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## Original article

# Seed size variation in the palm *Euterpe edulis* and the effects of seed predators on germination and seedling survival

Marco A. Pizo<sup>a,\*</sup>, Christiane Von Allmen<sup>b</sup>, L. Patricia C. Morellato<sup>b</sup>

<sup>a</sup> Programa de Pós-graduação em Biologia, Universidade do Vale do Rio dos Sinos (UNISINOS), Centro 2, Av. Unisinos, 950, 93022-000 São Leopoldo-RS, Brazil

<sup>b</sup> Departamento de Botânica, Plant Phenology and Seed Dispersal Group, Universidade Estadual Paulista (UNESP), C.P. 199, 13506-900 Rio Claro, São Paulo, Brazil

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## ABSTRACT

Intraspecific variation in seed size is common in wild plant populations and has important consequences for the reproductive success of individual plants. Multiple, often conflicting evolutionary forces mediated by biotic as well as abiotic agents may maintain such a variation. In this paper we assessed seed size variation in a population of the threatened, commercially important palm *Euterpe edulis* in southeast Brazil. We investigated (i) how this variation affects the probability of attack by vertebrate and invertebrate post-dispersal seed predators, and (ii) if seed size influences the outcome of seeds damaged by beetles in terms of seed germination and early survival of seedlings. *Euterpe edulis* seeds varied in diameter from 8.3 to 14.1 mm. Neither insects nor rodents selected the seeds they preyed upon based on seed size. Seed germination and total, shoot and root biomasses of one-year seedlings were significantly and positively affected by seed size. Root biomass and seedling survival were negatively affected by seed damage caused by a scolytid beetle (*Coccotrypes palmarum*) whose adults bore into seeds to consume part of the endosperm, but do not oviposit on them. Seed size had a marginally significant effect on seedling survival. Therefore, if any advantage is accrued by *E. edulis* individuals producing large seeds, this is because of greater seed germination success and seedling vigor. If this is so, even a relatively narrow range of variation in seed size as observed in the *E. edulis* population studied may translate into differential success of individual plants.

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## 1. Introduction

Considerable seed size variation often occurs within a plant species, with important consequences for the reproductive success of individual plants (Harper, 1977; Stanton, 1984; Silvertown, 1989). Multiple factors may maintain such variation. For instance, large seeds may be favored because they

produce larger and more vigorous seedlings with better chances of survival than small seeds (Howe and Richter, 1982; Moegenburg, 1996; Khan, 2004; Moles and Westoby, 2004). Small seeds, however, may be ingested and dispersed more often (Levey, 1987), may be dispersed by a wider range of seed dispersers (Moermond and Denslow, 1985), and may be dispersed longer distances (Pizo and Oliveira, 2001) compared to large seeds. On the other hand, because resources for producing seeds may be limited, small seeds are generally produced in great numbers than large ones (Smith and Fretwell, 1974). Therefore, conflicting evolutionary forces

\* Corresponding author.

E-mail address: [mapizo@unisinos.br](mailto:mapizo@unisinos.br) (M.A. Pizo).

mediated by biotic as well as abiotic agents potentially act upon plants to produce the seed size distributions observed in natural plant populations (Harper, 1977; Foster, 1986).

