

SHORT COMMUNICATION

Seed predation under high seed density condition: the palm *Euterpe edulis* in the Brazilian Atlantic Forest

Christiane von Allmen, L. Patricia C. Morellato and Marco A. Pizo¹

Departamento de Botânica, Plant Phenology and Seed Dispersal Group, Universidade Estadual Paulista (UNESP), C.P. 199, 13506-900, Rio Claro, São Paulo, Brasil
(Accepted 16 June 2003)

Key Words: Arecaceae, Atlantic Forest, *Euterpe edulis*, seed predation

Over recent decades, studies on post-dispersal seed predation have revealed some general patterns despite dealing with a highly variable phenomenon (reviews in Crawley 1993, Hulme 1998). Most of these studies, however, were carried out with plant species whose population density range from low to moderately high (Hulme 1998). Only rarely has seed predation been studied in very dense stands of a given plant species (Schupp 1988*a, b*, 1992). In such a situation, seed predators might respond to the local availability of seeds in a manner that differs from their response under conditions of low seed density. For instance, a high density of seeds beneath a fruiting plant may attract seed predators, causing a positive correlation between predation and seed density (Janzen 1970). Schupp (1992), however, noted that at a population scale, a high density of seeds could satiate predators, resulting in a negative correlation between predation and seed density (see also Burkey 1994).

Therefore, empirical studies encompassing the full range of possible natural seed densities will aid in understanding the responses of seed predators and the possible consequences of seed predation to plant populations. With this in mind, we examined a very dense population of the palm *Euterpe edulis* Mart. in the Atlantic Forest of south-east Brazil to investigate seed exploitation by insect and rodent seed predators. We specifically asked: (1) does seed predation vary temporally from the beginning to the end of the palm fruiting season? Other studies indicate that, as a result of predator satiation, predation pressure on seeds may vary through the fruiting season (Forget *et al.* 1999, Wright 1990); (2) does seed predation vary spatially among distinct microhabitats within the forest? It has been shown that seed survival

might differ among distinct microhabitats if seed predators use them non-randomly (Kiltie 1981, Whelan *et al.* 1991, Willson 1988); and (3) do seeds beneath fruiting plants embedded in a matrix of overall high seed density suffer high predation?

We conducted this study from May to October 2000 and May to August 2001 in the lowland Atlantic Forest (Saibadela Research Station; 24°14'S, 48°04'W; 70 masl) of the Parque Estadual Intervales (PEI), a 49 000-ha reserve located in São Paulo state, south-east Brazil. The site receives a mean annual rainfall of over 4000 mm, with rains well distributed throughout the year; no month receives less than 100 mm of rainfall. A period of less-intense and less-frequent rains occurs between April and August, roughly coinciding with the fruiting period of *E. edulis* (see below). Average (\pm SD) minimum and maximum daily temperatures for the period 1994–1996 are 20.8 \pm 2.5 °C, and 25.7° \pm 2.8 °C, respectively. The forest is predominantly old-growth forest (*sensu* Clark 1996) with an open understorey and canopy height of 25 m, with a few emergent trees reaching 30 m high (Almeida-Scabbia 1996).

Euterpe edulis is widespread in the Atlantic Forest. It inhabits the coastal forest from 15° S to 29° S and penetrates into the interior through gallery forests to reach Paraguay and Argentina (Henderson *et al.* 1995). Individual palms produce 1–5 infructescences annually bearing on average over 3000 fruits each (Mantovani & Morellato 2000). Fruits are globose drupes containing a single seed (mean \pm SD = 13.5 \pm 1.3 mm length, 14.2 \pm 1.2 mm width, $n = 10$) covered by a thin black pulp. Fruits are eaten by a variety of animals, including birds and mammals, which disperse the seeds effectively (Galetti *et al.* 1999).

