ARBORESCENT PALM SEED MORPHOLOGY AND SEEDLING DISTRIBUTION

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(With 1 figure)

ABSTRACT

This study examines how the seed morphology of two large arborescent palms, *Attalea maripa* (Aubl.) Mart. and *Astrocaryum aculeatum* G. Mey, may affect their seed shadow in a seasonally dry Amazonian forest. In addition to being smaller and produced in larger numbers than those of *A. aculeatum*, *A. maripa* seeds also presented a substantially lower amount of nutritional reserves available for the embryo. However, *A. maripa* seedlings were found in much higher numbers than those of *A. aculeatum*. The results suggest that, within the spatial scale considered, the seed rain of *A. maripa* is more restricted to the area surrounding around reproductive conspecifics than that of *A. aculeatum*. Furthermore, in comparison with those of *A. aculeatum*, the smaller seeds of *A. maripa* might be less attractive to scatterhoarding rodents (e.g. *Dasyprocta aguti*). The pattern observed emphasizes the importance of scatterhoarding rodents as dispersers of large-seeded plant species in Neotropical forests.

Keywords: Amazonia, *Astrocaryum aculeatum*, *Attalea maripa*, scatterhoarding, seed shadow.

RESUMO

Morfologia de sementes e distribuição de plântulas de palmeiras arborescentes

Foi investigada a relação da morfologia das sementes de duas palmeiras arborescentes de grande porte, *Attalea maripa* (Aubl.) Mart. e *Astrocaryum aculeatum* G. Mey, com a chuva de sementes, em uma floresta amazônica sazonalmente seca. As sementes de *A. maripa* são menores e produzidas em maiores quantidades que aquelas de *A. aculeatum*. Tais sementes também têm uma quantidade de reservas nutricionais disponível para o embrião substancialmente menor. As plântulas de *A. maripa* foram encontradas em números muito maiores que as de *A. aculeatum*. Os resultados sugerem que, na escala espacial considerada, a chuva de sementes de *A. maripa* é mais restrita ao redor de palmeiras reprodutivas que aquela de *A. aculeatum*. As sementes de *A. maripa*, menores, devem ser menos atraentes para roedores que estocam seu alimento difusamente enterrando-o (e.g. *Dasyprocta aguti*). O padrão observado enfatiza a importância de tais roedores como dispersores de sementes de grande porte nas florestas neotropicais.

Palavras-chave: Amazônia, *Astrocaryum aculeatum*, *Attalea maripa*, estocagem dispersa, chuva de sementes.

INTRODUCTION

Seed size and shape represent compromises between constraints associated with the most efficient means for both packing and dispersing embryo reserves (Harper *et al.*, 1970). There is an obvious trade-off between seed size and number since small seeds can be produced in much larger quantities than larger ones for any given amount of overall reproductive investment. Thus, there is always a selective pressure for the production of larger quantities of smaller seeds (Harper *et al.*, 1970; Fenner, 1985).

The benefits of large seed-size for plant survival are relatively higher in environments where seedlings experience density stress. Under such conditions, large seeds have a better chance of establishing themselves because of their larger nutritional reserves. Such reserves, stored within the seed, enable the seedling to produce a more extensive root system and to have a greater initial growth. Thus, single large seeds can produce large and more vigorous seedlings that have a higher establishment and recruitment probability (Harper *et al.*, 1970; Fenner, 1985; Saverimuttu & Westoby, 1996; Walters & Reich, 2000).

Much of the enormous inter-specific variation in seed shape in plants is related to seed dispersal mechanisms (Fenner, 1985; Foster, 1986). The size and shape of seeds can also influence plant establishment probability by affecting the distance over which seeds can be dispersed.

With respect to plant distribution and abundance, small-seeded species exhibit a wide range of abundance and distribution, whereas larger-seeded species generally present lower abundance and narrower distribution (Guo *et al.*, 2000). Smaller seeds are likely to be ingested whole by a wider range of animal dispersal agents (Harper *et al.*, 1970; Harper, 1977; Jackson, 1981; Howe & Smallwood, 1982; Howe *et al.*, 1985; Fenner, 1985; Foster, 1986; Hegde *et al.*, 1991).

