THE IMPORTANCE OF FOREST DISTURBANCE FOR THE RECRUITMENT OF THE LARGE ARBORESCENT PALM *ATTALEA MARIPA* IN A SEASONALLY-DRY AMAZONIAN FOREST

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Abstract

The hypothesis that forest disturbance is important for the recruitment of the large arborescent palms *Attalea maripa* was tested with a natural experiment in the Pinkaití site ($7° 46'S$; $51° 57'W$), a seasonally-dry Amazonian forest. A 8,000 m long trail, that crosses, in its lower half, an open forest along the Pinkaití stream bottomlands and, on its upper half, a dense forest on a hill, was divided in 160 0.15 ha (50x30 m) sampling units. At each unit, adult palms were counted and percentage of canopy openness was measured with a concave spherical densiometer. The palms were nearly five times more abundant at the bottomlands, whose forest had a canopy 14.8% more open than that of the hill; supporting the hypothesis that disturbance is important for their recruitment.

Key words: Attalea maripa, Forest dynamics, Palm trees, Forest regeneration

Resumo

A hipótese de que a perturbação florestal é importante para o recrutamento da palmeira arborescente de grande porte *Attalea maripa* foi testada com um experimento natural na base de pesquisas do Pinkaití ($7° 46'S$; $51° 57'W$), uma floresta Amazônica sazonalmente seca. Uma trilha de 8.000 m de comprimento que cruza, em sua metade baixa, uma floresta aberta ao longo da baixada do rio Pinkaití e, em sua metade alta, uma floresta densa em uma serra, foi dividida em 160 unidades amostrais de 0,15 ha (50x30 m). Em cada unidade, palmeiras adultas foram contadas e a percentagem de abertura do dossel foi medida com um densiômetro hemisférico côncavo. As palmeiras foram quase cinco vezes mais abundantes na baixada, cuja floresta teve um dossel 14,8% mais aberto que aquele da serra, apoiando a hipótese de que perturbação é importante para seu recrutamento.

Palavras-chave: Attalea maripa, Dinâmica florestal, Palmeiras arborescentes, Regeneração florestal

1. Introduction

Because the stem of palms is entirely primary, with no addition of secondary vascular or thickening tissues, the establishment phase imposes considerable limitation on the overall habit of the plant (Tomlinson 1990). Palm trees compensate for the increasing mechanical support requirements during height growth by a combination of initial development of a stem that has sufficient diameter, sustained cell expansion and increase of stiffness and strength of the stem tissue with age. In some cases, there is also cell division within the ground tissue (Rich 1987). The establishment phase of most species of arborescent palms is carried through with the shoot apex close to, or below, the ground level. In such condition, palms are rosettes of large leaves emerging from forest floor, where, "locked", the stem develops to diameter largely compatible with arboreal support requirements. Such condition coincides with a period when the palms have growing energetic demands, as the fraction of biomass allocated to leaves declines with the stem development (Hallé et al. 1978).

Traveling across the Amazon basin, most of the earlier naturalists were attracted by palms – "the most characteristic components of the Amazonian landscapes" (Kahn & de Granville 1992) – and the general rarity of large arborescent palm trees in dense forests was noticed (Spruce 1871). Ecologists soon related the developmental constraints imposed by the establishment phase of large arborescent palms to the general rarity of palm trees in areas on dense forest, with closed canopy (Kahn 1986, de Granville 1992, Kahn & de Granville 1992). Field studies that support the theory that forest disturbance is very important for palm trees recruitment and, thus, distribution, made paired comparisons of palm density estimates in forest areas affected by distinct disturbance regimes. Kahn & Castro (1985) compared topographic sequences in a primary forest near Manaus, which includes dense forests in hilly well drained areas, where palm trees are rare, and bottomlands, where, due to seasonal flooding, forest disturbance is intense, and palms dominate the canopy. Kahn (1986) also found that in a dense forest in Central Amazonia with modest-sized trees and smaller gaps, arborescent palms were rare. However, in an open forest in Eastern Amazonia, characterized by giant broad-trunk trees which falling create huge gaps, those palms were abundant. Clark et al. (1995) found that within an old-growth rain forest in Costa Rica, among the topographic positions considered, the density of palms was higher on the slope crests and steeper slopes, where forest height was lower and gaps were more frequent.

