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Aspectos da Dinâmica de Populações da Palmeira *Attalea humilis* Mart. ex. Spreng. em Fragmentos de Floresta Atlântica Sujeitos ao Fogo

Orientador: Dr. Fernando Roberto Martins

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CONTEÚDO

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Como a maioria dos trabalhos científicos, esta tese é o produto final do esforço direto e indireto de várias pessoas. Em primeiro lugar, ela não teria sido possível sem o apoio e ajuda constante de meus pais Paulo e Tânia, aos quais eu tanto devo. A idealização do projeto coube à Dra. Dalva M. Silva Matos, que foi também responsável pelo desenho amostral e pela grande realização que foi a criação e execução do projeto sobre o efeito da fragmentação nas populações vegetais em Poço das Antas (RJ). A coleta de dados foi feita dentro deste projeto maior, e só foi possível graças a ajuda de vários colegas: Flávio N. Ramos, Filipe Caluca, Mariana C. Torres, Ludmila P. Siqueira, Janduí Amorim, Antonio M. Rosa e do Dr. Luiz F. L. Duarte. O financiamento da Fundação O Boticário de Proteção à Natureza e da Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) tornaram possível a implantação do projeto, enquanto que a Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) tornou possível sua continuidade como minha tese de Mestrado através da concessão da bolsa de estudos (processo nº 98/01263-3).

A análise do grande volume de dados coletados ao longo dos três anos de campo no Rio, bem como sua interpretação e contextualização na teoria corrente de dinâmica de populações de plantas tropicais, incluindo os fatores ligados à fragmentação e ao impacto representado pelo fogo, representaram para mim um grande desafio intelectual. Para superá-lo, tive a felicidade de contar com a orientação do Dr. Fernando R. Martins, que guiou muitas vezes o raciocínio biológico que permeia os trabalhos aqui contidos. De grande valor foram também as discussões com os Drs. Elena R. Alvarez-Buylla (UNAM - México), Fábio R. Scarano (UFRJ), Flávio M. Santos (UNICAMP) e Gislene M. S. Ganade (UNICAMP).

RESUMO

Um estudo da dinâmica de populações da palmeira acaulescente *Attalea humilis* Mart. ex. Spreng foi conduzido em três fragmentos (1,6; 6,4 e 9,9 ha) da Floresta Atlântica, no sudeste do Brasil, entre 1996 e 1999. Durante o período de estudo, os fragmentos foram atingidos por um incêndio antrópico que devastou parte da reserva na qual estão incluídos. O número de folhas e o comprimento da raquis da folha mais recentemente expandida foram medidos para todas as palmeiras encontradas em duas transecções perpendiculares de 10 m de largura cruzando os fragmentos de borda a borda. Os seguintes aspectos da ecologia de populações da espécie foram estudados:

1) Caracterização de estádios ontogenéticos. Cinco estádios ontogenéticos foram distinguidos: Plântulas encontravam-se ligadas a restos seminais geralmente enterrados e apresentavam folhas inteiras; Juvenis apresentavam segmentação incompleta do limbo foliar. Indivíduos não reprodutivos com folhas pinatissectas foram divididos morfometricamente em dois grupos: os Imaturos, com menor número de folhas e comprimento da folha mais jovem menor e altamente variável , e os Virgens, com mais e maiores folhas, mas com comprimento da folha mais jovem mais constante. O tamanho crítico de copa para o qual imaturos e virgens puderam ser identificados variaram de acordo com o fragmento e o ano. Palmeiras Reprodutivas apresentavam estruturas reprodutivas.

2) *Dinâmica da hierarquia de tamanhos.* Não foram encontradas evidências consistentes de dependência da densidade no tamanho dos indivíduos das populações estudadas, avaliados através de analises de regressão entre variáveis ligadas ao tamanho da copa e a densidade das parcelas. Tanto para o número de folhas quanto para o comprimento da raquis da folha mais nova em todas as populações, diferenças de tamanho entre palmeiras em uma mesma categoria ontogenética tenderam a diminuir ao longo do processo de maturação da espécie.

Palmeiras jovens foram danificadas heterogeneamente pelo fogo, enquanto a maioria das palmeiras imaturas tiveram 50 - 75% de sua copa destruída, e os adultos mostraram uma grande proporção de plantas sem nenhum sinal de destruição da copa. Dezoito meses após o incêndio os indivíduos tenderam a apresentar uma menor desigualdade em relação ao número de folhas entre categorias ontogenéticas em todos os fragmentos. Sugerimos que a heterogeneidade ambiental, poderia agir como filtros ambientais selecionando os indivíduos que são recrutados para a categoria imatura. Estes indivíduos apresentariam crescimento e sobrevivência maiores e tamanhos menos desiguais:

3) *Distribuirão espacial de estádios ontogenéticos.* As palmeiras estavam significativamente agregadas em várias escalas, mas uma redução no grau de agregação ocorreu de plântulas para adultos em todos os fragmentos. O fogo aumentou temporariamente o grau de agregação dos jovens. Estádios ontogenéticos não foram encontrados nas mesmas parcelas com maior freqüência do que esperado ao acaso na maioria dos casos, mas uma associação positiva significativa de reprodutivos em diferentes anos foi encontrada em dois fragmentos. A distribuirão das palmeiras entre setores dos fragmentos variou de acordo com o estádio, fragmento e o ano, mas foi consistente no tempo sendo pouco afetado pelo fogo. Não foi encontrada uma relação geral entre a densidade de palmeiras e a distância da borda do fragmento, mas sim uma resposta complexa e esporádica. Sugerimos que a dispersão de sementes a curta distância por roedores pode resultar em agregados discretos e de baixa densidade de palmeiras jovens dissociados de plantas reprodutivas e que estádios posteriores ficam restritos a sítios mais abertos, perturbados e sujeitos ao fogo:

4) *Demografia.* Em todos os anos a densidade de palmeiras no fragmento de tamanho intermediário (750 - 900 palmeiras ha^{-1}) foi significativamente maior e apresentou maior

amplitude do que nos outros fragmentos (130 - 200 palmeiras ha^{-1} e 120 - 150 palmeiras ha^{-1}).A estrutura de estádios das populações variou com o fragmento e o ano, mas em geral os estádios posteriores foram mais abundantes do que os iniciais. A população no fragmento mais denso estava concentrada em seu setor mais perturbado. Tanto a taxa de crescimento populacional (λ) projetada quanto a observada foram significativamente maiores do que a unidade no menor fragmento mas similar á unidade no fragmento maior. Taxas de crescimento populacional baseadas em modelos matriciais foram mais sensíveis a mudanças na sobrevivência de plântulas, virgens e imaturos, e relativamente insensíveis a mudanças no crescimento e fecundidade. Depois do fogo, as populações permaneceram estáveis em todos os fragmentos exceto no de tamanho intermediário, onde uma tendência decrescente foi observada. A estrutura de estádios de todas as populações foi marcadamente alterada pelo fogo através da concentração da maioria dos indivíduos no estádio imaturo, de tamanho intermediário, mas esta tendência foi parcialmente revertida no segundo ano após o incêndio. Estes resultados poderiam indicar que a habilidade de rebrota de *A. humilis*, juntamente com sua tendência de persistir e crescer em áreas perturbadas promovem o crescimento populacional em fragmentos florestais pequenos e impactados, mas este crescimento pode ser revertido pelo crescimento secundário denso que tem lugar após incêndios ocasionais.

ABSTRACT

A study of the population dynamics of the acaulescent palm *Attalea humilis* Mart. ex. Spreng was conducted in three fragments (1.6, 6.4 and 9.9ha) of the Atlantic Forest, in southeastern Brazil, from 1996 to 1999. In late 1997, the fragments were damaged by a wildfire that burned part of the reserve they are part of. Leaf number and leaf rachis length of the newest expanded leaf were measured for palms in two 10 m-wide transects which cut across each fragment. The following aspects of the population ecology of the species were studied:

1) *Characterisation of ontogenetic stages.* Five ontogenetic stages were distinguished: Seedlings were attached fruit remains that were buried and presented entire leaves; Juveniles possessed incomplete segmentation of the blade. Pinnatifid-leafed, pre-reproductive individuals were morphometrically divided in two groups: the Immature, with fewer leaves and smaller but highly variable youngest leaf length, and Virginile, with more and larger leaves, but more constant youngest leaf length; the critic crown size by which immature and virginile could be identified varied with fragment and year. Reproductive palms presented reproductive structures.

2) *Size hierarchy dynamics.* We found scant evidence of density-dependent size in the populations studied, as measured by regression analysis between crown size variables and plot density. For both leaf number and newest leaf rachis length and all populations, size differences among palms in the same ontogenetic category tended to diminish along the species' maturation process. Young palms were heterogeneously damaged by fire, while most immature palms had 50 – 75% of their crown destroyed, and adults showed a high proportion of plants without any sign of crown destruction. Eighteen months after fire individuals tended to show reduced inequality in regard to the number of leaves among

ontogenetic categories in all fragments. We suggest that environmental heterogeneity could act as environmental sieves selecting individuals that are recruited to the immature category. These individuals would show enhanced growth and survival and less unequal sizes;

3) *Spatial distribution of ontogenetic stages*. Palms were significantly clumped in a range of scales, but a marked reduction in clumping degree occurred from seedling to the adult stage in all fragments. Fire increased temporarily the clumping degree of the young. Ontogenetic stages were not found in the same plots more often than expected by chance in the majority of cases, but a significant positive association of reproductive palms between years was found in two of the fragments. Palm distribution among fragments sectors varied with stage, fragment and year, but was consistent between years, being little affected by fire. No general relationship between palm density and distance from fragment edge could be detected, but a complex and sporadic response was found instead. We suggest that short-distance seed dispersal by scatterhoarding rodents results in discrete, low-density clumps of young palms dissociated from reproductive plants and that later stages are mostly restricted to more open, disturbed and fire-prone sites;

4) *Demography*. For all years, palm density in the medium-sized fragment (750 – 900 palms ha^{-1}) was significantly higher and varied in a broader range than in the two other fragments (130 - 200 palms ha^{-1} and 120 – 150 palms ha^{-1}). The stage structure of the populations was dependent on fragment and year, but later stages were generally more abundant than initial ones. The population in the denser fragment was concentrated within its disturbed sector. Both observed and projected population growth rates (λ) were greater than one in the smallest fragment but similar to one in the largest fragment. Population

growth rates based on matrix models were most sensitive to changes in survival of seedlings, virgins and the immature, and relatively insensitive to changes in growth and fecundity. After fire, populations remained stable in all fragments but the medium-sized one, where a declining tendency took place. After fire, most individuals were concentrated in the medium-sized, immature stage, but by the second year after fire most populations had returned to pre-fire stage structure. These results could indicate that the resprouting ability of *A. humilis*, coupled with its tendency to persist and thrive in disturbed areas promote population growth in disturbed small forest fragments, but this growth may be hindered by dense secondary regrowth following occasional fires.

INTRODUÇÃO GERAL

Devido ao fato de as florestas tropicais abrigarem um grande número de espécies (Wilson & Peter 1988) e de estarem sendo destruídas a taxas alarmantes (Whitmore 1997), sua conservação tornou-se um dos maiores desafios tanto da comunidade científica internacional quanto de organizações civis e governamentais preocupadas com a realização de um modelo de desenvolvimento sustentável ambientalmente (Whitmore & Sayer 1992, Goodland 1995). Entretanto, a maioria das paisagens tropicais não é mais dominada por florestas contínuas, mas por um mosaico de unidades de paisagem antrópicas, entremeadas por fragmentos florestais de diferentes tamanhos e graus de conservação (Thomlinson *et al.* 1996, Metzger 1999). Esta realidade levou, nas últimas duas décadas, a um crescente esforço de pesquisa voltado para os efeitos da fragmentação sobre a perda de espécies e mudanças estruturais nos habitats remanescentes (e.g. Lovejoy *et al.* 1986, Leigh *et al.* 1993, Turner 1996, Scariot 1999). Um menor número de trabalhos, porém, tem investigado os mecanismos causadores da perda de espécies em fragmentos florestais tropicais em nível demográfico, apesar da importância da ecologia de populações para a conservação *ex-situ* de espécies (Simberloff 1988, Schemske *et al.* 1994, Alvarez-Buylla *et al.* 1996, mas veja Barrow *et al.* 1993, Ratsirarson *et al.* 1996, Silva Matos *et al.* 1999).

Nesta tese apresentamos um conjunto de trabalhos que abordam aspectos da ecologia de populações de uma espécie endêmica em fragmentos da floresta Atlântica brasileira entre 1996 e 1999. A floresta Atlântica epitomisa o processo de conversão da maioria das florestas tropicais em áreas de uso antrópico. Uma das formações florestais mais ricas e diversas do planeta, com altos níveis de diversidade vegetal (Mori *et al.* 1981) e de endemismo de espécies animais e vegetais (Brown & Brown 1992), a floresta

Atlântica vem sofrendo os efeitos do desflorestamento e da fragmentação desde o início da colonização européia no Brasil, no século XVI (Dean 1996). Hoje esta grande formação vegetal encontra-se reduzida a fragmentos florestais em sua maioria com área restrita e em propriedades particulares (Ranta *et al.* 1998), que juntos somam cerca de 5% de sua área original (Viana & Tabanez 1996).

A compreensão da dinâmica de populações de espécies presentes em remanescentes da floresta Atlântica é, pois, um dos pré-requisitos para a conservação e manejo destes remanescentes florestais. Nesta tese, temos como objetivos gerais descrever aspectos da dinâmica de populações da palmeira *Attalea humilis* Marx. ex. Spreng. em três fragmentos florestais com características físicas e estruturais diferentes, bem como avaliar a resposta desta espécie à perturbação antrópica representada pelo fogo. *A. humilis* é uma espécie endêmica da região centro-sul da Floreststa Atlântica (Lorenzi *et al.* 1996), ocorrendo principalmente nas planícies costeiras do Espírito Santo e Rio de Janeiro. Apesar de sua distribuição restrita, *A. humilis* é abundante na maior parte das localidades onde ocorre. Além disso, é comumente encontrada formando densos agregados em áreas desmatadas, sendo mesmo considerada invasora de pastagens (Lorenzi *et al.* 1996).

Especificamente, visamos verificar se a as populações presentes nos fragmentos apresentavam tendências demográficas distintas em fragmentos com características estruturais diferentes, a fim de criar hipóteses de trabalho acerca das respostas populacionais à pressão antrópica sobre seu ambiente. Sendo assim, três perguntas gerais guiaram o desenvolvimento dos trabalhos: 1) a densidade populacional de *A. humilis* apresenta diferenças em fragmentos estruturalmente distintos? 2) as populações encontradas em tais fragmentos estão em crescimento, declínio ou estão estáveis? 3) há padrões morfométricos, demográficos ou espaciais que sugiram as causas biológicas das tendências demográficas observadas?

Na tentativa de responder às questões levantadas acima, foi necessário formular diversas outras, relacionadas a aspectos básicos da autoecologia da espécie e desenvolvidas nos trabalhos que se seguem, uma vez que, como a grande maioria das espécies tropicais, a biologia de *A. humilis* é praticamente desconhecida.

Organização Geral da Tese

A tese está dividida em quatro capítulos, que constituem trabalhos independentes, com objetivos, análise e discussões próprias, embora em conjunto representem um quadro geral da ecologia populacional da espécie estudada. No primeiro capítulo identificamos os estádios ontogenéticos (fases de desenvolvimento) naturais da espécie, com base em análises morfológicas e morfométricas. Estes estádios serviram como base para o desenvolvimento de todas as análises posteriores. No segundo capítulo analisamos a formação de hierarquias de tamanho nos diferentes estádios ontogenéticos e a variação espaço-temporal do grau de hierarquização nos diferentes fragmentos estudados. No capítulo seguinte investigamos a distribuição espacial dos indivíduos em cada estádio ontogenético nos fragmentos, ao longo do tempo. O padrão espacial de uma espécie é fruto de uma seqüência de interações bióticas e abióticas ao longo da ontogenia de cada indivíduo e pode oferecer importantes informações acerca do comportamento da espécie em face a um grande número de fatores. Por fim, no capítulo quatro apresentamos a demografia das populações estudadas, incluindo uma análise de seu ciclo de vida e estimativas das taxas de crescimento populacional.

Todos os quatro trabalhos aqui reunidos abordam as populações estudadas como "caixas pretas", uma vez que não nos foi possível conduzir experimentos ou fazer observações acerca da maioria dos mecanismos responsáveis pelos padrões que encontramos. Entretanto, acreditamos que estes trabalhos representam um passo importante na compreensão da biologia de populações de espécies perenes tropicais, e das respostas destas espécies aos impactos humanos representados pela fragmentação e pelo fogo.

Porquê Inglês?

Uma observação final é necessária sobre o idioma empregado no corpo principal da tese. Todos os quatro capítulos foram redigidos em língua inglesa, de acordo com a deliberação recente (001/98) da CCPG, que dispõe a respeito do formato das teses de Mestrado e de Doutorado aprovadas pela UNICAMP. Optamos pelo uso deste idioma visando à sua publicação em periódicos internacionais. Essa opção foi feita com o objetivo de facilitar e agilizar a publicação dos trabalhos em revistas científicas de circulação internacional e, desta forma, garantir sua disponibilidade a um maior número de profissionais interessados no assunto.

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CAPÍTULO 1: Detecting ontogenetic stages of the palm *Attalea humilis* Mart. ex Spreng. in fragments of the Brazilian Atlantic Forest [1, 2]

1 - Trabalho submetido à revista *Canadian Journal of Botany*

2 – Tabelas e Figuras no final do Capítulo

RESUMO

Um estudo da dos estádios ontogenéticos da palmeira acaulescente *Attalea humilis* Mart. ex. Spreng foi conduzido em três fragmentos (1,6; 6,4 e 9,9 ha) da Floresta Atlântica, no sudeste do Brasil, entre 1996 e 1999. Durante o período de estudo, os fragmentos foram atingidos por um incêndio antrópico que devastou parte da reserva na qual estão incluídos. A macromorfologia externa e medidas do número de folhas e do comprimento da raquis da última folha expandida permitiram a distinção de cinco estádios ontogenéticos: Plântulas encontravam-se ligadas a restos seminais geralmente enterrados e apresentavam folhas inteiras; Juvenis apresentavam segmentação incompleta do limbo foliar. Indivíduos não reprodutivos com folhas pinatissectas foram divididos morfometricamente em dois grupos: os Imaturos, com menor número de folhas e comprimento da folha mais jovem menor e altamente variável , e os Virgens, com mais e maiores folhas, mas com comprimento da folha mais jovem mais constante. O tamanho crítico de copa para o qual imaturos e virgens puderam ser identificados variaram de acordo com o fragmento e o ano. Palmeiras Reprodutivas apresentavam estruturas reprodutivas. Plântulas, juvenis e imaturos apresentaram menos folhas do que virgens e reprodutivos. O comprimento foliar foi similar entre plântulas e juvenis, mas apresentou aumentos nos estádios posteriores. As características de cada estádio foram bastante constantes ao longo dos anos de estudo nos três fragmentos, e foram pouco afetados pelo fogo, indicando que os estádios que identificamos são importantes no programa de desenvolvimento de *A. humilis*.

Abstract: A study of the ontogenetic stages of the acaulescent palm *Attalea humilis* Mart. ex. Spreng was conducted in three fragments (1.6, 6.4 and 9.9ha) of the Atlantic Forest in southeastern Brazil. The fragments were damaged by fire during the study period (1996-1999). External macromorphology and quantitative measures of leaf number and length of the newest leaf's rachis allowed the distinction of five ontogenetic stages: Seedlings were attached to buried fruit remains and presented entire leaves. Juveniles possessed incomplete segmentation of the blade. Pinnatifid-leafed, non-reproducing individuals were morphometrically divided in two groups: immature, with fewer leaves and smaller but highly variable youngest leaf length, and virginile, with more and larger leaves, but more constant youngest leaf length; the critical crown size by which immature and virginile could be identified varied according to fragment and year. Reproductive palms presented reproductive structures. Seedlings, juveniles and immatures had fewer leaves than virginile and reproductive individuals. Leaf length was similar between seedlings and juveniles, but increased in later stages. The characteristics of each stage were fairly constant throughout the study years in the three fragments, and were little affected by fire, indicating that the stages we define in this study are important in the developmental program of *A. humilis*.

Key words: stage-structured populations, ontogenetic stages, forest fragments, fire, leaf size, leaf number

Introduction

Knowledge of population biology is fundamental for the understanding of natural systems, and constitutes, along with community ecology, the main tool in conservation programs (Simberloff 1988). Most demographic studies on South American forests were carried out in Amazonia (Turner 1996), and only recently information on the Atlantic moist forests of Brazil has been published (e.g. Viana et al. 1997, Silva Matos et al. 1998*a*,*b*). The Brazilian Atlantic moist forests present some of the highest plant diversity and endemism in the world (Mori et al. 1981), but have been subjected to extensive deforestation, and its currently protected area network underrepresents natural landscape heterogeneity (Viana et al. 1997). Fire is one of the many hazards the Atlantic forest remnants face, and is used as a way of eliminating the forest cover to benefit other land uses, as well as a tool applied in agriculture and pasture management (Dean 1996). Fire exerts a crucial influence on the life history of many plant populations, but there have been few opportunities to study species in fire-prone forest fragments in a conservation unit of the Atlantic Forest.

Life history is considered to be the interface between an organism's ontogeny and its environment (Klingenberg 1998). The size of plants, in its turn, is the most important life-history variable determining individual fate (Silvertown and Lovett Doust 1993, Begon et al. 1996*b*), and the fact that plant populations have both a stage and an age structure is well known in the plant population dynamics literature (Silvertown and Lovett Doust 1993, Begon et al. 1996*b*). Hence, sound plant population studies must rely on clearly identified life stages with biological meaning. Gatsuk et al. (1980) used 'age states' to classify individuals on an ontogenetic or developmental basis. They created a classification scheme that uses biological criteria to indicate the state of development of a plant (e.g. seeds, seedlings, juveniles, adults). According to these authors, the age state of an individual could be defined by a complex of quantitative and qualitative features, and is generally characterised by the appearance of structures which are absent in earlier stages of development, and by the loss of previous ones. However, as discussed by Wellington and Noble (1985), the use of the term 'age' is unfortunate since, as Gatsuk et al. (1980) themselves pointed out, there is often no relationship between the biological 'age state' of a plant and its calendar age. Indeed, the word 'stage' has been commonly used with referrence to the ontogenetic or age states (e.g. Ash 1988, Carvalho et al. 1999). For these reasons, the term 'ontogenetic stage' (Carvalho et al. 1999) is used here rather than 'age state'.

Although the effects of disturbances, as the fire regime, have been studied in relation to the demographic variables (e.g. Wellington and Noble 1985, Begon et al. 1996*b*) and life history variation of plant populations (Silvertown and Lovett Doust 1993, Begon et al. 1996*a*), few studies have considered the effects fire could have on the maturation process of plant populations, *i.e.*, the progression through the various stages of ontogeny (Klingenberg 1998). This paper addresses the following questions concerning the maturation process of the palm *A. humilis* Mart. ex. Spreng.: 1) what are the post-germinative ontogenetic stages undergone by this species? 2) how do morphometric features related to crown size in each stage vary among fragments of the Atlantic Forest with different size, shape and structure? 3) are these morphometric features constant in time? 4) what are the effects of disturbance by fire on these morphometric variables?

Methods

Study Site

The study was carried out in the National Biological Reserve of Poço das Antas (22°30'-22°33'S, 42°15'-42°19'W), county of Silva Jardim, Rio de Janeiro state, southeastern Brazil. The Reserve covers ca. 5000 ha of Atlantic Forest, with a perimeter of 44 km (IBDF/FBCN 1981) and maximum elevation of 205 m above sea level. Pastures, agriculture and secondary forests surround the area. The regional climate is classified as Walter and Lieth's Equatorial type (Walter 1971). Rainfall is well distributed throughout the year (the average annual rainfall is 2092 mm, data from 1987 to 1997 period), with a less-rainy period extending from May to August.

The sites selected are part of the complex locally known as the 'Barbados' archipelago, a mosaic of eight forest fragments located on small hills. The fragments are embedded in a vegetation matrix dominated by grasses, patches of the bracken fern (*Pteridium aquilinum*) and isolated stands of *Cecropia* sp. (Cecropiaceae) and *Trema micrantha* (Ulmaceae). In the fragments, different kinds of soil form an indiscriminate grouping of alic Oxisols/Ultisols, with moderate A horizon and clayey to very clayey texture (Takizawa 1995). Three forest fragments were selected, ranging in size from 1.6 to 9.9 ha. The fragments present differences in forest structure, productivity and microclimate. Mean canopy is higher in fragments II and III (9.4 and 9.3 m, respectively) than in the smallest one (7.6 m), and tree density decreases from 797 trees/ha in the largest to 426 trees/ha in the smallest fragment (Silva Matos et al. 1998*a*). Mean annual litterfall also decreases from fragment III (5.7 ton ha^{-1} y^{-1}) to fragment I (4.1 ton ha^{-1} y^{-1})(Silva Matos *et al* 1998*b*). Additionally, the smallest fragment presents higher air and soil temperatures and lower air relative humidity and soil moisture content, besides suffering higher wind penetration (Silva Matos et al. 1998*b*).

Study species

A. humilis Mart. ex. Spreng. (Arecoideae: Cocoeae: Attaleinae, Uhl and Dransfield 1987), is a monoecious, solitary, acaulescent palm (sensu Dransfield 1978) that develops a saxophone-axis type stem (Tomlinson and Jeffrey 1990), which is short, subterranean or rarely aerial (Lorenzi et al. 1996). The apical meristem, protected by the surrounding leaf sheaths, is also subterranean, as well as the basal portion of the petioles. The crown has 5 - 16 pinnatifid, spineless leaves, each 1 - 7 m long with 75 – 120 pairs of segments up to 1 m long. Each reproductive palm produces separate male and female inflorescences at the end of the rainy season. *A. humilis* is restricted to the central-southeastern Atlantic Forest, ranging from the state of Bahia to the state of São Paulo (Lorenzi et al. 1996). It grows both in the forest understory and in open areas, like abandoned pastures or secondary, disturbed forests, often forming large, nearly homogeneous stands. Through most of its range, *A. humilis* occupies mainly the crests or slopes of hills, but rarely flooded sites.

Sampling method and data analysis

We censused palms in two perpendicular 10 m wide transects that cut across each fragment. Each transect was divided in 10 x 10 m contiguous plots. The sampled area covered from 7 to 18 % of each fragment area. Following the recommendation of Gatsuk et al. (1980), we made qualitative observations (phyllotaxy, leaf shape, presence of reproductive structures) and quantitative measurements of some external macromorphological structures of each plant. We recorded the shape of the newly opened leaf since the series of leaf forms that characterise the transition to the adult vegetative stage in palms is highly constant and characteristic for each species (Tomlinson and Jeffrey 1990). The number of leaves, length of the newly expanded leaf rachis, and occurrence of reproductive structures were also recorded. The moisture content percentage of whole fruits was calculated on a fresh-mass basis (100[mass water/fresh seed mass]) after drying the fruit at 105 °C for 24 h (Brasil 1992). Dead leaves were not counted, and a leaf was considered alive if at least 50% of its blade carried green segments. We chose length of the newly opened leaf lamina as a size measure because leaves are progressively larger in palms, at least until they reach the adult vegetative stage (Tomlinson and Jeffrey 1990).

Data were collected from July 1996 to January 1997 (1996 field survey) and between July and August 1997 (1997 field survey). At the end of the 1997 dry season (August-September) a fire damaged ca. 1000 ha of the Reserve, including the study area. Fire prevented the conclusion of the 1997 field survey, and data could not be collected in fragment II. In order to access the effects fire had on the ontogenetic stages of the populations under study, subsequent field surveys were carried out in April 1998 and in June 1999, after the reconstruction of the destroyed plots. In 1999 thirty seedlings and juveniles were excavated along one transect arm in fragment II in order to verify whether they where attached to fruit remains.

To test for the existence of distinct developmental stages among plants with the same macromorphological features, differences in leaf length between individuals with different number of leaves were assessed by Kruskal-Wallis ANOVA and nonparametric multiple comparisons (Zar 1996). This procedure was chosen due to large differences in the number of data in each group compared, as well as to the heterogeneity of variances between them. Leaf length variability was compared by testing the homogeneity of coefficients of variation (V) according to Zar (1996), after correction for small samples (Sokal and Rohlf 1995): $V = (SD/\bar{x})(1+1/4n)$, where n is the sample size. Notched box plots (McGill et al. 1978) assessed significance of differences between ontogenetic stages for both leaf number and length. All analyses were performed on SYSTAT, version 9.0 (SPSS, Inc. 1998).

Results

Definition of ontogenetic stages

The qualitative observations on the external macromorphological structures allowed the distinction of three pre-reproductive and one reproductive ontogenetic stages in the populations (Fig. 1). These four stages were characterised as follows:

Seedling.- The first expanded leaves or eophylls (Tomlinson 1960) are simple, entire and lanceolate, sometimes slightly indented at the apex, and have a distichous arrangement in the crown (Fig. 1e). All seedlings in the study area presented underground meristems, with partially buried leaves. Out of the 30 young plants excavated, four seedlings and three juveniles showed no fruit remains, nevertheless seventeen seedlings and six juveniles (see below) were attached to fruit remains at a depth of 4.1 ± 2.2 cm ($\bar{x}$ ± SD, range 0-10 cm, n = 23). A few individuals were found germinating under the litter layer, and these presented remote germination, with shoot developing at some distance from the seed due to an extended cotyledonary axis (Fig. 1d). No seedlings were found in fragment I in 1996, although they were present in fragments II and III in that year and in all fragments in subsequent surveys.

Juvenile - possesses transitional or 'juvenile' leaves (*sensu* Tomlinson and Jeffrey 1990), which are bifid, with incomplete segmentation of the blade (Fig. 1f). At this stage a spiral arrangement of leaves supersedes the distichous one. Juvenile plants may present both entire and transitional leaves. All the fruit that remained attached to the excavated juveniles were rotten. They were absent from the three fragments in 1996, but occurred in all fragments in the subsequent years.

