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ASPECTOS DA DINÂMICA POPULACIONAL DE UMA PALMEIRA CLONAL NA FLORESTA PALUDÍCOLA DA RESERVA MUNICIPAL DE SANTA GENEBRA (CAMPINAS, SP)

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Conteúdo

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RESUMO

Nesta tese, investigamos aspectos da ecologia de uma espécie de palmeira clonal endêmica das florestas paludícolas da América do Sul, *Geonoma brevispatha*. Buscando inserir o estudo demográfico em seu contexto florestal, ampliamos o escopo da tese de forma a incluir um estudo sobre a estrutura e dinâmica do fragmento de floresta paludícola onde *G. brevispatha* foi estudada. De forma geral, nosso principal objetivo foi a detecção de padrões e tendências populacionais no sistema ecológico estudado. A tese está dividida em quatro capítulos, que abordaram os seguintes aspectos do sistema estudado:

1) *Estrutura e dinâmica da floresta paludícola*. Clareiras e áreas sucessionais compreenderam, respectivamente, 7,5% e 69,75% da área em 2002. A análise demonstrou grande imprevisibilidade da variação de fundo na abertura de dossel, mas áreas com graus mais elevados de abertura concentraram-se em um arco ao longo da direção nordeste-sudoeste. A abertura de dossel aumentou entre 2001 e 2002. No período estudado, os pontos alagados diminuíram em 40,4%. A abertura de dossel e a densidade de árvores pequenas foram independentes da umidade do solo, não sendo correlacionadas. Árvores grandes ocorreram agregadas na área estudada em escalas maiores do que 40 m, enquanto palmeiras arborescentes ocorreram agregadas em todas as escalas avaliadas (1 - 50 m).

2) *Estádios ontogenéticos e estratégias de crescimento*. Nós investigamos os padrões de crescimento e reprodução da palmeira clonal arbustiva *Geonoma brevispatha*, baseados na identificação dos estádios ontogenéticos pós-seminais, em um período de três anos. A espécie desenvolve-se como genetas (indivíduos genéticos) os quais crescem através da produção de rametas (indivíduos morfologicamente diferentes porém geneticamente

iguais). Os rametas passam por quatro estádios ontogenéticos (juvenis de folhas bífidas, imaturos acaulescentes de folhas pinatissectas, virgens não reprodutivos e com estipe, e reprodutivos, com estipe). Durante a ontogenia, o tamanho da folha, o número de folhas e a taxa de produção de novas folhas aumentam, as a taxa de crescimento em diâmetro é mais elevada apenas entre os rametas imaturos, sendo estatisticamente igual entre os demais estádios. O comprimento do estipe, o número de nós e o comprimento da raquis foliar foram positivamente correlacionados em todos os estádios, mas a altura da copa foi menor do que o comprimento do estipe entre os rametas reprodutivos devido ao tombamento freqüente do estipe. O número de folhas e a fecundidade sexual aumentaram proporcionalmente ao comprimento do rameta, mas declinaram nos rametas maiores, o que foi interpretado como sinal de senescência. A fecundidade clonal precedeu a fecundidade sexual, e ambas as fecundidades aumentaram continuamente com o tamanho do geneta.

3) *Especialização de micrositíos e distribuição espacial da espécie.* Neste capítulo, testei as hipóteses segundo as quais (1) genetas reprodutivos de *Geonoma brevispatha* seria mais abundante em micrositíos mais iluminados, mas a abundância dos juvenis não seria responsiva à disponibilidade de luz; (2) a espécie seria restrita às regiões de transição entre micrositíos alagados e secos; (3) se as hipóteses (1) e/ou (2) fossem aceitas, a especialização de microhabitat que elas representariam deveriam refletir-se na distribuição espacial dos indivíduos em escalas distintas. A umidade do solo foi autocorrelacionada espacialmente em distâncias menores do que 1 m, refletindo o padrão microtopográfico de depressões e canais delimitados por elevações mais secas no terreno. A primeira hipótese foi rejeitada, mas a segunda foi aceita. Nenhum geneta ocorreu em micrositíos alagados. A terceira hipótese foi aceita. Genetas individuais apresentaram distribuição especial aleatória, correspondente à distribuição da umidade

do solo, mas apresentaram-se agregados em escalas maiores. Genetas juvenis estavam associados positivamente com genetas reprodutivos.

4) *Dinâmica populacional*. A mortalidade de genetas estabelecidos foi < 2,0%, e foi concentrada em rametas solitários. As taxas demográficas no interior de cada geneta foram afetadas principalmente pelo tamanho do geneta, mais do que por fatores ambientais diretos. A sobrevivência de juvenis solitários (27,8%) foi muito menor do que a de juvenis produzidos vegetativamente (79,3%), indicando subsídios para o estabelecimento, através da integração fisiológica no interior dos genetas. As taxas de produção vegetativa de rametas foram positivamente relacionadas com o tamanho dos genetas em ambos os anos. No Segundo ano, houve uma redução importante na sobrevivência dos rametas reprodutivos, em grande parte devido a um aumento na pressão de predação por macacos. Modelos populacionais matriciais predisseram que a taxa de crescimento da população geral de rametas foi significativamente maior do que a unidade no primeiro ano de estudo, mas significativamente menor do que 1,0 no ano seguinte. Simulações periódicas e estocásticas indicaram que longas seqüências de anos desfavoráveis seriam necessárias para reduzir as taxas de crescimento populacionais.

ABSTRACT

In this thesis, we investigate aspects of the population ecology of the clonal palm *Geonoma brevispatha*,which is endemic to the swamp forests of South America. Seeking to insert the demographic study in the context of forest ecology, we expanded the thesis scope to include a study of the structure and dynamics of the swamp forest fragment where *G. brevispatha* was accompanied. Our main goal was to detect the main population patterns and tendencies and tendencies in the studied ecological system. The thesis is divided in four chapters:

1) *Swamp forest structure and dynamics*. Building patches and treefall gaps comprised, respectively, 69.75% and 7.5% of the area in 2002. Spatial analyses showed large unpredictability of background variation in canopy openness, but patches with high canopy openness values concentrated along the South and East plot borders. Overall canopy openness increased from 2001 to 2002. In 2001, flooded sites comprised 38.19% of the study area, and were not spatially autocorrelated. Large trees aggregated at scales larger than 40 m, while arborescent palms were aggregated at all scales.

2) *Ontogenetic stages and growth strategies.* We investigated the patterns of growth and reproduction of the understory clonal palm *Geonoma brevispatha* based on the identification of post-germinative ontogenetic stages, over a 3-yr period. Ramets pass through four ontogenetic stages (bifid-leafed juveniles, pinnatifid-leafed stemless immatures, stemmed non-reproductive virgins, and reproducers). Leaf size, leaf number and leaf production rate increased during ontogeny, but diameter growth rate was higher among immatures. Stem length, number of nodes and leaf rachis length were positively correlated across ontogenetic stages, but crown height was smaller than stem length in adult palms due to frequent leaning. Leaf number and sexual fecundity increased with

ramet size, but declined in larger, senescent ramets. Clonal fecundity preceded sexual fecundity, and sexual and clonal fecundity increased continuously with genet size. No relation was found between sexual and clonal fecundity.

3) *Microsite specialization and spatial distribution.* We tested the hypotheses that: (1) reproductive *Geonoma brevispatha* is most abundant in more brightly lit microsites but the abundance of juveniles is not responsive to light availability; (2) the species is restricted to the transitional zones between flooded and well-drained microsites; (3) if hypotheses (1) and/or (2) are accepted, the microhabitat specialization they represent should be reflected in the spatial distribution of the individuals at distinct scales. Soil moisture was autocorrelated at distances up to ca. 1 m, reflecting a fine-scale microtopographic pattern of flooded pits and channels delimited by drier mounds. The first hypothesis was rejected, but the second hypothesis was accepted. No genets occurred on flooded microsites. The third hypothesis was accepted. Individual genets were randomly distributed at scales corresponding to soil moisture patches, but were aggregated at larger scales. Juvenile genets were positively associated with reproducer genets.

4) *Population dynamics.* Mortality of established genets was < 2.0%, and was concentrated on solitary ramets. Within-genet ramet vital rates were mainly affected by genet size, rather than by direct environmental factors. Solitary juvenile survivorship (27.8%) was much lower than the survivorship of juvenile ramets produced vegetatively (79.3%), indicating establishment support through physiological integration within genets. Rates of vegetative ramet production were positively related to genet size in both years. In the second year, there was a marked reduction in the survivorship of reproducer ramets, largely attributable to increased predation pressure by *Cebus apella nigritus* monkeys. Matrix models predicted that the growth rate of the overall ramet

population was significantly greater than unity in the first study year, but it was significantly smaller than 1.0 in the next. Massive predation by monkeys on the crowns of reproductive ramets and prolonged dry season were probably responsible for population decrease. Periodic and stochastic simulations indicated that long sequences of unfavourable years would be necessary to reduce population growth rates.

INTRODUÇÃO GERAL

Nas últimas décadas, as florestas tropicais têm sido alvo de um crescente número de publicações científicas. Intensos esforços de pesquisa têm revelado padrões na distribuição geográfica de seus táxons (Terborgh e Andersen 1998, ter Steege *et al.* 2000) e de sua diversidade arbórea (Scudeller *et al.* 2001, ter Steege *et al.* 2003), bem como ampliado nossa compreensão acerca dos complexos mecanismos envolvidos na estrutura e dinâmica de suas comunidades vegetais (*e.g.*, Condit *et al.* 1992, 2000, Wills *et al.* 1997, Harms *et al.* 2001). Em nível populacional, um número crescente de estudos demográficos utilizando modelos matriciais exponenciais tem revelado que a maioria das espécies estudadas encontrava-se em equilíbrio (Alvarez-Buylla *et al.* 1996).

Entretanto, apesar destes avanços, muitos aspectos da ecologia vegetal tropical permanecem obscuros. Dois destes aspectos são a ecologia das florestas paludícolas (*i.e.*, florestas que ocorrem sobre solos permanentemente alagados), e de populações clonais. Nas florestas tropicais, as espécies clonais são particularmente abundantes no sub-bosque (Sagers 1993; Richards 1996, van Groenendael *et al.* 1997; Kammesheidt 1999). As florestas paludícolas, por sua vez, têm sido alvo de descrições florístico-fitossociológicas (*e.g.*, Ivanauskas *et al.* 1997, Toniato *et al.* 1998), mas sua estrutura e dinâmica são pouco conhecidas (ter Steege *et al.* 2003). Para compreendermos a ecologia de plantas clonais endêmicas de florestas paludícolas, precisamos de um conhecimento prévio das conseqüências ecológicas do crescimento clonal, assim como de uma melhor compreensão da estrutura e dinâmica de seu ambiente.

Nesta tese, investigamos aspectos da ecologia de uma espécie de palmeira clonal endêmica das florestas paludícolas da América do Sul, *Geonoma brevispatha*. Buscando inserir o estudo demográfico em seu contexto florestal, ampliamos o escopo da tese de forma a incluir um estudo sobre a estrutura e dinâmica do fragmento de floresta paludícola onde *G. brevispatha* foi estudada. De forma geral, nosso principal objetivo foi a detecção de padrões e tendências populacionais no sistema ecológico estudado.