Saibadela Station has a dense population of *E. edulis* (256 plants (dbh > 5 cm) ha⁻¹; Almeida-Scabbia 1996). During the 1995 fruiting season, a total of 10.5 seeds

¹Corresponding author. E-mail: pizo@rc.unesp.br

m⁻² dropped on the floor of Saibadela forest, and during the 1996 fruiting season, *E. edulis* was responsible for 17–98% of the monthly fleshy fruitfall (in terms of fresh weight) (M. A. Pizo, unpubl. data). Fruit maturation in the study site generally extends from April to September, peaking in June–July (Galetti *et al.* 1999).

Post-dispersal predation of *E. edulis* seeds at Saibadela is caused by a scolytid beetle (*Coccotrypes palmarum* Eggers 1933, Scolytidae) and rodents (Pizo & Simão 2001). *Coccotrypes* are specialized at exploiting palm seeds (Janzen 1972). Adults of *C. palmarum* were present in 96.6% of the 268 insect-attacked seeds of *E. edulis* collected on the floor of the study site, the remainder being infested by larvae of an unidentified insect (Pizo & Simão 2001). Seeds of *E. edulis* offered to non-starved captive rodents were completely consumed by *Nectomys squamipes* and *Oryzomys intermedius*, the two most abundant rodents at the study site (Vieira 1999). Both of these species are diet generalists, eating a variety of fruits, seeds and invertebrates (Emmons & Feer 1997, E. M. Vieira, unpubl. data).

To investigate temporal variation in the proportion of seeds preyed upon by insects and rodents, a group of five seeds was placed at each of 63 experimental stations arranged linearly 2–3 m off-trail along three 1-m-wide trails that crossed the study site. Stations were spaced at least 50 m apart. Seeds used in this experiment and in experiments described below were collected on the floor of the Saibadela forest. Most had been regurgitated by birds and none showed signs of predation by rodents or insects. Seeds were set at the beginning (May), peak (July) and end (September) of the 2000 fruiting season. For each of these periods, the number of seeds removed by rodents and/or preyed upon by insects was checked 1 mo later. After 1 mo seeds usually began to germinate. The high abundance of rodents (Vieira 1999) coupled with the general low abundance of other seed-eating vertebrates at the study site makes rodents the most likely seed remover. We considered seeds not found within 30 cm of their original position or seeds found but cracked to have been preyed upon by rodents. Insect predation was indicated by the typical entrance hole left by adult beetles boring into the seeds. Unless rodents avoid insect-infested seeds, it is possible that we underestimated insect predation if insect-infested seeds were removed by rodents prior to our censuses (see Silvius 2002).

Spatial variation in the proportion of seeds preyed upon by insects and rodents was investigated separately by setting out groups of five seeds in experimental stations located in five different microhabitats: (1) along old fallen trunks whose canopy gap has closed over, (2) open tree-fall gaps ranging in area from 28.2–1215.0 m² (mean \pm SD = 205.6 \pm 446.3 m²), (3) along stream margins (< 1 m from water), (4) at the bases of buttressed trees and (5) in the forest understorey, with

none of the previous microhabitats nearby. We followed 20 replicates per microhabitat. Each experimental station was at least 50 m from others, and at least 5 m from any fruiting palm. Seeds were set at experimental stations during peak fruit production in July 2000, and the number of predated seeds was checked 1 mo later.

In the two previous experiments, we could easily differentiate between experimental seeds and seeds that might have fallen into the area during the intervening month because *E. edulis* seeds exposed to weather became darker with time.

