

Seed banks on *Attalea phalerata* (Arecaceae) stems in the Pantanal wetland, Brazil

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- **Background and Aims** Seeds can accumulate in the soil or elsewhere, such as on the stems of palms when these are covered by persistent sheaths. These sheaths could act as a safe site for some species. Here, we studied whether persistent sheaths of the palm *Attalea phalerata* (Arecaceae) are available sites for seed accumulation in the Pantanal wetland of Brazil. We also investigated whether the composition, richness and diversity of species of seeds in the persistent sheaths are determined by habitat (riparian forest and forest patches) and/or season (wet and dry).
- **Methods** All accumulated material was collected from ten persistent sheaths along the stems of 64 *A. phalerata* individuals (16 per habitat and 16 per season). The material was then individually inspected under a stereomicroscope to record seed species and number.
- **Key Results** Of the 640 sheaths sampled, 65 % contained seeds ($n = 3468$). This seed bank included 75 species belonging to 12 families, and was primarily composed of small, endozoochoric seeds, with a few abundant species (*Cecropia pachystachya* and *Ficus pertusa*). Moraceae was the richest family (four species) and Urticaceae the most abundant (1594 seeds). Stems of *A. phalerata* in the riparian forest had 1.8 times more seeds and 1.3 times more species than those in forest patches. In the wet season we sampled 4.1 times more seeds and 2.2 more species on palm stems than in the dry season. Richness did not differ between habitats, but was higher in the wet season. Abundance was higher in forest patches and in the wet season.
- **Conclusions** *Attalea phalerata* stems contain a rich seed bank, comparable to soil seed banks of tropical forests. As most of these seeds are not adapted to grow in flooding conditions, palm stems might be regarded as safe sites for seeds (and seedlings) to escape from the seasonal flooding of the Pantanal.

Key words: *Attalea phalerata*, *Cecropia pachystachya*, *Ficus*, hemi-epiphyte, palm tree, palm seed bank, phorophyte, seed community, seed dispersal, Pantanal wetland, Brazil.

INTRODUCTION

In tropical forests, the forest soils have been the main subject of studies on seed banks and are often regarded as the final place where plant diaspores are deposited (Butler and Chazdon, 1998; Dalling *et al.*, 1998; Grombone-Guaratini and Rodrigues, 2002; Grombone-Guaratini *et al.*, 2004). However, there are other sites of seed deposition that have received only minor attention (Benzing, 1990; Fischer and Araujo, 1995). Considering the great variety of dispersal modes and diaspore traits, it might be expected that seeds may land on plant substrates throughout the vegetation strata (Nadkarni and Haber, 2009). Indeed, epiphytes and parasite plants have some features that facilitate the seeds attachment on plant substrates (phorophytes; Benzing, 1990; Fischer and Araujo, 1995). Therefore, studies of seed banks on different plant substrates can provide more reliable knowledge about forest regeneration (Putz and Holbrook, 1989; Nadkarni and Haber, 2009).

Seed accumulation on vegetation may be high on rough and large trunks, branch forks or dense foliage (Putz and Holbrook, 1989; Bernal and Balslev, 1996; Nadkarni and Haber, 2009). Several palm trees have a canopy architecture resembling a

funnel, produced by concentric leaves that intercept falling objects and carry them toward to the stem (Putz and Holbrook, 1989; Bernal and Balslev, 1996). In addition, some palm tree species keep senescent leaf sheaths (persistent sheaths hereafter) covering all the stem. These very rough stems favour accumulation of nutrient-rich sediments that allow plant development and may contain a particular seed bank (Putz and Holbrook, 1989; Bernal and Balslev, 1996; Nadkarni and Haber, 2009). Palm stems can represent safe sites for seed species, providing decreasing mortality risk there than in other sites. Seeds of epiphytic species are expected to be common on palm stems, as they depend on phorophytes to establish seedlings (Benzing, 1990; Fischer and Araujo, 1995). Composition and richness of seeds deposited on palm stems may change according to each palm's neighbouring vegetation, and may vary seasonally due to plant phenologies (Dalling *et al.*, 1998; Grombone-Guaratini *et al.*, 2004; Hopfensperger, 2007). Animal-dispersed seeds commonly show a fruiting peak during the wet season, whereas wind-dispersed seeds do so in the dry season (Howe and Smallwood, 1982; Fischer and Araujo, 1995; Turner, 2001; Ragusa-Netto, 2002).