The aim of this work is to verify the importance of forest disturbance for the recruitment of the large arborescent palm *Attalea maripa*, by comparing palm abundance between forest areas subjected to different disturbance regimes, in the Pinkaití site, a seasonally-dry forest of Southeastern Amazon.

2. Material and Methods

2.1 *Attalea maripa* (Aubl.) Mart.

Attalea maripa are tall (10-25 m in height), massive and solitary arborescent palm. They fit the growth form of palm trees that remains "locked" in the forest floor, as their stems have a reduced capacity of increasing in diameter after the shoot is formed (Salm 2004). The subterraneous stems of several palm species, after germination, develop with an obliquely horizontal orientation before turning upwards. In *Attalea* spp. such curvature is exaggerated, since the axis is initially positively geotropic and subsequently negatively, giving a "saxophone shape" to the developing stem (Tomlinson 1990).

The natural distribution of *A. maripa* is circumscribed to the Amazon, although widespread towards its peripherical, seasonally-dry forests, where it can be very common (Uhl & Dransfield 1987, Henderson *et al.* 1995). In terra firme forests, the species is not naturally dominant over large areas, but often dominates secondary forests (Kahn & de Granville 1992). Patches of this species are often encountered in remote, primarily indigenous areas in the Xingu River basin (May et al. 1985). The fruits of *A. maripa* are frequently a main food source for the vertebrate community (Bodmer 1991, Kahn & de Granville 1992, Fragoso 1997, 1998, 1999).

2.2 Study site

This study was conducted in the Pinkaití Research Station (7° 46'S; 51° 57'W), managed by the NGO Conservation International do Brasil (CI-Brasil). The Pinkaití is located at the border of the Riozinho river, a second-order tributary of the upper Xingu river, within the Kayapó Indian village territory of A' Ukre, at the municipality of Ourilândia do Norte, Southern Pará, Brazil (Fig. 1).

The study site lies within the pre-Cambrian crystalline shield of Brazil. Elevation ranges from 200 to 450 m above sea level and the relief is irregular, characterized by rolling slopes that are interrupted by rock outcrops. Rocky ridges throughout the area are 100-250 m in altitude. The climate is tropical dry, with monthly temperatures ranging between 25 and 27°C (Holdridge 1967, Salati & Marques 1984). At the forest management farm Marajoara, 130 km on a straight line eastward from the Pinkaití, annual precipitation between 1995 and 2001 ranged from 1636 to 2170mm, with >90% falling between November and May; in some years no rain fell for 3-4 moths during the dry season (Grogan 2001). Following a westward gradient of increasing rainfall in Eastern Amazonia (Nimer 1977), the climate in the Pinkaití is slightly wetter with average rainfall close to 2200 mm.yr^{-1}.