Pinnatifid-leafed, non-reproducing palms - The palms present at least the youngest leaf with fully segmented blade. Segments are uniseriate (Tomlinson and Jeffrey 1990), *i.e.*, they are regularly distributed along the rachis and spread on the same plane. Above ground there is a gradual change in leaf position from nearly vertical, during blade expansion, to nearly horizontal, during petiole elongation, conferring a spherical shape to the crown. Under ground, the plumular axis grows obliquely down, and leaves are reoriented almost 180° to form the erect portion of the shoot. The base of the leaves develops a bulbous protuberance, which protects the meristem and probably assists the axis in forcing its way into the soil (Tomlinson and Jefffrey 1990) (Fig. 1g).

<u>Reproducer</u> - The palms present reproductive structures. Infructescences mature at ground level, are 18 - 40 cm long, with a thick, long petiole (24 - 70 cm) and bear 42 - 157 fruits. The fruit (51.4 ± 10.9 g; n = 80) is brownish nuculanium (sensu Spjut 1994), obovoid and tapers to the apex, having a thick, fibrous pericarp differentiated in a hardened endocarp enclosing 1 - 3 white, fleshy seeds. Fruit moisture content is 44.8 ± 2.1%. The continuous positive geotropic growth of the seedling axis can bury the leaf basis and the meristem of reproductive palms to a depth of ca. 1 m. One excavated individual showed a bulbous protuberance of 30 cm diameter buried at 1.2 m (Fig. 1h).

Analysis of morphometric data showed that a further distinction could be made among pinnatifid-leafed, non-reproducing palms. In 1996, palms in this category bearing at least 5 and 7 leaves had significantly longer leaf rachis in fragments II and III, respectively (Table 1)(Kruskal-Wallis ANOVA, fragment I: $H = 16.6$, $df = 6$, $P = 0.011$; fragment II: $H = 189.6$, $df = 12$, $P < 0.001$; fragment III: $H = 38.5$, $df = 8$, $P < 0.001$). Furthermore, the coefficients of variation of leaf rachis length were not homogeneous among plants with different leaf numbers (fragment I: $\chi^2 = 11.7$, $df = 5$, $P < 0.05$; fragment II: $\chi^2 = 71.0$, df =

12, $P < 0.001$; fragment III: $\chi^2 = 21.1$, $df = 8$, $P < 0.01$). Palms with larger crowns (≥ 6 leaves in fragment I, and ≥ 5 leaves in fragments II and III) showed reduced rachis length variation (Table 1). These results indicate that pinnatifid-leafed, non-reproducing individuals could comprise two distinct groups of plants: those with fewer leaves and smaller but highly variable youngest leaf length, and those with more and larger leaves, and more constant youngest leaf length. Following Gatsuk et al. (1980), these groups were recognised as "immature" and "virgin" stages, respectively. As these phases were characterised by changes in two population estimates (leaf rachis length and its variation), the critical crown size by which they could be identified varied in each fragment. Thus, palms were assigned to the virgin stage upon presenting crown of 6 or more leaves in fragment I and 5 or more leaves in fragments II and III.

These limits remained relatively constant in 1997. In fragment III virginal individuals had 6 or more leaves, presenting longer ($H = 26.8$, $df = 8$, $P = 0.001$) and less variable ($\chi^2 = 65.1$, $df = 7$, $P < 0.01$) leaf rachises than co-occurring plants with fewer leaves (Table 1). Both Kruskal-Wallis and Homogeneity of Coefficients of Variation test failed to detect significant differences in leaf rachis length or variation in fragment I, but notched box plot comparisons allowed the recognition of virginal individuals from 5 leaves on (Fig. 2a).

In 1998, after the 1997 fire, almost all immature palms had up to 4 leaves in fragment I, with no differences in leaf size or variability (Table 1). Hence, fire temporally eliminated the virgins from this fragment. In fragment II, the virgin stage could be assigned by leaf length and variation of leaf rachis to palms with at least 6 leaves ($H = 124.7$, $df = 11$, $P < 0.001$; $\chi^2 = 26.1$, $df = 8$, $P < 0.001$); and in fragment III by leaf length to palms with at least 7 leaves ($H = 34.2$, $df = 9$, $P < 0.001$)(Table 1). In 1999, almost two years after the fire, virginal individuals still could not be detected in the smallest fragment, and all individuals had relatively small, highly variable leaf sizes (Table 1). In fragment II, leaf length differed among palms with different number of leaves ($H = 89.0$, $df = 7$, $P < 0.001$), but these did not form clear groups. Leaf size variation, however, was not homogeneous among these plants ($\chi^2 = 18.0$, $df = 6$, $P < 0.01$), suffering a reduction in palms with 6 or more leaves, which were then assigned to the virgin stage (Table 1). In the largest fragment (III) the coefficients of variation were homogeneous, and plants with larger number of leaves showed progressively larger leaves ($H = 32.7$, $df = 8$, $P < 0.001$)(Fig. 2b). Palms with 6 or more leaves were assigned to the virgin stage since this was the largest leaf number presenting a significant increase in leaf rachis length.

Morphometric comparisons between ontogenetic stages

Plants in different stages showed marked differences in both leaf number and size, which tended to increase through the ontogenetic development (Table 2). These differences were rather constant among fragments, as showed by median confidence interval comparisons. Seedlings, juveniles and immatures had similar number of leaves, as well as virginal and reproductive individuals, but these two stages presented a greater number of leaves (Fig. 3). Leaf rachis length was similar between seedlings and juveniles, showed significant increases in the immature and virgin stages and, in fragments I and II in 1996 and in fragment III in 1997, also increased in the reproductive stage (Fig. 4). There was little, if any, site difference among palms in the same stage for both leaf number and length. Only in 1996 in fragment I, reproductive plants had longer leaves, and in fragment III the virgins had more leaves than in the other fragments. There was a marked reduction in leaf number variation from seedlings to the next stages in the years before fire, but this trend disappeared in 1998 and 1999 (Table 2). Leaf rachis length variation tended to be reduced in the virgins and reproducers. These trends showed to be consistent among fragments.

The morphometric relationships among ontogenetic stages did not change from 1996 to 1997 and was little affected by fire (Figs. 4 and 5). However, fire did provoke a generalised reduction in leaf number in all stages in all fragments, and different stages were unevenly affected by fire in different fragments. In fragment II reproducers showed the most remarkable reduction in leaf number, while virgins presented an increased number of leaves. In fragment I fire eliminated the virgins and severely reduced juveniles and reproducers. The 1999 data revealed a generalised return to before-fire values for most stages in all fragments. The reversal in size between virgins and reproducers in fragment II soon after fire was not found in 1999. After the fire in fragment I, leaf number and rachis length of seedlings and juveniles were higher than before. Thus, despite fire-induced differences, the general trends of increased leaf number in the virgin and reproductive stage, gradual increase in leaf rachis length, and gradual reduction in rachis length variation through the maturation process were confirmed from a dynamic perspective in both space and time.

Discussion

The ontogenetic stages identified in the present study for *A. humilis* ontogenetic development fit well with the general characterisation presented by Gatsuk et al. (1980) for the main age states of seed plants. It does not correspond completely, however, to the developmental phases of most palms (Tomlinson and Jeffrey 1990), due to the absence of an aerial stem, the formation of which defines both establishment and adult phases in palms with an aerial stem.

Studies on palm demography generally identify the seedling stage as having entire or poorly divided leaves (e.g. Piñero et al. 1984, Ash 1988, Orellana and Ayora 1993). This stage is also characterised by partially heterotrophic nutrition (Gatsuk et al. 1980), and palm seedlings remain attached to fruit remnants until the exhaustion of seed reserves (Tomlinson and Jeffrey 1990). Virtually all *A. humilis* seedlings emerged from buried fruits, and two non-exclusive explanations could account for this finding. First, the high moisture content of seeds generally implies high oxygen-consumption rates and desiccation sensitivity (Broschat and Donselman 1988, Garwood and Lighton 1990). Second, *A. humilis* fruit fits the rodent seed dispersal syndrome (Price and Jenkins 1986, Zona and Henderson 1989), and, as many large-seeded species, may depend on animals, especially scatterhoarding rodents, for successful seed dispersal and establishment (e.g. Price and Jenkins 1986, Smythe 1989, Forget 1992). Hence, it is possible that *A. humilis* seeds are dependent to some degree on burial mechanisms, probably a disperser with a characteristic behaviour, in order to escape desiccation and/or seed predation.

The ability of litter-covered *A. humilis* seeds to germinate indicates that, under favourable conditions (e.g., high humidity microenvironment, lack of seed predators), burial is not a prerequisite for seed germination. However, the development of a cotyledonary axis (i.e., remote germination) in seedlings originated from litter-covered seeds indicates that burial seems to be needed for the development of the newly established palm, since the extended cotyledonary axis develops a positive geotropism and buries the plumule, a process that may promote rooting (Tomlinson and Jeffrey 1990). Thus, it is possible that, in the species studied, the development of a cotyledonary axis depends on environmental conditions. In this case, germination type would be a heteromorphic trait (sensu Silvertown and Lovett Doust 1993). Both remote germination and saxophone-like stem development in the genus *Attalea* are regarded as correlated with drier climates, occurring most often in open, savannah-like situations (Tomlinson and Jeffrey 1990), as in the cerrado vegetation of central Brazil (e.g. Rawitscher and Rachid 1946), and in fire-prone areas (Henderson et al. 1995, Begon et al. 1996*a*). This view is reinforced by the appearance of small seedlings six months after the fire in fragments I and II. *A. humilis* germinative and stem growth strategies seem to have enabled it to thrive in the now fire-prone fragmented Atlantic Forest.

The seedling stage in palms is commonly long-lasting, ranging from years to decades (Piñero et al. 1984, Ash 1988, McPherson and Williams 1996). Regulation of phase change in shoot development has important consequences for the morphogenesis and evolution of plants through different selective advantages conferred by each stage (Lawson and Poethig 1995). In palm species with saxophone-type axis, the duration of the establishment phase depends on individual growth, and is strongly influenced by local conditions (McPherson and Williams 1996). Although we did not estimate the duration of ontogenetic stages, growth and development of pinnatifid, longer leaves in *A. humilis,* could be adaptive traits if they constitute a response of seedlings to consistent increases in light availability. Although palm leaf size and shape have strong phyllogenetic constrains (Tomlinson 1960), they are also strongly influenced by environmental conditions (Parkhurst and Loucks 1972). Changes of local conditions may impose the development of distinct leaf forms through their influence on plant size (Lawson and Poethig 1995), and the production of a new leaf becomes advantageous only under more favourable light conditions (Parkhurst and Loucks 1972, Chazdon 1986*a*). The light environment in the forest understory is highly heterogeneous, varying greatly both spatially and temporally (Chazdon 1986*b*, Chazdon and Pearcy 1991). Chazdon (1986*b*) found that seedlings of the palms *Asterogyne martiana*, *Geonoma congesta* and *G. cuneata* growing in gap edges had larger leaves than seedlings growing in a closed-canopy understory site. Indeed, the establishment of palms and the associated elaboration of adult-sized leaves require progressively higher levels of light intensity (Kahn and Granville 1992, but see Svenning 1999), generally associated with openings in the canopy. In *A. humilis* the production of adult-shaped leaves begins in the immature stage, and the very low number of juveniles, as well as their absence in all fragments in 1996 suggest that the transition from entire to pinnatisect leaf blade is quite a short period.

As showed by Chazdon (1986*b*), most of the light under a closed-canopy site comes from directly above the plant, and a difference in mean height of less than 1 m resulted in increased light availability for reproductive individuals of *Asterogyne martiana*. Hence, the observed change of leaf position in the immature stage of *A. humilis* from nearly vertical, during expansion, to nearly horizontal during petiole elongation, in addition to the spiral arrangement of leaves in the crown, achieved in the previous juvenile stage, could minimise leaf overlapping and optimise photosynthetic efficiency (Chazdon 1986*a*). A minimum critical size, from which further increases in crown size would not compensate for the energetic costs involved, should be achieved to allow the formation of reproductive structures. Considering that the effects of structure on performance are nonlinear and environment-dependent, the performance of an organism is meaningful only in its actual environment (Koehl 1996). Hence, the optimum leaf size of each ontogenetic stage of *A. humilis* may be different in each fragment. Although not developing an aerial stem, *A. humilis* photosynthetic surface increased from the seedlings and juveniles in the lower layers of the forest, through the production of larger leaves by immatures and virgins, to reproducers with leaves up to 7 m height. The production of longer leaves would tend to increase the amount of photosynthetically active radiation intercepted not only through increased leaf area but also by gaining access to areas of the vertical space richer in this resource. The tendency to increase leaf length during the ontogenetic development, however, may be limited by mechanical and physiological constraints, since larger leaves have disproportionately higher energetic costs (Parkhurst and Loucks 1972, Chazdon 1986*a*). Thus, the increased leaf size of reproductive individuals of *A. humilis* observed in fragment I in 1996 and subsequent increases in leaf number and size found in many stages after the fire could be related to increased light penetration resulting from disturbed conditions; on the other hand, the fact that increased leaf rachis length was not always accompanied by increased leaf number could come from the eventual reduction in light interception efficiency associated with increased leaf overlap due to greater number of leaves (Chazdon 1985). The ability of *A. humilis* to persist and thrive in disturbed areas (Henderson et al. 1995) may be due in part to their improved photosynthetic response in open areas, such as river margins, clearings or light gaps (Hogan 1988).

The differentiation of stages and phases in the pre-reproductive period of some species is difficult or even impossible, because the structure of their leaves, shoots and root system hardly changes during this period (Gatsuk et al. 1980). Indeed, the transition to the reproductive stage was not sharply marked in *A. humilis* regarding either length or number of leaves, indicating that virgin and reproductive could be reversible ontogenetic stages, and that at least part of the virginal individuals were in fact non-reproducing palms. Furthermore, reproduction at small sizes, due to precocity or damage, frequently constitutes a life-history response to increase fitness under low survival probability (Silvertown and Lovett Doust 1993). Thus, the size reversal in both number and length of leaves between virgins and reproducers soon after fire may have resulted from the reversal of some of the larger, previously reproductive plants to the virgin stage, while seriously injured ones might have invested their reserves in reproduction.

The three fragments were very different in a number of ways, and probably represented distinct environments from the smaller, more disturbed to the larger, more closed one. Moreover, the passage of fire altered substantially the light environment of the fragments, provoking a large-scale leaf fall and death of most understory plants (Silva Matos et al. in prep.). Despite these differences, both morphological and size characteristics of each stage were fairly constant in the study years, indicating that they are important in the developmental program of *A. humilis*.

Morphometric variables measured in different parts of an organism can show different ontogenetic trends, and their evolutionary history may be either independent or linked to that of other such parts (Klingenberg 1998). The fact that environment-dependent leaf size convergence to an optimum does not seem to be accompanied by changes in leaf number in *A. humilis* may indicate that each character is subjected to distinct environmental pressures, as the mechanical and absorptive trade-offs to which leaf length is subjected, and the trade-off between leaf arrangement and shading to which leaf number must account for.

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Table 1. Statistical parameters of leaf rachis length (cm) for pinnatifid-leafed, non-reproducing palms of *Attalea humilis* with different number of leaves in three forest fragments in the National Biological Reserve of Poço das Antas, Rio de Janeiro state, southeastern Brazil. V = corrected coefficient of variation.

	Number of Leaves													
Fragment	1	2	3	4	5	6	7	8	9	10	11	12	13	TOTAL
							1996							
I														
Median		111.0	208.5	124.0	200.0	300.0	254.5		330					
V *		0.62	0.72	0.52	0.66	0.14	0.15							
n		4	2	7	5	8	4		1					31
II														
Median	100.0	80.0	150.0	190.0	260.0	300.0	300.0	360.0	325.0	375.0	375.00	410.0	400.0	
V **	0.56	0.75	0.49	0.46	0.34	0.26	0.30	0.22	0.32	0.18	0.11	0.20	0.33	
n	8	46	59	73	53	42	30	14	12	8	2	6	4	357
III														
Median	53.0	89.0	130.0	226.5	260.0	250.0	375.0	230.0	400.0					
V **	0.21	1.01	0.44	0.37	0.22	0.25	0.27	0.47	0.16					
n	2	4	11	16	7	7	6	3	5					62
							1997							
I														
Median			150.0	135.5	271.5	298.0	318.0	427						
V ns			0.70	0.51	0.35	0.21	0.20							
n			5	4	10	5	4	1						29
III														
Median		145.0	180.0	187.0	265.0	280.0	269.0	320.0	270.0	335.0				
V **		0.46	0.51	0.45	0.43	0.28	0.15	0.17		0.07				
n		8	13	8	10	9	6	3	1	2				60

Table 1. (*Concluded*).

	Number of Leaves													
Fragment	1	2	3	4	5	6	7	8	9	10	11	12	13	TOTAL
							1998							
I														
Median	179.5	148.0	219.0	240.0		230.0		307.0						
V ns	0.98	0.62	0.47	0.22										
n	2	19	8	3		1		1						34
II														
Median	130.0	127.0	220.0	272.0	227.0	349.0	450.0	392.0	417.5		354.0	472.0		
V **	0.52	0.59	0.42	0.27	0.40	0.22	0.14	0.08	0.14					
n	13	160	186	45	16	4	2	5	6		1	1		440
III														
Median	130.0	126.0	172.0	265.0	224.0	253.0	367.0	360.0	317.0	445.0				
V ns	0.14	0.50	0.37	0.61		0.64	0.17	0.22		0.16				
n	3	30	16	5	1	3	6	5	1	2				71
							1999							
I														
Median			266.5	201.0	222.0	276.0	381.0	330.0	248.0	256.0				
V ns			0.47	0.15	0.38	0.63	0.01							
n			2	7	7	2	2	1	1	1				23
II														
Median		174.0	159.5	229.5	303.0	330.0	377.5	325.0	395.5					
V **		0.29	0.34	0.36	0.31	0.19	0.20	0.05	0.30					
n		4	40	124	91	36	14	2	2					313
III														
Median	90.0	99.5	153.0	187.5	246.5	340.0	306.0	349.0	374.0					
V ns		0.39	0.48	0.37	0.29	0.21	0.53	0.35	0.27					
n	1	4	14	20	14	5	2	3	2					65

Note: Homogeneity of coefficients of variation test: * $P < 0.05$ ** $P < 0.01$. ns = non significant.

Table 2. Quantitative characteristics of ontogenetic stages and phases of *Attalea humilis* in three forest fragments in the National Biological Reserve of Poço das Antas, Rio de Janeiro State, southeastern Brazil. V = corrected coefficient of variation. S = seedling, J = juvenile, I = immature, V = virgin, R = reproductive.

Stage	Fragment	Number of Leaves			Leaf Length (cm)			n
		median	V	range	median	V	range	
1996								
I	I	4	0.31	2 – 5	131.0	0.61	29 – 420	18
V	I	6	0.14	6 – 9	300.0	0.14	220 – 350	13
R	I	7	0.39	6 – 13	450.0	0.14	320 – 450	5
S	II	3	0.45	1 – 6	26.5	0.72	4 – 107	38
I	II	3	0.30	1 – 4	150.0	0.57	11 – 400	186
V	II	6	0.30	5 – 13	300.0	0.30	20 – 600	171
R	II	8	0.30	2 – 16	350.0	0.23	173 – 620	152
S	III	3	0.44	1 – 4	26.0	0.50	7 – 60	17
I	III	3	0.28	1 – 4	160.0	0.54	20 – 380	33
V	III	7	0.23	5 – 10	300.0	0.32	143 – 550	29
R	III	8	0.21	6 – 12	320.0	0.22	250 – 500	19
1997								
S	I	3	0.31	2 – 5	30.0	0.46	14 – 85	20
J	I	3.5	0.18	3 – 4	29.3	0.35	17 – 36	4
I	I	3	0.15	3 – 4	138.0	0.60	98 – 420	9
V	I	5.5	0.17	5 – 8	300.5	0.28	105 – 427	20
R	I	7.5	0.26	5 – 10	380.0	0.20	328 – 540	6

Table 2. (*Continued*).

Stage	**Fragment**	**Number of Leaves**			**Leaf Length (cm)**			**n**
		median	**V**	**range**	**median**	**V**	**range**	
1997								
S	III	2	0.61	1 - 5	25.5	0.45	1 - 50	22
J	III	2.5	0.31	2 - 3	28.5	0.36	22 - 35	2
I	III	3	0.31	2 - 5	180.0	0.48	29 - 360	40
V	III	7	0.18	6 - 10	300.0	0.21	92 - 400	21
R	III	8	0.21	4 - 11	350.0	0.12	300 - 410	21
1998								
S	I	2	0.45	1 - 5	23.5	1.26	12 - 165	12
J	I	2	-	-	25.0	-	-	1
I	I	2	0.50	1 - 8	171.5	0.53	24 - 380	34
R	I	9	-	-	344.0	-	-	1
S	II	2	0.48	1 - 5	25.0	0.40	8 - 48	25
J	II	2.5	0.32	2 - 3	38.5	0.48	27 - 50	2
I	II	3	0.30	1 - 5	194.0	0.50	13 - 480	420
V	II	8	0.25	6 - 14	401.5	0.14	310 - 503	20
R	II	3	0.58	2 - 12	328.5	0.24	190 - 480	27
S	III	2	0.44	1 - 4	25.0	0.68	6 - 59	7
J	III	3	0.49	2 - 5	25.0	0.31	17- 31	3
I	III	2	0.41	1 - 6	148.0	0.50	24 - 388	58
V	III	8	0.14	7 - 10	370.5	0.19	253 - 490	14
R	III	9.5	0.31	3 - 11	394.0	0.12	315 - 481	10

Table 2. *(Concluded)*.

Stage	**Fragment**	**Number of Leaves**			**Leaf Length (cm)**			**n**
		median	**V**	**range**	**median**	**V**	**range**	
1999								
S	I	4	0.27	3 - 6	38.0	0.19	23 – 44	10
J	I	5	0.12	4 - 5	40.0	0.28	35 – 65	5
I	I	5	0.34	3 - 10	222.0	0.33	120 – 385	23
R	I	8	0.42	5 - 12	341.0	0.05	337 – 370	3
S	II	3	0.30	2 - 4	33.0	0.19	21 – 42	13
J	II	4	0.21	3 - 6	58.0	0.38	23 – 117	26
I	II	4	0.17	2 - 5	245.0	0.34	65 – 445	177
V	II	6	0.12	6 - 9	349.0	0.20	166 – 471	55
R	II	6	0.32	3 - 13	390.0	0.17	59 – 544	105
S	III	3	0.27	2 - 4	34.0	0.08	30 – 36	4
J	III	4	0.00	4	62.5	0.06	60 – 65	2
I	III	4	0.26	1 - 5	188.0	0.44	42 – 420	53
V	III	7	0.17	6 - 9	343.0	0.25	204 – 438	12
R	III	9	0.28	4 - 15	426.5	0.13	350 – 530	14

Note: Values presented for cases where n = 1 report the size of the single individual measured.

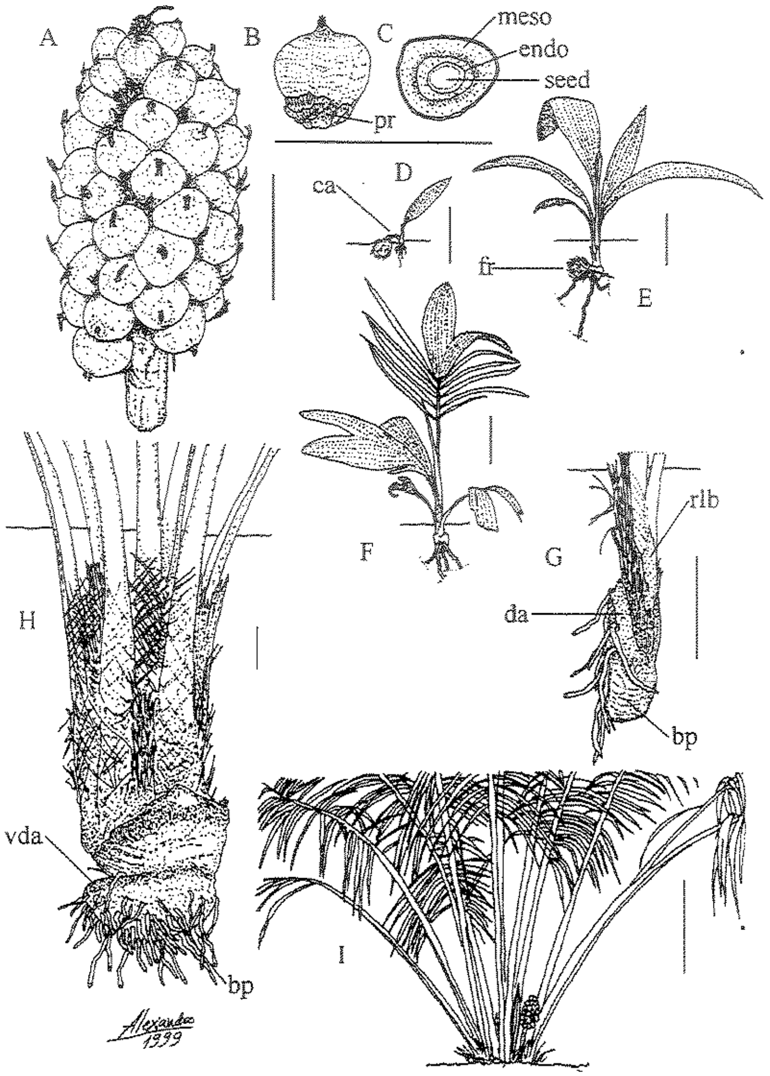

Fig. 1. Ontogenetic stages of *A. humilis humilis*. A) mature infructescence; B) external view of fruit; pr = perianth remains; C) transversal section of fruit; meso = fibrous mesocarp, endo = hardened endocarp; D) recently germinated seedling; ca = extended cotyledonary axis; E) established seedling; fr = fruit remains; F) juvenile, with transitional, but still distichous leaves; G) immature subterranean system; bp = bulbous protuberance, da = descending axis, rlb = reorientated leaf bases; H) reproductive subterranean system, with adventitious roots; vda = vestigial point of insertion of the degenerated descending axis, bp = bulbous protuberance; I) reproductive plant with spiral arrangement of leaves and mature infructescence. Scale bars: 10 cm for Figs. A – H, 1 m for Fig. I.

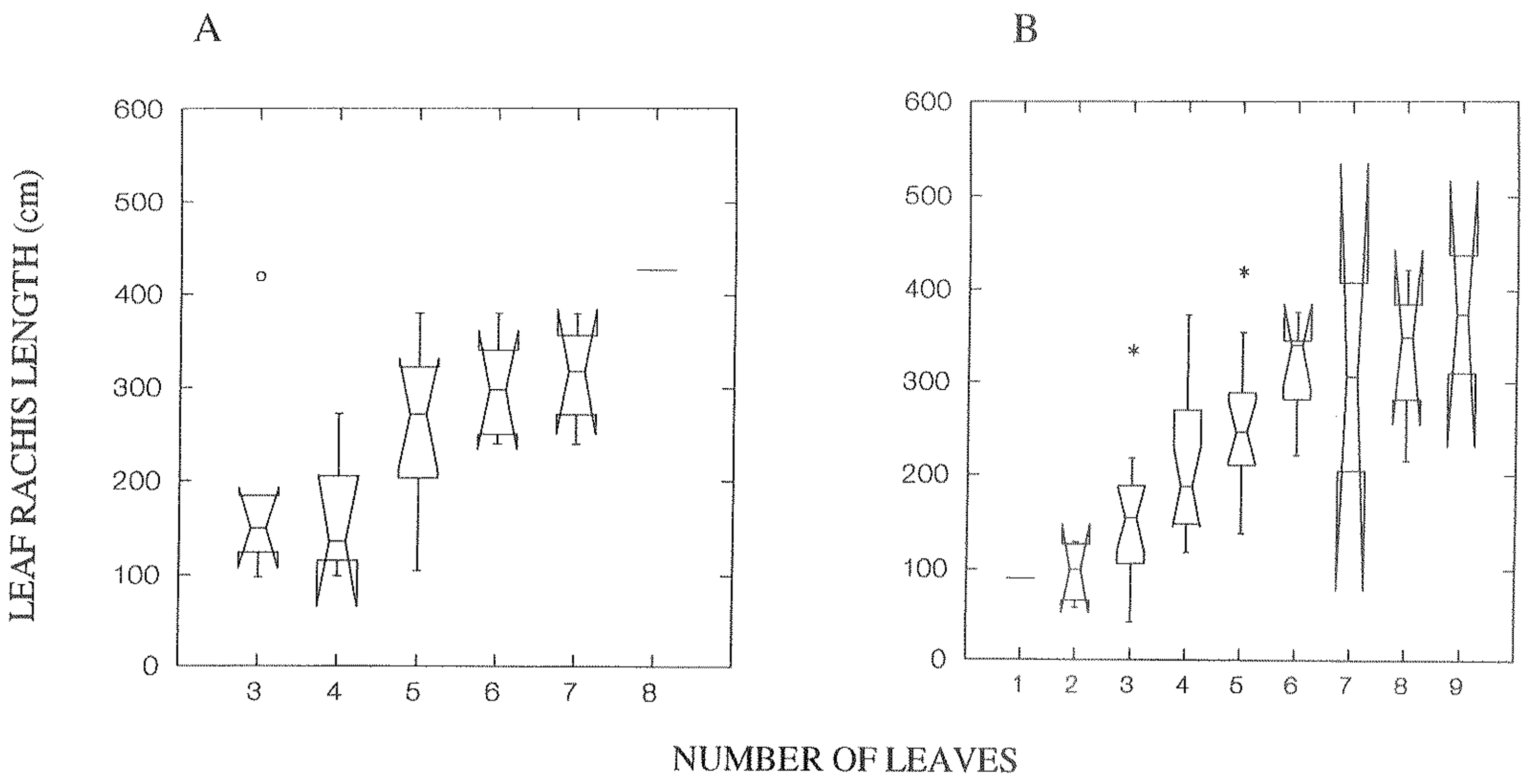

Fig. 2. Leaf rachis length of pinnatifid-leafed, non-reproducing individuals of *Attalea humilis* with different number of leaves. A) fragment I in 1997; B) fragment III in 1999. Central horizontal bars represent median values; upper and lower vertical bars (whiskies) represent 4th and 1st percentiles, respectively; notches surrounding the median represent median 95% confidence intervals; vertical bars connect the minimum and maximum values measured; o = extreme value; * = outlier. Non-overlapping of notches indicate significant difference at 95% confidence level.

