

Seed deposition patterns and the survival of seeds and seedlings of the palm *Euterpe edulis*

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Abstract – The seed deposition pattern created by a seed disperser is one of the components of the efficiency of a species as seed disperser, and ultimately may influence the recruitment of a plant species. In this study, we used the seeds of a bird-dispersed forest palm, *Euterpe edulis*, to investigate the effects of two distinct seed deposition patterns created by birds that defecate (clumped pattern) and regurgitate seeds (loose-clumped pattern) on the survival of seeds experimentally set in an *E. edulis*-rich site, and of seedlings grown under shade-house conditions. The study was conducted in the lowland forest of Parque Estadual Intervales, SE Brazil. Clumped and loose-clumped seeds were equally preyed upon by rodents and insects. Although clumped and isolated seedlings had the same root weight after 1 year, the isolated seedlings survived better and presented more developed shoots, suggesting intraspecific competition among clumped seedlings. Our results indicate that animals that deposit *E. edulis* seeds in faecal clumps (e.g. cracids, tapirs) are less efficient seed dispersers than those that regurgitate seeds individually (e.g. trogons, toucans). Intraspecific competition among seedlings growing from faecal clumps is a likely process preventing the occurrence of clumps of adult palms. © 2001 Éditions scientifiques et médicales Elsevier SAS

Atlantic forest / *Euterpe edulis* / seed deposition pattern / seed dispersal / seed predation / seedlings

1. INTRODUCTION

The seed deposition pattern created by a seed disperser is one of the components of the efficiency of a species as seed disperser [30]. Through differential survival, seed deposition patterns influence the fate of seeds and the successful establishment and development of seedlings, ultimately determining the recruitment of the plant [13].

As a consequence of the disperser foraging behaviour, morphology (e.g. gape size), physiology (e.g. gut passage rate) and seed size, seeds can be deposited in clumps or singly [18, 19]. Clumped seeds have been shown to suffer higher predation than isolated seeds [11, 35], but this is not a universal trend, being dependent upon the system and the type of seed

predator considered [7, 22, 25]. Additionally, seedlings that develop from clumped seeds may be at a disadvantage in relation to isolated seedlings because of intra- or interspecific competition [13, 20].

Using an economically important bird-dispersed forest palm, *Euterpe edulis* Martius [9, 10, 26], we investigated the effects of two distinct seed deposition patterns on the survival of seeds experimentally set in an *E. edulis*-rich site and of seedlings grown under shade-house conditions. Although *E. edulis* fruits are eaten both by birds that defecate the seeds in clumps and by birds that regurgitate them one by one, adult plants rarely occur clumped (mean distance among adult plants \pm SD = 5.7 ± 5.6 m; [27]). We hypothesize that the former birds are less efficient seed dispersers than the latter because the deposition of seeds in clumps seems to be detrimental to the recruitment of *E. edulis*. This study aimed to identify at which point in development from seed to adulthood this detrimen

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tal effect occurs. Does it depend upon the susceptibility of seeds to insect and rodent predators or on the survival and early development of seedlings? We specifically addressed the following questions: (1) Does the probability of seed predation by insects and rodents differ between clumped and loose-clumped seeds? (2) Do clumped and isolated seedlings differ in survival and growth?

1.1. Natural history background

The palm *Euterpe edulis* Martius is endemic to the Atlantic forest [12] where it is frequently the dominant understorey tree species [32]. The historical, unplanned, and often illegal extraction of palm hearts (the edible apical meristem) led to the disappearance of *E. edulis* from many areas, causing serious concerns for its long-term existence [6].