Here we address the richness and composition of seed banks on persistent sheaths on *Attalea phalerata* (Arecaceae) stems, by far the most abundant and widely distributed palm tree in the Pantanal floodplain of central South America (Pott and Pott, 1994). At the study site, there are two natural forest habitats, riparian forest and forest patches called capões. In the riparian forest the flooding season is more frequent and extended than in capões. Also, the spatial distribution of *A. phalerata* individuals differs between habitats, being aggregated in capões but sparse in riparian forests (Damasceno et al., 1999).

We first investigated if *A. phalerata* stems maintain a seed bank, and then tested the following hypotheses: (1) community parameters (richness of seeds, seed species composition and abundance) are higher on palm stems in capões than in riparian forest because riparian forest palm sheaths could remain longer under water and seeds that had accumulated could be taken out; and (2) community parameters (richness of seeds and abundance) are higher on palm stems in the wet season than in the dry season, as most plant species fruit in the wet season in the Pantanal (Teixeira et al., 2009; Ragusa-Netto, 2004).

MATERIAL AND METHODS

Study site and species

The Pantanal floodplain (approx. 160 000 km²) is part of the upper Paraguay basin in central South America. The climate is tropical (Aw of Köppen), with a dry season from April to September and a wet season from October to March (Cadavid-Garcia, 1984; Teixeira et al., 2009). Mean monthly temperatures vary from 20 to 27 °C and annual rainfall from 800 to 1400 mm (Teixeira et al., 2009). Vegetation is represented by semi-deciduous riparian forests and capões (0.5–5 ha), forest patches surrounded by seasonally flooding fields and water bodies with aquatic plants (Prance and Schaller, 1982; Araujo and Sazima, 2003). Data collection was carried out in capões and riparian forest habitats in the region of Pantanal do Miranda (approx. 19°34'S, 57°01'W), Corumbá, Mato Grosso do Sul, Brazil.

Attalea phalerata (Arecaceae) is the most common palm tree among nine palm species that occur in the Pantanal (Pott and Pott, 1994). Individuals are found either in the understorey, forest borders or open sites. Its leaves are concentrated at the apex with long petioles and broad, invaginant sheaths (Joly, 1991) that remain attached after leaf abscission, covering the entire stem (Fig. 1). The number of persistent sheaths per *A. phalerata* stem varies from 70 to 500 depending on stem length (0.8–4.0 m). The sediment accumulated on persistent sheaths is acidic (pH = 5.4) with a high proportion of organic matter and a fine clay texture. Cation exchange capacity is 27.6 meq 100 cm⁻³ and elements found in the sediment are P (42.3 µg cm⁻³), K (1.38 meq 100 cm⁻³), Ca (10.7 meq 100 cm⁻³), Mg (5.8 meq 100 cm⁻³), Al (0.6 meq 100 cm⁻³), Fe (7.7 mg dm⁻³), Mn (70.4 mg dm⁻³), Cu (0.33 mg dm⁻³) and Zn (29.2 mg dm⁻³) (C. E. Corrêa, unpubl. res.).

Data collection

Sixty-four adult individuals of *A. phalerata* were haphazardly selected for sampling of seeds deposited on persistent sheaths, 32 in the wet season (March) and 32 in the dry season (September). In each season, 16 individuals of *A. phalerata* were sampled per habitat (capões and riparian forest), with at least 50 m between them. All material deposited on ten persistent sheaths distributed along the stem of each palm was collected. The material from each sheath was individually wrapped in paper bags, weighed and later inspected in the laboratory under a stereomicroscope to separate seeds. We slightly pressed seeds manually to identify rotten ones, which were not included in counts. Only angiosperm seeds larger than 0.5 mm in width or length were included. Seeds were identified through comparisons with herbarium material and identification guides (Lorenzi, 1992, 1998; Lobova and Mori, 2002; Carvalho, 2003); unidentified seeds were classified as morphospecies. To describe the seeds deposited on persistent sheaths we weighed (to ± 0.001 g) and classified them according to habit (hemi-epiphyte, herbaceous,