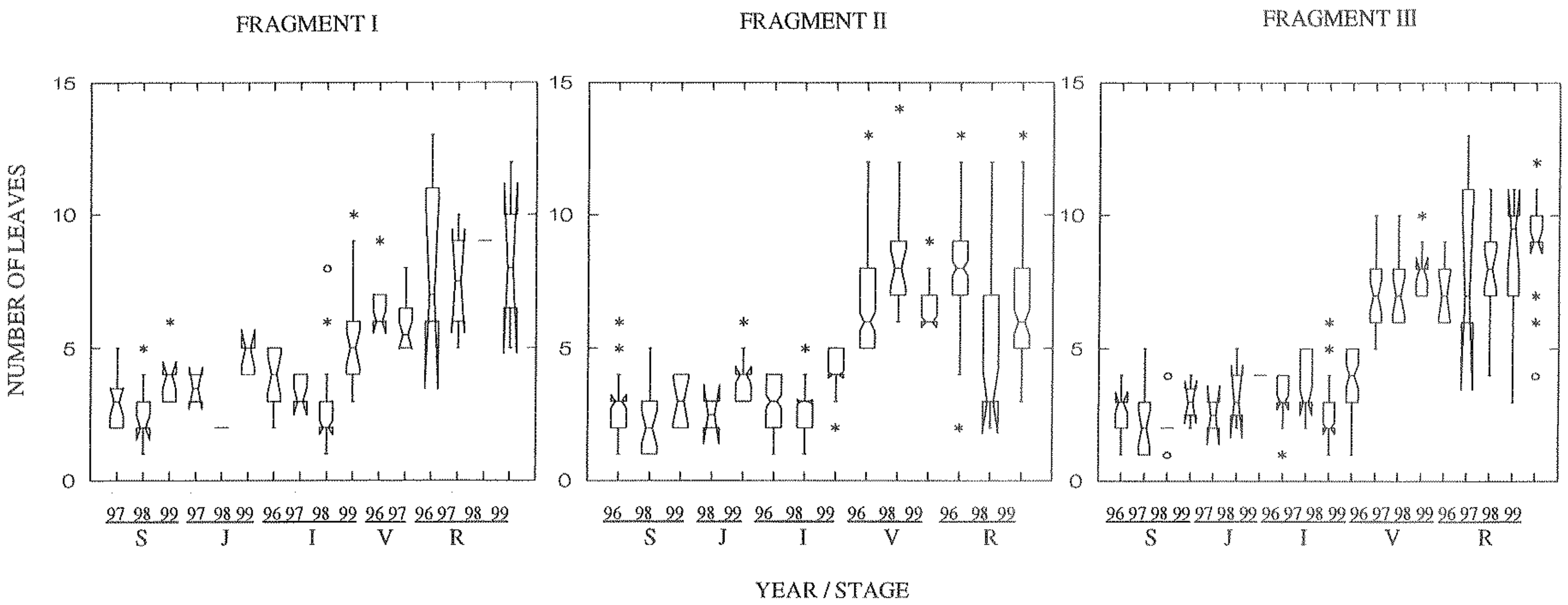

Fig. 3. Leaf number of individuals of *Attalea humilis* in different ontogenetic stages in three forest fragments in 1996, 1997 and after the 1997 fire in the National Biological Reserve of Poço das Antas, southeastern Brazil. Box and ontogenetic stage symbols as in Fig. 2.

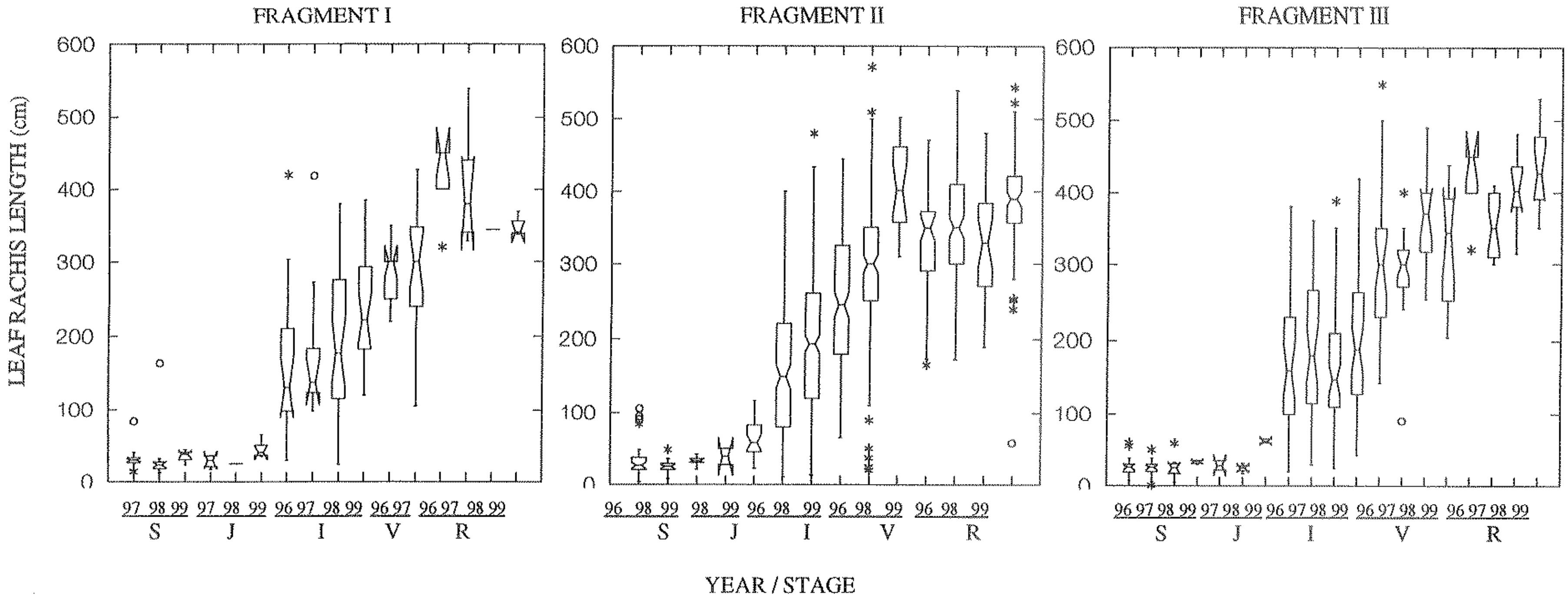

Fig. 4. Leaf rachis length of individuals of *Attalea humilis* in different ontogenetic stages in three forest fragments in 1996, 1997, and after the 1997 fire at the National Biological Reserve of Poço das Antas, southeastern Brazil. Box and ontogenetic stage symbols as in Fig. 2.

CAPÍTULO 2: Size Hierarchy Dynamics of *Attalea humilis* Mart. ex Spreng. (Arecaceae) in Fragments of the Brazilian Atlantic Forest[1]

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1 – Tabelas e Figuras no final do Capítulo

RESUMO. Nós utilizamos o número de folhas e o comprimento da raquis da folha mais recentemente expandida para estudar o grau de desigualdade de tamanho de categorias ontogenéticas da palmeira acaule *Attalea humilis*, no período de 1996 - 1999, em três populações estabelecidas em fragmentos da Floresta Atlântica. Mudanças no grau de desigualdade de tamanho de cada população puderam ser estudadas após a passagem do fogo porque um incêndio de origem antrópica atingiu os fragmentos durante o estudo. Os três fragmentos estudados variavam de tamanho (1.6, 6.4 e 9.9 ha) e estrutura. Não foram encontradas evidências de dependência da densidade no tamanho dos indivíduos nas populações estudadas, segundo análises de regressão linear entre a densidade das parcelas e as variáveis de tamanho escolhidas. Para ambas as variáveis e todas as populações, diferenças de tamanho entre palmeiras na mesma categoria ontogenética tenderam a diminuir ao longo do processo de maturação da espécie, embora as desigualdades tenham sido mais fortes para o comprimento da raquis. Palmeiras jovens foram atingidas pelo fogo de maneira heterogênea, apresentando uma amplitude de intensidades de dano, enquanto a maioria dos imaturos tiveram 50 – 75% de sua copa destruída e os adultos tiveram uma alta proporção de plantas sem nenhum sinal de destruição. Embora o padrão de desigualdade de tamanho encontrado antes do fogo entre as categorias ontogenéticas tenha sido pouco afetado imediatamente após o fogo, 18 meses depois do incêndio o número de folhas tendeu a apresentar reduções no grau de desigualdade entre categorias em todos os fragmentos. É possível que a heterogeneidade ambiental selecione os indivíduos que são recrutados para a categoria imatura. Estes apresentariam maior crescimento e sobrevivência e tamanhos menos desiguais. O aumento na variabilidade temporal de tamanho encontrada

entre adultos pode ser uma conseqüência da alocação sazonal de recursos para a reprodução.

ABSTRACT. We used the number of leaves and rachis length of the newest expanded leaf to study the degree of size inequality of ontogenetic categories of the acaulescent palm *Attalea humilis* over a four-year period, in three populations established on fragments of the Brazilian Atlantic Forest. Changes in each population's degree of size inequality could be followed after fire because a human-induced fire damaged the fragments during the study. The three fragments studied varied in size (1.6, 6.4 and 9.9 ha) and structure. Individuals of *Attalea* occurred at low densities in the fragments studied, and we found scant evidence of density-dependent size in the populations studied, as measured by regression analysis between size variables and plot density. For both variables and all populations, size differences among palms in the same ontogenetic category tended to diminish along the species' maturation process, though inequalities were stronger for leaf rachis length. Young palms were heterogeneously damaged by fire, showing a range of damage intensities, while most immature palms had 50 – 75% of their crown destroyed and adults showed a high proportion of plants without any sign of crown destruction. Although the pre-fire pattern of size inequality among ontogenetic categories was little altered immediately after fire, 18 months after fire the number of leaves tended to show reduced inequality among ontogenetic categories in all fragments. We hypothesize that, in the forest fragments studied, environmental heterogeneity in both time and space, represented by local differences in forest structure and the combined effects of edges and disturbed sectors, act as environmental sieves selecting individuals that are recruited to the immature category. These individuals would show enhanced growth and survival and less unequal sizes. Adults showed increased variability in the degree of size inequality through time, which could partly be due to the seasonal allocation of resources to reproduction.

INTRODUCTION

Size is a fundamental feature of most plant life histories. Large plants have increased survival probabilities, increased fecundity (Solbrig 1981, Silvertown & Lovett Doust 1993, Begon *et al.* 1996), and enhanced competitive ability (Weiner & Thomas 1986). Most plant populations exist as size hierarchies of individuals, *i.e.* the individuals varies enormously in size, generating positively skewed size distributions in which relatively few individuals contribute most of the population's biomass (Weiner & Solbrig 1984). This has important ecological and evolutionary consequences. Size hierarchies can reduce the effective population size, and an inordinately large proportion of a plant population's genes may be descended from a very small number of individuals (Weiner & Thomas 1986, Weiner 1990, Silvertown & Lovett Doust 1993).

Size hierarchies are the result of interactions among six major factors (Weiner & Thomas 1986): age differences, genetic differences, environmental heterogeneity, maternal effects, differential effects of herbivores, parasites and pathogens, and competition. Most work on this topic has been done on experimental even-aged monospecific stands of annual herbaceous plants. A common, though not universal result is that the degree of size inequality of the population increases from young to old stands, and from low-density to high-density populations (Benjamin & Hardwick 1986, Weiner & Thomas 1986). These results have been attributed mainly to a) the distribution of growth rates resulting from differences among individuals because of random genetic and/or environmental effects (Westoby 1982, Geber 1989); and b) competitive interactions, whereby larger individuals suppress the growth of smaller ones (Bonan 1988, 1991). The distinction between symmetric and asymmetric competition has dominated the literature on the formation of size hierarchies (Turner & Rabinowitz 1983, Weiner 1985, Bonan 1988, 1991, Geber 1989, Schwinning & Weiner 1998), largely after Weiner (1985, 1990) and Weiner & Thomas (1986) proposed that greater size inequalities would emerge when larger plants obtain a disproportionate share of resources and suppress the growth of smaller neighbors (asymmetric competition).

However, in natural populations exposed to habitat heterogeneity, distinct patterns of size variability may emerge. The population biomass may be concentrated on isolated individuals released from competition (*e.g.* Harmon & Stamp 1992) or be positively correlated with local density (Hartgerink & Bazzaz 1984, Silvertown & Lovett Doust 1993, Wilson & Gurevitch 1995), as the clumping of plants in favorable sites may override the effects of competition with neighbors (Firbank & Watkinson 1987, Fowler 1988). Thus, there is some evidence that, at least in natural populations of iteroparous plants, environmental heterogeneity frequently overrides competition in the creation of size hierarchies.

Even less studied are the effects natural or human-induced disturbances may have on the formation of size hierarchies. In this regard the study of natural populations occurring in forest fragments is a valuable opportunity to test the predictive power of our current understanding on the formation of size hierarchies. The distinct environmental pressures leading to size inequalities should have different relative intensities in different forest fragments, which commonly present very distinct biotic and abiotic characteristics depending on their size, shape, and human interference (Saunders *et al.* 1991, Camargo & Kapos 1995, Murcia 1995). Moreover, the analysis of size distribution patterns in such populations is of practical importance, helping in the recognition of population responses to local environmental changes in isolated conservation units.

Most plant populations have an ontogenetic stage structure (Silvertown & Lovett Doust 1993), in which each stage may have distinct ecological requirements. We expect the degree of size inequality to decrease from young to immature stages because the initial size variability should be reduced by differential mortality imposed by the environmental sieve the distribution of favorable sites represent. The enhanced growth and survival in such sites would then lead to more even-sized individuals. Furthermore, unless mature plants exhibit high synchrony during reproductive events, the degree of size hierarchy should be more dynamic in the reproductive stage, due to the periodic allocation of resources to reproduction, which constrains the size and rate of production of vegetative structures during reproductive events. Also, due to the range of patch types (light gaps, closed forest, disturbed secondary forest, forest edge) and population densities commonly found in forest fragments (Viana & Tabanez 1996, Oliveira-Filho *et al.* 1997, Benítez-Malvido 1998), we expect that, in slow-growth species in which size limitation occur long before survivorship reduction under competitive pressure, stronger size hierarchies develop: (1) in fragments or patches with high population densities, due to increased intraspecific competition; (2) in preserved, more closed fragments or patches where resources, mainly light, are scarcer and more patchily distributed. Additionally, large-scale, human-induced disturbances, such as fire, should reduce size inequalities through size-dependent mortality or reduction of the size of the larger plants, thus concentrating the surviving individuals around intermediate sizes.

In this paper we evaluate the degree of size inequalities in populations of the palm *Attalea humilis* Mart. ex. Spreng. in three fragments of the Atlantic forest in southeastern Brazil. The studied fragments present a range of biotic and abiotic conditions, including the density of palms. Additionally, the fragments were burned in late 1997, and population assessments made thereafter allowed us to estimate the immediate effect of fire on the size structure of the populations.

MATERIALS AND METHODS

Study Site

The study was carried out in the Poço das Antas National Biological Reserve (22°30'-22°33'S, 42°15'-42°19'W), municipality of Silva Jardim, State of Rio de Janeiro, southeastern Brazil. The Reserve is located in the Atlantic Forest domain, and represents one of the last refuges of the coastal lowland forests that once covered the Brazilian coastal plains. The Atlantic moist forests are among the most diverse forests of the world (Mori *et al.* 1981), and have suffered extensive deforestation since colonial times (Viana *et al.* 1997). Therefore, there is a potential conservation value to any effort to understand the dynamics of populations in its remnants. The Reserve covers ca. 5000 ha of Atlantic Forest surrounded by pastures, cultures and secondary forests, with maximum elevation of 205 m a.s.l. (IBDF/FBCN 1981). The regional climate is classified as Walter and Lieth's Equatorial type (Walter 1971). Rainfall is well distributed throughout the year, with a discrete dry season from May to August. The sites selected are part of a mosaic of eight forest fragments located on small hills, near the left margin of the São João River. The fragments are embedded in a vegetation matrix dominated by grasses, patches of the bracken fern (*Pteridium aquilinum*), and isolated stands of *Cecropia* sp. (Cecropiaceae) and *Trema micrantha* (Ulmaceae). Three forest fragments were selected (1.6, 6.4 and 9.9 ha) that showed differences in density and mean height of trees ≥ 10 cm DBH, litterfall and shape, as well as contrasting densities of *Attalea humilis* (Table 1). Additionally, the smaller fragment exhibit higher air and soil temperatures, lower air relative humidity and soil moisture content, and suffers higher wind penetration than the other fragments (Silva Matos *et al.* 1998*b*). See Chapter 1 for further description of the area.

Study Species

Attalea humilis Mart. ex. Spreng. (Arecoideae: Cocoeae: Attaleinae, Uhl & Dransfield 1987), hereafter *Attalea*, is a monoecious, solitary, acaulescent palm (*sensu* Dransfield 1978), endemic to the central-southeastern Atlantic forest (Lorenzi *et al.* 1996), which develops a short, subterranean stem (Chapter 1). The apical meristem, protected by the surrounding leaf sheaths, is also subterranean. *Attalea* grows both in the forest understorey and in open areas, like abandoned pastures or secondary, disturbed forests, often forming large, nearly homogeneous stands. Through most of its geographical range *Attalea* occupies mainly the crests or slopes of hills but rarely flooded sites.

Following Gatsuk *et al.* (1980), we distinguished five ontogenetic stages in *Attalea*, according to morphological and morphometrical analysis (Chapter 1). Seedlings present entire, distichous leaves, which are replaced in the juvenile stage by bifid, incompletely segmented leaves. Immature individuals present completely segmented leaf blade, being distinguished from virginile ones by having fewer leaves and smaller but highly variable youngest leaf length. The reproductive stage is recognized by the production of flowers and fruits.

Sampling method and data analysis

Palms were censused along two perpendicular 10 m wide transects that cut across each fragment. Each transect was divided in 10 x 10 m contiguous plots. The sampled areas covered 7 - 18 % of each fragment area (Table 1). Plant size may be assessed in various ways, including shoot dry mass in herbaceous species, trunk diameter in trees, and number of leaves in palms (Hutchings 1997). As *Attalea* has a subterranean stem, we recorded the number of leaves and rachis length of the newly expanded leaf of each individual as size measures. Length of the newly-opened leaf lamina was chosen as a size measure since leaves are progressively larger in palms, at least until they reach the adult vegetative stage (Tomlinson & Jeffrey 1990). Dead leaves were not counted, and a leaf was considered alive if at least 50 % of its blade carried green segments.

Data were collected from July 1996 to January 1997 (1996 field survey) and between July and August 1997 (1997 field survey). At the end of the 1997 dry season (August-September) a fire damaged *ca.* 1000 ha of the Reserve, including the study area. Fire prevented the conclusion of the 1997 field survey, and data could not be collected in fragment II. In order to assess the effects fire had on the populations under study, field surveys were carried out in April 1998 and in June 1999, after reconstruction of the destroyed plots. If fire affected each stage homogeneously, we did not expect it to change the previous degree of size inequality. In the 1998 census, we assigned each palm to one of the following classes of crown destruction as a measure of fire damage intensity: 0) no apparent damage, 1) from zero to 25%, 2) from 25 to 50%, 3) from 50 to 75%, 4) more than 75% and 5) entirely destroyed.

In the analysis, individuals in the seedling and juvenile stages (hereafter the 'young') were pooled together due to the low number of juveniles and to the fact that their leaf number and length are not different (Chapter 1). Virginile and reproductive individuals were also grouped (hereafter 'adults'), since they present extensive leaf number and size coincidence and together probably represent the potentially reproductive individuals (Chapter 1). Thus, in the analysis we considered the young, the immature and adult as ontogenetic categories. Notched box plots (McGill *et al.* 1978) were used to assess significance of differences between plot densities for each fragment and year. To assess possible effects of density on individual size in each ontogenetic category, leaf number and size were regressed against the density of the plot where each individual was found, using SYSTAT (SYSTAT 1998). In each case, normal probability plots of residuals were used to assess strong departures from normality (SYSTAT 1998), and regression of the residuals against the estimated values allowed for an estimate of heteroscedasticity (Zar 1996). When necessary, the data were ln-transformed. For each ontogenetic category and fragment, a Kolmogorov-Smirnov test (Zar 1996) was performed on the distribution of palms among classes of fire-induced crown destruction to test for the null hypothesis of uniform distribution of individuals in the classes.

Patterns of size distribution were described by the Gini coefficient corrected for small samples, calculated for each ontogenetic category according to Weiner & Solbrig

(1984): $G = \sum_{i=1}^{n}\sum_{j=1}^{n} \left| x_i - x_j \right| / 2n(n-1)\bar{x}$, $i \neq j$, where n is the number of individuals, x_i and x_j are leaf number or length for palms i and j, and $\bar{x}$ is the mean leaf number or length. The degree of the size inequality is the degree to which the population's biomass is concentrated among a few larger individuals (Weiner & Solbrig 1984). Therefore larger coefficients represent larger inequalities. Means and standard deviations for Gini coefficients were determined using a "bootstrapping" technique with 1000 bootstrap samples (Manly 1991). All bootstrapping and pairwise comparisons between estimated means were carried out on WINGINI (Santos 1996).

RESULTS

Except for the extended range of densities in fragment I in 1997, fragments I and III had similar, low number of palms per plot (Table 2). In contrast, fragment II presented much higher and variable densities. This picture was slightly altered after fire due to small reductions in density values in 1998 and 1999.

Density did not have a significant effect on either leaf number or rachis length in most cases (Table 3). Only 16 out of 62 regression coefficients were significant. With few exceptions, significant regressions showed no consistency of density effects on both variables or between fragments or ontogenetic categories. Moreover, density could account for only up to *ca*. 20% of the variation in size in most significant cases. Before fire, the young had shorter leaves in denser plots in both the smallest (1996) and largest (1996,

1997) fragments. Adults, on the contrary, had more leaves in denser plots in fragment III (1996, non-significant but still positive coefficient in 1997). Such loose trends disappeared after fire. Young palms in denser plots had more leaves in fragment I (63.3% of variance explained), but this relation was restricted to the year just after fire. In 1999, adult palms in the same fragment had fewer and smaller leaves in denser plots (59.0 and 76.3% of variance explained for leaf number and length, respectively).

The inequalities for leaf number distributions were generally lower than those for leaf rachis length (Tables 4 and 5). In the years preceding fire distinct patterns of inequality occurred for leaf number and rachis length. For both size measures, the degree of inequality decreased from young to adult palms, though the immature showed stronger hierarchies in relation to leaf rachis length. Values of the Gini coefficient for leaf number were similar between fragments in 1996, but differed in the next year, when the largest, more closed fragment (III) presented stronger hierarchies in the young and immature categories (Table 4). The significant decrease in size inequality of leaf rachis length from the immature to adults held for both years and all fragments, with the exception of fragment I in 1997, where the degree of inequality did not differ among categories (Table 5).

The distribution of palms among fire damage classes differed in each population and in each ontogenetic category (Figure 1). The young were heterogeneously damaged in fragments I and III, with a similar number of individuals in each damage class. In fragment II *ca.* 70% of the young showed no signs of burn. In contrast to the young, most immature palms had 50 – 75% of their crown destroyed by fire in all fragments. The adults showed to be the least damaged ontogenetic category, showing a high proportion of plants without any sign of crown destruction. There was a generalized lack of plants with extensive proportions of crown destroyed (class 4) or with completely burnt crowns (class 5). This result could be partly due to the fact that almost all palms presented a new, expanding leaf clearly constructed after fire (pers. obs.).

Size distributions of both number and size of leaves were little altered after the passage of fire (1998 data). The only exception was the distribution of leaf number of the immature in fragment I, which showed increased inequality in relation to the pre-fire (1997) distribution (difference between corrected Gini coefficients = 0.1432, $P < 0.0001$). However, it did not differ from the 1996 or 1999 values, and could hardly be regarded as a relevant consequence of fire. In fragment II, on the contrary, the immature showed the weakest inequality, while the adults were as hierarchised as the young (Table 4).

In 1999 the previously recognized pattern of relative inequalities between ontogenetic categories was blurred for leaf number, and a similar degree of size inequality seems to have been achieved in all categories and fragments, except for the immature in fragment II, which still showed to be less unequal. The degree of inequality for leaf rachis length, however, was similar between the young and the immature, but dropped significantly in adults in all fragments in both years after fire (Table 5).

DISCUSSION

Although palms occurred in the fragments as loose clumps of individuals (Chapter 3), adding up hundreds of individuals per ha, we found scant evidence of density-dependent size in the populations studied. Apparently, the observed range of densities did not suffice to promote the overlap of individual crowns and induce strong competitive effects in most cases. However, the use of measures of local crowding (*e.g.* density) to explain the performance of individual plants (and infer the 'absence' of competition) may not be satisfactory, and may account for only a relatively small proportion of the variation in individual plant yield (Firbank & Watkinson 1987). Nevertheless, the lack of correlation between palm size and plot density in most cases indicate that local population density has little influence on palm size, and that intraspecific competition is unlikely to be a driving force in the formation of size hierarchies in the populations studied. This is in agreement with Fowler's (1988) and Wilson and Gurevitch's (1995) field results and Hartgerink and Bazzaz's (1984) experiment, in which aggregation in favorable microsites outweighed the effects of competition in the populations studied.

The fragment with highest density (fragment II) showed in fact a broad range of values, a picture that fire did not alter. This fragment presents high structural heterogeneity (*pers. obs.*), and the palm population, except for the young, is concentrated in its disturbed sectors, where it forms large, dense stands (Chapter 3). In this situation there is extensive overlap among individual crowns (*pers. obs.*), which are spherical and composed of 5 – 8 spirally arranged, up to 6 m-long leaves (Chapter 1). In crowded populations without mortality, asymmetric competition generally acts to exaggerate relative size differences arisen by variation in relative growth rates of individuals over what they would be without or with symmetric competition (Weiner 1990). To generate size asymmetric resource competition, a resource must be "pre-emptable", and light is believed to be the primary example of this kind of resource (Schwinning & Weiner 1998). However, the degree of size inequality was not significantly higher in fragment II for any ontogenetic category or size measure. Thus, compensatory mechanisms must be acting to enable coexistence of close neighbors despite overlap among individual areas of influence, which is regarded as a measure of competitive pressure (Brisson & Reynolds 1997). Plant form can dramatically affect competitive ability, and greater competitive asymmetry emerges in species whose morphology leads to greater between-plant shading (Ellison & Rabinowitz 1989, Geber 1989, Ellison & Vikites 1991). *Attalea* presents an open crown architecture, with few large feather-shaped leaves positioned in space by up to 3.5 m-long petioles, enabling extensive inter-crown penetration which reduces between-plant shading. It is possible that, in the dense stands of *Attalea* found in degraded secondary forests (like some sectors of fragment II; Table 1) and open areas (like pastures, Lorenzi *et al.* 1996), asymmetric competition for light is compensated by the plant's open crown architecture, allowing for a tight packing of individuals.

Size inequalities were not similar between *Attalea* ontogenetic stages. Rather, in the two years before fire size differences between palms in the same ontogenetic category tended to diminish along the species' maturation process, as expected. This holds despite the striking differences between the fragments studied. It is well established that levels of selectively relevant variation within small local populations and the very persistence of species in heterogeneous environments may arise from genetic polymorphism or phenotypic plasticity, or a combination of both (Scheiner & Goodnight 1984, Silvertown & Lovett Doust 1993, Begon *et al.* 1996). In any case, however, variance is maintained largely due to environmental heterogeneity. Seed size, genetic variability and emergence time are known to strongly influence size variation in seedlings (Firbank & Watkinson 1987, Hutchings 1997). In the populations studied, increased seedling growth and survival in patches with increased light (Chazdon 1986*a*, Cintra & Horna 1997) and/or nutrient (Barot *et al.* 1999) availability probably enhance such variation, leading to the widely variable seedling sizes observed.

Considering that mortality may be higher among the young occurring out of resource-rich patches, the immature might comprise palms that had grown up in favorable sites. Such an environmental sieve could help explain why size inequalities among the immature were similar to (newest leaf rachis length) or predominantly lower (leaf number) than in the young. On the other hand, the small number of young palms found during the study period and the numerical predominance of the immature (Chapter 4) suggest that prolonged survival in the seedling and juvenile stages is not likely, and that the immature represent a large array of ages. Additionally, the immature were found in almost all fragments' sectors (Chapter 3). Hence, the strong size inequality it frequently showed in regard to the newest leaf rachis length may result from both variable ages and extended exposure to conditions that are probably even more heterogeneous than those faced by the young (*i.e.*, gaps, fragment edges, shaded understorey, nutrient-rich fragment edges, nutrient-poor forest interior [Didham 1998]). These results agree with the suggestion made previously (Chapter 1) that leaf number and length are restricted in different ways by the prevailing environmental pressures.

Adults tended to produce less variable leaf sizes. Mechanisms giving rise to such a reduction in size inequality in relation to previous categories include mortality of smaller individuals occurring in unfavorable sites (*e.g.* Mohler *et al.* 1978), as suggested for the immature, as well as released growth of smaller individuals induced by changing environmental conditions (*e.g.* Macdonald & Yin 1999). Additionally, as a converse aspect of plastic expression, through which under a consistent environmental pressure different genotypes will produce the same habit and morphology (Sultan 1987), adult palms with differing growth capabilities could converge to a narrow range of crown sizes (*i.e.*, leaf number and size). This could result from the trade-off between increased light availability and homogeneity along the forest profile (Chazdon 1986*a,* Walsh 1996) and increased energetic costs of leaf production (Parkhurst and Loucks 1972, Chazdon 1986*b*), which may restrict leaf size and number for adult individuals.