We tested the effect of the proximity to a fruiting plant by selecting 25 fruiting palms of *E. edulis* and establishing two experimental stations at each, one directly under the palm canopy, and the other 5 m from either the focal palm or any other fruiting palm. Given the high density of *E. edulis* in the study area, it is hard to be more than 5 m away from any fruiting palm. The ‘away’ treatment experienced the overall high *E. edulis* seed density characteristic of Saibadela forest, while the ‘under’ treatment experienced even higher seed density conditions. To reduce the chance of underestimating insect predation as explained above, we applied exclusion and non-exclusion treatments to each station. In the exclusion treatment seeds were set under a wire cage (16 \times 16 \times 9 cm, 1-cm mesh) that only permit access by insect seed predators, while in the non-exclusion treatment both vertebrate and invertebrate seed predators had access to seeds. The exclusion treatment provided the amount of insect predation, while the number of seeds removed from the non-exclusion treatment was the figure for vertebrate predation. At each station, the two treatments, each with five seeds, were 30 cm apart. Due to the constant input of seeds from the fruiting plant, we differentiated experimental seeds by marking them with a small dot of white enamel paint. Seeds were set at stations during the peak of the 2001 fruiting season in July and the number of predated seeds was recorded 1 mo later.

We separately examined seed exploitation by rodents and insects as the proportion of seeds preyed upon by each of these seed predators at a given station. We used Kruskal–Wallis tests to analyse temporal and spatial variation in seed exploitation. To investigate the influence of proximity to a fruiting tree on seed exploitation patterns, we used Wilcoxon paired-sample tests to compare under and away treatments. All tests were performed using Statistica[®], version 5.5.

Seed exploitation by insects did vary through the fruiting season ($H = 22.1$, $df = 2$, $P < 0.001$), decreasing from the beginning to the end of the fruiting season. Seed removal by rodents also varied ($H = 9.91$, $df = 2$, $P = 0.007$), but tended to increase (Figure 1). Microhabitats did not differ significantly in seed exploitation, either

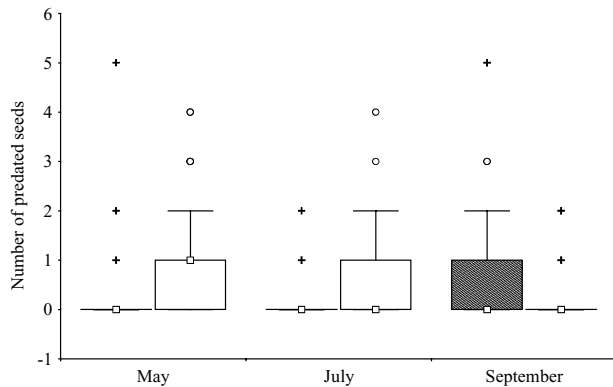


Figure 1. Box-and-whisker plots showing the number of *Euterpe edulis* seeds preyed upon by insects (opened boxes) and rodents (filled boxes) per experimental station set at the beginning (May), peak (July) and end (September) of the 2000 fruiting season at the Saibadela forest, Parque Estadual Intervales, south-east Brazil. Sixty-three stations were set at each period, each station with five seeds. Represented are medians (small squares), first-third quartile ranges (boxes), non-outlier ranges (set at $\pm 1.5 \times$ the height of the box; vertical lines), outliers (circles) and extreme values (crosses).

by insects ($H = 5.62$, $df = 4$, $P = 0.23$) or by rodents ($H = 7.47$, $df = 4$, $P = 0.11$). Similarly, predation on seeds placed under and away from fruiting trees did not differ for either insects or rodents ($Z_{\text{insects}} = 0.03$, $df = 1$, $P = 0.98$; $Z_{\text{rodents}} = 1.01$, $df = 1$, $P = 0.31$).

Above results showed that predation of *E. edulis* seeds by rodents and insects at the Saibadela forest was by no means homogeneous in time and reflected patterns already detected in other studies. Seed exploitation by insects was more intense at the beginning of the *E. edulis* fruiting season, decreasing towards its end. A similar pattern was found by Wright (1990) and Forget *et al.* (1999) for different plant and insect species. Such a pattern may occur when only one generation of the insect seed predator develops during the fruiting season of its plant host. As a consequence, predators become gradually satiated and late-fruiting plants experience a decreasing amount of seed predation (Wright 1990).