A floristic inventory based on two 1ha plots (1000x10m) at the study site revealed approximately one hundred tree species per hectare at this site. This species
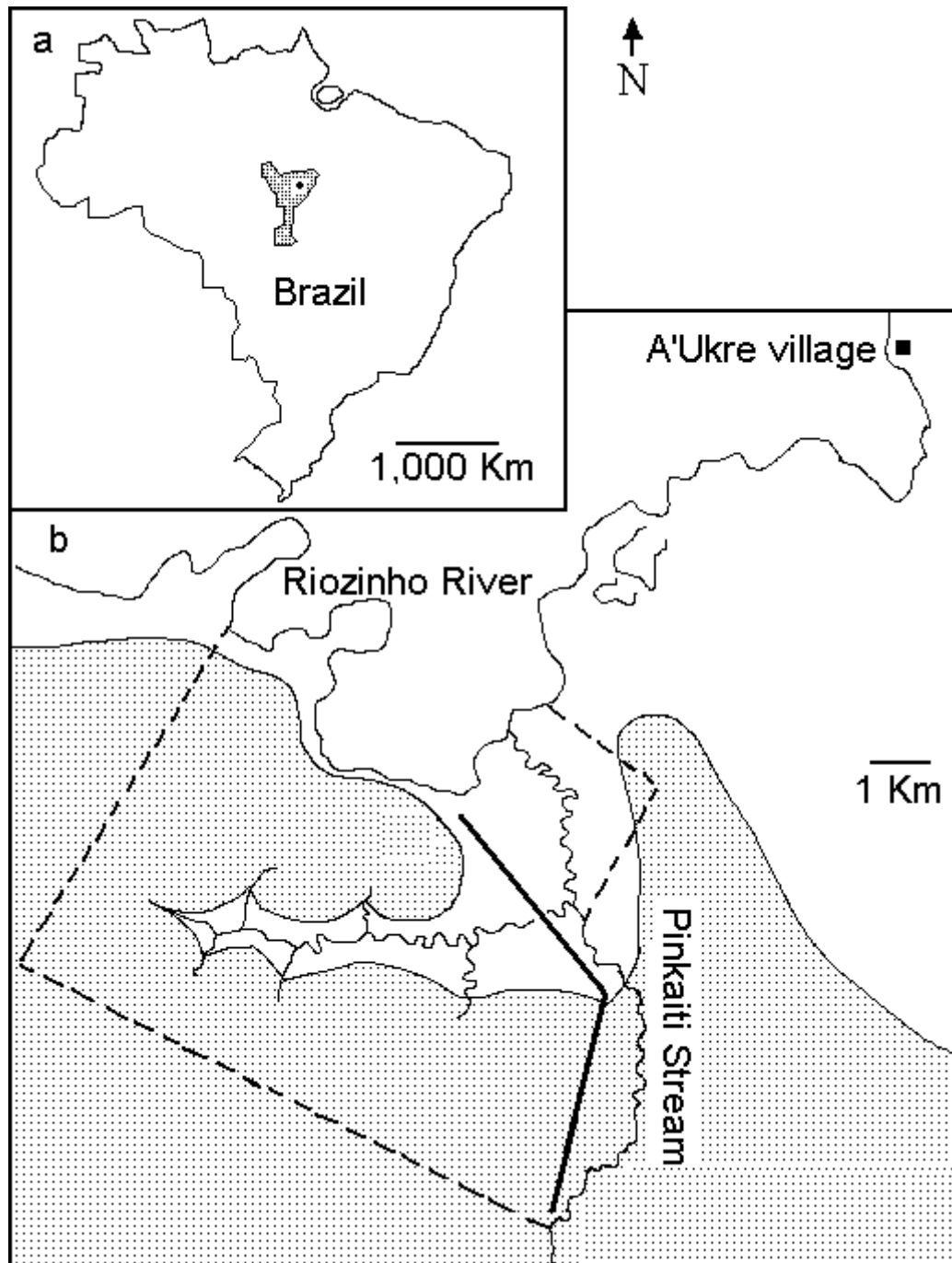
FIGURE 1. The study set up. (a) Within the map of Brazil, the block of Xingu indigenous lands (14,197,666 ha); the black dot indicates the Pinkaití site position (FUNAI 2004; adapted). (b) A'Ukre village position and the limits of the Pinkaití research station, presented by the Pinkaití stream and Riozinho