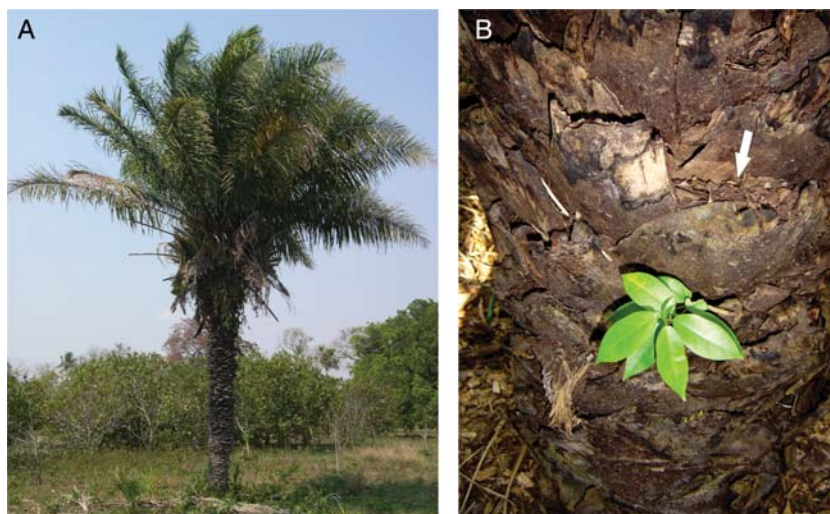


FIG. 1. *Attalea phalerata* individual (A), and the stem showing persistent sheaths with accumulated sediment (arrow) and one epiphyte seedling of *Ficus* sp. (B), in the Pantanal do Miranda, Brazil.

shrub or tree) and dispersal mode (zoochoric, anemochoric or autochoric) based on diaspore morphology and the literature (Howe and Smallwood, 1982; Pott and Pott, 1994; Turner, 2001; Carvalho, 2003; Teixeira *et al.*, 2009). Seeds heavier than 0.001 g were individually weighed; otherwise they were weighed in groups of ten seeds per species.

Data analysis

To evaluate whether the species richness and abundance on *A. phalerata* stems differed between habitats and between seasons, we used a general linear model (GLM) with Poisson distribution, as recommended for count data (Crawley, 2007). In this analysis, abundance (relative abundance) was defined as the number of persistent sheaths in which a given seed species occurred, as it is closer to the number of dispersal events than the number of seeds. As the amount of sediment on each sheath might introduce bias on sampling efforts, we tested for differences of sediment mass on persistent sheaths between habitats and between seasons, using two-way ANOVA. GLM and ANOVA were performed in the R program (R Development Core Team, 2010). To estimate richness of seeds on *A. phalerata* stems and to evaluate completeness of our sample we computed the Chao 2 estimator based on 100 randomizations using EstimateS 7.5 (Colwell, 1997; Chao, 2005).

To summarize patterns of seed bank communities (species composition and relative abundance) among *A. phalerata* stems (individuals) we used the hybrid multidimensional scaling (HMDS) technique and the Chord index of dissimilarity, in the PATN program (Faith *et al.*, 1987). To test for effects of habitat and season (independent variables) on similarity of seed banks among *A. phalerata* stems (values of HMDS axes 1 and 2; dependent variables), we used multivariate analysis of variance (MANOVA) and the Pillai Trace statistic, with Systat 11. Cited means are shown \pm s.e.

RESULTS

We recorded 3468 seeds of 75 species/morphospecies on persistent sheaths of *A. phalerata* in the Pantanal. We found 54.2 ± 10.6 seeds, and 3.6 ± 0.3 species/morphospecies per palm stem ($n = 64$). These seeds were distributed on 75 ± 8 % persistent sheaths on each palm tree. The 20 seed species (27 %) identified to family level or lower belonged to 12 families and 13 genera (Table 1). Most species/morphospecies (95 %) had small seeds (≤ 1 g), and were zoochoric (40 %) or anemochoric (34 %). The only large-seeded (approx. 15 g) species on *A. phalerata* stems was its own seed.