However, for large-seeded species, vertebrate predation is generally believed to be a disadvantage, presumably because their seeds represent a richer energy source and are more visible than small seeds are to vertebrates. Thus, the advantages of greater energy reserves associated with large seeds could be offset by possible dispersal limitations and predation risks (Vander Wall, 1990; Hulme, 1993). For example, in Neotropical forests, caviomorph rodents such as agoutis (*Dasyprocta spp.*) and accouchis (*Myoprocta spp.*) have been described as important seed dispersers of neotropical large-seeded palms (Smythe, 1978; Forget, 1991, 1994). However, because these rodents habitually scatterhoard their prey-seeds, they may fail to retrieve a small proportion of them. Thus, they also function as seed dispersers (Smythe, 1978; Forget, 1990, 1994; Forget & Milleron, 1992; Forget *et al.*, 2001; Peres *et al.*, 1997).

The Amazonian large arborescent palm *Attalea maripa* (Aubl.) Mart. has thick (> 30 cm DBH), tall, single stems with no spines. The fruits consist of a fibrous outer shell and mesocarp that somewhat viscous when immature. The seed is enclosed in a smooth woody yellowish-brown shell with a sharp point (Henderson *et al.*, 1995). Almeida & Dantas da Silva (1997) describe *A. maripa* seeds as being 3-4 cm in length and 2 cm in diameter. Although typically having 2, the seeds may have from 1 to 3 kernels. These authors report an average 33% moisture content in the fresh fruit. The dry fruit mass averages 18 g and comprises the outer shell (16%), mesocarp (26%), woody inner shell (49%), and oily kernels (9%) (Almeida & Dantas da Silva, 1997).

The upper parts of the massive trunks of *Astrocaryum aculeatum* G. Mey, also a large arborescent palm restricted to the Amazon (Henderson *et al.*, 1995), have long black spines arranged in regularly spaced rings. As the palm grows, the old spines fall, and the lower parts of the trunk typically become bare. The yellowish-green fruit of *A. aculeatum* palms consists of a dense, yellowish, farinaceous mesocarp that envelops a nearly black, woody shell. The single kernel is white, oily and hard, and covered with an adherent brown testa (Pesce, 1985; Almeida & Dantas da Silva, 1997).

The aim of this study is to examine the effects of seed size and shape on seedling distribution; this will be done through a comparative study of *A. maripa* and *A. aculeatum* in a seasonally dry Amazonian forest. Laboratory measurements of seed anatomy will be considered together with mapping of seedlings and adults of both species growing in a 16 ha grid system that crosses two areas presenting contrasting forest structure and floristic composition.

METHODS

Seeds of *Attalea maripa* (Aubl.) Mart. and *Astrocaryum aculeatum* G. Mey were collected at the Pinkaití Research Station (7° 46' 18" S; 51° 57' 42" W), located along Riozinho River, a second-order tributary of the Xingu River. These were taken to the Plant Anatomy Laboratory of the University of São Paulo (USP) for measurement. Seed length and width were measured to the nearest millimeter. Seed volume was estimated following seed immersion in a graduated beaker. The seeds were broken and the kernel volume was measured. One fruiting palm tree of each species was destructively sampled; fruits were counted and used for seed predation and seed dispersal experiments.

Seed shadow is not always spatially congruent with seedling distribution (Rey & Alcantara, 2000). However, because of the practical difficulty of determining seed shadow through direct means, I used the seedling distribution in relation to reproductive palms as a proxy measure. Furthermore, since seedlings of *A. maripa* and *A. aculeatum* differ morphologically, arbitrary boundaries were set for their respective definitions. Thus, *A. maripa* seedlings were defined as plants having petioles of up to 7 mm in diameter measured at 10 cm from the ground. For *A. aculeatum*, the limit was 4 mm at the same height.

The seedling distribution pattern of *A. maripa* and *A. aculeatum* in relation to reproductive adults of each species was quantified within a 16 ha section of the main grid system at Pinkaití. This grid system progresses from an open forest with a high abundance of arborescent palms in its western portion, to a more built-up forest where palm trees were rare in the eastern portion. To investigate palm seedling distribution of each species in relation to reproductive adults, the grid area was demarcated with flag stakes placed at 25 m intervals, creating 0.0625 ha subplots. Within this area, all adult trees of each palm species were mapped and tagged. Thereafter, every adult *A. maripa* and *A. aculeatum* palm was inspected for evidence of past reproductive activity, i.e., accumulation of old seed remnants beneath the crown. Here, the term "reproductive" denotes fruit-producing individuals, which excludes palms that may also be reproductive through pollen production from male flowers.