A investigação de aspectos pouco compreendidos das florestas tropicais é necessária por razões mais do que acadêmicas. Devido ao fato de as florestas tropicais abrigarem um grande número de espécies (Wilson e 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 ambientalmente sustentável (Whitmore e Sayer 1992, Goodland 1995). Neste contexto, o estudo de populações vegetais em fragmentos florestais, além de contribuir para o conhecimento ecológico dos sistemas estudados, tem potencial para subsidiar ações conservacionistas de caráter prático.

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 e de seu ambiente.

No primeiro capítulo, apresentamos uma descrição da estrutura espacial de alguns elementos da floresta paludícola onde o estudo foi desenvolvido, bem como alguns aspectos de sua dinâmica. Neste capítulo, nossa ênfase foi na organização espacial horizontal de alguns dos principais elementos florestais com potencial para influenciar a dinâmica de populações de *G. brevispatha*.

No segundo capítulo, identificamos os estádios ontogenéticos (fases de desenvolvimento) da espécie, com base em análises morfológicas e morfométricas. Estes estádios serviram como base para o desenvolvimento das análises posteriores. Também neste capítulo, exploramos algumas implicações do hábito clonal para as estratégias reprodutivas e de crescimento da espécie.

No terceiro capítulo, investigamos a distribuição espacial dos indivíduos, bem como sua especialização em determinadas porções de seu hábitat natural. O padrão espacial de uma população é fruto de uma seqüência de interações bióticas e abióticas ao longo da ontogenia da espécie, e pode oferecer importantes indícios de processos ecológicos importantes.

Por fim, no quarto capítulo apresentamos a demografia da população estudada, incluindo uma análise de seu ciclo de vida e estimativas das taxas de crescimento populacional.

Por que Inglês?

Uma observação 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 da Comissão Central de Pós-Graduação do Instituto de Biologia da UNICAMP (001/98), que dispõe a respeito do formato das teses de Mestrado e Doutorado aprovadas pela UNICAMP. Optamos pelo uso deste idioma visando à publicação dos capítulos em periódicos de circulação internacional. Esta opção foi feita com o objetivo de facilitar e agilizar a publicação dos trabalhos neste tipo de veículo, de forma a garantir sua disponibilidade a um maior número de profissionais interessados no assunto.

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CAPÍTULO 1. Spatial variation and dynamics of flooding, canopy openness, and structure in a neotropical swamp forest.[1]

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[1] – Tabelas e figuras no final do capítulo. Trabalho formatado segundo as normas da revista *Plant Ecology*.

Resumo

Um passo importante na determinação dos impactos ambientais de atividades econômicas é o desenvolvimento de ferramentas científicas capazes de detectar mudanças em sistemas naturais. Neste estudo, aplicamos métodos geoestatísticos à investigação da degradação florestal em um fragmento florestal urbano impactado pela poluição atmosférica e pelos efeitos de borda. Nós medimos as mudanças temporais e a variação especial da umidade do solo e da disponibilidade de luz no sub-bosque (medida como abertura de dossel) em 2001 e 2002. Medimos também a densidade de árvores pequenas (5 ≤ diâmetro à altura do peito < 10 cm), a fase sucessional florestal e a distribuição espacial de árvores grandes (diâmetro à altura do peito ≥ 10 cm) em 1 ha de floresta paludícola (floresta de brejo) na Reserva Municipal de Santa Genebra (Campinas, SP). Clareiras e áreas sucessionais compreenderam, respectivamente, 7,5% e 69,75% da área em 2002. Semivariogramas indicaram segregação especial das fases sucessionais, com áreas maduras predominando no norte, e clareiras e áreas abertas no sul e na margem leste do hectare estudado. A exclusão de pontos com valores extremos demonstrou grande imprevisibilidade da variação de fundo na abertura de dossel, mas áreas com graus mais elevados de abertura concentraram-se em um arco ao longo da direção nordeste-sudoeste. A abertura de dossel aumentou entre 2001 e 2002. No período estudado, os pontos alagados diminuíram em 40,4%. A abertura de dossel e a densidade de árvores pequenas foram independentes da umidade do solo, não sendo correlacionadas. Árvores grandes ocorreram agregadas na área estudada em escalas maiores do que 40 m, enquanto palmeiras arborescentes ocorreram agregadas em todas as escalas avaliadas (1 - 50 m). Nossos resultados sugerem que as florestas paludícolas tropicais representam ambientes muito heterogêneos. Padrões em grandes escalas indicaram a ocorrência de degradação florestal generalizada na área estudada. Esta

degradação parece ser particularmente avançada em alguns setores florestais, e provavelmente é resultado do reduzido tamanho do fragmento florestal, da chuva ácida e concentrações elevadas de ozônio presentes na região metropolitana de Campinas, as quais resultam de atividades industriais. Práticas de manejo são necessárias para conservação da floresta estudada e da Reserva, a qual constitui o maior remanescente florestal Atlântico do município.

Keywords: Crown densiometry, Forest degradation, Forest dynamics, Ground-surface heterogeneity, Ripley's K function

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Abstract.

We investigated temporal changes and spatial variation of soil drainage and understory light availability in 2001 and 2002, and small stem ($5 \leq$ dbh < 10 cm) density, forest successional phase and large stem (dbh ≥ 10 cm) spatial distribution in one ha of tropical swamp forest in SE Brazil. Building patches and treefall gaps comprised, respectively, 69.75% and 7.5% of the area in 2002. Semivariograms indicated spatial segregation of successional phases, with mature areas predominating in the North and gaps aggregated in the South. Exclusion of outliers showed large unpredictability of background variation in canopy openness, but patches with high canopy openness values concentrated along the South and East plot borders. Overall canopy openness increased from 2001 to 2002, and was locally autocorrelated between two consecutive years. In 2001, well-drained and flooded sites comprised 46.75% and 38.19% of the study area, respectively, and were not spatially autocorrelated. In the study period, the number of flooded sites decreased by 40.4%. Canopy openness and small stem density were independent from drainage and were not correlated. Large trees aggregated at scales larger than 40 m, while arborescent palms were aggregated at all scales. Our findings suggest that tropical swamp forests represent highly heterogeneous environments, which are not adequately described by the gap/non-gap dichotomy.

Patterns at larger scales pointed to the occurrence of widespread forest degradation, which seems to be particularly advanced in some forest sectors.

Introduction

Although tropical forests have been the focus of a growing number of studies in the last two decades, only recently the spatial heterogeneity of their constituent elements begun to be explicitly addressed (Núñez-Farfán & Dirzo 1988, Molofsky & Augspurger 1992, Trichon *et al.* 1998, Nicotra *et al.* 1999, Denslow & Guzman 2000, Montgomery & Chazdon 2001). Swamp forests are characterised by high spatial and temporal variability (Joly 1991, Klinge *et al.* 1990), largely due to the aquatic-terrestrial gradient they represent (Malanson 1993). However, despite their importance as exclusive habitats for a number of specialised taxa (Leitão Filho 1995, Ivanauskas *et al.* 1997, Harms *et al.* 2001, Marques *et al.* 2003), protective systems of springs and water bodies, and atmospheric carbon sinks (Esteves 1998), swamp forest structure, dynamics and internal heterogeneity have received little attention.

Tropical swamp forests develop on soils that are permanently waterlogged, and are capable of bearing high forest similar in many aspects to the climax forests of well-drained sites in which they are embedded (Richards 1996). They are regarded as edaphic climaxes because the extreme environmental conditions to which these forests are subjected prevent them from reaching the climatic climax of the region (Richards 1996, Scarano 2002). They are less diverse, but floristically distinct, from the semideciduous or rain forests in which they are embedded, presenting many specialized taxa, higher tree density and lower canopies (Oliveira-Filho *et al.* 1994a,b, Leitão Filho 1995, Ivanauskas *et al.* 1997, Imbert *et al.* 2000, Harms *et al.* 2001, Marques *et al.* 2003). In the case of the Atlantic coastal vegetation complex of Brazil, swamp forests occur in stressful habitats marginal to the Atlantic rainforest and semideciduous forest (Scarano 2002).

Natural communities are characterized by spatial heterogeneity at several scales (Palmer 1988), and appropriate quantification of such heterogeneity is dependent on the distinction and measurement of its different aspects, such as grain, extent, complexity and variability (Li & Reynolds 1995). Spatio-temporal heterogeneity in the distribution of environmental conditions and resources influences resource acquisition in clonal plants (Oborny 1994), establishment patterns of forest trees (Núñez-Farfán & Dirzo 1988, Molofsky & Augspurger 1992), species distribution (Svenning 2000), and coexistence (Chesson 2000).

Light availability, water regime and the size and distribution of trees are at one time key conditions and resources in tropical forest communities. Light availability is one of the main factors determining tropical forest regeneration by means of its influence on seed germination and seedling survival and growth (Vásquez-Yanes & Orozco-Segovia 1993, Webb 1999). Tree regeneration is also influenced by the size and spatial distribution of adult trees, which may be at one time a source of propagules and natural enemies, as well as local resource-depletion agents (Clark & Clark 1984, Condit *et al.* 1992, Barot *et al.* 1999).

Studies of tree distribution and microsite conditions in tropical forests have traditionally been carried out in the framework of gap-phase theory. These studies generally measure tree regeneration and light availability in forest patches defined *a priori* as mature, gap or building, and have found that light availability and seedling/sapling growth and survival is consistently higher in tree-fall gaps than in the intact forest understorey (Martínez-Ramos *et al.* 1989, Clark 1990, Clark *et al.* 1993, Osunkoya *et al.* 1993, Trichon *et al.* 1998, Svenning 2000). Yet, a growing body of evidence has pointed to the insufficiency of the gap/non-gap dichotomy to adequately describe tropical forest environments in face of the continuous nature of most variables involved (Lieberman *et al.* 1989, Smith *et al.* 1992, Connell *et al.* 1997, Nicotra *et al.* 1999, Wirth *et al.* 2001). Here we examine the spatial and temporal heterogeneity in the distribution of light availability and soil drainage, as well as the distribution of trees and the traditional gap-phase scheme in a neotropical swamp forest.

Specifically, we ask the following questions: (1) What is the complexity of the distribution of soil drainage (i.e., flooding)? Complexity regards the spatial heterogeneity of a categorical variable, and is measured by the composition and configuration of patches (Li & Reynolds 1995). (2) Is the spatial distribution of soil drainage categories stable in time? (3) What is the variability of light availability in the understorey environment? Variability refers to the characterization of spatial heterogeneity of a numerical variable, and is measured by variation in autocorrelation and anisotropy (Li & Reynolds 1995). (4) What is the spatial and temporal dynamics of understory light availability? (5) Are light availability in the understory and measures of forest structure, such as tree basal area and stem density, associated with soil drainage? (6) What is the spatial distribution of the main determinants of forest structure, i.e., large trees and palms?