Moraceae was the richest family ($n = 4$ species) on stems, but 92 % (637/694) of these seeds belonged to one species, *Ficus pertusa*. Urticaceae was the most abundant family ($n = 1594$ seeds), represented only by *Cecropia pachystachya*. Other families comprised three or fewer species of seeds on *A. phalerata* stems, and occurred on 23 % (15/64) or less of them. The seed community on persistent sheaths showed a markedly high dominance of two species, *C. pachystachya* and *F. pertusa* (Table 1), which occurred on 84 and 63 %, respectively, of the palm individuals. Eighteen species occurred

on 3–20 % of the palm stems, and 55 species occurred on 1.5 %.

The number of seed species in the seed bank found on *A. phalerata* stems did not differ ($z = 103.08$, $P = 0.32$) between riparian forests ($n = 49$) and capões ($n = 38$). On the other hand, it was higher ($z = 69.49$, $P < 0.01$) in the wet season ($n = 57$) than in the dry season ($n = 26$). Eight species were common to both seasons and 13 to both habitats. Estimated richness of seeds on palm stems was 171 in riparian forests (95 % CI from 94 to 373) and 96 in capões (95 % CI from 58 to 206), and 137 in the wet season (95 % CI from 89 to 254) and 127 in the dry season (95 % CI from 56 to 365). The number of persistent sheaths containing seeds was higher ($z = 287.67$, $P < 0.01$) in riparian forests ($n = 277$) than in capões ($n = 206$), and was higher ($z = 202.12$, $P < 0.01$) in the wet season ($n = 341$) than in the dry season ($n = 142$). Accumulated material per persistent sheath weighed 17.2 ± 1.2 g ($n = 32$) and did not differ between habitats ($F_{1,28} = 0.78$, $P = 0.38$) or between seasons ($F_{1,28} = 0.02$, $P = 0.88$), and therefore the amount of accumulated material was not a source of bias among samples.

The community structure of seed banks on palm stems, based on species composition and their relative abundances (HMDS: $r^2 = 0.81$; stress = 0.23), differed between habitats ($P < 0.01$; MANOVA – Pillai Trace = 0.008) but not between seasons ($P = 0.198$; MANOVA – Pillai Trace = 0.31), and there was no effect of habitat and season interaction ($P = 0.38$; MANOVA – Pillai Trace = 0.24). Seed species composition was less similar among palm stems in capões than among those in riparian forests.

DISCUSSION

Palm stems as seed banks

Our results indicate that persistent sheaths of *A. phalerata* stems are accessible sites for arrival of seeds of several forest species in the Pantanal, resulting in a palm seed bank. Most sheaths (65 %) accumulate seeds in amounts comparable to soil seed banks (Butler and Chazdon, 1998; Grombone-Guaratini and Rodrigues, 2002; Grombone-Guaratini *et al.*, 2004), even considering that the limited space between the sheath and stem restricts the number of seeds that can accumulate. The limited space on persistent sheaths is probably a first barrier to retaining large seeds. These are also rare in soil seed banks because they are generally recalcitrant, produced in small quantities and susceptible to predation (Fenner, 1985; Thompson, 1987; Louda, 1989; Gross, 1990; Murdoch and Ellis, 2000; Moles *et al.*, 2004).

Overall, the palm seed banks included 4 % of angiosperm species and 10 % of the angiosperm families already reported in the Pantanal (Pott and Pott, 1994). In addition, the richness and abundance of seeds on *A. phalerata* persistent sheaths in the Pantanal (75 species and 3468 seeds) are higher than those often found in soil seed banks of tropical forests (< 50 species) (e.g. Butler and Chazdon, 1998; Grombone-Guaratini and Rodrigues, 2002; Grombone-Guaratini *et al.*, 2004). This richness may be due to a high accumulation of seeds in a limited space (*A. phalerata* stems) and low rates

TABLE 1. Frequency of occurrence, life forms, mass and dispersal mode of 20 seed species recorded on persistent sheaths in stems of *Attalea phalerata* (Arecaceae) palm trees in the Pantanal do Miranda, Brazil

