**UNIVERSIDADE FEDERAL DE SÃO CARLOS**

CENTRO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE

Programa de Pós Graduação em Ecologia e Recursos Naturais

# A importância das palmeiras arborescentes de grande porte na dinâmica das florestas amazônicas sazonalmente secas

RODOLFO AURELIANO SALM

Tese de Doutorado apresentada ao Programa de Pós Graduação em Ecologia e Recursos Naturais, do Centro de Ciências Biológicas e da Saúde da Universidade Federal de São Carlos, como parte dos requisitos para a obtenção do título de Doutor em Ciências, área de concentração em Ecologia e Recursos Naturais.

Orientadora: Profa. Dra. Michèle Tomoko Sato

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**UNIVERSIDADE FEDERAL DE SÃO CARLOS**
Centro de Ciências Biológicas e da Saúde
**PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E RECURSOS NATURAIS**
Via Washington Luiz, Km. 235 - Caixa Postal 676
**Telefax:** (016) 3351-8305
CEP 13.565-905 - São Carlos - SP – Brasil
**E-mail** : ppgern@power.ufscar.br

ATA DO EXAME DE TESE DE DOUTORADO DO(A) CANDIDATO(A): **RODOLFO AURELIANO SALM.**

Aos dez dias do mês de julho de dois mil e cinco, às 14h00 no Anfiteatro do CCBS da Universidade Federal de São Carlos, reuniu-se a Banca Examinadora nas formas e termos dos **artigos 32º, 33º e 35º** do regimento do Programa de Pós-Graduação em Ecologia e Recursos Naturais, composta pelos seguintes membros: Dra. Michele Tomoko Sato (Presidente), PPG-ERN/UFSCar, Dr. José Eduardo dos Santos, PPG-ERN/UFSCar, Dra. Dalva Maria da Silva Matos, PPG-ERN/UFSCar, Dr. Euphly Jales Filho, USP/ Ribeirão Preto/SP e Dr. Yuri Tavares Rocha, USP/SÃO PAULO/SP, para Exame de Tese de Doutorado sob o título: **"A importância das palmeiras arborescentes de grande porte na dinâmica das florestas amazônicas sazonalmente secas"**. A sessão foi aberta pelo(a) presidente Dra. Michele T. Sato. Após a explanação, o(a) candidato(a) passou a palavra aos componentes da Banca Examinadora. Terminada a arguição a Banca Examinadora reuniu-se em sessão secreta para atribuição dos níveis, os quais se transcrevem: Dra. Michele Tomoko Sato, nível "A", Dr. José Eduardo dos Santos, nível , "A", Dra. Dalva Maria da Silva Matos, nível "A", Dr. Euphly Jales Filho, nível "A" e Dr. Yuri Tavares Rocha, nível "A". De acordo com os **parágrafos 1º, 2º e 3º do artigo 32º** o(a) candidato(a) foi considerado(a) aprovado com nível "A" com distinção .-.-.-.-.-.-.-.-.-.-.-.-.-.-. Encerrada a sessão secreta, o Presidente informou o resultado do concurso. Nada mais havendo a tratar, eu, João Augusto da Silva Affonso, secretário do Programa de Pós-Graduação, lavrei a presente ata que assino juntamente com os membros da Banca Examinadora.

Profa. Dra. Michele Tomoko Sato

Prof. Dr. José Eduardo dos Santos

Dalva M. Silva Matos
Profa. Dra. Dalva Maria da Silva Matos

Prof. Dr. Euphly Jales Filho

Prof. Dr. Yuri Tavares Rocha

Prof. Dr. José Eduardo dos Santos
Coordenador
PPG-ERN/UFSCar

João Augusto da S. Affonso
Secretário PPG-ERN/UFSCar

P.S. A defesa foi realizada aos sete dias do mês de julho e não aos dez dias do mês de julho supracitado.

Prof. Dr. José Eduardo dos Santos
Coordenador
PPG-ERN/UFSCar

## CANÇÃO DO EXÍLIO

"Minha terra tem palmeiras,

Onde canta o Sabiá;

As aves, que aqui gorjeiam,

Não gorjeiam como lá.

....

Minha terra tem primores,

Que tais não encontro eu cá;

Em cismar — sozinho, à noite —

Mais prazer encontro eu lá;

Minha terra tem palmeiras,

Onde canta o Sabiá.

Não permita Deus que eu morra,

Sem que eu volte para lá;

Sem que desfrute os primores

Que não encontro por cá;

Sem qu'inda aviste as palmeiras,

Onde canta o Sabiá."

**Gonçalves Dias**

*À memória de minha mãe, Tona*

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## Sumário

## Resumo

Foram estudados os determinantes biogeográficos da riqueza e abundância de palmeiras em uma escala local, ao longo de um gradiente de umidade em uma floresta amazônica sazonalmente seca, comparados com padrões observados em uma grande escala, que abrange todo o território brasileiro. Vulnerabilidade climática parece determinar fortemente a distribuição de palmeiras, sendo a importância relativa de umidade consistente nas duas escalas.

Um modelo da importância de palmeiras arborescentes de grande porte na dinâmica das florestas amazônicas sazonalmente secas foi concebido para orientar o trabalho de investigação desta tese. Aspectos do Modelo foram examinados com um experimento ecossistêmico que se aproveitou de uma mancha de floresta secundária rica em palmeiras (=palmeiral) próxima à base de pesquisas do Pinkaití, no sudoeste da Amazonia, imersa em uma matriz de florestas sazonalmente secas notavelmente bem protegida para fins de investigação científica e preservação. Focamo-nos nas palmeiras *Attalea maripa* e *Astrocaryum aculeatum*, a primeira naturalmente abundante e a segunda rara no Pinkaití, buscando estabelecer comparações entre as duas espécies, sempre que possível.

A floresta do Pinkaití apresenta grande heterogeneidade em sua estrutura e composição florística. Tais diferenças se devem à perturbação natural, característica das espécies arbóreas mais importantes e ao histórico de uso do solo. Moderadamente dominado pela palmeira *A. maripa*, o palmeiral apresentou alta diversidade de árvores e é floristicamente semelhante às florestas primárias da base de pesquisas.

Apesar de superficialmente semelhantes, as palmeiras *A. maripa* e *A. aculeatum*, são distintas na estrutura e desenvolvimento de seu caule. O caule dissecado de *A.*

*aculeatum* apresentou gradientes mais íngremes de densidade, tanto do topo para a base, quanto da sua parte interna para a parte externa, se comparado com o caule de *A. maripa* examinado. A diferença tem importantes implicações para a ecologia destas espécies. O crescimento e a idade das palmeiras foram estudados com uma formula que incluí o número médio de cicatrizes foliares, e a taxa anual de queda de folhas em uma população amostrada na base do Pinkaití. Foi estimado que *A. aculeatum* também tem gradientes mais íngremes de declínio de crescimento do caule a medida que o caule cresce em altura. A diferença pode explicar a vantagem numérica de *A. maripa* sobre *A. aculeatum* nas matas tipicamente abertas das florestas amazônicas sazonalmente secas. Vantagem esta, que é provavelmente revertida a favor de *A. aculeatum* nas florestas densas da Amazônia Central e Ocidental.

O estudo da distribuição da palmeira *A. maripa* em relação a perturbação florestal sugere que, tanto a perturbação natural, como a antrópica, afetam sua ocorrência favoravelmente. Entretanto, devido ao longo tempo de desenvolvimento das palmeiras arborescentes em relação à escala compatível com a experimentação científica ordinária, o estudo da importância da perturbação florestal para o desenvolvimento das palmeiras deve considerar a perspectiva histórica e variações explícitas da distribuição das palmeiras ao longo da paisagem.

As sementes de *A. aculeatum* são substancialmente maiores que as de *A. maripa* e carregam mais reservas para o embrião. O estudo da chuva-de-sementes das duas espécies, baseado nos padrões de distribuição das plântulas em relação aos adultos reprodutivos de suas espécies, contradiz padrões gerais das angiospermas pois, na escala espacial considerada, as sementes de *A. aculeatum*, maiores, estavam dispersas mais homogeneamente que as sementes de *A. maripa*. O resultado pode ser explicado pelos “serviços” de dispersão de sementes prestados por roedores caviomorfos (cotias, *Dasyprocta aguti*) que estocam sementes espalhadas. Aparentemente os roedores preferem as sementes mais ricas em reservas de *A. aculeatum*, para quem seriam dispersores mais eficientes, se comparado com *A. maripa*, que lhes “paga” coquinhos menores pelo trabalho de dispersão.

O modelo de Janzen-Connell, que pretende explicar a alta diversidade de árvores das florestas tropicais chuvosas em relação a florestas equivalentes na região temperada pela maior diversidade de herbívoros hospedeiro-específicos nos trópicos, foi investigado. O sistema estudado inclui a palmeira *A. maripa*, o besouro bruquídeo, *Pachymeris cardo*, e uma guilda generalista de vertebrados predadores de sementes de grande porte. Os resultados são consistentes com a previsão de Janzen-Connell de que, quando acidente histórico produzir densidades variadas de adultos reprodutivos de uma dada espécie, em florestas tropicais chuvosas, a mortalidade média das sementes causada por um predador hospedeiro específico deve ser uma função inversa da densidade de árvores reprodutivas adultas.

Os resultados apresentados nos capítulos de dados desta tese sugerem que o modelo proposto é apropriado e que seu estudo é gratificante para a compreensão da importância das palmeiras arborescentes de grande porte na dinâmica das florestas amazônicas sazonalmente secas. Desta forma, sobressai seu papel como ferramenta para a reconstituição ambiental em um provável futuro de desmatamentos em larga escala na Amazonia.

## Abstract

We investigated and compared the determinants of palm diversity at different spatial scales: along a moisture gradient in a seasonally dry Amazonian forest and using a climatic model comprising the entire Brazilian territory. Climatic hazards seem to strongly determine the distribution of palms, with the relative importance of moisture being highly consistent across scales.

A model that represents the importance of large arborescent palms on the dynamics of seasonally dry Amazonian forests was conceived to guide this thesis. Specifically, the model is aimed at guiding the investigation of the role of large arborescent palms on forest regeneration and succession. Aspects of the model were examined with a ecosystem experiment that took advantage of a palm-rich secondary forest patch (=*palmeiral*) close to the Pinkaití research station, south-eastern Amazon, immersed in a matrix of notably well protected seasonally dry forests, preserved to the purpose of scientific investigation and preservation. We focused on the palms *Attalea maripa* and *Astrocaryum aculeatum*, the first naturally abundant and the second rare at the Pinkaití, attempting to establish comparisons between the two species, whenever possible.

The Pinkaití, like other seasonally dry forests, have great heterogeneity in forest structure and composition, associated with biotic characteristics of the most important tree species, natural disturbance and history of land-use. The palm grove, moderately dominated by the arborescent palm *Attalea maripa* (Aubl.) Mart., presented high tree species diversity and was floristically similar to undisturbed forests at the study site.

Despite being superficially similar, the palms *A. maripa* and *A. aculeatum* are distinct in the structure and development of their stem. The samples of *A. maripa* stem were more homogeneous in density than those of *A. aculeatum*, both from the internal to the

external, and from the lower to the upper parts of the stem. Field estimates of stem growth rates revealed that *A. maripa* growth is also more constant through development in height. Short *A. aculeatum* palms had faster growth rates than *A. maripa*, as they get taller, stem growth rates are reduced and approach *A. maripa* rates. The difference could explain the numerical advantage of *A. maripa* over *A. aculeatum* at the typically open seasonally dry Amazonian forest. Advantage, which is probably reverted in favor of *A. aculeatum* at the dense forests of Central and Western Amazon.

The study of *A. maripa* palms distribution in relation to forest disturbance suggests that, both natural and anthropic disturbance affects favorably their occurrence. However, due to the long time of palms development in relation to ordinary scientific research, the study of the importance of forest disturbance to the development of arborescent palms must consider the historical perspective and explicit variations of palms distribution across the landscape.

The seeds of *A. aculeatum* are substantially larger that those of A. maripa and carry more reserves to the embryo. The study of the seed rain of both species, based in the seedling distribution patterns in relation to reproductive adults contradict general patterns among Angiosperms as, at the considered scale, the seeds of *A. aculeatum*, larger, were more homogeneously dispersed than the seeds of *A. maripa.* The result can be explained by the seed dispersal services paid by scatterhoarding caviomorph rodents (agoutis, *Dasyprocta aguti*). The rodents apparently prefer the nutrient richer seeds of *A. aculeatum*, being more efficient disperser to this palm, if compared with their behavior towards *A. maripa*, which "pays" smaller bites for the seed dispersal service.

Hypotheses for the maintenance of tropical forest tree diversity were tested with a system that includes the palm *Attalea maripa*, the beetle *Pachymerus cardo* and vertebrate predators of large seeds in a palm patch and its adjacent forest in Southeastern Amazon. Seed predation was affected by host-specificity degree of the animals involved. Seed survivorship depended on the distance from the palm-patch but was unrelated to distance from individual fruiting palms.

The result presented in the data chapters of this thesis suggests that the proposed model is appropriate and that its study is rewarding to the understating of the importance of large arborescent palms on the dynamics of seasonally dry Amazonian forests. As a result, highlights their role as tools for the environmental reconstitution in a likely future of larger scale deforestation in the Amazon.

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# Especial

# Exploração de palmeiras *Attalea*: uma alternativa para a crise energética

***Rodolfo Salm***

O gênero *Attalea* compreende as palmeiras inajá, indaiá, babaçu, piaçava, bacuri, palheira, aricuri, dois-por-dois, catolé e pindobaçu. Suas folhas são usadas para a cobertura de casas e a confecção de cestos, tapetes e vassouras. A polpa e a amêndoa de seus frutos, de onde se extrai um óleo excelente para a culinária, são comestíveis crus ou assadas. Seu palmito também é muito apreciado. Nos trópicos do Novo Mundo, as palmeiras *Attalea* sustentam boa parte da fauna silvestre de frugívoros.

Segundo o botânico russo Gregório Bondar, o grande estudioso das palmeiras *Attalea*, falecido em Salvador em 1959, os seus cocos fazem um excelente combustível que, queimado diretamente ou convertido em carvão, gera até 8.010 calorias por grama. Durante a Primeira Guerra Mundial, quando o conflito limitou o comércio mundial de carvão mineral, coquinhos de *Attalea* foram queimados aos milhares de toneladas no Brasil, utilizados para fins industriais, em substituição ao carvão mineral. Exportados para os Estados Unidos, os cocos serviram de combustível à marinha norte-americana.

Nas palavras de Bondar: "*o coco destas palmeiras é um carvão mineral que cresce em árvores sem a mina nunca se esgotar, e seu óleo pode facilmente substituir o óleo dos motores a diesel. O carvão pode ser produzido a um custo modesto e vendido à industria siderúrgica, companhias de navegação e de transporte ferroviário*".

Uma tese de doutorado defendida este ano na faculdade de Engenharia Mecânica da Unicamp demonstrou que a tecnologia de geração de energia elétrica a partir de bagaço de cana-de-açúcar, com ligeiras adaptações, pode gerar o equivalente a 105 MW, ou 2% da matriz energética nacional, com cerca de 1 milhão de toneladas de cascas de babaçu por ano ("Caracterização Energética do Babaçu e Análise do Potencial de Cogeração", Autor:Marcos Alexandre Teixeira, Orientador: Luiz Fernando Milanez. 2003).

A queima de combustíveis fósseis e a construção de grandes hidrelétricas na região amazônica, com desmatamentos invariavelmente associados, muito contribuem para o efeito estufa, com conseqüências sinistras para o futuro da vida na Terra. Em contraste, a queima dos coquinhos de palmeiras é inofensiva à biosfera, pois o carbono que contêm é recapturado no processo de fotossíntese.

Nos imensos campos devastados dos estados do Acre, Rondônia, Mato Grosso, Tocantins e Pará – o arco de desmatamento da Amazônia –, exércitos de palmeiras lutam contra o capim. Até a formação de um dossel sombreado, pragas de clareira como cipós, taquaras e touceiras de gramíneas infernizam espécies da mata madura como o mogno e a castanheira, estancando a sucessão ecológica. O crescimento das palmeiras é o próprio restabelecimento da floresta. Por isso são consideradas, e tratadas, como pragas pelos fazendeiros, que preferem os campos às matas. Há localidades no Norte do Brasil onde as palmeiras *Attalea* são tão abundantes e a produção de frutos tão intensa que o chão fica completamente coberto de frutos acumulados. Em áreas cultivadas, palmeirais chegam a produzir anualmente 1.500 kg de coquinhos por hectare.

Os 30 milhões de hectares já desmatados da Amazônia, se reflorestados com palmeiras, produziriam muitos milhões de toneladas de carvão, que poderiam gerar algo próximo a toda a demanda nacional por energia elétrica. Como a coleta de frutos é manual e trabalhosa, a ampla utilização da energia das palmeiras criaria muitos milhões de empregos no campo. Com os imensos palmeirais, recuperaríamos a mata já devastada e prescindiríamos de novas hidrelétricas, como Belo Monte, no Xingu, salvando-nos de suas nefastas e inevitáveis conseqüências ambientais.

**Rodolfo Salm, doutorando em Ecologia e Recursos Naturais pela Universidade Federal de São Carlos (PPG-ERN/UFSCar), é pesquisador do projeto Pinkaiti Aldeia A'Ukre.**

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## Capítulo-1

# Introdução geral

O objeto deste estudo é o papel ecológico desempenhado pelas palmeiras arborescentes de grande porte na dinâmica das florestas amazônicas sazonalmente secas. Abordaremos este objeto através de um modelo simplificado do sistema florestal, porém concebido para ser capaz de dar conta dos atributos funcionais por mim considerados relevantes. Para nossos propósitos, não consideramos como necessário que o modelo concebido comportasse a quantificação das conexões estabelecidas. Como se verá, o Modelo, em que pese sua extrema esquematização, mostrou-se suficiente e pertinente ao nosso objeto de estudo.

## O Modelo

O modelo proposto para a representação da dinâmica das florestas amazônicas sazonalmente secas está representado na Figura 1. O propósito do Modelo é guiar a investigação do papel de palmeiras arborescentes de grande porte na regeneração da floresta, entendida como o seu retorno para a maturidade ou clímax, a partir de perturbações. Foram incluídas relações entre um conjunto de variáveis de diferentes naturezas envolvendo três grupo de plantas, "árvores", "palmeiras" e "lianas". O ciclo successional da floresta é heuristicamente dividido em "clareira", "regeneração" e "maturidade". Eventos de perturbação sempre podem trazer a floresta de volta para a fase de clareira. A regeneração leva à maturidade e uma vez na fase madura, apenas um novo evento de perturbação pode trazer a floresta de volta para a fase de clareira. O grupo de plantas adultas que dominam o estrato superior da vegetação, que recebe incidência direta da maior fração da radiação solar, depende do histórico da performance prévia de seus jovens. Tal performance, por sua vez depende das condições de luminosidade nos extratos inferiores. O desenvolvimento dos jovens varia negativamente com a capacidade do grupo

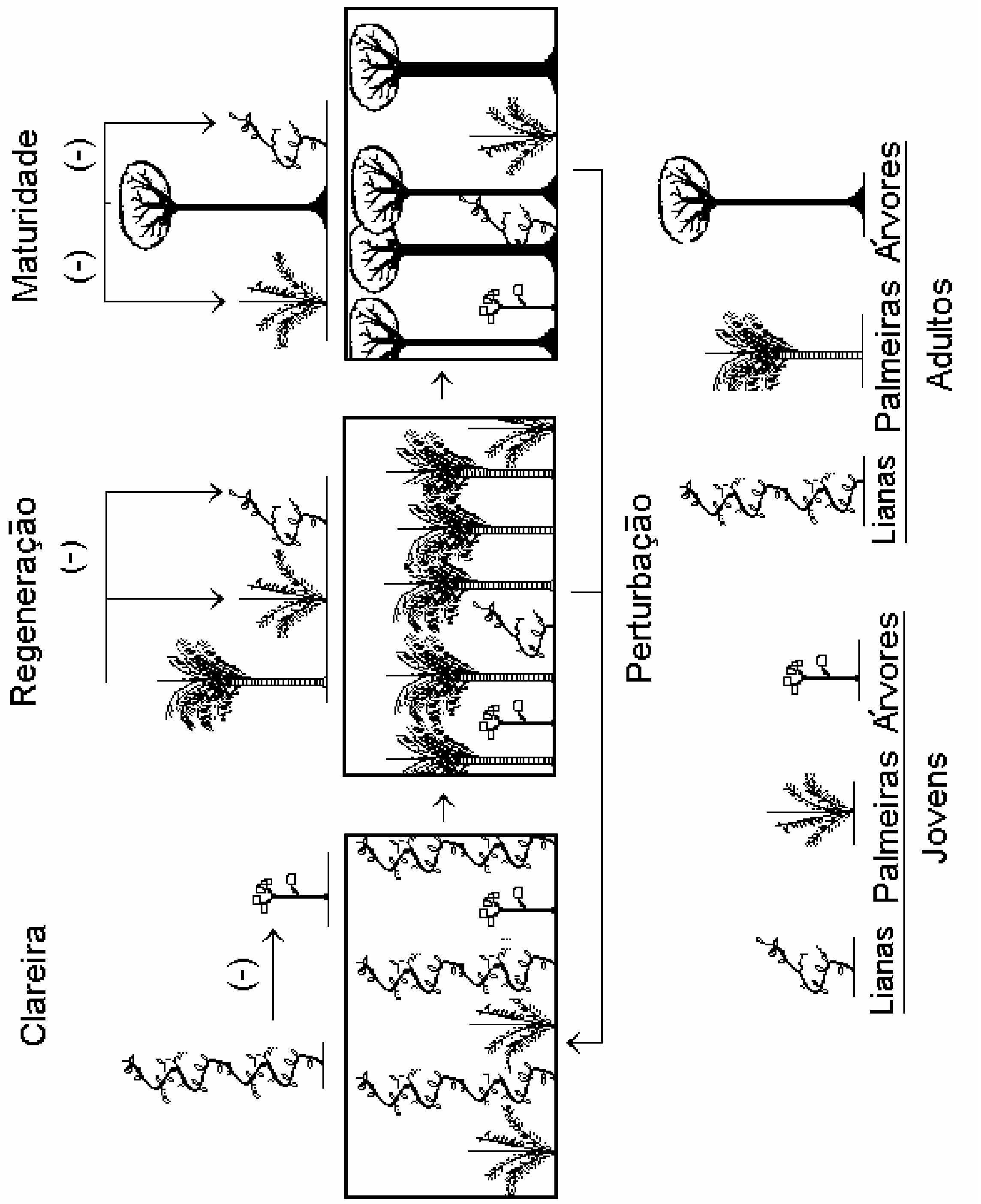

**Figura 1-** Modelo esquemático da importância de palmeiras arborescentes de grande porte para a dinâmica das florestas amazônicas sazonalmente secas.

de se desenvolver em condições de baixa luminosidade. Árvores têm as menores taxas de crescimento e a maior capacidade de crescer à sombra, no interior da floresta. Lianas têm as taxas de crescimento mais elevadas quando expostas a condições de luminosidade ótimas e a capacidade mais baixa de sobreviver à falta de luz. Palmeiras são o grupo intermediário nos dois aspectos. Na fase de florestas madura, o dossel formado pelo conjunto das árvores é alto e denso, impedindo o desenvolvimento de palmeiras e lianas. O equilíbrio pode ser rompido com um evento de perturbação que cause o colapso do dossel, criando uma clareira na mata, onde a radiação solar se aproxime do nível do solo. A alta luminosidade permite a proliferação de lianas que, quase que imediatamente, dominarem a clareira. Lianas são desprovidas de capacidade de auto suporte, mas podem escalar ao longo das árvores. Usando sua estrutura como suporte, cipós suprimem severamente o crescimento e ameaçam a sobrevivência das árvores. Entretanto, devido à sua arquitetura colunar, palmeiras não são severamente afetadas por lianas. A floresta progride para a fase de regeneração, a medida que as palmeiras crescem e o dossel é gradualmente elevado, se tornando mais denso, obstruindo progressivamente a passagem de luz. Palmeiras são auto-limitantes porque o desenvolvimento dos jovens é restrito do pela sombra produzida pelos adultos. Além do mais, sofrem mortalidade dependente de densidade. Com a redução da luminosidade nos extratos inferiores da floresta, causada pela formação de um dossel dominado por palmeiras, o recrutamento de lianas é limitado e seu impacto negativo sobre as árvores diminui, liberando-as para se desenvolver. Com o crescimento e senescência (envelhecimento) das palmeiras, e sua conseqüente substituição pelas árvores da floresta madura, a antiga clareira progride para a maturidade, e a estrutura da floresta se estabiliza, até que outro evento de perturbação a traga de volta para a fase de clareira.

## 2- Estrutura da tese

Com exceção deste capítulo introdutório, e das considerações finais, esta tese é composta por os capítulos correspondentes a artigos publicados, no prelo ou em preparação, conforme descrito em suas respectivas capas. O **Capítulo-2**, **“**Determinantes da distribuição das palmeiras em diferentes escalas”, corresponde minha mais recente viagem de campo à Amazônia, em outubro/novembro de 2004, e é metodológico e conceitualmente independente dos outros seis artigos, relacionados ao modelo da importância das palmeiras arborescentes de grande porte na dinâmica das florestas amazônicas sazonalmente secas.

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Em uma apreciação clássica do estado da arte do estudo das palmeiras, CORNER (1966) protestou pelo fato de que, nenhum dos grupos principais de plantas era tão negligenciado em seu estudo quanto elas, dada a sua importância ecológica e econômica. A razão, segundo ele, é que a maioria dos cientistas, europeus ou norte-americanos, estranhos às terras das palmeiras, as consideram excessivamente grandes e intratáveis para a investigação científica ordinária e que “é necessário viver com as palmeiras por muitos anos para aprender a apreciá-las” (CORNER, 1966, pg.2). Hoje, questões básicas relacionadas à distribuição e abundância das principais palmeiras amazônicas não estão resolvidas. O modelo proposto pretende ser um instrumento heurístico na investigação da importância das palmeiras arborescentes de grande porte na dinâmica do ecossistema das florestas amazônicas sazonalmente secas. Aspectos do Modelo são abordados através de um experimento ecossistêmico, definido por CARPENTER (1998) como o estudo de campo com unidades amostrais grandes o bastante para incluir o contexto necessário para a elucidação de aspectos de processos relevantes para a escala de ecossistemas. Desta forma, o presente estudo tirou proveito de um encrave de floresta secundária, caracterizado pela abundância de palmeiras (=palmeiral), em uma matriz de florestas primárias, a poucas centenas de metros da base do Pinkaití (descritos mais abaixo). O modelo que provê o arcabouço teórico desta tese é apresentado no **Capítulo-3,** em parte traduzindo elementos desta introdução para o formato de publicação em inglês. Diferentes aspectos deste experimento são tratados nos cinco artigos que constituem os capítulos centrais (4 a 8) desta tese.

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Florestas sazonalmente secas cobrem uma porção substancial da bacia amazônica, distribuídas ao longo de gradientes de pluviosidade em direção a seus limites com formações externas mais secas. As florestas amazônicas sazonalmente secas consistem de uma coleção de tipos de vegetação, geralmente caracterizada por alta descontinuidade do dossel e níveis variáveis de perda de folhas na época de estiagem. Estas florestas têm menor diversidade de árvores por hectare que as áreas mais úmidas da Amazônia e possuem fortes variações de composição de espécies arbóreas em macromosaicos florísticos (PIRES, 1984; GENTRY, 1988; DALY e PRANCE, 1989).

Evidências indicam que o manejo cultural e a perturbação de florestas por povos indígenas, ao longo dos milênios, transformaram muito das florestas amazônicas sazonalmente secas com grande impacto na distribuição dos tipos de floresta e cerrado (ANDERSON e BENSON, 1980; UHL, 1982; SPONSEL, 1986). Florestas de liana são amplamente distribuídas ao longo de vastas áreas da Amazonia que sofrem de forte sazonalidade pluviométrica. Tais florestas são definidas por suas áreas basais notavelmente baixas, tipicamente com 18-24 $m^2$/ha, e são caracterizadas por um dossel geralmente baixo, com árvores emergentes cobertas por grandes quantidades de lianas. Tais florestas ocupam cerca de 100.000 km$^2$ da Amazônia brasileira, principalmente entre os rios Tocantins e Xingu (PIRES, 1973; PIRES e PRANCE, 1985). Não há evidência de que solos sejam fatores limitantes para florestas de liana, uma vez que tais florestas crescem em uma variedade de solos, incluindo formas relativamente férteis (FALESI, 1972). A possibilidade de que florestas de liana sejam um tipo de anti-clímax, conseqüência de milênios interferência humana no processo de sucessão natural já foi repetidamente discutida (SMITH, 1982; BALLÉE e CAMBELL, 1990). Áreas de poucos a vários hectares amplamente dominadas por palmeiras em florestas amazônicas de terra firme estão frequentemente relacionadas a um passado de perturbação humana (BALLÉE, 1988; BALLÉE E CAMBELL, 1990; ANDERSON et al., 1991; KAHN e GRANVILLE, 1992).

Por muito tempo depois que os primeiros Europeus chegaram às Américas a região das florestas amazônicas sazonalmente secas, ao sul e a lesta da bacia amazônica, foram ocupadas exclusivamente por povos indígenas. Mudanças substanciais na ocupação da Amazonia foram impulsionadas, no começo do século vinte, pelas primeiras economias extrativistas desenvolvidas na região, notavelmente, a economia-da-borracha, *Hevea brasiliensis*, e a castanha-do-Pará, *Bertholletia excelsa*. Como estas industrias usavam o sistema de rios da Amazonia como vias de acesso, e eram baseadas em produtos não madeireiros, os desmatamentos eram desprezíveis, restritos às necessidades de produção alimentícia de subsistência (WEINSTEIN, 1983; DEAN, 1987).

Padrões de assentamentos humanos nas florestas de transição começaram a mudar mais rapidamente no começo da década de 1960 com a implementação de planos governamentais para promover a colonização da região (FORESTA, 1991; FEARNSIDE, 1993). Desde então, estradas pavimentadas abriram acesso a vastas áreas nos flancos sul e leste da Amazônia. Em décadas recentes, usinas hidrelétricas imensas foram construídas para a suportar a industria mineradora e o desenvolvimento urbano na região. A construção do complexo composto pela rodovia Belém-Brasília, a hidrelétrica de Tucuruí, e o Projeto Grande Carajás promoveram uma onda de imigração da Região Nordeste para o sul do Pará (CARVALHO, 2001). Devido às altas taxas de desmatamento que caracterizam as áreas mais acessíveis ao longo dos limites da floresta amazônica, esta região ficou conhecida como o "arco-do-desmatamento" da Amazonia (FEARNSIDE e FERRAZ, 1995).

Embora inúmeros impactos sociais e a eminência da perda da identidade cultural amazônica, no domínio das florestas amazônicas sazonalmente secas, a Terra Indígena Kayapó[1], com 3.284.005 hectares, homologada pelo decreto 316, de 29/10/1991, DOU de 30/10/1991 (ISA, 2000), destaca-se pelo excelente estado de preservação de seus ecossistemas, se comparado o entorno da reserva, no Sul do Pará, inserido em uma das principais fronteiras de ocupação da Amazônia (ZIMMERMAN et al., 2001). As taxas de desmatamento nos arredores da terra indígena são as mais altas da Amazônia brasileira (ALVES et al., 1998), mas os desmatamentos acabam abruptamente nas fronteiras da reserva. Até o momento, as principais ameaças à cobertura da floresta na Amazonia, como a criação de gado, a pavimentação de estadas e a construção de usinas hidrelétricas, não adentram as terras dos índios Kayapó (ZIMMERMAN et al., 2001).

Os Kayapó se envolveram com atividades madeireiras através de concessões ilegais feitas a empresas madeireiras, permitindo-lhes que cortem o mogno (*Swietenia macrophylla*), a espécie madeireira de maior valor na região (VERISSIMO et al., 1995;

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[1] Terras Indígenas são terras tradicionalmente ocupadas pelos índios para a sua posse e usufruto exclusivo. Habitadas por eles em caráter permanente, destinam-se às "atividades produtivas imprescindíveis à preservação dos recursos ambientais" necessários a seu "bem-estar, e reprodução física e cultural, segundo seus usos, costumes e tradições" (Artigo 231 da Constituição brasileira).

TURNER, 1999). Estima-se que 85% da população adulta de mogno já foi cortada no território Kayapó (ZIMMERMAN et al., 2001). Apesar da maquinaria pesada que é usada para a abertura de estradas e arraste de toras, os danos a florestas associados ao corte de mogno é baixo pois a espécie é naturalmente rara. A espécies está principalmente restrita a área de baixada e geralmente ocorre em densidades de poucos adultos por hectare. Entretanto, há áreas onde o mogno foi totalmente explorado, como no território da aldeia Gorotire, próximo a borda leste da reserva Kayapó, região que já sofre do esgotamento de seus estoques madeireiros e outras espécies de valor inferior se tornaram visadas. A exploração de novas espécies resulta na abertura de mais estradas e trilhas de arraste, aumentando assim, progressivamente, o impacto das atividades madeireiras sobre a estrutura e composição da floresta (NEPSTAD et al., 1999)

Como as florestas amazônicas sazonalmente secas são historicamente inacessíveis (DUCKE e BLACK 1953) e possuem baixa resiliência ao impacto de atividades antrópicas, fazendo com que o acesso moderno a estas áreas esteja invariavelmente seguido por forte degradação ambiental, a ecologia de tais florestas permanece muito pouco compreendida. Desta forma, a base de pesquisas do Pinkaiti (7° 46’18”S; 51° 57’42”W), localizada às margens do rio Riozinho, um tributário de segunda ordem do rio Xingu, representa uma rara oportunidade para o desenvolvimento de programas de pesquisa e conservação em uma área vasta e amplamente preservada de florestas amazônicas sazonalmente secas.