Methods

The study was conducted at Santa Genebra municipal reserve (22°44'S, 47°06'W; 670 m a.s.l.), a 251.8-ha urban reserve of semideciduous tropical forest in the municipality of Campinas, state of São Paulo, southeastern Brazil. Total yearly rainfall is ca. 1360 mm, mostly falling in the wet season extending from November to April, and mean annual temperature is 20.6°C (Leitão Filho 1995). The reserve is surrounded by crop cultures and a residential district. The study was carried out in an evergreen swampy area of ca. 10 ha where the water table never falls far below the soil surface, even in the dry season (maximum water table depth is ca. 60 cm on the highest elevations in the driest months; lowest sites never dry out, Lobo-Faria 1998).

Data were collected in a one-ha plot (100 x 100 m) divided in 400 contiguous 5 x 5 m subplots. The sampled area roughly corresponds to 10% of the entire swamp forest, and was considered sufficient in face of the goal of studying fine-scale heterogeneity in forest structure. Subplot size was chosen to correspond to the average size of crown diameters of dominant tree species in tropical forests (Montgomery & Chazdon 2001), since these trees form the basic structural units of the forest mosaic (Riéra *et al.* 1998). The sample area was ca. 77 m distant from the reserve border, which at this point was limited by sugar cane monoculture. Low secondary semideciduous forest constitutes most of the vegetation between the study site and this border.

Light availability and soil drainage

We assessed forest light environment by measuring percent canopy openness. Canopy openness was estimated using a spherical densiometer, a concave mirror with an engraved grid system (Lemmon 1957). In May 2001, four readings of canopy openness were made in the centre of each 5 x 5-m subplot from four different directions. The densiometer was hand-held at elbow height (ca 1.30 m). The average of the readings was used as a measure of canopy openness in each subplot. Canopy openness has been shown to be related to microclimate, and is regarded as a better measure of the local environment plants face than physical gap size (Whitmore *et al.* 1993). Although indirect methods may not yield accurate enough estimates of light conditions at a single site, needed for example for detailed ecophysiological studies (Whitmore *et al.* 1993, Engelbrecht & Herz 2001), they are well suited to rank understory light conditions among a large number of sites (Engelbrecht & Herz 2001). In particular, densiometer measurements are correlated with total site factor and weighted-canopy openness estimates derived from hemispherical photographs (Englund *et al.* 2000, but see Engelbrecht & Herz 2001). In order to assess the dynamics of canopy openness, new series of measurements were made in May 2002 and 2003 in 100 randomly chosen 5 x 5 m subplots. The same subplots were used in both years.

Soil drainage depended on local topography. Subtle topographic variations created a network of channels (where water drained freely), pits (permanently flooded) and well-drained mounds of different sizes. Waterlogged areas occurred between the well-drained mounds and nearby flooded sites. We classified local soil drainage as flooded, waterlogged or well-drained. In May 2001, we assessed soil drainage using a simple apparatus made of a steel cone 15 cm deep, perforated by 48 holes attached to an iron holder. Holes were 3 mm in diameter. It was used to distinguish between the waterlogged and well-drained categories. At each sampling location, the cone was completely inserted into soil, which was classified as waterlogged if water drained into the cone. In flooded sites, the depth of the water column was measured to the nearest centimeter. Preliminary observations revealed that mosaic of water saturation occurred at a smaller scale than the 5 x 5 m plots. We thus divided each plot in four 2.5 x 2.5 m subplots and measured soil drainage at the center of each subplot (N = 1600). A second series of measurements was made in May 2002 in the same 100 randomly chosen 5 x 5 m subplots selected for the canopy openness measurement.

Tree spatial distribution and forest structure

In June 2001, all stems ≥ 10 cm in diameter at breast height (dbh), hereafter referred to as large stems for brevity, were mapped (N = 844). Polar coordinates within the 100 x

100 m plot were measured relative to a reference 10 x 10 m grid delimited by poles. For each stem, we measured dbh and overall height. Tree height was estimated with the aid of a pole of known length. Due to their distinct architecture and ecological requirements, stems were identified as either dicot trees or arborescent palms. Arborescent palms occurring in the study area were *Euterpe edulis* Mart. and *Syagrus romanzoffiana* (Cham.) Glassman., but individual stems were not assigned to species. In the same period, basal area and density of all stems 5 ≤ dbh < 10 cm, hereafter referred to as small stems, were measured in the same 100 randomly chosen 5 x 5 m subplots mentioned above.

In order to relate the variables measured to the commonly used framework of gap-phase regeneration mosaic of tropical forests, we assigned each 5 x 5 m subplot to one of three basic successional phases in the whole 1-ha plot in May 2002 (N = 400), and in the 100 randomly chosen subplots in April 2003. We distinguished gap, building and mature forest phases, and thereby followed the basic division and terminology used in forest dynamics studies (Watt 1947, Whitmore 1975). Gaps were distinguished according to Brokaw (1982). Mature patches were distinguished by the presence of a continuous large tree-canopy, while successional patches were dominated by small trees and lacked a continuous canopy-tree cover. Tabanez & Viana (2000) recognized four physiognomic units that would be recurrent within fragments of semideciduous Atlantic forest and proposed their utilization in studies of the regional vegetation. However, their classification scheme is largely dependent on the prevalence of bamboo and liana tangles, and thus is not applicable in swamp forests, where these elements are rare or absent.

Statistical analyses

Spatial structure of most biological variables shows some degree of spatial autocorrelation (i.e., spatial dependence) and thus violates the independence assumption of conventional statistical methods (Robertson 1987, Legendre & Fortin 1989).

We measured spatial autocorrelation in both canopy openness and soil drainage using semivariograms combined with maps. The semivariogram is a graph of the semi-variance statistic as a function of distance intervals (h) in a data set. The shape of this plot describes the degree of autocorrelation (Robertson 1987). There are three basic parameters in semivariograms used to interpret the spatial features of a variable: (1) The range, if present, is the distance where the spatial influence disappears, that is, the semi-variance ceases to increase and the variable is considered spatially independent. (2) The sill is the semi-variance value reached by the semivariogram at the range. In theoretical variograms, the sill equals the overall variance of the variable. (3) The nugget effect is the ordinate value of the semivariogram at distance zero; it needs not be equal to zero. The ratio of the nugget effect to the sill is referred to as the relative nugget effect and may be used to evaluate sampling error and short-distance spatial effects. More information on these methods can be found in Legendre & Fortin (1989) and Rossi *et al.* (1992). Since samples were collected at 5-m intervals, the smallest interval h separating any two points in the grid was 5 m, and the largest was 95 m. (Robertson 1987). In order to check for anisotropy (i.e., when the semi-variance is dependent on both the Euclidean distance between sites and direction), semivariograms were constructed in four geographic directions (Rossi *et al.* 1992): 0° (north-south: N-S), 45° (NE to SW), 90° (east-west: E-W), and 135° (NW to SE).

In the analysis of canopy openness, we found unusually large data (i.e., outliers), which corresponded to hyperdisturbed sites at the core of extensive patches with reduced canopy cover. As outliers can greatly affect the interpretation of spatial dependence when using semivariogram analysis (Rossi *et al.* 1992), we compared the results of the analysis in the presence and in the absence of large values. This allowed the detection of the spatial pattern of both background (i.e., undisturbed) and overall canopy openness. As the data on canopy openness are proportions, all statistical analyses, semivariograms included, were performed on arcsine-transformed values (Sokal & Rholf 1995). In addition to semivariograms, soil drainage (a categorical variable) spatial heterogeneity was characterized by its complexity in composition (the number and proportions of patch types) and configuration (patch size distribution), following Li & Reynolds (1995). To analyze the spatial pattern of forest successional phases, we transformed the nominal categories into an ordinal variable with values 1, 2 and 3 for the gap, building and mature phases, respectively.

To test for the presence of a relationship between canopy openness and basal area and density of small stems, we rescaled data on soil drainage by aggregation. This was necessary because soil drainage was measured at a finer-grained scale than the other variables (Li & Reynolds 1995). Rescaling was achieved by classifying each 5 x 5 m plot according to the number of flooded 2.5 x 2.5 subplots it had (5 categories, ranging from 0 to 4). All geostatistical and conventional statistical analyses were performed on SYSTAT, version 10.0 (SPSS, Inc. 2000).

As our data on the spatial distribution of large stems consisted of a map of points, we used spatial point pattern analyses based on Ripley's K-function (Ripley 1981, Diggle 1983). These methods consist of density functions using the second moment, i.e., they use all point-to-point distances for a statistical description of two-dimensional distribution patterns. They test the significance of the departure of observed samples from randomness and whether the relationship between two types of sampled points suggests spatial association, repulsion, or independence. The K-function involves measuring the average number of points located within a given distance *d* of each sampled point and testing against the null hypothesis of complete spatial randomness. The calculation of K for a range of distances allows for the study of spatial pattern at a range of scales, which is a very attractive feature of this test, since the degree of clumping in nature is frequently strongly influenced by the spatial scale considered (Hurlbert 1990). Cases of *d* greater than the distance to the nearest plot boundary require an edge-correction (Diggle 1983, Haase 1995).

The derived variable $L(d) = \sqrt{[K(d)/\pi]}$ enables the interpretation of the type of spatial pattern as a function of distance by plotting $L(d) - d$ against d. For a completely random pattern $L(d) - d = 0$; $L(d) - d$ becomes negative when the pattern is regular and positive when trees are clustered (Haase 1995). The K function was computed with a 1-m step up to $d = 50$ m. Edge corrections were calculated using local weighting method (Haase 1995). Test significance was estimated by means of the Monte Carlo procedure to simulate randomly generated plots of the same density and dimensions as the observed plot. We used 1000 simulations of each of the univariate patterns. The means ± 1.96 standard deviation (2.5 % tails) of the 1000 simulations were used to construct a confidence envelope for the *L*-statistic (data) for each value of *d* (Haase 1995). All point pattern analyses were performed on SPPA 1.1.1 software (Haase 1999).

Results

The forest mosaic

In 2002, building patches dominated the study plot, comprising 69.8% of the area. They formed an almost continuous network in which gaps and mature sites were embedded (Fig. 1a). They represented a diverse array of forest development phases: a) dense secondary vegetation following recent treefall gaps; b) thinning stands dominated by pioneer and young trees; c) degrading patches represented by standing dead trees; and d) patches dominated by invasive ruderal species. Eighteen gaps were present, comprising 7.5% of the area. Individual gap areas ranged from 25 m^2 to 125 m^2, but most gaps occupied only one sampling unit (25 m^2). Mature patches represented 22.75% of the plot, forming larger mosaic units of up to 1600 m^2.

Figure 1

Semivariograms revealed significant anisotropic spatial structure in the distribution of forest mosaic units (Fig. 2). Relative nugget effects ranged from 35% to 62%, indicating that a large portion of the variance among forest mosaic units was associated with the spatial pattern. Semivariance ranges were larger in the E-W (ca. 30 m) than in the N-S (ca. 10 m) direction, suggesting that mosaic units were roughly elliptical in the E-W direction. Increased semi-variance values in the N-S direction at scales larger than 40 m indicated that the mosaic units were spatially segregated at this scale, with mature areas predominating in the North and gaps aggregated in the South (Fig. 1a). On the other hand, reduced semi-variance values at larger scales in the E-W direction resulted from the dominance of the eastern and western sectors of the plot by building patches, as a band of mature and gap patches ran N-S across the centre of the area (Fig. 1a).