rivers, as well as dotted lines (≅10,000 ha). White and shaded areas are bellow and above 300 m height limit, in relation to the sea level, according to a 1:50,000 IBGE (1985) map. The bold line approximately follows the orientation of the Waterfall trail.
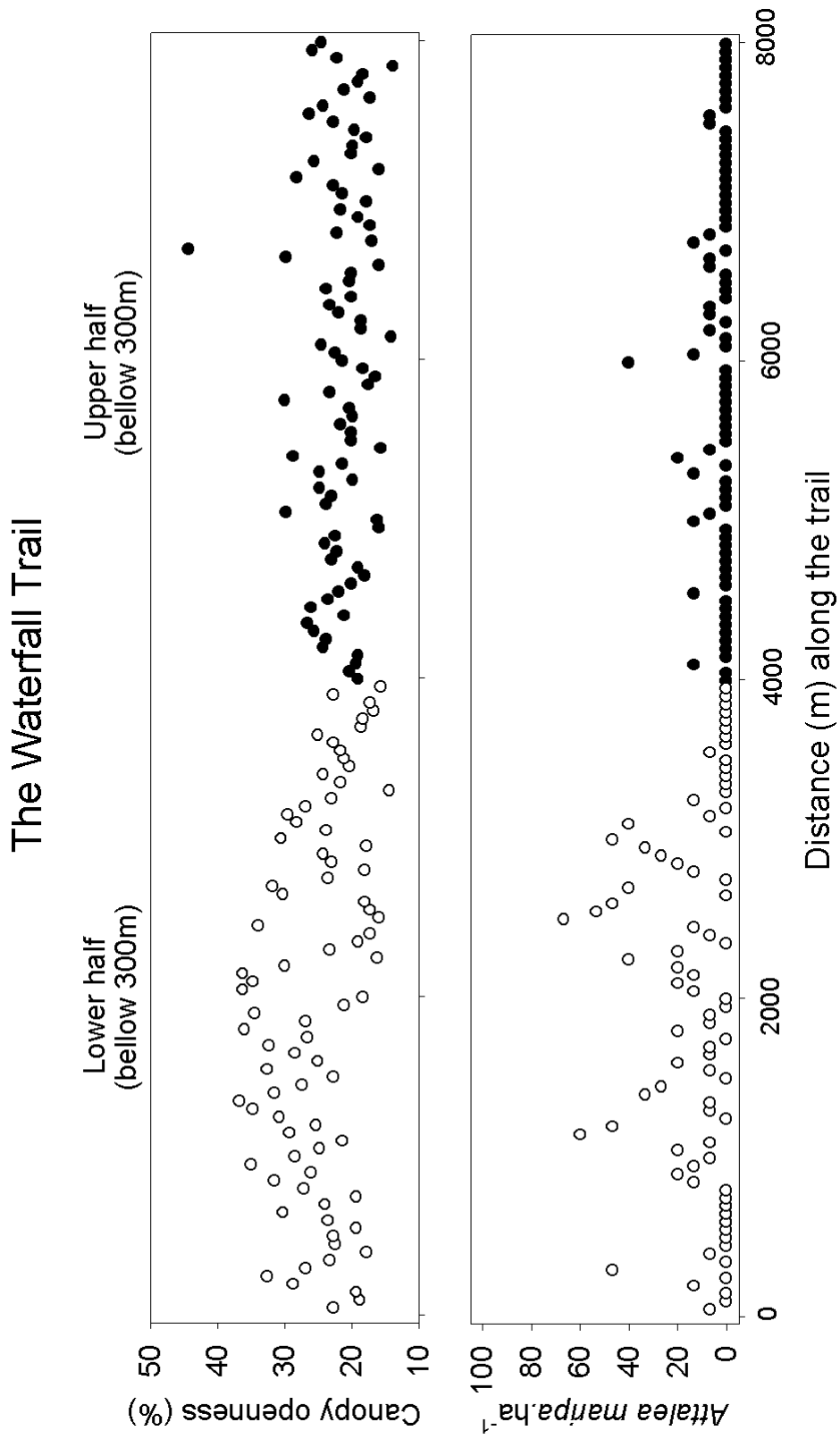
FIGURE 2. Percentage of canopy openness and density of *A. maripa* adults per hectare, along an 8,000 m trail, open and dense circles represent sampling units at lower and upper half of the trail, respectively.