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A base de pesquisas do Pinkaiti (7° 46’18”S; 51° 57’42”W), no território da Aldeia A’Ukre, administrada pela Conservation International do Brasil (CI-Brasil), deu apoio logístico a este trabalho. A Dra. Bárbara Zimmerman, professora da Universidade de Toronto (Canadá), e atual diretora do Projeto Pinkaití, convidada por esta comunidade, em

1992 iniciou um projeto de estudos do mogno na área Kayapó. Para tal, a aldeia reservou cerca de 10.000 hectares de suas terras onde se comprometeu a não caçar ou retirar madeira. Nesta área foi construída a base de pesquisas do Pinkaití, que conta com duas casas de alvenaria equipadas com placas solares, rádio de ondas curtas, uma cozinha, e estrutura de alojamento para receber até 20 pessoas; além de duas casas tradicionais na aldeia, para dar apoio aos pesquisadores em sua interação com esta comunidade. Inicialmente voltadas ao estudo do mogno, as atividades do Pinkaití logo se diversificaram e já foram feitos estudos envolvendo diversos elementos da fauna e da flora local (ZIMMERMAN et al., 2001). Em uma das áreas mais devastadas da Região Amazônica, a base de pesquisas do Pinkaití representa uma rara oportunidade para o desenvolvimento de programas de pesquisa e conservação em uma área vasta, e amplamente preservada, de florestas amazônicas de transição e de Cerrado.

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Entendemos que o estudo de duas espécies de palmeiras arborescentes de grande porte, ao invés do foco em apenas uma espécie, seria de maior utilidade para a investigação de aspectos do Modelo devido às possíveis inferências feitas a partir da análise comparativa. Desta forma, concentramo-nos nas palmeiras inajá, *Attalea maripa*, e tucumã, *Astrocaryum aculeatum*, pertencentes a gêneros evolutivamente próximos (pertencem à tribo cocoeae) e superficialmente semelhantes (altas, massivas e solitárias). Porém, diferenças anatômicas, e de atividade reprodutiva das espécies têm prováveis implicações ecologicamente relevantes para o Modelo. Como as palmeiras *A. maripa* são geralmente muito mais abundantes que *A. aculeatum* nesta área de estudos, e problemas amostrais relacionados à relativa raridade de *A. aculeatum* limitam análises estatísticas, focamo-nos exclusivamente nas primeiras, em dois dos artigos desta tese.

*Attalea maripa*, conhecidas popularmente como inajás, são palmeiras altas (10 a 15 m de altura), massivas e solitárias (Figura 2). Seu caule não tem espinhos. As folhas pinadas atingem 5 m de comprimento e os folíolos estão inseridos em grupos de três ou quatro na raquis. A infrutescência é grande e contém várias drupas ovóides. Estas são compostas de uma casca fibrosa e o mesocarpo, viscoso quando os frutos não estão maduros. A semente fica encapsulada em uma "concha" lisa de 3-4 cm de comprimento e 2 cm de diâmetro com uma extremidade pontiaguda, tipicamente com dois embriões (variando de 1 a 3). Frutos maduros têm um conteúdo médio de 33% de umidade. O fruto seco pesa cerca de 18 g (UHL e DRANSFIELD, 1987; ALMEIDA e DANTAS DA SILVA, 1997). Nas florestas de terra firme da a Amazônia, *A. maripa* não parece ser dominante em grandes áreas, mas palmeirais dominados por esta espécie são freqüentemente encontrados em florestas remotas da bacia do Rio Xingu (MAY et al., 1985). A distribuição natural de *A. maripa* esta restrita à floresta Amazônica, sendo freqüentemente substituída por *A. phalerata* em direção à sua área periférica (Figura 3). Os frutos desta palmeira são freqüentemente a principal fonte alimentar da comunidade de vertebrados em diferentes áreas da Amazônia (BODMER, 1991; KAHN e GRANVILLE, 1992, FRAGOSO, 1997). O óleo de seu mesocarpo e endosperma se assemelha ao do dendê, *Elais oleifera*, tendo aroma agradável e podendo ser utilizado para culinária sem precisar ser refinado; o mesocarpo pode ser comido cru ou assado; o palmito pode ser comido na salada e é tão palatável quanto o de *Euterpe* spp; as folhas sao frequentemente utilizadas na cobertura de casas. (MILLIKEN et al., 1986; ANDERSON, 1990).

**Figura 2-** Aspécto de uma palmeira *A. maripa* (Foto: C.BAIDER)

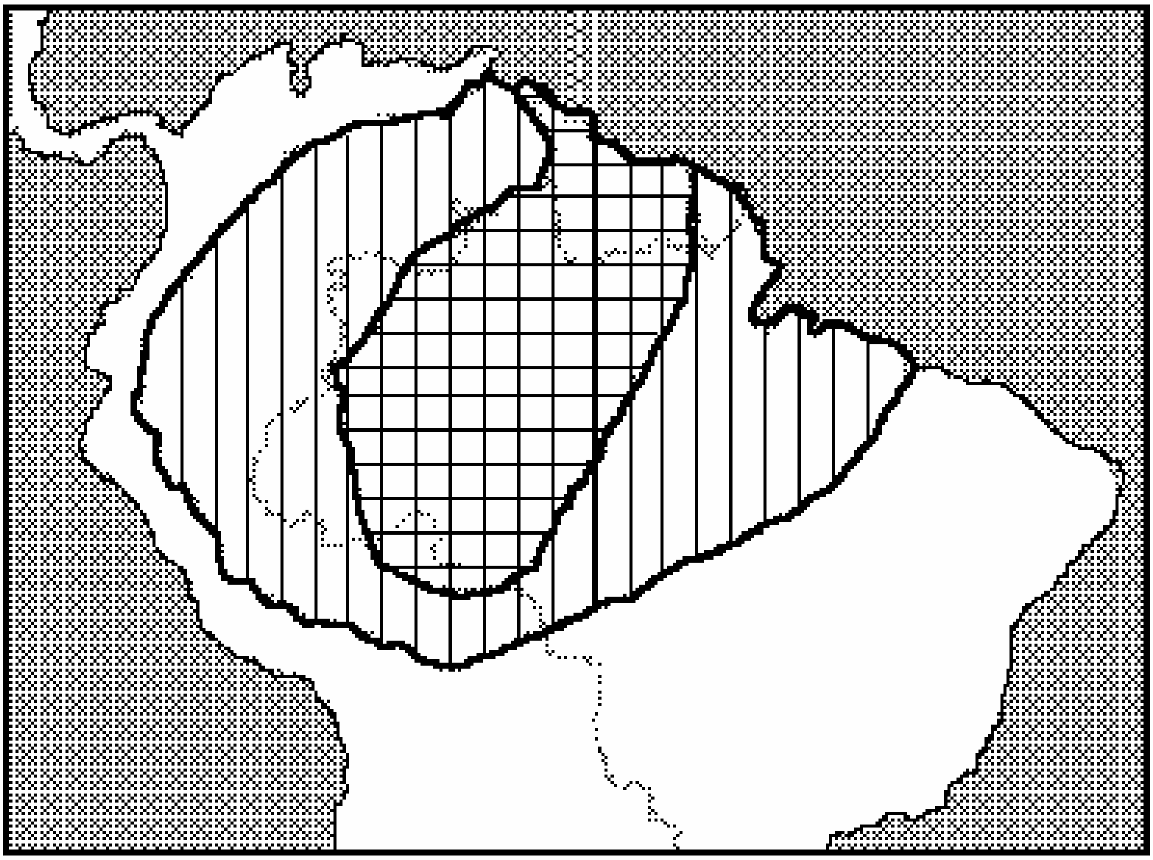

**Figura 3-** Distribuição de *Attalea maripa* (linhas verticais) e *Astrocaryum aculeatum* (linhas horizontais) (adaptado de HENDERSON et al., 1995).

*Astrocaryum aculeatum*, conhecidas popularmente como tucumãs, são palmeiras altas (10 a 25 m de altura), massivas e solitárias (UHL e DRANSFIELD, 1987) (Figura 4). A parte superior de seu caule é armada com longos espinhos negros arranjados em anéis regulares; à medida que as palmeiras crescem, os espinhos mais velhos caem, de forma que a parte inferior do caule geralmente não tem espinhos. As folhas são pinadas e têm de 4 a 5 metros de comprimento, com espinhos em toda a sua extensão, mais concentrados em sua base. A infrutescência tem 1,5 m de comprimento com flores femininas em sua parte basal e flores masculinas ocupando a parte apical. Os frutos amarelo-esverdeados de *A.*

*aculeatum* consistem de um mesocarpo oleoso, denso, amarelo-alaranjado que circunda uma semente de cor quase preta, caracterizada por uma concha extremamente dura. O endosperma, branco, duro e oleoso tem uma testa aderente marrom (ALMEIDA e DANTAS DA SILVA, 1997). Em comparação com as palmeiras *A. maripa*, *A. aculeatum* é mais restrito ao centro da região amazônica (HENDERSON et al., 1995; Figura 3). Não há concenso sobre a distribuição natural de *A. aculeatum*, entretanto esta claro que é uma espécie restrita a região amazônica. Sua abundância em florestas secundárias da Amazônia central é atribuída à dispersão proposital por populações tradicionais (KAHN e GRANVILLE, 1992). O óleo de *Astrocaryum* ssp., assim como o de *A. maripa*, também é adequado para a culinária e comestivel sem que precise ser refinado (WESSELS BOER, 1965). A fibra de palmeiras desta espécie é amplamente utilizada em várias partes do Brasil, sendo aplicada na confecção de redes de pescar, redes, bolsas e pulseiras (BONDAR, 1938).

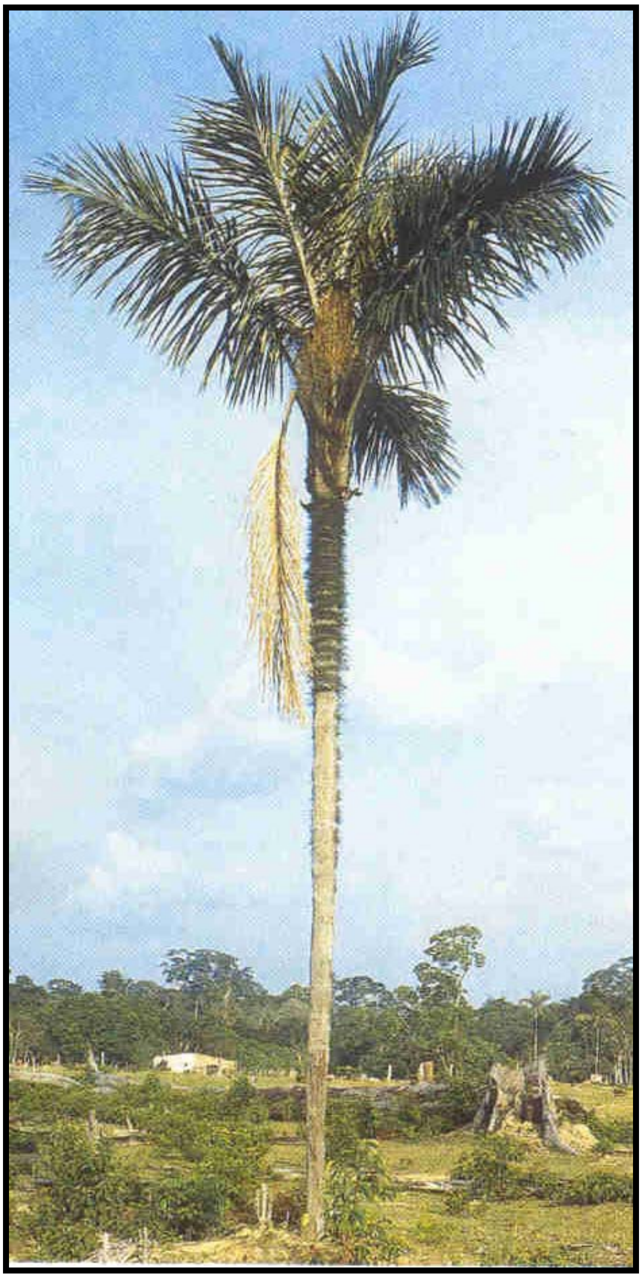

**Figura 3-**Aspécto de uma palmeira *A. aculeatum* palm (Foto: H. LORENZI).

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Experimentos ecossistêmicos, observou CARPENTER (1988), são limitados, não apenas pela sua dinâmica lenta, mas também por problemas ligados a aspectos da cultura acadêmica e limitações institucionais. Porém, respeitado o âmbito das possíveis inferências feitas a partir de tais experimentos, problemas ligados a replicações, seriam de importância menor diante da necessidade de se avaliar explicações alternativas para processos na escala de interesse. Entendemos que a comparação de parâmetros ecológicos de duas áreas de floresta, uma em fase de regeneração rica em palmeiras (o palmeiral) e outra adjacente em estado de maturidade (a floresta primária circundante) poderia elucidar aspectos relevantes da importância das palmeiras para a dinâmica da floresta, conforme o modelo proposto. Este palmeiral é plenamente visível por cima, a partir de um afloramento granítico de cerca de 250 m de altura e tem um limite bastante claro com a matriz de florestas primárias onde as palmeiras arborescentes são muito menos evidentes. Identificamos uma árvore emergente, no limite do palmeiral e, tomando-a como ponto de partida, construímos a grade de trilhas necessária para a amostragem ecológica das duas áreas de floresta. Distintos recortes desta grade de trilhas, que abrange uma área total de aproximadamente 20 ha, foram usados nos diferentes artigos constituintes da tese.

De acordo com os Kayapó (Ukarurü, Bemp-totí, Tikirí), este palmeiral cresceu sobre uma roça voltada à produção de cultivos de subsistência pertencente a uma família de caboclos, que foi abandonada na primeira metade do século passado. Os Kayapó têm a sua gênese histórica na região do encontro dos rios Tocantins e Araguaia, mas migraram para o oeste ocupando o vale do rio Xingu no princípio do século XX, devido a pressões de elementos da sociedade nacional brasileira que principiavam a colonização da atual área de influência da rodovia Belém-Brasília, na parte leste do estado do Pará (TURNER, 1999). Os caboclos, provavelmente associados à economia-da-borracha, que já estava em declínio neste momento (WEINSTEIN, 1983), viviam onde hoje fica a base de pesquisas do Pinkaití e foram expulsos pelos índios em sua migração para o atual território da aldeia A'Ukre.

Não é possível definir precisamente o ano do confronto que expulsou os caboclos que viviam onde hoje fica a base de pesquisa do Pinkaití devido à tradição exclusivamente oral dos Kayapo. Entretanto, uma aproximação é possível, uma vez que apenas os poucos homens mais velhos da aldeia, quando jovens, participaram do combate. Potes de ferro fundido, eventualmente encontrados na floresta, são os únicos indícios materiais deixados por estes brasileiros no local em que viveram. Aqui, buscamos compreender melhor suas marcas deixadas na floresta. Assim, podemos ter mais detalhes na compreensão da dinâmica florestal, através de seus símbolos e marcas remanescentes.

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No **Capítulo-4**, cujo título em português seria "Diversidade de espécies arbóreas em uma floresta sazonalmente seca: o caso da base de pesquisas do Pinkaití, na Terra Indígena Kayapó, limite sudeste da Amazonia", concentramo-nos na estrutura e composição de espécies arbóreas da floresta do Pinkaití. Nesta sessão, é feita uma descrição mais minuciosa da geologia, relevo e clima da área de estudos. O estudo florístico necessário à elucidação de aspectos ligados tanto à evolução da estrutura, quanto da composição da floresta, em estágios distintos de desenvolvimento foi possível graças ao senhor Manuel dos Reis Cordeiro, técnico da Embrapa Amazonia Oriental, e ao botânico Eduardo Mariano que fizeram as medidas de diâmetro de altura das árvores assim como a sua identificação. A equipe mediu e identificou todas as árvores com DAP $\geq$ 10 cm em um grupo de 52 parcelas de 0,0625-ha (25x25-m) regularmente dispostas tanto no palmeiral, quanto na floresta primária adjacente.

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O **Capítulo-5**, “Densidade do caule e crescimento de *Attalea maripa* e *Astrocaryum aculeatum*: implicações para a distribuição de palmeiras arborescentes pela floresta amazônica”, traz uma descrição detalhada do caule de um indivíduo adulto de cada das duas espécies de palmeira. A velocidade de crescimento do caule das palmeiras é relevante para o Modelo pois, a partir da fase de clareira, é este crescimento que promoveria a elevação do extrato superior da vegetação e a formação do dossel, que limitaria o desenvolvimento das lianas, possibilitando o desenvolvimento das espécies de árvores típicas da floresta madura e o amadurecimento da floresta. Como *A. maripa e A. aculeatum* são palmeiras superficialmente semelhantes, com orçamentos energéticos comparáveis, seria de se esperar que diferenças em sua estrutura fossem acompanhadas de diferenças no desenvolvimento. Os padrões de crescimento do caule das duas espécies foram estimados com uma metodologia descrita por P.B. TOMLINSON (1990), que considera o número médio anual de produção ou queda de folhas e os padrões de cicatrizes foliares encontrado ao longo do caule das palmeiras.

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A importância da perturbação florestal para o recrutamento das palmeiras arborescentes de grande porte é um pressuposto fundamental do Modelo. Palmeiras arborescentes de grande porte são notoriamente raras nas florestas tropicais chuvosas densas e comuns nas florestas abertas, marcadas por fortes períodos de seca. Além do mais, a dominância de palmeiras em extensas áreas de florestas da região amazônica está frequentemente associada a desmatamentos, um processo que é visível nos pastos que margeiam as estradas amazônicas. Entretanto, SVENNING (1999) alega ter refutado a teoria de que perturbação florestal seja importante para o desenvolvimento das palmeiras, baseado nos estudos de sua distribuição no Parque Nacional de Yasuní, Equador. No **Capítulo-6**, a hipótese de que a perturbação florestal é importante para o recrutamento da palmeira arborescente de grande porte *A. maripa* foi testada com um experimento natural na base de pesquisas do Pinkaití. 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.

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A dispersão de sementes das palmeiras é outro elemento fundamental do Modelo. Isto porque ele assume que, uma vez que uma grande clareira é formada criando condições de luminosidade favoráveis ao desenvolvimento das palmeiras, já haverá plântulas de palmeirais, ou sementes serão trazidas para o local, para que possam usufruir da alta luminosidade e se desenvolver. O pressuposto, não é necessariamente verdadeiro, uma vez que as sementes destas palmeiras dependem fundamentalmente de animais para que possam se dispersar.

A relação da morfologia dos propágulos das palmeiras *A. maripa* e *A. aculeatum* com a chuva-de-sementes, na floresta do Pinkaití foi estudada no **Capítulo-7**, “morfologia de sementes de palmeiras arborescentes e a distribuição de suas plântulas”. Este artigo também foi concebido como um estudo comparativo das duas espécies, focado em sua estratégia reprodutiva. O volume e dimensões das semente, assim como a quantidade de reservas disponíveis para o embrião de *A. maripa* e *A. aculeatum*, foram medidos em laboratório. Por outro lado, a distribuição das plântulas das duas espécies em relação aos adultos que produzem frutos foram estudados no palmeiral do Pinkaití e na sua floresta primária adjacente.

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Os mecanismos que mantém a diversidade de espécies arbóreas nas florestas tropicais, há muito fascinam cientistas (WALLACE, 1878; DENSLOW, 1980). Desde a década de 1930, os efeitos da distância das árvores parentais sobre a sobrevivência de sementes e plântulas  têm sido considerado um fator determinante para a manutenção da diversidade de plantas nas florestas tropicais chuvosas, se comparadas com florestas equivalentes das regiões temperadas (JANZEN, 1970). Desde que JANZEN (1970) e CONNELL (1971) publicaram independentemente seu modelo para a diversidade de árvores de florestas tropicais, este recebeu considerável atenção (HOWE e SMALLWOOD, 1982; CLARK e CLARK, 1984). Dentre várias teorias para a diversidade de árvores de florestas tropicais, o modelo é o único que atribuí um papel a animais, herbívoros que criariam forte discrepância  entre a chuva-de-sementes e o padrão de recrutamento das espécies por eles afetadas (TERBORGH et al., 2002).

O Modelo aborda o problema da diversidade de árvores uma vez que postula que no processo successional que se seque a formação de uma grande clareira, com o amadurecimento da floresta, as palmeiras arborescentes de grande porte são progressivamente substituídas por uma comunidade mais diversa, das árvores típicas da floresta madura. Esta substituição é consequência do sombreamento criado pelas palmeiras adultas, demasiadamente severo para o desenvolvimento de novas lianas e palmeiras, mas suficiente para o crescimento das árvores jovens. Porém, o Modelo pressupõe o estabelecimento plântulas de árvores na floresta em regeneração, para que esta possa se amadurecer. Este pressuposto também não é necessariamente verdadeiro pois em regiões do Brasil Central, palmeirais de babaçu, *A. phalerata*, sobre antigas áreas desmatadas têm o chão forrado por carpetes tão densos de jovens palmeiras que não há espaço suficiente para colonização das árvores da floresta madura (KAHN e GRANVILLE, 1992). O resultado é que o sistema pode permanecer preso indefinidamente neste estágio successional sem que nunca a maturidade da floresta, com a diversidade de árvores que lhe é típica, seja atingida.

Finalmente, o **Capítulo-8**—"Predação de sementes da palmeira amazônica *Attalea maripa* por invertebrados e vertebrados: implicações para o mecanismo de espaçamento de Janzen-Connell"—aborda o papel de animais na criação de mecanismos dependentes de densidade que limitem, dando um caráter necessariamente transitório à dominância desta palmeira em uma grande clareira. Foram investigados os efeitos de densidade e distância de árvores reprodutivas no palmeiral e na floresta primária adjacente, pobre em palmeiras, sobre os padrões de predação de sementes pelos besouros bruchideos *Pachymeris cardo* e uma guilda generalista de vertebrados predadores de sementes grandes e bem protegidas.

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Palmeiras arborescentes, além de serem úteis na regeneração de áreas degradadas (BALICK, 1987; BALLÉ, 1988; ANDERSON, 1990), são importantes para as populações locais e seus produtos têm grande potencial econômico e valor industrial, que é subtilizado (CORNER 1966, KAHN e GRANVILLE, 1992). O óleo extraído dos frutos de *A. maripa* é similar ao do babaçu, *A. phalerata* e ao do óleo de dendê, *Elais oleifera.* Ele tem odor agradável e pode ser usado para cozinhar sem que seja refinado. A polpa pode ser comida crua ou cozida e o palmito pode ser comido como salada e é tão saboroso quanto os de *Euterpe* spp., os palmitos mais apreciados na América do Sul. Por muitos anos, o Brasil exportou frutos de palmeiras *Attalea* para a produção de uma gama de objetos pequenos

(BONDAR, 1941). BONDAR (1941) observou que os coquinhos das palmeiras *Attalea* são um “excelente combustível”, queimado diretamente ou convertido em carvão. Durante a Primeira Guerra Mundial, milhares de toneladas de frutos de *Attalea* foram queimadas como combustível no Brasil e usadas pela marinha nacional em substituição ao carvão mineral. A América Central também exportou toneladas de frutos de *Attalea* para fins industriais para os Estados Unidos como a produção de carvão ativado e para a produção de máscaras de gás, uma vez que o carvão das *Attalea* retém gases tóxicos em quantidades muito maiores que outros carvões (BONDAR, 1938; BONDAR, 1941; ANDERSON, 1990). BONDAR (1941) comparou as os coquinhos a “um carvão mineral que cresce em árvores sem a mina nunca se acabar”, e constatou que seu óleo produziria ótimo biodiesel. O carvão das palmeiras poderia ser produzido a  um baixo custo e vendido para indústria metalúrgica e companhias de navegação e ferroviárias. De acordo com o autor, dos estoques existentes na época, na América do Sul, a produção potencial seria enorme, limitada apenas pela escassez de mão-de-obra para a coleta dos frutos e pela precariedade nos transportes. O óleo extraído dos frutos de *Astrocaryum* ssp. também é excelente para a culinária e comestível sem ser refinado. Ele é usado para cozinhar no interior do estado do Pará e pode ser usado para a produção de margarina, competindo com sucesso com óleo do coco-da-bahia  (*Cocos nucifera*) e babaçu (*A. phalerata*), devido ao seu ponto de derretimento mais alto (WESSELS BOER, 1965). Finalmente, as conchas extremamente duras dos coquinhos de *A. aculeatum* são amplamente usadas para a manufatura de artesanato por nativos da Amazonia, e vendidas para várias partes do Brasil.

Todas as projeções para o futuro da Amazonia ao longo do século atual, mesmo sob cenários otimistas, prevêem desmatamentos em larga escala na região. Ameaças críticas para a floresta no Brasil são postas por planos governamentais de expandir ainda mais a rede de estradas pavimentadas e outros megaprojetos de infraestrutura (LAURANCE et al., 2004). No período de 2002-2003, a taxa de desmatamento na Amazonia brasileira escalou para o alarmante patamar de 2.400.000 hectares por ano. O aumento resultou principalmente da rápida destruição das florestas sazonalmente secas ao sul e a leste da bacia. Em relação à média do período de 1990-2001, a perda de florestas cresceu 48% em 2002-2003 nos estados do Pará, Rondônia, Mato-Grosso e Acre, que compreendem o arco-do-desmatamento da Amazônia. O crescimento está evidentemente dirigido pelo aumento nos desmatamentos e especulação fundiária ao longo de novas rodovias e rotas planejadas (GRUPO PERMANENTE DE TRABALHO INTERMINISTERIAL SOBRE O DESMATAMENTO NA AMAZÔNIA, 2004). Historicamente, a criação de gado bovino é o principal responsável pelos desmatamentos na Amazônia (KAIMOWITZ et al., 2004). O atual aumento na produção de soja contribuí diretamente para os desmatamentos mas tem efeitos indiretos muito mais perversos justificando a implementação de projetos massivos de infraestrutura que catalisam os desmatamentos como, por exemplo, a pavimentação da rodovia Cuiabá-Santarém (LAURANCE et al., 2002; FEARNSIDE e LAURANCE 2003), a oeste da Terra Indígena Kayapó. A pavimentação desta rodovia fará com que a Terra Indígena, hoje pressionada pela frente de desmatamentos associada a rodovia Belém-Brasília em flanco leste, mas ainda praticamente contínua com o corpo principal da floresta amazônica a oeste rapidamente se transforme em uma imenso fragmento florestal.

Desmatamentos e fragmentação florestal em larga escala na Amazonia tem consequências ecológicas potenciais que variam da extinção de espécies (GASCON et al., 2002), a impactos sobre o clima local e global (LAURANCE, 2004), que por sua vez resulta no crescimento da probabilidade de incêndios acidentais das florestas remanescentes, gerando novas áreas desmatadas (COCHRANE e LAURANCE, 2002; LAURANCE, 2003).

O problema dos desmatamentos envolve questões tanto políticas quanto técnicas. Atualmente, o debate acerca da conservação da Amazonia está mais focado na contenção do crescimento das taxas anuais de desmatamento do que no reflorestamento das áreas degradadas. Entretanto, o Caderno de Subsídios para o Debate, do Programa de Governo do Partido dos Trabalhadores (SECRETARIA NACIONAL DE MEIO AMBIENTE DE DESENVOLVIMENTO DO PT, 2002), em nome da ruptura com o modelo de desenvolvimento caracterizado pela degradação ecológica, propôs a realização de um mutirão de recuperação florestal a fim de reverter a tendência dos desmatamentos nos estados de Rondônia, Mato-Grosso, Tocantins e Pará. Porém, mesmo que a reconstituição das áreas devastadas estivesse hoje no topo da agenda política, problemas técnicos associados com conhecimento insuficiente acerca das espécies ecologicamente mais importantes e da dinâmica de regeneração natural da floresta, dificultariam esforços virtuosos.

Espera-se que o presente estudo contribua para a elucidação dos processos ecológicos naturais associados à regeneração das florestas amazônicas sazonalmente secas e que este conhecimento seja útil a possíveis esforços direcionados à recuperação de áreas desmatadas e à utilização plena dos benefícios potenciais das palmeiras.

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## Capítulo-2

# Determinantes meta-espaciais da distribuição de palmeiras

# *Cross-scale determinants of palm species distribution*

SALM, R., SALLES, N.V., ALONSO, W.J. & SCHUCK-PAIM, C. Cross-scale determinants of palm species distribution. Submetido à Biota Neotropica.

# ABSTRACT

**Aim** In this study we investigate the biogeographic determinants of palm species richness and abundance at a local scale, along a moisture gradient in a seasonally-dry Amazonian forest, and compare it to the patterns observed at a large scale, comprising the entire Brazilian territory.

**Methods** At a local scale, the association of forest structure, palm density and richness with moisture was studied along the Mokoti, a seasonally-dry river from southeastern Amazon. The hills, uplands and bottomlands of this river basin were studied by the establishment of sampling plots respectively at the spring, an intermediate position and the mouth of the river. We used published distribution maps of all palms present within the Brazilian territory and climate maps generated with information obtained from ground-based meteorological stations. The Brazilian territory was divided into 49 units of approximately 150,000 km$^2$ each, and the number of species in the center of each square counted. Species richness was then tested against a number of eco-climatic variables estimated for the same geographical points. With the results obtained for the Brazilian territory we generated a climatic model with which palm richness is predicted at a global scale.

**Results** A total of 694 palms belonging to 10 species were sampled at the Mokoti River basin. Although the species showed diverse distribution patterns, we found that local palm abundance, richness and tree basal area increased significantly from dryer to wetter areas, and that both niche specialization and chance seemed to determine palm community composition. The analyses at the larger spatial scale was consistent with these patterns, revealing a strong influence of vapor pressure (a measure of moisture content of the air, in turn modulated by temperature) and seasonality in temperature: the richest regions were those where temperature and humidity were simultaneously high, and which also presented a lower degree of seasonality in temperature.

**Main conclusions** Climatic hazards seem to strongly determine the distribution of palms, with the relative importance of moisture being highly consistent across scales. This finding support the idea that, by ‘putting all eggs in one basket’ (a consequence of survival depending on the preservation of a single irreplaceable bud), palms have become vulnerable to extreme environmental conditions, hence having its distribution limited to those tropical and sub-tropical regions with constant conditions of (mild to high) temperature and moisture all year round. The climatic model proposed here additionally promotes the understanding of the limits placed by eco-climatic variables on the distribution and richness of this family.

***Key Words***

*Amazon, diversity, moisture, palms, tropical forests.*

# INTRODUCTION

Explaining the high diversity of plant species in wet lowland tropical forests is a major challenge for ecologists, who have explored the potential influence of factors ranging from climate (Gentry, 1988) and chance (Hubbell, 1979) to niche specialization (Terborgh, 1985; Svenning, 2001) on the high number of species in these areas.

The family Arecaceae, with approximately 2800 species and high morphological diversity, constitutes one of the best-known tropical families of flowering plants (Tomlinson, 1979), and seems to be a suitable model for the investigation of the relative importance of those factors. Although possessing a wide range of ecological adaptations (Uhl *et al.*, 1987), an extreme vulnerability to climatic hazards is found among palms, a consequence of their general constitution as “solitary perennating bud”, with no “reserve buds”— if the apex is injured, the whole shoot dies (Richards, 1996). Globally, low temperatures seem to be the major climatic restriction for the distribution of the family, as most species are found throughout the tropical and subtropical region, with very few occurring at temperate areas (Uhl *et al.*, 1987). Within the tropics, however, moisture appears to play a more important role. Palms are absent from deserts and semideserts, with the exception of where groundwater is near the surface, showing a strong preference for wet habitats, where they might be dominants (Tomlinson, 1979). The paucity of palm species in Africa as compared to that in the Neotropical region and southeastern Asia exemplifies this, having been explained as a consequence of the history of draught of that continent - a possibility supported by the relatively high diversity of palms in the adjacent and moister Madagascar (Moore, 1973).

In the Amazonian region there is a general increase in plant-species richness with increasing precipitation (Gentry, 1988), and palms seem to follow this trend (Svenning, 2001). Remarkably diverse palms communities, with up to 34 species within 21 genera, are found in terra firme forests in the Peruvian Amazon (Kahn & Mejia, 1991). Palm species diversity hits its highest point in terra firme forests of wetter central and western Amazonian lowlands, decreasing eastwards towards the seasonally-dry Amazonian forests. The palm family is also noticeably abundant - although not particularly diverse - in flooded forests located in the floodplains of the major rivers, as well as in the network of valleys weathered by small rivers draining the plateaus of the Amazon, where soils are permanently waterlogged and inundations occur irregularly during the rainy season (Kahn & Castro, 1985, Kahn & de Granville, 1992).