The single-seeded, medium-sized fruits of *E. edulis* (mean seed size \pm SD = 13.5 \pm 1.3 mm length, 14.2 \pm 1.2 mm width, n = 10) are eaten and primarily dispersed by 22 bird species at the study site [10, 17]. This assemblage can be divided into two groups in relation to the way they deposit seeds. The cracids (especially the guans *Pipile jacutinga* and *Penelope* spp., Cracidae) defecate groups of seeds, thus providing a clumped seed distribution. Reis [27] observed a captive Dusky-legged guan (*Penelope obscura*) defecating groups of three to four seeds at 15–20 min intervals starting 4 h after fruit ingestion. All of the other avian consumers of *E. edulis* fruit regurgitate the seeds [17], thus providing a more scattered or loose-clumped seed distribution. These birds, especially the trogons (Trogonidae), toucans and toucanets (Ramphastidae), typically perch motionless while regurgitating the seeds one by one at short intervals. A Saffron-billed toucanet (*Bailloni bailloni*) was observed regurgitating eight seeds under the same perch during a 12-min period (M.A. Pizo, pers. obs.). Seeds defecated by cracids and regurgitated by *B. bailloni* had a high germination success (> 95 %; [17]).

Birds that regurgitate *E. edulis* are more abundant in terms of species and individuals at the study site than those that defecate them [1]. As a result, only eight out of 99 feeding bouts recorded on *E. edulis* fruits at the study site were for bird species that defecate the seeds [10]. Birds, however, are not the only fruit consumers of *E. edulis* fruits [10]. Up to fifty seeds were found under bat feeding roosts [17], while a single tapir (*Tapirus terrestris*) dropping found at Parque Intervales contained 300 seeds [28].

Post-dispersal predation of *E. edulis* seeds is caused by a scolytid beetle (*Coccotrypes palmarum* Eggers 1933, Scolytidae) and rodents. Adults of *C. palmarum*

were present in 96.6 % of the 268 insect-attacked seeds collected at the study site, the remainder being infested by an unidentified insect larvae. Seeds of *E. edulis* offered to non-starved rodents in captivity were completely eaten by *Nectomys squamipes* and *Oryzomys intermedius*, the two most abundant rodents at the study site [34].

2. METHODS

2.1. Study site

This study was conducted in the lowland forest of the Parque Estadual Intervales (Saibadela Research Station; 24°14' S, 48°04' W), a 49 000-ha reserve located in the municipality of Sete Barras in São Paulo state, south-east Brazil. This site bears a dense population of *E. edulis* (255.6 plants (dbh > 5 cm)-ha⁻¹; [2]) relatively undisturbed by illegal harvesting (but see [8]). During the 1995 fruiting season (April to September), a total of 10.5 seeds·m⁻² dropped on the floor of Parque Intervales (M.A. Pizo, unpubl. data).

The site received a mean annual rainfall of 4 216.2 \pm 245.5 mm between 1994–1996. Rains were well distributed throughout the year with no month receiving less than 100 mm. We can distinguish, however, a period of less intense and less frequent rains between April and August. During this period, low temperatures may occur but rarely dropping below 10°C (mean \pm SD = 20.8 \pm 2.5°C for the study period), which contrasts with the wetter period when maximum temperatures may reach 42°C (25.7 \pm 2.8°C). The forest is predominantly an old-growth forest (sensu Clark [5]) with an open understorey and canopy height of 25 m with a few emergent trees reaching 30 m [2].

2.2. Seed predation

The effects of deposition patterns on seed predation were investigated in July 1995 (peak of fruit production) by placing seeds on two parallel thirty-station transects established 2–3 m off-trail on opposite sides of a 1-m wide trail that crossed the study site. The number of seeds preyed upon by rodents and insects was recorded 1 month later. Consecutive stations on the same transect were spaced 25 m apart, and at least 5 m distant from the nearest station on the opposite transect. Each station received five seeds, a number chosen because it is close to the mean number of seeds contained in cracid faeces found in the field (mean \pm SD = 5.7 \pm 2.2, range 3–10, n = 10). In one of the parallel transects, the five seeds/station were set up in close proximity to each other to simulate a cracid defecation clump (clumped treatment). In the opposite

transect, one seed was placed in each corner of a 1-m² quadrat, with the fifth seed in the centre, simulating the deposition pattern provided by birds that regurgitate seeds individually while perched (loose-clumped treatment). Thus, we had 150 seeds (30 stations × 5 seeds/station) assigned to each of the two treatments. All the seeds used in the transects had been regurgitated by birds and collected in the field. The position of the seed clump, and of each individual seed in the loose-clumped treatment was marked with wooden stakes. We considered every seed not found in an area of 30 cm around the stakes to be preyed upon by rodents. Insect predation was verified by looking for the typical entrance hole left by insects entering the seeds. We may have underestimated insect predation because insect-attacked seeds might have been removed by rodents prior to our census (but see [29]).