richness is much lower than in the richer Amazonian sites and is typical of transitional Amazonian forests (Baider 2000). At the distribution limit of the Amazon, the forest at the study site is structurally heterogeneous, consisting of clearly distinguishable mosaics of open and dense forests (RADAM 1974). There, both strong draught in the austral winter, and intense rainfall in the summer, contribute for forest disturbance. During the dry season, when there is no rain whatsoever for the period of up to three months, the Riozinho river and the Pinkaití stream are the only perennial water bodies in the area. During this period, close to 16% of tree species at the study site shed their leaves, a high value if compared to rainier areas of Central Amazon, but still low enough to be considered an evergreen forest (Baider 2000).

Open forests, distinguished by great discontinuity of canopy, occur along the limits of the Amazon on isolated patches or on bottomlands (Pires 1984, Prance & Brown 1987, Daly & Prance 1989). At the Pinkaití site, open forests are mainly concentrated along the bottomlands of the Riozinho river and the Pinkaití stream (RADAM 1974). Such bottomlands are percolated by a netlike system of seasonal streams which, following storm periods, at the top of the rainy season, cover the whole area with up to a meter of water, creating soil instability and increasing the tree-fall probability. Most clearings at this area are small (up to 100 m^2), but large tree falls (≥ 400 m^2) are common, especially when associated with a domino effect, when a large tree falls upon others that do not resist and fall as well (Baider 2000). In addition, under intense disturbance regime, the light environment is propitious for the growth of lianas. Such vines hinder the development of the trees which they use for support to grow and, connecting the crown of neighboring trees, upon a tree fall pulls others, further increasing forest disturbance (Phillips at al. 2002, Grauel & Putz 2004). This positive disturbance feedback results in the degeneration of large areas across the seasonally-dry Amazonian forests (RADAM 1974).

Dense forests, characterized by a rather uniform 25 to 45 m high continuous and evergreen canopy with sparse emergent trees taller than 50 m, are found in well drained areas at the Pinkaití site (RADAM 1974). At the upper Pinkaití stream valley, during the drought period, the humidity retained by the relief has an attenuating effect on dryness and, during the rainy season, declivity prevents flooding and the soil instability associated. The basal area of trees with DBH $\geq$ 10cm at the uplands of the Pinkaití stream valley (40 m^2.ha^{-1}) is remarkably high (Baider 2000).

At the Pinkaití site, *A. maripa* seeds are efficiently dispersed by agoutis, which may carry seeds for up to hundreds of meters and scatterhoard them for future consumption, eventually failing to retrieve them (Jorge 2000). Furthermore, tapir feces containing more than a hundred *A. maripa* seeds are often found at the study site. Both seed dispersers are relatively abundant at the Pinkaití, where they are found at densities of 43.3 and 0.6 individuals per km^2, respectively (Peres 2000).

2.3 Experimental procedures

Associations of canopy openness and adult *A. maripa* distribution along the 8,000 m long Waterfall Trail (Fig. 1) were investigated. The trail crosses, in its lower half, the bottomlands of the Pinkaití stream valley, and in its upper half, the well drained areas that follow this river along the hills. All adult *A. maripa* palms up to 15 m on both sides of the trail were counted in 50 m intervals, resulting in 80 (50x30 m – 0.15 ha) sampling units, in each vegetation type. Perpendicular distances from transects was not measured, unless the palm appeared to be close to the distance cut-off point to ensure census accuracy. Canopy openness measurements made every 50 m (one measure per sampling unit) along the trail, using a spherical densiometer (a pocked-size concave mirror with 96 divisions), was chosen as a proxy for forest light environment. The canopy openness and palm densities at the bottom- and uplands of the Pinkaití valley were compared through the Mann-Whitney test.