Seed predators, either vertebrates or invertebrates, may be among the most important selection agents acting on seed size because they may choose large seeds that offer a better cost-benefit balance (Janzen, 1969; Ernst et al., 1989; Moegenburg, 1996; Brewer, 2001). These so-called seed predators may not always cause seed death, however, but instead may act as parasites (Hulme, 1998). Some seed species, including both tropical (Dalling et al., 1997; Harms and Dalling, 1997; Mack, 1998; Dalling and Harms, 1999) and temperate species (Ollerton and Lack, 1996), are able to germinate and produce healthy seedlings despite some degree of damage (that may reach 80%) of their cotyledonary tissue (Mack, 1998). Some seeds even have enhanced germination after damage (Karban and Lowenberg, 1992), and, in an extreme example of such relationship, insects boring into hard seeds with impermeable seed coats act as scarification agents and are essential to seed germination (Takakura, 2002). The outcome of the interaction, i.e. whether the seed is able to sustain a given level of cotyledonary damage, may depend on seed size. Artificially cutting portions of the cotyledon of several seed species (ranging in size from 4 to 180 g) from a forest in Papua New Guinea, Mack (1998) found that larger seeds are more likely to survive after damage. Similarly, Harms and Dalling (1997) observed that only seeds larger than 5 g were able to produce seedlings that resprout after simulated herbivory (see also Khan, 2004). This led to the development of the hypotheses that large seed sizes observed in many tropical tree species is an adaptation to resist herbivory (Mack, 1998).

In the present paper we assessed seed size variation in a population of the palm species *Euterpe edulis* Martius in southeast Brazil, and investigated how this variation affects the probability of attack by rodent and scolytid-beetle post-dispersal seed predators. Under greenhouse conditions, we investigated whether seed size affects the ability of beetle-damaged seeds to germinate and their seedlings survive. Our ultimate goal was to identify factors likely responsible for the maintenance of seed size variation we observed in the *E. edulis* population.

## 2. Study site and species

The study took place in the lowland Atlantic Forest (Saibadela Research Station; 24°14'S, 48°04'W; 70 m asl) of the Parque Estadual Intervales (PEI), a 49,000-ha reserve located in São Paulo state, south-east Brazil (see description of the site in Almeida-Scabbia, 1996; Guilherme et al., 2004). Annual rainfall is around of 4000 mm. Although there is not a really dry period, a cooler and less humid season occurs between May and September, and a warm, very wet season between November and April. The vegetation is predominantly evergreen old-growth forest (sensu Clark, 1996); the understory is open and the canopy is 25–30 m tall. Saibadela Station has a dense population of *E. edulis* (255.6 plants [dbh > 5 cm] ha<sup>-1</sup>; Almeida-Scabbia, 1996), which produces thousands of fruits annually (Galetti, 1996; Von Allmen et al., 2004). Fruits

are eaten by a variety of animals, including birds and mammals, which disperse the seeds (Galetti et al., 1999). Fruit maturation in the study site generally extends from April to September, peaking in June–July (Galetti et al., 1999).

*Euterpe edulis* fruits are globose drupes containing a single rounded seed which averages 12 mm in diameter (see below). Post-dispersal predation of *E. edulis* seeds at Saibadela is by a scolytid beetle (*Coccytrypes palmarum* Eggers 1933, Scolytidae), and rodents (Pizo and Simão, 2001; Von Allmen et al., 2004). Adults of *C. palmarum* bore into seeds to consume part of the endosperm, but do not oviposit on them. It is the predominant insect predator of *E. edulis* seeds at the study site, being present in 96.6% of 268 insect-attacked seeds collected from the forest floor; the remainder were infested by larvae of an unidentified insect (Pizo and Simão, 2001). Although up to four entrance holes could be found in a single seed, thus denoting multiple infestations, 75% of 509 insect-attacked seeds had only one hole (M.A. Pizo, unpublished data). Feeding trials with captive rodents performed at the study site showed that rodent species larger than 70 g, which includes the locally most abundant species (*Nectomys squamipes* and *Oryzomys intermedius*), consume and totally destroy *E. edulis* seeds (Vieira et al., 2003).

## 3. Methods

To assess seed size variation in the *E. edulis* population we collected 136–515 ripe fruits from each of 10 individual palms and removed the thin mesocarp that covers the seed. For each seed we measured the diameter with a caliper to the nearest 0.01 mm. We used the seed diameter to categorize seed size because it could be easily and accurately measured under field conditions, and was highly correlated with seed weight (Pearson correlation on log-transformed data:  $r = 0.94$ ,  $n = 52$ ,  $P < 0.001$ ). We then investigated the influence of seed size on the probability of predation by insects and rodents using the extremes of the size distribution. Small seeds were < 11 mm in diameter (24.7% of the 2364 seeds measured), whereas large seeds were those with a diameter > 13 mm (12.8% of the seeds).