Two drawbacks limit the interpretation of these results. First, the groups of individuals considered here represent developmental ontogenetic categories rather than cohorts of even-aged individuals. Hence, as mentioned above palms of different ages probably accumulate to some extent in the same ontogenetic category. This blurs conclusions based solely on the temporal or spatial dimensions because under conditions where growth is exponential, even small age differences will lead to increasing size inequality over time (Weiner & Thomas 1986). Second, confidence intervals obtained from the Gini coefficient through bootstrapping procedures are too narrow when calculated from samples smaller than 50 individuals (Dixon *et al.* 1987). Though the unbiased sample estimator of the Gini coefficient used in this study reduced this bias (Dixon *et al.* 1987), significant but small differences between Gini coefficients estimated for ontogenetic categories should be viewed with caution, since most estimations were calculated using N < 50.

The present results showed that size hierarchies are dynamic, fluctuating between years in each population. Though generally lacking in studies reporting size inequalities in natural plant populations, this is not surprising. Leaf production depends on the availability of light and nutrients (Parkhurst and Loucks 1972, Chazdon 1986*b*), and varies among individuals inhabiting different patch types (Martínez-Ramos *et al.* 1988). In forest fragments, decomposition rates (Didham 1998) and light intensity (Saunders *et al.* 1991, Murcia 1995) respond in complex, unpredictable ways to environmental gradients such as edge distance and fragment size. Moreover, nutrient fluxes are often pulsed in tropical forests (Lodge *et al.* 1994), having strong influences on the fates of nutrients in ecosystems. Therefore, it is likely that leaf production, size and longevity are influenced by spatial and temporal heterogeneity of the resources available in forest fragments. This, in turn, could alter the position individuals hold in the size hierarchies and also alter the degree of size inequality found in the populations themselves. In this way, disturbances such as fire could lead to further increases in size variability.

Nevertheless, the relative degree of inequality between ontogenetic categories for both leaf number and size was little altered after fire. This is not surprising since fire action was quite homogeneous on both the immature, for which most plants had 50 – 75% of crown destroyed, and the adults, which were largely unaffected. Thus, it seems that different ontogenetic categories were damaged in similar proportions, thus maintaining the populations' size structure. The almost complete lack of extensively or completely burnt individuals could represent an underestimation of real values for the young due to the difficulty of finding small, burnt leaves amidst the thick layer of dead leaves that covered the ground in the months following fire. However, it is known that in monocots leaf arrangements and rigid leaf bases (Whelan 1995), as well as the possession of specialized underground organs (Crawley 1997) can insulate otherwise susceptible buds from the peak of heat in a fire. Thus, for immature and adult palms, it is probable that the rosette-like arrangement of leaves and buried meristem described in Chapter 1 for *Attalea* allows both protection of inner, younger leaves and leaf primordia, and production of new leaves shortly after fire.

The rise in leaf number inequality in adult palms immediately after fire in fragment II fits well with the subdivision of the population in two contrasting groups in similar proportions: undamaged (~ 50% of palms) and damaged to class three (~ 40%). Also, the discrepant concentration of immature and adult palms in such different levels of crown destruction (class three and unaffected, respectively), could result from the fact that fire was not homogeneously distributed and that these two ontogenetic categories had partially non-overlapping spatial distributions (Chapter 3). This is supported by the prevalence of unburned palms among the adults (Figure 1).

The reversal in the trend of decreasing size inequality from the young to adults for leaf number in 1999 was probably a result of increased environmental heterogeneity (Hartgerink & Bazzaz 1984) provoked by fire. Fires are generally patchy in their extent (Whelan 1995), and disturbed forests are more prone to natural or induced fires (Whelan 1995, Cochrane & Schulze 1999). The 1997 fire was patchy in the fragments (*per. obs.*), damaging mainly sites already disturbed as edges and the east and west portions of fragments I and II respectively. These sites experienced intense secondary growth, and most individuals of *Attalea* were overtopped by the formation of dense liana tangles and bamboo thickets, resprout of burnt trees and shrubs and growth of pioneer species. Thus, it is likely that the few reproducing individuals found in these plots had smaller sizes than the ones found in more preserved patches. The fact that this took place in relation to leaf number but not rachis length conforms to the suggestion of Souza *et al.* (1999) that leaf number and length are subjected to distinct selective pressures in *Attalea*.

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Table 1. General characterization of the study forest fragments at the National Biological Reserve of Poço das Antas, Rio de Janeiro State, southeastern Brazil.

Fragment	Area (ha)	Perimeter (m)	P:A[a]	Number of 10 x 10 m Plots	Sampled Area[b] (m^2)	Trees/ha[c] (DBH $\geq$ 10 cm)	Mean Height[c] (m)	Litterfall[d] (ton ha^{-1} y^{-1})	Density of *Attalea humilis*[e] (palms ha^{-1})
I	1.6	325	0.020	29	2900 (18.1)	426	7.6	4.1	130.0
II	6.4	650	0.010	61	6100 (9.5)	514	9.4	5.3	900.0
III	9.9	775	0.008	70	7000 (7.1)	797	9.3	5.7	140.0

a - Perimeter (m): area (m^2) proportion; b - Percent area of each fragment sampled in parenthesis; c - Silva Matos *et al.* (1998*a*); d - Silva Matos *et al.* (1998*b*); e - Calculated from Souza *et al.* (1999) data for 1996.

Table 2.Densities (mean number of individuals per 100 m^2 ± SD) of *Attalea humilis* in three fragments of the Atlantic Forest. Minimum and maximum density values are shown in parenthesis. Dashed line indicates the occurrence of fire.

	Year			
Fragment	1996	1997	1998	1999
I	1.3 ± 1.4	2.0 ± 3.1	1.7 ± 2.1	1.5 ± 2.5
	(0 – 4)	(0 – 15)	(0 – 9)	(0 – 12)
II	9.0 ± 8.3	–	8.1 ± 7.0	7.5 ± 6.1
	(0 – 32)		(0 – 26)	(0 – 22)
III	1.4 ± 1.6	1.5 ± 1.7	1.3 ± 1.4	1.2 ± 1.4
	(0 – 9)	(0 – 8)	(0 – 5)	(0 – 6)

Table 3. Linear regression coefficients of individual leaf number and rachis length on plot density. S = seedling, I = immature, A = adult; r^2 = coefficient of determination.

			Number of Leaves		**Leaf Rachis Length**	
Category	**Fragment**	n	Slope	r^2	Slope	r^2
1996						
I	I	18	-0.259	0.057	-0.328$^{(1)}$*	0.290
A	I	18	0.375	0.051	10.417	0.027
S	II	38	0.024	0.010	-1.113	0.053
I	II	186	-0.023*	0.030	-0.166	0.000
A	II	323	-0.029	0.010	0.239	0.000
S	III	17	-0.189	0.207	-3.004*	0.360
I	III	33	0.025	0.005	-8.932	0.061
A	III	48	0.587**	0.249	12.779	0.045
1997						
S	I	24	-0.053	0.094	-0.805	0.094
I	I	9	-0.083	0.037	-46.833	0.301
A	I	26	-0.047	0.025	2.308	0.013
S	III	24	-0.348*	0.221	-3.154**	0.278
I	III	39	0.029	0.003	-17.704**	0.197
A	III	42	0.127	0.023	9.877	0.088
1998						
S	I	13	0.163$^{(1)}$**	0.633	5.968	0.084
I	I	35	0.100	0.023	4.925	0.010
S	II	27	0.001	0.000	-0.450	0.099
I	II	420	-0.003	0.001	-2.186	0.020
A	II	47	-0.215**	0.185	-4.926*	0.095
S	III	10	-0.215	0.078	-0.823	0.007
I	III	58	0.227*	0.076	3.307	0.003
A	III	24	0.027	0.000	-1.180	0.000

* $P < 0.05$ ** $P < 0.01$; (1) ln-transformed data; seedlings were absent from fragment I in 1996.

Table 3. Continued.

Category	**Fragment**	**n**	**Number of Leaves**		**Leaf Rachis Length**	
			Slope	r^2	Slope	r^2
			1999			
S	I	15	0.047	0.045	-0.027$^{(1)}$	0.226
I	I	23	-0.066	0.020	-0.099	0.000
A	I	13	-0.073$^{(1)}$**	0.590	-0.0203$^{(1)}$ **	0.763
S	II	39	0.004	0.000	-0.217	0.002
I	II	260	0.008	0.004	-1.656	0.011
A	II	160	-0.080**	0.085	-2.050*	0.033
S	III	6	0.667	0.200	4.333	0.024
I	III	54	-0.148	0.052	-0.070$^{(1)}$	0.046
A	III	26	0.048	0.066	23.596*	0.162

* $P < 0.05$ ** $P < 0.01$; (1) ln-transformed data; seedlings were absent from fragment I in 1996.

Table 4. Mean corrected Gini coefficients ± SD for leaf number distributions in ontogenetic phases of populations of *Attalea humilis* in three forest fragments. For each year, means accompanied by different letters (upper case for lines, lower case for columns in the same year) differ at 5% significance level. Dashed line indicates the occurrence of fire; – indicates the absence of the phase.

Fragment	**Ontogenetic Phase**		
	Seedling	**Immature**	**Adult**
		1996	
I	—	0.161 ± 0.031 *aA*	0.163 ± 0.059 *abA*
II	0.233 ± 0.030 *aB*	0.159 ± 0.009 *aA*	0.170 ± 0.006 *bA*
III	0.236 ± 0.041 *aB*	0.145 ± 0.028 *aA*	0.134 ± 0.011 *aA*
		1997	
I	0.163 ± 0.019 *aB*	0.072 ± 0.013 *aA*	0.113 ± 0.017 *aB*
III	0.300 ± 0.033 *bC*	0.171 ± 0.016 *bB*	0.107 ± 0.012 *aA*
		1998	
I	0.191 ± 0.053 *aA*	0.214 ± 0.043 *aA*	—
II	0.241 ± 0.032 *aB*	0.158 ± 0.006 *aA*	0.269 ± 0.025 *bB*
III	0.216 ± 0.062 *aB*	0.201 ± 0.025 *aB*	0.113 ± 0.023 *aA*
		1999	
I	0.117 ± 0.023 *aA*	0.175 ± 0.028 *bA*	0.194 ± 0.057 *aA*
II	0.140 ± 0.019 *aB*	0.092 ± 0.005 *aA*	0.140 ± 0.010 *aB*
III	0.119 ± 0.045 *aA*	0.138 ± 0.017 *bA*	0.145 ± 0.024 *aA*

Table 5. Mean corrected Gini coefficients ± SD for leaf rachis length distributions in ontogenetic phases of populations of *Attalea humilis* in three forest fragments. For each year, means accompanied by different letters (upper-case for lines, lower-case for columns in the same year) differ at 5% significance level. Dashed line indicates the occurrence of fire; – indicates the absence of the phase.

	Ontogenetic Phase		
Fragment	**Seedling**	**Immature**	**Adult**
		1996	
I	—	0.311 ± 0.052 *aB*	0.173 ± 0.050 *aA*
II	0.336 ± 0.044 *aB*	0.322 ± 0.016 *aB*	0.152 ± 0.008 *aA*
III	0.244 ± 0.046 *aAB*	0.302 ± 0.038 *aB*	0.157 ± 0.016 *aA*
		1997	
I	0.185 ± 0.050 *aA*	0.260 ± 0.070 *aA*	0.157 ± 0.028 *bA*
III	0.230 ± 0.050 *aB*	0.268 ± 0.032 *aB*	0.097 ± 0.017 *aA*
		1998	
I	0.344 ± 0.157 *aA*	0.324 ± 0.038 *aA*	—
II	0.216 ± 0.036 *aB*	0.283 ± 0.009 *aB*	0.124 ± 0.013 *aA*
III	0.280 ± 0.081 *aB*	0.273 ± 0.022 *aB*	0.092 ± 0.014 *aA*
		1999	
I	0.126 ± 0.030 *aB*	0.178 ± 0.021 *aB*	0.027 ± 0.008 *aA*
II	0.251 ± 0.020 *bB*	0.211 ± 0.008 *abB*	0.103 ± 0.008 *bA*
III	0.161 ± 0.047 *abAB*	0.244 ± 0.020 *bB*	0.124 ± 0.021 *bA*

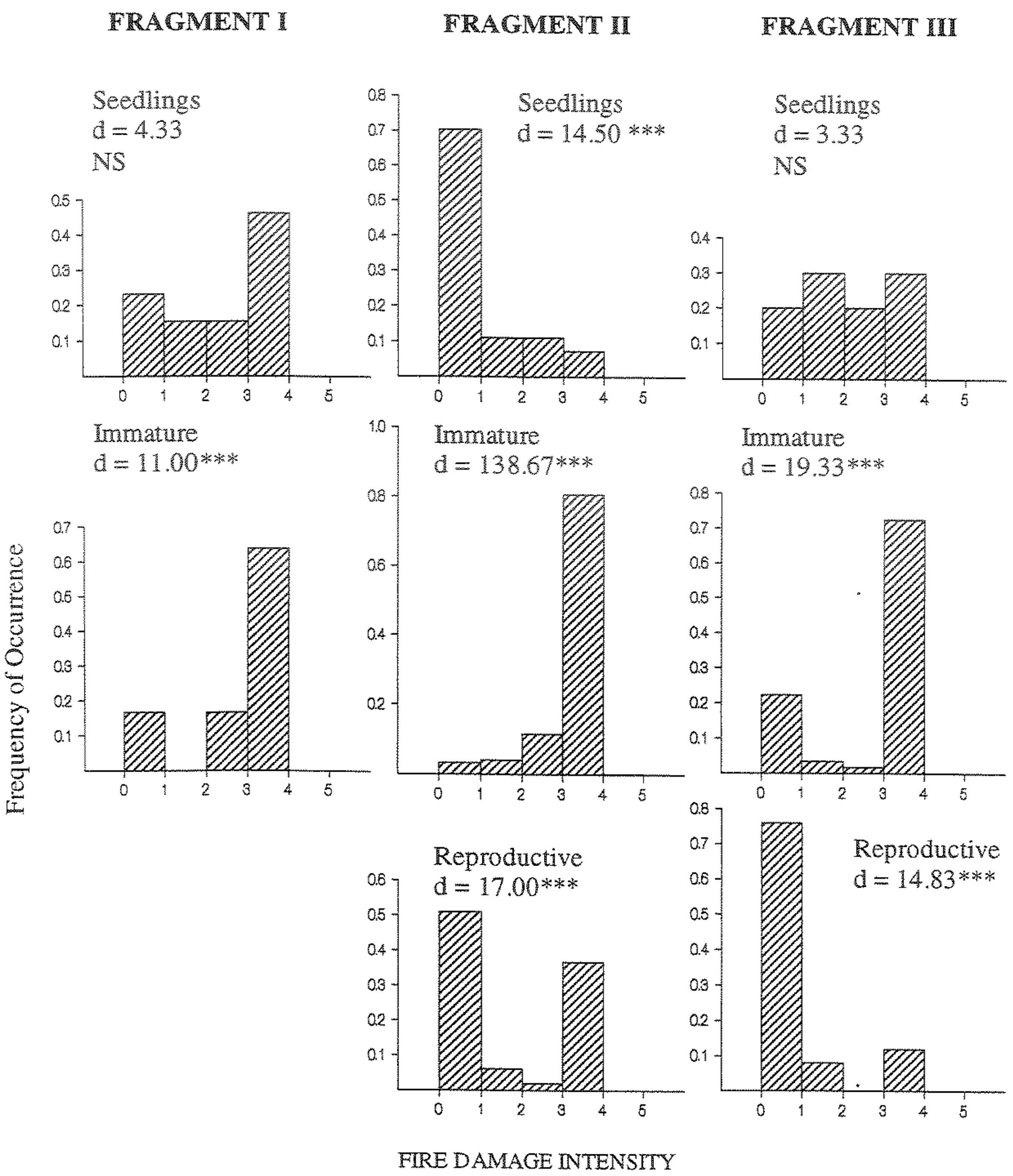

Figure 1. Distributions of the degree of crown damage by fire in *Attalea humilis* in three ontogenetic phases, in three forest fragments at the National Biological Reserve of Poço das Antas. Degrees of crown damage: 0) no apparent damage, 1) from zero to 25%, 2) from 25 to 50%, 3) from 50 to 75%, 4) more than 75% and 5) entirely destroyed. The fits of uniform distributions to the data were tested using the Kolmogorov-Smirnov test on the categorical data. d = maximum absolute difference between two cumulative distributions. *** $P < 0.001$; NS = non significant. Sample sizes as in Table 2.

CAPÍTULO 3: Spatial Distribution of the Palm *Attalea humilis* Mart. ex Spreng. in Fragments of the Brazilian Atlantic Forest: Combined Effects of Habitat Heterogeneity, Dispersers, and Fire?[1,2]

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1 – Trabalho formatado segundo as regras da revista *Plant Ecology*

2 – Tabelas e Figuras no final do Capítulo

RESUMO. Um estudo da distribuirão espacial das categorias ontogenéticas da palmeira acaule *Attalea humilis* foi conduzido em três fragmentos da Floresta Atlântica, cujo tamanho ia de 1.6 a 9.9 ha, de 1996 a 1999. Análises espaciais basearam-se no índice de dispersão de Morisita, calculado para várias escalas, análises de correlação entre a densidade de palmeiras e a distância da borda da floresta e comparaçãoes entre lados dos transectos amostrais voltados para as quatro direções cardinais. A associação entre categorias foi testada com dados de presença/ausência. Os principais resultados foram: (1) as palmeiras estavam significativamente agregadas na maioria das escalas, mas uma redução no grau de agregação ocorreu de jovens para adultos em todos os fragmentos; (2) os padrões espaciais variaram pouco entre os anos; um incêndio aumentou temporariamente o grau de agregação dos jovens; (3) categorias ontogenéticas não foram encontradas nas mesmas parcelas com mais frequencia do que esperado ao acaso na maioria dos casos, mas uma associação significativa entre palmeiras reprodutivas entre anos sucessivos foi encontrada em dois fragmentos; (4) a distribuirão das palmeiras entre os lados das transecções variou com a categoria, o fragmento e o ano, mas apresentou estabilidade entre anos, sendo pouco afetada pelo fogo; (5) não foi encontrada uma relação geral entre a densidade de palmeiras e a distância da borda dos fragmentos, mas sim uma resposta complexa e esporádica. Sugerimos que a dispersão de sementes a curta distância realizada por roedores resulta em agregados discretos e de baixa densidade de jovens, dissociados dos reprodutivos. Categorias posteriores ficam restritas principalmente a sítios mais abertos e perturbados. Estes seriam representados por clareiras no fragmento maior e mais preservado, e por setores contínuos perturbados no fragmento de tamanho intermediário,

formando manchas contínuas de palmeiras. Este padrã oparece ser reforçado pelo fogo, que tende a ocorrer em sítios queimados anteriormente. Para a espécie estudada, a heterogeneidade ambiental em larga escala parece ser mais importante do que o efeito de borda.

Key words: Edge effects, Ontogenetic stages, Tropical forests

Abstract

A study the spatial distribution of ontogenetic stages of the acaulescent palm *Attalea humilis* was conducted in three fragments of the Brazilian Atlantic forest ranging in size from 1.6 to 9.9 ha from 1996 to 1999. We analysed data on the number of palms in each stage in two perpendicular transects subdivided in 10 x 10 m plots that cut across each fragment. Spatial analysis were based on Morisita's index of dispersion calculated at a range of quadrat sizes, correlation analysis between the palm density and distance from forest edge and comparisons among transect sides facing each of the cardinal points. Association between stages was tested with binary presence or absence data. The main results were as follows: (1) palms were significantly clumped at most scales, but a marked reduction in clumping degree occurred from seedling to the adult stage in all fragments; (2) spatial patterns showed subtle variations among fragments and years; fire increased temporarily the clumping degree of the young; (3) ontogenetic stages were not found in the same plots more often than expected by chance in the majority of cases, but a significant association of reproductive palms between years was found in two of the fragments; (4) palm distribution among transects sides varied with stage, fragment and year, but showed stability between years, being little affected by fire; (5) no general relationship between palm density and distance from fragment edge could be detected for any stage, fragment, or year, but a complex and sporadic response was found instead. We hypothesise that short-distance seed dispersal by scatterhoarding rodents results in discrete, low-density clumps of

young palms dissociated from reproductive plants. Later stages are mostly restricted to more open, disturbed sites. These are represented by canopy gaps in the larger, more closed fragment, thus generating the randomly distributed clumps of palms observed there. In the other fragments, the presence of large disturbed sectors promotes the formation of large, continuous stands of palms. This pattern seems to be reinforced by fire, which tends to burn already disturbed patches. For the species studied, large-scale spatial habitat heterogeneity seems to be more important than restricted edge effects.

Introduction

The study of tropical forest fragmentation represents a challenge for ecologists. The process of fragmentation brings a series of complex and synergistic effects to the already complex issues of community structure and composition, population biology, and species interactions in tropical forests (Saunders *et al.* 1991, Bierregaard *et al.* 1992). The Brazilian Atlantic forest constitutes one of the most dramatic examples of forest fragmentation. It extends along the Brazilian coast, where a long history of land clearing and the concentration of the largest part of the country's population nowadays makes it one of the most threatened tropical forest ecosystems in the world (Dean 1996, Viana & Tabanez 1996). This forest constitutes a unique biome characterised by one of the highest levels of species diversity and endemism in the world (Mori *et al.* 1981, Fonseca 1985). Most of the remaining cover of the Atlantic forest is represented by small, privately owned fragments (Fonseca 1985, Ranta *et al.* 1998). These fragments are frequently exposed to human-induced fires (Dean 1996), which represents a further threat to their preservation.

The acceleration of forest clearing and creation of forest fragments (Whitmore 1997) has given opportunity to many studies on the consequences of fragmentation on the number of species retained in these remnants (Turner 1996). However, effective conservation efforts must rely on an understanding of both community and population biology, which are the main tools of conservation science (Simberloff 1988). Knowledge of the responses of particular species to the changes fragmentation produces in their habitats is extremely necessary nowadays as a mean to understand the processes that lead to the observed patterns of species loss (Crome 1997). Yet comparatively few long-term studies have been conducted on aspects of the population biology of particular plant species in tropical forest fragments.

Studies of plant spatial distribution bring promising opportunities of understanding the combined effects of various ecological forces, allowing the formulation of testable hypotheses about the underlying processes, that link demography, plant spatial patterns and environmental heterogeneity (Barot *et al.* 1999*a*,*b*). The spatial distribution of established plant populations is an outcome of the interplay between the spatial distribution of seed-producing plants and of the seed rain, the behaviour of seed and seedling predators, and the spatial distribution of suitable germination sites determine the final spatial distribution of adults (Hutchings 1997). In forest fragments human-induced impacts (Oliveira-Filho *et al.* 1997, Svenning 1998) and edge effects (Murcia 1995) also influence the spatial distribution of plants.

The studies by Henriques & Sousa (1989) and Oliveira-Filho ·*et al.* (1996) are among the few published for tropical plant populations in Brazil, and only the latter was carried out in a fragment of the Atlantic forest. In this paper we present data on the spatial distribution of populations of *Attalea humilis*, an endemic palm of the Brazilian Atlantic forest, in small forest fragments from 1996 to 1999. We adopted the life-stage demographic approach (Barot *et. al* 1999*a*) which considers the developmental stages that composes the species life cycle as the study units. Specifically, we addressed the following questions: (1) how does the spatial distribution of different life stages vary between fragments of different sizes? Life stages generally comprise groups of individuals sharing specific morphological and physiological traits (Lawson & Poethig 1995), and thus present potentially distinct ecological requirements. We expect that the contrasting environments represented by different forest fragments act differently on each stage, generating distinct spatial patterns; (2) are the life stages spatially associated, implying a general concordance in their responses to local environmental conditions or attraction by one or both stages by the other (Ludwig & Reynolds 1988)? *A. humilis* produces large seeds that frequently accumulate beneath parent plants (Chapter 1). We thus expect seedlings to be associated to adult plants; (3) are the spatial patterns aggregation and concentration of palms in specific fragments sectors) in each fragment stable through time? Since *A. humilis* is a perennial, long-lived species, we expect changes in its spatial distribution to be slow and difficult to detect in short time-periods; (4) what are the changes in the spatial pattern after a disturbance, like fire? Since established individuals bear a protected, subterranean meristem (Chapter 1) we expect the main changes in the spatial distribution to take place among younger stages, which bear superficial underground systems and are thus more susceptible to fire-induced mortality.

Methods

StudysSite and study species

Field data were collected in the Poço das Antas National Biological Reserve (22°30'-22°33'S, 42°15'-42°19'W), municipality of Silva Jardim, State of Rio de Janeiro, southeastern Brazil (Fig. 1a). The Reserve covers ca. 5000 ha of lowland (maximum elevation of 205 m a.s.l.) Atlantic forest, and comprises a mosaic of vegetation patches with different successional phases (IBDF/FBCN 1981). The area is surrounded by pastures, cultures and secondary forests. The regional climate is classified as Walter and Lieth's Equatorial type (Walter 1971). Despite large variation in rainfall between years, all months are considered perhumid (precipitation over 100 mm), but less rainfall occurs in the period extending from May to August, when drought episodes are not absent (Fig. 1b).

The sites selected are part of the complex locally known as the 'Barbados archipelago' (Fig. 1c), a mosaic of eight forest fragments located on small hills originally isolated by permanent waterlogging, near the left margin of the São João river. Since the building of the Juturnaíba dam in 1981, the water regime of the São João River was altered, draining the area surrounding the fragments. The fragments are now embedded in a vegetation matrix dominated by grasses, patches of the bracken fern (*Pteridium aquilinum*) and isolated stands of *Cecropia* sp. (Cecropiaceae) and *Trema micrantha* (Ulmaceae). Matrix soils are classified as Histosols (USDA 1990), a type of organic soil originated from peat, while the soils in the fragments form an indiscriminate grouping of alic Oxisols/Ultisoils, with moderate A horizon and clayey to very clayey texture (Takizawa 1995). The lower levels of the matrix suffer annual inundation during the rainiest months (December through March). The Barbados archipelago has been subject to a defaunation process due to clandestine hunting, which concentrates on large mammals and birds.

As part of a larger project (Silva Matos *et al.* 1998*b*), three forest fragments were selected, ranging in size from 1.6 to 9.9 ha (Fig. 1). The fragments present differences in density and mean height of trees ≥ 10 cm DBH (Silva Matos *et al.* 1998*a*), litterfall (Silva Matos *et al* 1998*b*) and shape (Table 1). The smallest fragment is subjected to higher air and soil temperatures and lower air relative humidity and soil moisture content, as well as larger wind penetration distances (Silva Matos *et al.* 1998*b*). Since the drainage of the matrix in 1981, the area suffered recurrent, man-induced fires in 1982, 1990, 1993 and 1997. These fires have taken place during the driest months and frequently invaded the fragments, causing variable damage.

The study species, *Attalea humilis* Mart. ex. Spreng., hereafter referred to as *Attalea*, is a monoecious, solitary palm with a short, subterranean stem (saxophone-axis type, Tomlinson & Jeffrey 1990; see Souza *et al.* 1999 for a morphological description). The apical meristem, protected by the surrounding leaf sheaths, is also subterranean. The aerial portion is composed by the crown, which has 5 - 16 pinnatifid, spineless, up to 7 m long leaves (Souza *et al.* 1999). The species is restricted to the central-south-eastern Atlantic Forest, ranging from the state of Bahia to the state of São Paulo (Henderson *et al.* 1995, Lorenzi *et al.* 1996). It grows both in the forest understory and in open areas, like abandoned pastures or secondary, disturbed forests. In more open sites it often forms large, nearly homogeneous stands (Henderson *et al.* 1995), being sometimes regarded as a pasture invader (Lorenzi *et al.* 1996). Through most of its range, *Attalea* occupies mainly the crests or slopes of hills but rarely flooded sites. Based on morphological and morphometrical analysis, we distinguished five ontogenetic stages in *Attalea* (Souza *et al.* 1999): seedlings present entire, distichous leaves; juveniles present bifid, incompletely segmented ones; immature individuals produce completely segmented leaf blades, being distinguished from virginile ones by having fewer leaves and smaller but highly variable youngest leaf blade length; reproductive palms are recognised by the production of flowers and fruits.

Sampling method and data analysis

Palms were censused along two perpendicular 10 m wide transects that cut across each fragment (Fig. 1c). Transects were aligned as closely as possible with the north-south and east-west directions, and divided in 10 x 10 m contiguous plots. The sampled area covered 7 - 18 % of each fragment area (Table 1). In each plot we censused all individuals of *Attalea* from July 1996 to January 1997 (1996 field survey) and between July and August 1997 (1997 field survey). At the end of the 1997 dry period (August-September) a fire damaged *ca.* 1000 ha of the Reserve, including the study area. Fire prevented the conclusion of the 1997 field survey, and data could not be collected in fragment II. To access the effects of fire on the populations under study, field surveys were carried out in April 1998, after reconstruction of destroyed plots, and in June 1999. In the analysis, individuals in the seedling and juvenile stages (hereafter the 'young') were pooled together due to the low number of juveniles and to the fact that their leaf number and length are not different (Chapter 1). Virginile and reproductive individuals were also grouped (hereafter 'adults'), since they present extensive leaf number and size coincidence and together probably represent the potentially reproductive individuals (Chapter 1). Thus, in the analysis we considered the young, the immature and adult as ontogenetic categories.

The degree of clumping in different stages was determined through the Morisita index of dispersion I_M (Morisita 1962), calculated with the NEGBINOM procedure of the Krebs/WIN program (Krebs & Brzustowski 1998). The value of the index $I_M = 1.0$ for randomly distributed individuals, > 1.0 for clumped individuals and < 1.0 for regularly distributed individuals. The statistical significance of the departure of each I_M from 1.0 was tested with the statistic $\chi^2_{(df=Q-1)} = (Q - 1)\ s^2/\bar{x}$ (David & Moore 1954), where Q is the number of plots in the sample and s^2 and $\bar{x}$ are the sample variance and mean, respectively. As the degree of clumping in nature is frequently strongly influenced by the spatial scale considered (Hurlbert 1990), we calculated I_M and the significance of its departure from 1.0 at a range of plot sizes using the Two-Term Local Quadrat method of plot pooling (Ludwig & Reynolds 1988). Plots were pooled until plot size approximated the scale of one arm of a transect, i.e. 600 m^2 in fragment I and 1500 m^2 in fragments II and III.