3. Results

At the bottomlands of the Pinkaití stream, a total of 145 adult *A. maripa* palms were found (12.1 palms.ha^{-1} or 1.8 $\pm$ 2.4 S.D. individuals.0.15ha^{-1}), and the average percentage of canopy openness was 24.6%. On the hills, on the other hand, only 30 palms were found (2.5 palms.ha^{-1} or 0.4 $\pm$ 0.9 S.D. individuals.0.15ha^{-1}), and the average percentage of canopy openness was 21.5%. The palms were, thus, significantly more abundant at bottomlands (Mann-Whitney U, p<0.001), which also had higher canopy openness (Mann-Whitney U, p<0.001; Fig. 2).

4. Discussion

The finding that, in a comparison of *A. maripa* abundance and canopy openness at the bottomland and the hills of the Pinkaití River valley, palms were nearly five times more abundant at the earlier area, which also had a canopy 14.8% more open, supports the hypothesis that disturbance is important for the recruitment of these large arborescent palms. However, the lowland and highland forests may differ in other respects relevant for the ecology of this species and, thus, theoretically, this association could spurious or be related to a third, determinant factor. Therefore, our conclusions should be taken with care. More conclusive evidence would involve relating a proxy measure of disturbance and the density of palms with more independent replicates. Nevertheless, such measurement is hindered by two sets of limitations: First, the choice of sufficient number of satisfactorily independent samples in a region where the vegetation varies structurally in a wide range of spatial scales would involve random dislocation over very large areas, which is not practical in tropical forests. Second and more

important, environmental conditions are dynamic and there may be a considerable lag between gap formation and palms recruitment. Probably, the small-scale variation in vegetation structure seen at present is not the same that influenced individual palm recruitment decades ago.

Canopy gaps of varied sizes are constantly formed in tropical forests by the fall of branches and trees, and such clearings are quickly filled by the growth of adjacent standing canopy trees, pre-existing smaller trees, seedlings or colonizers (Richards 1996). The formation of thick liana mats may also rapidly reduce the intensity of light that reaches the understory (Phillips at al. 2002, Grauel & Putz 2004). As a result, studies that investigate forest disturbance and palm trees regeneration through paired comparisons of areas subjected to different disturbance pattern support the hypothesis that disturbance is important for the recruitment of large arborescent palms (Kahn & Castro 1985, Kahn 1986, Clark et al. 1995), while the hypothesis is denied by the search of correlations between palm abundance and forest structure (Svenning 1999).

Small palms are widespread at the understory of tropical forests, even at the energetic restricted conditions of dense shade from the canopy (Chazdon 1986). According to Tomlinson (1990), establishing palms, if in energetic equilibrium, could live indefinitely in the forest interior, waiting for a gap to develop further the size of their leaves and the diameter of their subterraneous stem, unless killed by fallen trunks and branches or diseases. However, this author observed that the opportunity for the recruitment of *Attalea* palms is time-limited. Although buried to a considerable depth after germination, once their plumule starts growing upward, because palms can not produce leaves by the means of a secondary meristem, every new leave has to be produced at an upper level.

Therefore, establishing palms may eventually become too shallow to produce an obconical stem buried enough to give stability to a viable mature palm before developing a stem with sufficient diameter for future support requirements. Furthermore, highly disturbed forest patches and areas of low disturbance probability, spread in a mosaic-like fashion, may function as sources and sinks allowing the formation of a bank of seedling and juvenile, as well as rare adults, in areas of dense forest that, otherwise, would not support viable *A. maripa* populations. I conclude that, investigating the importance of forest disturbance for large arborescent palms, disturbance has to be considered in historical or probabilistic perspectives, and the palms examined trough demographic variation along the landscape.

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