Since marked differences were found in the abundance of *A. maripa* and *A. aculeatum* seedlings, their respective spatial distributions were estimated with two different methodologies. Thus, *A. maripa* seedlings, found to be more abundant than those of *A. aculeatum*, were sampled within 100 5 x 5 m plots, which were regularly spaced across the grid system. The much rarer seedlings of *A. aculeatum* were exhaustively sampled throughout the entire grid system. Two previously trained field assistants searched each 0.0625 ha plot, where all seedlings were located. Using tape and a compass, they tagged and mapped each in relation to the nearest grid stake.

RESULTS

The elongated seeds of *Attalea* were significantly smaller than the globose seeds of *Astrocaryum* (t- test, $p < 0.001$; Fig. 1, Table 1). The seeds of *Attalea* had 1, 2, or 3 loci (38.7%, 38.7, and 22.5% N = 31) whereas *Astrocaryum* seeds always had one locus with a single embryo. A total of 2283 fruits were counted from a single bunch of a felled *Attalea* tree. In contrast, the *Astrocaryum* tree had three bunches and a total of 557 fruits (mean of 186 fruits per bunch).

The density of reproductive *Attalea* palms in the forest plots with high palm density (26.2 trees.ha^{-1}) was significantly higher than that of the low palm-density forest eastwards (2.5 trees.ha^{-1}) (Mann-Whitney U, $p = 0.001$). In the grid system as a whole, there was a significant negative correlation between the seedling density

TABLE 1
Volume of *A. maripa* and *A. aculeatum* seeds collected at the Pinkaití Research Station, Brazil.

	***Attalea maripa* n = 91**	***Astrocaryum aculeatum* n =12**
	Mean ± S. D. (min.-max.)	
Seed volume (mL)	9.2 ± 2.5 (5-17)	32.5 ± 8.5 (16-44)
Endosperm volume (mL)	1.9 ± 0.6 (1.0-3.0)	12.0 ± 3.6 (7.0-15.0)

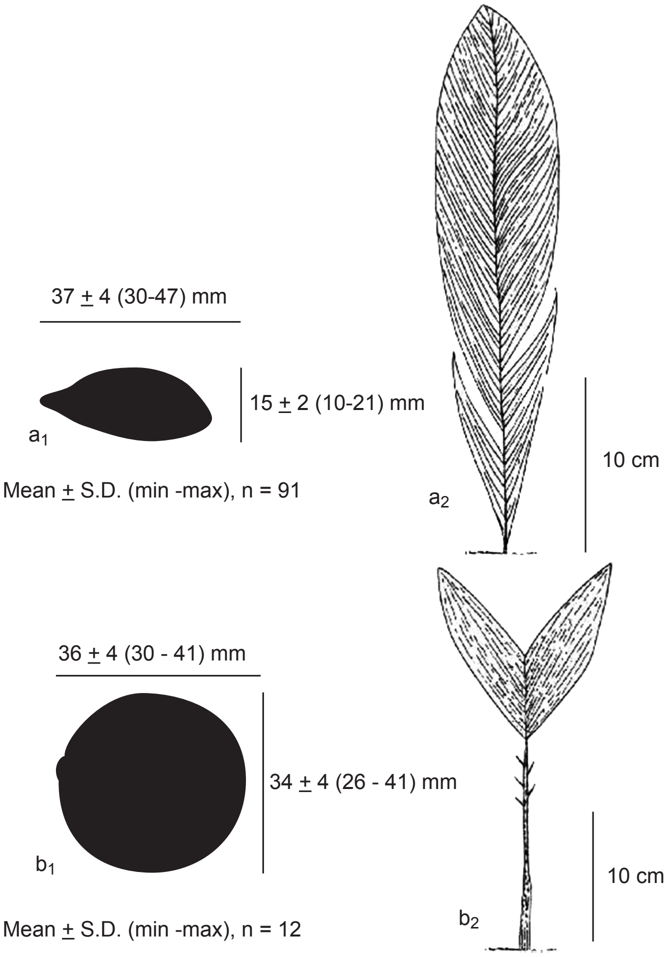

Fig 1. — Dimensions of a) *Attalea maripa* and b) *Astrocaryum aculeatum* 1) seed and 2) seedling.