As significant clumping was found for most cases at larger scales, we tested for differences in palm density among transect arms. Exploratory data analysis showed strong deviance from normality in most cases, which was not satisfactorily corrected with either log or square root transformations. As transect arms were not equal, we performed plot-based comparisons among them with nonparametric Kruskal-Wallis analysis of variance. When significant differences were found, nonparametric multiple comparisons were carried out using the *Q* statistic with a standard error for unequal sample sizes (Zar 1996).

Two-way contingency tables were used for testing the independence of each pair of stages with binary (presence or absence)-reduced data (Ludwig & Reynolds 1988, Zar 1996). Pearson's Chi-square and Fisher's exact test were computed for each case, and an association was considered significant when the two statistics were concordant (Wilkinson 1999). Yates's corrected Chi-square was used instead of Pearson's Chi-square in cases where any cell in the table had an expected frequency < 1 or more than two cells had expected frequencies < 5 (Ludwig & Reynolds 1988). The Jaccard index was computed for significant cases as a measure of the degree of association between the stages (Ludwig & Reynolds 1988). Significant trends in palm density as a function of both distance from fragment edge and density of other ontogenetic categories were tested using the nonparametric Spearman's rank correlation coefficient (Zar 1996). When all three ontogenetic categories showed significant pairwise correlation we expressed their relationship through Kendall's coefficient of concordance (Zar 1996). All analysis were performed with SYSTAT software (SYSTAT 1998) at the 5% significance level.

Results

Clumping degree at various scales

During the study years, the three fragments had different densities of palms in each category (Table 2). Palms were significantly clumped at most scales, but a marked reduction in clumping degree occurred from the young to the adult category (detailed statistical results are given in the Appendix; summary results in Fig. 2). I_M of the young decreased from its highest values in the smaller plot sizes towards unity as plot size increased. This result, however, could be partly attributed to the mathematical properties of the index, which maximum value is always the maximum number of plots. Despite this scale-dependent reduction, the young exhibited significant clumping at all scales (see Appendix). This pattern indicates the existence of patches of high population density, away from which density decreases more or less abruptly (Hubbell 1979). Considering all fragments and years, plots with higher densities had 4 – 7 young palms, with the exception of fragment I, where one plot had 11 young palms in 1997. Adult and immature plants, on the other hand, showed to be loosely clumped at all scales, with small variation of I_M as quadrat size increased, indicating the presence of large clusters of palms over extensive areas of each fragment.

These patterns were dynamic, showing subtle variations between fragments and years. The young were less clumped in fragment II than in the other two fragments, with smaller I_M values at all scales (Fig. 2). The immature were randomly dispersed at all scales in fragment I. In fragment III the immature shifted from clumped to random dispersion at the 200 m^2 scale, which was successively reversed at 500 m^2 and 600 m^2 (see Appendix), indicating the presence of randomly dispersed clumps. This picture remained stable from 1996 to 1997, and presented few changes after fire (Fig. 2). In 1998, six months after fire, the young were much more clumped than in previous years in all three fragments. Adults were randomly dispersed at scales up to 500 m^2 and beyond 600 m^2 in fragment II. In fragment III adults showed clumping at all scales in spite of the shifting pattern found previously. In 1999 the spatial patterns resembled those of the years before fire: the clumping degree of young was reduced in all fragments, the immature and adults showed little but significant clumping at all scales in fragment II, and in fragment III immature palms showed shifting patterns at increasing scales. Exceptions were adults, randomly dispersed in fragment I and significantly clumped at all scales in fragment III.

Association between ontogenetic categories

Despite generally occurring as more or less definite clusters of palms, *Attalea* ontogenetic categories were not found in the same plots more often than expected by chance. Only two out of 29 possible site- and time-specific associations between categories were significant: the young were positively associated with the immature in fragment II in 1996 ($\chi^2 = 15.8$, df = 1, $P < 0.0001$; Jaccard = 0.46), and with adults in fragment III in 1997 ($\chi^2 = 8.4$, df = 1, $P = 0.004$; Jaccard = 0.28).

As only a fraction of adult individuals actually reproduced each year, the lack of association between young and adult palms could hide existing associations between young and reproductive palms. Thus we also tested for associations involving the reproductive stage (apart from the virgin stage). In the two largest fragments, reproductive individuals were significantly associated in successive years (Fig. 3), though in fragment II the association was nearly half as strong as in fragment III. This suggests that the palms reproducing each year were not a random assemblage of adults, but to a large extent represented the same individuals, concentrated in a few plots. Young palms found in successive years, in turn, were not the same in most cases (Fig. 3). Significant but weak associations between young and reproductive palms occurred in fragments II and III in the years before fire, but were not present after fire anymore. Although patterns were difficult to distinguish in the smallest fragment, fire apparently changed the inter-annual association between the reproductive from 1996 to 1997, but a 40% association appeared between the young from 1998 to 1999.

Covariances between ontogenetic categories

The overall pattern of lack of association between ontogenetic categories (adult palms considered) could hide a larger number of significant covariances (Table 3). In 1996 all categories in fragment II were positively correlated with each other (Kendall's coefficient of concordance $W = 0.60$, $\chi^2 = 109.9$, $df = 61$, $P < 0.001$). This mutual concordance between the abundance of ontogenetic categories disappeared after fire, but returned in 1999, although not as strongly as in 1996. In 1999 the immature and adult categories were also correlated in fragment I. In fragment III the sole significant case was a weak correlation between the young and adults in 1997, expected by their qualitative association (see above).

Palm distribution among fragments' s sectors

Palm distribution between transect arms varied with ontogenetic category, fragment and year (Table 4). In the small- and medium-sized fragments (I and II), immature and adult palms were concentrated in the west arm, while in the largest fragment the adults were more common in the south arm (Table 5). These patterns were consistent.through the study years, presenting minor changes even after fire. In the smallest fragment, the east arm presented the lowest palm densities during the study period, and in 1999 no palms were found in it. Similarly, in fragment II palms remained aggregated in the west arm in all years except 1988, when adults were evenly found in all transect arms. The south transect arm of fragment III remained denser in adults until 1999, when distinct concentration of ontogenetic categories between arms could no more be detected. Young density per plot did not differ between transect arms in any fragment or year.

Relationship between palm density and fragment edge

No general relationship between palm density and distance from fragment edge could be detected for any stage, fragment, or year. Instead, a complex response of palms emerged in relation to distance from fragment edge depending on transect arm (Table 6). In the smallest fragment, the number of adults decreased towards the edge in the arm with lower densities of palms (east arm) before fire. In fragment II, the abundance of all ontogenetic categories increased towards the fragment edge in the east, but the immature showed the opposite trend in the north and west arms, as well as adults in the west. In the years before fire, palm numbers were not responsive to the distance from the edge in the largest fragment.

Apparently, fire weakened any tendency of varying density with distance from fragment edge (Table 6). In 1998 not the adults but the immature were negatively related to the distance from the edge in the eastern transect arm of fragment I, while in fragment II only the immature were responsive to increased distance from the edge. In both cases, however, both correlation sign and strength were similar to before-fire values. In fragment III the density of immatures increased towards the fragment centre in the north arm and decreased in the west arm. In 1999 no palms were found in the eastern side of fragment I, and the density in the west arm was positively associated with the distance from the edge. In fragment II all stages were again associated with the edge in the east, but the previously strong positive relation of the immature with the centre of the fragment disappeared in the south. A significant increase of the number of young palms towards the fragment edge, however, appeared in the west side. In fragment III the positive relationship between the density of immatures and the distance from the edge held in the north arm, and was also detected in the east.

Discussion

In all forest fragments, irrespective of year, young *Attalea* occurred in patches of a few individuals, away from which virtually no young palms were found. Additionally, the young were not associated with adult or reproductive palms, as we would expect for a ground-bearing, large-seeded species. Why would it be so? *Attalea* fruits fit the dispersal syndrome by hoarding mammals (Howe & Westley 1997), and all seedlings emerge from buried seeds, being probably dispersed by squirrels and agoutis (Chapter 1). Seeds found beneath reproductive palms were either desiccated or rotten, often with signs of insect attack (*pers. obs.*). Seed predators commonly attack undispersed seeds accumulated under parent plants (Wilson & Janzen 1972, Lott *et al.* 1995, Pizo 1997), and it has been suggested that seedling production of *Attalea* is dependent upon scatterhoarding rodents (Chapter 1).

Squirrels and agoutis are known to bury large seeds intact (Smythe 1970, Paschoal & Galetti 1995, Peres & Baider 1997), usually in caches of individual seeds near natural objects (Kiltie 1981) over their whole home range (Dubost 1988), generating a diffuse surface of caches of single seeds (Peres & Baider 1997). Sist (1989) attributed to this behaviour the random distribution of seedlings of *Astrocaryum sciophilum* found in French Guiana. However, studies on rodent caching behaviour usually do not consider explicitly the spatial distribution of caches, and refer to harvested seeds irrespective of species. The process of seed dispersal generally produces a heterogeneous pattern of seedfall across the landscape, with many seeds falling in some patches and a few landing in others (Martínez-Ramos *et al.* 1989, Schupp 1993). Rodents transport seeds over short distances, usually of a few meters from feeding places, often generating spatially restricted seed shadows (Price & Jenkins 1986, Forget 1990, Forget *et al.* 1994, Peres & Baider 1997). Furthermore, although agoutis cache seeds individually, their tendency to locate caches near reference objects such as fallen trunks, palms, roots and trees (Kiltie 1981, Cintra 1998) implies in clusters of caches near such objects. As reproductive *Attalea* are clumped, we could expect rodent cache behaviour and short-distance seed dispersal to generate a clumped seed shadow, with caches not necessarily associated to the distribution of seed-producing plants.

The distribution of dispersed seeds near objects is reflected in the distribution of seedlings (Kiltie 1981). Clumped distribution of more developed ontogenetic categories is generally associated with limited dispersal of seeds (Hubbell 1979). Thus, the clumped distribution of young *Attalea* is likely to result from limited seed dispersal by rodents superimposed to the distribution of patches suitable to germination. These may be represented by shaded sites with low drying potential (Broschat & Donselman 1988), since palm seeds are sensible to desiccation and are buried at only a few centimetres from the surface (Peres & Baider 1997, Chapter 1).

An overall tendency towards a less aggregated pattern along the life cycle has been found in a number of tropical palm (Sterner *et al.* 1986, Barot *et al.* 1999*a*) and tree species (Hubbell 1979, Henriques & Sousa 1989, Oliveira-Filho *et al.* 1996). Density-dependent mortality (self-thinning) has been invoked in the majority of studies as the main reason for this reduction in clumping degree along the life cycle. In most cases, however, the local seedling density is very high compared with later stages, and seedlings occur in dense clumps around reproductive plants (*e.g.* Henriques & Sousa 1989, Silva Matos & Watkinson 1998, Barot *et al.* 1999*a*), where competition, seedling predation and pathogen attack are intense (Janzen 1970, Augspurger 1984, Clark & Clark 1984, Barot *et al.* 1999*b*). However, this scenario is unlikely for *Attalea*, for the following reasons. The young occurred at very low local densities (maximum of 11 individuals per 100 m^2) throughout the fragments, and their higher clumping degree was largely a result of their relative absence from most plots. Young palms form discrete 'clumps' at the 100 m^2 and larger scales, but are not crowded at the individual level. Hence, intraspecific competition and attack of density-responsive herbivores are unlikely to take place regularly among such clumps. Additionally, considering that immature and adult palms show virtually no signs of herbivory (*pers. obs.*) and that the young were not associated with adults, distance-dependent survivorship is also a remote possibility.

Since seed-dispersing rodents concentrate their caches near natural objects a few meters from original seed sources, and considering that both reproductive palms and structural elements of forests are dynamic, it is likely that, as time goes on, loose clumps of young palms emerge at different places. This picture agrees with the weak and sporadic association found between clumps of young plants in each fragment in successive years. While seedlings of many palm species may subsist in shaded understorey due to their large seed reserves (Saverimuttu & Westoby 1996) and reduced physiological activity (Hogan 1988), their growth and survival are frequently enhanced by increased light availability in gaps and disturbed sites (Chazdon 1986, Kahn 1987, Hogan 1988, Martínez-Ramos *et al.* 1988, Cintra & Horna 1997).

Species of *Attalea* are known to thrive in disturbed areas such as river margins, clearings and light gaps (Henderson *et al.* 1995, Lorenzi *et al.* 1996), and have enhanced photosynthetic activity under increased light conditions (Hogan 1988). There is some evidence that the role of rodents in dispersing large seeds secondarily is more important for finding suitable sites merely by enlarging seed shadow than by directing dispersal to more open sites (Hoshizaki *et al.* 1999). Hence, the distribution of immature and adult individuals of *Attalea* in the studied fragments is likely to result from the interaction between the initial distribution of seedling 'clumps' and the distribution of more open patches, where recruitment to later ontogenetic categories is more probable.

In the largest, more closed fragment studied, open patches are restricted to the occurrence of natural treefall gaps, which are distributed through the whole area of the fragment (*pers. obs.*) as discrete events. The patchy distribution of favourable habitats is probably the main cause of the distribution of immature and adult *Attalea* as random, low-density clumps of palms. This was probably the distribution of *Attalea* populations in the originally continuous Atlantic Forest, and should still be found in fragments with preserved structure. However, most of the small Atlantic Forest fragments show marked structural heterogeneity in the form of disturbed sectors with lower canopy heights and basal areas per hectare, higher tree densities and liana tangles and sometimes bamboo-dominated patches (Viana & Tabanez 1996, Oliveira-Filho *et al.* 1997). Preliminary data (Silva Matos *et al.* 1998*a*,*b*) indicate that fragments II and I are marked by extensively disturbed sectors, which probably affect the distribution of *Attalea*.

Although presenting mean dossel height and tree density similar to those of fragment III (9.9 ha), fragment II (6.4 ha) is characterised by high internal structural variability, with disturbed, secondary forest dominating its west sector (D. M. Silva Matos unpub. data). The predominance of disturbed conditions over continuous sectors of this fragment may enable successive clumps of young palms in different years to find better chances of survival, leading to the formation of large, dense stands of palms in the west arm of the transect (Table 3). Thus, in this case, reduced clumping degree detected in later ontogenetic categories probably resulted from successful establishment of adjacent seedling clumps over extensive areas. In the smallest fragment, a converse aspect of habitat heterogeneity could lead to the concentration of *Attalea* in the transect west arm. This fragment presents highly altered biotic and abiotic characteristics (Table 1, D. M. Silva Matos unpub. data), and probably has no remaining 'core' habitat. Its east side is dominated by monospecific, dense stands of *Trema micrantha* (Silva Matos *et al.* 1998*b*), which probably outcompete most understorey species.

The overall response of palms to the distance from fragment edge was less pronounced than that related to fragment sector. Indeed, the large number of biotic and abiotic edge-responsive factors and the complexity of biological interactions blur the effects of most distance-responsive variables, and simple, unimodal patterns are not to be expected as a rule (Murcia 1995). In the populations studied the same spatial heterogeneity affecting the concentration of palms in some transect arms could produce variable relationships with the distance from the edge. Edges may represent quite distinct environments depending on fragment size, degree of isolation and orientation (Saunders *et al.* 1991) and vegetation structure (Murcia 1995, Didham & Lawton 1999). Therefore, a concordant arrangement of the conditions favourable to *Attalea* establishment and growth in a gradient from the edge to the forest interior is likely to be rare. Special cases were the east sector of fragment I, where field observations suggested that the densities of *Attalea* and *Trema micrantha* were probably inversely related, and the east sector of fragments II and III, where a more clear-cut difference between a closed-forest interior and open edge was observed. Additionally, in the northern and southern sides of fragments II and III, respectively, steep slopes probably create a drainage gradient, to which palms are known to be responsive (Kahn 1987).

What was the effect of fire on the spatial patterns discussed so far? First, it accentuated the clumping degree of the young. The extent of fires in nature is strongly influenced by environmental features such as topography, vegetation structure and the amount of litter, and generally is highly patchy (Whelan 1995). In forest fragments fire penetration is highly influenced by edge structure. Edges closed by dense vegetation growth act as barriers to fire encroachment (Kellman *et al.* 1996, Didham & Lawton 1999). Young *Attalea* do not have the developed subterranean system present in immature and adult palms (Souza *et al.* 1999), and thus are more susceptible to fire. Hence, fire may have acted eliminating some clumps of young palms while leaving others unharmed, and thus enhancing the patchiness of their distribution.

Burned forest environments are extremely heterogeneous, with unburned patches occurring within burned areas (Whelan 1995, Cochrane & Schulze 1999). Indeed, the fragments showed differing patterns of fire damage (*pers. obs.*): the largest fragment was mainly burned in the edge, the medium-sized one was most affected in its disturbed, *Attalea*-rich sectors (west sector and east edge), while the smallest one was extensively burnt. This burning pattern seems not to have substantially altered the pre-fire distribution of palms, since neither major changes in the relative clumping degree between stages nor the distribution of individuals between transect arms occurred. The minor changes observed in relation to distance from forest edge are likely the result of patchy mortality due to fire and post-fire altered environmental conditions.

Burning generally increases fire susceptibility of forests (Cochrane & Schulze 1999). Thus, the recent history of recurrent anthropogenic fires in the study fragments makes it probable that the distribution of palms we found could result from a process of progressive forest degradation due to the combined effects of reduced fragment size, increased edge effects and successive fire encroachment. Moreover, our data suggest that in small forest remnants, ‘edge’ effects may not be restricted to a marginal zone but spread over entire fragment sectors.

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Appendix. Statistical properties of the spatial distribution of *Attalea humilis* in three forest fragments at different scales for the period 1996-1999. I_M = Morisita index of dispersion.

		Fragment/Stage								
			I			II			III	
Scale (m^2)	I_M/χ^2	Y	I	A	Y	I	A	Y	I	A
						1996				
100	I_M	-	1.18	2.16	3.97	2.01	1.62	7.89	2.42	1.2
	$\chi^2_{(df)}$	-	$32.0_{(29)}$	$48.7_{(29)}$*	$179.4_{(61)}$***	$247.0_{(61)}$***	$262.0_{(61)}$***	$187.0_{(70)}$***	$115.0_{(70)}$**	$79.2_{(70)}$
200	I_M	-	0.92	2.10	2.52	1.83	1.49	4.58	1.39	1.33
	$\chi^2_{(df)}$	-	$11.6_{(13)}$	$31.8_{(13)}$**	$85.2_{(29)}$***	$181.3_{(29)}$***	$185.0_{(29)}$***	$9.8_{(34)}$***	$46.5_{(34)}$	$49.7_{(34)}$*
300	I_M	-	1.06	1.67	3.24	1.75	1.51	3.91	1.26	1.14
	$\chi^2_{(df)}$	-	$9.0_{(8)}$	$21.4_{(8)}$**	$102.0_{(19)}$***	$166.1_{(19)}$***	$180.0_{(19)}$***	$71.4_{(22)}$***	$30.4_{(22)}$	$28.7_{(22)}$
400	I_M	-	1.01	1.69	2.62	1.71	1.48	3.56	1.06	1.3
	$\chi^2_{(df)}$	-	$5.2_{(5)}$	$16.7_{(5)}$**	$69.8_{(13)}$***	$133.7_{(13)}$***	$151.0_{(13)}$***	$59.4_{(16)}$***	$18.0_{(16)}$	$29.9_{(16)}$*
500	I_M	-	1.11	1.44	1.57	1.65	1.43	3.4	1.62	1.09
	$\chi^2_{(df)}$	-	$5.9_{(4)}$	$11.4_{(4)}$*	$29.4_{(10)}$**	$123.3_{(10)}$***	$140.0_{(10)}$***	$52.8_{(12)}$***	$30.6_{(12)}$**	$16.5_{(12)}$
600	I_M	-	1.23	1.60	2.01	1.55	1.44	2.30	1.043	1.23
	$\chi^2_{(df)}$	-	$6.0_{(3)}$	$15.0_{(3)}$**	$46.2_{(9)}$***	$110.9_{(9)}$***	$148.0_{(9)}$***	$32.1_{(10)}$**	$11.3_{(10)}$	$20.8_{(10)}$*
1500	I_M	-	-	-	1.19	1.26	1.35	1.52	1.04	1.17
	$\chi^2_{(df)}$	-	-	-	$7.8_{(2)}$*	$40.4_{(2)}$***	$93.8_{(2)}$***	$11.8_{(3)}$**	$4.2_{(3)}$	$10.4_{(3)}$*

Appendix. Continued.

		Fragment/Stage								
		I			II			III		
Scale (m^2)	I_M/χ^2	Y	I	A	Y	I	A	Y	I	A
						1997				
100	I_M	8.59	1.67	1.57	-	-	-	5.92	1.73	1.15
	$\chi^2_{(df)}$	$204.0_{(29)}$***	$34.3_{(29)}$	$43.2_{(29)}$*	-	-	-	$183.0_{(70)}$***	$98.5_{(70)}$*	$73.6_{(70)}$
200	I_M	4.36	1.00	1.46	-	-	-	3.80	1.46	1.42
	$\chi^2_{(df)}$	$90.3_{(13)}$***	$13.0_{(13)}$	$24.6_{(13)}$*	-	-	-	$98.5_{(34)}$***	$51.6_{(34)}$*	$51.3_{(34)}$*
300	I_M	5.67	1.75	1.38	-	-	-	2.67	1.39	1.28
	$\chi^2_{(df)}$	$116.0_{(8)}$***	$14.0_{(8)}$	$17.6_{(8)}$*	-	-	-	$60.3_{(22)}$***	$37.1_{(22)}$*	$33.6_{(22)}$
400	I_M	3.78	1.29	1.20	-	-	-	2.34	1.22	1.38
	$\chi^2_{(df)}$	$69.0_{(5)}$***	$7.0_{(5)}$	$10.0_{(5)}$	-	-	-	$46.8_{(16)}$***	$24.2_{(16)}$	$31.7_{(16)}$*
500	I_M	3.15	1.53	1.14	-	-	-	2.73	1.54	1.15
	$\chi^2_{(df)}$	$53.5_{(4)}$***	$8.2_{(4)}$	$7.5_{(4)}$	-	-	-	$51.8_{(12)}$***	$32.7_{(12)}$**	$18.0_{(12)}$
600	I_M	2.75	2.29	1.24	-	-	-	0.17	1.05	1.34
	$\chi^2_{(df)}$	$41.5_{(3)}$***	$12.0_{(3)}$**	$9.1_{(3)}$*	-	-	-	$25.5_{(10)}$**	$12.1_{(10)}$	$24.0_{(10)}$**
1500	I_M	-	-	-	-	-	-	1.28	1.07	1.24
	$\chi^2_{(df)}$	-	-	-	-	-	-	$9.3_{(3)}$*	$5.5_{(3)}$	$12.0_{(3)}$**

Appendix. Continued.

		Fragment/Stage								
		I			II			III		
Scale (m^2)	I_M/χ^2	Y	I	A	Y	I	A	Y	I	A
						1998				
100	I_M	11.53	1.29	-	6.01	1.82	1.32	12.62	1.25	2.60
	$\chi^2_{(df)}$	$55.8_{(29)}$***	$39.0_{(29)}$	-	$104.4_{(61)}$***	$403.0_{(61)}$***	$76.3_{(61)}$	$175.0_{(70)}$***	$84.0_{(70)}$	$108.0_{(70)}$**
200	I_M	5.39	1.20	-	2.99	1.72	1.10	4.86	1.23	2.57
	$\chi^2_{(df)}$	$65.6_{(13)}$***	$20.0_{(13)}$	-	$80.8_{(29)}$***	$326.0_{(29)}$***	$33.7_{(29)}$	$64.9_{(34)}$**	$47.0_{(34)}$	$71.6_{(34)}$**
300	I_M	7.61	1.19	-	1.99	1.68	1.19	3.19	1.09	2.22
	$\chi^2_{(df)}$	$87.4_{(8)}$***	$14.5_{(8)}$	-	$44.9_{(19)}$**	$301.0_{(19)}$***	$28.1_{(19)}$	$39.6_{(22)}$*	$26.9_{(22)}$	$51.4_{(22)}$**
400	I_M	6.00	1.17	-	1.51	1.62	1.05	3.78	1.12	2.44
	$\chi^2_{(df)}$	$60.0_{(5)}$***	$10.8_{(5)}$	-	$23.8_{(13)}$*	$256.0_{(13)}$***	$15.2_{(13)}$	$38.2_{(16)}$**	$22.9_{(16)}$	$50.5_{(16)}$***
500	I_M	4.23	1.10	-	1.45	1.56	1.23	2.89	1.29	1.98
	$\chi^2_{(df)}$	$42.8_{(4)}$***	$7.6_{(4)}$	-	$18.5_{(10)}$*	$228.0_{(10)}$***	$20.6_{(10)}$*	$27.1_{(12)}$**	$28.9_{(12)}$**	$34.5_{(12)}$**
600	I_M	4.00	1.36	-	1.45	1.52	1.17	1.53	1.04	2.24
	$\chi^2_{(df)}$	$36.0_{(3)}$***	$14.3_{(3)}$**	-	$20.8_{(9)}$*	$226.0_{(9)}$***	$17.3_{(9)}$*	$14.200_{(10)}$	$12.3_{(10)}$	$39.7_{(10)}$***
1500	I_M	-	-	-	0.94	1.34	1.03	1.78	1.0709	1.41
	$\chi^2_{(df)}$	-	-	-	$1.0_{(2)}$	$118.6_{(2)}$***	$3.2_{(2)}$	$9.2_{(3)}$*	$6.620_{(3)}$	$12.9_{(3)}$**

Appendix. Continued.

		Fragment/Stage								
		I			II			III		
Scale (m^2)	I_M/χ^2	Y	I	A	Y	I	A	Y	I	A
						1999				
100	I_M	10.00	1.90	2.00	2.43	2.47	1.45	9.47	1.44	2.62
	$\chi^2_{(df)}$	$74.1_{(29)}$***	$48.7_{(29)}$*	$34.0_{(29)}$	$115.0_{(61)}$***	$300.0_{(61)}$***	$132.0_{(61)}$***	$112.0_{(70)}$**	$93.3_{(70)}$*	$111.0_{(70)}$**
200	I_M	5.73	1.72	0.93	1.82	2.19	1.31	4.67	1.22	3.02
	$\chi^2_{(df)}$	$79.2_{(13)}$***	$28.7_{(13)}$**	$12.7_{(13)}$	$60.2_{(29)}$**	$238.0_{(29)}$***	$78.2_{(29)}$***	$52.3_{(34)}$*	$45.8_{(34)}$	$84.4_{(34)}$***
300	I_M	7.80	1.39	2.40	1.57	2.14	1.32	3.07	1.17	2.26
	$\chi^2_{(df)}$	$103.0_{(8)}$***	$16.5_{(8)}$*	$15.0_{(8)}$	$40.5_{(19)}$**	$219.0_{(19)}$***	$69.6_{(19)}$***	$32.3_{(22)}$	$31.2_{(22)}$	$53.6_{(22)}$**
400	I_M	5.20	1.25	0.80	1.76	2.14	1.33	2.27	1.25	2.04
	$\chi^2_{(df)}$	$63.8_{(5)}$***	$10.2_{(5)}$	$4.0_{(5)}$	$39.4_{(13)}$**	$206.0_{(13)}$***	$60.7_{(13)}$***	$22.3_{(16)}$	$29.1_{(16)}$*	$42.0_{(16)}$**
500	I_M	4.33	1.40	1.33	1.49	2.10	1.20	1.73	1.44	1.40
	$\chi^2_{(df)}$	$50.7_{(4)}$***	$12.9_{(4)}$*	$5.7_{(4)}$	$25.1_{(10)}$**	$195.0_{(10)}$***	$38.1_{(10)}$***	$15.7_{(12)}$	$35.1_{(12)}$**	$22.0_{(12)}$*
600	I_M	4.00	1.35	1.07	1.42	2.13	1.25	1.47	1.22	1.73
	$\chi^2_{(df)}$	$42.0_{(3)}$***	$10.4_{(3)}$*	$3.3_{(3)}$	$24.8_{(9)}$**	$208.0_{(9)}$***	$48.9_{(9)}$***	$12.3_{(10)}$	$21.5_{(10)}$*	$28.2_{(10)}$**
1500	I_M	-	-	-	1.55	1.62	1.23	2.67	1.02	1.60
	$\chi^2_{(df)}$	-	-	-	$16.2_{(2)}$**	$199.4_{(2)}$***	$29.7_{(2)}$***	$11.3_{(3)}$*	$4.1_{(3)}$	$16.1_{(3)}$**

Y = young, I = immature, A = adults; * $P < 0.05$, ** $P < 0.01$, *** $P< 0.001$

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Table 1. General characterisation of the study forest fragments in the National Biological Reserve of Poço das Antas, Rio de Janeiro State, south-eastern Brazil.

Fragment	Area (ha)	Perimeter (m)	P:A[a]	Number of 10 x 10 m Plots	Sampled Area[b] (m^2)	Trees/ha[c] (DBH ≥ 10 cm)	Mean Height[c] (m)	Litterfall[d] ($ton\ ha^{-1}\ y^{-1}$)
I	1.6	325	0.020	29	2900 (18.1)	426	7.6	4.1
II	6.4	650	0.010	61	6100 (9.5)	514	9.4	5.3
III	9.9	775	0.008	70	7000 (7.1)	797	9.3	5.7

a - Perimeter (m): area (m^2) proportion; b - Percent area of each fragment sampled in parenthesis; c - Silva Matos *et al.* (1998*a*); d - Silva Matos *et al.* (1998*b*).

Table 2. Densities (number of individuals/ha) of *Attalea humilis* ontogenetic categories in the forest fragments studied. The dashed line indicates the occurrence of fire.