Within this framework, the aim of this work was three-fold: firstly, to contribute to the understanding of the climatic determinants of palm richness and distribution both at a local and regional spatial scale. Secondly, to compare the consistency of the findings at the two levels to determine the relative importance of macro and microclimatic factors on the diversity of palms. Finally, with the climatic model obtained to explain the regional richness of palms we generate a predictive map in which palm richness is estimated at a global scale.

## *METHODS*

### *Local patterns of palm distribution*

The Pinkaití Research Station (7° 46'S; 51° 57'W), managed by the NGO Conservation International do Brasil (CI-Brasil), is located at the Kayapo Indigenous Land, municipality of Ourilância do Norte, State of Pará, Brazil. The research station comprises an area of 10,000 ha within the territory of A'Ukre village, where the native indigenous population has committed to stop any hunting or logging activities in order to enable the development of scientific research in an undisturbed area of seasonally-dry forest within one of the most degraded regions of the Amazon (Zimmerman et al., 2001).

The climate in the study region is tropical dry, with monthly temperatures ranging from 25 to 27°C (Holdridge, 1967; Salati & Marques, 1984). At the forest management farm Marajoara, 130km far from the Pinkaití Station, annual precipitation between 1995 and 2001 ranged from 1636 to 2170 mm, with more than 90% falling between November and May and, in some years, no rainfall for approximately 3 to 4 months during the dry season (Grogan, 2001). Following a westward gradient of increasing pluviosity in the Eastern Amazon (Nimer, 1977), the climate in the Pinkaití is slightly wetter, with average annual rainfall indexes close to 2200 mm.

Geologically, 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 granitic outcrops. Rocky ridges throughout the area are 100-250 m high (RADAM, 1974). The soils distribution patterns follow predictable sequences across the topographic relief, with gray or bleached-white sandy profiles predominating on low ground adjacent to the lowest order seasonal streams and dense dark red clays found at higher elevations, often mixed with lateritic gravel (Grogan, 2001). In the rainy season, the water level rises up to 7 m in Riozinho river (Baider, 2000); for long periods, thereafter, large floodplain areas remain submersed under more than a meter of water usually for few days.

The vegetation maps produced by the RADAM Project (1974) with the use of radar imagery and field inventories still provide the most comprehensive description of the study region. The Pinkaití Station area is described in Volume 4 (page sb.22 corresponding to 'Araguaia' and the section of page sc.22 corresponding to 'Tocantins'), within the map Gorotire (SB.22-oY-D). The Gorotire region is highly representative of the vegetation mosaics of the southern Amazon known as 'dry belt archway'. The forest at the study site is structurally heterogeneous, consisting of easily distinguishable types that form mosaics of dense forest (mostly insular in residual plateaus) and open forest (in isolated patches or bottomlands), including extensive areas of liana forest (sensu Pires & Prance, 1985). Woodland and grassland savannahs are more concentrated to the east, following the rainfall gradient. Patches of grassland savannah at this site also seem to coincide with edaphic conditions that are unfavorable to forest cover (RADAM, 1974) and their distribution seems to be affected by fires occasionally started by the Kayapó Indians. Approximately 15% of an 80 x 80 km area (640,000 ha) centered around the A'Ukre's village is savannah, distributed largely along a few upland plateaus (Malcolm *et al.*, 1999). A corridor of grassy savannah running more or less across the Pinkaití site region divided the forests of the upper and lower Amazon during dry periods of the Pleistocene and during a dry post-Pleistocene episode (Haffer, 1969).

Similarly to other seasonally-dry Amazonian forests (RADAM, 1974; Gentry, 1988), relatively small group of species have become dominant in the tree community in the Pinkaití forest (Salm, 2004). Indeed, Baider (2000) estimated the diversity of tree species in the Pinkaití area by setting up two 1 ha (10x1000m) in regions of tall open forest and found low diversity indexes if compared to sites of less pronounced seasonality elsewhere in the Amazon (Gentry, 1988).

The structure of palm communities, species composition and abundance, and the forest structure (basal area and number of trees) in the hills, uplands and bottomlands of the

Pinkaití Research Station were studied in respectively three regions: at the spring, at an intermediate position and at the mouth of the Mokoti, the main river that crosses the area (Fig. 1a). The Mokoti river spring is 281 m high relative to the sea level. The river extends along a meandrous for 8347 m until reaching the left margin of the Pinkaití river, at 254 m of altitude and 5061 m far from the spring. At the hills, the Mokoti River is narrow (from one to two meters wide) and shallow (half meter deep), becoming gradually wider and deeper towards its mouth, where its width ranges from 4 to 6 m and its depth can reach up to 4 m. At the hills, the bottom of the Mokoti riverbed is covered with stones which in the uplands, at an intermediate position along the river, are replaced by sand and subsequently by mud when close to its mouth, at the bottomlands of the Pinkaití site. Due to the morphological and demographic diversity of the studied palms, different inclusion criteria to the adult class had to be used to the different groups of species. First, among those species that develop a subterraneous stem (which emerge to the surface with its approximated maximal diameter) the individual palms with an external and visible stem were considered as adults. Secondly, among the arborescent palms, whose stems grow externally in diameter, we considered as adults those individuals with diameter at breast height (DBH) ≥ 5cm. Finally, among abundant clonal species, those genets that revealed signs of present or past reproductive activity were counted as adults.

One group of ten plots of $600m^2$ (60x10m) was established at the hills, another at the uplands and another at the bottomlands of the Pinkaití site. Within each plot all adult palms were identified and counted and all trees with DBH ≥10cm measured. To capture a wide and standardized range of edaphic conditions within the areas, the plots were centered at curves of the river, being 10 m wide at both river margins and extending for 30 m inland

- parallel to the main curve axis - in both sides of the river (total plot extension = 60 m; see Fig.1b).

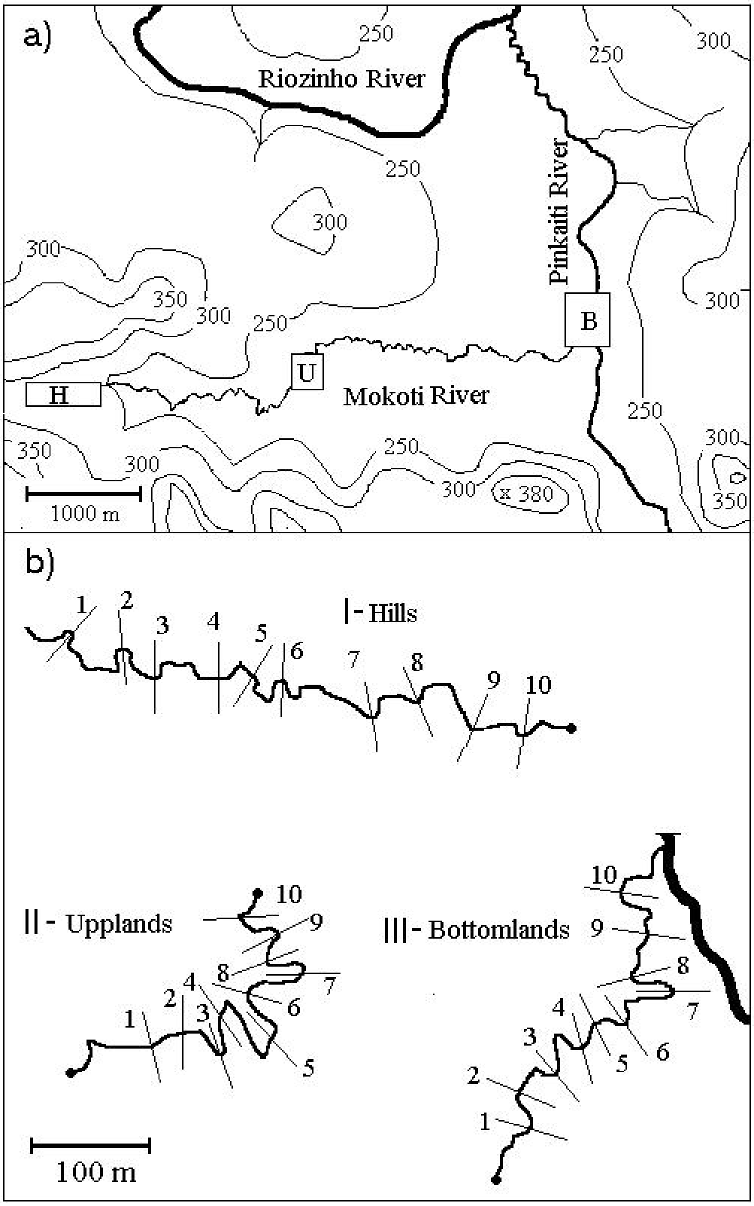

Figure 1. Local palm study setup, illustrating (a) the location of the areas sampled at the hills (H), uplands (U) and bottomlands (B) of the Mokoti river basin and (b) the positioning of the 10 plots of 600m$^2$ (60x10m) at each of the areas.

To reduce the effect of environmental variation associated to the transitions from the hills to the uplands and bottomlands, while still preserving the independence of the sampling units, within each area the plots were set in river curves that were as close as possible to one another, provided they did not overlap (Fig. 1b).

The structure of the forest in the three plot types, measured through the number and basal area of trees with DBH ≥10cm, as well as the number of individuals of each palm species, was compared with the use of Kruskal-Wallis tests corrected for tied groups, followed by non-parametric Tukey multiple comparisons tests, when suitable (Zar, 1999). Detrended Correspondence Analysis (DCA) was carried out using CANOCO 4.0 for Windows. The ordination arranges the floristic plots as points in a scatter diagram in an ecologically structured way. Data points that are close together correspond to plots that are compositionally similar, whereas those that are farther apart are more dissimilar. Species are also represented as points, and those that tend to occur in the same plots converge in the scatter plot, whereas those that occur in different plots appear farther apart. If the species are plotted onto the same diagram of floristic quadrats, they tend to appear near the quadrats where they are most abundant. To reduce the importance of rare species, whose distributions are difficult to explain ecologically and could weaken the overall ordination results (Jongman *et al*., 1995), only those tree species with more than 10 individuals were included in the DCA.

***Large-scale patterns of palm distribution***

Regional patterns of palm richness were estimated from maps showing occurrence points of the 283 species, sub-species and varieties of palms found within the Brazilian territory (Lorenzi *et al*., 2004). The territory was divided into 49 units of approximately 150,000 km$^2$ and species richness was inferred for the point corresponding to the center of each square. To understand the potential role of climate on palm richness and distribution we obtained the environmental variables corresponding to each of the 49 points specified above. To this end, we used worldwide climate maps generated by the interpolation of climatic information obtained from ground-based meteorological stations (New *et al.*, 1999). The mean climate surfaces were available for the period from 1961 to 1990, with a monthly temporal resolution and 0.5º (latitude) by 0.5º (longitude) spatial resolution (New *et al.*, 1999). The climatic variables used were: precipitation, maximum, minimum and mean temperature, ground frost frequency, saturation vapor pressure, ground-frost frequency and wet-day frequency. The minimum and maximum monthly temperature estimates were calculated from the original climate surfaces by subtracting or adding, respectively, half the diurnal temperature range from the mean monthly temperature (New *et al.*, 1999). In order to summarize the information contained in this time-series and capture the seasonal features of the data, each climatic variable was processed with temporal Fourier analysis (processed dataset kindly provided by Professor D. J. Rogers; see Rogers & Williams, 1994; Rogers *et al.*, 1996; Rogers, 1998; Rogers, 2000), extracting in this process each variable's mean (a0) value; amplitude of annual (a1), biannual (a2), and triannual (a3) cycles and maximum (mx) and minimum (mn) values and the phase variables (reflecting the timing of occurrence of cyclic events). This process essentially smoothes out the inter-annual variability, while leaving the seasonal characteristics intact. To explore the potential role of climate on variation in palm richness within the country we then conducted a stepwise regression analysis to determine which factors would better explain the observed patterns of richness. We scrutinized the data to determine whether it satisfied the assumptions of the regression, and (log or square-root) transformed those variables with distribution significantly departing from normality, discarding those variables for which normality was not achieved after transformation. After determining the eco-climatic constraints currently defining the distribution and richness of the palm family within the Brazilian territory, the resulting climatic model was used to generate a predictive map of palm richness at a global scale (the climatic variables corresponding to all regions of the world were collected and processed in the same way as that described for the Brazilian territory).

## *RESULTS*

### *Local patterns of palm distribution*

A total of 694 individual palms belonging to 10 species were sampled at the Mokoti River basin: *Astrocaryum aculeatum* G. Mey, *Astrocaryum gynacanthum* Mart., *Attalea maripa* (Aubl.) Mart., *Bactris acanthocarpa* Mart., *Bactris tomentosa* Mart., *Desmoncus poliacanthos* Mart., *Euterpe precatoria* Mart., *Geonoma baculifera* (Poit.) Kunth, *Oenocarpus distichus* Mart. and *Socratea exorrhiza* (Mart.) H. Wendl. Table 1 shows the mean values of abundance of each palm species observed at the hills, uplands and bottomlands of the Mokoti river basin, together with the overall values of abundance, number of species and tree basal area at each of these regions. There was a significant increase in the abundance (Kruskal Wallis test, H=19.444; $p < 0.001$) and richness (Kruskal Wallis test, H= 13.046; $p = 0.001$) of palms between the hills, uplands and bottomlands of the Mokoti basin river (see Table 2 for Post-hoc Tukey tests showing the direction of the differences for the two tests mentioned above and those following below). This increase in richness and abundance follows a significant increase in tree basal area (Kruskal Wallis test, H=8.308; $p = 0.024$). The total number of sampled trees also increased along the three regions, although not significantly (Kruskal Wallis test, H=4.457; $p = 0.108$; Fig. 2).

Table 1. Forest structure (first four rows) and mean abundance of each palm species observed at the hills, uplands and bottomlands of the Mokoti river basin, southeastern Pará, Brazil. Different letters (“a” and “b” or “a”, “b” and “c”), within a line, represent significant differences between plot types. Conversely, there were no significant differences among plots marked with the same later “a” or “b” (Non-parametric Tukey, p≤0.05). The numbers between brackets indicate total values.

| | Average ± SD (total values) | | |
|---|---|---|---|
| | Hills | Uplands | Bottomlands |
| Number of trees | 27.1 ± 7.1 (271) | 31.0 ± 7.7 (310) | 34.4 ± 9.3 (344) |
| Tree basal area | 1.3 ± 1.3 (12.2) $^{a}$ | 1.4 ± 0.6 (13.6) $^{ab}$ | 1.6 ± 0.6 (16.3) $^{b}$ |
| Number of palms | 10.0 ± 4.2 (100) $^{a}$ | 11.4 ± 5.1 (114) $^{a}$ | 48.0 ± 19.4 (480) $^{b}$ |
| Palm species | 3.4 ± 0.8 (6) $^{a}$ | 4.6 ± 1.3 (8) $^{b}$ | 5.5 ± 0.8 (9) $^{c}$ |
| *Desmoncus polyacanthos* | _ | _ | 1.7 ± 5.3 (1) |
| Oenocarpus distichus | _ | _ | 1.7 ± 5.3 (1) |
| *Astrocaryum aculeatum* | 1.7 ± 5.3 (1) | 6.7 ± 8.6 (4) | 1.7 ± 5.3 (1) |
| *Astrocaryum gynacanthum* | _ | 35.0 ± 29.8 (21) | _ |
| *Attalea maripa* | 6.7 ± 16.1 (4) $^{a}$ | 10.0 ± 11.7 (6) $^{a}$ | 23.3 ± 11.7 (14) $^{b}$ |
| *Socratea exorrhiza* | 28.3 ± 27.3 (17) | 6.7 ± 8.6 (4) | 15.0 ± 9.5 (9) |
| *Bactris tomentosa* | 31.7 ± 26.6 (19) $^{a}$ | 1.7 ± 5.3 (1) $^{b}$ | 20.0 ± 13.1 (12) $^{a}$ |
| *Bactris acanthocarpa* | 40.0 ± 30.6 (24) | 61.7 ± 40.9 (37) | 30.0 ± 23.3 (18) |
| *Euterpe precatoria* | 58.3 ± 40.3 (35) $^{a}$ | 58.3 ± 51.1 (35) $^{a}$ | 223.3 ± 137.3 (134) $^{b}$ |

| | | | |
|---|---|---|---|
| *Geonoma baculifera* | _ | 10.0 ± 16.1 (6) $^{a}$ | 483.3 ± 313.6 (290) $^{b}$ |

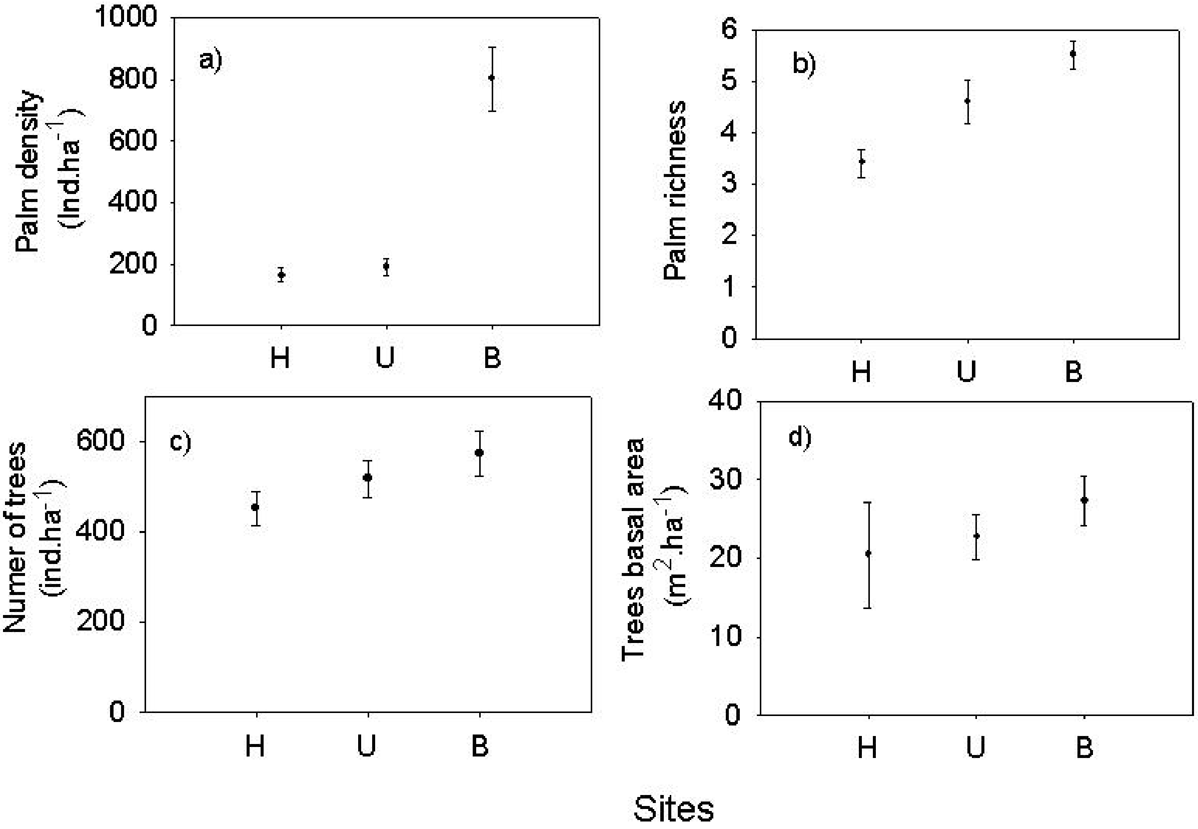

Figure 2. Average palm density (a), richness (b), number of trees (c) and total tree basal area (d) at the hills (H), uplands (U) and bottomlands (B) of the Mokoti river basin, southeastern Para, Brazil.

The palm species *A. aculeatum*, *D. poliacanthos* and *O. distichus* were represented by less than 10 individuals and therefore not included in the ordination analysis. In Axis 1 of the scatter-diagram resulting from the DCA the plots at the bottomlands of the Mokoti River are separated from those at the hills and uplands, which are in turn set apart in Axis 2

(Fig.3). *G. baculifera* and *E. precatoria* were strongly associated with the bottomlands. The former is found in this area at densities of hundreds of individuals per hectare, while it occurs at low densities at uplands and is totally absent from the hills (Kruskal Wallis, $H=23.654$; $p < 0.001$). The latter is found in all sampled areas, but its density grows significantly along the river (Kruskal Wallis, $H=11.004$; $p = 0.004$). *A. gynacanthum* was found exclusively at the uplands. The two species of the genera *Bactris* appear to have opposite behavior: *B. acanthocarpa* was associated with the uplands, where the species is found at higher densities (although this difference was not significant: Kruskal Wallis, $H=4.054$, $p = 0.132$), whereas B. tomentosa was associated with the hills, where it is more abundant, followed by the bottomlands, being finally rarer at the uplands (Kruskal Wallis, $H= 11.097$, $p = 0.004$). It is possible to see in the scatter diagram that A. maripa lies at an intermediate position between the uplands and bottomlands plots. The density of palms of this species grew significantly along the river basin (Kruskal Wallis, $H=9.050$, $p = 0.011$). *S. exorrhiza*, in contrast, was associated with the hills, where it reached its highest density, followed by the bottomlands and uplands, showing no significant difference in abundance between the three regions (Kruskal Wallis, $H= 5.545$, $p = 0.063$).

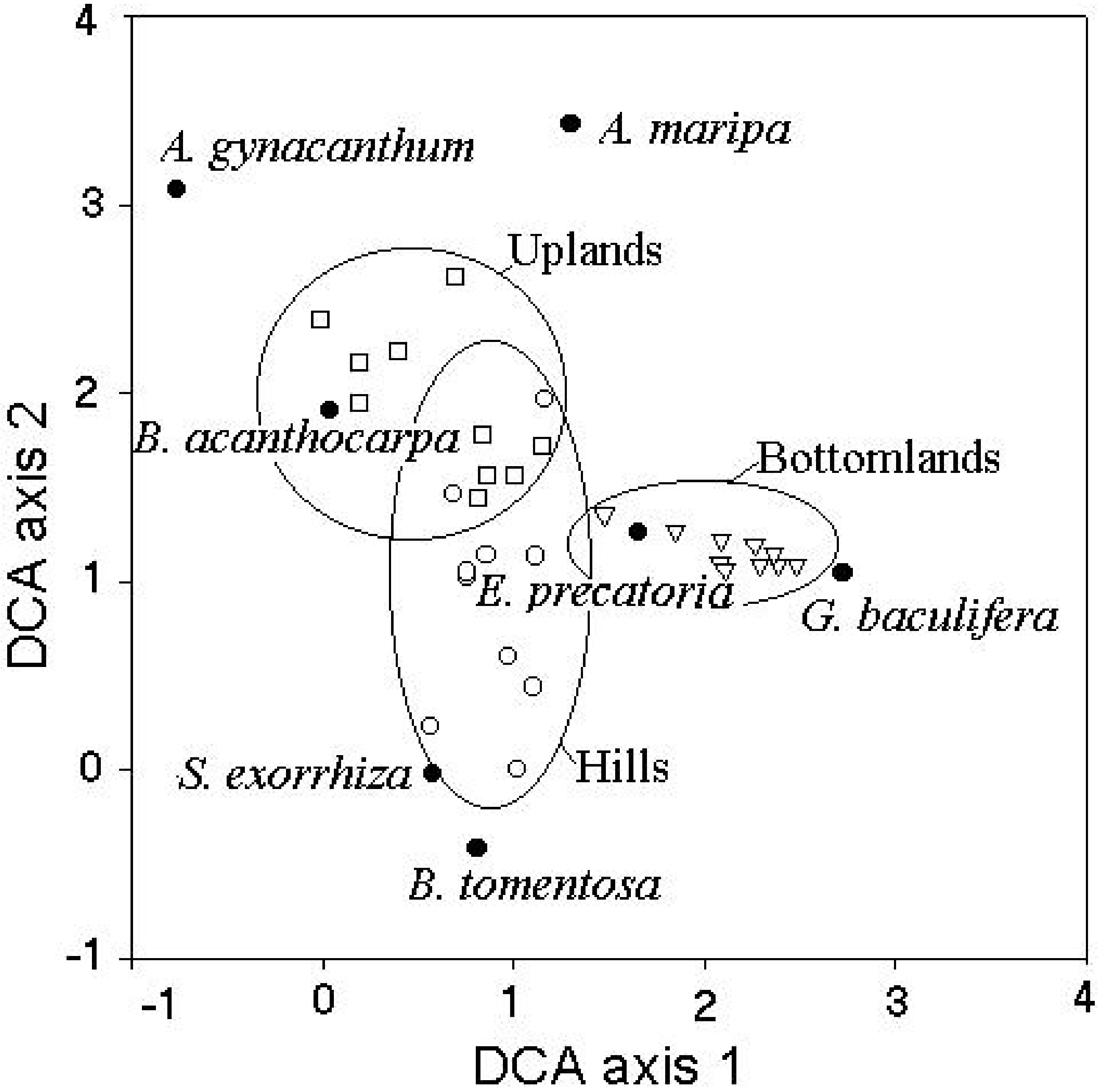

Figure 3. Detrended Correspondence Analysis ordination of palm plots. Solid and open symbols represent species and plots, respectively, with squares corresponding to plots on uplands, circles to plots on hills and triangles to plots on bottomlands (Lengths of gradient 2.483 and 2.619 SD-units; Eigenvalue Axis 1=0.4897 and Axis 2=0.1847).

### ***Large-scale patterns of palm distribution***

Within the Brazilian territory, palm richness reaches its highest values, with more than fifty species found per 150,000 $km^2$ squares, at two areas in the Amazon, one at the center of the basin, around the city of Manaus, and the other at its westernmost parts, in the State of Acre. From these areas, palm richness decreases towards dryer areas to the north, south and west. The major South American disjunction (Brieger, 1969), a wide transversal corridor roughly superposed to the distribution of the Central Brazilian savannahs, with lower annual rainfall, where the richness of palms falls to levels between ten and twenty species, separates the Amazon and the Atlantic forests. The wetter Atlantic forest constitutes another center of high species diversity, with more than thirty species found in the State of Espirito Santo and adjacent Southern Bahia. From this area, species richness decreases towards the interior of the country and along the cost, to the north and to the south. Less than ten species are found at the dry region in the northeast of the country. Within Brazil the effects of minimum temperature on palm species distribution are more evident at the southernmost part of the country, with less than 10 palm species per sampled region. These values are found up to the Pantanal in Mato-Grosso do Sul, where low minimum temperatures are common during the austral winter due to invasions of polar winds, which transpose the Andes on a continental route (Nimer, 1972).

The environmental model resulting from the stepwise regression analysis shows the limiting role of eco-climatic factors on palm distribution and richness, and provides us with additional insights (Table 2). The first predictor selected, which alone accounted for approximately 53% of the variance in palm richness, was minimum vapor pressure (namely, the annual mean of the minimum values of vapor pressure registered monthly).

Table 2. Results of the stepwise regression analysis. Parameters are shown in order of entrance in the stepwise regression model. The last row shows the parameters and total variance (R-square) explained by the full model. In all cases $P < 0.001$.

| Parameter | b* | N° Parameters in the Model | F | $R^2$ |
|---|---|---|---|---|
| (P1) Minimum Vapor Pressure | 0.17 | 1 (P1) | 52.7 | 0.53 |
| (P2) Amplitude of the Annual Cycle of Temperature (Maximum Temp.) | -12.86 | 2 (P1, P2) | 34.6 | 0.60 |
| (P3) Mean Annual Maximum Temperature | -0.25 | 3 (P1, P2, P3) | 35.6 | 0.70 |

Intercept for the full Model = 96.7, *unstandardized coefficients.

Vapor pressure results from the number of water vapor molecules in the air (the greater the moisture vapor content of air, the greater the vapor pressure), and is thus linearly related to absolute humidity. It is also modulated by temperature, with higher values of vapor pressure corresponding to warmer places. The selection of this variable therefore indicates that richness hits its highest levels in simultaneously warmer and more humid places, specifically in those places where the interaction of temperature and humidity (which is in turn strongly influenced by precipitation) does not allow vapor pressure to fall below certain levels. Table 2 also shows that the second best predictor of richness (negatively related to it) was the amplitude of the annual cycle of temperature (maximum temperature), meaning the degree of seasonal variation in the maximum observed values of temperature along any one year. This is an interesting result, as it suggests that richness is higher in places with more stable maximum temperatures than in those regions characterized by a strong seasonality in this parameter. Finally, the last predictor selected was the mean of maximum temperature (i.e. the average of the maximum temperatures registered per month), which was negatively associated to richness, thus suggesting that in those places where maximum temperatures were highest palm richness was lower. It seems to us, however, that the latter association has resulted from the fact that, within the Brazilian territory, those regions with highest maximum temperatures correspond to regions where there is a very large variation in precipitation along the year (as indicated by the significant correlation between 'maximum temperature' and 'amplitude of the annual cycle of precipitation': $r=0.53$, $p<0.001$, where $p$ is Bonferroni-corrected). Areas with stronger seasonality in precipitation levels might have less palm species due to the palms' general vulnerability to climatic hazards resulting from the lack of reserve buds previously mentioned (Tomlinson, 1990; Richards, 1996).

The climatic model resulting from the regression analysis was subsequently used to generate a predictive map of palm richness at a global scale. Given the discussed specificity of the last predictor selected (mean of maximum temperature) with the ecosystems of the Brazilian territory we decided to exclude this factor from the model to generate the predictive map for the globe, retaining the first two best predictors of richness. Fig. 4 shows the resulting map. The color-coded levels of richness effectively indicate the predicted number of palm species in each region as based on their environmental suitability (in terms of vapor pressure and seasonality in temperature).

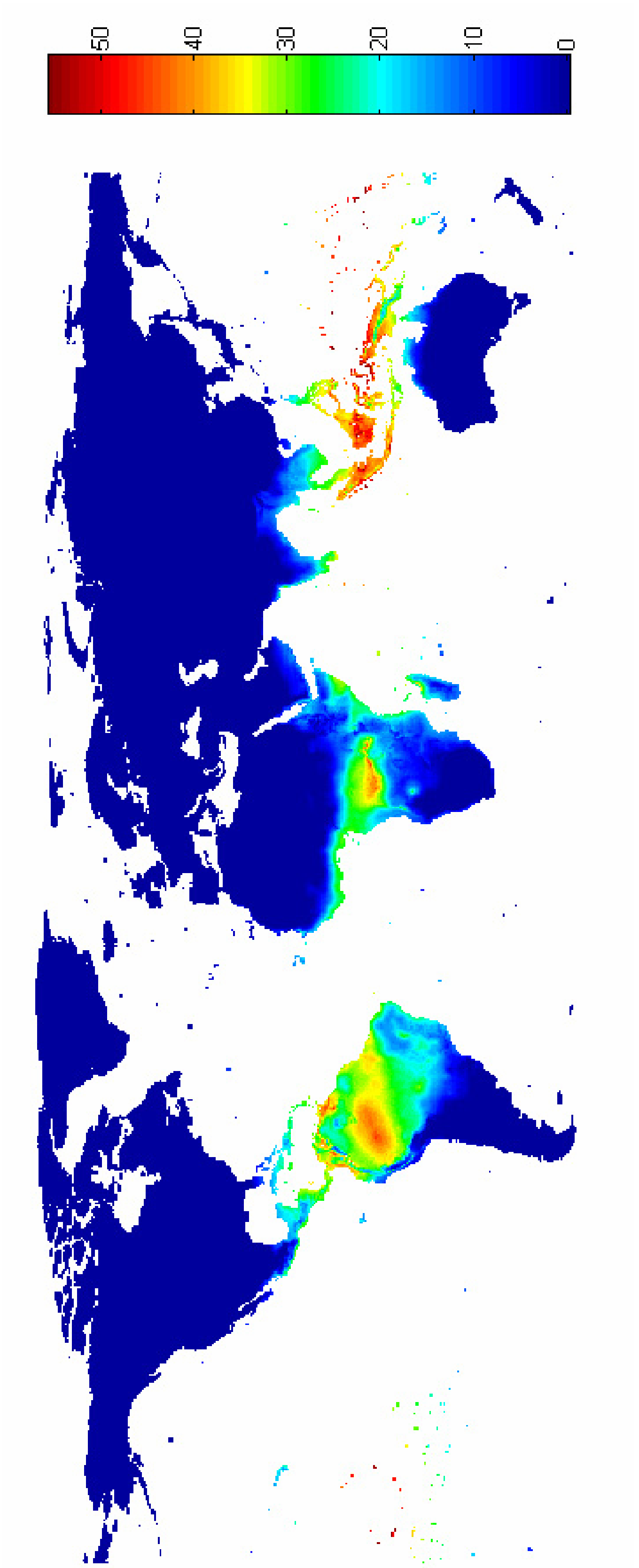

Figure 4. Predictive map of palm richness at a global scale. Color-coded levels of richness indicate the predicted number of palm species in each region as based on their environmental suitability in terms of vapor pressure and seasonality in temperature.