In May 2001 seed groups consisting of three large and three small seeds were placed at each of 62 experimental stations arranged linearly 2–3 m off-trail along 1-m-wide trails that crossed the study site. Stations were marked with wooden stakes, and were set at least 50 m from each other. The number of seeds removed by rodents and/or preyed upon by insects was checked one month later. After one month 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 removers. We considered seeds not found within 30 cm of their original position or seeds found but cracked to have been preyed upon by rodents. Available evidence indicates that rodents do not act as secondary dispersers of *E. edulis* seeds (Voltolini, 2004). Insect predation was indicated by the typical entrance hole left by adult beetles boring into the seeds. With this procedure, it is possible that we have underestimated insect predation if insect-infested seeds were removed by rodents prior to our

cenuses. However, we have no information if rodents avoid or not insect-infested seeds (Silvius, 2002).

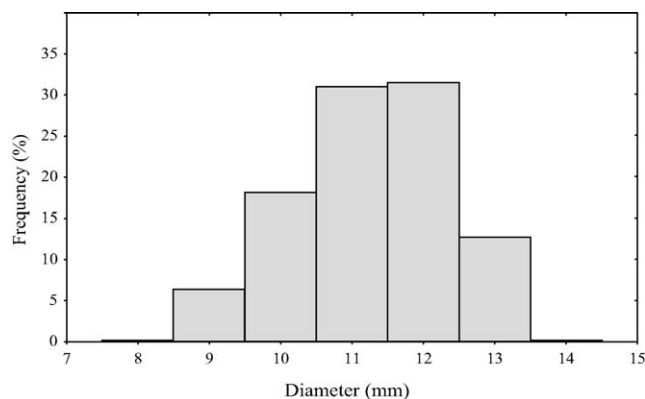
In June 2001, 100 intact seeds of each extreme size category (small and large), and 34 seeds damaged by *C. palmarum* (i.e. with the entrance hole left by this insect) of each size category were collected from the floor of the study site and placed to germinate in a greenhouse. Each seed was placed in an individual plastic tube (3 × 12 cm) filled with a sterilized, porous mineral (vermiculite). Seeds were watered daily, and checked periodically for 2 months for the protrusion of the radicle indicating germination. Seeds that had not germinated after this period showed clear signs of decay. After 5 months, the resulting seedlings were transplanted into plastic bags (10 cm wide × 15 cm tall) filled with soil (horticultural mixture) and kept in the same greenhouse for 7 months. After this 1-year period, the surviving seedlings (including roots) were harvested, washed, and dried for 72 h in an oven at 50 °C. We weighed separately the belowground and aboveground parts of each seedling to the nearest 0.01 g.

The Wilcoxon paired test (Zar, 1996) applied to the proportions of seeds preyed upon by rodents and insects was used to check for the influence of seed size upon seed choice by predators. We cross-classified all germinated seeds and surviving seedlings by seed size (small × large) and damage (intact × damaged) categories. We performed log-linear analysis on the resulting two-way frequency table to examine whether seed size and seed damage (design variables) affected seed germination and seedling survival (response variables). The significance of each design variable and their interactions were assessed with Maximum Likelihood Chi-square relative to the model to which it was added (Test of Marginal Association; Statsoft Inc., 1996). The effects of seed size and damage upon the total seedling biomass as well as its component parts, shoot and root biomasses, were tested using a two-way ANOVA design applied to log-transformed data. All statistical tests were performed using STATISTICA version 5.5 (Statsoft Inc., 1996).