Figure 2

In a one-year period, a forest patch could remain without a change in state, or it could change by one state (Table 1). Most gaps advanced to the successional stage, but almost 40% remained in the gap phase. The large majority of building patches remained in this category, and only 5.6% advanced to the mature phase. Conversely, almost half of the mature sites regressed to the building phase without passing through the gap phase. Although this partly reflects small sample size, it also results from the standing death of trees and branch fall. These transition probabilities show an overall tendency towards the increase in the number of building patches over the number of mature ones.

Table 1

Light availability

In 2001, percent canopy openness ranged from 4.9 to 41.1% (mean = 14.5, SD = 6.3, N = 400). Most plots (60%) had from 10 to 20% canopy openness. Percent canopy openness showed anisotropic spatial structure (Fig. 3). Relative nugget effects were generally high, ranging from 43% to 78%, implying weak spatial dependence. Considering all data, including the extreme values found in some hyperdisturbed patches, canopy openness showed a clear gradient structure in the N-S direction, and large-scale patchiness in the E-W, NE-SW and NW-SE directions. These results describe an arch of more open canopies extending along the South and East plot borders (Fig. 1b). This pattern largely disappeared with the exclusion of high canopy openness values (> 28%, Fig. 3). Analysis of this data set showed ranges of ca. 30 m and a weak spatial structure, although large-scale patchiness persisted in the NE-SW direction. This corresponded to the occurrence of three areas with large canopy openness values (Fig. 1b). Background variation in canopy openness, however, was largely unpredictable, as can be seen in the semivariograms of patches with values < 14% (Fig. 3). Weak or absent spatial dependence was also expressed in the high relative nugget effects for these data. This implies that, at the spatial scales studied (> 5 m), neighbor sites are no more alike than sites separated by large distances.

Figure 3

Canopy openness increased from 2001 to 2002, but did not change signficantly from 2002 to 2003 (Repeated Measures ANOVA, df = 2, F = 6.96, P = 0.001, N = 100, Fig. 4). Canopy openness was positively autocorrelated between consecutive years (2001-2002: Pearson *r* = 0.453, P < 0.001, 2002-2003: *r* = 0.653, P < 0.001, N = 100). This suggests that canopy dynamics was synchronous in most subplots, and that canopy opening was widespread. Yet, the relatively low correlation indicated that changes were sizeable in some regions of the forest. The greatest decrease in canopy openness at a single plot was 16.9% (2002-2003) and the greatest increase was 26% (2001-2002).

Figure 4

Soil Drainage

In 2001, most soil microsites were well-drained (46.8%, N = 1600), followed by flooded sites (38.2%, Fig. 1c). Together, they formed a network of channels and flooded pits around well-drained mounds. Waterlogged sites corresponded to transitional zones between the other two predominant categories, and comprised a smaller portion (15.1%) of the area. Size distributions of both well-drained and flooded patches showed high positive asymmetry. Excluding the large homogeneous well-drained area in the southeast, where the swamp forest was replaced by semideciduous forest, single-plot patches (5.5 m^2) corresponded to 80% and 70% of well-drained and flooded area, respectively (Fig. 1c). The largest well-drained and flooded patches were 429 m^2 and 302.5 m^2, respectively. Depth of flooded sites ranged from 1.0 to 65.0 cm (mean = 13.4 cm, SD = 7.7 cm), but most flooded sites (81.7%) were shallower than 20 cm.

We found no evidence for autocorrelation between adjacent sampling points at the spatial scales studied (Fig. 5). Soil drainage was unpredictable at the small scale as it

Figure 5

was at the larger spatial scale as evidenced by the semivariogram and high relative nugget effect (80%).

In a one-year period, soil drainage could remain without a change in state, or it could change by one or two states (Table 2). The transition probabilities varied between the three categories, with an overall tendency towards the reduction of soil moisture degree. Most well-drained sites remained in this category, but the majority of waterlogged sites were well-drained in 2002. Although 41.6% of the previously flooded sites were still submerged in 2002, 31.8% of them had become well-drained. Overall, the number of well-drained and waterlogged patches increased by 16.2% and 57.4%, respectively, while the number of flooded patches decreased by 40.3%.

Table 2

Canopy openness and soil drainage were independent at the 25 m^2 scale (soil drainage measured as the number of 2.5 x 2.5 m flooded subplots, ANOVA, df = 4, F = 1.625, P = 0.167).

Forest structure and tree spatial pattern

Small stems (5 ≤ dbh < 10 cm) basal area (2.8 m^2 ha^{-1}) and density (700 stems ha^{-1}) were highly variable among the 100 randomly chosen 5 x 5 m plots (coefficients of variation = 98.6% and 100.9% for stem basal area and density, respectively). Small stem density ranged from 0 to 6 stems per 5 x 5 m plot, and was independent of the number of flooded 2.5 x 2.5 m subplots in each 25-m^2 plot (ANOVA on square-root transformed values, df = 4, F = 1.653, P = 0.168). Small stem density and canopy openness were not correlated (Pearson *r* = - 0,183; *t* = 1,843; df = 98; P > 0.05).

Large stem (dbh ≥ 10 cm) density and basal area in the 1-ha study plot were 844 and 21.9 m^2, respectively. Most large stems (80.5%) were in the 10 – 20 cm dbh size class, and the largest dbh was 65.1 cm. Stem height distribution was unimodal (mean ± SD = 8.5 ± 1.7 m), ranging from 3 to 16 m. Arborescent palms (N = 360) had significantly smaller dbh than dycot trees (Mann-Whitney ANOVA, U = 57452.500, $P < 0.0001$). Neither the density (Pearson $r = -0.060$, df = 98, $P > 0.05$) nor the basal area of large stems ($r = -0.105$, df = 98, $P > 0.05$) were correlated with canopy openness. Large stems were aggregated at scales from 3 to 20 m and > 28 m (Figs. 1d and 6). This pattern, however, resulted from the occurrence of distinct spatial distribution patterns of trees and arborescent palms (Fig. 6). Trees were randomly distributed at all scales up to ca. 40 m, being significantly aggregated thereafter. On the other hand, palms were strongly aggregated at all scales larger than 1 m.

Discussion

More than describing the structure of a tropical swamp forest, our results showed that different forest elements may have contrasting spatial structures at distinct scales. In natural systems, the scales of patterns may suggest the scales at which the processes responsible for such patterns operate (Chesson & Murdoch 1986, Levin 1992, Barot *et al.* 1999). In the Santa Genebra swamp forest, pattern emerged at two scale ranges, each of which indicates distinct processes and gives rise to distinct working hypotheses.

Background structure of the swamp forest

At linear scales smaller than ca. 40 m (1600 m^2), the distribution of soil drainage, canopy openness and large stems were homogeneous (sensu Li & Reynolds 1995), i.e., the value of each of these variables at any one point in space was uncorrelated with neighbouring values.

The spatial independence of soil drainage and canopy openness at small scales we registered formally describes the heterogeneity that other authors have qualitatively attributed to the Atlantic forest swamps (Klinge *et al.* 1990, Ivanauskas *et al.* 1997, Scarano *et al.* 1997, Scarano 1998, Marques & Joly 2000, Marques *et al.* 2003). In swamp forests, the distribution of soil moisture is complicated by the interactions between microtopograhy and fluctuations of the soil water table. This creates a variety of situations ranging from elevated, well-drained mounds, which may be subjected to seasonal drought, to permanently flooded pits and channels. This configuration seems to be common in the swamp forests of southeastern Brazil (Ivanauskas *et al.* 1997, Scarano *et al.* 1997, Scarano 1998, Marques & Joly 2000, Marques *et al.* 2003). Soil moisture is a key factor controlling seed germination and seedling establishment (Silva Matos & Watkinson 1998, Souza *et al.* 1999, Battaglia *et al.* 2000), and the lack of spatial autocorrelation in soil drainage we found adds to the unpredictable nature of the local establishment environment (Núñez-Farfán & Dirzo 1988, Molofsky & Augspurger 1992).

Flooding affects soils by altering soil structure, depleting dissolved oxygen, accumulating carbon dioxide, inducing anaerobic decomposition of organic matter, and reducing iron and manganese (Kozlowski 1997). It thus affects negatively the distribution of woody plants as much as drought conditions, since most species of the tropical humid forests cannot establish in either flood- or drought-prone sites (Burslem *et al.* 1996, Kozlowski 1997, Scarano *et al.* 1997, Souza *et al.* 1999). Even species characteristic of seasonally flooded forests may not germinate under a water column of more than a few centimeters (Souza *et al.* 1999), which excludes most flooded microsites in the Santa Genebra swamp forest (mean depth ca. 10 cm). Therefore spatial heterogeneity of soil moisture is likely to restrict the proportion of microsites favorable for seedling establishment to the transitional zones between flooded and well-drained microsites (‘waterlogged’ in *Results*). Fluctuations in flooding intensity may thus have important consequences for plant regeneration dynamics, and the increase in the proportion of well-drained patches we registered from 2001 to 2002 showed that sizeable changes in the swamp forest overall drainage may take place in an annual basis, likely due to fluctuations in rainfall. However, whether the increase in the proportion of well-drained patches we observed represents a long-term drought tendency or just a yearly fluctuation is not clear from such short-term data.

According to Lieberman & Lieberman (1994), the unsuitable habitats flooded microsites represent could avoid tree saturation in swamp forests and the consequent competition-mediated hyperdispersed spatial distribution of large trees. Furthermore, Imbert *et al.* (2000) reported that, in swamp forests in the island of Guadeloupe, trees of the dominant species *Pterocarpus officinalis* formed large clumps where well-drained soil patches were aggregated in large hummocks alternated with large flooded hollows, but were randomly dispersed where the topography was more uniform. The random distribution of large trees we found at scales < 40 m matches such pattern, which implies that the basic conditions for tree regeneration are homogeneously distributed at small scales.

The Santa Genebra swamp showed to be a low-stature (maximum height = 16 m) forest characterized by a high density of small stems and small size of large stems (maximum dbh = 65.1 cm). Canopy gaps were small (up to 125 m^2), and canopy openness was large, mostly between 10% and 20%. These figures correspond with the values Martins & Rodrigues (2002) reported for the range of canopy openness (8.7% -

17.3%) in treefall gaps in the semideciduous forest in Santa Genebra. Overall, this picture is in agreement with the basic description of other tropical swamp forests as short, dense and relatively open-canopy formations (Torres *et al.* 1994, Duivenvoorden 1996, Richards 1996, Ivanauskas *et al.* 1997, Toniato *et al.* 1998, Imbert *et al.* 2000, Bianchini *et al.* 2001, Wiser *et al.* 2002) when compared with non-flooded forests, where openning is up to 5% (Smith *et al.* 1992, Duivenvoorden 1996, Trichon *et al.* 1998, Svenning 1999, Grove *et al.* 2000, Bianchini *et al.* 2001).