## DISCUSSION

The finding that palm richness in Brazil is best predicted by minimum vapor pressure and the amplitude of the annual cycle of temperature, with a marked presence of palms in stable areas of simultaneously high humidity and temperatures, reflects the basic physiological constraints characteristic of the palm family and its vulnerability to climatic hazards (Richards, 1996), particularly given by the presence of a single, irreplaceable terminal bud (Tomlinson, 1990). Within the tropics, the predictive map of global palm diversity is consistent with the general knowledge of global palm distribution - with the major centers of diversity aligned along the Equator in the Amazon, the Congo basin and Southeastern Asia, with the largest number of species found in the latter area (Corner, 1966). The island of New Guinea, for example, which hosts 145 palms species belonging to 32 genera within its 808, 510 $km^2$ of territory (Bachman *et al.*, 2004), is shown as a hotspot of palm diversity in the model.

Rather than attempting to provide a global map of diversity for the family - whose global distribution is relatively well known through direct evidence - the model is aimed at exploring the limits placed by eco-climatic variables on the distribution and richness of the family. In this sense, the overall consistency between its predictions and general reports of palm diversity around the globe highlights the major role played by climate – and particularly the variables selected in our analyses – on palm diversity. The model is additionally aimed at serving as a heuristic tool for the investigation of those cases in which factors other than climate might underlie the discrepancy between the model's prediction and the reality. For example, although it predicts an absence of palms in the Middle East, the importance of palms in the region is known from biblical times. In Jewish traditions, for example, the "Tree of Life" is understood to be the date palm *Phoenix dactylifera* L.— a species referred to by the Italic people as *palma*, a name then extended to the whole family (Lorenzi *et al*., 2004). Yet although palms can survive in such a dry region, they do so only in those areas where the ground water approaches the soil surface. Since this latter variable was not made available to our analyses, it was not captured by the model (notice, however, that in any case palm diversity is extremely low in the Middle East, hence being close to the model's prediction). A similar case occurs in the Palm Valley Oasis in arid central Australia: although the model predicts an absence of palms in this region, the actual occurrence of large stands of *Livistona mariae* F.Muell. (Wischusena & Fifield, 2004) results from the presence of subterraneous water close to the surface in this valley. The dynamics of island biogeography (MacArthur & Wilson, 1967) also seems to be the cause of some of the differences between the predicted and observed diversity of palms in some tinny islands of Micronesia: although the model predicts areas with richness values as high as 40 species per 150,000 km$^2$, well-known effects of insularity such as island size and distance from continental lands seem to underlie the less pronounced diversity observed in these islands. Within Brazil, the effects of insularity and the presence of subterraneous water may respectively explain the structure and diversity of palm communities in ecosystems subjected to human induced or natural fragmentation (Scariot, 1999) and the formation of palm-dominated forests in areas that are climatically unsuitable for their occurrence (Lorenzi *et al*., 2004).

At a local scale, the distribution maps of Lorenzi *et al.* (2004) indicate that the 150.000 km$^2$ area including the Pinkaití research station, located at the limits of the Amazon forest with the Cerrado of Central Brazil, has a number of species typical of the dryer regions of Central Brazil (with richness ranging from 10 to 20 species in areas of similar size). Five palms species were however found at the Mokoti basin beyond their distribution limits proposed: *Attalea maripa*, *Astrocaryum aculeatum*, *Bactris tomentosa*, *Euterpe precatoria* and *Geonoma baculifera*. With these species, the richness of the region climbs to those ranges typical of the seasonally dry forest at the limits of the Amazon (20 to 40 species in areas of similar size).

Within the field study site, the palm family became more abundant and richer from the open and drier forest of the Mokoti hills to the denser forests at the uplands and, subsequently, to the bottomlands of this river basin, consistently with the importance of moisture found at a regional scale. To explain the composition of the palm community we are left, however, with a two-sided question: why would it be that, out of the regional pool of 23 palm species, 13 (*Bactris brongniartii* Mart. , *Bactris major* (Mart.) Drude, *Bactris simplicifrons* Mart., *Euterpe longibracteata* Barb. Rodr., *Geonoma brevispatha* Barb. Rodr., *Geonoma deversa* (Poit.) Kunth, *Mauritia flexuosa* L. f., *Oenocarpus bataua* Mart., *Orbignya phalerata* Mart., *Syagrus cocoides* Mart., *Syagrus comosa* Mart., *Syagrus petraea* (Mart.) Becc., *Syagrus vermicularis* Noblick) are not representative of the palm community of the Mokoti river basin and, conversely, which factors would enable the coexistence of the 10 palm species observed in the basin (*Astrocaryum aculeatum*, *Astrocaryum gynacanthum*, *Attalea maripa*, *Bactris acanthocarpa*, *Bactris tomentosa*, *Desmoncus polyacanthos*, *Euterpe precatoria*, *Geonoma baculifera*, *Oenocarpus distichus*, *Socratea exorrhiza*) within the same area?

Our field data indicates that moisture also limits forest structure at the Mokoti basin, as suggested by the increase in total tree basal area observed along the river – a result also expected given its positioning at the southeastern extreme of the Amazon forest distribution area, a few kilometers from a large patch of savannah typical of Central Brazil (RADAM 1974). Yet, although the vegetation becomes evidently dryer from the bottomlands to the uplands and the hills, savannahs do not penetrate the river basin as isolated patches of open vegetation do in nearby valleys. This absence of an exclusively open formation is in fact sufficient to explain the absence of *G. brevispatha*, *S. comosa* and *S. petraea* in the basin, as these are species which, according to Lorenzi *et al.* (2004), are restricted to the Cerrado. Similarly, it could also explain the absence of *M. flexuosa*, which is observed in the Cerrado formations in the regional area but not associated to forests, characteristic of the smaller area comprising the Mokoti River basin (R. Salm, personal observation).

The other ten forest species, which could otherwise thrive in the Mokoti river valley but were not found in the area, may have either never been dispersed to the basin or, alternatively, existed there being subsequently locally extinct due to deterministic and/or random factors. For instance, evidence indicates that the effects of forest fragmentation on the diversity of palm communities are significant (Scariot, 1999). During the geological dry periods when the forests of the upper and lower Amazon were divided by a corridor of grassy savannah running through the Pinkaití site region (Haffer, 1969), the forest patches remaining at the area were probably fragmented into relatively small isolated patches, increasing overall extinction probability.

Within the plant community, the dynamics of extinction may also be affected by niche specialization. In Costa Rica, for example, the distribution of five common palm species in an old-growth lowland forest is related to soil type, topographic position and slope angle, with closely related palm species having strong opposite edaphic associations (Clark *et al.*, 1995). In the Peruvian amazon, the distribution of closely related palm populations is also heterogeneous in relation to topography (Kahn, 1987). The hypothesis that niche specialization affects palm community structure is also, at least partially, supported by our data, as those species with dissimilar morphology and behaviour were more likely to be associated. For example, the association of the prostrate *G. baculifera* and the medium-sized palm with erect stem *E. precatoria* was clearly observed for the bottomlands region, probably as a consequence of their distinctive habits: *Geonoma* was restricted to areas subjected to seasonal flooding, while *Euterpe* was found throughout the basin, in progressively lower densities towards the hills. Associations between the two genera, which might be stabilized due to their great morphological dissimilarity, are indeed widespread and found even at the disjunt Atlantic forest (Silva-Matos, personal communication). Also, among the 5 species of *Bactris* ocurring at the Pinkaití region, the two small palms with erect stem found at the Mokoti basin show antagonistic behavior, as *B. tomentosa* was found in higher densities at the hills and the bottomlands and lower densities in the uplands while *B. acanthocarpa* had the opposite distribution. The large arborescent palms *A. maripa* and *S. exorrhiza* also showed opposite distribution patterns, *Attalea* being found at higher densities towards the bottomlands and *Socratea* being associated to the sampled plots at the hills.

These observations would suggest that, by being under higher competitive pressure, those species with similar niches would be more likely to have been locally extinct. Another way of testing this hypothesis is the following: if one assumes that those species that are phylogenetically closer tend to have on average more similar habits, closely related species should be more likely to be locally extinct. Thus, the local palm community at the Mokoti river basin should not be a random assemblage of the pool of species found at the larger (150,000 km$^2$) region comprising the basin site. Instead, the number of genera in the river basin should be over represented, given the higher probability of extinction of species within the same genus than that of species belonging to different genera. To test this we conducted a Monte Carlo simulation, drawing (50,000 times) random samples of 10 species out of the total pool of 23 species in the region, subsequently counting in each simulation the number of genus observed. The resulting distribution showed, however, that the observed number (8 genera observed at the Mokoti out of 11 genera in the larger area) was not significantly different from what it would be expected by chance ($p>0.05$). If, on the one hand, it is possible that the role played by niche specialization in the composition of the palm community may have not been strong enough so as to be detected by our analyses, on the other, chance may have had a stronger influence on community composition than what suggested by the pattern of associations among the species. It is more likely though that these two factors have historically interacted so as to produce the patterns we observed.

The role played by niche specialization was evidently clearer in a seasonally flooded forest in Serra dos Carajas, 200 km towards the northeast of the country, where eight species belonging to eight different genera were found in one hectare (Scariot *et al.*, 1989). In Ecuador, the distribution of palm species in relation to mountainous heterogeneity suggests that niche specialization - besides recruitment limitation, which is evidenced by strong clumping - plays an important role in the ecology of a Andean palm community (Svenning, 2001). Similarly, in a lowland palm community, antagonistic patterns of microhabitat preferences were recognized among pairs of small and medium palms, although not among canopy palms (Svenning, 1999).

Our results stress the importance of climate as a major determinant of gradients of palm richness. Particularly, it highlights the importance of the combined effect of moisture and temperature, as well as seasonality, across different spatial scales. These findings give support to the idea that, by ‘putting all eggs in one basket’ (a consequence of survival depending on the preservation of a single bud), palms have become vulnerable to extreme environmental conditions, hence having its distribution limited to those tropical and subtropical regions with constant conditions of (mild to high) temperature and moisture all year round. Additionally, our model forecast at a global scale can be used in the identification of those factors other than climate underlying regional patterns of diversity. At a local scale, the data collected at the Mokoti river basin indicates that both chance and niche specialization are important to define palm community assemblage. Future studies involving palm communities in different valleys at the limits of the Amazon forest, with different histories of fragmentation and coalescence, would contribute to determine the ultimate importance of each of these factors.

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## Capítulo-3

# Um modelo da importância de palmeiras arborescentes de grande porte na dinâmica das florestas amazônicas sazonalmente secas

# *A model for the importance of large arborescent palms on the dynamics of seasonally-dry Amazonian forests*

SALM, R., JALLES FILHO, E e PAIM, C.S. A model for the importance of large arborescent palms on the dynamics of seasonally-dry Amazonian forests. Submetido à Biota Neotropica.

## Abstract

In this study we propose a model that represents the importance of large arborescent palms on the dynamics of seasonally-dry Amazonian forests. Specifically, the model is aimed at guiding the investigation of the role of large arborescent palms on forest regeneration and succession. Following disturbance, the high level of luminosity reaching recently formed forest gaps favors the quick proliferation of lianas that, by casting shade on tree crowns and increasing tree-fall probability, suppress forest succession. Due to their columnar architecture palm trees are, however, not severely affected by vines. As the palms grow, the canopy at the gaps becomes gradually higher and denser, progressively obstructing the passage of light, thus hindering the growth of lianas and enabling tree development and forest regeneration. Owing to the long time associated with forest regeneration, the model cannot be tested directly, but aspects of it were examined with field data collected at an *Attalea maripa*-rich secondary forest patch within a matrix of well-preserved seasonally-dry forest in the Southeastern Amazon. The results indicate that (1) forest disturbance and (2) seed dispersal by scatter-hoarding rodents are important for the recruitment of large arborescent palms species, (3) palms can grow rapidly after an event of disturbance, restoring forest canopy height and density, (4) density-responsive invertebrate seed predators limit palm dominance and (5) secondary forest dominated by palm species may be floristically similar to nearby undisturbed forests, supporting the hypothesis that the former has undergone regeneration, as purported in the model. Further investigation on the effects of lianas on tree development and the impact of palms' growth upon vines' populations may additionally contribute to determine the importance of palms to seazonally-dry Amazonian forest dynamics and their potential utility as tools to encourage forest regeneration.

***Key words:*** *Amazon, Attalea maripa, Forest dynamics*, *Palm trees, Regeneration*

## 1. Introduction

Seasonally-dry forests, consisting of an assemblage of ecologically diverse vegetation formations generally characterised by high discontinuity of their canopy, variable level of deciduousness and strong spatial variation in floristic macromosaics, cover a substantial area of the Amazon basin. These forests are distributed mostly along rainfall gradients defining the limits between the Amazonian forest and external dryer vegetation biomes (Pires 1984, Gentry 1988, Daly & Prance 1989), an area often referred to as 'Deforestation Arc of Amazonia' (Fearnside 1993, Fearnside & Ferraz 1995). In this study we investigate the role played by large arborescent palms on the dynamics of seasonally-dry Amazonian forests. Specifically, we propose a simplified model of the forestall system, in which the role of palms on the dynamics of forest succession and regeneration is explored (Figure 1).

The understanding of succession processes in natural communities as well as their effects upon community stability and organization were among the major concerns of early ecologists (Cowles 1899). Initially, succession was described by a relatively rigid sequence of species successively invading a site (Clements 1916), a notion subsequently expanded to include predictable changes in characteristics of forest structure other than species composition, such as biomass, productivity, diversity and niche breath (Odum 1969). Although in these studies ecosystems were viewed as highly predictable and organized systems, objections to this concept arose early, reaching a critical point in the early seventies (Connell 1972; Drury & Nisbet 1973) due to a lack of clearly defined and testable hypotheses about the mechanisms underlying succession events, an ignorance at the time

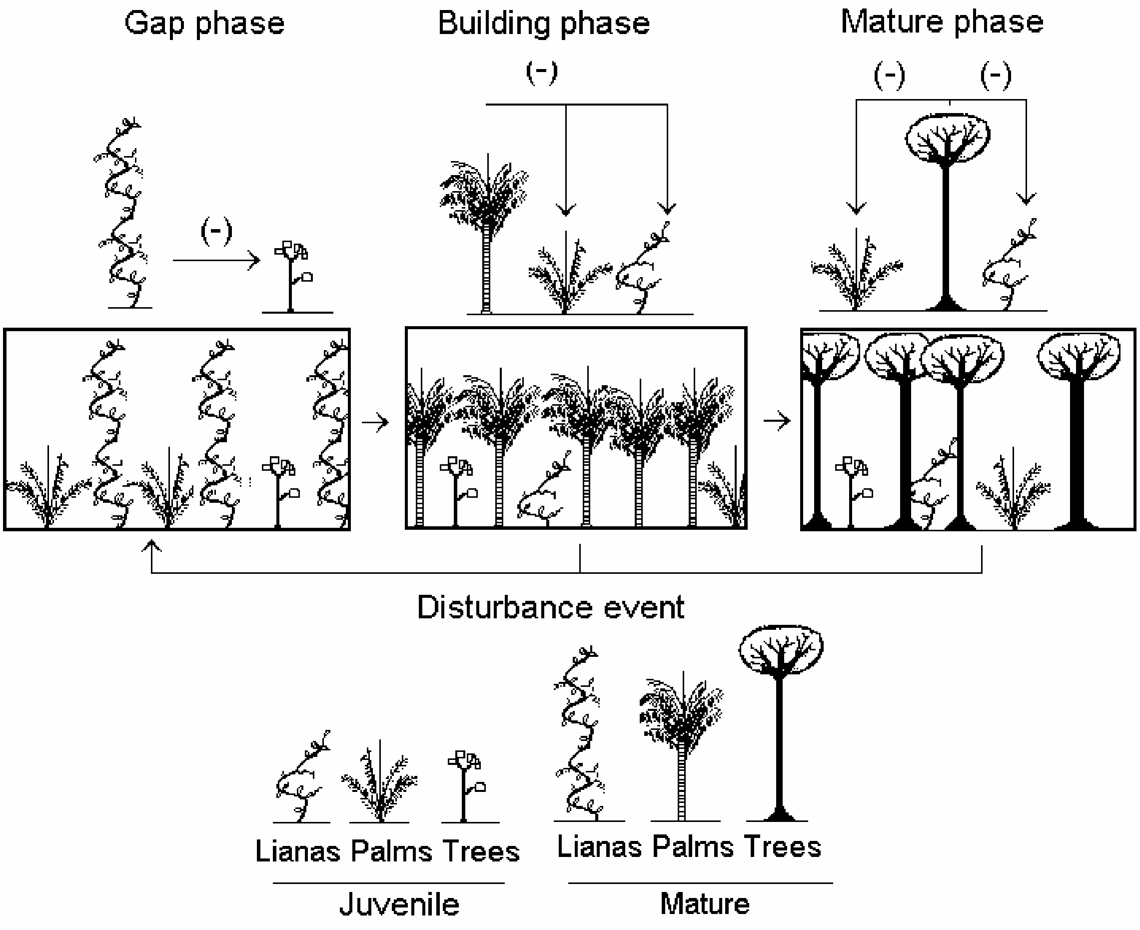

Figure1. Pictorial model of the importance of large arborescent palm on the regeneration dynamics of seasonally dry Amazonian forests. The negative sign indicates an inhibition effect, whereby the growth of one functional plant group is inhibited, e.g. by another group (for instance, in the gap phase, the presence of lianas inhibit the growth of trees). For a definition of the plant groups and regeneration phases, see the text.

about the role played by animals on such events and an absence of direct evidence of late succession stages (Connell & Slatyer 1977).

To contribute to this matter, Connell & Slatyer (1977) described three models to explain the succession process after an event of disturbance: the facilitation model, the tolerance model and the inhibition model. All models purport that certain species can become established before others due to the presence of "colonizing" characteristics such as rapid growth and a high level of investment on reproduction. The three models differ, however, in the mechanisms whereby new species colonize the area later in the succession cycle: the facilitation model assumes that only certain "early succession" species are able to colonize the site immediately following perturbation, modifying the environment so that it is more suitable for later succession species to invade and grow to maturity — the original conception of succession (Clements 1916). The other two models, conversely, assume that any arriving species, including those which usually appear later in the succession process, can colonize a disturbed site. However, they differ in that while the tolerance model assumes that the modification brought about by earlier colonists neither increases nor reduces the recruitment rate and probability of growth to maturity of later colonists, the inhibition model proposes that once earlier colonists secure space or other resources, succession is suppressed.

The influence of large arborescent palms on the dynamics of succession proposed here, incorporates elements of these three models, as we shall explain as follows. Before proceeding, some explanations are however necessary. Our model considers three functional groups of plants: "lianas", "palms" and "trees" Additionally, forest succession is heuristically partitioned here into three phases: a "gap phase", a "building phase" and a "mature phase" (Aubréville 1938). The first phase corresponds to that immediately following an event of disturbance, which leads as a by-product to the opening of clearings in the forest, hence the terminology ‘gap’. Regeneration leads to maturity, namely the reestablishment of canopy height and density and the re-colonization of the area by species of trees typical of mature forests. Once at the mature phase, only a new disturbance event can bring the forest back to the gap phase.

Although dissimilar in many aspects, one difference of special relevance to the present discussion is the distinct response of the three mentioned groups of plants to light: while trees have the lowest growth rate on maximum light intensity (and highest survival likelihood under low light intensity), lianas show the opposite response (highest growth rate at maximal light intensity and the lowest capacity to survive light shortage), with palms being intermediate in both respects. The effect of arborescent palms on forest regeneration can be then understood by considering the following dynamics. At the mature phase, the canopy is composed mainly by the group of trees, being dense to a point that the reduced light conditions below it prevents palm (Chazdon 1986, Kahn 1986, Tomlinson 1990, Kahn & Granville 1992) and liana growth (RADAM 1974, Schnitzer *et al.* 2000, Alvira et al. 2004). Such an equilibrium can be broken by an event of disturbance, which by opening clearings in the forest enables solar radiation to reach the soil level with a higher intensity. Lianas are then able to proliferate almost immediately, becoming dominant in this gap phase (RADAM 1974). Although lacking self-support capacity, lianas can climb the trees by using their structure as support, thus severely suppressing tree growth and survival (see e.g. RADAM 1974 and Richards 1996 for examples in seasonally-dry forests). Additionally, they cast shade on tree crowns and increase tree-fall probability (Schnitzer *et al.* 2000, Alvira et al. 2004), thus suppressing forest succession. Due to their columnar architecture palm trees are, however, not severely affected by vines (Richards 1996). Palm trees are dispersed to gaps from surrounding areas by scatter-hoarding rodents (e.g. agoutis *Dasyprocta ssp.*, Smythe 1989, Forget 1991) and from long-distances by large frugivores (e.g. tapir *Tapirus terrestris*, Fragoso 1997, Fragoso *et al.* 2003). As the palms grow, the canopy at the gaps becomes gradually higher and denser, progressively obstructing the passage of light, thus hindering the growth of lianas and consequently favoring tree development and forest regeneration. Palms are self-limiting because the development of juveniles is hampered by the shadow produced by adult palms. Furthermore, they suffer density dependent mortality due to the action of host-specific efficiency enemies (Janzen 1970). The negative effect of these animals on population recruitment declines with increasing distance of the juvenile from their parents and other adult palms, as proposed by Janzen (1970). With tree growth and palm senescence, the gap phase progresses to maturity, and forest structure stabilizes again.

Similarly to Connell & Slatyer's facilitation model (1977), the model just described above is fundamentally facilitative, as it states that once a disturbance opens a relatively large space releasing resources (light and space), palms are among the early succession species to become established, modifying the environment so that it becomes less suitable for the subsequent recruitment of early succession species, but more suitable for the recruitment of late succession species. It also incorporates a component of "tolerance" when it assumes that lianas are replaced by palms which, in turn, are replaced by other trees, so that the sequence of species is determined, not solely but fundamentally, by life-history characteristics that enable survival and growth despite the shade cast by early succession species. Inhibition is also considered in our model, since lianas limit trees and, as long as they persist, continue to exclude or suppress subsequent colonists of the mature forest.

It is important to highlight that the influence of palms on forest succession as proposed here is specially attributed to the large arborescent forms of palms. Neotropical palms range widely from shade tolerant to needing high levels of light (Svenning 2001). 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). Thus, arborescent palms become increasingly light-demanding with increasing size (de Granville 1992) and generally depend on large gaps for recruitment to the adult stage (Kahn 1986), whereas small palms are widespread at the understorey of tropical forests, even under the energetically restricting conditions of dense shade cast by the canopy (Chazdon 1986). Indeed, ecologists soon related the developmental constraints imposed by the establishment phase of large arborescent palms to the general rarity of palm trees in areas of dense forest with closed canopy (Kahn 1986, de Granville 1992, Kahn & de Granville 1992). While these palms are generally rare in pristine, well drained areas, they often dominate secondary forests in the Amazon (Spruce 1871, Kahn & Castro 1985, Kahn *et al.* 1988, Kahn & Granville 1992, Ballée 1988, 1989). For example, large areas dominated by palm trees in the Brazilian State of Maranhão are related to a secular colonization frontier at this region (Kahn & Granville 1992), and forest patches at the State of Para were associated through archaeological evidence to abandoned Indian villages (Ballée, 1988, 1989, 1990). Palm trees are also often dominant in cleared areas around roads across the seasonally dry Amazonian forests, which concentrate most of the areas so far deforested in the Amazon region.

Also of importance is the observation that the proposed model is, in its present form, restricted to seasonally-dry Amazonian forests, since the dynamics of regeneration is likely to follow different routes under conditions other than those found in these biomes. In the seasonally-dry Amazonian forests, the alternating annual periods of strong rainfall and drought create a high level of natural disturbance, suitable for the growth of gigantic trees like mahoganies (*Swietenia macrophylla*) and Brazil-nuts trees (*Bertholletia excelsa*), which create enormous gaps upon their deaths further increasing disturbance, thus establishing the ideal circumstances for the recruitment and growth of large arborescent palms (Kahn, 1986). But regeneration not necessarily involving palms as ecologically important colonizing-trees seem to prevail elsewhere. In Central Amazon, for example, secondary forests are colonized by pioneer dicotyledonous species of the genus *Cecropia* or *Vismia* (Mesquita *et al.* 2001). Palm trees indeed appear to be of much less important for regeneration both in the rainier areas of the Amazon and on the Atlantic forest, where palm trees are naturally rarer. One reason behind the difference in the influence of palm trees on regeneration among ecosystems might be associated to the relative competitive advantage of lianas over mature forest trees in seasonally dry areas, due to the vines' ability to produce deeper roots than trees with the energy that these climbers save by not producing a self-sustained stem. Such deep roots allow the vines to reach the phreatic water for a longer period at the dry-season—an advantage that is relatively less important in wetter forests (Nepstad *et al.* 1994).

The model treats large arborescent palms as a single functional group, but differences among species within this group might also have relevant consequences on forest dynamics. For example, although apparently similar, the palms species *A. maripa* and *A. aculeatum* differ in the structure and development of their stem, with expected implications for growth rate and breakage probability, and thus, for their capacity to colonize different types of gaps: a dissected stem of *A. aculeatum* showed steep density gradients, both from the internal to the external, and from the lower to the upper parts of the palm (Salm 2004a). Field estimates of stem growth rates also revealed that *A. maripa* growth is more constant with height development: the stem of *A. maripa* reaches 8 m in 16 years on average, whereas *A. aculeatum* reaches the same height at half of this time (Salm 2004a). Forest structure does not seem to affect the abundance of *A. maripa* and *A. aculeatum* in the same way as growth rate, since the abundance ratio of the former to the latter species increases as the forest become structurally more open (Salm 2005). The higher overall stem density of the shorter *A. maripa* palms make it structurally more resistant to potential fatal damages by physical disturbance during early stem growth - a special advantange under high disturbance regimes typical of more open forests. Conversely, in spite of its larger stem diameter, *A. maripa* seems to have a lower capacity to increase stem density during later phases of the stem development process, something likely to make taller palms of this species more vulnerable to stem breakage. As a consequence, this would impinge a disadvantage for *A. maripa* compared to *A. aculeatum* in more built-up, taller forests (Salm 2004a).

Differences in dispersion rates and patterns among palm species might also lead to differences in their relative influence on the process of regeneration. In Neotropical forests, seed dispersal and recruitment of many large-seeded plants depend on large caviomorph rodents such as the acouchies (*Myoprocta sp.*) and agoutis (*Dasyprocta sp.*) (Smythe 1978, Forget 1991). The ecological association of large rodents with large-seeded trees is complex and, in many cases, rodents serve as both important dispersal agents and major seed predators. These animals store diffuse seed caches, each of which containing a fruit or seed for retrieval during times of food scarcity (Smythe 1978, 1989, Dubost 1988). The animals inevitably fail to recover a small fraction of the seeds, which, once protected from other invertebrate seed predators, apparently enjoy a higher survival rate (Smythe 1978, 1989, Dubost 1988, Forget 1991). Seed burial by agoutis and other scatter-hoarding rodents thereby seem to play a key role on seedling establishment. Hence, a differential treatment by these animals to the seeds of different palm species could have important consequences for seed dispersal patterns and gap colonization and, therefore, for the role that a palm species may have on forest regeneration.

Finally, density dependent mortality due to the action of host-specific efficiency enemies (Janzen 1970) is also a key component of our model. The role played by herbivores, often neglected in studies of plant succession (Connell & Slatyer 1977), is explicit in our hypothesis as it incorporates elements from the Janzen-Connell model (Janzen 1970, Connell 1971). According to Janzen (1970), their model is an extension to the plant community of the proposition that the local diversity of animal species is related to the number of predators in the system and their "efficiency", responding positively to density and negatively to distance (Janzen 1970), in preventing a single species from monopolizing a limited resource (Paine's 1966). Jansen's hypothesis is based on the generalization that wet lowland tropical forests have more tree species and, consequently, lower density of adults of each species, if compared to temperate-zone forests of similar area, topographic diversity and edaphic complexity. It then and predicts that the higher number of tree species observed in the tropics would be allowed by the efficiency of density-responsive, host-specific, herbivores in preventing tree species to dominate the forest space. As one moves to dryer or temperate zones, the increasing severity and unpredictability of the physical environment would make predators progressively less apt to specialize in a single prey species, keeping it from competitively dominating the habitat (Janzen 1970). In dryer areas of Central Brazil, for example, seedlings of the babassu palms (*Attalea phalerata*), are so abundant that hinder someone's progression through the forest and physically impede the development of mature forest trees, actually arresting succession (Kahn & Granville 1992). Therefore, under such conditions, the facilitative dimension of palm trees role on forest succession, proposed by our model, does not apply.

## 2. Empirical evidence

In this section some aspects of the model are examined with field data collected at an *Attalea maripa*-rich secondary forest patch within a matrix of well-preserved seasonally-dry forest in the Southeastern Amazon. To this end, we studied a patch of secondary forests where palm trees were abundant, in a matrix of primary forests, a few hundred meters from the Pinkaití research station (7° 46'18"S; 51° 57'42"W), at the Kayapó Indigenous Lands, South-eastern Amazon, Brazil. A palm grove that, according to the Kayapó indigenous population at the area, was cleared for the plantation of subsistence crops and subsequently abandoned in the first half of last century, was adjacent to a large isolated hillside, the *mirante*, which provided a panoramic view of the study area. The study area was formed by a forest of several hectares largely dominated by palm trees, being adjacent to a denser forest, where few palm trees can be seen. In a 16 ha grid system, established at the limit between these areas, adult palms were exhaustively searched and 569 *A. maripa* and 71 *A. aculeatum* palms were mapped. Within this grid, and at a surrounding undisturbed forest, studies were conducted on the importance of forest disturbance for the recruitment of large arborescent palms (Salm 2005), palm growth (Salm 2004a), palm seed dispersal (Salm 2006, in press), invertebrate and vertebrate predation of palm seeds (Salm, submitted), and tree species diversity (Salm 2004b).

The results of these studies show that large arborescent palms are generally rare at undisturbed areas of the Pinkaití (Salm *et al.*, in preparation), but abundant in naturally disturbed (Salm 2005) and dominant at a patch of secondary forests within the study site (Salm 2004a). These findings support the proposed notion of large arborescent palms as light demanding successional species that depend on large events of disturbance to become ecologically dominant - a view that, although disputed (Svenning 1999), is largely accepted (Kahn 1986, de Granville 1992, Kahn & de Granville 1992), and essential to our model.

A relatively fast rate of palm growth in height - necessary for the constitution a minimally closed canopy that will keep the sun from directly reaching the soil and therefore limit the growth of lianas - is an important factor of our model. Supporting this assumption, growth rate estimates showed that, once the palm's stem of adult diameter is developed, a palm-dominated canopy could be formed within a decade (Salm 2004a). This finding also highlights the potential importance of large arborescent palms as facilitative "tools" in programs of regeneration of deforested areas within the largely destroyed and endangered (Zimmerman *et al.* 2001) seasonally-dry Amazonian forests.

Furthermore, as postulated in the model, seed dispersal by scatter-hoarding rodents, abundant at the studied forest (Jorge & Peres, in press) seemed to be important for palm recruitment, affecting the relative role played by each palm species on forest regeneration. This is exemplified by considering the differences observed in the dispersion patterns of the seeds of two palm species by these animals (Salm, in press). The seeds of *A. maripa* are produced in much larger number and have significantly lower endosperm reserves available for the development of seedlings than those of *A. aculeatum*. Animals seem to have an important role on the dispersal of these seeds: large quantities of *A. maripa* seeds where found in tapir (*Tapirus terrestris*) dung piles, as elsewhere in the Amazon (Bodmer 1990, Fragoso 1997, Salm unpublished data). Seeds of *A. maripa* have also been found in tortoise (*Geochelone sp*.) faeces at the study site (Jerozolimski 2005). However, given the size of *A. aculeatum* seeds, whole propagules of this species are unlikely to be ingested by any living species. Such differences are likely to influence the spatial distribution, and thus recruitment patterns, of these palms. Salm (in press) shows in this sense that the seedlings of *A. maripa* are widespread in *terra firme* forest areas, being up to two orders of magnitude more abundant than those of *A. aculeatum*. They are also significantly more clumped around reproductive trees, suggesting a more restricted seed shadow - a result in odds with the patterns found for wind or gut dispersed species (Harper et. al. 1970, Harper 1977, Howe & Smallwood 1982, Fenner 1985) – probably as a consequence of the strong mutualistic association with caviomorph rodents, which preferentially remove large seeds and tend to disperse them farther (Vander Wall 1990). *A. maripa* seedlings are more clumped around reproductive trees since, given their lower level of energy reserves, it pays scatterhoarding rodents to invest more into dispersal of the more nutritive *A. aculeatum* seeds.

The implications for palm gap-colonization suitability in structurally distinct forests are clear: *A. aculeatum* should reach more efficiently the smaller and more evenly dispersed gaps of the dense forests of central Amazon, whereas *A. maripa* should be more suitable to colonize the large gaps of seasonally-dry Amazonian forests, as observed by Salm (in press) and consistently with the geographic distribution of these palms (both species are restricted to the Amazon region but *A. maripa* is more widespread abundant towards its periphery; Uhl & Dransfield 1987, Kahn & Granville 1992).

