in a random sample of 247 pyrenes out of the 900 collected, we found that 18.6% were classified in a different state when opened. We found a difference between the apparent evaluation and the real evaluation of the pyrenes that we analyzed (c^2=30.205; p=0.000).

Seed predators selected the size of pyrenes: The vertebrates preyed on pyrenes with the largest diameter (F=6.128; p=0.002) while beetles prefer the ones with the largest length (F=13.25; p=0.000). In relation to the number of seeds inside the pyrenes, 96% of the pyrenes that we opened had one seed and 4% had two seeds. In relation to pyrenes with two seeds, 33.3% of them had one seed preyed upon by beetles, while the other remained intact; 50.1% had both seeds intact and 16.6% had both preyed upon.

We found a negative relationship between the distance from the closest adult of *A. dubia* and the proportion of seed predation by beetles beneath the mother palm (F=7.17; p=-0.032); i.e., the predation by beetles is higher within a shorter distance between palms. We did not find any relationship between the variables that we measured and the seed predation by vertebrates.

Seed removal and fate experiment. There was no seed removal after seven days, suggesting that seed removal by rodents in the study site had little role in aspects of seed dispersal and predation, at least in the period observed. A similar experiment with *Astrocaryum aculeatissimum* using the same period of seed exposure had 36% of removal (Donatti 2004, Galetti et al. 2006).

Discussion

We found that beetles are the most important seed predators of *Attalea dubia* at Ilha do Cardoso. This may be because beetles are more specialized (Janzen 1980), while rodents can feed on a variety of different food resources (Paschoal & Galetti 1995, Silvius & Fragoso 2003). Nevertheless, squirrels (*Sciurus ingrami)* that are considered the main seed predator and disperser of the palm *Attalea dubia* (Voltolini 2004), are uncommon on Cardoso Island (Bernardo & Galetti 2004). Understanding the impact of vertebrates and invertebrates on seed predation is important because vertebrates can adversely impact the populations of invertebrates close to the mother plant (Herrera 1989, Traveset 1992). Our data indicate that the low rate of predation and absence of seed removal by rodents or other large seed dispersers (such as tapirs) can contribute to the high rates of seed predation by beetles beneath the mother plants.

Janzen (1970) suggested that the seed mortality increases with the proximity of a reproductive adult, and this relation was also clear in several other studies (Wilson & Janzen 1972, Wright 1983, Schupp 1988b). Our data indicate that predation by beetles is higher in areas with more availability of seeds and also in palms that have close conspecific adults.

In five apparently intact pyrenes, we found either larva or adult beetles. It is possible that the fibers covering the pyrene hide the holes made by this invertebrate because there is a high growth of fibers in pyrenes that suffered damage (C.E. Steffler, personal observation). Some pyrenes proved to be intact regardless of the obvious small holes in their endocarps. These data echo the consideration brought up by Pires (2006) that it is important to open the pyrenes for a clear understanding of their real state, but few studies have done this (Wright et al. 2000).

Besides the selection in the pyrene size by beetles (Fox & Mousseau 1995, Campbell 2002, Scherer & Romanowski 2005), Westoby et al. (1992) showed that rodents prefer the largest seeds. In the case of scatter-hoarding rodents, they can be limited by the weight of the pyrenes. Our data show that the pyrenes selected by beetles have the largest diameter while the ones selected by rodents have the largest length, indicating that this preference may occur because rodents can better handle pyrenes with this shape.

Even though most of the pyrenes of *Attalea dubia* have only one seed (Reitz 1974, Voltolini 2004, this study), pyrenes with two seeds have the highest chance of escaping predation (Bradford & Smith 1977) because they are only partially attacked. Our data agree with these findings because 33.3% of the pyrenes with two seeds were just partially predated, meaning that fruits with more than one seed do not always have all seeds attacked by beetles. The presence of two or more seeds per fruit can be a strategy for escape of predation (Bradford & Smith 1977, Scherer & Romanowski 2005). Therefore, the combined effects of the behavior of rodents and the high seed predation by beetles can be a consequence of pyrene size in this species.

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About the Covers

The stunning images on the covers and table of contents page come to us from IPS member Angela Blakely of Hawaii. Angela wrote, "Growing up in inland Southern California and seeing the same old landscape palms – *Phoenix canariensis*, *Syagrus romanzoffiana*, *Washingtonia robusta* – over and over again, I never paid much attention to the colors of palms. For me they were always green. When I later learned that *C. macrocarpa* has a red emergent leaf, my first response was disbelief! My second was, 'Where can I get my hands on one?' The red new leaf of *C. macrocarpa* was a revelation. From the moment I laid eyes on that red leaf I was transformed into an enthusiast." She went on, "As an artist, I am drawn to the intense colors of tropical foliage… Many of the palms with red emergent leaves are so eye-catching that they have really inspired me to share their beauty through my photography." Angela now lives in Hawaii, on the Big Island, where, as she said, "a whole new colorful world of palm options is open to me."

Angela's favorites include *Chambeyronia macrocarpa* (Front Cover) and *Welfia regia* (Back Cover). "I shall never forget the first time I saw a *Welfia regia* in habitat during the IPS Biennial in Costa Rica," Angela wrote. "We were in an aerial tram traveling through the trees of the predominantly green rain forest. I looked down and saw a bright red new leaf of *W. regia*. It was spectacular, a bright red beacon in a sea of green." Of *Chambeyronia*, Angela wrote, "I have three 6-m (20-ft.) tall *C. macropcarpa* that are five-years old and have been planted as a group. We are still waiting for a 'trifecta' of color, for all three to push out new leaves at the same time; so far, we have had no such luck."

Actinokentia divaricata (Table of Contents, p. 107) is another of Angela's favorites, along with the "Mad Fox," *Dypsis marojejyi*. Of the latter, she wrote, "Its changing beauty reminds me of a sunset. As the new frond just barely starts to open, some parts catch the light and almost glow a brilliant orange, especially on overcast days. At first, the leaf shifts from orange-red to red. After the leaf opens fully, it changes to a burgundy color. As it matures, it becomes increasingly purple. Eventually the sunset ends, and it finally fades to green." Angela has posted a number of her beautiful images of red new leaves on PalmTalk, but we cannot resist one last image (below), that of the new leaf of *Calyptrocalyx lauterbachianus* with contrasting bright green stripes on the leaflets.

– The Editors