Treefall gaps occurring both in the moister areas of the Atlantic forest (Tabarelli & Mantovani 1999) and in the semideciduous forest in Santa Genebra (Martins & Rodrigues 2002) are much larger (up to ca. 500 m^2) than those we registered for the swamp forest. There is a correlation between gap size and surrounding canopy height (Martins & Rodrigues 2002), and thus small gap size in swamps could be attributed to the lack of large trees, since small individuals do not open big gaps when they fall. Small adult tree sizes are probably related to mechanical instability on flooded soils (Imbert *et al.* 2000). In Central American tropical forests, shorter, more homogeneous canopies of young, secondary growth stands have smaller gap size and a more even distribution of openings in the canopy, resulting in fine-grained distribution of light availability (Nicotra *et al.* 1999, Denslow & Guzman 2000). Our results suggest that canopy architecture of swamp forests may be similar to secondary growth forests on upland, well-drained sites, generating a similarly fine-grained, spatially uncorrelated distribution of light availability and canopy openness.

The lack of correlation we found between measures of forest structure and light availability agrees with the results of Clark *et al.* (1996) and Montgomery & Chazdon (2001), who found that canopy height and tree density or basal area were weak predictors of light availability in both old growth and secondary growth forests in Costa

Rica. This is likely due to the fact that canopy openness, measured in the understory, results from the complex distribution of shrubs and saplings in the understory and canopy and subcanopy vegetation, creating a highly variable pattern of light availability, which is probably more dynamic than the treefall-gap disturbance regime (Connell *et al.* 1997, Trichon *et al.* 1998, Montgomery & Chazdon 2001, Wirth *et al.* 2001). Accordingly, our results reinforce the view that the quantification of continuous variables may yield important insights into forest structure and light availability that would not be possible based only on the gap/non-gap paradigm (Lieberman *et al.* 1989, Smith *et al.* 1992, Connell *et al.* 1997, Wirth *et al.* 2001).

Large-scale patterns

A recurrent pattern found in three out of four variables studied (i.e., forest successional phases, canopy openness, and large stem distribution) was the occurrence of large-scale spatial structure in the data, as opposed to weak or absent small-scale spatial organization. Although our sampling effort was restricted to 1 ha, it represents a reasonable proportion (ca. 10%) of the Santa Genebra swamp forest. Furhtermore, it was directed to the small scales in which the interactions between individual plants and their environment take place (Purves & Law 2002). Altogether, our results seem to indicate the presence of a disturbed belt along the South and Southeastern sectors of the study plot (Fig. 1).

Several features of the Santa Genebra swamp forest indicated an overall tendency towards a degenerating sylvigenic cycle. First, the distribution pattern of large stems at scales > 40 m showed significant clumping, which in this case, arises from the occurrence of large areas with reduced tree density (Fig. 1) reflecting the concentration of multiple treefall gaps in some areas of the forest (Pélissier 1998, pers. obs.). As mentioned before, tree distribution on flooded soils with fine-grained topography tend to be randon (Lieberman *et al.* 1994, Imbert 2000). It is worth remembering that the studied swamp forest is located < 100 m from the edge of a small forest fragment (251.8 ha). Forest fragments exhibit elevated tree mortality, damage and turnover rates in relation to continuous forests (Esseen 1994, Laurance *et al.* 1998). These effects penetrate up to 300 m from forest edges and result from increased windthrow and microclimate changes (Laurance *et al.* 1998, 2002), which are ameliorated but not stopped by the presence of secondary vegetation at the forest edge (Mesquita *et al.* 1999, Laurance *et al.* 2002). Furthermore, as an urban fragment embedded in a intensely urbanized and industrial landscape, Santa Genebra is exposed to the increased air ozone concentrations and acid rain that occur in Campinas region (Tresmondi 2003). While ozone is a pollutant of injurious potential to plants (Matyssek & Sandermann 2003), the effects of acid rain on tree survivorship are likely to be particularly negative in swamps, where tree root systems are permanently immerse in standing water. Although tree mortality was not directly assessed here, tree spatial patterns strongly indicate the occurrence of increased mortality of large trees.

Palm clumping at all scales results from the concentration of most palms in a dense aggregate in the southwest of the study area (Fig. 1). This area corresponds to an open forest sector, with low tree density, and reflects the growth of an even-aged, mono-dominant patch of *Euterpe edulis* (pers. obs.). *Euterpe edulis* shows increased population growth in the studied area (Silva Matos *et al.* 1999), and may represent a case of disturbance-driven population increase, also found in other tropical forest fragments (e.g., Souza & Martins 2003).

The density of large stems (dbh ≥ 10 cm, 844 stems ha^{-1}) was much larger than the 260 – 446 stems ha^{-1} Lieberman & Lieberman (1994) found in their review of patterns of density and dispersion of lowland tropical forest trees. On the other hand, small stem ($5 \leq$ dbh $<$ 10 cm) density (7000 stems ha^{-1}) was higher than the values reported for other flood-prone areas (Oliveira-Filho *et al.* 1994a, Torres *et al.* 1994, Ivanauskas *et al.* 1997). Hence, the swamp forest structure resembles that of degraded forest edges and sectors, which have lower canopy heights and basal areas per hectare, higher tree densities and liana tangles and sometimes bamboo-dominated patches (Tabanez & Viana 2000, Oliveira-Filho *et al.* 1997, Lykke & Goudiaby 1999). Indeed, most of the studied area was not in the mature successional, but in the building phase. Furthermore, the proportion of building patches tended to increase over mature patches with time. Although the building stage of the tropical forest regeneration cycle usually represents forest succession in treefall gaps, its dominance in the Santa Genebra swamp forest suggests forest degradation over large areas rather than closure towards the mature phase. This view is confirmed by the proportion of the forest opened by canopy gaps (7.5%), which was much higher than the average values found for one-time gap surveys in other localities (Clark 1990: 1.0 – 1.05%, Yavitt *et al.* 1995: 4.3%, van der Meer & Bongers 1996: 1.1%). This picture confirms the prediction of Laurance *et al.* (1998) that, due to high tree mortality and damage near edges, forest fragments would have high proportions of their area in gap and building phases of forest dynamics.

Canopy openness followed the large-scale North-South trend of disturbance that the distribution of forest successional phases exhibited. However, due to its continuous nature, canopy openness formed a gradient of light availability from the closest sites in the North to the hyperdisturbed sites in the South-Southeast. The main consequences of this were the wide range of light availability conditions found under building patches and the occurrence of open forest understories in the Southern forest sector. Canopy openness is known to play a significant role in the distribution and dynamics of many tree and palm species (Clark *et al.* 1993, Lieberman *et al.* 1995, Svenning 2000). Hence, if the increase in canopy openness from 2001 to 2002 were to persist, we expect the gradient of canopy openness in the Santa Genebra swamp forest to drive directional shifts in species composition and abundance of the forest community towards increasing dominance by pioneer and ruderal species.

Forest degradation by large-scale edge effects (Laurance 2000) is known to progressively destroy fragments surrounded by aggressive environments like cultures, roads and human settlements (Gascon *et al.* 2000). This process is just beginning to be detected in the small fragments of the Atlantic Forest (Tabanez & Viana 2000, Souza & Martins 2003). Santa Genebra is the largest remnant of the Atlantic forest in the heavily developed Campinas region, and represents a rare case of well-documented announced death of small forest reserves, judging by the unfavourable characteristics of its size, irregular shape and isolation (Laurance *et al.* 2002), high abundance of exotic understory species (Martins & Rodrigues 2002), overabundance of liana tangles on trees (Rodrigues 1995), disruption of seed dispersal systems (Pizo 1997, Silva Matos & Watkinson 1998), invasion of generalist matrix species of snakes (Sazima & Manzani 1995) and birds (Aleixo & Vielliard 1995), at the expense of forest-interior species, as well as the altered spatial structure of its swamp forest we present. We suggest that protective management options be put in practice as quikly as possible in order to try to conserve as much of forest structure and function as possible.

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Figure Legends

Figure 1. Maps of the horizontal distribution of the studied variables in a tropical swamp forest. a) forest successional phases; b) % canopy openness (contour line increments = 4%); c) soil drainage; d) spatial distribution of large stems (dbh > 10 cm; circle diameter proportional to stem diameter). Note different spatial resolution of each variable. Map a: 2002 data, maps b – d: 2001 data.

Figure 2. Semivariograms of forest successional phases in a tropical swamp forest from four different directions. Inset numbers are relative nugget effects.

Figure 3. Semivariograms of % canopy openness in a tropical swamp forest. CO = canopy openness. Inset numbers are relative nugget effects.

Figure 4. a) Box-plots of percent canopy openness in 2001, 2002 and 2003. In each graph, each box comprises 50% of data. Boxes are notched (narrowed) at the median and return to full width at the lower and upper 95% confidence interval values. Inner and outer fences are defined by interquartile ranges. Asterisks are outliers. When confidence intervals do not overlap, the median of the stages are different (McGill *et al.* 1978).

Figure 5. Semivariogram of soil drainage categories. Inset number is relative nugget effects.

Figure 6. Second-order spatial analysis of large stems (dbh ≥ 10 cm) in a tropical swamp forest. The sample statistic *L(d) – d* is plotted against *d* (solid line). The dotted lines give a 95% confidence envelope for complete spatial randomness.