Density-responsive invertebrate seed predators also seem to prevent palms from establishing as dominants during the regeneration process, as our proposal assumes. Although *A. maripa* seedlings are found in high densities at the study site (Salm in press), they never reach a density comparable to the seedlings of the congener *A. phalerata* in dryer areas of Central Brazil, where succession is suppressed (Kahn & Granville 1992). This is probably related to the efficiency (sense Paine 1966) of the bruchid beetle *Pachymerus cardo* as a predator of *A. maripa* seeds, as found by other studies on bruchid predation of palm seeds (Janzen 1970, Wright 1983, Smythe 1989, Cintra & Horna 1997, Fragoso 1997, Silvius & Fragoso 2002, Fragoso *et al.* 2003). By imposing strong mortality on *A. maripa* seeds, the bruchid beetle *P. cardo* may thus hinder the palm tree to keep the monopoly of space, allowing other species to grow. This behaviour is in agreement with Janzen's (1970) prediction that, regardless of the seed crop in a given year as well as the distance between seeds and parent trees, density-responsive predators will "pursue seeds" until their density is so low that search is no longer profitable.

Additionally, the studied patch of secondary forest seems to be in an advanced stage of regeneration, having senescent palm populations (Salm 2004a) and floristically resembling the pristine areas of the Pinkaití Research Station. The successional nature of the palm grove is in fact evident on the structure of this forest patch. Its basal area is extremely low (15 $m^2.ha^{-1}$), significantly lower than that of the adjacent pristine forest (Salm 2004b). Such basal area is even lower than the limits (18-24 $m^2.ha^{-1}$) considered for liana forests (Pires & Prance 1985). The average height of the palm grove forest, on the other hand, is not significantly different from that of the adjacent forest (Salm 2004b).

These observations support the model's proposed role for arborescent palms on the regeneration of ecosystem structure, given its reconstituting role of canopy height and density.

Taken together, these results support the proposed role or arborescent palms on the regeneration of seasonally dry Amazonian forests. A final remark is however necessary. Despite its importance in the model, the negative effects of lianas on the growth of mature forest trees as well as on palms were not directly studied here due to the practical difficulties to identify vines and measure their biomass and, perhaps most importantly, the limitations associated to the temporal scale needed for such an investigation. Still, their suppressive effects on mature forest trees, by shading their crowns and increasing tree fall probability, is recognized by the Kayapó Indians (who are used to cut the vines that climb useful tree species) and well-known in the forestry literature (Alvira et al. 2004; Bongers et al. 2002). In Central America (Barro Colorado Island), vines dominate gap-phase regeneration and seem to inhibit non-pioneer tree survival (Schnitzer et al. 2000) but are significantly more abundant in younger than in older forests (Dewalt et al. 2000).

In conclusion, our model provides the basis for new lines of investigation that will allow the ecology of palm trees to be better understood within the context of Amazonian forests. Moreover, it highlights the potential role of palms as tools for environmental reconstitution in a likely future of large-scale deforestation in the Amazon. It is our hope that it contributes for the development of further studies applied to the conservation of the highly threatened seasonally-dry forests of the Amazon, and to the sustainable exploitation and management of these ecologically important and economically valuable palm species.

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### Capítulo-4

# Diversidade de espécies arbóreas em uma floresta sazonalmente seca: o caso da base de pesquisas do Pinkaití (PA), na Terra Indígena Kayapó, limite sudoeste da Amazônia

*Tree species diversity in a seasonally-dry forest: the case of the Pinkaití site, in the Kayapó Indigenous Area, southeastern limits of the Amazon*

SALM, R. 2004. Tree species diversity in a seasonally-dry forest: the case of the Pinkaití site, in the Kayapó Indigenous Area, Southeastern limits of the Amazon. Acta Amaz. 34: 435-443.

## Abstract

This study investigates patterns of forest structure and tree species diversity in an anthropogenic palm grove and undisturbed areas at the seasonally-dry Pinkaití research station, in the Kayapó Indigenous Area. This site, managed by the Conservation International do Brasil, is the most southeastern site floristically surveyed in the Amazon until now. The secondary and a nearby undisturbed forest were sampled in a group of 52 floristic plots of 0.0625-ha (25x25-m) where all trees with DBH ≥ 10 cm were measured and identified. The analyses were complemented with other two floristic plots of 1-ha (10x1000-m). The present study has shown that the Pinkaití, like other seasonally-dry forests, have great heterogeneity in forest structure and composition, associated with biotic characteristics of the most important tree species, natural disturbance and history of land-use. The palm grove, moderately dominated by the arborescent palm *Attalea maripa* (Aubl.) Mart., presented high tree species diversity and was floristically similar to undisturbed forests at the study site. It is discussed the importance of large arborescent palms for the seasonally-dry Amazon forests regeneration.

Key words: Amazon, anthropogenic forest, arborescent palms, floristics, tropical forests

# Diversidade de espécies arbóreas em uma floresta sazonalmente seca: o caso da base de pesquisas do Pinkaití (PA), na Terra Indígena Kayapó, limite sudoeste da Amazônia

Resumo

Este estudo compara a florística e estrutura e a diversidade de espécies arbóreas de um palmeiral antropogênico e áreas não perturbadas na floresta sazonalmente seca da base de pesquisas ecológicas do Pinkaití, na Terra Indígena Kayapó. Esta base de estudos, administrada pela Conservation International do Brasil, é a área mais ao sudoeste até o momento floristicamente amostrada na Amazônia. Uma mancha de floresta secundária e uma floresta não perturbada adjacente foram amostradas com um grupo de 52 parcelas de 0,0625-ha (25x25-m) onde todas as árvores com DAP≥ 10 cm foram medidas e identificadas. As análises foram complementadas com outras duas parcelas de 1-ha (10x1000-m). Este estudo mostrou que o Pinkaití, como outras florestas sazonalmente secas, tem grande heterogeneidade na estrutura e composição da floresta, associada com características bióticas das espécies arbóreas mais importantes, perturbação natural e histórico de uso do solo. O palmeiral, moderadamente dominado pela palmeira arborescente *Attalea maripa* (Aubl.) Mart., apresentou alta diversidade de espécies arbóreas e é floristicamente semelhante às florestas primárias da área de estudos. É discutida a importância de palmeiras arborescentes de grande porte no processo de regeneração das florestas amazônicas sazonalmente secas.

Palavras chave: Amazônia, florística, floresta antropogênica, floresta tropical, palmeiras arborescentes

# Introduction

The variety of seasonal forests that occur in the Amazon are difficult to define and grade continuously from dense to open and from evergreen to seasonally-dry forests. Dense forests, characterised by a rather uniform 25 to 45 m high continuous and evergreen canopy, with sparse emergent trees, frequently taller than 50 m, dominate wetter areas (>2500 mm rainfall per year). This is the dominant physiognomy in the central Amazon where the dry periods are relatively weak, and is frequently found in isolated patches along the transitional region. Semi-deciduous and deciduous forests occur in patches through the gradient between evergreen forests and savannah. Open forests, distinguished by the greater discontinuity of the canopy, are more frequently found in transitional zones, where savannahs gradually replace the forest (RADAM, 1974; Pires, 1984; Prance & Brown, 1987; Daly & Prance, 1989).

Seasonally-dry transitional forests, spread along the northern and southern limits of the Amazon basin, are connected by a large NW-SE arch which receives less than 2000 mm of rain annually. Their distribution coincides with one third of the Amazon that repeatedly experiences strong seasonal droughts (Nimer, 1977; Nepstad *et al.*, 1999). The Amazon forest extends as far as climate and edaphic constraints allows, and portions of its periphery show different types of transitional vegetation to extra-Amazonian floras and physiognomies. In general, the transitional forests of the northern Amazon are characterised by rather abrupt transitions from dense forest to savannah whereas the southern perimeter usually shows mosaic-like transitions involving semi-deciduous and liana forests (RADAM, 1974; Daly & Prance, 1989).

The transitional forests at the latitudinal limits of the Amazon lay upon the Precambrian shield of Guiana in the north and the Brazilian or Guaporé shield in the south (Putzer, 1984). Along the edges of the Amazon basin there are still intact sedimentary Precambrian plateaus and the vast majority of the highly weathered soils have been developing for over 20 million years from sediments derived from the rocks of the shields (Irion, 1978; Jordan, 1987). These regions show a variety of topographies, with numerous small elevations and are geologically more diverse than the core of the Amazonian intracratonic depression (Daly & Prance, 1989). Rivers dissecting these areas have well-defined beds, stable banks, and often form rapids, which mark the interface of the lower basin with the crystalline shields (Sioli, 1984).

For a long time, transitional forests have been considered as a distinct formation within the Amazon, although this notion has been changing historically (Daly & Prance, 1989). The strong presence of *Attalea phalerata* Mart. ex Spreng. (Babassu palm) and *Bertholletia excelsa* Humb., Bonpl. & Kunth (Brazil-nut) along the southeastern periphery of the Amazon was recognised early on, and considered as a distinct forest physiognomy denominated "zona dos cocaes" (Sampaio, 1945). More recently, forests with canopies highly entangled by lianas, and having a generally low basal area (18-24$m^2.ha^{-1}$), were described as "liana forests" (Pires & Prance, 1985).

The high α-diversity is one of the most distinctive ecological characteristics of tropical rain forests (Richards, 1996; Whitmore, 1990), especially the Amazon forests (Gentry, 1988). The Amazon forests have a large number of rare species and a few dominant (5-15) contributing up to 50% of the individuals (Pires & Prance, 1985). However, because plant α-diversity and annual rainfall across the Neotropics tend to be highly correlated, the local tree species richness in the transitional, seasonally-dry forest is expected to be generally lower than their equivalents in wetter areas of the Amazon (Gentry, 1988). But their composition often varies in a very complex way, even within areas of few hectares or less in extend, resulting in a high β-diversity (Oliveira & Mori, 1999; Richards, 1996). In the Amazon forest, large-scale variations both in the structure and the floristic composition seem to be chiefly determined by basin-wide variation in rainfall seasonality, but locally, geomorphology and hydrology play important roles (Gentry, 1988; Araújo *et al.*, 1999; Campbell *et al.*, 1986; Fearnside, 1999).

Nevertheless, physiognomic characteristics such as open canopy, low basal areas, large profusion of lianas and high abundance of pioneer tree species that typify a large part of the transitional Amazon forest have been interpreted as relics of anthropogenic activity and disturbance by pre-Columbian societies (Ballée & Campbell, 1990). Numerous monodominant forest enclaves of 2-3 ha of *Attalea* spp. in the Brazilian States of Pará and Maranhão are often associated with old human settlement sites and these species are usually considered good indicators of 'anthropogenic forests' (Balée, 1988, 1989). Indeed, large arborescent palms are among the most frequently noted disturbance indicators of Amazonian archaeological sites, and the vast palm forests, which cover almost 200,000 km$^2$ of the Brazilian Amazon, appear to be an artefact of intense human disturbance and use of the forest (May *et al.*, 1985).

The aim of this study is to investigate forest structure and composition variation, identifying patterns of tree species diversity within an anthropogenic palm grove, locally called *palmeiral*, and undisturbed areas at the Pinkaití research station, a seasonally-dry forest site on the Kayapó Indigenous Area, Southern Pará, Brazil. To identify spatial patterns of forest heterogeneity, detrended correspondence analysis (DCA) was conducted with 52 plots of 0.0625-ha (25x25m) spread along transects intercepting the *palmeiral* and a nearby, undisturbed, forest.

# Methods

## STUDY SITE

The Pinkaití Research Station (7$^{o}$ 46’18”S; 51$^{o}$ 57’42”W), managed by the NGO Conservation International do Brasil (CI-Brasil) is located at the municipality of Ourilândia do Norte, Southern Pará, Brazil (Fig 1a). It was build at the border of the Riozinho river (or Anfrísio’s Little River in some maps), a second-order tributary of the upper Xingu River, within the Kayapó Indigenous Area (3,284,005 ha). This area, contiguous with other eight contiguous indigenous areas form a continuous block of indigenous lands, with a great variety of indigenous peoples, which spans over more than 14 million ha in Pará and Mato Grosso (ISA, 2000).

The Kayapó, originally distributed along the Tocantins and Araguaia Rivers, since the beginning of the XIX century started shifting towards the Xingu river basin due to growing conflicts with the Brazilian national society, until their pacification in the decade of 1950 (Turner, 1999). Kayapó Indigenous Area protects a unique and vulnerable Amazonian forest type poorly represented in existing nature reserves. Several endangered vertebrate species typical of the seasonally-dry, transitional Amazonian forests were recorded at relatively high densities within this area (Nascimento, 1999).

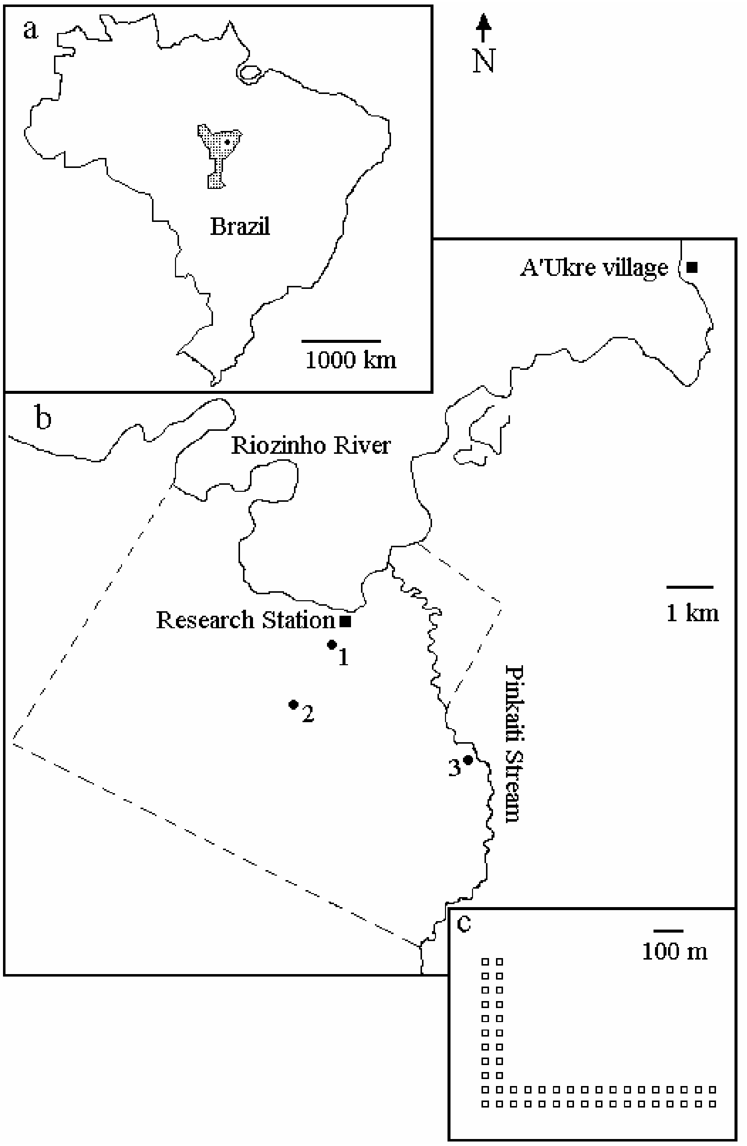

FIGURE 1. The study set up. (a) Within the map of Brazil, the 14,197,666 ha block of indigenous lands, composed by the Kayapó and the contiguous Badjonkore, Baú, Capoto/Jarina, Menkragnoti, Paraná, Batovi, Wawi and Parque do Xingu; the black dot indicates the Pinkaití site position (ISA, 2000; adapted). (b) The biological research station area; the numbers indicate the position of "1" the 52 0.0625-ha (25x25-m) floristic plots, "2" the Brazil-nut grove and "3" the Pinkaití stream 1-ha (1000x10-m) plots from C. Baider's (2000). (c) Distribution of the 52 0.0625-ha (25x25-m) plots.

In 1992, the Pinkaití project was initiated at the request of the leadership of the Kayapó Indian village of A'Ukre, which controls approximately 310,000 ha of forests and savannah, with the objective of providing economic alternatives to logging and protecting a population of mahogany trees. The Kayapó committed themselves to do not hunt or log in an area close to 10,000 ha, where the biological research station was set (Zimmerman *et al.*, 2001).

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 of the Pinkaití, annual precipitation between 1995 and 2001 ranged from 1636 to 2170 mm, 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 pluviosity in Eastern Amazonia (Nimer, 1977), the climate in the Pinkaití is slightly wetter with average rainfall close to 2200 mm yearly.

Geologically, 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, characterised by rolling slopes that are interrupted by granitic outcrops. Rocky ridges throughout the area are 100-250 m in altitude (RADAM, 1974). The soils distribution patterns follow predictable sequences across topographic relief with gray or bleached-white sandy profiles predominating on low ground adjacent to the lowest order seasonal streams and dense dark red clays found at higher elevations, often mixed with lateritic gravel (Grogan, 2001).

In the rainy season, the water level rises up to 7 m in Riozinho river (Baider, 2000); for long periods, thereafter, large floodplain areas are found and remain under more than a meter of water, usually for few days.

The RADAM Project (1974), with vegetation maps produced with the use of radar imagery and field inventories still provides the most comprehensive description of the studied area. The Pinkaití station area is approached in the volume 4 (FOLHA SB.22 ARAGUAIA E PARTE DA FOLHA SC.22 TOCANTINS), within the map Gorotire (SB.22-Y-D). The Gorotire region is highly representative of the vegetation mosaics of the southern Amazon known as dry belt archway. The forest at the study site is structurally heterogeneous, consisting of easily distinguishable types that form mosaics of dense forest (mostly insular in residual plateaus) and open forest (in isolated patches or bottomlands), including extensive areas of liana forest (*sensu* Pires & Prance, 1985). Woodland and grassland savannahs are more concentrated to the east, following the rainfall gradient. Patches of grassland savannah at this site also seem to coincide with edaphic conditions that are unfavourable to forest cover (RADAM, 1974) and their distribution seems to be affected by fires occasionally started by the Kayapó Indians. Approximately 15 % of an 80 x 80 km area (640,000 ha) centred around the A'Ukre's village is savannah, distributed largely on a few upland plateaus (Malcolm *et al.*, 1999). During dry periods of the Pleistocene and during a dry post-Pleistocene episode when the forests of the upper and lower Amazon had been divided by a corridor of grassy savannah running more or less across the Pinkaití site region (Haffer, 1969).

C. Baider (2000) estimated the Pinkaití tree species α-diversity with two 1-ha (10x1000m) quadrats set up in tall open forest type, and found that it is low, if compared to more aseasonal sites elsewhere in the Amazon (Gentry, 1988). One of them was located within a Brazil-nut (*Bertholletia excelsa* Humb., Bonpl. & Kunth) grove (hereafter, Brazil-nut grove plot), approximately 3 km inland from Riozinho River and had 594 trees of 102 species. The other crossed a forest along a permanent river valley (from now on, Pinkaití Stream plot) and had 540 individuals of 98 species (Fig 1b).

FLORISTIC PLOTS

To compare patterns of tree species diversity within an anthropogenic forest and undisturbed areas at the Pinkaití, was selected a palm grove that, according to the Kayapó, was cleared for subsistence crops (*roças*), in the first half of last century. A member of A'Ukre community, Beptoti Pompe, related that when his father, the old chief Tiquiri was young, the Kayapos displaced a group of *caboclos* (probably rubber-tapers) who lived on the area now occupied by the research station.

As the old Kayapó are illiterate and did not know to count the years, it is difficult to precise exactly when these Indians occupied the Riozinho River valley, displacing the *caboclos* that lived where today is the Pinkaití Research station. However, iron tools found in the palm grove testify its former occupation and the conflict with the *caboclos* is recalled by the oldest members of A'Ukre village. Their fields were, probably, similar to those found around A'Ukre village, where *terra firme* (= unflooded) forest patches of a few hectares, are periodically cleared, mainly for the cultivation of manioc, corn, beans, yam and sweet potatoes (Morsello, 2002). Some of these cops are still occasionally found in the immediacy of the Pinkaití station's houses. The proximity of the research station with the probable site occupied by the Brazilians that lived in this area is not incidental, since this is one of the rare land patches along the Riozinho river that do not flood at the top of the rainy season.

Departing from a point more or less in the centre of the palm grove dominated by the large arborescent palm *Attalea maripa* (Aubl.) Mart., 52 plots of 0.0625-ha (25x25-m) were set, distant at least 25 m from each other, established along two orthogonal transects. The first transect was 600 m in length and progressed northwards towards the Riozinho River. The other was 800 m in length, extended to the east, crossing an undisturbed area with low palm density, visibly dominated by the legume tree *Cenostigma tocantinum* Ducke, locally known as *pau-preto* (Figure 1c).

In all quadrats, all trees reaching diameter ≥ 10 cm at 1.3 m height were measured to the nearest millimetre, and the height of all trees (upper crown) was visually estimated. Samples were taken for almost all individuals except the very easily identifiable ones, like *Bertholletia* or palms. Field identification was performed in the field by Mr. M. R. Cordeiro, and confirmation at IAN Herbarium (from Embrapa Amazonia Oriental, Belém), where all material has been deposited.

### *DATA ANALYSIS*

Correspondence analysis was carried out using CANOCO for Windows 4.0. The ordination arranges the floristic plots as points in a scatter diagram in an ecologically structured way. Data points that are close together correspond to plots that are compositionally similar, whereas those that are farther apart are more dissimilar. Species are also represented as points, and those that tend to occur in the same plots, converge in the scatter plot, whereas those that occur in different plots appear farther apart. If species are plotted on the same diagram of floristic quadrats, they tend to appear near the quadrats where they are most abundant (Jongman *et al.*, 1995).

To reduce the importance of rare species, whose distributions are difficult to explain ecologically and could weaken the overall ordination results (Jongman *et al.*, 1995), only tree species with more than 10 individuals were included in the analysis. This procedure resulted in the selection of only 29 out of a total of 175 tree species. To strengthen the interpretation of the Detrended Correspondence Analysis, 52 randomly assorted samples of 6,25% of the Brazil-nut grove and Pinkaití were selected and incorporated in the analyses.

For the fitossociological analysis of the Pinkaití site, four different areas were considered: (1) the palm grove, with 24 0.0625-ha plots and (2) the *pau-preto* forest, with 28 0.0625-ha plots, whose distinction was observed in the field and confirmed by the ordination analysis of tree species abundance and composition (see below), the (3) The Brazil-nut grove and the (4) Pinkaití Stream 1-ha plots, from C. Baider (2000). To describe the structure of the main populations of the four areas, were calculated importance value index (IVI), Shannon diversity and similarity indices (Whittaker, 1972; Pielou, 1975).

## Results

The scatter-diagram from the DCA confirmed the separation of the 24 0.0625-ha plots from the palm grove plots from the 28 0.0625-ha plots in the adjacent *pau-preto* forest. The plots of the anthropogenic palm grove were clustered with the 52 randomly assorted samples of the Brazil-nut grove and Pinkaití the stream forest (Fig 2). In contrast, Sorensen Similarity Index indicated that the composition of the palm grove is more similar to the adjacent *pau-preto* forest than to the Brazil-nut grove and the Pinkaití stream forest (Table 1).

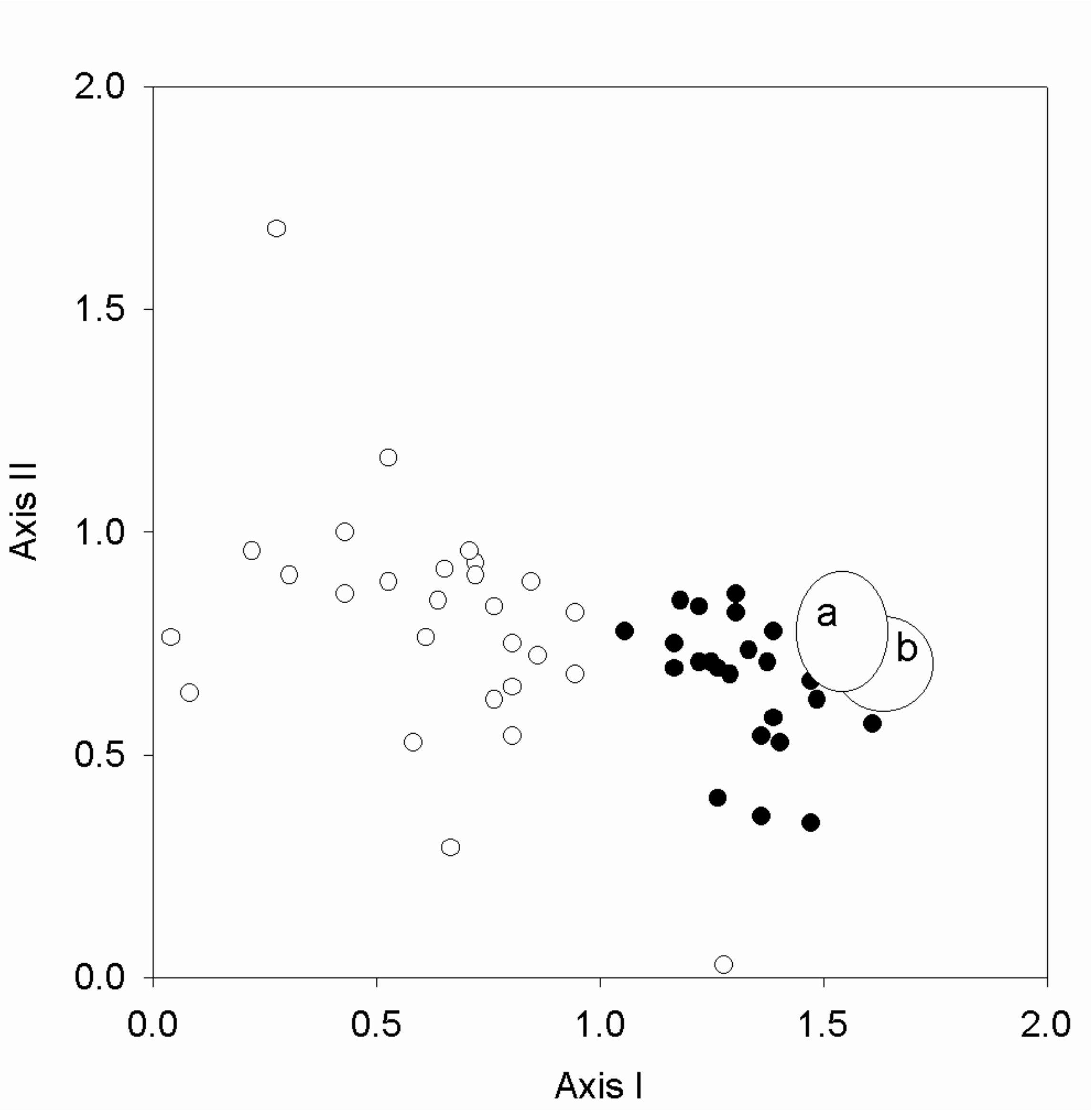

FIGURE 2. Detrended Correspondence Analysis ordination of floristic plots. Solid and open circles represent the palm grove and the *pau-preto* forest plots (0.0625-ha), respectively. The areas delimited by “a” and “b” mark the distribution of 52 randomly assorted samples of 6,25% of the Brazil-nut grove and Pinkaití stream plots, respectively. DCA axis 1 and 2 explained 25.6 % and 5.4 % of variation in species data, respectively (length of gradient 2.271 and 1.675 SD-units).

TABLE 1. Floristic similarities estimated with the Sorensen Similarity Index, among the four considered areas at the Pinkaití, Southern Pará, Brazil.

| | *pau-preto* forest | Brazil-nut grove* | Pinkaití Plot* |
|---|---|---|---|
| Palm grove | 0.590 | 0.449 | 0.449 |
| *Pau-preto* forest | - | 0.505 | 0.505 |
| Brazil-nut grove | | - | 0.495 |

* C. Baider (2000).

The palm *Attalea maripa* (Aubl.) Mart. was the most important species in the palm grove, followed by *Metrodorea flavida* Krause (Rutaceae), *Tetragastris altissima* (Aubl.) Swart (Burseraceae), *Theobroma speciosum* Willd. Ex Spreng. (Sterculiaceae) and *Protium subserratum* (Engl.) Engl. (Burseraceae). The *pau-preto* forest is strongly dominated by *pau-preto* trees (*Cenostigma tocantinum* Ducke, Leguminosae), followed in importance by *T. altissima*, *M. flavida*, *A. maripa* and *Cheiloclinium cognatum* (Mierc.) A.C. Smith (Hippocrateaceae). In both the Brazil-nut grove and Pinkaití the stream forest, *T. altissima* was the most important species. It is followed by *Astronium gracile* Engler (Anacardiaceae), *M. flavida*, *T. speciosum* and *Brosimum lactescens* (S. Moore) C. C. Berg (Moraceae) in the Brazil-nut grove and *M. flavida*, *Pouteria trilocularis* Cronq. (Sapotaceae), *Trichilia quadrijuga* Kunth (Meliaceae) and *B. lactescens* in the Pinkaití stream forest. The Shannon diversity index indicated that the Palm grove was, floristically, the most diverse area, followed by the Pinkaití Plot, the Brazil-nut grove and the *pau-preto* forest (Table 2).

TABLE 2. Forest composition at the four study areas considered at the Pinkaití site, Southern Pará, Brazil. For each area, are presented the 5 tree species with the highest importance value index (In parenthesis is the species percentage of IVI) and the Shannon diversity index.

| | Palm grove | *pau-preto* forest | Brazil-nut grove* | Pinkaití Plot* |
|---|---|---|---|---|
| 1st Species in IVI | *Attalea maripa* (14%) | *Cenostigma tocantinum* (29%) | *Tetragastris altissima* (15%) | *Tetragastris altissima* (8%) |
| 2nd Species in IVI | *Metrodorea flavida* (10%) | *Tetragostris altissima* (8%) | *Astronium gracile* (4%) | *Metrodorea flavida* (5%) |
| 3rd Species in IVI | *Tetragastris altissima* (4%) | *Metrodorea flavida* (7%) | *Metrodorea flavida* (10%) | *Pouteria trilocularis* (4%) |
| 4th Species in IVI | *Theobroma speciosum* (3%) | *Attalea maripa* (5%) | *Theobroma speciosum* (3%) | *Trichilia quadrijuga* (4%) |
| 5th Species in IVI | *Protium subserratum* (3%) | *Cheiloclinium cognatum* (4%) | *Brosimum lactescens* (3%) | *Brosimum lactescens* (3%) |
| Shannon Index | 3.95 | 3.17 | 3.75 | 3.84 |

* C. Baider (2000).

All plots showed that Leguminosae, including the families Fabaceae, Mimosaceae and Cesalpiniaceae, was the most species-rich family. The Rutaceae, mostly represented by the understorey tree *M. flavida* is almost ubiquitous across all *terra firme* forest plots. At the palm grove, the Rutaceae was the family with the highest number of stems, followed by the Leguminosae and Palmae. At the *pau-preto* forest, Leguminosae was the most abundant family, chiefly represented by *C. tocantinum*. The Burseraceae and Rutaceae were the second-ranking families in number of individuals, mainly represented by *T. altissima* and *M. flavida*, respectively. In both the Brazil-nut and Pinkaití Stream plots, the Burseraceae was the most abundant family, chiefly represented by *T. altisissima* (Fig 3).

The palm grove had, by far, the lowest basal area, followed by the Brazil-nut grove, the *pau-preto* forest and the Pinkaití Stream Plot. The palm grove had the same median tree height as the *pau-preto* forest, substantially lower than the Brazil-nut grove and the Pinkaití Stream Plot (Table 3). The 24 0.0625-ha plots of the palm grove, compared to the adjacent 28 plots at the *pau-preto* forest had significantly lower basal area (Mann-Whitney U, $p<0.001$). However, no significant difference was found between the median height of these forest plots (Mann-Whitney U, $p=0.646$).