Family/species	Frequency*		Life form	Seed mass (g)	Dispersal mode
	Capões	Riparian forest			
Urticaceae					
<i>Cecropia pachystachya</i> Trec.	23 (543)	31 (1051)	Tree	0.001	Zoochory
Moraceae					
<i>Ficus pertusa</i> L. f	23 (165)	17 (472)	Hemi-epiphyte	<0.001	Zoochory
<i>Ficus gardneriana</i> (Miq.) Miq	1 (3)	0	Hemi-epiphyte	<0.001	Zoochory
<i>Ficus</i> sp. 1	1 (1)	4 (52)	Hemi-epiphyte†	<0.001	Zoochory
<i>Ficus</i> sp. 2	1 (1)	0	Hemi-epiphyte†	0.001	Zoochory
Arecaceae					
<i>Attalea phalerata</i> Mart. ex. Spreng.	9 (20)	4 (13)	Tree	14.95	Zoochory
Annonaceae					
<i>Ammonia</i> sp.	3 (24)	2 (11)	Shrub	<0.001	Zoochory
<i>Unonopsis lindmanii</i> R. E. Fries	0	1 (2)	Shrub	0.153	Zoochory
Fabaceae					
<i>Aeschynomene</i> sp.	0	1 (1)	Herb	0.044	Autochory
<i>Deguelia costata</i> (Benth.)A.M.G.Azevedo	0	1 (1)	Tree	0.001	Zoochory
<i>Pterogyne nitens</i> Tul.	0	1 (2)	Tree	0.07	Anemochory
Anacardiaceae					
<i>Astronium fraxinifolium</i> Schott ex Spreng	1 (1)	0	Tree	0.034	Anemochory
Caryophyllaceae					
<i>Drymaria cordata</i> (L.) Willd. ex Schult.	1 (1)	1 (1)	Herb	0.002	Autochory
Ulmaceae					
<i>Trema</i> sp.	1 (1)	0	Shrub	<0.001	Zoochory
Myristicaceae					
<i>Virola</i> sp.	0	1 (1)	Tree	0.056	Zoochory
Malpighiaceae					
<i>Byrsonima</i> sp.	2 (2)	0	Shrub	<0.001	Zoochory
Sapindaceae					
Morphospecies 1	2 (2)	2 (2)	–	0.002	Zoochory
Sterculiaceae					
Morphospecies 2	3 (9)	0	–	0.002	Anemochory
Morphospecies 3	1 (1)	0	–	<0.001	Zoochory

* Frequency is the number of palm individuals which contained seeds for each species; the total number of seeds recorded is given in parentheses.

† Two of the six species of *Ficus* that occur in the study site are not described as hemi-epiphytic.

of seed movement. Palms are also more frequently used than other trees as feeding perches by seed dispersers.

Seed banks on *A. phalerata* stems in the Pantanal mainly comprised small endozoochoric and dormant seeds, with a few dominant species, as found for soil seed banks in tropical forests (Thompson, 1987; Gross, 1990; Butler and Chazdon, 1998; Leishman *et al.*, 2000; Murdoch and Ellis, 2000). The two dominant species in palm seed banks – *C. pachystachya* and *F. pertusa* – are the two most frequent seeds found in the faeces of *Artibeus jamaicensis* (Phyllostomidae), by far the most abundant fruit-eating bat in the Pantanal (Teixeira *et al.*, 2009). This indicates that bats are probably the main vectors of seeds to *A. phalerata* stems (Marinho-Filho, 1992).

The palm sheaths can provide a safe site as they maintain specific conditions of humidity and nutrients (Howe and Smallwood, 1982; Eriksson and Ehrlen, 1992; Bernal and Balslev, 1996), and could provide protection against predation and flooding in the Pantanal. The sandy Pantanal soil is drier (when not flooded) and poorer in nutrients than the palm sheaths (see also Bernal and Balslev, 1996), and thus *A. phalerata* stems may favour seed germination and seedling establishment. In addition, during the wet season seeds and seedlings in palm stems may stay above inundation level (<1 m deep) so escaping from flooding. Seedlings of several

tree species in the Pantanal, including *C. pachystachya*, are not flood-tolerant (Damasceno *et al.*, 2005).

For epiphyte or hemi-epiphyte species, the arrival of seeds on palm stems is clearly expected to improve their survival and growth; in fact, many epiphyte/hemi-epiphyte species are unable to establish directly on forest ground (Benzing, 1990). Although seeds of epiphytes/hemi-epiphytes represented few of the species recorded, they are among the commonest seed species in palm seed banks. *Cecropia pachystachya* has been not described as an epiphyte/hemi-epiphyte, but we have found reproductive trees in the Pantanal that germinated on *A. phalerata* stems and their roots connected to soil after establishment. Therefore, the massive arrival of seeds on palm stems (this study) combined with a negative effect of flooding on recruitment on forest soils (Damasceno *et al.*, 2005; Marques *et al.*, 2009) might favour the hemi-epiphyte habit found for some individuals of *C. pachystachya* in the Pantanal.