of this species and distance to reproductive *Attalea* trees (r_s = - 0.366, $p < 0.001$). Seedling abundance was positively correlated with reproductive palm density (10 m: r_s = 0.221, p = 0.014; 20 m: r_s = 0.290, p = 0.002; 50 m: r_s = 0.284, p = 0.002). However, there was a significantly higher density of *Attalea* seedlings in this high palm-density area (t-test, $p < 0.001$). These relationships were not significant when only the high palm-density (10 m: r_s = 0.078, p = 0.275; 20 m: r_s = 0.090, p = 0.244; 50 m: r_s = 0.207, p = 0.055) or the low palm-density (10 m: r_s = - 0.180, p = 0.256; 20 m: r_s = 0.179, p = 0.144; 50 m: r_s = 0.253, p = 0.061) areas were considered.

The density of reproductive *Astrocaryum* trees in the high-density portion of the grid was significantly higher than that of low palm-density (Mann-Whitney U, p = 0.013). The seedlings of this species, in turn, were significantly less abundant in the low palm-density half of the grid (Mann-Whitney U, $p < 0.001$). There was no spatial correlation between the abundance of seedlings and the abundance of reproductive adults of this species (high and low-density: r_s= - 0.086, p = 0.228; high-density: r_s = - 0.009, p = 0.459; low-density: r_s = 0.017, p = 0.444).

DISCUSSION

Although there was no difference in seed length between the two species (p = 0.680), the seeds of *Attalea* were significantly narrower than those of *Astrocaryum* ($p < 0.001$), whose length and width were roughly equivalent. Also, *A. maripa* seeds presented up to three embryos each, while those of *A. aculeatum* invariably had only one.

Thus, *Attalea* seeds had significantly smaller endosperm reserves available for seedling development than those of *Astrocaryum* ($p < 0.001$), which was compensated for by the far greater fruit crop size of the former. This represents a trade-off in that, while the long-shaped seeds of *A. maripa* carry smaller nutrient reserves, they may be ingested by some vertebrate species, whereas seed dispersal of *A. aculeatum* is only carried out by scatterhoarding rodents.

Large quantities of *A. maripa* seeds were found in tapir (*Tapirus terrestris*) dung piles at Pinkaití, which is consistent with observations made elsewhere in the Amazon (Bodmer, 1990; Fragoso, 1997). Seeds of *A. maripa* have also been found in tortoise (*Geochelone sp.*) feces at this site (Jerozolimski, 2005). The Kayapó Indians have also reported finding *A. aculeatum* seeds in tapir feces. However, given the size of these seeds, this probably occurs rarely as no *A. aculeatum* seeds were found in a number of dung piles inspected, and no other species is likely to ingest these seeds whole.

The seedlings of *A. maripa* are widespread in *terra- firme* forest areas at Pinkaití, with results showing that these seedlings were up to two orders of magnitude more abundant than those of *A. aculeatum*. The larger number of fruit-producing trees of this species, the greater seed-crop size, and the broader spectrum of animal dispersal agents may all explain this difference. This comparative study also showed that seedlings of the smaller-seeded *A. maripa* are more densely clumped around reproductive trees than those of the larger-seeded *A. aculeatum*, suggesting that the seed shadow of *A. maripa* is more restricted than that of *A. aculeatum*. Needless to say, this pattern is unlike that found for wind or gut-dispersed species (Harper *et al.*, 1970; Harper, 1977; Howe and Smallwood. 1982; Fenner, 1985).

The wider seed shadow of *A. aculeatum* might be a consequence of this species's stronger mutualistic relationship with caviomorph rodents. Thus, because larger seeds contain greater food reserves, scatterhoarding rodents preferentially remove large seeds and tend to disperse them farther (Vander Wall, 1990). In addition, the fruits of *A. aculeatum* are an important food source for agoutis at Pinkaití, particularly during the dry season when alternative food resources for this species are scarce (Jorge, 2000).

This study supports the view that caviomorph rodents are especially important in large-seeded plant dispersal because of their high relative abundance and widespread distribution. Furthermore, by decreasing the probability of seed predation and by actively promoting seedling establishment, burying seeds in scattered caches potentially enhances plant recruitment.

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