	Fragment/Ontogenetic Category								
	I			**II**			**III**		
Year	**Y**	**I**	**A**	**Y**	**I**	**A**	**Y**	**I**	**A**
1996	-	58.0	58.0	60.0	295.2	512.7	23.9	46.5	67.6
1997	77.4	29.0	83.9	-	-	-	33.8	56.3	59.2
1998	41.9	109.7	3.2	42.9	666.7	74.6	14.1	81.7	33.8
1999	48.4	74.2	9.7	61.9	280.9	254.0	8.5	74.6	36.6

Y = young, I = immature, A = adults.

Table 3. Spearman rank correlation coefficients for the relationship between the abundances of *Attalea humilis* ontogenetic categories in the three forest fragments studied. Bold numbers indicate significant ($P < 0.05$) coefficients.

		Fragment/ Ontogenetic Category					
		I		**II**		**III**	
Year		Y	**I**	Y	**I**	Y	**I**
1996	**I**	-		**0.509*****		0.102	
	A	-	0.285	**0.478*****	**0.705*****	0.118	-0.019
1997	**I**	0.196		0.243		0.168	
	A	0.343	0.284	0.088	-0.032	**0.297***	0.055
1998	**I**	0.174		-		0.102	
	A	-	-	-	-	-0.047	-0.053
1999	**I**	0.170		-0.011		0.167	
	A	0.070	**0.377***	0.057	**0.471*****	0.125	-0.057

Y = young, I = immature, A = adults; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 4. Kruskal-Wallis analysis of variance of the number of palms in each ontogenetic category per transect side. df = 3. Bold numbers indicate significant effects.

	Fragment/Ontogenetic Category								
	I			**II**			**III**		
	Y	I	A	Y	I	A	Y	I	A
					1996				
H	-	8.54	8.55	3.23	15.51	19.85	7.68	0.36	11.61
P	-	**0.036**	**0.036**	0.357	**0.001**	**0.000**	0.053	0.949	**0.009**
					1997				
H	1.69	7.37	11.45	-	-	-	4.30	1.49	13.55
P	0.640	0.061	**0.010**	-	-	-	0.231	0.684	**0.004**
					1998				
H	3.30	9.94	-	1.04	15.56	0.62	5.57	5.00	14.31
P	0.348	**0.019**	-	0.791	**0.001**	0.892	0.134	0.172	**0.003**
					1999				
H	5.17	12.42	5.88	3.87	29.69	14.85	6.64	4.15	6.86
P	0.160	**0.006**	0.118	0.276	**0.000**	**0.002**	0.084	0.245	0.077

Y = young, I = immature, A = adults

H = Kruskal-Wallis statistic, P = probability values

Table 5. Multiple comparisons of transect rank sums for the Kruskal-Wallis analysis of variance of the number of palms in each ontogenetic category per transect side. Number of plants per transect shown. In each line and fragment, values with the same letter are not significantly different.

	Fragment/Transect Side											
	I				**II**				**III**			
	N	S	E	W	N	S	E	W	N	S	E	W
n	5	5	9	9	9	9	21	21	17	17	18	18
						1996						
I	4^{AB}	3^{AB}	0^{A}	8^{B}	5^{A}	36^{A}	34^{A}	105^{B}	-	-	-	-
A	0^{A}	2^{AB}	2^{A}	13^{B}	28^{A}	27^{A}	66^{A}	190^{B}	4^{A}	22^{B}	12^{A}	10^{A}
						1997						
A	0^{A}	5^{AB}	2^{A}	15^{B}	-	-	-	-	4^{A}	21^{B}	9^{AB}	8^{AB}
						1998						
I	4^{A}	6^{A}	3^{A}	20^{B}	19^{A}	64^{AB}	77^{A}	244^{B}	-	-	-	-
A	-	-	-	-	-	-	-	-	3^{AB}	15^{B}	3^{A}	4^{AB}
						1999						
I	1^{AB}	8^{B}	0^{A}	12^{B}	0^{A}	2^{A}	39^{AB}	135^{B}	-	-	-	-
A	-	-	-	-	11^{A}	15^{AB}	40^{A}	88^{B}	-	-	-	-

I = immature, A = adults; n = number of plots.

Table 6. Spearman rank correlation coefficients for the relationship between the abundance of *Attalea humilis* ontogenetic categories and distance from the forest edge in transect sides in three forest fragments. Results for the period 1996-1999. Bold numbers indicate significant coefficients.

	Fragment/Transect Side											
	I				II				III			
	N	S	E	W	N	S	E	W	N	S	E	W
						1996						
Y	-	-	-	-	0.411	0.342	**-0.636****	-0.283	0.102	0.299	0.270	-
I	0.335	-0.289	-	-0.089	**0.757***	**0.920****	**-0.727*****	-0.016	0.448	0.085	0.329	0.074
A	-	0.289	**0.725***	-0.376	0.560	**0.932****	**-0.779*****	-0.415	0.396	-0.231	0.268	-0.380
						1997						
Y	0.000	0.354	0.000	-0.564	-	-	-	-	-	0.193	0.383	-0.204
I	0.354	.	0.411	-0.347	-	-	-	-	0.448	0.398	0.330	0.174
A	-	0.000	**0.725***	-0.214	-	-	-	-	0.396	-0.176	0.246	-0.439
						1998						
Y	0.000	-	-	-0.518	0.274	0.251	-0.027	-0.135	-	-0.298	-	0.006
I	0.335	0.103	**0.730***	-0.449	0.561	**0.975*****	**-0.826*****	-0.199	**0.603***	0.138	0.267	0.180
A	-	-0.707	-	-	0.634	0.303	-0.181	0.098	0.220	-0.061	0.257	**-0.618****

Column headlines: N = North, S = South, E = East, W = West; otherwise Y = young, I = immature, A = adults

* P < 0.05, ** P < 0.01, *** P< 0.001

Table 6. Continued.

	Fragment/ Transect Side											
	I				II				III			
	N	**S**	**E**	**W**	**N**	**S**	**E**	**W**	**N**	**S**	**E**	**W**
						1999						
Y	0.354	-	-	**-0.762***	-0.142	0.383	**-0.553***	**-0.479***	-	-0.094	0.351	-
I	0.000	0.821	-	-0.329	-	-0.311	**-0.555***	-0.126	**0.528***	0.232	**0.536***	-0.174
A	-	-0.577	-	0.219	0.448	0.547	**-0.446***	-0.064	0.234	-0.299	-0.110	-0.043

Column headlines: N = North, S = South, E = East, W = West; otherwise Y = young, I = immature, A = adults

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

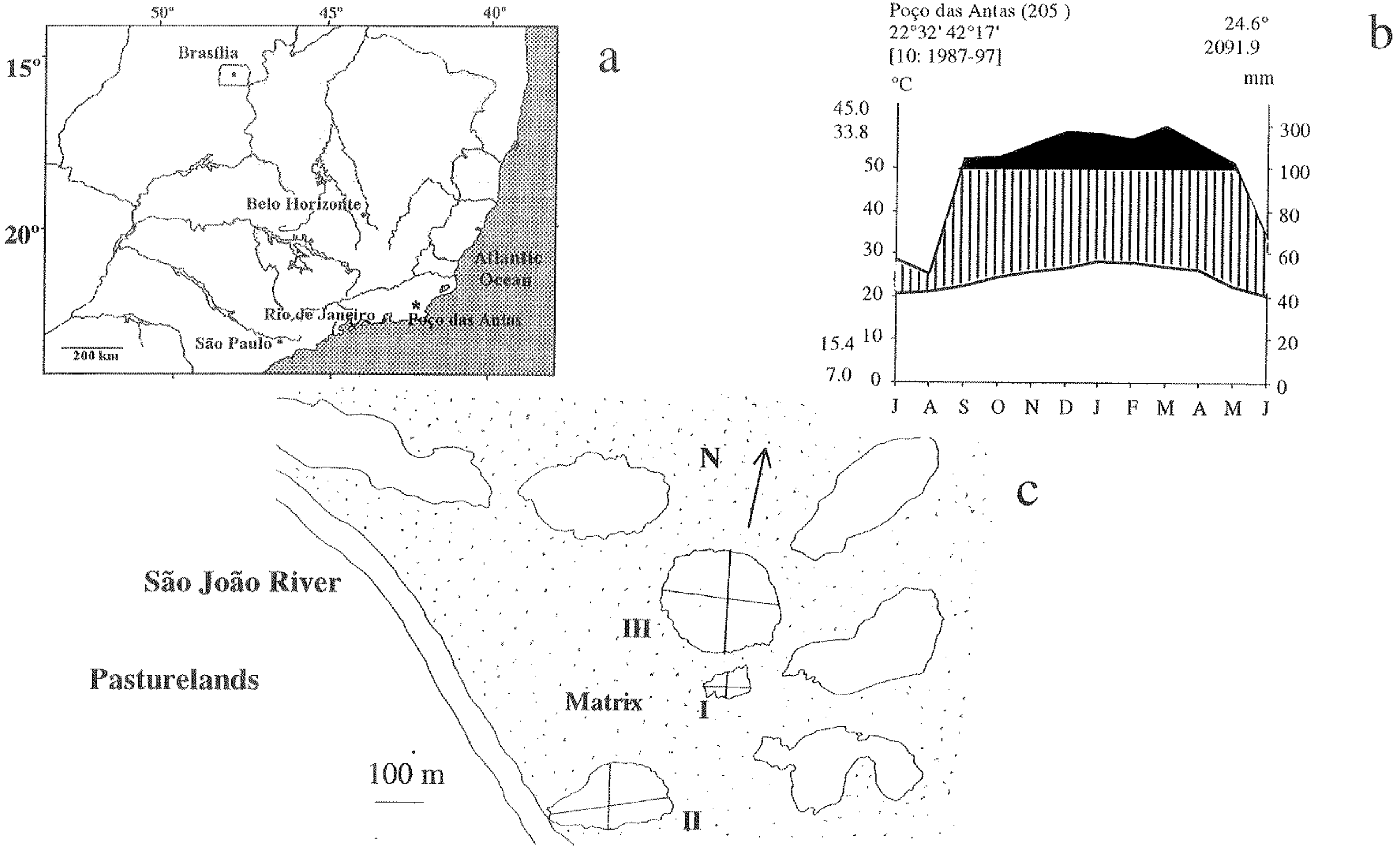

Figure 1. a) Geographical situation of the study area (National Biological Reserve of Poço das Antas) in southeastern Brazil; b) Walter & Lieth climatic diagram for the Reserve (diagram follows Walter 1971) and c) location of the studied fragments. Solid lines represent transects.

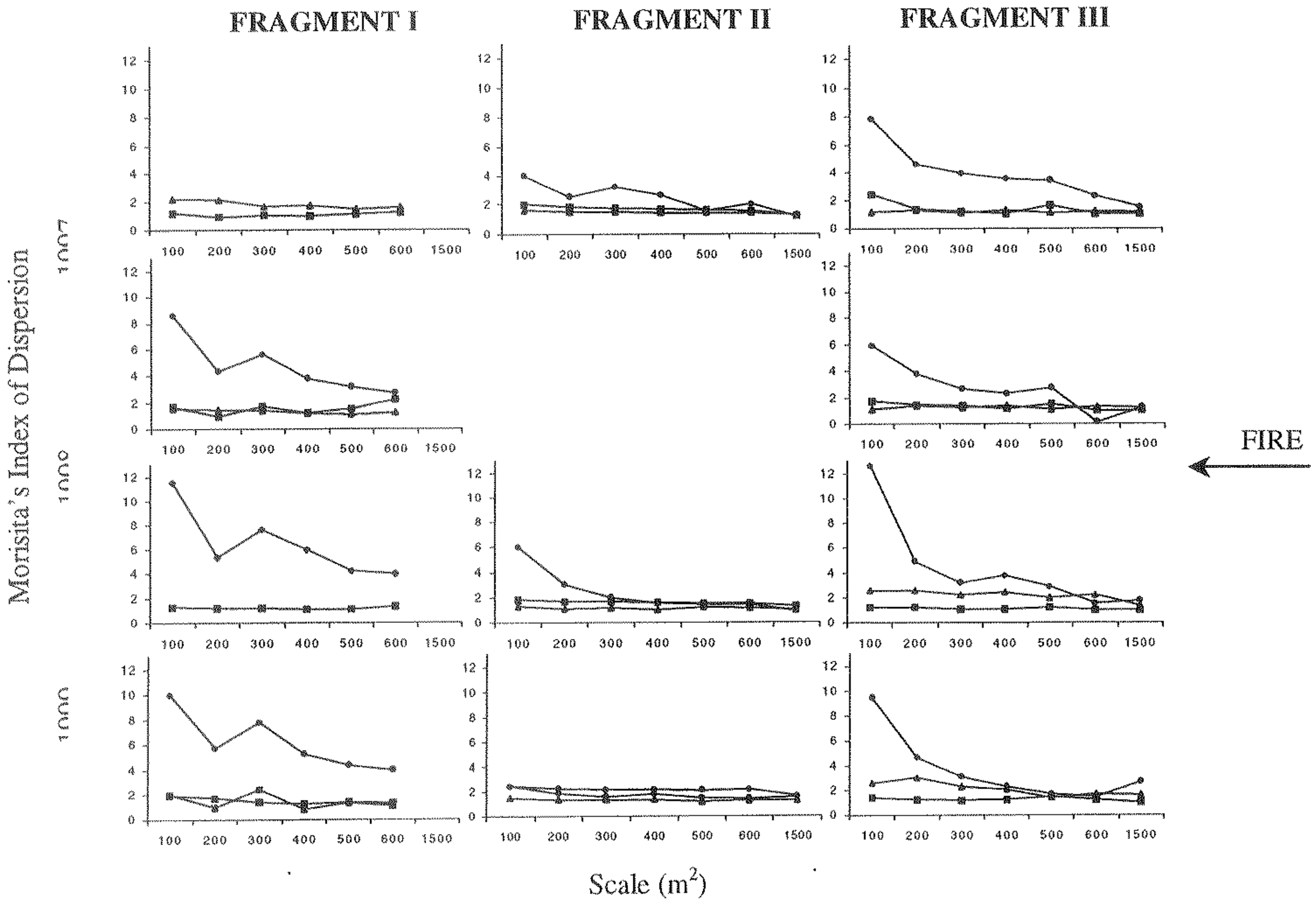

Figure 2. Values of Morisita's Index of Dispersion (I_M) at increasing scales for the young (-●-), immature (-■-) and adult (-▲-) *Attalea humilis* in three forest fragments of the Atlantic forest, southeastern Brazil.

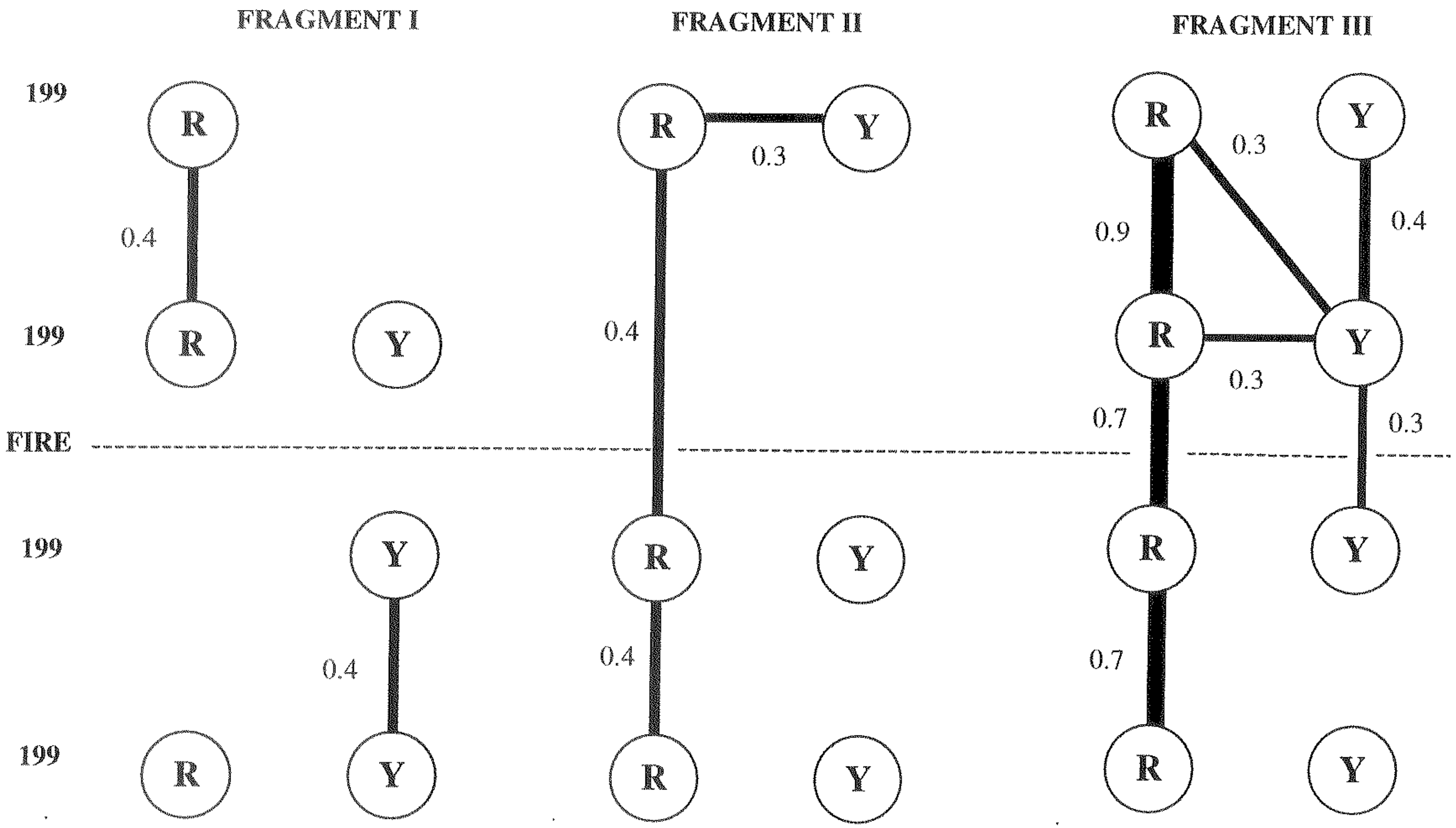

Figure 3. Partial correlation diagrams for the young (Y) and reproductive (R) *Attalea humilis* in three forest fragments of the Atlantic Forest, southeastern Brazil. Solid lines represent significant associations ($P < 0.05$); accompanying numbers are Jaccard's Index of association strength.

CAPÍTULO 4: Population Dynamics of a Neotropical Palm in Fire-Impacted Fragments of the Brazilian Atlantic Forest[1]

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[1] – Tabelas e Figuras no final do Capítulo

RESUMO. – A demografia da palmeira acaule *Attalea humilis* foi estudada no período de 1996 - 1999 em três fragmentos (1.6 ha a 9.9 ha) da Floresta Atlântica. Modelos matriciais baseados em estádios ontogenéticos foram utilizados para determinar probabilidades de transição entre estádios e para projetar taxas de crescimento populacionais, juntamente com flutuações populacionais observadas e mudanças na estrutura de estádios das populações antes e depois de um incêndio que atingiu a área de durante o estudo. A heterogeneidade interna de um dos fragmentos foi explorada através da comparação da estrutura e densidade entre setores perturbados e preservados. Em todos os anos, a densidade de palmeiras no fragmento de tamanho intermediário (750 – 900 palmeiras ha^{-1}) foi significativamente maior e apresentou maior amplitude do que nos outros dois fragmentos (130 - 200 palmeiras ha^{-1} e 120 – 150 palmeiras ha^{-1}). A estrutura de estádios das populações foi dependente do fragmento e do ano, mas em geral estádios posteriores foram mais abundantes do que os iniciais; plântulas representaram apenas 2.8% – 33.9% dos indivíduos. O fragmento mais denso apresentou maior heterogeneidade interna, com seu setor perturbado concentrando a maior e mais densa subpopulação. Ambas as taxas de crescimento populacional (λ) projetadas e observadas foram maiores do que a unidade no fragmento menor, mas semelhantes à unidade no maior fragmento. As taxas de crescimento populacional foram mais sensíveis a mudanças na sobrevivência de plântulas, virgens e imaturos, e relativamente insensíveis a mudanças no crescimento e fecundidade. Após o fogo, as populações permaneceram estáveis em todos os fragmentos, exceto no de tamanho intermediário, onde uma tendência ao declínio foi observada. A estrutura de estádios de todas as populações foi marcadamente alterada pelo fogo através da concentração de

indivíduos no estádio imaturo, mas esta tendência foi parcialmente revertida no segundo ano após o fogo. Estes resultados indicam que a habilidade de rebrotamento de *A. humilis*, juntamente com sua tendência a persistir e prosperar em áreas perturbadas promovem o seu crescimento em fragmentos florestais pequenos, mas este crescimento pode ser obstruído pelo crescimento secundário denso que se segue a incêndios ocasionais.

ABSTRACT. – The demography of the subterranean-stemmed palm *Attalea humilis* was studied during a four-year period in three fragments of the Atlantic Forest, in south-eastern Brazil. Fragment sizes ranged from 1.6 ha to 9.9 ha. Stage-based matrix models were used to determine stage-specific transition rates and to project population growth rates, along with observed population fluctuations and the ontogenetic stage structure of the populations before and after a man-induced fire that damaged the populations during the study period. Internal heterogeneity of one of the fragments was explored by comparing population structure and density between disturbed and preserved sectors. For all years, palm density in the medium-sized fragment (750 – 900 palms ha^{-1}) was significantly higher and presented a broader range than in the two other fragments, where density remained consistently low (130 - 200 palms ha^{-1} and 120 – 150 palms ha^{-1}). The stage structure of the populations was dependent on fragment and year, but in general later stages were more abundant than initial ones; seedlings represented only 2.8% – 33.9% of individuals. The denser fragment showed high internal heterogeneity, with its disturbed sector concentrating the largest and denser subpopulation. Both observed and projected population growth rates (λ) were greater than unity in the smallest fragment but similar to unity in the largest fragment. Population growth rates were most sensitive to changes in survival of seedlings, virgins and the immature, and relatively insensitive to changes in growth and fecundity. After fire, populations remained stable in all fragments but the medium-sized one, where a declining tendency took place. The stage structure of all populations was markedly altered by fire through the concentration of most individuals in the medium-sized, immature stage, but this trend was partly reversed by the second year after fire. These results indicate that the resprouting ability of *A. humilis*, coupled with its tendency to persist and thrive in disturbed areas promote population growth in disturbed small forest fragments, but this growth may be hindered by dense secondary regrowth following occasional fires.

Key words: *Attalea humilis*, tropical forest, Brazil, demography, matrix analysis, elasticity analysis, stage structure

INTRODUCTION

High deforestation rates have converted formerly continuous tropical rain forests to anthropogenic landscapes, where forest habitats are reduced to scattered forest fragments of varying sizes and quality (Noss & Csuti 1997, Whitmore 1997). This process has taken place with different intensities at different times in tropical regions. Thus, while most deforestation activities in the Amazon basin occurred in the last century, the fragmentation process in the Brazilian Atlantic Forest initiated in the beginning of the 16th century (Brown & Brown 1992, Dean 1996). The Atlantic Forest presents some of the highest plant diversity in the world (Mori *et al.* 1981), high plant and animal endemism (Brown & Brown 1992) and a protected area network that underrepresents its natural landscape heterogeneity (Viana & Tabanez 1996). Extensive and rapid deforestation have reduced this forest to less than 5% of the total pre-settlement forest area (Viana & Tabanez 1996). The vast majority of this remnant area consists of many small, privately-owned forest fragments (Ranta *et al.* 1998), which are frequently exposed to human-induced fires. In Brazil fire is commonly used as a way of eliminating the forest cover in benefit of other land uses, and as a tool applied to agriculture and pasture management (Dean 1996).

Much effort has been made to access the effects of fragmentation on species richness (Turner 1996), but comparatively few researchers have devoted attention to the population dynamics of individual long-lived plant species in tropical forest fragments (but see Barrow *et al.* 1993, Ratsirarson *et al.* 1996, Silva Matos *et al.* 1999). As the population is the ecologically and evolutionarily functional unit, it should be the focus of efforts directed towards the species level of conservation plans (Pulliam & Dunning 1997). Hence, the conservation and management of habitats may be frequently guided by the knowledge of the population dynamics of at least some of their species. Indeed, the Sustainable Biosphere Initiative suggested the study of the unknowns of structure and function of biological systems, including the consequences of natural and man-induced environmental variability for the maintenance of natural populations (Lubchenco *et al.* 1991). Accordingly, there has recently been much concern on the viability of small and isolated populations (Gilpin & Soulé 1986, Pulliam & Dunning 1997) and the use of both demographic and genetic models in conservation biology (Alvarez-Buylla *et al.* 1996).

Palms are abundant in tropical and subtropical systems (Henderson *et al.* 1995) and commonly play an important role in many ecological processes (*e.g.* Price & Jenkins 1986, Smythe 1989). However, studies on the population dynamics of palm species in tropical forests are relatively recent (e.g. Bullock 1980, Piñero *et al.* 1984, Pinard 1993, Olmsted & Alvarez-Buylla 1995, Bernal 1998), and few researchers have paid attention to the demography of fragmented populations (e.g., Barrow *et al.* 1993, Ratsirarson *et al.* 1996). The study of Silva Matos *et al.* (1999) on the demography of *Euterpe edulis* in a fragment of semideciduous forest is among the few published for tropical plant populations in the Atlantic Forest. In this paper we aim to study the population dynamics of *Attalea humilis*, an endemic and abundant understorey palm of the Atlantic Forest in fire-impacted forest fragments, using a stage-based matrix approach. Apart from the results of this project (Chapters 1, 2 and 3), there has been no ecological study done on this species.

Specifically, we asked the following questions: (1) what are the probabilities of survival, growth and shrinkage for each ontogenetic stage; (2) how do these descriptors differ between forest fragments? This question is based on the assumptions, strengthened by some initial evidence (see *Material and Methods: Study site and species*), that fragmentation altered the microclimate and structure of studied forest environments in a number of ways, and that each species respond to these changes through its demographic descriptors, which will, thus, differ between fragments of distinct size and conservation status; (3) how does the stage structure of the populations vary through space and time?; (4) what is the effect of fire on both population growth and stage structure in fragments differing in size, shape and structure?

MATERIAL AND METHODS

Study site and species

The study was carried out in the National Biological Reserve of Poço das Antas (22°30'-22°33'S, 42°15'-42°19'W), municipality of Silva Jardim, state of Rio de Janeiro, south-eastern Brazil. The Reserve covers ca. 5000 ha of lowland Atlantic Forest ('floresta pluvial baixo-montana', according to Rizzini 1979), with maximum elevation of 205 m a.s.l., and comprises a mosaic of vegetation patches at different successional phases (IBDF/FBCN 1981). The Reserve is surrounded by pastures, cultures and secondary forests. The climate is classified as Walter and Lieth's Equatorial type (Walter 1971), with mean annual rainfall of ca. 2100 mm (1987 – 1997 data). There is no distinct dry season and, despite large variation between years, a drier period normally extends from May to August.

Field data were collected at three forest fragments that are part of the complex locally known as the 'Barbados archipelago', a mosaic of eight forest fragments located on small hills originally isolated by permanent waterlogging, near the left margin of the São João river. Distances between adjacent fragments ranged from ~ 33 m to 190 m. The studied fragments ranged in size from 1.6 to 9.9 ha, and present a number of structural and physical differences, summarised in Table 1. The smallest fragment is subjected to higher air and soil temperatures and lower air relative humidity and soil moisture content, as well as larger wind penetration distances (Silva Matos *et al.* 1998*b*). The "Barbados archipelago" has been subject to a defaunation process due to clandestine hunting, which concentrates on large mammals and birds. The matrix surrounding the fragments, originally represented by a low-stature, waterlogged forest, was drained in 1981 after the alteration of the water regime of the São João River by the building of the Juturnaíba dam. The fragments are now embedded in a vegetation matrix dominated by grasses, patches of the bracken fern (*Pteridium aquilinum*) and isolated stands of *Cecropia* sp. (Cecropiaceae) and *Trema micrantha* (Ulmaceae). Matrix soils are classified as Histosols (USDA 1990), a type of organic soil originated from peat. The lower levels of the matrix suffer annual inundation during the rainiest months (December through March). In the fragments, soils form an indiscriminate grouping of alic Oxisols/Ultisoils, with moderate A horizon and clayey to very clayey texture (Takizawa 1995). Since the drainage of the matrix in 1981, the area suffered recurrent, man-induced fires in 1982, 1990, 1993 and 1997. These fires have taken place during the driest months and frequently invaded the fragments, causing variable damage.

Attalea humilis Mart. ex. Spreng., hereafter *Attalea*, is a monoecious, solitary palm with a short, subterranean stem (saxophone-axis type, Tomlinson & Jeffrey 1990; see Souza *et al.* 1999 for a morphological description). The apical meristem, protected by the surrounding leaf sheaths, is also subterranean. The aerial portion is composed by the crown, which has 5 - 16 pinnatifid, spineless, up to 7 m long leaves (Souza *et al.* 1999). The species is restricted to the central-south-eastern Atlantic Forest, ranging from the state of Bahia to the state of São Paulo (Henderson *et al.* 1995, Lorenzi *et al.* 1996). Based on morphological and morphometrical analysis, we distinguished five ontogenetic stages in *Attalea* (Chapter 1): seedlings present entire, distichous leaves; juveniles present bifid, incompletely segmented ones; immature individuals produce completely segmented leaf blades, being distinguished from virgins by having fewer leaves and smaller but highly variable youngest leaf blade length; reproductive palms are recognised by the production of flowers and fruits.