Figure 1. Souza & Martins

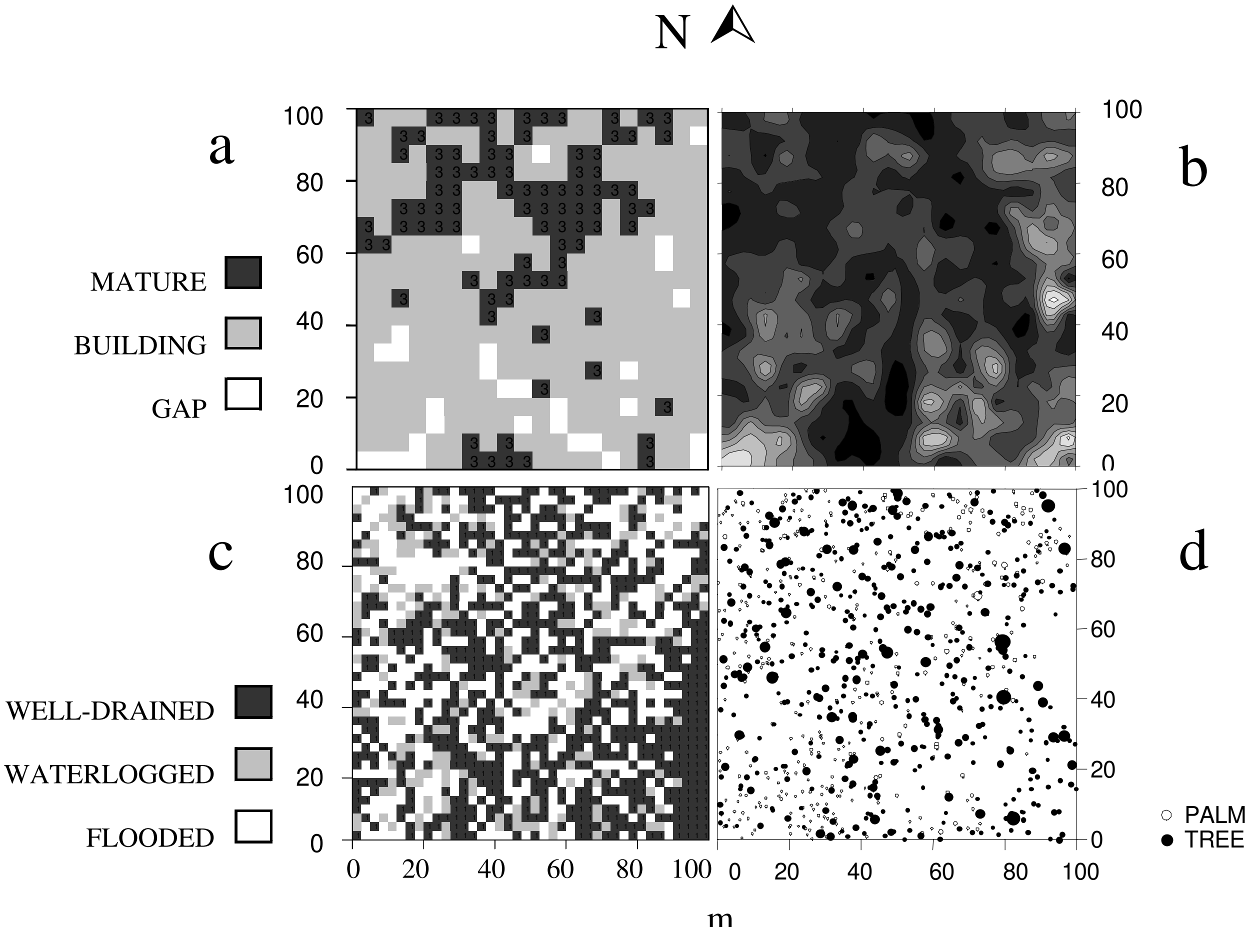


Figure 2. Souza & Martins

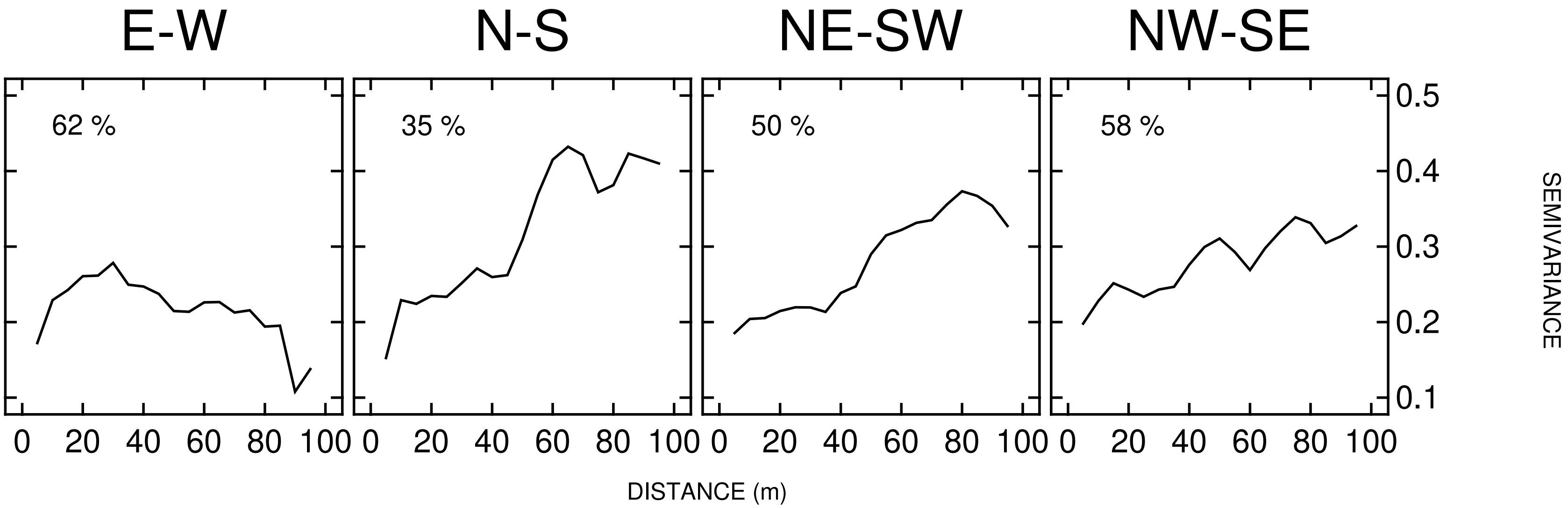


Figure 3. Souza & Martins

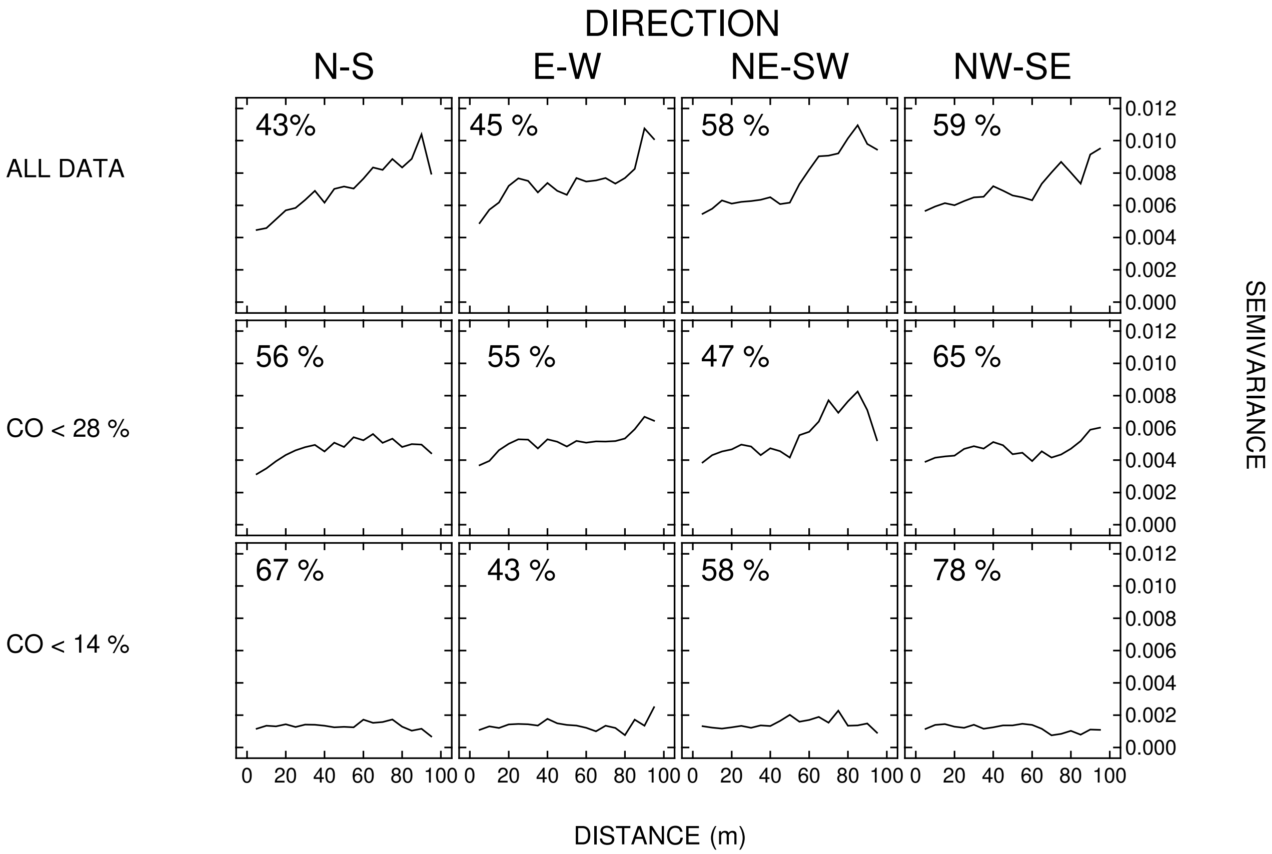
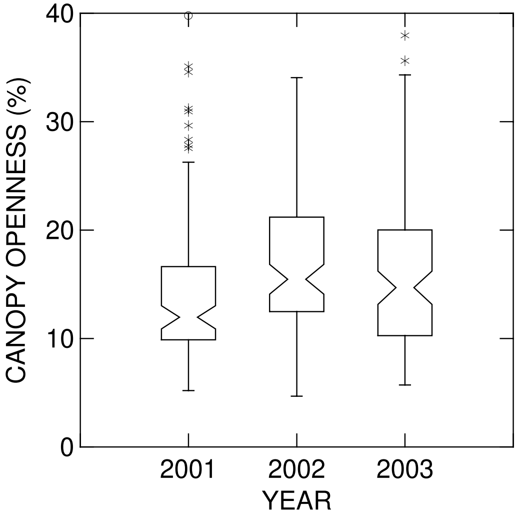


Figure 4. Souza & Martins



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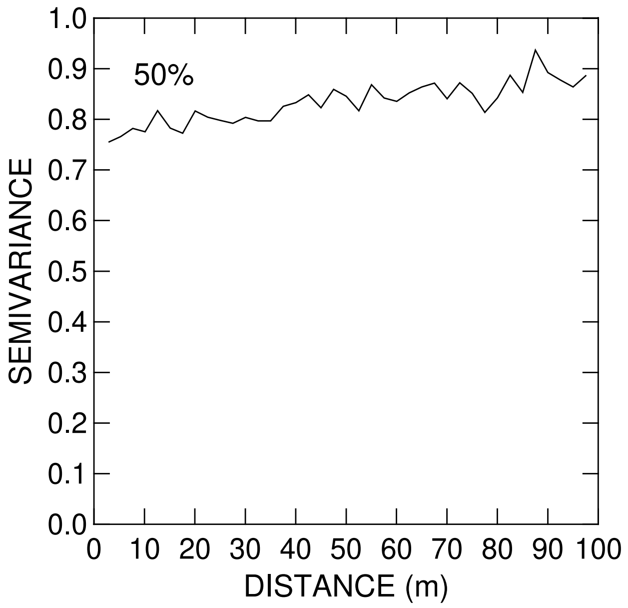

Figure 6. Souza & Martins

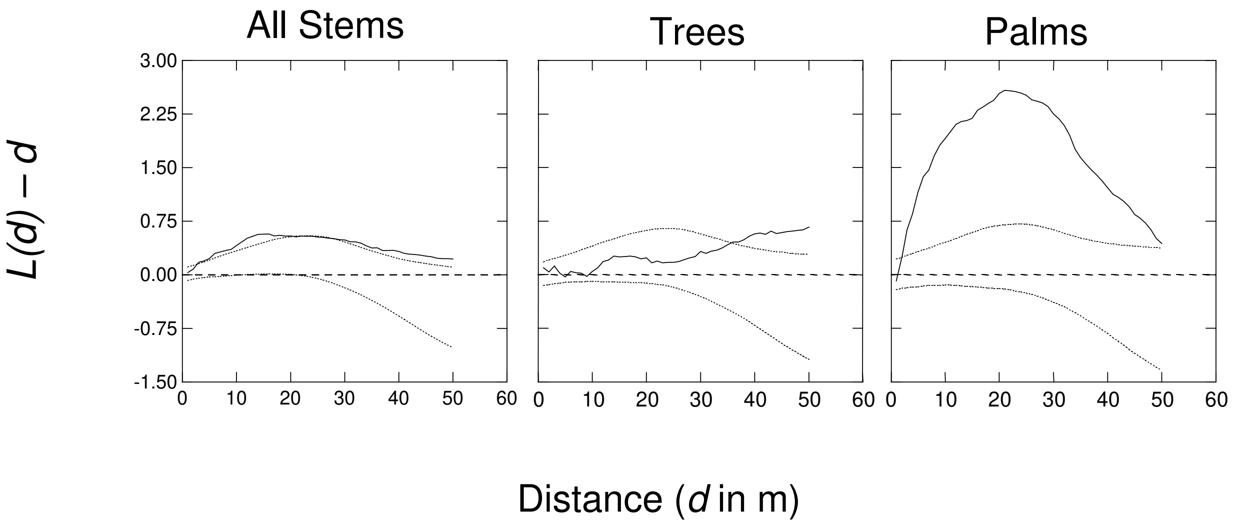

Table 1. Transition probability matrix for successional phases in a tropical swamp forest in south-eastern Brazil.