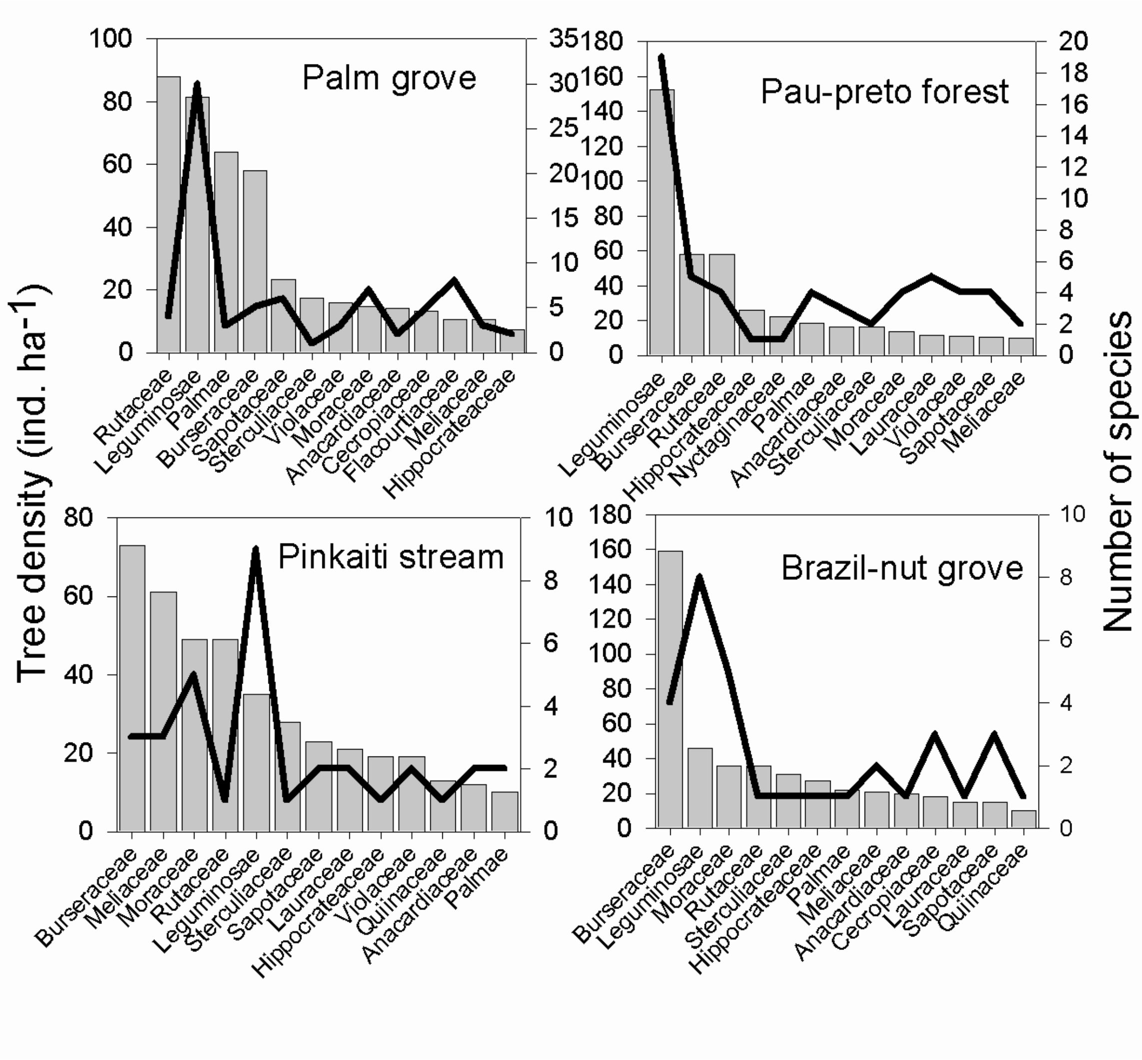

FIGURE 3. Rank of family abundance in relation to density and species richness at the four study areas. Solid lines indicate number of species and bars indicate stem densities.

TABLE 3. Forest structure at the four study areas considered at the Pinkaití site, Southern Pará, Brazil. For each area, are presented the median tree DBH, median three Height and basal area per hectare.

| | Palm grove | *pau-preto* forest | Brazil-nut grove* | Pinkaití Plot* |
|---|---|---|---|---|
| Median DBH | 14.8 cm | 16.7 cm | 16.2 cm | 17.7 cm |
| Median Height | 11 m | 11 m | 17 m | 18 m |
| Basal area | 15 $m^2 .ha^{-1}$ | 27 $m^2 .ha^{-1}$ | 24 $m^2.ha^{-1}$ | 40 $m^2.ha^{-1}$ |

* C. Baider (2000).

# Discussion

The findings of this study show that at the Pinkaití forest, like in other seasonally-dry Amazonian forests (RADAM, 1974; Gentry, 1988), a relatively small group of species, can occasionally become dominant in the tree community. The comparison of the palm grove with the adjacent *pau-preto* forest, the Brazil-nut grove, and the Pinkaití stream plots revealed that this palm dominated forest in an advanced stage of regeneration, floristically resembles the undisturbed areas of the Pinkaití Research Station. The successional nature of the palm grove is evident on the relative importance of the most abundant species and on the structure of this forest patch.

Large arborescent palms are generally rare in Amazonian dense, *terra firme* forests, where large palm trees are chiefly restricted to areas with high levels of natural or anthropogenic disturbance (Spruce, 1871; Kahn and Castro, 1985; Kahn *et al.*, 1988; Kahn and Granville, 1992; Ballée, 1988, 1989). The evidence from this study agree with others that found *Attalea maripa* to appear on sites of previous human disturbance (Pesce, 1985). The large arborescent palm *A. maripa* is the most important tree species in the palm grove, with 53 individuals per hectare. The palm was the second species in number of trees, after the Rutaceae *Metrodorea flavida*. Its higher percentage of IVI resulted mainly from the larger diameter of the palm's stem. The Sorensen Similarity Index indicated that the palm grove is floristically similar to the adjacent undisturbed *pau-preto* forest. The main compositional difference between these areas was mainly related to the strong dominance of *Cenostigma tocantinum* in the latter. Both the Brazil-nut grove and the Pinkaití Plots are moderately dominated by the Burseraceae *Tetragastris altissima.* Indeed, closed-canopy forests throughout the whole Gorotire region ($7^{o}$ 00 S-$8^{o}$ 00 S; $51^{o}$ 00W-$52^{o}$ 30'W), where the study site is inserted, are largely dominated by *T. altissima* (RADAM, 1974).

The Shanon Diversity Index indicated that the tree species community of the palm grove is even more diverse than that of the Pinkaití river valley, among the undisturbed sites, the most diverse compared area. The Brazil-nut grove was intermediate in tree species diversity and the lowest values were found in the *pau-preto* forest.

The high tree species diversity of the palm grove forest might result from the advanced stage of forest succession and the environmental heterogeneity created by the *caboclos* that lived in this area. The area abandonment allowed the forest succession to proceed, with the development of pioneers, and their gradual replacement for late successional species dispersed from the undisturbed surrounding forest. High diversity have been related to intermediate levels of disturbance in widely different ecosystems like rainforests and coral reefs (Connell, 1978).

Among the forest plots, the DCA ordination indicated that the most floristically distinctive plots are those in the *pau-preto* forest, that also had the lowest diversity of tree species among the compared areas. The results are explained by the high dominance, both numeric and in terms of the total basal area, of the legume tree *C. tocantinum*. This species is typically restricted to large river edges in the study area, which is consistent with the local distribution of *Cenostigma* spp. elsewhere in the Xingu River basin (Campbell *et. al*, 1986). These species have great sprouting capacity and large hollow trunks that frequently dismount, giving "birth" to new trees, which, utilising resources from the original tree, can develop well in shaded areas. The palm grove, despite being a few hundred meters from the main perennial river of this area, never floods due to the proximity to an isolated mount by the river. In contrast, the *pau-preto* forest, further away from the mount is affected by flash floods that create the competitive conditions for *C. tocantinum* dominance.

In the southeastern limits of the Amazon, the Pinkaití research station is just a few kilometers from a large savannah patch on an upland plateau (Malcolm *et al.*, 1999), similar to the *cerrado* of Central Brazil (RADAM, 1974). The relatively high tree species diversity of the Pinkaití Stream Plot was expected and is consistent with the observation that in the Amazon there is a strong positive correlation between precipitation and community level plant species richness (Pires & Prance, 1985; Gentry, 1988; Campbell *et al.*, 1986; Daly & Prance, 1989). The benevolent environmental conditions created by the humidity of the Pinkaití River valley probably allowed the maintenance of the tropical rainforest while most of surrounding areas was replaced for open formations. Today, such humidity allows the maintenance of an evergreen forest at the valley while the forest in most of the research station area suffers from different levels o water stress and leaves shading (Baider, 2000).

Seasonally-dry Amazonian forests are typically characterised by high structural heterogeneity compared to more aseasonal forests of the central-western Amazon (Pires & Prance, 1985; Daly & Prance, 1989). The results presented here show that the Pinkaití forest is, structurally, highly variable, and these are conservative given that more open vegetation types occurring in the wider study area, such as vegetation associated with rock outcrops, were not sampled. The basal area of the Stream Plot (39.9 $m^2.ha^{-1}$) was the highest recorded in a sample of 14 one-hectare floristic plots spread across the Eastern Amazon (Baider, 2000).

The successional nature of the palm grove is evident on the structure of this forest patch. Its basal area is extremely low (15 $m^2.ha^{-1}$), significantly lower than that of the adjacent *pau-preto* forest. Such basal area is even lower than the limits (18-24 $m^2.ha^{-1}$) considered for liana forests (Pires & Prance, 1985). The average height of the palm grove forest, on the other side, is not significantly different from the adjacent forest.

With the *caboclo's* displacement and the abandonment of their crop fields, succession probably proceeded in this large forest gap as it does in large gaps in the region. In a first phase, grasses and bamboos rapidly form thick mats that hinder the growth and survival of mature forest species. Furthermore, lianas, using the structure of trees as support, severely suppress tree growth and survival (RADAM, 1974). Forest succession progresses to a second phase with the establishment and growth of large arborescent palms, chiefly *A. maripa* but also *Astrocaryum aculeatum* G. Mey , *Socratea exorrhiza* (Mart.) H.Wendl. and *Oenocarpus distichus* Mart. Palm trees are often spared in the process of trees felling for forest clearance, not only due to their utility for humans but also because of the hardness of their stem that makes their felling extremely laborious (Kahn & Granville, 1992).

At the Pinkaití, *A. maripa* seeds are avidly consumed, and dispersed, by agoutis (*Dasyprocta agouti*) particularly during the dry season, when alternative food resources are scarce (Jorge, 2000). Furthermore, large quantities of *A. maripa* seeds are often found in tapir (*Tapirus terrestris*) dung piles (Salm, 2002). Both the seed dispersors are relatively abundant at the Pinkaití where agoutis and tapirs are found at densities of 43.34 and 0.62 individuals per km$^2$ (Peres, 2000). As a result, *A. maripa* seedlings are virtually ubiquitous across this site, being found in the *pau-preto* forest at densities of approximately 10,000 per hectare (Salm, 2002).

Furthermore, a particularity of the *Attalea* stem development is the remote-tubular seedling development. After germination, the seedling stem has a positive geotropism characterised by the growth of a descending subterranean stem before ascending to develop the above-ground trunk (Bondar, 1964). Therefore, the underground palm stems are not easily destroyed by fire, which gives them an enormous advantage as a pioneer in burnt areas and to persist under severe disturbance regimes (Henderson *et al*., 1995).

In full-light conditions, the growth in height of *A. maripa* is relatively rapid and the stem of these palms can reach 8-m height aboveground in 16.5 ± 2.8 (S.D.) years after its emergence (Salm, 2004). During this phase, the canopy height is gradually raised and the canopy closes, reducing the light that reaches the juveniles. Palms are self-limiting because their regeneration is hampered by the shadow produced by adult palms. With the reduction of light in the understorey, liana recruitment becomes less frequent and their negative impact on the trees diminishes, liberating the trees to develop further. With the tree growth and the palm senescence, and replacement, the forest tends to progress to the mature stage.

The forests at the Pinkaití research station have great heterogeneity in composition and structure, associated with topography, soils and drainage (RADAM, 1974; Malcolm *et al.*, 1999; Baider, 2000). Beside habitat condition, the present study has shown that such differences are associated with biotic characteristics of the sampled population and history of land-use. Further studies of large arborescent palms distribution are necessary to shed additional light into the ecological consequences of human disturbance and their potential role for restoration of degraded areas within the seasonally-dry Amazonian forests.

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**Capítulo-5**

# Densidade do caule e crescimento de *Attalea maripa* e *Astrocaryum aculeatum*: implicações para a distribuição de palmeiras arborescentes na floresta Amazônica

# *Stem density and growth of* Attalea maripa *and* Astrocaryum aculeatum*: implication for arborescent palms distribution across Amazonian forests*

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# Abstract

## Stem density and growth of *Attalea maripa* and *Astrocaryum aculeatum*: implication for arborescent palms distribution across Amazonian forests

This study examines aspects of the stem density and growth of two large arborescent palms *Attalea maripa* and *Astrocaryum aculeatum* and discusses their implication for the palm trees distribution in Amazonia. Stem density and growth were investigated through both laboratory measurements and field estimates of growth rates. The densities of stem samples collected within one individual of each studied species were very distinct. The samples of *A. maripa* stem were more homogeneous in density than those of *A. aculeatum*, both from the internal to the external, and from the lower to the upper parts of the stem. Field estimates of stem growth rates revealed that *A. maripa* growth is also more constant through development in height. Short *A. aculeatum* palms had faster growth rates than *A. maripa*, as they get taller, stem growth rates are reduced and approach *A. maripa* rates. The implications for arborescent palms distribution across Amazonian forests are discussed.

Key words: Amazonia, *Astrocaryum aculeatum*, *Attalea maripa*, Distribution, Palms, Stem density

# Resumo

## Densidade do caule e crescimento de *Attalea maripa* e *Astrocaryum aculeatum*: implicações para a distribuição de palmeiras arborescentes na floresta Amazônica

Este estudo examina aspectos da densidade do caule e crescimento de duas palmeiras arborescentes de grande porte *Attalea maripa* e *Astrocaryum aculeatum* e discute suas implicações para a distribuição de palmeiras arborescentes na Amazônia. Densidade dos caules e crescimento foram investigados através de uma combinação de medidas de laboratório e estimativas de campo de taxas de crescimento. As densidades de amostras do caule coletadas de um indivíduo de cada espécie foram muito distintas. As amostras do caulde de *A. maripa* foram mais homogêneas em densidade que aquelas de *A. aculeatum*, tanto das partes internas para externas, como inferiores para superiores dos caules. Estimativas de campo de crescimento do caule revelaram que o crescimento de *A. maripa* também é mais constante ao longo do desenvolvimento. Palmeiras *A. aculeatum* baixas tiveram crescimento mais rápido que *A. maripa*, palmeiras mais altas têm seu crescimento reduzido a níveis semelhantes ao de *A. maripa.* São discutidas as implicações para a distribuição de palmeiras na Amazônia.

Palavras-chave: Amazônia, *Astrocaryum aculeatum*, *Attalea maripa*, Densidade do caule, Distribuição, Palmeiras.

## 1. **Introduction**

The occurrence of disturbance seems to be a limiting factor for the distribution of different life-forms of palms in tropical forests. Early naturalists noticed the general rarity of palm trees in dense, well-drained forest areas (Spruce 1871). In the Amazonian *terra firme* forests, the distribution of the arborescent palms is partly determined by heterogeneity in topography (Kahn & Granville 1992, Svenning 1999) and canopy cover (Richards & Williamson 1975, Svenning 1999, 2000). Palm trees are abundant in open forests, which tends to be less developed architecturally, with large and complex canopy gaps, permitting greater level of light penetration through the understorey (Kahn & Castro 1985, Kahn 1987).

The importance of forest disturbance regime as a determinant of palm tree occurrence and distribution has been attributed to their high light requirements for early establishment (Kahn & Castro 1985, Kahn 1987, Kahn & Granville 1992, but see Svenning 1999). The ecological light compensation point of establishing and adult palms increases throughout palm development. This occurs because the relative amount of support tissues in the leaves grow with leaf size and the fraction of biomass allocated to leaves declines with stem height (Givnish 1979, 1988, Tomlinson 1990).

In large gaps, trees along gap edges are relatively inefficient in promoting canopy closure. Thus, forest regeneration is mainly a result of new tree development, which takes considerably longer than regeneration from bordering trees on small gaps. Therefore, in large canopy gaps, light demanding palm trees often have sufficient time to complete their establishing growth under such favourable light conditions (Kahn 1986, Kahn & Granville 1992, de Granville 1992).

Palms lack a lateral vascular cambium and, in the absence of any secondary thickening meristem, thickness growth is entirely primary, and confined to the apical meristem. Thus, stem girth growth largely precedes the completion of extension growth. The consequence is that palm trees, in contrast to dicotyledonous trees, are more limited in their capacity to increase stem diameter by cell division (Tomlinson 1961, 1979, Tomlinson & Zimmermann 1967).

Palm trees represent exceptionally dynamic structures in which major age-dependent changes occur in mechanical properties (Rich 1986). The mechanical structure of arborescent palms is therefore fundamentally different from that of dicotyledon trees. The palm stem is more heterogeneous and undergoes more marked internal changes. Within the palm tree stem, density tends to be higher towards both the stem periphery and its base (Richolson & Swarup 1977, Sudo 1980, Killmann 1983). Stiffness increase within palm stems prevents a steep growth in the risk of mechanical failure (Tomlinson & Zimmerman 1967, Tomlinson 1979, 1990). Density of peripheral stem tissues at the base of mature palm trees is higher than that of most dicotyledon, while the density of the central core, toward the crown, tends to be lower than most woods. Thus, a single mature arborescent palm can encompass the full range of published values of wood density (Williamson 1984).

The imbalance between the development of the palm stem and their mechanical support requirements poses anatomical constraints for arborescent palms in tropical forests. Inter-specific variation in stem development among Neotropical palm tree species might affect species growth rates and their performance in forests of contrasting architecture (Rich 1987a, Tomlinson 1990).

The aim of this study is to examine aspects of the stem structure and development of two large arborescent palms in a seasonally dry Amazonian forest and the ecological correlates of stem development. The establishment growth of *Attalea maripa* and *Astrocaryum aculeatum* was related to the morphometrics of both palm species. Stem structure and development were investigated through laboratory measurements of density and field estimates of stem growth rates.

## 2. Material and Methods

*Attalea maripa* is a tall (10 to 15 m height), massive, solitary and monoic palm (Uhl & Dransfield 1987). The species is found throughout the Amazonian region, being widespread towards the open forests of its periphery, but it is not found outside Amazonia (Uhl & Dransfield 1987, Kahn & Granville 1992). *A. maripa* can become common in highly seasonal forests and is frequently dominant in secondary forests across their distribution range (Henderson *et al.* 1995). The fruits of this palm represent a major food source for the vertebrate community in several parts of the Amazon (Bodmer 1991, Kahn & Granville 1992, Fragoso 1994, 1997, 1998, 1999).

*Astrocaryum aculeatum* is also a tall (10 to 25 m height), massive, solitary and monoic palm (Uhl & Dransfield 1987). The upper part of its stem is armed with long black spines arranged in regularly spaced rings. As the tree grows, the oldest spines drop off, and lower trunk parts generally have no spines. This species is restricted to the Amazon region although less widespread than *A. maripa* towards its periphery (Uhl & Dransfield 1987, Kahn & Granville 1992). This species can become common in the dense forest of central

Amazonia where it occasionally dominates secondary forests (Kahn & Granville 1992, Henderson *et al.* 1995).

This study was conducted at the Pinkaití forest of southeastern Amazonia (7$^{o}$ 46’18”S; 51$^{o}$ 57’42”W). Geologically, the study area lies on the pre-Cambrian crystalline shield of Brazil. Annual rainfall is approximately 2000 mm.yr$^{-1}$ and there is a severe dry season from June to September, when total rainfall is close to nil. The Pinkaití site is floristically much heterogeneous and its tree species diversity is low, compared to more aseasonal sites elsewhere in the region (Baider 2000, Salm 2002), which is typical of transitional forests of southern and eastern Amazonia (Pires & Prance 1985, Campbell *et al.*, 1986). It is chiefly dominated by open forests, typically characterised by a high abundance of lianas (Ballé and Campbell 1990), and dense forests, that predominates in residual plateaus and other upland areas (Radam 1974). At the study site, there is a generally high density of *A. maripa* (6.7 ! 11.2 S.D palms. ha$^{-1}$) that is consistently more abundant than *A. aculeatum* (1.6 ! 3.8 S.D palms. ha$^{-1}$). The palm family, in addition to *A. maripa* and *A. aculeatum*, also includes the arborescent *Euterpe precatoria* and *Socratea exorrhiza*, which are found in lower densities (Salm 2002).

The morphometrics and the field estimates *A. maripa* and *A. aculeatum* stem growth rates were measured within a 16 ha grid system set in a forest path where the forest had apparently been cleared for subsistence crops in the first half of last century (U. Kayapo, pers. comm.). The Rutaceae is the family with highest number of stems, chiefly represented by *Metrodorea flavida*, the most numerous tree species in this assemblage. The palm A. maripa was the tree species with the highest basal and the second highest numerical abundance. On the other hand, *A. aculeatum* was the 16th most common species in terms of basal area and the 10th in individuals number (Salm 2002).

### *2.1* Stem structure and development

The diameter of 111 *A. maripa* and 50 *A. aculeatum* trees with above-ground stem were measured within the 16 ha grid system. It was possible to determinate the reproductive development stage of a total of 246 *A. maripa* and 41 *A. aculeatum* palms by an inspection for evidence or absence of past reproductive activity, as indicated by the accumulation of old seed and flower remnants underneath the crown. Heights were estimated using a 8 m long pole for reference from the ground to the lowest leaf-bearing node.

One individual palm of each species was destructively sampled outside the grid-system near the Pinkaiti research station. The *A. maripa* palm sampled was 8m tall and had a cross-section of the stem collected at 0, 4 and 8m above ground. The *A. aculeatum* sampled was 16 m tall and had samples collected at 0, 4, 8, 12 and 16 m. Both palms were reproductive adults and occurred under similar environmental condition, with the crown fully exposed, above the canopy.

Three whole cross-sections of *A. maripa* and five of *A. aculeatum* corresponding to the different height along the stem were taken to the Plant Anatomy Laboratory of the University of São Paulo (USP) for density measurements. Stem sections were photographed and milled into cubes. From each stem sections, 9 cubic samples were extracted, three of each from its central, intermediate and external parts. Because of practicality, stem tissue density was measured as oven-dry weight per dry volume. After samples were dried at 60°C for 30 days. All samples were weighed in a precision scale and their volume subsequently measured as the water volume displaced by the immersion of the sample in a graduated beaker.

### *2.2* Growth rate estimates

The palm family is characterised by a continuous production of leaves, and many palm species produce permanent leaf scars on the stem. Rates of leaf formation, internode distances, or rate of leaf expansion have been used to estimate the growth rate and age of palms (Corner 1964, Sarukhan 1978, Savage and Ashton 1983, Piñero *et al.* 1984, Uhl & Dransfield 1987). It is feasible to estimate the growth rate of palms with data collected at relatively short periods of time. However, extrapolations from mean values should be considered with caution (Tomlinson 1979, 1990, Rich 1987a). Furthermore, age estimates of stemmed individuals still require information about the seedling and juvenile lifespan which in most large arborescent palms is difficult since their stems are protected and remain invisible below ground (Corner 1964, Tomlinson 1990).

For this study, leaf scar production rates were estimated by counting the number of leaves that fell from 81 adult *A. maripa* and 36 *A. aculeatum* during a 1-year period. At the beginning of this investigation period all fallen leaves were removed from the surroundings of the focal palms selected for observation. Fallen leaves, hanging from branches of surrounding trees were also removed. Fallen leaves were defined as those that had no base contact with the palm stems. All focal palms were subsequently monitored during three occasions (at four months interval) when all the new fallen leaves were counted and removed. The time interval between consecutive leaf counts was short enough to ensure that fallen leaves did not decay on the forest floor.

Leaf scars were counted with the assistance of a pair of binoculars along 67 adult *A. maripa* and 38 *A. aculeatum* stems. Leaf abscission marks are conspicuous in both *A. maripa* and *A. aculeatum.* Counts were classed within 1 m intervals, with reference to a 8 m long banded pole placed next to the focal palm stem. Leaf scars above 8 m along the palm stems were counted together as a single class. Counts were classed within 1 m intervals, with reference to a 8 m long banded pole placed next to the focal palm stem. Leaf scars above 8m along the palm stems were counted together as a single class. Dividing the number of leaf marks along the stem by annual leaf production rates allowed stem growth rates to be estimated.

The palms considered for the leaf scar production rates estimation were not necessarily the same of those where leaf scars were counted, because of the distinct requirements of good visual access to the stem, and to the crown, in a forest where heavy liana loads cover most of the trees.

## 3 Results

### 3.1 *Stem structure and development*

The diameter of the *A. maripa* palms (26.7 cm +/- 4.1 SD) was significantly higher than those of *A. aculeatum* (23.7 cm +/- 3.9 SD) (Independent sample T p=0.001). The height of the sampled *A. maripa* population (8.2 m +/- 3.9 SD) is significantly lower of that of *A. aculeatum* (14.4 m +/- 4.3 SD) (Mann-Whitney U p=0.001) (Fig. 1). There was a positive relationship between palm girth and height in *A. maripa* ($r_s$=0.304; p=0.001), while no such correlation is found with *A. aculeatum* ($r_s$=0.024; p=0.871). The low number of *A. aculeatum* trees, especially those of low height, hinders interpretation of the pattern found.

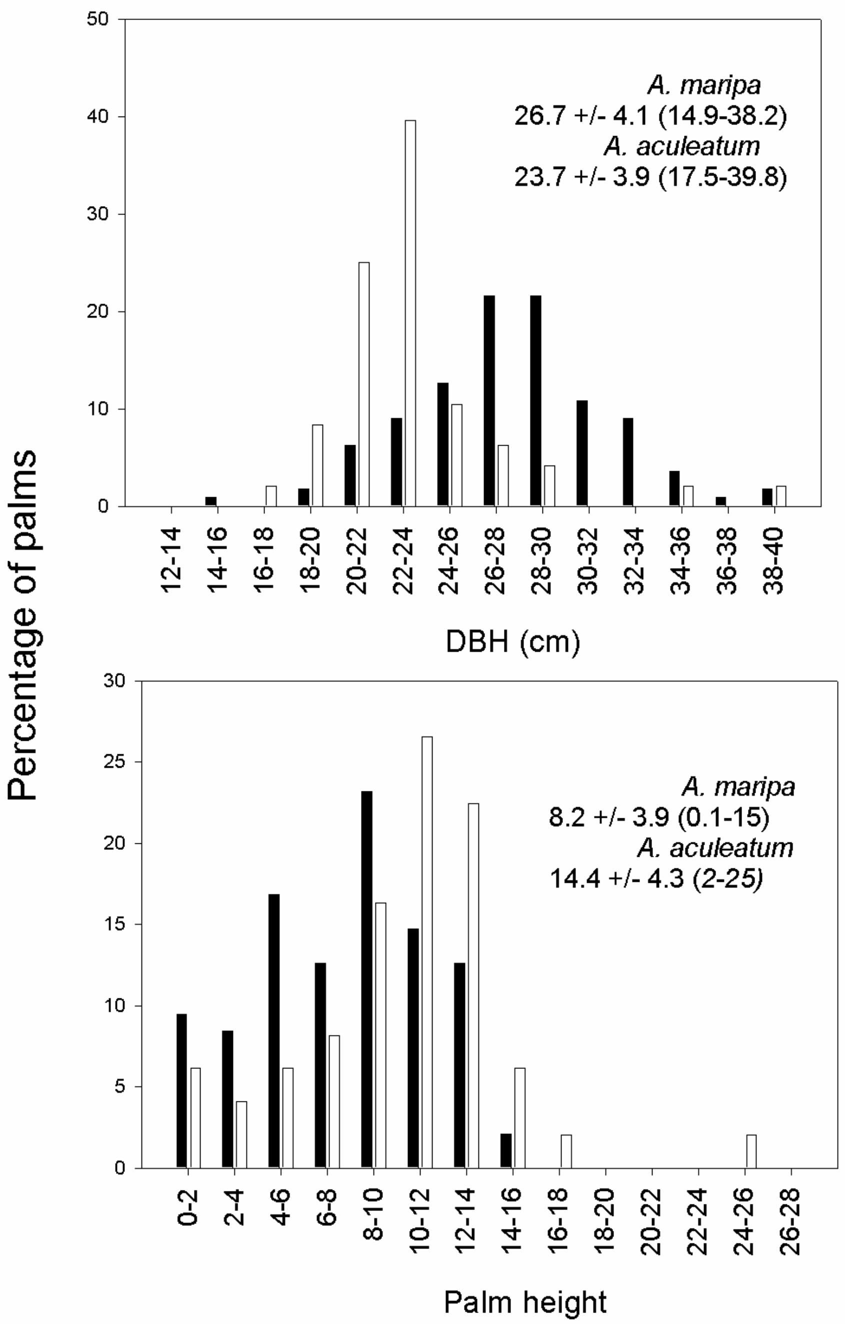

FIGURE 1. Frequency diagrams of the trunk DBH and height for 111 individual *A. maripa* (black) and 55 *A. aculeatum* (white) in the Pinkaití research station –Mean +/- SD (min-max).

Among the palms, which the reproductive development stage could be accessed, nonreproductive *A. maripa* were significantly shorter (2.4+/- 2.2 m; n=33) than reproductive ones (10.0+/- 2.6 m; n=213) (Mann-Whitney U, p=0.001). Non-productive *A. aculeatum* were also significantly shorter (4.4+/- 2.0 m; n=5) than reproductive ones (13.1+/- 4.3 m; n=36) (Mann-Whitney U, p=0.001). All the non-productive virgin palms were less than 9 m tall, while most of the reproductive ones where taller than such limit (Fig. 2).

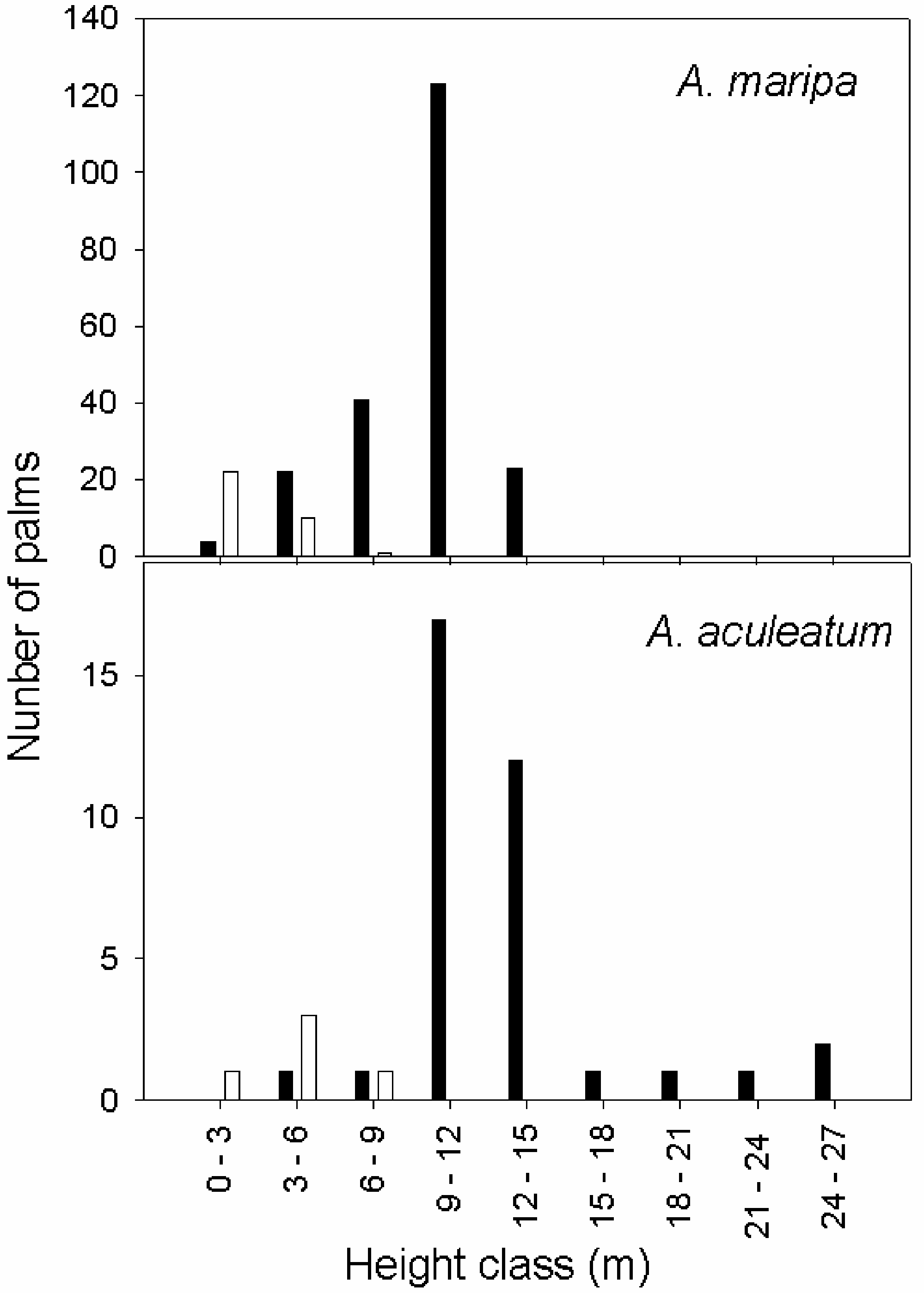

FIGURE 2. Frequency diagrams of reproductive stage and height of 246 individual *A. maripa* and 41 *A. aculeatum*. White and black bars represent, non-reproductive and reproductive palms, respectively.

Variations were found in the aspect and density of *A. maripa* and *A. aculeatum* stem sections, both from the border to the centre and from the lower to upper parts of the palm. Fibrous bundles were more abundantly found towards the stem periphery. Both *A. maripa* and *A. aculeatum* showed higher density of fibrous material at lower and external parts of their stems, a pattern which is more conspicuous for *A. maripa* than *A. aculeatum*. Density of *A. maripa* and *A. aculeatum* is higher towards both the lower and the external parts of the stem, a pattern that is substantially less clearly defined for *A. maripa* than for *A. aculeatum* (Fig. 3).