Data collection

Palms were censused along two perpendicular 10 m-wide transects that cut across each fragment. The transects were divided in 10 x 10 m contiguous plots, and covered 7 - 18 % of each fragment area (Table 1). All individuals of *Attalea* were tagged with a numbered plastic label from July 1996 to January 1997 (1996 field survey), and the fates of the plants were subsequently monitored in July-August 1997 (1997 field survey), when all new plants were also tagged. Morphometrical measurements allowed later assignment of individuals to each of the ontogenetic stages mentioned above (Chapter 1). At the end of the 1997 drier period (August-September) a fire damaged *ca.* 1000 ha of the Reserve, including the study area. Fire prevented the conclusion of the 1997 field survey, and data could not be collected in fragment II. Furthermore, fire destroyed most plastic tags, thus preventing monitoring the fates of individual plants in subsequent years. To access the effects of fire on the structure of populations under study, field surveys were carried out in April 1998, after reconstruction of destroyed plots, and in June 1999. During April and May 1997, the number of fruits produced was recorded for all reproductive individuals in all fragments. Infructescences with signs of fruit removal or abortion were excluded from calculations of individual fecundity, because perianth remains difficult exact determination of the number of fruits lacking.

Data analysis

Abundance and population structure

To test whether observed population sizes changed significantly from one year to the next, we compared population sizes at successive pairs of years (t_i, t_{i+1}) with uniform distributions considering t_i values. Population density was compared non-parametrically between fragments with Kruskal-Wallis ANOVA. To determine whether the stage structure of the populations varied through space and time, we performed a log-linear analysis considering stage S, year Y, and fragment F (three fragments), by building a three-way contingency table (Sokal & Rohlf 1995). We tested the null hypothesis of three-factor interaction by fitting the fully saturated model (SYF term present)(Sokal & Rohlf 1995).

Previous spatial pattern analysis (Chapter 3) showed that the population in fragment II was mostly concentrated in the western, disturbed sector of the fragment. We explored such internal heterogeneity by performing a series of tests of proportions with the data from this fragment. We tested the null hypotheses that the proportion of the population in the western sector was proportional to the sampled area (pooled data from all years), that it was constant through the study years (two-way contingency table, sector [west, others] x year), and that the stage structure was independent of fragment sector and year (log-linear analysis considering stage S, year Y, and sector D).

Life cycle and matrix models

Data collected in the plots were used to build a Lefkovitch, stage-based matrix model with five ontogenetic stages. Matrix models and their inherent assumptions are discussed in Caswell (1989). This approach relies on using information on the transition probabilities among life cycle categories from one time period to the next, in order to describe and project population dynamics through a square matrix **A** and a vector (**v**). The following parameters are required for construction of **A**: the probability that an individual in stage i will survive and remain within stage i (P_i); the probability that an individual in stage i will survive and grow into stage $i + 1$ (G_i); and reproductive output or fecundity (F_i). The **v** vector defines the number of individuals in the population for each stage at time t. When the matrix **A** is multiplied by the vector **v** one can obtain the population vector at time $t + 1$.

The data summarised in Figure 4 were put in two projection matrices corresponding to fragments I and III (fire prevented identification of individuals in fragment II). Following the ontogenetic stages identified in Chapter 1, we constructed matrix models with only one category of reproductive plants. Entries of matrix **A** represents transition probabilities in a 1-year period (1996-1997). The data in the first row represent the contribution of each stage i to the seedling stage, which was estimated by dividing the number of new seedlings emerged at time $t + 1$ by the number of reproductive palms observed at time t. Data on fruit production were pooled from the three fragments, due to small sample sizes when considering only integer infructescences by site ($N_I = 1$, $N_{II} = 14$, $N_{III} = 4$). In the model, the fruit category was omitted because from one year to the following, all seeds either germinate or die.

As in 1996 both seedlings and juveniles were absent from fragment I, the transition from seedling to juvenile in this fragment was estimated from the stage distribution by dividing the mean number of juveniles in the period 1997-1999 by the mean number of seedlings in the same period. We opted for using means instead of values from the observed stage structure from any one year due to remarkable year-to-year variation in the stage structure (see *Results*). The same was not possible for the transition from the juvenile to the immature stage because immature individuals outnumbered juveniles in all fragments and years. In this case we attributed a probability of 0.999 to this transition. This probably does not seem unrealistic in face of the transitional character of the juvenile stage, indicated on morphometrical grounds (Chapter 1). We assigned a probability value of dying of 0.001 to those stages in which no individuals died (Piñero *et al.* 1984). The same was done for the transition probabilities from the virginile to the reproductive stage in fragment I, and from the immature to the virginile stage in fragment III. These transitions were not observed because the time period considered in the model is short compared to the timing of natural events in the life cycle of a long-lived perennial like *Attalea*. Both transitions were observed in one of the fragments, and biologically meaningless developmental sequences would be assumed if zero values were attributed to them (*e.g.*, palms would have to reproduce before entering the virginile stage in fragment III). We estimated confidence intervals for λ by drawing 1000 bootstrap samples from the original data, building a life table and a matrix for each (Alvarez-Buylla & Slatkin 1991), and solving it for λ.

To determine whether transition probabilities varied between fragments, we performed a log-linear analysis (Caswell 1989, Sokal & Rohlf 1995), considering stage (five stages, as above) in time t, fragment (fragments I and III, as above), and fate (stage in time $t + 1$), as the categorical variables. This analysis was based in a three-way contingency table defined by the factors stage S, fragment P, and fate F. We tested the null hypothesis of conditional independence of fate and fragment, fitting the model SF, SP (Caswell 1989). The finite rates of population increase (λ) were calculated from the dominant eigenvalues using the power method (Caswell 1989), as well as the corresponding right eigenvector (*i.e.*, the stable-stage distribution). The elasticity is a measure of the relative change in the population finite rate of increase in response to small changes in the value of a matrix element (de Kroon *et al.* 1986). Elasticity analysis has mathematical constraints derived from the relationship between the elasticities of growth and fecundity (Matos & Silva Matos 1998). However, they are still useful for comparisons between studies and between the vital rates of populations occurring at different areas in a given time period. Thus, an elasticity analysis was performed to determine the most critical stages of the life cycle.

The population finite rate of increase (λ) and the stable distribution are asymptotic properties of the populations under the initial environmental conditions (the 1996-1997 period, in this case)(Caswell 1989). To examine the transient dynamics of the populations, we projected the stage-structure and total population size in fragments I and III in 1997, 1998 and 1999 by multiplying the transition matrix of each fragment by the initial (1996) population vector of each fragment (*i.e.*, a column vector whose elements n_i are the number of individuals in each stage). To examine whether observed populations were significantly different from the stable-stage and projected distributions, we did G tests comparing observed and expected distributions for each fragment and year. To determine how similar two distributions were, we calculated the PS, the proportional similarity index, as in Horvitz and Schemske (1995),

$$\mathrm{PS} = \sum_{n}^{i=1} \min\,(a_i, b_i) \times 100,$$

where there are n stages and a_i is the proportion of individuals in the i^{th} stage of the stable-stage distribution and b_i is the proportion of individuals in the i^{th} stage of the observed stage distribution. All log-linear analysis were done after adding 0.5 to each cell (Sokal & Rohlf 1995). Analysis were performed with SYSTAT software (SYSTAT 1998) at the 5 percent significance level.

RESULTS

Abundance and population structure

Mean density of *Attalea* in the fragments ranged from 1.2 to 9.0 palms per 100m^2 plot (*i.e.* 120 to 900 palms ha^{-1}). There was more variation among fragments than among years for a given fragment (Figure 1). For all years, palm density in fragment II (750 – 900 palms ha^{-1}) was significantly higher and presented a broader range than in the two other fragments, where density remained consistently lower (130 – 200 palms ha^{-1} and 120 – 150 palms ha^{-1} in fragments I and III, respectively). Fragment II had a projected initial population size of 5758 palms (based on the observed number of individuals and the percentage of the total area sampled), while the other two had smaller projected populations (199 and 1394 palms in fragments I and III, respectively). Before fire (1996 – 1997 period), observed finite rate of increase was significantly greater than unity in fragment I but not in fragment III (Table 2). In the period comprising the occurrence of fire and after it, all population growth rates were smaller than, but not significantly different from unity. Considering the entire study period, population sizes in fragments I and III remained at equilibrium, but the population in fragment II decreased.

The stage structure of the populations (*i.e.*, the relative densities of the ontogenetic stages) was dependent on fragment and year (three-way log-linear model, $G = 76.8$, $df = 20$, $P < 0.0001$), varying in a complex way across both space and time (Figure 2). Generally, later stages were more abundant than initial ones; seedlings represented only 2.8% – 33.9% of individuals, and in most cases outnumbered only juveniles. The juvenile was the least abundant stage, and was absent from all fragments in 1996. The population in fragment I had the most dynamic stage structure, while the one in fragment III, the most stable. Seedlings were absent from fragment I in the first year, but in the second year a recruitment event seems to have took place, and both seedlings and juveniles were present, the first at relatively high numbers. Fragments II and III had a similar stage structure, with prevalence of the immature, virgin and reproductive stages.

Fire had a striking effect on the structure of all populations. Six months after the burning (1998 data), the immature was the prevalent stage in the all fragments, accounting for 62.4% - 84.7% of individuals. The juvenile, virgin and reproductive stages disappeared from fragment I, but the number of seedlings remained nearly unchanged. The population in fragment II showed the strongest concentration of plants in the immature stage, while the one in fragment III showed the smallest structural change. In 1999, despite the fact that the immature was still the most abundant stage in all three populations, its prevalence was reduced, for juvenile and reproductive palms were observed in fragment I, and the relative abundance of virgin and reproductive palms increased in the other fragments.

The denser population (fragment II) was marked by strong internal heterogeneity. A significantly large proportion of it was concentrated in the western sector of the fragment (William's corrected $G = 234.5$, $df = 1$, $P < 0.001$), irrespective of year ($G = 4.2$, $df = 2$, $P = 0{,}123$). Considering all the study years, mean density in the western sector ranged from 11.6 to 15.6 palms per plot (mean CV = 47.4%), while in all other sectors pooled it ranged from 5.5 to 5.9 palms per plot (mean CV = 5.7%). Log-linear analysis revealed that stage structure differed between sectors ($G = 46.5$, $df = 14$, $P < 0.0001$)(Figure 3) and was dependent on year ($G = 396.0$, $df = 12$, $P < 0.0001$). In the year before fire the stage structure presented the highest similarity (PS = 67.4%) between the western sector and the others pooled, but the proportion of reproductive plants was higher in the western sector. After fire, the concentration of individuals in the immature stage was higher and juveniles were absent in the western sector, leading to reduced similarity with the distribution in the other sectors (PS = 61.0%). In 1999 the proportion of seedlings and juveniles was lower in the western sector.

Life cycle and matrix models

Life cycles of the populations of *Attalea* at fragments I and III are illustrated in Figure 4. In a one-year period, palms could survive without a change in stage, or they could shrink by one stage or grow by one or two stages. The proportion of individuals that changed from one stage to the next after a one-year period varied widely, ranging from 0.1% for the virgins in fragment I and the immature in fragment III to 99.0% for juveniles in both fragments. Seedling survival was remarkably high (79.0% in fragment III). In general, the probability of surviving and staying in the same stage presented the higher values, along with the transition from the juvenile to the immature stage. The transition from seedling to the immature stage, observed in fragment III was absent from fragment I. The average fruit production of 19 reproductive palms was 75.3 ± 29.3 fruits individual^{-1} year^{-1} ($\overline{X} \pm$ SD).

The transition coefficients of the two fragments were marginally different (log-linear analysis, $G = 31.762$; $df = 20$; $P = 0.046$). Besides the absence of the transition from seedling to the immature stage in fragment I, the probabilities of surviving and staying in the same stage for seedlings and virgins were lower in fragment III than in fragment I, while the opposite was true for the immature. Therefore, the data from each fragment were used to build two separate matrices (Table 3). Population finite rates of increase were greater than unity in both fragments, and the population in fragment I was growing at an annual rate (21.8-24.0%) larger than the population in fragment III (5.9-7.3%). Overall survivorship (stasis) was the most important life-history parameter that affected the finite rate of increase, accounting for 58.6% and 83.4% of total elasticity in fragments I and III, respectively (Table 4). Growth (31.5% and 10.1% in fragments I and III, respectively) was the second most influential parameter in both fragments, but in fragment I the elasticity of reproduction (9.3%) was higher than the elasticity for shrink (2.7%). In fragment III the elasticity for reproduction (3.5%) was much lower than in fragment I, and was similar to shrink (3.0%). Despite the importance of stasis for the population growth rate in both fragments, there were conspicuous differences between the populations. The population in fragment III was much more dependent on stasis than the population in fragment I, which was dependent on the pathway seedling → juvenile → immature → reproductive to a greater extent. Furthermore, the individual matrix parameters with the largest elasticity values in fragment I were the stasis of seedlings and reproductive plants, while in fragment III the stasis of the immature and the reproductive presented the largest values.

The models predicted different stable stage distributions for the two fragments (Figure 5). Seedlings made up the highest proportion of the population in fragment I (49.9%), followed by the virgins (23.4%), while the distribution in fragment III was dominated by the immature (54.7%), followed by seedlings (22.1%) and reproductive palms (17.0%). All except one (fragment I in 1997) of the observed stage distributions differed significantly from the expected stable stage distribution (Table 5). Nevertheless, the proportional similarities indicated that observed distributions in fragment III ($\overline{X} =$ 78.8%, SD = 4.1) were much closer to the stable stage distributions than in fragment I ($\overline{X} =$ 54.0%, SD = 19.4). Predicted transient dynamics for the two populations, as represented by stage distributions projected for the years after fire, were significantly different from observed distributions (Figure 6), but projected stage distributions in fragment III were much closer to the actual distributions than in fragment I (see Figure 2).

DISCUSSION

The three forest fragments studied were strikingly different and represented a range of conditions from the smallest, more disturbed fragment to the largest, more preserved one (Table 1). However, abundance differences among natural *Attalea* populations in the fragments did not follow an intuitive pattern. The mid-sized fragment had by far the largest population, while the other two had smaller projected populations, at similar low densities. Although these projections are tentative at best, because the populations are not uniformly distributed (Souza *et al.* 1999*b*), they give a rough picture of the magnitude of the differences in population size among the fragments.

This picture could be largely attributed to the internal heterogeneity of the fragments. Small tropical forest fragments are normally characterised by high internal heterogeneity, with preserved sectors surrounded by disturbed sectors and edges, where species diversity and canopy heights are generally lower and tree densities, canopy openings, and abundance of pioneer and climbing species use to be higher (Laurance 1997, Oliveira-Filho *et al.* 1997, Lykke & Goudiaby 1999). Many species of the genus *Attalea* have the ability to persist and thrive in disturbed areas (Hogan 1988, Henderson *et al.* 1995). *A. humilis* is not an exception to this pattern, often forming large colonies in more open or disturbed sites (Henderson *et al.* 1995, Lorenzi *et al.* 1996). Indeed, a previous spatial analysis of the same data (Chapter 3) showed that most individuals of *Attalea* in the fragments were concentrated in the disturbed sectors of each fragment.

Accordingly, the analysis of the internal heterogeneity of the population in fragment II showed that in most of its sectors, palm density was similar to values found for the other fragments, and that the large population size in this fragment results from increased density in the western sector. This is the most degraded sector of the fragment, with high incidence of liana tangles and low canopy cover and density of large trees (personal obs.). The ability to increase photosynthetic activity in response to increased light incidence (Hogan 1988) and to occur at high densities with no detectable effects on the size of established individuals (Souza *et al.* 1999*a*) may partly account for the success of *Attalea* in such open patches.

Why, then, was the population in the smallest fragment found at lower densities, similar to those found in the largest fragment? This could be attributed to the hyper-disturbed conditions of the smallest fragment, which could counterbalance increased light availability resulting from reduced canopy cover. Very small fragments can be devastated by frequent wind disturbance and edge effects, becoming virtually all edge habitat (Esseen 1994, Noss & Csuti 1997). This seems to be the case in fragment I, which present markedly altered microclimate and vegetation structure (Table 1). Furthermore, a large portion of this fragment is dominated by monospecific, dense stands of the pioneer tree *Trema micrantha* (Silva Matos *et al.* 1998*b*), with associated increased occurrence of vines and understory bamboos (pers. obs.). *Attalea* is absent from these patches (Chapter 3), where it has been probably excluded from by competition with dense secondary vegetation and fast-growing pioneer trees. This process is probably already in course in the western sector of the fragment, where the population was mostly restricted to (Chapter 3).

The stage structure of *Attalea* populations was characterised by low frequencies of seedlings and juveniles, although their relative frequencies varied in time and space. Reduced frequency of initial stages could result from lower survival in these stages, differential growth of individuals in each stage, or low population growth rates (Condit *et al.* 1998). No population growth rate was smaller than unity before fire in the fragments, even in fragment I, where seedlings were absent in 1996. The analysis of the *Attalea* life cycle in fragments I and III indicated that observed pre-fire stage structures resulted from the very distribution of transition probabilities among ontogenetic stages. Indeed, the stable-stage distribution for fragment III predicted higher concentration of individuals in the virgin stage, while the one for fragment I predicted a concentration in the immature stage, besides the prevalence of seedlings. Populations of the palms *Iriartea deltoidea* (Pinard 1993) and *Phytelephas seemannii* (Bernal 1998) also showed a concentration of individuals in intermediate-sized classes.

Analyses of matrix population projection models are normally limited by low numbers of individuals to provide accurate transition probabilities, the short time period spanned by most studies and the failure of the most commonly used form of the model to account for density-dependent vital rates (Bierzychudek 1999). Our analysis is not free from these shortcomings, and thus should be viewed as only a first approximation to the actual situation. Population growth rates were equal or greater than unity, thus indicating that the habitats occupied by *Attalea* favoured its persistence in the fragments before the fire (Horvitz & Schemske 1995). A similar result has been found for other palm species in forest fragments (Ratsirarson *et al.* 1996, Silva Matos *et al.* 1999), and reflects the ability of these species to couple with the altered forest environment in these fragments. However, its worth noting that the population in the largest fragment was the most stable of the three populations studied, since it showed neither the fluctuation seen in fragment I nor the declining tendency seen in fragment II after fire (Table 2). This picture is reinforced by the high similarity between observed and stable stage structures in this fragment. It remains to be seen whether the stability found in other palm species in continuous forests (Bullock 1980, Piñero *et al.* 1984, Pinard 1993, Olmsted & Alvarez-Buylla 1995, Bernal 1998) would be maintained in fragments.

Population growth rate was mainly dependent on stasis, specially of seedlings and non-reproductive large plants, a pattern found by Silvertown *et al.* (1993) for woody plants in general and by Horvitz and Schemske (1995) for the understory rhizomatous herb *Calathea ovandensis*. Thus, our study species behaved like other rhizomatous plants and trees, in which survival is most important (Caswell 1989, Silvertown *et al.* 1993), than like herbs. The concentration of palms in the immature and virgin stages may be the outcome of the accumulation of individuals from successive cohorts, as well as previously reproductive palms that moved back to the virgin stage. The same process was found by Bernal (1998) for *Phytelephas seemannii*. Due to its preserved structural characteristics, the occurrence of open, resource-rich sites in the largest fragment is mostly restricted to natural treefall canopy openings. The low degree of clumping of the population in this fragment and the random distribution of its diffuse aggregates were attributed in Chapter 3 to the unpredictability of such openings. As both growth and the probability of reproduction of understory palms are greatly enhanced under canopy gaps (Martínez-Ramos *et al.* 1988, Abrahamson 1999), it is likely that both the fast growth of seedlings into the immature stage and the moving of virgins and immature palms into the reproductive stage (see Figure 4) take place predominantly in recently opened gaps.

The pre-fire dynamics of the population in fragment I requires additional explanation. Many large-seeded species are dependent on rodents for successful seed dispersal and establishment (Price & Jenkins 1986, Forget 1997), and *Attalea* successful germination and establishment are thought to depend on the activities of scatterhoarding agoutis (Chapter 1). The absence of seedlings in fragment I in 1996 was followed by a large recruitment event in the next year, where 20 seedlings (33.4% of the sampled population in that year, Figure 2) emerged, almost all of them in a single aggregate in the *Attalea*-rich sector of the fragment (Chapter 3). This seedling outburst was the main cause of the high population growth rates found for this fragment. Since all seedlings emerged from buried seeds (Chapter 1), it is likely that this recruitment event resulted from the failure of a rodent disperser to recover a large aggregate of caches. This result suggests that *Attalea* may be recruitment-limited by seed predation by rodents, but the success of seed dispersal and establishment be dependent on the same animals (Smythe 1989, Crawley 1997). This could partly account for the relatively low number of seedlings found each year in the populations of all fragments. Agoutis and other fruit-eating rodents tend to disappear from small fragments of the Atlantic Forest due to illegal hunting and to the proliferation of secondary vegetation and lianas (Chiarello 1999). This could threaten the persistence of *Attalea* in such fragments, since virtually all undispersed fruits die from desiccation or insect attack (pers. obs.). Indeed, this may be already occurring in fragment I, since no new emerging seedlings were observed after the 1997 event (spatial data in Souza *et al.* 1999b and pers. obs.).

Attalea population growth rates showed high stability to fire. The most depressing effect fire had was the reduction of the population growth rate in fragment I to values indistinguishable from 1.0 (Table 2). On the other hand, the stage structure of populations were resilient to fire. Although there had been a marked concentration of individuals in the immature stage six months after the burning (Figures 2 and 6), this change was mostly reversed one year later. Palm (Barrow *et al.* 1993, Ratsirarson *et al.* 1996) and tree (Uhl & Kauffman 1990) species adapted to rain forest environments, where fire is not a natural part of the ecosystem, typically experience high adult mortality when impacted by fire. Although we do not have data on individual survivorship after 1997, our results concerning population density and stage structure, along with a previous analysis of the distribution of palms among fire damage classes (Chapter 2), strongly suggest that the majority of larger individuals did not die but shrinked to the immature stage. To a large extent, this results derive from the fact that the apical meristem is buried and well-insulated by leaf bases (Chapter 1), becoming protected from fire highest temperatures (McPherson & Williams 1998), a common habit among species from fire-prone habitats (Whelan 1995).

Most surprising, though, was the constancy of the number of seedlings recorded in all fragments after fire. Although high concentration of carbohydrate reserves may permit some palm seedlings to recover well after defoliation (McPherson & Williams 1999), young plants are unlikely to survive fire due to their undeveloped of subterranean system and, hence, superficial meristem position (McPherson & Williams 1998). This was indicated by the disappearance of juveniles and the reduction in the number of seedlings in the western sector (which was more strongly affected by fire, *pers. obs.*) of fragment II after fire (Figure 3). Fire is usually considered to be extremely rare in intact tropical moist forests (Uhl & Kauffman 1990), but fragmentation of such forests results in greater exposure to fires propagated in the surrounding non-forest landscape (Kellman & Meave 1997). Forest fires, however, are normally patchy (Whelan 1995) and tend to occur predominantly at the outer boundaries of fragments (Kellman & Meave 1997), at open, disturbed forest patches and at previously burned forest sectors (Cochrane & Schulze 1999). Seedling and juvenile persistence in the studied populations is better explained by the spatial segregation between seedlings and established plants, which lead to a large proportion of seedling clusters to emerge in closed patches of the fragments, since most established plants are concentrated in more opened sites (Chapter 3). Thus, *Attalea* seedlings and juveniles, occurring mainly in more closed, protected sectors, are likely to escape the majority of fires.

Many species of *Attalea* occur in savannah-like ecosystems, where fire is an important process, and have short or subterranean stems (Henderson *et al.* 1995), so that the habit and resprout strategy of *A. humilis* could be regarded as preadaptations to fire. Considering that *Attalea* population growth rate rely heavily on survivorship of seedlings and immature and virgin plants, it is unlikely that fire threatens its persistence in the fragments in face of the resprouting ability of established plants and as long as seed disperser activity permit new seedlings to emerge in relatively protected sites. Nevertheless, if fire frequency becomes too high, even populations of resprouting species may experience increased mortality of established plants and suffer rapid changes (Whelan 1995). Thus, provided fires did not become too frequent, it could promote *Attalea* population growth through the combined effects of increased fecundity after burning (Abrahamson 1999) and growth under opened canopies (Martínez-Ramos *et al.* 1988), and increased nutrient availability. Indeed, both simulated effects of increased fire frequency on woody plants of the cerrado savannas of Brazil (Hoffmann 1999) and theoretical studies (Iwasa & Kubo 1997) showed that burning (or periodic removal of aerial parts) promotes success of low-stature, long-lived resprouting species. This scenario could lead to a species-impoverished, palm dominated system in the forest fragments studied (McPherson & Williams 1998), as seems to be the case of the disturbed western sector of fragment II.

Nonetheless, at the current fire frequency (*ca.* one occurrence at each 5-year interval), the disturbed, fire-susceptible sectors of the fragments that harbour denser subpopulations of *Attalea* are giving place to dense successional stands dominated by vine and liana tangles, understorey bamboos, fast-growing pioneer tree species and a suite of sun-loving species, a common process in degraded tropical forest patches (Viana & Tabanez 1996, Laurance 1997, Oliveira-Filho *et al.* 1997). Most individuals of *Attalea* occurring in these patches were overtopped by regrowth vegetation in 1999 (*pers. obs.*). The open crown architecture, low stature and slow growth of *Attalea* may make it a poor competitor in such dense milieu. The absence of *Attalea* individuals from the *Trema*-dominated sectors in fragment I and the declining population size in fragment II (Table 2) could result from competitive exclusion from hyper-disturbed patches following fire.

Finally, although the proximity of the fragments may permit pollinator-mediated gene flow between populations in different fragments (Meffe & Carroll 1997), the large size of *Attalea* fruits and its probable dependence on scatterhoarding rodents for effective seed dispersal (Chapter 1) makes it unlikely that migration between fragments be frequent or even possible. Chance events, in this case represented by demographic and environmental stochasticity, and natural or man-induced catastrophes (Pulliam & Dunning 1997) can interact to draw small populations in an extinction vortex (Gilpin & Soulé 1986). Indeed, despite its apparently successful resprouting strategy, the population at the smallest fragment is already very small and possibly in danger of local extinction. The present results can be viewed as a warning that reduced fragment area, habitat degradation and man-induced fires can interact to threaten the persistence of even abundant, preadapted to such disturbances species, like *Attalea*.

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Table 1. General characterisation of the study forest fragments in the National Biological Reserve of Poço das Antas, Rio de Janeiro state, south-eastern Brazil.

Fragment	Area (ha)	Perimeter (m)	P:A^a	Number of 10 x 10 m Plots	Sampled Area^b (m^2)	Trees/ha^c (DBH ≥ 10 cm)	Mean Height^c (m)	Litterfall^d (ton ha^{-1} y^{-1})
I	1.6	325	0.020	29	2900 (18.1)	426	7.6	4.1
II	6.4	650	0.010	61	6100 (9.5)	514	9.4	5.3
III	9.9	775	0.008	70	7000 (7.1)	797	9.3	5.7

a - Perimeter (m): area (m^2) proportion; b - Percent area of each fragment sampled in parenthesis; c - Silva Matos *et al.* (1998*a*); d - Silva Matos *et al.* (1998*b*).

Table 2. Observed finite rates of increase ($\lambda = N_{t+1}/N_t$) and the significance of the departure of fluctuations in observed population size from a uniform distribution of population sizes.

	Time Period							
	1996 - 1997		1997 – 1998[1]		1998 – 1999		1996 - 1999	
Fragment	λ	χ^2	λ	χ^2	λ	χ^2	λ	χ^2
I	1.639	14.7***	0.848	1.4 ns	0.880	0.7 ns	1.222	1.8 ns
II	—	—	—	—	0.925	2.8 ns	0.838	14.5***
III	1.071	0.5 ns	0.877	1.6 ns	0.924	0.5 ns	0.869	1.7 ns

1 – time period comprising the fire. *** $P < 0.001$, ns = non significant.

Table 3. Transition matrices for *Attalea humilis* populations at two fragments of the Atlantic Forest. The corresponding value of λ for each matrix is also given. Missing matrix elements all have value of zero.

Stage at time $t + 1$	Stage at time t				
	S	J	I	V	R
Fragment I (λ = 1.229 ± 0.011)					
S	0.807				4.000
J	0.192				
I		0.999	0.444	0.077	
V			0.333	0.921	0.200
R			0.111	0.001	0.799
Fragment III (λ = 1.066 ± 0.007)					
S	0.556				0.632
J	0.056				
I	0.167	0.999	0.909	0.241	
V			0.001	0.654	0.105
R			0.030	0.103	0.894

S = seedling, J = juvenile, I = immature, V = virgin, R = reproductive.

Table 4. Elasticity matrices for *Attalea humilis* populations at two fragments of the Atlantic Forest.

Stage at time $t + 1$	Stage at time t				
	S	J	I	V	R
Fragment I					
S	21.39				9.33
J	9.33				
I		9.33	7.34	2.31	
V			1.83	8.44	0.34
R			9.54	1.43	21.38
Fragment III					
S	4.18				3.49
J	0.86				
I	2.63	0.86	35.43	0.87	
V			0.07	3.98	2.16
R			4.29	1.36	39.83

Elasticity values were multiplied by 100 to be represented as percentages. Missing matrix elements all have value of zero. S = seedling, J = juvenile, I = immature, V = virgin, R = reproductive.

Table 5. Statistical results of comparisons between actual and stable stage distributions predicted by the models for two fragments of the Atlantic Forest. The proportional similarity index (PS), indicating the magnitude of the difference between the two distributions, is given.

	Fragment					
	I			III		
Year	G	P	PS (%)	G	P	PS (%)
1996	110.7	< 0.0001	41.8	26.2	< 0.0001	73.6
1997	8.0	0.093 NS	82.5	13.4	0.01	77.4
1998	88.5	< 0.0001	42.0	15.6	0.004	81.2
1999	71.8	< 0.0001	49.5	16.9	0.002	82.9

df = 4 in all cases.