	State at time *t*		
State at time *t* + 1	Gap	Building	Mature
Gap	0.375	0.042	0
Building	0.625	0.903	0.476
Mature	0	0.056	0.524

Table 2. Transition probability matrix for soil drainage in a one-ha of tropical swamp forest in south-eastern Brazil.

	State at time *t*		
State at time *t* + 1	Well-drained	Waterlogged	Flooded
Well-drained	0.750	0.556	0.318
Waterlogged	0.135	0.333	0.266
Flooded	0.115	0.111	0.416

CAPÍTULO 2. Clonal growth and reproductive strategies of the understory tropical palm *Geonoma brevispatha*: an ontogenetic approach[1]

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1 – Trabalho publicado na revista *Canadian Journal of Botany*. Cópia no *Apêndice*.

Resumo

Nós investigamos os padrões de crescimento e reprodução da palmeira clonal arbustiva *Geonoma brevispatha*, baseados na identificação dos estádios ontogenéticos pós-seminais, em um período de três anos. A espécie desenvolve-se como genetas (indivíduos genéticos) os quais crescem através da produção de rametas (indivíduos morfologicamente diferentes porém geneticamente iguais). Os genetas foram monitorados em 100 parcelas de 5 x 5 m e 100 sub-parcelas de 2 x 2 m, em uma área de 1 hectare na floresta paludícola da Reserva Municipal de Santa Genebra (Campinas, SP). Os rametas passam por quatro estádios ontogenéticos (juvenis de folhas bífidas, imaturos acaulescentes de folhas pinatissectas, virgens não reprodutivos e com estipe, e reprodutivos, com estipe). Durante a ontogenia, o tamanho da folha, o número de folhas e a taxa de produção de novas folhas aumentam, as a taxa de crescimento em diâmetro é mais elevada apenas entre os rametas imaturos, sendo estatisticamente igual entre os demais estádios. O comprimento do estipe, o número de nós e o comprimento da raquis foliar foram positivamente correlacionados em todos os estádios, mas a altura da copa foi menor do que o comprimento do estipe entre os rametas reprodutivos devido ao tombamento freqüente do estipe. O número de folhas e a fecundidade sexual aumentaram proporcionalmente ao comprimento do rameta, mas declinaram nos rametas maiores, o que foi interpretado como sinal de senescência. A fecundidade clonal precedeu a fecundidade sexual, e ambas as fecundidades aumentaram continuamente com o tamanho do geneta. Nenhuma relação foi encontrada entre as fecundidades clonal e sexual. As estratégias de crescimento e sobrevivência de *G. brevispatha* foram consistentes com padrões encontrados em outras espécies clonais tropicais. As fecundidades sexual e clonal parecem ser dois processo integrados favorecidos pelas condições ambientais que também sustentam o crescimento dos rametas estabelecidos.

CAPÍTULO 3: Microsite specialization and spatial distribution of *Geonoma brevispatha*, a clonal palm in southeastern Brazil[1]

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1 – Tabelas e figuras no final do capítulo. Trabalho formatado segundo as regras da revista *Ecological Research.*

Resumo

Neste capítulo, testei as hipóteses segundo as quais (1) genetas reprodutivos de *Geonoma brevispatha*, uma palmeira clonal do sub-bosque, seria mais abundante em microsítios mais iluminados, mas a abundância dos juvenis não seria responsiva à disponibilidade de luz; (2) a espécie seria restrita às regiões de transição entre microsítios alagados e secos; (3) se as hipóteses (1) e/ou (2) fossem aceitas, a especialização de microhabitat que elas representariam deveriam refletir-se na distribuição espacial dos indivíduos em escalas distintas. A umidade do solo foi autocorrelacionada espacialmente em distâncias menores do que 1 m, refletindo o padrão microtopográfico de depressões e canais delimitados por elevações mais secas no terreno. A primeira hipótese foi rejeitada, mas a segunda foi aceita. Nenhum geneta ocorreu em microsítios alagados. Um experimento de emergência de juvenis demonstrou que as sementes não são capazes de germinar sob condições de alagamento, mas a abertura de dossel não influenciou o número de juvenis que emergiram. A terceira hipótese foi aceita. Genetas individuais apresentaram distribuição especial aleatória, correspondente à distribuição da umidade do solo, mas apresentaram-se agregados em escalas maiores. Genetas juvenis estavam associados positivamente com genetas reprodutivos. Nossos resultados indicam que palmeiras podem especializar-se em partes restritas de gradientes de umidade em florestas paludícolas, e que esta especialização pode excluí-las mesmo de microhabitats sutilmente distintos.

ABSTRACT

We tested the hypotheses that: (1) reproductive *Geonoma brevispatha*, an understorey clonal palm endemic to South American swamps, is most abundant in more brightly lit microsites but the abundance of juveniles is not responsive to light availability; (2) the species is restricted to the transitional zones between flooded and well-drained microsites; (3) if hypotheses (1) and/or (2) are accepted, the microhabitat specialization they represent should be reflected in the spatial distribution of the individuals at distinct scales. The study was carried out in a swamp forest in south-eastern Brazil. Soil moisture was autocorrelated at distances up to ca. 1 m, reflecting a fine-scale microtopographic pattern of flooded pits and channels delimited by drier mounds. The first hypothesis was rejected, but the second hypothesis was accepted. No genets occurred on flooded microsites. A juvenile emergence experiment showed that seeds were unable to develop into juveniles under flooded conditions, but canopy openness did not influence the number of juveniles emerging. The third hypothesis was accepted. Individual genets were randomly distributed at scales corresponding to soil moisture patches, but were aggregated at larger scales. Juvenile genets were positively associated with reproducer genets. Our results indicate that palms may specialize on narrow parts of moisture gradients in swamp forests, and that this specialization may exclude them from even subtly distinct microhabitats.

Key-words: Atlantic forest, point pattern analysis, Santa Genebra Municipal Reserve, spatial autocorrelation, tropical forests

INTRODUCTION

Two central paradigms in tropical rain forest plant ecology are: 1) survival and growth of plants in the understorey are light-limited; and 2) resource partitioning between trees exists in their differential regeneration along light gradients created by treefall gaps of different sizes and spatial distribution (Connell 1978; Denslow 1987; Svenning 2001b). Differences in performance associated with a gap-understorey environmental mosaic have been recorded for a number of species at distinct spatial scales (Bazzaz 1991; Denslow 1987; Nuñez-Farfán & Dirzo 1988; Svenning 2000, 2001b; Vandermeer *et al.* 1997). Indeed, niche differentiation is thought to be an essential mechanism for species coexistence (Chesson 2000), and the differential utilisation of the light environments that forest gaps create is possibly one important factor in the maintenance of the high local species richness in tropical rain forests (Denslow 1987; Svenning 2001b). This view arises as one of the main developments of Grubb's (1977) regeneration niche hypothesis to explain the maintenance of species diversity in forest plant communities.

Nevertheless, a large portion of the variance of species abundance and distribution remains unexplained in the studies relating the occurrence of species in distinct light environments (Harms *et al.* 2001; Lieberman *et al.* 1995; Svenning 2001b). There is an ongoing debate on whether this reflects the lack of study of aspects of habitat and microhabitat specialization other than those related to light gaps, or the prevalence of non-equilibrium conditions in most forest communities, by which most species would be generalist and species composition would not remain constant (Chesson 2000; Connell 1978; Hubbell & Foster 1986a; Terborgh *et al.* 1996). At the spatial scale of habitats, one manifestation of resource-based niche differentiation is habitat specialization such that species abundance in different habitats may reflect habitat-dependent differential competitive abilities (Chesson 2000; Svenning 2001b). Accordingly, many tree and palm species have been found to be significantly positively or negatively associated with slopes, swamps and low-lying plateaux in lowland tropical forests (Harms *et al.* 2001; Hubbell & Foster 1986b; Svenning 1999, 2001b), as well as aspect, altitude and particular local conditions, such as gaps or dry soils in mountain forests (Svenning 2001a).

With regard to niche differentiation in resource-use by tropical plants, an important set of variables, which is just beginning to be explored, is related to soil factors. It is well documented that palm species occur differentially in major soil-related habitat types, e.g., forests on floodplain or well-drained soil (Clark *et al.* 1995; Kahn & de Granville 1992). Some recent evidence, however, suggests that palms may also be specialised on particular microhabitats within these major habitat types (Scariot *et al.* 1989; Svenning 1999, 2001b). Microhabitat refers to environmental conditions varying at scales less than 10^3 m, e.g., treefall gaps or local topographic variation (Svenning 1999).

Here we evaluate the distribution of an understorey clonal palm with regard to both light availability and soil relative moisture in a neotropical swamp forest, using the individual-based approach (Hubbell *et al.* 2001). The premise of this approach is that whatever microhabitat specialization mechanisms were or are operating in the studied population, they should leave a spatial signature that could be detected by making explicit maps of individual plant locations in the forest (Hubbell *et al.* 2001).

Tropical swamp forests are less diverse, but floristically distinct, from the lowland semideciduous or rain forests in which they are embedded, having many specialised taxa, higher tree density and lower canopies (Harms *et al.* 2001; Lieberman *et al.* 1985; Scarano 2002). They are characterised by high spatial and temporal variability in abiotic conditions, largely due to the aquatic-terrestrial gradient they represent (Scarano 1998). Swamp forests present complex physiography (i.e., strong fine-scale soil moisture heterogeneity, Lieberman *et al.* 1985; Scarano *et al.* 1997; Walker & Kenkel 2001). The concept of physiography incorporates both superficial topography and drainage, being an important determinant of landscape complexity (Walker & Kenkel 2001). Such complexity may be an important, albeit little-studied, factor in the ecology of neotropical palms. For example, it has recently been suggested that palms divide swamps into numerous microtopographic niches along two hydrological niche axes, namely flooding and drainage (Svenning 2001b).