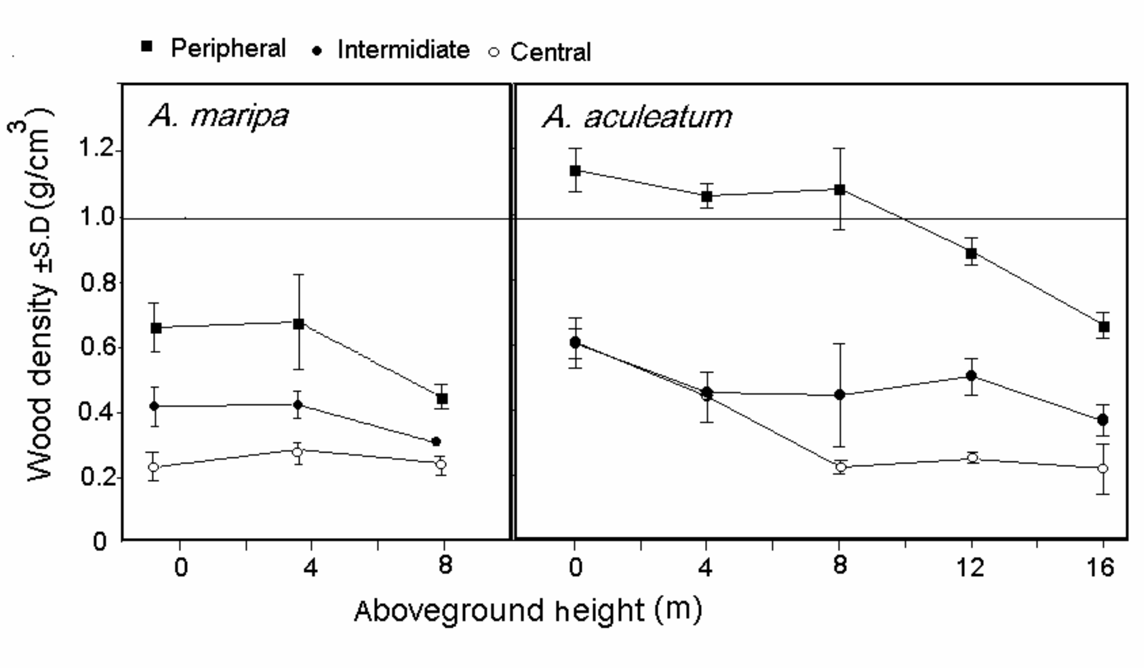

FIGURE 3. Distribution of stem tissue density in longitudinal section within a 8-m-tall *A. maripa* and a 16-m-tall *A. aculeatum.* Dry density is plotted as a function of height above ground for peripheral, intermediate and central stem tissue. Dry density is expressed as oven-dry weight over volume. N=9 for each position and height.

### 3.2 *Stem growth*

In the year period from April 1998 to April 1999, the mean number of new leaves (+/-SD) produced by *A. maripa* and *A. aculeatum* was 3.6+/- 1.5 (n=81) and 4.0+/- 1.5 (n=37). Because there was no significant correlation between palm height and the number of leaves produced for either species (*A. maripa*-$r_s$=0.183 p= 0.053; *A. aculeatum*- $r_s$=0.195 p= 0.128), the average values were used to estimate palm growth rate. As said in methods, dividing the number of leaf marks along the stem by annual leaf production rates allowed stem growth rates to be estimated. Stem growth rate is higher in *A. aculeatum.* Growth rates of both species decrease with height (Fig. 4). The rate of decrease however is initially higher for *A. maripa* and consequently the species takes significantly longer than *A. aculeatum* to reach 8 m height aboveground (Fig. 5, Chi-square value, p=0.006).

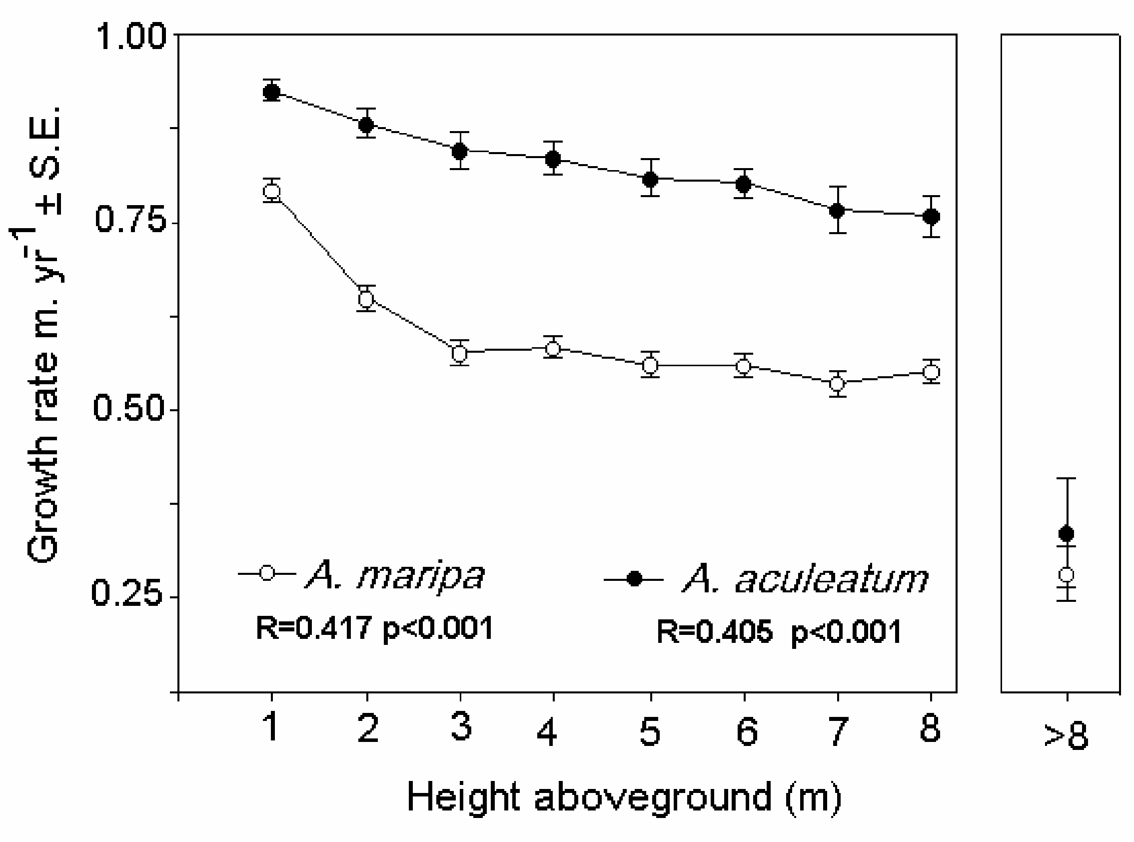

FIGURE 4. The relationship between growth rate and height of *A. maripa* and *A. aculeatum* at Pinkaití Site, Brazil. based on leaf scar per (m) and average production rates.

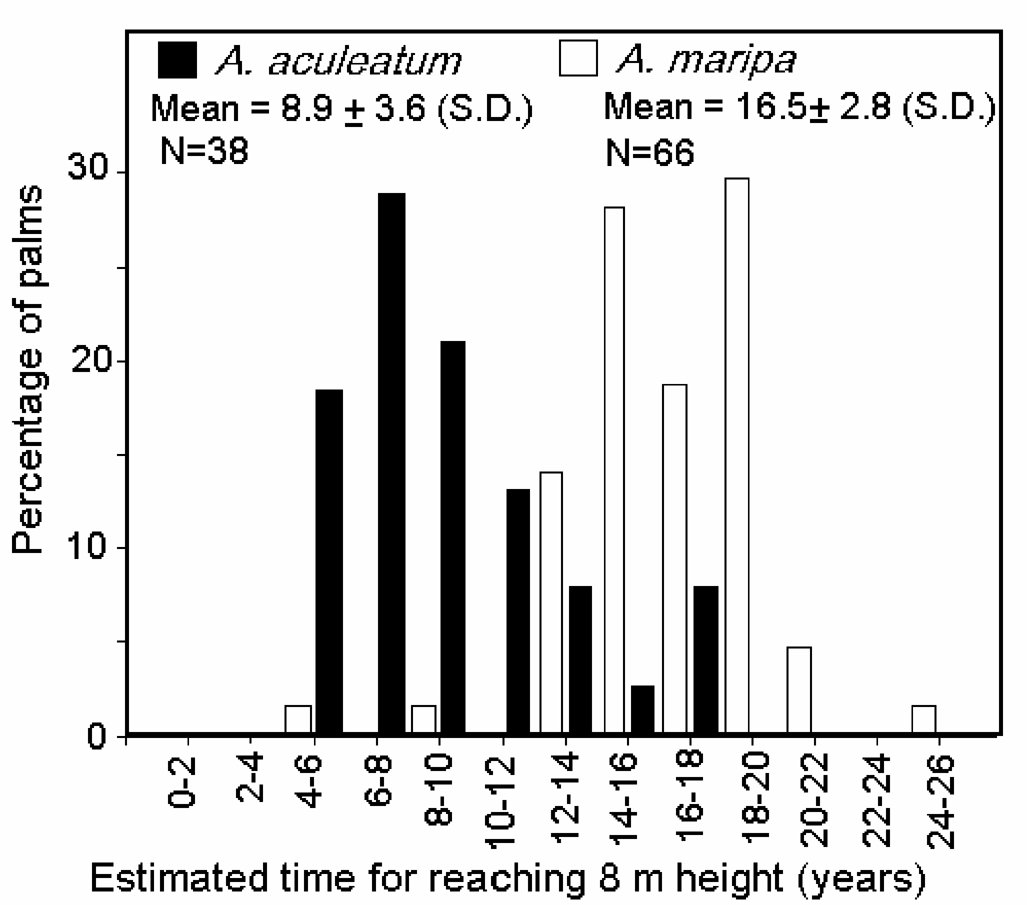

FIGURE 5. Frequency distribution of estimated time of stem development since emergence up 8 m height for *A. maripa* and *A. aculeatum* at the Pinkaití site, Brazil.

## 4. **Discussion**

Neotropical palms range widely from shade tolerant to needing high levels of light (Svenning 2001). For example, cloning, in tropical forest palms, is a strategy that allow specimens to grow and persist under highly shaded conditions by the physiological integration of ramets, allowing the distribution of resources, from sites of acquisition, to sites where the resource is scarce (Souza *et al*. 2003). Arborescent palms, in particular, become increasingly light-demanding with increasing size (de Granville 1992) and generally depend on large gaps for recruitment to the adult stage (Kahn 1986). J.-C. Svenning (1999) predicted that, if microhabitat niche differentiation is important for maintaining the species richness of the community, palms of similar growth form will show antagonistic microhabitat relationships. However, he could not find antagonistic patterns of microhabitat preferences among arborescent canopy palms.

The niche diversification hypothesis (Connell 1978) states that species coexist by occupying different niches. Because the arborescent palms *Attalea maripa* and *Astrocaryum aculeatum* are close relatives (both belong to the tribe cocoeae), are superficially similar, have comparable total leaf area, and comparable energy budget for their stem development, these species are likely to be direct competitors. However, the species coexist in vast areas of the core of the Amazonian region, where their distribution is superimposed (Henderson *et al.* 1995). The present work shows marked differences on the stem density and growth of these palms. Such differences, on palms of similar growth, through their probable implication for the species distribution, could be a large contribution to the "microhabitat niche differentiation" necessary for their stable co-existence.

The stems of *A. maripa* are significantly thicker than those of *A. aculeatum* and their DBH is weakly positively correlated with palm height. Such a relationship has been understood as evidence of capacity to increase in stem diameter by means of sustained cell expansion or primary cell division within the ground tissue (Corner 1964, Rich 1987a, 1987b, Waterhouse and Quinn 1978). It would be inappropriate to attach much meaning to the absence of a correlation between *A. aculeatum* stem height and girth, in light of the small sample size of short *A. aculeatum* trees in the sampling areas.

The range of density values of *A. maripa* and *A. aculeatum* stems covers a large part of the total observed variation in wood density values of Amazonian forest dicotyledonous trees, as predicted by Williamson (1984). Stem densities decreased in *A. maripa* and *A. aculeatum*, both from the stem periphery to the core and from the bottom to the top. Differences were found between the density patterns found across the stem of *A. maripa* and *A. aculeatum*. Stem density of *A. maripa* was substantially more homogeneous both from the centre to its external parts, and from the base of the stem towards the crown.

The results show that the stem growth rates of both *A. maripa* and *A. aculeatum* are higher at an earlier period after emergence from the ground level, compared to the late development period. On the other hand, the reproductive activity of palms of both species was lower at an earlier period after emergence from the ground, and increased at a later development period. Stem growth rate of *A. maripa* was high at the first metre of aboveground development, declining sharply from 1 to 2 m and then stabilising before substantially decreasing in taller palms at heights greater than 8 m. The stem growth rate of *A. aculeatum*, in turn, was higher when compared to that of *A. maripa* and had a smoother decline during the early development period, becoming similarly low at late maturity.

That stem density increases towards the stem periphery and the base has been reported to occur, to varying extents, among other arborescent palms (e.g. *Cocos nucifera*: Richolson & Swarup 1977, Sudo 1980, Killmann 1983, *Iriartea gigantea*, *Socratea durissima*: Rich 1987a). The finding that *A. maripa* stem density is much more homogeneous than that of *A. aculeatum* is also consistent with observations that palm tree species can range widely in the extent to which density varies across the stem (Tomlinson 1961, 1979, 1990, Zimmermann 1973, Rich 1987b, 1987a).

Within energetic constraints, stem density should be inversely related to stem growth, a relationship that holds among tropical forest trees (Richards 1952, Whitmore 1975, 1984, 1989, Fearnside 1997). The smaller differences in early and late growth rates of *A. maripa* stem, when compared to *A. aculeatum*, is likely to be directly related to the smaller differences in density patterns found across the stem of this species. A reduction in growth rate in mature to senescent palms has also been observed to be a common feature in palm tree species. Its adaptive value is likely to be related to both decreasing net benefits from greater luminosity and increasing probability of stem breakage in taller plants. Although the energetic costs associated with the reproductive activity of mature individuals might be a confounding variable (Corner 1964, Tomlinson 1990, Alvarez-buylla & Garay 1994, Alvarez-Buylla *et al.* 1996).

Sample size limitation, at the present work, hindered refinements on the relationships between environmental heterogeneity created by the vegetation and the density, structure and growth of the stems of each specie. However, the information available is enough to draw a broad picture of large arborescent palm developmental contrasts, and the main differences between *A. maripa* and *A. aculeatum*. At the Pinkaití site, palm trees, as a group, are more abundant in more open forests. The same pattern holds at the scale of the entire Amazon basin, as large arborescent palms are more frequently found in structurally open, seasonally dry forests, that predominate along the Southern and Eastern fringes of the region (Kahn & Granville 1992). However, forest structure does not seem to affect the abundance of *A. maripa* and *A. aculeatum* in the same way, since the abundance ratio of the former to the latter is increases with structurally more open forests (Salm 2002).

Large forest patches dominated by palm trees do not occur naturally in terra firme forest at the Pinkaití site. Indeed, palm-dominated forest patches in well-drained areas of Amazonia of a few to several hectares, seem to be related to past human disturbance (Ballée 1989, Ballée and Cambell 1990, Anderson *et al*. 1991, Kahn and Granville 1992). Numerous monodominant forest enclaves of 2-3 ha of *Attalea phalerata* (babassu) in the Brazilian State of Maranhão are often associated with old human settlement sites (Ballée 1984). In fragments of the Atlantic forest, in Southeastern Brazil, the presence of large disturbed sectors promotes the formation of large, continuous stands of the acaulescent palm *Attalea humilis* (Souza & Martins 2002).

The higher overall stem density of the shorter *A. maripa* palms, in comparison to *A. aculeatum*, give this species a wider structural safety margin during early stem growth. Such safety margin should make this species less likely to be fatally damaged by physical disturbance at an early stage. This is especially advantageous under the high disturbance regime that is typical of structurally more open forests like many parts of the Pinkaití forest. Despite having larger stem diameter, *A. maripa* seems to have a lower capacity to increase density later on during the stem development process, which is likely to make taller palms of this species more vulnerable to stem breakage. This could confer a further disadvantage for *A. maripa*, in relation to *A. aculeatum*, in more built-up, taller forests. Such patterns are consistent with the distributional contrasts of *A. maripa* and *A. aculeatum* across structurally distinct forests and could provide a mechanism for avoiding the competitive exclusion of either species across most of the Amazon.

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**Capítulo-6**

# A importância de perturbação para a regeneração da palmeira arborescente *Attalea maripa* em uma floresta Amazônica sazonal

# *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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http://www.biotaneotropica.org.br/v5n1/pt/abstract?article+BN00305012005

Abstract

# The importance of forest disturbance for the recruitment of the large arborescent palm *Attalea maripa* in a seasonally-dry Amazonian forest

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 ($7^{o}$ 46’S; $51^{o}$ 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 importância de perturbação para a regeneração da palmeira arborescente *Attalea maripa* em uma floresta Amazônica sazonal

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 ($7^o$ 46'S; $51^o$ 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 $27^o$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$^{-1}$.

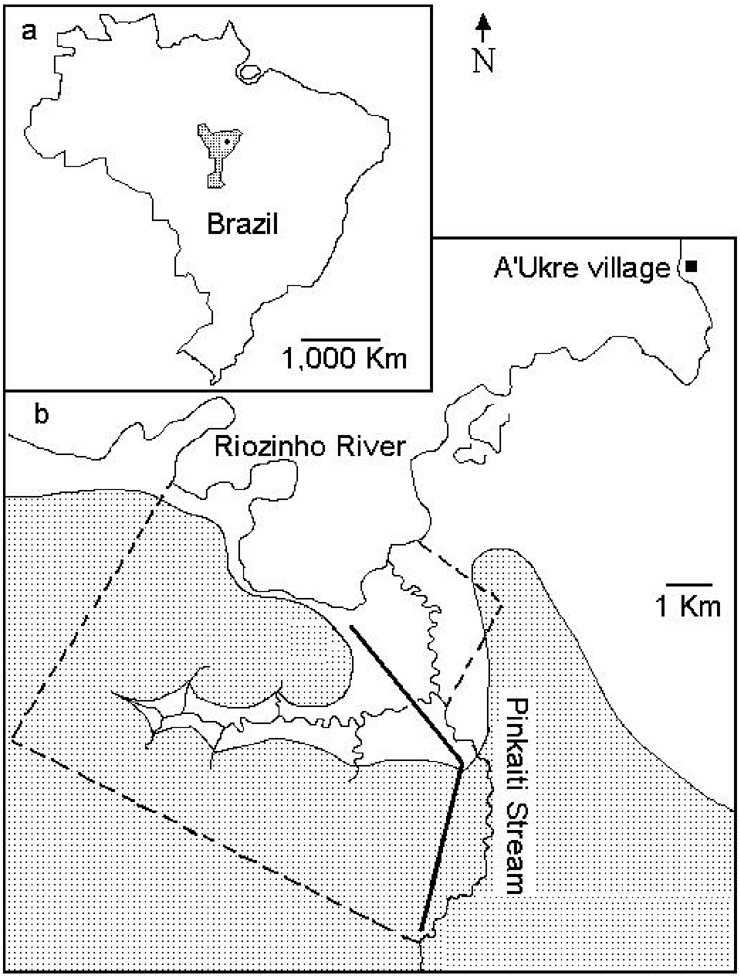

FIGURE 1. The study set up. (a) Within the map of Brazil, the block of Xingu indigenous lands (14,197,666 ha); the black dot indicates the Pinkaití site position (FUNAI 2004; adapted). (b) A'Ukre village position and the limits of the Pinkaití research station, presented by the Pinkaití stream and Riozinho 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.

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 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 ($\geq$ 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 ≥ 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 ± 2.4 S.D. individuals.0.15$ha^{-1}$), 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 ± 0.9 S.D. individuals.0.15$ha^{-1}$), 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).

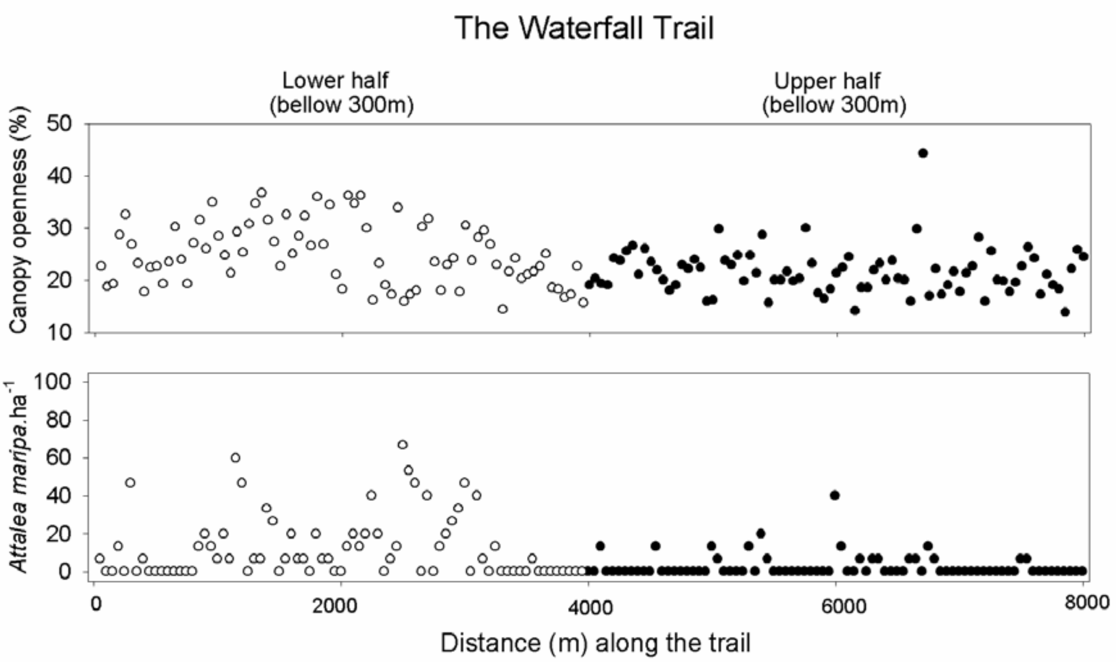

FIGURE 2. Percentage of canopy openness and density of *A. maripa* adults per hectare, along an 8,000 m trail, open and dense circles represent sampling units at lower and upper half of the trail, respectively.

## 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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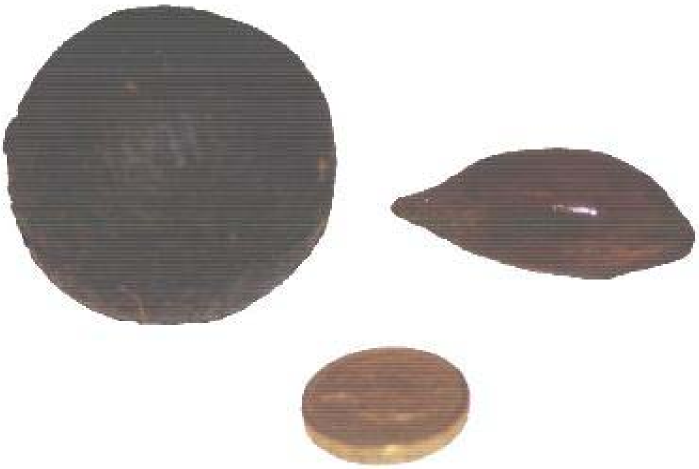
## **Capítulo-7**

# Morfologia de sementes e distribuição de plântulas de palmeiras arborescentes

## Arborescent palm seed morphology and seedling distribution

SALM, R. 2006 (in press). Arborescent palm seed morphology and seedling distribution. Braz. J. Biol. 66 (1).



# 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. Seeds of *A. maripa* were smaller and produced in larger numbers than those of *A. aculeatum*. *A. maripa* seeds also had a substantially lower amount of nutritional reserves, available for the embryo. *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 around reproductive conspecifics than that of *A. aculeatum*. The smaller seeds of *A. maripa* might be less attractive to scatterhoarding rodents (e.g. *Dasyprocta aguti*). The observed pattern emphasizes the importance of scatterhoarding rodents as dispersers of large-seeded plant species in Neotropical forests.

# 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.

## INTRODUCTION

Seed size and shape represent compromises between constraints associated with the most efficient means for packing the embryo reserves and for dispersing them (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 becoming an established, because they carry a larger nutritional reserves than small seeds. 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 that seeds can be dispersed. 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). Seed size is correlated with plant distribution and abundance, as small-seeded species exhibit a wide range of abundance and distribution, whereas larger-seeded species generally exhibit lower abundance and narrower distribution (Guo et al. 2000).

Vertebrate predation is generally believed to be a disadvantage for large seeded-species, however, presumably because large seeds represent a richer energy source and are more apparent to vertebrates than small seeds. Thus, the advantages of large reserves associated with large seeds could be offset by possible disadvantages in dispersal limitation and predation risks (Vander Wall 1990, Hulme 1993).

In tropical forest, tree species have been classified as pioneer or persistent based on the environmental conditions necessary for their successful establishment (Whitmore 1989). The adaptive value of seed size, seed number and the stored reserve associated with the embryo may be in conflict with one another to such an extent that reproductive efficiency in a particular habitat may depend upon a compromise between all such demands (Stebbins 1971). Species requiring open, luminous, or early successional habitats tend to have smaller seeds than those tolerating denser, darker or late successional habitats (Richards 1952, Harper et al. 1970, Denslow 1980, Foster & Janson 1985, Foster 1986).

In Neotropical forests, caviomorph rodents, such as agoutis (*Dasyprocta spp.*) and accouchis (*Myoprocta spp.*) are important seed predators of large-seeded species. However, because these rodents habitually scatterhoard their prey-seeds, but eventually fail to retrieve a small proportion of them, they also function as seed dispersers (Smythe 1978, Forget 1990, 1994, Forget & Milleron 1992, Forget et al. 2001, Peres et al. 1997). Caviomorph rodents have been described as important seed dispersers of neotropical large-seeded palms (Smythe 1978, Forget 1991, 1994).

The Amazonian large arborescent palm *Attalea maripa* (Aubl.) Mart. have tall, massive (>30 cm DBH), solitary stems with no spines. The fruits consist of a fibrous outer shell and a mesocarp pulp, which is somewhat viscous when immature. The seed is enclosed within a smooth woody shell yellowish-brown with a sharp point (Henderson et al. 1995). Almeida and Dantas da Silva (1997) describe *A. maripa* seeds as having 3-4 cm in length and 2 cm in diameter. The seeds typically have 2 kernels, but may have 1 to 3. These authors report on average moisture content of the fresh fruit at 33%. The dry fruit mass is on average of 18g and is comprised of an outer shell (16%), a mesocarp (26%), a woody inner shell (49%) and oily kernels (9%) (Almeida and 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), are armed, with 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 green- yellowish fruit of *A. aculeatum* palms consists of a farinaceous, dense, yellowish mesocarp pulp that surrounds a nearly black woody seed shell. The single kernel is white, oily and hard, and covered with an adhering brown testa (Pesce 1985, Almeida and 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 at a 16-ha grid system which crosses two areas with 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$^{o}$ 46’18”S; 51$^{o}$ 57’42”W), located along Riozinho River, a second-order tributary of the Xingu River, and taken to the Plant Anatomy Laboratory of the University of São Paulo (USP) for measurements. Seed length and width were measured to the nearest millimeter. Seed volume was estimated through 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, and fruits were counted and used for seed predation and seed dispersal experiments.

Seed shadow is not always spatially congruent with seedling distribution (Rey and Alcantara 2000). However, because of the practical difficulty in accessing seed shadow through direct means, I used the seedling distribution in relation to reproductive palms as a proxy measure. The palm seedling phase has been defined as the interval between germination and the exhaustion of the seed reserves (Tomlinson 1990). The seedlings of *A. maripa* and *A. aculeatum* differ morphologically and different arbitrary boundaries were set for their definition. *A. maripa* seedlings were defined as plants that had petioles of up to 7 mm in diameter measured at 10 cm from the ground. For *A. aculeatum* this cut-off was 4 mm at the same height.

The pattern of seedling distribution of *A. maripa* and *A. aculeatum* in relation to reproductive adults of each species was quantified within at a 16-ha section of a main grid system at Pinkaití. This grid system progresses from an open forest with high abundance of arborescent palms in its western portion to a more built up forest where palm trees were rare in its eastern portion. For the investigation of palm seedling distribution of each species in relation to the reproductive adults, the grid area was demarcated with flag stakes distributed every 25m, denoting subplots of 0.0625 ha. Within this area, all adult trees of each palm species were mapped and tagged. Every adult *A. maripa* and *A. aculeatum* palm was inspected thereafter for evidence of past reproductive activity, as indicated by the accumulation of old seed remnants underneath the crown. Here, the term “reproductive” is reserved for fruit-producing individuals, which excludes palms that may also be reproductive through pollen production from male flowers.

The spatial distribution of *A. maripa* and *A. aculeatum* seedlings were estimated with two different methodologies, due to marked differences in their abundance. *A. maripa* seedlings were more abundant than those of *A. aculeatum* and were sampled within 100 5x5m plots, which were regularly spaced across the grid system. Seedlings of *A. aculeatum*, on the other hand, were much rarer and could be exhaustively sampled throughout the entire grid system. Two previously trained and skilful field assistants carefully searched each 0.0625 ha plot, where all seedlings were located, and tagged and mapped then with a tape and compass in relation to the nearest grid stake.

## RESULTS

The elongated seeds of *Attalea* were significantly smaller than the globose seeds of *Astrocaryum* (t- test, $p<0.001$; Figure 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).

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

| | *Attalea maripa* n= 91<br>Mean ± S. D. (min.-max.) | *Astrocaryum aculeatum* n=12 |
|---|---|---|
| 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) |

The density of reproductive *Attalea* palms in the high-palm-density forest plots (26.2 trees.ha$^{-1}$) was significantly higher than that at 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 density of seedlings of this species and distance to reproductive *Attalea* trees ($r_s=-0.366$, $p<0.001$). Seedling abundance was positively correlated with the density of reproductive palms (10m: $r_s=0.221$, $p=0.014$; 20m: $r_s=0.290$, $p=0.002$; 50m: $r_s=0.284$, $p=0.002$). 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 (10m: $r_s=0.078$, $p=0.275$; 20m: $r_s=0.090$, $p=0.244$; 50m: $r_s=0.207$, $p=0.055$) or the low-palm-density (10m: $r_s=-0.180$, $p=0.256$; 20m: $r_s=0.179$, $p=0.144$; 50m: $r_s=0.253$, $p=0.061$) areas were considered.

The density of reproductive *Astrocaryum* trees in the high-density portion of the grid was significantly higher than at the low-palm-density side of the grid system (Mann-Whitney U, $p=0.013$). The seedlings of this species, in turn, were significantly less abundant at 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: $r_s =0.017$, $p=0.444$).

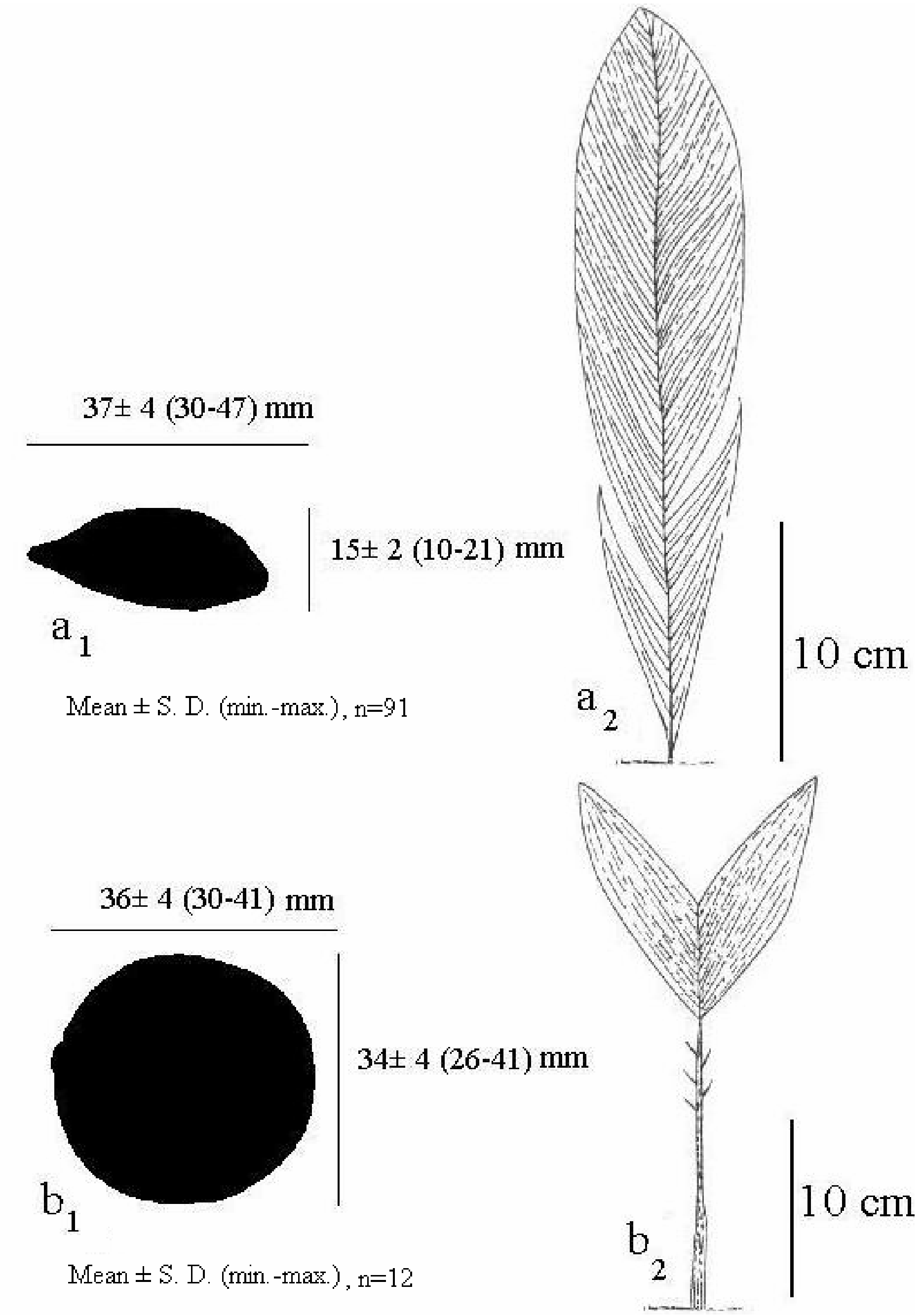


Figure 1. Aspect and dimensions of (a) *Attalea maripa* and (b) *Astrocaryum aculeatum* (1) seed and (2) seedling.