The seed predation data we obtained were non-parametric, thus we used the Wilcoxon paired-sample tests [37] to investigate the effect of deposition patterns on seed predation by rodents and insects. *P*-values are reported using the normal approximation with continuity correction [33].

2.3. Seedling competition

We examined the consequences of clumped vs. loose-clumped deposition patterns on seedling development by planting seeds in a shade-house and recording seedling survival and biomass 1 year later. In June 1996, we collected germinating seeds (seeds with protruding radicles) with no sign of insect or fungus infestation from the field and planted them into plastic bags (17 cm diameter × 20 cm tall) filled with soil collected at the study site. Germinating seeds were used to prevent the effect of priority of emergence on size and subsequent fate of seedlings [24]. The seedlings were kept in a shade-house (25 % full sunlight) constructed in the field especially to nurse *E. edulis* seedlings. Watering consisted of natural rainfall. Two treatments were considered: (1) 45 seeds were planted

individually (isolated treatment), thus simulating seedlings that would develop from loose-clumped seeds; and (2) 75 seeds were planted in groups of five in each plastic bag (clumped treatment), thus simulating seedlings growing from clumped seeds. After 1 year, seedlings (including roots) were harvested, washed, and dried for 8 h in a furnace set at 80°C. The same procedure was repeated 1 year later with 35 seeds planted individually and 75 seeds planted in groups of five. To distinguish root from shoot competition, we weighed separately the subterranean and aerial parts of each seedling to the nearest 0.01 g. As shoot and root weights did not differ between 1995 and 1996 for any treatment (*t*-tests: all *P* > 0.10), data from both years were pooled for analysis. We applied the *t*-test to root and shoot dry weights to compare the effect of isolated vs. clumped treatments on seedling biomass.

3. RESULTS

Seed deposition treatment did not significantly affect the proportion of seeds preyed upon by rodents or insects (table I). Similarly, the number of experimental stations 'discovered' by predators (those that had at least one seed attacked) did not differ in rodent (Chi-square tests with Yates correction: $\chi^2 = 0.08$, *P* = 0.77) or insect predation ($\chi^2 = 0.00$, *P* = 1.00) between clumped and loose-clumped treatments.

Clumping pattern also had no effect upon the weight of the roots of 1-year-old seedlings (table I). However, a significant difference was detected in the aerial portion of the seedlings; isolated seedlings had more developed shoots than clumped ones (table I). Moreover, a higher proportion of isolated seeds survived the 1-year study period for both the 1995 (0.75 vs. 0.52 for isolated and clumped seedlings, respectively; $\chi^2 = 5.60$, *df* = 1, *P* = 0.02) and the 1996 cohorts (0.57 vs. 0.19; $\chi^2 = 14.79$, *df* = 1, *P* < 0.001). Only one of

Table I. Proportion of *Euterpe edulis* seeds preyed upon by rodents and insects, and the dry weight of roots and shoots of 1-year-old seedlings according to two contrasting clumping treatments.

Deposition pattern	Mean proportion ± SD seeds preyed/station		Mean weight (g) ± SD seedlings	
	Insects	Rodents	Root	Shoot
Clumped	0.39 ± 0.28	0.06 ± 0.10	0.33 ± 0.16 (50)	0.97 ± 0.41 (50)
Loose-clumped seeds (or isolated seedlings)	0.44 ± 0.30	0.08 ± 0.14	0.36 ± 0.16 (51)	1.15 ± 0.42 (52)
<i>P</i> -level ^a	0.54	0.52	0.46	0.04

^a Wilcoxon paired-sample tests and *t*-tests used for predation and weight comparisons, respectively.