#### 4. Results

Mean seed diameter (± S.D.) was 11.7 ± 1.1 mm, ranging from 8.3–14.1 mm (n = 2364; Fig. 1). The within-plant coefficient of variation (C.V.) ranged from 2.1% to 6.3%. Although individual palms differed from one another in mean seed size (F<sub>9, 2354</sub> = 1544.59, P < 0.001), the difference was of low magnitude (C.V. = 9.0%). Further, seed size did not affect the probability of attack by seed predators. Insect attacks were detected in 18.3% and 17.7% of small and large seeds, respectively, yielding a non-significant difference (T = 169.00, P = 0.87). Similarly, no significant difference was detected for seed size selection by rodents (T = 74.5, P = 0.63), which removed or consumed without moving a total of 26.3% and 24.7% of the small and large seeds, respectively.

Seed germination was, however, significantly affected by seed size, with large seeds having a greater germination success than small seeds (χ<sup>2</sup> = 5.90, df = 1, P = 0.01). Seed damage and the interaction between seed size and damage had no effects on germination (χ<sup>2</sup> = 0.12, df = 1, P = 0.72, and



**Fig. 1 – Frequency distribution of seed diameter in *Euterpe edulis*. The distribution was based on 2364 individually measured seeds gathered from 10 different plants of the studied population.**

χ<sup>2</sup> = 0.00, df = 1, P = 1.00, respectively; Table 1). Seedling survival, in contrast, was strongly affected by seed damage. Seedlings produced by intact seeds had significantly greater survival than seedlings from damaged seeds (χ<sup>2</sup> = 10.01, df = 1, P = 0.001). Seed size had a marginally significant effect on seedling survival (χ<sup>2</sup> = 3.18, df = 1, P = 0.07), while the interaction between seed size and damage had no significant effect (χ<sup>2</sup> = 0.00, df = 1, P = 0.99) (Table 1).

Seed size significantly affected total seedling biomass (F<sub>1, 118</sub> = 26.44, P < 0.001) as well as each of its components, shoot (F<sub>1, 118</sub> = 11.90, P < 0.001) and root biomasses (F<sub>1, 118</sub> = 51.51, P < 0.001). Large seeds produced larger seedlings with larger shoots and roots (Table 1). A marginally significant effect of insect damage upon total seedling biomass was detected (F<sub>1, 118</sub> = 3.57, P = 0.06), which was greatly influenced by the detrimental effect of insect damage upon root biomass (F<sub>1, 118</sub> = 8.94, P = 0.003) rather than on shoot biomass (F<sub>1, 118</sub> = 2.55, P = 0.11). The interaction between seed size

**Table 1 – Results of seed germination, seedling survival, and total, shoot and root biomasses of *Euterpe edulis* seedlings surviving over one year classified according to seed size (small or large), and seed damage (intact or damaged) categories. Sample sizes are given in parentheses. Mean and standard deviations are presented for biomasses**

	Small seeds	Large seeds
<b>Seed germination (%)</b>		
Intact seeds	86.0 (100)	95.0 (100)
Damaged seeds	85.3 (34)	94.1 (34)
<b>Seedling survival (%)</b>		
Intact seeds	50.0 (86)	62.1 (95)
Damaged seeds	27.5 (29)	37.5 (32)
<b>Total biomass (g)</b>		
Intact seeds	0.46 ± 0.16 (43)	0.69 ± 0.24 (59)
Damaged seeds	0.33 ± 0.08 (8)	0.68 ± 0.34 (12)
<b>Shoot biomass (g)</b>		
Intact seeds	0.37 ± 0.15 (43)	0.54 ± 0.22 (59)
Damaged seeds	0.27 ± 0.07 (8)	0.51 ± 0.31 (12)
<b>Root biomass (g)</b>		
Intact seeds	0.09 ± 0.02 (43)	0.15 ± 0.04 (59)
Damaged seeds	0.06 ± 0.02 (8)	0.17 ± 0.18 (12)

and damage affected neither total biomass ( $F_{1, 118} = 1.48$ ,  $P < 0.22$ ) nor its component parts (shoot:  $F_{1, 118} = 0.45$ ,  $P = 0.50$ ; root:  $F_{1, 118} = 3.08$ ,  $P = 0.08$ ). A close inspection on Table 1 reveals that small seeds presented the greatest biomass differences between intact and damaged seeds.