Rodents, in contrast to insects, preyed more intensively upon seeds at the end of the *E. edulis* fruiting season. Forget *et al.* (1994) similarly found that rodents preyed more heavily upon seeds of *Attalea butyracea* (= *Scheelea zonensis*) at the end of its fruiting season, possibly influenced by the generally low availability of alternative seeds at Barro Colorado Island, Panama. The same mechanism may underlie the activity of rodents as predators of *E. edulis* seeds at Saibadela. Working for 6 y at the site, we noted a general scarcity of fruits at the end of the drier period (August–September), which corresponds to the end of the *E. edulis* fruiting season.

As a consequence of the contrasting temporal patterns of seed predation caused by insects and rodents, *E. edulis*

seeds dispersed at the middle (peak) of the fruiting season appear to have a greater chance of survival than those dispersed at the beginning or at the end of the fruiting season because they are subjected to an overall low probability of predation (pooled percentages of preyed seeds at the beginning, middle and end of the fruiting season: 22%, 11% and 17%, respectively).

Seed predation either by rodents or insects did not vary substantially among different microhabitats or in relation to the proximity to an adult fruiting tree. Several studies have shown that vertebrate seed predators, including rodents, concentrate their foraging activities in certain microhabitats of the forest, leading to spatial variation in survival probabilities for seeds (Kiltie 1981, Whelan *et al.* 1991, Willson 1988). Microhabitat use by vertebrate seed predators is partially influenced by the availability of seeds. Density-responsive rodents, for instance, concentrate their activities beneath fruiting plants where they usually find many seeds (Janzen 1970, Peres *et al.* 1997). Given the high abundance of *E. edulis* seeds at Saibadela, it is not surprising that little spatial variation in seed removal was detected. Rodents probably find seeds everywhere in the forest and have no necessity to search for seeds in a particular microhabitat, be it under a fruiting palm or anywhere else. Our results are similar to those obtained by Schupp (1988a, b, 1992), who investigated the predation of *Faramea occidentalis* (Rubiaceae) seeds by vertebrates at Barro Colorado Island (BCI) in Panama. *Faramea* occurs in variable densities at BCI ($< 30 \rightarrow 300$ adults ha^{-1}), and Schupp (1988b, 1992) found that seed survival 5 m from adults is greater than survival beneath adults at low to moderate adult densities, but not at very high densities of adults (i.e. ≥ 200 adults ha^{-1} ; Schupp 1988a).

Even more than generalist rodents, specialist insect seed predators tend to concentrate their activities beneath fruiting plants (Howe *et al.* 1985, Janzen 1972, Pizo 1997, Traveset 1990). At Saibadela, however, *C. palmarum* equally infested seeds placed under or 5 m away from *E. edulis* fruiting trees. Once again, we believe that the spatial homogeneity in insect seed predation was influenced by the high availability of *E. edulis* seeds. Under such conditions, insects may find seeds not only under fruiting plants but everywhere in the forest.

Therefore, under the conditions of high seed density experienced by *E. edulis* seeds at Saibadela, escaping predation is more a question of when a seed is dispersed than of where it is deposited. If the timing of fruit ripening is under genetic control (see Forget *et al.* 1994, Wright 1990), and seed predation indeed limits recruitment in such a high-density *E. edulis* population (see Andersen 1989), then seed predation may represent a selective pressure favouring the synchronicity of fruit production.

ACKNOWLEDGEMENTS

We are grateful to the Fundação Florestal do Estado de São Paulo, especially to Jeannete V. Geenen, for making possible our work at Parque Intervales. We thank Valesca Zipparro who kindly collected many *E. edulis* seeds, and Mauro Galetti for the cages used in the enclosure experiments. We also thank Peter Feinsinger, Eugene Schupp, and two anonymous reviewers for critical comments which greatly improved the manuscript. Financial support came from fellowships from CAPES, FAPESP (no. 98/11185-0), and CNPq to CvA, MAP, and LPCM, respectively, and from a FAPESP grant (no. 95/0269-6) for fieldwork. Data analysis was facilitated by support from FAPESP at UNESP/Rio Claro. The facilities provided by the Departamento de Botânica of this Institution to MAP made possible the preparation of this paper.

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