Thirty stations (with five seeds each) were used to assess rodent and insect predation. Sample sizes for root and shoot weights are indicated between parentheses.

the thirty clumped replicates (1995 and 1996 data combined) had the five original seedlings alive after 1 year.

4. DISCUSSION

Rodents and insects discovered and attacked clumped and loose-clumped *E. edulis* seeds equally. This result contrasts with Hammond [11] who found lower predation rates on single seeds than on clumped seeds of four tree species in Mexican forests. Although Lott et al. [22] did not detect any difference between the proportions of isolated and clustered *Normanbya normanbyi* palm seeds eaten by pigs, rodents and insects in an Australian rainforest, their results indicate that the latter two predators discovered more clusters than single seeds. Contrasting with our experimental design, however, these studies used truly isolated seeds that may be less prone to predation than our loose-clumped seeds simply because it has been shown that the discovery probability of a seed depot by rodents is a function of seed number [4, 35]. Therefore, at least from a rodent point of view, our loose-clumped treatment, with seeds separated from each other by 0.7–1 m, may not differ substantially from the clumped treatment. This hypothesis is corroborated by Notman et al. [25] who found that the removal of seeds of two tree species by rodents in a Peruvian rainforest did not differ between clumped and loose-clumped treatments. In any case, the loose-clumped treatment bears biological significance because it simulates the pattern of seed deposition produced by birds that regurgitate a series of seeds under a given perch, as trogons and toucans often do. The likelihood of predation for truly isolated seeds regurgitated singly on a given spot while the seed disperser is moving throughout the forest remains to be investigated.

The seed-searching behaviour of *Coccytrypes palmarum* is poorly known, so we can not assert what kind of difference the clumped and loose-clumped treatments represent for these insects, although evidence from the literature suggests that they may also not differ substantially. Wilson and Janzen [36] found that predation on *Scheelea* palm seeds by bruchid beetles was lower on isolated than on clumped seeds. In contrast, Forget and Milleron [7] observed that infestation by insects on loose-clumped seeds of *Virola surinamensis* (Myristicaceae) set 1 m apart from each other did not differ from infestation on clumped seeds.

Seedling competition, especially through shoot competition, is the process that most decisively pre-

vents the development of a clump of *E. edulis* adults from cracid faeces (see [14] for similar results with *Virola surinamensis*). Competition was thought to be the factor that decreased the probability of *E. edulis* seedling survival and growth with increasing density in 1 × 1 plots set in a Brazilian semi-deciduous forest fragment by Matos and Watkinson [23]. In a clump of seedlings, asymmetric competition for light may occur and, as a consequence, taller individuals suppress the growth of smaller ones (see [31] and references included). In such a situation, seed size, through its influence on seedling vigour, is a key factor in determining which seedling will survive [14]. Seeds of *E. edulis* vary five-fold in size (range 0.4–2.4 g; M.A. Pizo, unpubl. data), but it is not known if seeds of contrasting sizes, possibly from different individuals, occur in the same cracid faecal load.

In respect to the pattern of seed deposition, cracids might be regarded as less effective dispersers of *E. edulis* seeds when compared to birds that regurgitate seeds. However, disperser effectiveness is a complex and multi-factor trait that also incorporates aspects related to the quantity of seeds dispersed [21, 30]. Low deposition quality by cracids may be compensated by the large quantities of seeds they eat. Laps [17], for example, observed a jacutinga (*Pipile jacutinga*) eating 140 fruits of *E. edulis* in a single feeding bout.

Based on our results, we can assume that, as observed for experimental clumps, *E. edulis* seeds found in the large clumps typically produced by mammals (e.g. below bat feeding roosts, in tapir faeces; [17, 28]) are not likely to survive. Although rodents sometimes mine seeds from mammal dung [15, 16], as Howe [13] pointed out, this probably represents predation rather than seed dispersal. This loss of seeds may be irrelevant for the demography of the *E. edulis* population at the study site where there is probably an excess of seeds in relation to safe sites for recruitment (see [3]), but it may be of great importance for the recovery of depleted *E. edulis* populations in the many private forests that surround Parque Intervales.

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