## 5. Discussion

We did not detect any difference in the probability of predation of *E. edulis* seeds by either insects or rodents based on the size of seeds, indicating that these seed predators are not sensitive to the range of seed sizes produced by the population of *E. edulis* studied. These results contrast with other studies showing that, within a plant species, rodents (Hulme, 1993; Brewer, 2001) and insects (Ernst et al., 1989; Moegenburg, 1996) select certain size classes of seeds to exploit likely based on the amount of energy they offer. The range of seed sizes produced by *E. edulis*, however, may be too narrow to render any significant difference in seed exploitation by rodents. For instance, Brewer (2001) and Moegenburg (1996) found more than 120% variation in the size of the palm seeds they studied, compared with 70% reported here. For insects, contrary to bruchid beetles for which seed size selection was reported (Ernst et al., 1989; Moegenburg, 1996), *C. palmarum* do not oviposit on *E. edulis* seeds. If it did, we would expect an active selection of seeds with sufficient reserves to guarantee the successful development of offspring. Moreover, because *C. palmarum* adults are tiny insects ( $\approx 1.5$  mm total length compared to 13 mm length of a *E. edulis* seed; Pizo and Simão, 2001) that usually consume only part of the seeds' endosperm, small and large *E. edulis* seeds may equally provide enough food for them. Bruchid beetles, in contrast, are much larger than *C. palmarum* (Ernst et al., 1989; Moegenburg, 1996).

If any advantage is accrued by *E. edulis* individuals producing large seeds, this is because of greater seed germination success and seedling vigor (Lin, 1976; Andrade et al., 1996; this study). Other studies have pointed out a positive relationship between seed size and germination success (Stanton, 1984; Khan, 2004), while seedling vigor has been shown to be especially important in determining the success of seedlings under competitive conditions (Stanton, 1984; Eriksson, 1999). As a shade tolerant species that produces thousands of easily germinating seeds annually, a persistent bank of *E. edulis* seedlings occurs in patches of great density where competitive conditions likely prevail. Therefore, seed size may be an important factor determining which individuals succeed in the high density patches of seedlings that one may find in the forest understory (Matos and Watkinson, 1998; Pizo and Simão, 2001).

Although *C. palmarum* did not reduce the germination capacity of the seeds they exploit, the subsequent survival of seedlings was negatively affected, probably due to a reduction in the root biomass of the seedlings produced. Because large seeds naturally produce vigorous seedlings and likely lose a relatively smaller proportion of endosperm tissue to *C. palmarum*, they tend to resist better to the attack of this beetle, which is consistent with the findings of Mack (1998). Although the proportion of seeds attacked by this beetle was

low in this study ( $\approx 18\%$ ), it varies annually and may reach 44% over the entire fruiting season in some years (Pizo and Simão, 2001; Pizo and Vieira, 2004). Therefore, in years of intense attack by *C. palmarum*, plants producing large seeds may have an advantage in terms of seedling survival, partly due to an inherent advantage and partly due to a reduced effect of insect damage.

In conclusion, seed selection by seed predators is not likely a factor promoting the variation in seed size we observed in the *E. edulis* population. If any selective pressure exists benefiting individuals that produce larger than average seeds, it is apparently in the greater seed germination success and resistance to *C. palmarum*, and in better seedling performance (Moles and Westoby, 2004). If this is so, it is important to note that even a relatively narrow range of variation in seed size as observed in the *E. edulis* population studied may translate into differential success of individual plants and, thus, be subjected to natural selection.

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