The scarcity of seeds of epiphytes or hemi-epiphytes indicates that most species in the *A. phalerata* stems are not adapted to grow up on phorophytes. However, their low density in palm seed banks may not be relevant in terms of overall recruitment for their local populations, as only a small proportion of seeds would die on palm stems. In

contrast, a massive arrival in palm seed bank could be disadvantageous for species that have no adaptations to grow up on trees. Thus, even though occasional individuals of *C. pachystachya* were recorded on palm trees, additional data are needed to support the hypothesis that palm stems represent safe sites for its seeds.

Richness, abundance, and composition between habitats and seasons

The estimated richness of seeds in palm seed banks was far higher than the observed number of seed species on *A. phalerata* sheaths due to the very high number of rare species. Several rare species are expected to be added with increasing number of sampled palm stems at the study site, as deposition of seeds on palm stems occurred only once or twice for many species. Therefore, most diaspores appear to arrive accidentally at *A. phalerata* stems, probably related to forest community structures that commonly have a large number of rare species (Felfili et al., 2000; Wittmann et al., 2008).

The lower number of sheaths containing seeds among palm trees in riparian forests than for those in capões might be related to differences between habitats in the arrival and/or in retention of seeds on palm stems. In the riparian forest *A. phalerata* individuals are surrounded by taller (10–20 m) trees with dense canopies, which could be used by the fruit-eating bats as feeding roosts. By contrast, palms in capões commonly have conspecific neighbourhoods and represent the main place suitable as bat feeding roosts. In addition, the high intensity of flooding in riparian forest might flush out the seeds deposited on palm stems, whereas the lower flooding in capões would maintain most of them. The increased richness of seeds and number of sheaths containing seeds during the wet season may be explained by the largely seasonal fruiting seasons of the zoochoric species in the Pantanal (Ragusa-Netto, 2004).

Community structure between habitats and between seasons

Composition and structure of *A. phalerata* seed banks in forest patches (capões) had lower similarity among them than did palm seed banks in riparian forest. This pattern is probably related to the patchy nature of capões, with a wide range of size, degree of isolation and flooding regime, whereas the riparian forests are continuous formations under a similar flooding regime throughout their extent (Silva et al., 1998; Cunha and Junk, 1999; Damasceno et al., 1999, 2005). The dominant species on palm seed banks, *C. pachystachya* and *F. pertusa*, are year-round fruiting plants which occur in capões and riparian forests (Ragusa-Netto, 2004; Teixeira et al., 2009), and thus they contribute to the increased similarity of palm seed banks between seasons. Moreover, the similar community structures between seasons indicate that an accumulation of seeds occurs over time mainly due to the two dominant species.

Conclusions

Attalea phalerata stems maintain seed banks in the Pantanal which have general characteristics similar to those described

for the soil seed banks of tropical forests. Therefore, factors which determine overall patterns of soil seed bank structures are probably the same as those shaping the traits of palm seed banks described here. Seeds of fig species and *C. pachystachya* dominate palm seed banks and they are able to successfully establish seedlings on palms and become adults, but other less abundant seed species would depend on secondary dispersal. Ants are regular visitors of *A. phalerata* and they commonly carry a wide diversity of small seeds to their nests (Leal et al., 2007), and thus several seed species deposited in *A. phalerata* stems might be removed to surrounding sites. In this way palm stems could provide seeds with a place to wait for better conditions and ensure the maintenance of seed species in the forest. *A. phalerata* is a pioneer forest species which contains a source of seeds from the local community, so it could play a key role in successional processes in the Pantanal. Additional studies focusing on seed survival and secondary dispersal after deposition on palm stems are necessary to understand the role of *A. phalerata* seed banks in forest regeneration. Knowledge of alternative places for seed deposition, other than forest soil, and the traits of such uncommon seed banks might provide new approaches to conservation and restoration.

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