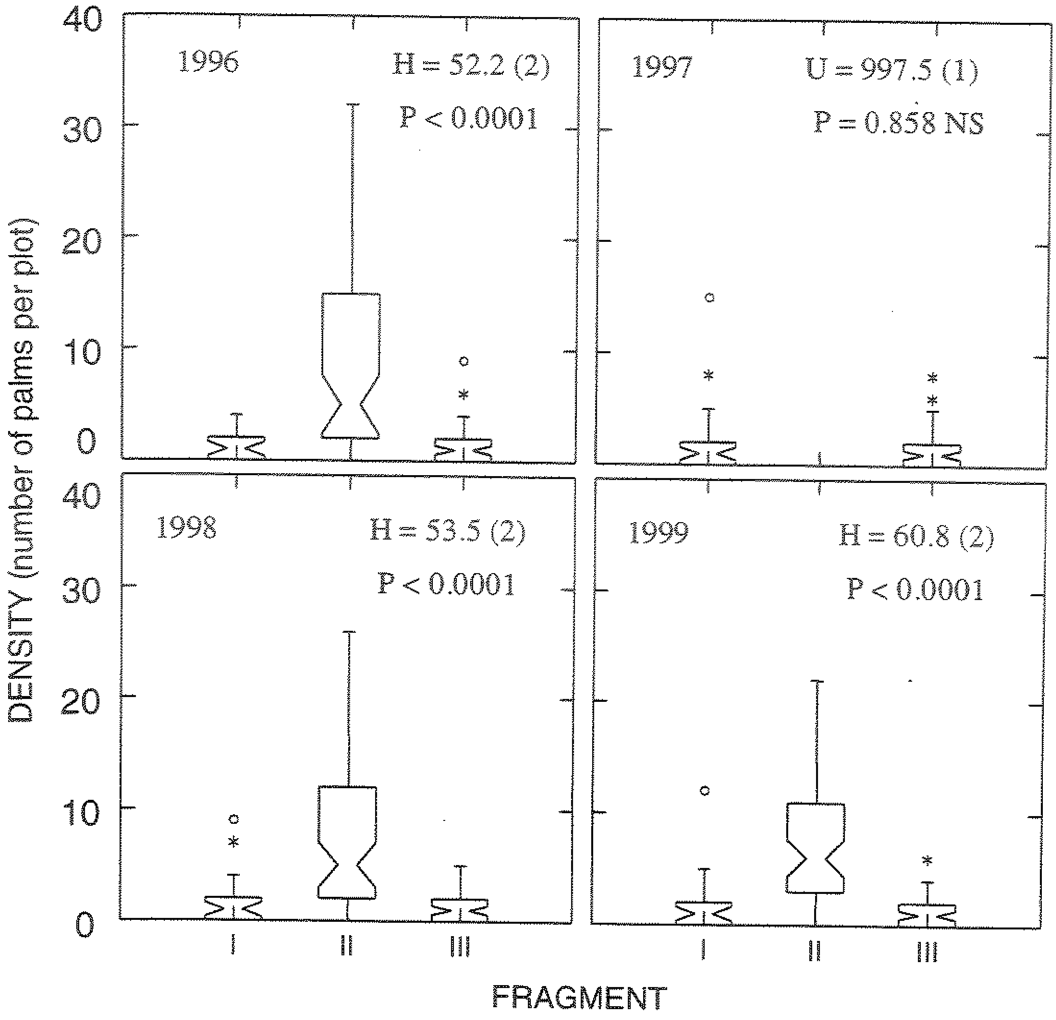

Figure 1. Density of *Attalea humilis* at three fragments of the Atlantic Forest. Central horizontal bars represent median values; upper and lower vertical bars (whiskies) represent 4th and 1st percentiles, respectively; notches surrounding the median represent median 95% confidence intervals; vertical bars connect the minimum and maximum values measured; o = extreme value; * = outlier. Non-overlapping of notches indicates significant difference at 95% confidence level. The results of the Kruskal-Wallis ANOVA (H) or the Mann-Whitney test (U), indicating whether there is a significant difference between the densities of the three fragments, is given; df for each case in parentheses.

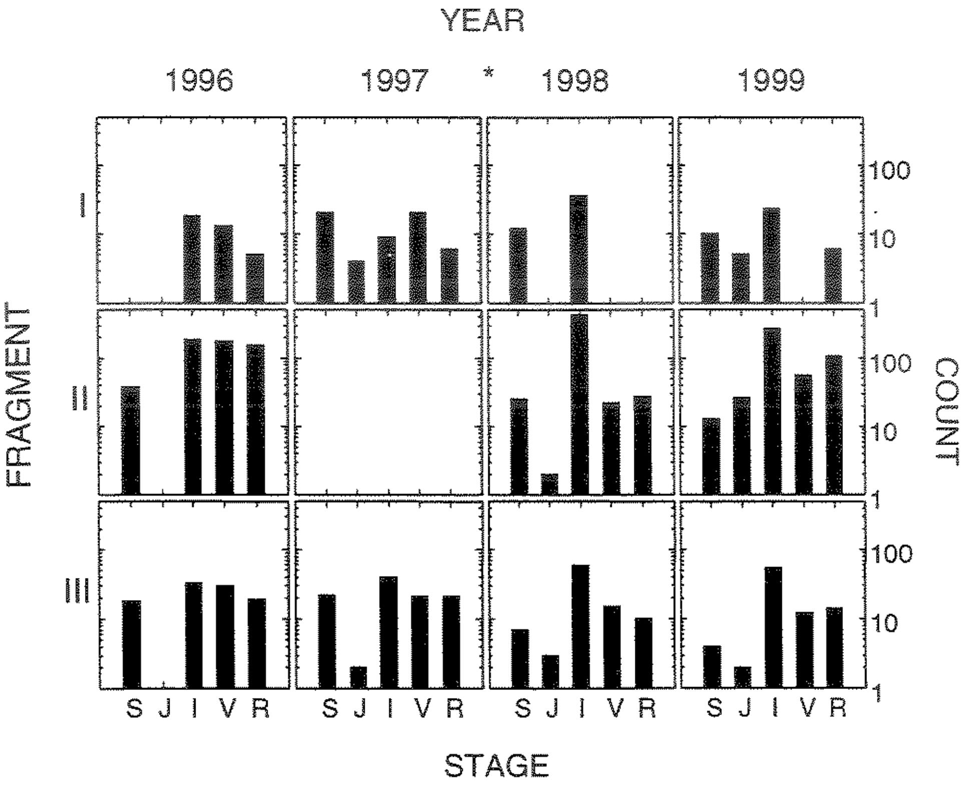

Figure 2. Frequency distributions of stages for the three populations of *Attalea humilis*. * indicates the occurrence of fire. S = seedling, J = juvenile, I = immature, V = virgin and R = reproductive.

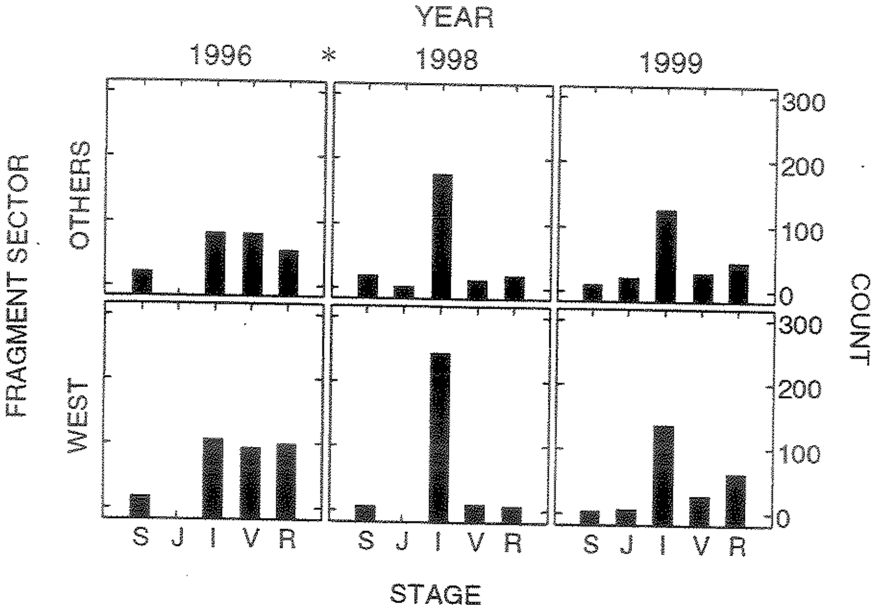

Figure 3. Frequency distributions of stages for the sub-populations of *Attalea humilis* in the western, disturbed sector of a fragment of the Atlantic Forest, and in the other sectors pooled. * indicates the occurrence of fire. S = seedling, J = juvenile, I = immature, V = virgin and R = reproductive.

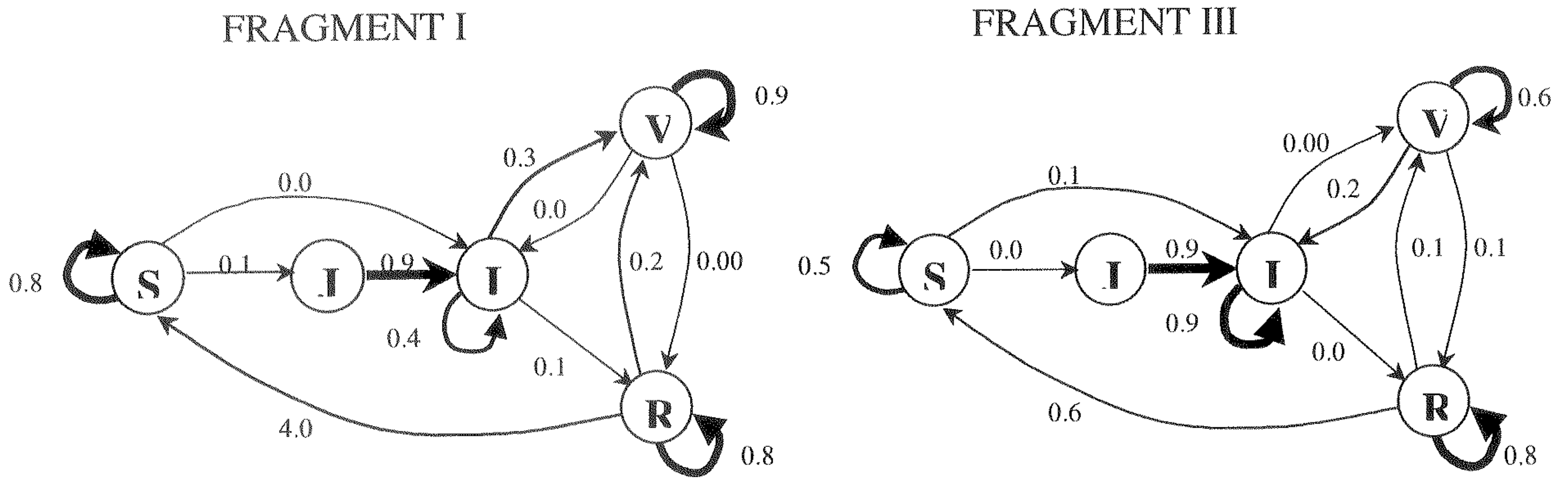

Figure 4. Life cycle diagram for *Attalea humilis* at two forest fragments of the Atlantic Forest. Values along arrows represent transition probabilities between stages (from one circle to another), or stasis probabilities (from a circle to the same one). S = seedling, J = juvenile, I = immature, V = virgin and R = reproductive.

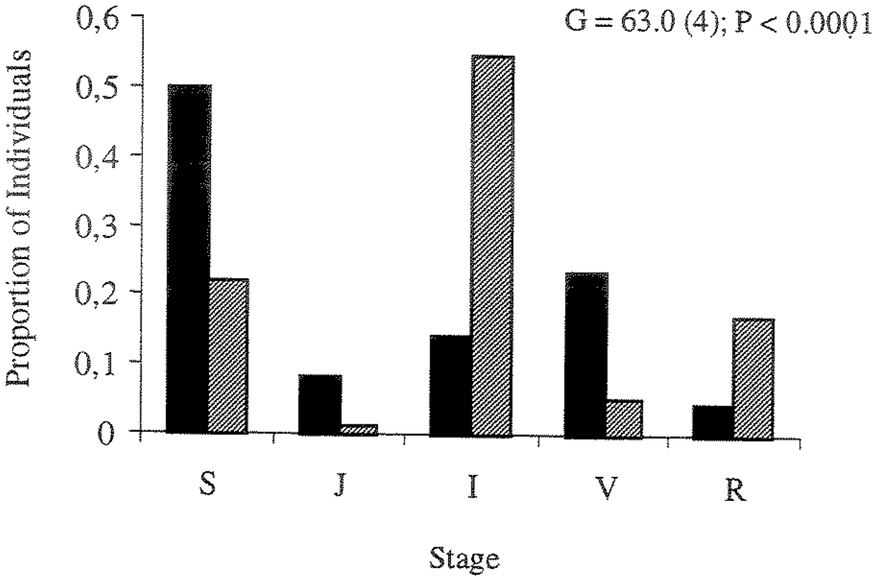

Figure 5. The stable-stage distribution for fragments I (solid bars) and III (hatched bars). The *G* statistic, indicating whether there is a significant difference between the two distributions, is given. S = seedling, J = juvenile, I = immature, V = virgin and R = reproductive.

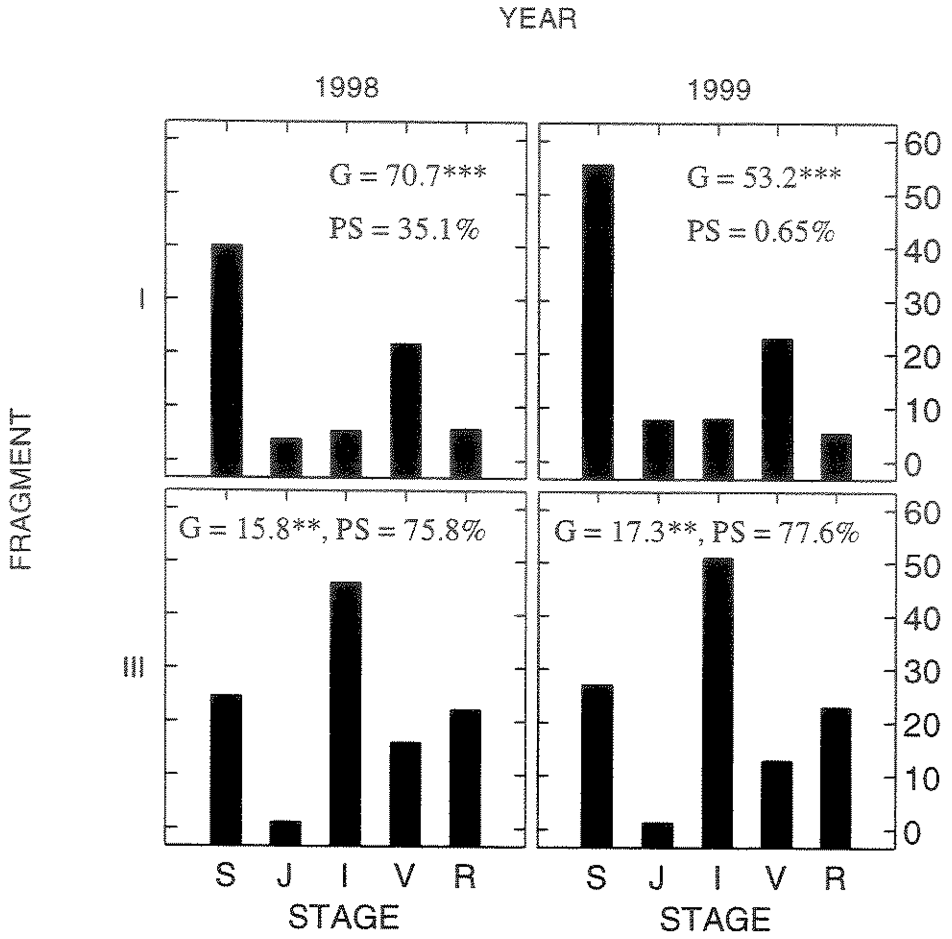

Figure 6. Transient analysis for *Attalea humilis* by projection of the stage structure at two fragments of the Atlantic Forest. The G statistic, indicating whether there is a significant difference between the projected and the observed distribution, and PS, indicating the magnitude of the difference between the two distributions, are given. df = 4 in all cases. ** $P < 0.01$, *** $P < 0.001$.

CONSIDERAÇÕES FINAIS

Como dissemos na Introdução Geral, os quatro trabalhos aqui reunidos abordaram aspectos da ecologia de populações de *Attalea humilis* visando à detecção de padrões e tendências populacionais. Sendo assim, não pudemos aqui elucidar as causas geradoras dos padrões observados nem prever exatamente em que condições poderão se repetir no futuro. Porém, através das análises apresentadas e das informações disponíveis na literatura, podemos propor, tentativamente, um cenário acerca do ciclo de vida de *Attalea humilis* nos fragmentos estudados. Este cenário, que mantivemos em sua forma mais simples possível, segundo o princípio da parcimônia (Barot *et al.* 1999), inclui uma série de hipóteses que podem ser testadas no futuro através de experimentos planejados para este fim. O cenário é o seguinte:

(1) O processo de dispersão de sementes de *A. humilis* ocorreria através do uso dos frutos por roedores de médio porte, que removeriam os frutos das proximidades das plantas mães e os enterrariam, isolados, próximo a elementos estruturais da floresta, formando agregados de baixa densidade. Os frutos não dispersos acumular-se-iam sob as palmeiras que os geraram e sofreriam altas taxas de mortalidade devido ao dessecamento e ao ataque de insetos.

(2) Os frutos não recuperados pelos dispersores germinariam, originando agregados de plântulas em baixas densidades, freqüentemente dissociados dos locais de maior ocorrência de adultos. As plântulas emergiriam com uma grande variação no tamanho foliar devido a diferenças genéticas e a diferenças no tamanho inicial dos frutos.

(3) As plântulas apresentariam altas taxas de sobrevivência, por contarem com os recursos do endosperma, ao qual permanecem ligadas por um período variável de tempo, por

serem capazes de armazenar carboidratos em tecidos de reserva e por apresentarem defesas contra a ação de herbívoros, principalmente altos teores de fibras e cristais de sílica nas folhas.

(4) Apesar dessa capacidade de sobreviver no estádio de plântulas, o crescimento para os estádios seguintes seria em grande parte dependente de aumentos na disponibilidade de recursos, representados principalmente pela luz, através da abertura de clareiras. Isso seria justificado pelo fato de que a luminosidade nas clareiras é grandemente aumentada em relação ao sub-bosque da mata fechada e a disponibilidade de nutrientes é muito mais variável e, em grande parte, imprevisível.

(5) Em resposta ao aumento de recursos, os indivíduos passariam rapidamente pelo estádio juvenil, de caráter transicional, e iniciariam a produção de folhas maiores e pinatissectas, entrando no estádio imaturo, iniciando a formação do sistema subterrâneo. A ocorrência de imaturos em locais de maior luminosidade, juntamente com as limitações fisiológicas à produção de novas folhas, reduziria a variação do número de folhas neste estádio, mas não no tamanho das folhas mais novas, dependente, em parte, das condições em que se encontra cada indivíduo.

(6) Uma vez estabelecidos, os indivíduos seriam capazes de sobreviver e crescer, embora lentamente, sob as condições de luminosidade reduzida do sub-bosque e, dependendo da ocorrência estacional de clareiras, atingir maiores taxas de crescimento. O caráter discreto das clareiras que se formam naturalmente nas florestas tropicais e a capacidade de os indivíduos da palmeira persistirem no sub-bosque implicariam na formação de agregados de baixa densidade de indivíduos em uma escala maior do que a das plântulas, devido ao recrutamento sucessivo de diferentes agregados de plântulas.

(7) Ao alcançarem um tamanho crítico, determinado, em grande parte, por relações de compromisso ('trade-offs') mecânicas e fisiológicas, os indivíduos passariam a reproduzir-se estacionalmente, durante a estação mais chuvosa do ano. A alocação periódica de recursos para a reprodução produziria um aumento na variabilidade do tamanho da copa dos indivíduos reprodutivos.

(8) Portanto, em condições florestais conservadas, o crescimento lento e a longevidade dos indivíduos, adicionados ao padrão de sobrevivência e fecundidade aqui sugeridos, permitiriam às populações manter um equilíbrio dinâmico entre as taxas de mortalidade e de natalidade e, portanto, apresentar taxas de crescimento populacional próximas à unidade.

(9) A perturbação antropogênica das florestas, através da retirada de madeira e de incêndios, provoca ocorrência de florestas perturbadas, com dossel aberto e mais baixo e, portanto, com maior penetração de luz. Nesses ambientes o recrutamento de indivíduos de *A. humilis* para os estádios mais desenvolvidos acelerar-se-ia, assim como a sobrevivência de plântulas de cada agregado inicial. Adicionalmente, o hábito da espécie, caracterizado por um meristema apical e um caule curto, ambos subterrâneos, representaria uma pré-adaptação a ambientes sujeitos a incêndios periódicos, permitindo uma alta sobrevivência dos indivíduos estabelecidos em relação ao fogo.

(10) Beneficiada pelo aumento da luminosidade em áreas perturbadas e pelo aumento da luminosidade e da disponibilidade de nutrientes que sucede aos incêndios florestais, haveria a formação de grandes colônias de indivíduos ocorrendo em densidades elevadas, em setores perturbados e sujeitos a incêndios. A arquitetura aberta da copa da espécie, composta de poucas folhas grandes, afastadas entre si, dispostas em espiral e

elevadas por longos pecíolos, permitiria a sobreposição das áreas de influência individuais, minimizando os efeitos negativos da competição intra-específica.

(11) Em condições perturbadas, as populações apresentariam taxas de crescimento maiores que a unidade, até que fatores dependentes da densidade passasssem a ser limitantes e estabilizassem sua densidade num novo patamar. Esse novo patamar, porém, seria muito maior que o anterior.

(12) A degradação contínua do habitat florestal, com a ocorrência de sucessivos incêndios poderia levar à proliferação de vegetação secundária de baixo porte, dominada por lianas, bambus e árvores pioneiras em alta densidade, seria capaz de eliminar competitivamente *A. humilis*. Os densos agregados da palmeira observados em pastagens seriam constituídos de indivíduos remanescentes de populações que aumentaram em florestas que foram perturbadas e depois eliminadas subitamente através do fogo ou de corte raso. Seriam, porém, populações inviáveis devido à falta de recrutamento de novos indivíduos, dada a ausência dos dispersores.

Implicações para conservação

Os resultados descritos nos capítulos da tese e o cenário demográfico sugerido acima apresentam importantes implicações para a conservação tanto da espécie estudada quanto de outras espécies com populações em fragmentos florestais nos trópicos.

A estimativa do tamanho populacional (Capítulo 4) projetou tamanhos variados para as populações nos fragmentos estudados. Segundo os cálculos, o menor fragmento (1.6 ha) tinha, em 1996, uma população de cerca de 200 indivíduos, o de tamanho intermediário

(6.4 ha), cerca de 6000 indivíduos e o maior (9.9 ha), aproximadamente 1400. Se considerarmos os indivíduos virgens e reprodutivos, que, em conjunto, provavelmente representam os com maior probabilidade de reprodução, obtemos estimativas dos tamanhos populacionais efetivos (N_e, Caughley 1994), ainda que grosseiras, de 99 indivíduos no fragmento I, 3399 indivíduos no fragmento II e 679 indivíduos no fragmento III.

Embora haja muito debate acerca da existência de um tamanho mínimo populacional viável universal, é um fato que populações pequenas têm probabilidade de extinção muito maior que populações grandes (Caughley 1994) em decorrência de processos genéticos e demográficos (Caughley 1994, Alvarez-Buylla *et al.* 1996). A longo prazo, acredita-se que os indivíduos de populações com pequeno tamanho efetivo sofram reduções em seu valor adaptativo ('fitness') devido a reduções na variabilidade genética resultante da perda de alelos e ao aumento da freqüência de indivíduos homozigotos com alelos semi-letais (Meffe & Carroll 1997). Tais efeitos negativos são fruto da deriva gênica (estocasticidade genética), 'gargalos' demográficos (a diversidade genética populacional é limitada ao conjunto gênico dos sobreviventes de reduções no tamanho populacional) e depressão de autocruzamento (Caughley 1994, Meffe & Carroll 1997). Para evitar esses efeitos nocivos, acredita-se que populações efetivas de pelo menos 50 indivíduos seriam necessárias e, para permitir a ocorrência dos processos evolutivos normais, as populações efetivas deveriam ter pelo menos 500 indivíduos (Franklin 1980). Por outro lado, é provável que um pequeno fluxo gênico seja suficiente para evitar a erosão da diversidade genética em populações pequenas (Meffe & Carroll 1997).

Nossas estimativas gerais para os tamanhos populacionais efetivos de *A. humilis* nos fragmentos estudados indicam, a princípio, que, se as populações nos fragmentos II e III se mantiverem em equilíbrio, como observado para o período estudado, há poucas chances de fatores genéticos desempenharem um papel relevante no risco de sua extinção. A população no menor fragmento, por sua vez, apresentou um tamanho populacional efetivo perigosamente próximo do mínimo proposto de 50 indivíduos, tornando mais provável a participação de fatores genéticos no processo de extinção local de *A. humilis* em fragmentos muito pequenos (*i.e.*, menores do que 6 ha). Entretanto, é provável que mesmo as populações reduzidas ocorrentes em fragmentos muito pequenos não corram um risco elevado de deterioração genética, se houver fluxo gênico de populações vizinhas. De acordo com as poucas informações disponíveis sobre o sistema reprodutivo de espécies do gênero *Attalea* (= *Scheelea, Orbignya* e *Maximiliana*, Uhl & Dransfield 1987), os agentes polinizadores incluem besouros, abelhas européias africanizadas (*Apis mellifera*) e meliponídeos, abelhas sem ferrão nativas do Brasil (Voeks & Dias 1985, Henderson 1986, 1988 e observação pessoal). As distâncias de vôo de abelhas estão ao redor de poucos quilômetros, mas podem chegar a dezenas de quilômetros em espécies maiores, não sendo normalmente inibidas por espaços abertos (Roubik 1989). Considerando a proximidade entre os fragmentos estudados (até ~300m entre fragmentos vizinhos) e entre a maioria dos fragmentos de floresta Atlântica em geral (Ranta *et al.* 1998), é provável que os agentes polinizadores ativos entre tais fragmentos sejam capazes de promover o reduzido fluxo gênico necessário para a prevenção dos efeitos deletérios da degradação genética das populações, apesar da tendência de substituição de abelhas nativas por abelhas européias africanizadas (Aizen & Feinsinger 1994) e da redução da riqueza e abundância de espécies de besouros (Klein 1989) em fragmentos florestais pequenos.

Se fatores genéticos têm poucas chances de aumentar significativamente as chances de extinção de *A. humilis* em fragmentos de floresta Atlântica, o mesmo não acontece com fatores demográficos. A estocasticidade demográfica e ambiental e a ocorrência de catástrofes naturais e induzidas pelo homem podem atuar sinergísticamente, levando populações reduzidas a um vórtice de extinção (Gilpin & Soulé 1986). Por esta razão, a existência de metapopulações tem recebido atenção cada vez maior em estudos de conservação de populações naturais, em face da possibilidade de muitas espécies dependerem da recolonização periódica de habitats após eventos de extinção local (Pulliam & Dunning 1997, Metzger 1999). Com base nas características reprodutivas de *A. humilis* (Capítulo 1), é possível supor que a existência de metapopulações no arquipélago dos barbados ou em outros complexos de fragmentos da Floresta Ombrófila Densa Atlântica seja dependente da presença de animais dispersores de sementes, provavelmente roedores de médio porte como cutias e pacas, para o transporte de frutos e a criação de condições favoráveis à germinação pelo enterramento dos frutos. Cutias são animais territoriais, cada casal dividindo um território de cerca de 1 ha (Dubost 1988) e cuja dieta compõe-se basicamente de frutos e sementes, encontrados em ambientes florestais (Dubost 1988, Henry 1999). Embora não haja informações disponíveis acerca do padrão de movimentação desses animais entre habitats separados por áreas abertas ou do grau de conectividade entre habitats necessário para que tal movimento se dê, é pouco provável que o transporte de frutos de *A. humilis* entre fragmentos, se ocorrer, se dê com freqüência suficiente para promover a recolonização de fragmentos após eventos de extinção local.

Além disso, roedores de médio porte estão entre os primeiros grupos a desaparecer de pequenos fragmentos da Floresta Ombrófila Densa Atlântica devido à degradação do habitat e à pressão de caça (Redford 1992, Chiarello 1999). É possível que mesmo as populações estabelecidas de *A. humilis* estejam sofrendo limitações no recrutamento de plântulas diante da ausência de dispersores, em mais um exemplo de efeito cascata do impacto humano em espécies dependentes de outras espécies (Redford 1992, Asquith *et al.*

1999). Este quadro, somado à capacidade de *A. humilis* de crescer oportunisticamente sob graus de perturbação antrópica intermediários, leva-nos a supor que a abundância desta espécie atingiria valores máximos em fragmentos florestais perturbados recentemente ou com graus de conservação intermediários, mas declinaria em fragmentos hiper-perturbados pela repetição de incêndios, efeitos de borda e caça atuando em conjunto. Considerando que palmeiras são organismos de vida longa, que tendem a responder lentamente a alterações no ambiente (Scariot 1999), é possível que muitos remanescentes florestais onde *A. humilis* ocorre como espécie dominante no sub-bosque – e muito provavelmente também os agregados remanescentes em pastagens (Lorenzi *et al.* 1996) – sejam populações inviáveis, sem recrutamento de novos indivíduos, com existência limitada à longevidade dos indivíduos já estabelecidos. Além da gravidade do fenômeno em si, a extinção local de *A. humilis* em fragmentos da Floresta Ombrófila Densa Atlântica pode funcionar como um círculo vicioso de causa e efeito, dificultando a sobrevivência ou o restabelecimento de populações de roedores de médio porte, para os quais frutos e sementes de palmeiras costumam constituir recurso-chave para a subsistência em períodos naturais ou induzidos de escassez de recursos alimentares (Terborgh 1986, Smythe 1989, Henry 1999).

Esse conjunto de possibilidades ressalta a importância da preservação do maior número possível de fragmentos florestais, conclusão a que têm chegado pesquisadores atuando em florestas tropicais pluviais (Turner & Corlett 1996) e semidecíduas (Janzen 1988). Fragmentos florestais de pequeno porte podem abrigar populações que, embora inviáveis a longo prazo, representam um valioso potencial para programas de recuperação de populações por reintrodução de dispersores e da coalescência de fragmentos através de programas de revegetação.

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