## 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 had up to three embryos each, while those of *A. aculeatum* invariably had only one.

Thus, *Attalea* seeds had a significantly smaller endosperm reserves available for the development of seedlings 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 the long-shaped seeds of *A. maripa* carry a smaller nutrient reserves but are also potentially ingested by some vertebrate species whereas seed dispersal of *A. aculeatum* is effectively restricted to scatterhoarding rodents.

Large quantities of *A. maripa* seeds were found in tapir (*Tapirus terrestris*) dung piles at Pinkaití, which is consistent with observations elsewhere in the Amazon (Bodmer 1990, Fragoso 1997). Seeds of *A. maripa* have also been found in tortoise (*Geochelone sp.*) faeces at this site (A. Jerozolimski, pers. comm.). The Kayapó Indians have also reported the presence of *A. aculeatum* seeds in tapir faeces. However, given the size of these seeds this is likely to be a much rarer event as no *A. aculeatum* seeds were found in a number of dung piles inspected, and whole seeds of this species are unlikely to be ingested by any other species.

The seedlings of *A. maripa* are widespread in *terra firme* forest areas at Pinkaití. The results showed that the seedlings of *A. maripa* 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 larger seed crop size, and the greater spectrum of animal dispersal agents may all explain such a difference. The findings of this comparative study, that seedlings of the smaller-seeded *A. maripa* are more 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* is at odds with the pattern 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 stronger mutualistic relationship with caviomorph rodents. Because larger seeds contain greater food reserves, scatterhoarding rodents preferentially remove large seeds and tend to disperse them farther (Vander Wall 1990). The finding that *A. aculeatum* have a substantially longer fruiting period than *A. maripa* is also consistent with the view that *A. maripa* is a generalist, opportunistic, species and that *A. aculeatum* is more specialized. 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 were scarce (Jorge 2000).

This study provides further support for the recognition of caviomorph rodents as especially influential in large-seeded plant dispersal because of their high relative abundance and widespread distribution. Burying seeds in diffuse caches potentially enhances plant recruitment by decreasing the probability of seed predation, and by actively promoting seedling establishment.

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### Capítulo-8

# Predação de sementes da palmeira amazônica *Attalea maripa* por invertebrados e vertebrados: implicações para o mecanismo de espaçamento de Janzen-Connell

## *Invertebrate and Vertebrate Seed Predation in the Amazonian palm* Attalea maripa*: Implications for the Janzen-Connell Spacing Mechanism*

SALM, R. Invertebrate and Vertebrate Seed Predation in the Amazonian palm *Attalea maripa*: Implications for the Janzen-Connell Spacing Mechanism. Submetido à Biotropica.

# ABSTRACT

Hypotheses for the maintenance of tropical forest tree diversity were tested with a system that includes the palm *Attalea maripa*, the beetle *Pachymerus cardo* and vertebrate predators of large seeds in a palm patch and its adjacent forest in Southeastern Amazon. Seed predation was affected by host-specificity degree of the animals involved. Seed survivorship depended on the distance from the palm-patch but was unrelated to distance from individual fruiting palms.

## RESUMO

Hipóteses para a manutenção da diversidade de árvores de florestas tropicais foram testadas com um sistema que incluí a palmeira *Attalea maripa*, o besouro *Pachymerus cardo* e vertebrados predadores de sementes, em um palmeiral e uma floresta adjacente, no sudoeste da Amazônia. A predação de sementes foi influenciada pelo grau de especialização dos animais envolvidos. Sua sobrevivência dependeu de sua posição em relação ao palmeiral, mas não esteve relacionada à distância de palmeiras em frutificação.

*Key words:* Attalea maripa, *bruchid, invertebrates, Janzen-Connell model,* Pachymerus cardo, *palms, seed predation, vertebrates*.

THE JANZEN-CONNELL MODEL (Janzen 1970, Connell 1971), since it was published, received considerable attention from ecologists (Howe & Smallwood 1982, Clark & Clark 1984). According to Janzen (1970), his model is an extension to the plant community, of Paine's (1966) proposition that local animal species diversity is related to the number of predators in the system and their "efficiency" in preventing a single species from monopolizing some limited resource. Indeed, several studies, recently reviewed by Leigh *et al.* (2004), show that increased activity of specialized pests in less seasonal climates seems to be a chief cause for the latitudinal gradient in tree diversity.

The importance of spatial scale for the maintenance of high diversity in tropical forests has long been acknowledged (Janzen 1970, Schupp 1992), but the Janzen-Connell model has been tested mainly at the so-called "agouti scale", at the level of individual trees (Fragoso 1997). However, the assumption that the seed predation patterns observed around adult individual trees can be used to predict the large-scale variation in adult density across the landscape is not necessarily true (Schupp 1992). In Maraca Island, Roraima (Brazil), for example, the abundant and widespread Amazonian palm *Attalea maripa* is highly aggregated. The study of the effects of seed dispersal by tapirs, *Tapirus terrestris*, and seed predation by bruchid beetles, *Pachymerus cardo*, revealed patterns that can only be understood at the scale of palm aggregations, meaningless in relation to individual trees (Fragoso *et al.* 2003).

The aim of this study was to test with field experimentation the predictions of Janzen's (1970) hypothesis for the high tree species diversity observed in tropical forests, and its spatial scale dependent component developed by Fragoso *et al.* (2003), against Hubbell's (1979) neutral theory of tropical forest dynamics, according to what, the species to what a tree belongs is irrelevant for its prospects of success. A system that includes the palm *A. maripa*, an invertebrate seed predator, the bruchid *P. cardo*, and a generalist guild of large-seed vertebrate predators was studied. The specific questions addressed in this study were: (1) how does seed predation vary between areas with high and low palm density? (2) Does distance to fertile conspecific adults affect the interactions between animals and seeds? And (3) how seed predation patterns are affected by the characteristics of the animals involved? The experimental design was chosen to test the effect of density of adult palms to interactions with seed predators, which includes an anthropogenically derived palm patch and adjacent undisturbed forest. Due to the trade-off that exists between the size of experimental units and replication, ecosystem-scale experiments often suffer from the absence of true replicates (Carpenter *et al.* 1998). Thus, rather attempting to test a null hypothesis the contrasts between the adjacent forests were compared to the propositions of the three models.

Field experimentation focused on a system that includes the widespread Amazonian palm, *A. maripa*, the host-specific bruchid beetle *P. Cardo*, and a guild of vertebrate predators of large well-protected seeds. We take advantage of a secondary, palm-rich forest patch (hereafter, *palmeiral*), adjacent to an old-growth forest where palm trees are rare, to evaluate the effects of vertebrate and invertebrate seed predators under different densities of fruiting palms.

Adult palms of *A. maripa* are tall (10 to 15 m in height) and have massive (>30 cm in DBH), solitary stems (Uhl & Dransfield 1987). Its infructescence is large and contains one to three thousand ovoid, drupaceous fruits (Fragoso 1997). The seed is enclosed within a hard woody shell, which is sharply pointed and has a smooth surface yellowish-brown in color, 3-4 cm in length, and 2 cm in diameter. Underneath the external shell, the pulp is oily and highly nutritive (Almeida & Dantas da Silva 1997).

The distribution of *A. maripa* is circumscribed to the Amazon region, and it is most abundant in the peripherical seasonally-dry forests (Uhl & Dransfield 1987, Henderson *et al.* 1995). In terra firme forests, the species is not naturally dominant over large areas, but often abounds on secondary forests (Kahn & Granville 1992). Patches of *A. maripa* are often encountered in remote, indigenous areas in the Xingu River basin (May *et al.* 1985).

Large-seeded palms have high seed predation rates by bruchid beetles during both pre-and post-dispersal stages (*e.g.*, Janzen 1971: *Attalea rostrata*, Kiltie 1981, Terborgh *et al.* 1993: *Astrocaryum macrocalyx*, Wright 1983: *Attalea butyraceae*, Smythe 1989: *Astrocaryum standleyanum*, Forget 1991: *Astrocaryum paramaca*, Fragoso 1997, Fragoso *et al.* 2003: *Attalea maripa*, Wright & Huber 2001: *Attalea butyraceae*). The beetle larvae invades the seed and feeds exclusively of its nutrient reserves up to maturity. Bruchids are seed predators that maximize the probability of successful reproduction in seeds by distinguishing uninfested seeds and dispersing their eggs uniformly among them (Wright 1983). Most studies show that bruchid predation is positively related to the density and distance to their prey-seed fruit-bearing trees (Wright 1983, Smythe 1989, Terborgh *et al.* 1993). However, opposite patterns, with negative relationships of bruchid attack and densities of fruit-bearing species have been recorded, suggesting that such predators may become satiated under certain fruit hyper-abundance conditions (Cintra 1997).

Rodents, peccaries (*Tayassu* spp.), deer (*Odocoileus virginianus* and *Mazama* spp.) eat the pulp of *A. maripa* fruits and spit out intact seeds, virtually all of then, within 25 m from the parent (Fragoso 1997). Tapirs (*Tapirus terrestris*), on the other hand, are specially important for this species because they are the only species capable of swallowing a large number of whole *A. maripa* seeds, often defecating them intact at distant sites (Fragoso 1997, Fragoso & Huffman 2000). At Maracá Island, Roraima, Brazil, where *A. maripa* occurs in large monodominant patches, the larvae of the bruchid beetle *P. cardo* killed most of seeds remaining near parent trees but virtually none of the seeds dispersed by tapirs to latrines away from the nearest palm clump (Fragoso 1997). A mesoscale map compiled from aerial photography, satellite imagery, and air- and ground-truthing revealed that *A. maripa* clumps are associated with tapir latrine sites, suggesting that long-distance seed dispersal by tapirs is important for the generation of palm patches and forest dynamics (Fragoso *et al.* 2003).

This study was undertaken within the Kayapo Indian Area, south-eastern Brazilian Amazonia. The Pinkaiti site ($7^{o}$ 46’18”S; $51^{o}$ 57’42”W) is located along the Riozinho River, a second-order tributary of the Xingu River. The terrain is characterized by a series of rocky ridges and granite outcrops interspersed with flat lowland river and stream valleys. Annual rainfall is close to 2000 mm with nearly no rain falling from June trough September.

The seasonal variation in fruit production was examined through observations of 58 *A. maripa* palms. Observations were conducted monthly from July 1998 to June 1999. Reproductive parts were identified as buds, flowers, immature or mature fruits. *A. maripa* reproduction was highly synchronous with a single annual period of fruit maturation and falling. Peaks of flowers, immature fruits and mature fruits followed a peak of buds. Mature fruits, eaten by animals or falling from the infructescence, were found from December to February.

The investigation of the consequences of different densities of fruiting *A. maripa* to seed predation probability was conducted in an area of contact between a patch of high palm-density forest (*palmeiral*) and its adjacent forest matrix with much lower palm density. According to the Kayapo Indians (U. Kayapo, pers. comm.) the *palmeiral* was an area cleared for subsistence crops (*roças*) and abandoned in the first half of last century. This high palm-density forest patch, that happens to be plainly visible from a 250-m high granitic outcrop, makes a fairly clear limit with a forest matrix where palm trees were much less evident. This limit was used as a reference to the establishment of a 16-hectare (800 x 200 m) grid system, half within the *palmeiral* and half in an adjacent, old-growth, palm-poor forest. All adult *A. maripa* trees were mapped with reference to trail flags marking the intersections of 25 x 25 m divisions across the whole study grid. A total of 358 *A. maripa* adult palms (44.7 ind. $ha^{-1}$) were located within the *palmeiral* at the western half of the grid system and only 29 palms (3.6ind. $ha^{-1}$) were found at the adjacent undisturbed forest. During the seed predation experiments, set at the second half of the palms fruit dropping period (February 1999), all adult palms within the grid system were systematically inspected every 10 days for fruit presence. It was found an average of 13.9 and 0.9 fruiting trees per hectare in the *palmeiral* and mixed-forest area, respectively, at the 1998-1999 fruiting season.

Seed predation experiments were conducted in 32 seed stations, each $\geq 50$ m from one another, placed along two 800-m long parallel trails that crosses the length of both high and low-palm-density portions of the forest plot. The distance to the nearest fruiting palm and the density of fruiting palms within 25 m radius, of the seed stations, were calculated from the mapped palms in the study grid. At each one of the 32 seed stations 10 *A. maripa* seeds were placed under iron mesh exclosures (with 30 cm of radius, 40 cm high and 1 cm of mesh-size), which allowed access to beetles but not to vertebrates. The experiment was repeated three times, on the 10th, 20 th and 25 th of February 1999, and a total of 960 *A. maripa* seeds were used. Because *A. maripa* fruits which are handled by vertebrates have a higher probability of infestation by bruchid eggs (Silvius & Fragoso 2002), to maximize oviposition probability, the exocarp and mesocarp of all experimental fruits were partially removed with a knife, simulating the vertebrates handling effects. The presence or absence of bruchid eggs on the seeds was checked 5 days after the seeds were placed in the seed stations. Ten infested seeds of *A. maripa* were taken to the laboratory and kept until adult emergence. Based on the observation of five adult specimens, S. Vannin from the Zoology Department at the University of São Paulo (IB-USP) identified the bruchid beetles as *P. cardo*.

To quantify the variation in vertebrate that dig into soils to eat the seeds of *A. maripa*, a total of 512 seeds were buried in groups of 16 at each of the 32 seed stations. At each seed station the seeds were buried individually into 3-5 cm deep soil pits to simulate a typical agouti scatterhoarding pattern. The pits were placed at the extremes of a 50 x 50 cm cross facing the cardinal directions, centered at four flags distant at least 2 m from another. The method, that allowed the precise location of cached seeds ensured that no seed was considered lost because they were not found as opposed to how many were actually removed. The seeds were cached in February 1999 and their presence and state or absence examined 7 months later (September 1999).

Seeds removed by rodents may have been recached but, because I could not follow seeds, I assumed that removed seeds were predated. Another possible confounding variable is that since the 16 ha grid is approximately twice the size of a home range of an agouti (Silvius & Fragoso 2003), one animal can have access to more than one station. Indeed, the home range of a radio-tracked agouti, living more or less at the center of the study plot was seasonally highly variable. It ranged from 6 hectares in July, at the top of the dry season, when fruits are scarce in the forest to only 1 hectare, in February, coinciding with A. maripa fruiting period (Jorge & Peres, in press), as observed elsewhere in the Amazon (Silvius & Fragoso 2003). Still, while the sampling scheme necessarily excludes the large parrots that also prey upon A. maripa seeds, we did not determined if rodents or actually white-lips (T. pecari) removed the seeds.

Nonparametric Spearman-$r_s$ correlations were used to investigate the relationship between the rates of invertebrate and vertebrate mediated seed predation upon *A. maripa* seeds and distance from fruiting trees. Correlations were considered significant at the 0.01 level (1-tailed).

*P. cardo* egg infestation upon all 320 seeds at each five-day experimental period increased from 2.5 to 9.1 and 31.9% at the three examined periods. Seeds were infected with high probability within the *palmeiral* and infestation dropped to nil towards the mixed non-palm forest. However, within the *palmeiral*, no significant correlation was found between infestation by *P. cardo* on seeds and distance to fruiting palms of this species (Period-1: $r_s$=0.087, $p$=0.375, n=16; Period-2: $r_s$=0.292, $p$=0.136, n=16; Period-3: $r_s$=0.125, $p$=0.322, n=16). The results of the seed predation by vertebrates was opposite. Virtually all seeds experimentally buried at the mixed non-palm forest were removed. Within the *palmeiral* there was no correlation between the odds of a seed being removed by vertebrates and distance to fruiting palms ($r_s$=0.009, $p$=0.487, n=16).

Within the *palmeiral*, the *P. cardo* seems to be an efficient predator (*sense* Paine 1966) of *A. maripa* seeds, as found by other studies of bruchids whose larvae are parasitic of palm seeds (Janzen 1970, Wright 1983, Smythe 1989, Cintra 1997, Fragoso 1997, Silvius & Fragoso 2002, Fragoso *et al.* 2003). The independence of bruchid *P. cardo* oviposition probability upon individual *A. maripa* seeds and the density or distance to fruiting adults of this palm suggests that the beetles search seeds thoroughly within a palm-rich forest patch. Indeed, beetle eggs were found even beyond the limits of the *palmeiral*, but this dropped to nil towards the palm-poor undisturbed forest only after a few tens of meters from the last scattered adult palms that surround the palm grove.

The studied case of bruchid predation on *A. maripa* seeds contradicts Hubbell's theory (1979) as the result show that the prospects of mortality of *A. maripa* seeds are much affected by their distribution in relation to the distribution of adult reproductive adults of this specie. The result is consistent with findings that, where palm distributions are clumped, survival rates of *A. maripa* seeds from bruchid predation is dependent on the seeds position in relation to aggregations, rather than at the scale of individual trees (Fragoso *et al.* 2003). The pattern fits the behavior of "density –responsive" seed predators, that search seeds at densities above a profitability threshold, independent of their distance from parent trees (Janzen 1970).

As predicted by Janzen (1970), agoutis, the vertebrate species that probably removed most of the cached *A. maripa* seeds, seems to be an inefficient predator of palm seeds. The rodents apparently become satiated by the seasonal abundance of nutritive resources at the *palmeiral*, which contrasts to the general scarcity of the adjacent undisturbed forest, where the fruits are searched thoroughly. Indeed, acting as seed predators, agoutis may actually contribute to making *A. maripa* even more clumped, allowing for a lower number of tree species in that part of the forest.

Peres *et al.* (1997), studying Brazil-nuts (*Bertholletia excelsa*) seed predation by agoutis at the same site, also found variation in relation to tree density at the scale of tree-patches rather than in relation to individual trees. However, while we found that *A. maripa* seeds were predated by rodents at lower probability at the palm grove, Brazil-nuts, in contrast, were removed at higher levels within high-density conspecific patches. This may have been due to differences in rodent search behavior or population density. Complication is added because, while being seed predators, agoutis are also important palm dispersors (Smythe 1989, Forget 1991). The net effect of rodents upon the distance between parent trees and recruits will depend on the rate of cached and recovered seeds (Forget *et al.* 2002).

Imposing strong mortality on *A. maripa* seeds, the bruchid beetle *P. cardo* may hinder the palm tree to keep the monopoly of space at *palmeiral* allowing other species to grow. Conclusions about *A. maripa* population dynamics based on a sample size of 1 are necessarily tentative but following strong forest disturbance, the growth rate of trees is expected to decline with forest maturation (Vandermeer *et al.* 1998). *A. maripa* was not the most abundant tree species within the *palmeiral. Metrodorea flavida* (Rutaceae) outnumbered the palm in number of adult stems in this gird and species like *Tetragastris altissima*, *Theobroma speciosum* and *Protium* spp., are found in high densities at this forest patch (Salm 2004).

In conclusion, the prospects of palm seed mortality due to the action of the invertebrate and the vertebrate predators was strongly affected by its position in relation to the areas of with high or low palm density, but distance to fruit-producing conspecific adults did not affect the interactions between animals and seeds. These findings corroborate studies of *A. maripa* seed ecology elsewhere in the Amazon (Fragoso 1997, Fragoso et al.

2003). The result also suggests that seed predation patterns are much affected by the characteristics of the animals involved, specially, their degree of host-specificity, as predicted by Janzen (1970) in his theory for the higher number of tree species in wet lowland tropical forests compared to temperate-zone forests.

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## Capítulo-9

# Considerações finais

## *Considerações Finais*

Desmatamentos na Amazônia geralmente levam à extinção da fauna, erosão do solo e desertificação (FEARNSIDE, 1999; NEPSTAD et al., 1999). Entretanto, o palmeiral que se desenvolveu sobre a velha roça abandonada, onde hoje fica a base de pesquisas do Pinkaití, ao invés de uma área degradada, destaca-se pela sua utilidade para a população local, devido à caça que sustenta, e também porque folhas de palmeiras são fundamentais para a construção do telhado de suas casas tradicionais. O experimento ecossistêmico (*sensu* CARPERNTER, 1998) realizado, examinando aspectos do modelo da importância de palmeiras arborescentes de grande porte para a dinâmica das florestas amazônicas sazonalmente secas, revelou que floresta secundária do palmeiral destaca-se também pela sua alta diversidade de árvores e progride, tanto em sua composição quanto em sua estrutura física, para a maturidade.

Os resultados apresentados no **Capítulo-4** mostram que o Pinkaití tem grande heterogeneidade na estrutura e composição da floresta, associada com características bióticas das espécies arbóreas mais importantes, perturbação natural e histórico de uso do solo, como outras florestas sazonalmente secas (CAMPBELL et. AL. 1989, PIRES e PRANCE 1985). Palmeiras arborescentes de grande porte destacam-se, e caracterizam a floresta secundária que cresceu sobre a roça abandonada de tal forma que ela é conhecida como "palmeiral". Entretanto, o presente estudo demostrou que o palmeiral é apenas moderadamente dominado pela palmeira *Attalea maripa*, tem alta diversidade de espécies arbóreas e é floristicamente semelhante às florestas primárias da área de estudos. A altura média da floresta no palmeiral não é significativamente diferente da floresta adjacente, mas sua natureza successional é evidente em sua reduzida área basal, mesmo para os limites naturais considerados para florestas de lianas (PIRES e PRANCE, 1985). Sob o ponto de vista do Modelo, o palmeiral encontra-se na transição do estado de regeneração para a maturidade, conforme o esquema descrito por VANDERMEER et al. (1998).

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O crescimento das palmeiras permitiu a elevação da altura do dossel e sombreia o interior da floresta que se reconstitui. Os resultados do **Capítulo-5** mostraram que, uma vez que as palmeiras *A. maripa* e *Astrocaryum aculeatum* concluem sua fase de estabelecimento, seu caule cresce em altura rapidamente, reconstituindo a cobertura florestal. Porém, a análise comparativa indicou que as duas espécies diferem em aspectos significantes da organização e do crescimento de seu caule, com prováveis implicações para a distribuição destas espécies em florestas estruturalmente distintas. A taxa de crescimento do cause de *A. maripa* tem um declínio forte nos primeiros três metros e estimamos que esta espécie demore significativamente mais que *A. aculeatum* para atingir oito metros de altura. Acima desta altura o crescimento do caule de ambas as espécies declina fortemente. O estudo da densidade do caule, uma medida de força, feita com o caule de um indivíduo de cada espécie, sugere que *A. aculeatum* tem crescimento mais íngreme na densidade do caule tanto das suas partes internas para as externas assim como do topo para a base do caule. Comparando palmeiras com orçamentos energéticos semelhantes, conferidos por copas adultas, taxas de crescimento mais elevadas implicariam em menor investimento em estrutura, revelado por menor densidade do caule (RICH, 1987). É possível que palmeiras *A. aculeatum* baixas tenham o caule mais frágil que os de *A. maripa.*

As diferenças encontradas têm implicações ecológicas relevantes para o Modelo, uma vez que um crescimento do caule inicial mais rápido é importante para a palmeira ascender sua copa mais rapidamente, acompanhando a regeneração da clareira. Isto é especialmente vantajoso nas florestas densas onde as clareiras são menores (KAHN, 1986) e a vantagem de crescer em altura maiores, comparado com as florestas abertas. Porém, se um crescimento mais rápido do caule implica na produção de estruturas mais frágeis, palmeiras que crescem mais rápido terão uma probabilidade maior de serem mortas quando atingidas por galhos ou árvores caindo. A fragilidade é mais grave em florestas abertas, onde a perturbação é mais intensa do que nas matas densas (RADAM, 1974). As limitações impostas pelo desenvolvimento e estrutura do caule poderiam explicar, em parte, a distribuição mais ampla de *A. maripa*, em relação a *A. aculeatum*, em direção às florestas sazonalmente secas, onde formações abertas substituem as florestas densas (KAHN e GRANVILLE, 1992). Na base do Pinkaiti, no limite de distribuição da floresta amazônica, *A. maripa* é aproximadamente dez vezes mais abundante que *A. aculeatum*.

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No **Capítulo-6**, quando a hipótese de que a perturbação florestal é importante para o recrutamento da palmeira arborescente de grande porte *Attalea maripa* foi testada, verificou-se que as palmeiras foram quase cinco vezes mais abundantes nas baixadas na base de pesquisas do Pinkaití, cuja floresta teve um dossel 14,8% mais aberto que aquele das terras altas, apoiando a hipótese de que perturbação é importante para seu recrutamento. Assim, o estudo confirma estudos clássicos (SPRUCE, 1871; DE GRANVILLE, 1992; KAHN e CASTRO 1985; KAHN, 1986, KAHN e DE GRANVILLE, 1992) e contraria trabalhos recentes sobre a questão (SVENNING, 1999).

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A comparação das estratégias reprodutivas de *A. maripa* e *A. aculeatum*, feita no **Capítulo-7**, também revelou diferenças relevantes para o Modelo. As sementes de *A.*

*maripa* são menores, produzidas numero mais alto e têm bem menos reservas, disponíveis para o embrião que as sementes de *A. aculeatum.* Não foi surpresa a constatação de que na área de estudos, plântulas de *A. maripa* são encontradas em densidades bem mais altas que aquelas de *A. aculeatum*, pois estão presentes, em maiores ou menores densidades por virtualmente toda a floresta. As sementes de *A. maripa*, menores, podem ser dispersas via intestinal por antas (FRAGOSO, 1997) ou mesmo jabutis (JEROZOLIMSKI, 2005) enquanto que as sementes de *A. aculeatum*, por serem bem maiores, não podem ser deglutidas por nenhuma das espécies da fauna local. Porém, na escala espacial considerada, a chuva de sementes de *A. maripa* estimada foi mais restrita nas proximidades de palmeiras desta espécie que aquelas de *A. aculeatum*. O resultado contradiz padrões estabelecidos para plantas com sementes de uma forma geral, segundo os quais, espécies com sementes maiores têm chuvas de sementes mais restritas (HARPER, et al. 1970; FENNER, 1985) e pode ser explicado com particularidades dos serviços de dispersão de sementes providos por roedores que praticam a estocagem difusa de sementes, nominalmente cotias, *Dasyprocta aguti* (FORGET, 1990; 1991; 1994; SMYTHE, 1978). As sementes menores de *A. maripa* devem ser menos atrativas para cotias e assim, geralmente mais negligenciadas ou levadas a distancias menores que as sementes de *A. aculeatum.*

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Os resultados do **Capítulo-8** demonstram uma intensa predação de sementes da palmeira *A. maripa* por besouros bruquídeos, *Pachymeris cardo*, no palmeiral onde a palmeira é abundante, que desaparece por completo a algumas dezenas de metros do palmeiral, sugerindo que estes insetos são eficientes (sensu PAINE, 1966) em limitarem a densidade das palmeiras, conforme previsto pela hipótese de Janzen-Connell (JANZEN, 1970; CONNELL, 1971). O resultado, também encontrado por outros autores que estudaram o problema (WRIGHT, 1983; TERBORGH et al. 1993; CINTRA, 1997; CLARK e CLARK, 1984; FRAGOSO, 1997; HARMS e DALLING, 2000) tem implicações fundamentais para o modelo do papel das palmeiras na dinâmica das florestas sazonais, pois os insetos permitem a substituição do dossel dominado por palmeiras pelas espécies de árvores típicas da floresta madura. A eficiência do besouro deriva de seu elevadíssimo grau de especialização, comum apenas entre os invertebrados, que constituem a maior parcela da biodiversidade tropical (TERBORGH, 1992).

* * * * *

O deslocamento dos caboclos pelos índios e o abandono de seus campos de cultivo à sucessão florestal, a poucas centenas de metros da base de pesquisas do Pinkaití, em uma matriz de florestas ecologicamente prístinas, é um valioso experimento natural. Sua importância advém da raridade da tendência, oposta aos padrões que dominam a região amazônica, possibilitado pela extensão e estado de preservação das terras dos Kayapo (ZIMMERMAN, et al. 2001).

Este estudo comprovou que o uso do modelo da importância de palmeiras arborescente de grande porte na dinâmica das florestas amazônicas sazonalmente secas é apropriado e gratificante para a investigação da ecologia de palmeiras e da regeneração destas florestas tão ameaçadas. Apoiado no Modelo, o experimento ecossistêmico, desenvolvido no palmeiral e na floresta primária adjacente, contribuiu para a elucidação de aspectos relevantes da dinâmica florestal. A regeneração da floresta sobre a roça abandonada demonstra que a recuperação de áreas desmatadas é possível e pode ser relativamente rápida, desde que preservados os dispersores de semente e a fonte de sementes de espécies de árvore típicas da mata madura.

Devido ao destacado papel ecológico e ao potencial econômico das palmeiras arborescentes de grande porte, é difícil superestimar sua importância em projetos de recuperação das florestas amazônicas sazonalmente secas.

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## **Anexo:** Legenda das fotos das capas dos capítulos

- **Capítulo-1:** Em cima, à esquerda, *Pilha de toras em uma madeireira em Redenção* (Rodolfo Salm); em cima, à direita, *Castanheira (Bertholletia excelsa) morta pelo fogo em pastagem* (Rodolfo Salm); embaixo, à esquerda, *Ôkiabôro, Cacique Geral dos Kayapó, discursando na Câmara dos Deputados* (Nefertiti Hass), embaixo, à direita, *Vista aérea do Rio Riozinho, próximo à aldeia A'Ukre* (Claudia Baider).
- **Capítulo-2:** Em cima, à esquerda, *Geonoma baculifera* (Rodolfo Salm); em cima, à direita, *Euterpe precatoria* (Rodolfo Salm); embaixo, à esquerda, *Jovem de Socratea exorrhiza* (Rodolfo Salm), embaixo, ao centro, *Bactris acanthocarpa com frutos* (Rodolfo Salm), embaixo à direita, *Astrocaryum gynacanthum* (Rodolfo Salm).
- **Capítulo-3:** Palmeiras *Attalea maripa* e *Astrocaryum aculeatum* na beira do Rio Riozinho (Rodolfo Salm).
- **Capítulo-4:** Em cima, à esquerda, *Bertholletia excelsa* (Claudia Baider); em cima à direita, *Attalea maripa* (Claudia Baider); embaixo, à esquerda, *Bixa sp.* (Claudia Baider); embaixo à direita, *Espécie não identificada* (Claudia Baider).
- **Capítulo-5:** À esquerda**,** *Caule de Astrocaryum aculeatum na base de pesquisas do Pinkaití* (Claudia Baider), à direita, *Caule de Attalea sp. no Jardim Botânico do Rio de Janeiro* (Rodolfo Salm)**.**
- **Capítulo-6:** *Vista aérea clareira da base de pesquisas do Pinkaití, Terra Indígena Kayapó, Pará* (Adriano Jerozolimski).
- **Capítulo-7:** Em cima, sementes de *Astrocaryum aculeatum* (esquerda) e *Attalea maripa* (direita) diante de moeda de uma Libra (Rodolfo Salm); embaixo, à esquerda, *Dasyprocta sp.* (Maria Luísa Jorge), embaixo, à direita, *Tapirus terrestris* (Carlos Peres).

- **Capítulo-8:** *Vista aérea da floresta no território da aldeia A'Ukre* (Claudia Baider).
- **Capítulo-9:** Em cima, à esquerda, *Mulheres da Aldeia A'Ukre dançando* (Adriano Jerozolimski), *Homens da Aldeia A'Ukre dançando* (Adriano Jerozolimski), embaixo à esquerda, *Criança Kayapó vestida para festividade* (Maria Luísa Jorge), embaixo à direita, *Neném Kayapó* (Adriano Jerozolimski).