Specifically, we tested the hypotheses that: (1) moisture-loving species, endemic to swamps, should be restricted to the transitional zones between flooded and well-drained microsites. Each of the above-cited hydrological variables, flooding and drainage, prevail in flooded pits or well-drained mounds. Microhabitat selection could occur through increased seed germination and/or juvenile establishment under specific combinations of drainage and flooding values, representing mild drainage and restricted flooding conditions (Scarano *et al.* 1997; Souza *et al.* 1999); (2) the abundance of young individuals should occur independently of light conditions, since seed germination and establishment of understorey non-pioneer species are not dependent on light (Souza *et al.* 1999; Swaine & Whitmore 1988), but adult palms should concentrate on brighter microsites (Svenning 2000, 2002); (3) if hypotheses (1) and/or (2) are accepted, the microhabitat specialization they represent should be reflected in the spatial distribution of the individuals at distinct scales. This hypothesis is based on the premise that the scales of patterns may suggest the scales at which the processes responsible for such patterns operate (Chesson & Murdoch 1986). Thus we expect individuals to aggregate at scales equal to or larger than those corresponding to the sizes of patches of soil relative moisture, but a random spatial pattern should emerge at smaller scales. Finally, we asked whether soil relative moisture is spatially autocorrelated at scales corresponding to the size of individual plants, which are likely to be the most important from the plant's perspective (Stuefer 1996).

METHODS

Study site and species

Fieldwork was carried out in July 2002 at the Santa Genebra Municipal Reserve (SGMR; 22°44'S, 47°06'W), municipality of Campinas, state of São Paulo, southeastern Brazil. Santa Genebra is a 250-ha urban reserve of semideciduous tropical forest. The mean annual rainfall of ca. 1360 mm is unevenly distributed throughout the year, with a wet season extending from November to April, and mean annual temperature is 20.6°C (Leitão Filho 1995). The study was carried out in an area of evergreen swamp forest of ca. 10 ha, where the water table never falls far below the soil surface, even in the dry season (maximum water table depth is ca. 60 cm in the driest months, Lobo-Faria 1998). Previous analyses revealed that soil water status (measured as flooded, waterlogged or well-drained) was unpredictably distributed at scales larger than 2.5 m, and that the forest shows signs of increasing tree mortality and canopy openness, probably due to edge effects (unpubl. data).

Geonoma brevispatha Barb. Rodr. (Arecaceae) is a monoecious, ornitochoric understorey palm with clonal growth. It is restricted to swamp forests at stream edges, gallery forest or lowland rain forest in central and southeastern South America (Henderson *et al.* 1995). As most species of the genus *Geonoma* (Chazdon 1986, Henderson *et al.* 1995), the scant information available indicates that *G. brevispatha* is moisture-loving and non-pioneer (Henderson *et al.* 1995, Souza *et al*. 2003). A *G. brevispatha* genet emerging from seed first establishes as a solitary juvenile and grows by adding new leaves to a vertical stem. A clumped arrangement of ramets is produced because the vegetative ramets develop from basal axillary buds, rooting next to the parent ramet. The successive production of new ramets by each daughter ramet results in the tight clump of varying-aged ramets representing a single genet (Souza *et al*. 2003). Genets are not connected and are easily distinguished in the field as individualized tufts separated in the space (*pers. observation*). Ramets pass through four ontogenetic stages (bifid-leafed juveniles, pinnatifid-leafed stemless immatures, stemmed non-reproductive virgins, and reproducers; Souza *et al*. 2003). Reproductive ramets possess an average 3.4 cm-thick and up to 5.3 m-long stem, with average crown diameter of 156.5 cm (N = 10). In this work, the stage of individual genets was classified by the stage of its most mature ramet, as this defines how the genet is functioning within the population (i.e., whether as a juvenile, immature, virgin or reproducer, De Steven 1989).

Field measurements

We assessed forest light environment by measuring percent canopy openness. Canopy openness was estimated using a spherical densiometer, a concave mirror with an engraved grid system (Lemmon 1957). In May 2002, four readings of canopy openness were made in four directions in the centre of 100 5 x 5 m plots randomly distributed within an area of 1 ha (study area) of the swamp forest (sampled area = 0.25 ha). The densiometer was hand-held at elbow height (ca 1.30 m), and the average of the four readings was used as a measure of canopy openness in each 5 x 5 m plot. Canopy openness has been shown to be related to microclimate, and is regarded as a better measure of the local environment than physical gap size (Whitmore *et al.* 1993). Densiometer measurements are correlated with total site factor and weighted-canopy openness estimates derived from hemispherical photographs (Englund *et al.* 2000, but see

Engelbrecht & Herz 2001). A detailed analysis of canopy openness in the study area will be the theme of a separate study.

Soil moisture was measured on a relative scale using a soil moisture meter (Lincoln Irrigation, Inc., Lincoln, Nebraska, USA), inserting the brass probe into the top soil (~ 5 cm). We measured soil relative moisture at 0.5-m intervals along three parallel 50-m transect lines 15 – 20 m distant from each other, in the forest understorey within the 1-ha study area (N = 303). Since most palms aggregate in the western half of the study area (see *Results* below), we distributed the three transects in the east-west direction in this plot half. As the sample points were distributed at random relative to soil microtopography, the soil relative moisture for these points estimates the background distribution of soil relative moisture in the study area. The soil moisture meter reads in a scale of 1 to 10, with 1 being completely dry and 10 indicating full saturation, and was calibrated to read 10 in flooded soil. Habitat specialization of *G. brevispatha* in regard to soil relative moisture was assessed by the frequency distribution of individuals relative to soil moisture and a germination experiment in the field. For the first approach, plants were censused within the 100 5 x 5 m plots. For each genet (N = 178), soil relative moisture was measured at stem base. Separate analyses were carried out for the population of genets as a whole as well as for recently established solitary juvenile genets (N = 28) and for reproductive genets, i.e., those with at least one ramet at the reproductive stage (N = 112).

From May to July 2001, all *G. brevispatha* genets present in the 1-ha study area were mapped (N = 576). Polar coordinates within the 100 x 100 m study area were measured relative to a reference 10 x 10 m grid delimited by pegs. Each mapped genet was classified as solitary juvenile, reproductive, or other.

Juvenile emergence experiment

The influence of both canopy openness and flooding on juvenile emergence from seed was evaluated experimentally in the field. For this experiment, mature fruits were collected from 25 reproductive genets from a nearby population, located in the campus of the Campinas State University (UNICAMP, 22°48'S, 47°03'W). To prevent pathogen infection from sites external to Santa Genebra, seeds were treated with 10% NaClO for 10 min before being stored in darkness and at room temperature during 4 d, without any drying treatment. Microsite treatments were established in six 5 x 5 m plots in a split-plot design. Canopy openness (CO) was the main plot factor in this experimental design, and two plots were randomly chosen from each of three levels: closed (CO < 14%), intermediate (14% < CO < 28%), and open (CO > 28%). The values of 14% and 28% correspond to the mode and the fourth quartile of the canopy openness frequency distribution in the area, respectively. Open sites corresponded to recent treefall gaps, while closed areas had a continuous tree canopy. Within each treatment, two 5 x 5 m plots were randomly chosen, separated by at least 20 m, following Clark *et al.* (1996), who suggested that tropical understorey light measurements would be uncorrelated at scales > 20 m. Soil water status (flooded vs non-flooded) was used as the subplot factor, corresponding to flooded pits and non-flooded mounds.

Experimental units consisted of 15 x 20 x 15 cm bags of 3 mm nylon mesh that retained *G. brevispatha* seeds but allowed water drainage. Each experimental unit was half-filled with commercial potting soil, and twenty seeds were sown on its top. Seeds were covered with 1 cm layer of the soil. In 1 April 2002, three experimental units were inserted into the soil at random positions in each soil water status sub-plot (a total of 36 bags and 720 seeds). In the flooded sub-plots, experimental units were tied to nearby trees to ensure later removal. The number of juveniles was determined in 14 March 2003. It is worth noting that in this experiment juvenile emergence resulted from the sequence of events related to seed survivorship (s) in soil, seed germination (g) and early juvenile establishment (j). Thus, although the experimental result (percent juvenile emergence, e) resulted from the product of a series of probabilities ($e = s \times g \times j$), these were not quantified. This approach was chosen because the intermediate events s, g, and j take place in a time frame smaller than one year, and our emphasis was in the demographic transition between the ontogenetic stages of seed and juvenile, which has an yearly cycle (see Bruna 2003 for a recent demographic application of this approach).

Data analyses

Data on canopy openness and palm density were collected following a plot-based approach, while the soil moisture data collected on transects and at palm bases followed an individual-based approach. Consequently, distinct analytical approaches must be followed in each case.

To test for the presence of a relationship between canopy openness and the number of *G. brevispatha* genets, we used the non-parametric Spearman coefficient of correlation due to strong deviations from normality in the distribution of the genet count data (Zar 1996). The data on forest understorey soil relative moisture (transect data) were analysed for the presence of spatial structure, i.e., spatial autocorrelation. We evaluated the spatial autocorrelation between points on each transect through correlograms using the Moran's I coefficient (Moran 1950) against 15 mutually exclusive distance lags of 0.5 m. The Moran's I coefficient varies generally from +1 to –1, but sometimes it can exceed these values (Legendre & Fortin 1989); positive values of Moran's I correspond to positive autocorrelation. A correlogram shows autocorrelation measures in distinct distance classes, thus allowing an evaluation of the effects of proximity between pairs of samples in the autocorrelation (see review in Legendre & Fortin 1989). Inferences on the underlying generative process from the shape of the correlogram are only valid when the correlogram is globally significant (Legendre & Fortin 1989). A global test of significance was performed by checking whether each correlogram contained at least one significant value at the $\alpha = 0.05/15 = 0.003$ significance level, according to the Bonferroni method of correcting for multiple tests (Legendre & Fortin 1989; Sokal & Rohlf 1995). In correlograms, the result of a test of significance is associated with each autocorrelation coefficient; the null hypothesis of this test is that the coefficient is not significantly different from zero. We tested this null hypothesis by performing a Monte Carlo test, through the creation of 1000 coefficients for 1000 permutations of the original data. Autocorrelation analyses were performed with the software Rookcase, an Excel® Visual Basic add-in (Sawada 1999).

Measures of kurtosis were calculated for the distributions of background soil relative moisture and at palm bases. The departure of each kurtosis value from 0 was tested using a *t* test with degrees of freedom $df = \infty$ (Sokal *&* Rohlf 1995). As soil moisture is a continuous variable, comparisons between its distributions in the forest understorey in general and at the bases of *G. brevispatha* genets were done using the Kolmogorov-Smirnov test for goodness of fit. The Kolmogorov-Smirnov test is applicable to continuous frequency distributions, where it has greater power than the *G* or chi-square tests for goodness of fit, and is especially useful with small samples (Sokal *&* Rohlf 1995). Spatial analyses of forest background soil relative moisture data (see *Results*) revealed autocorrelation between points closer than 1.0 m, and thus direct comparisons with the palm data using all data from transects were not valid. For these tests, we trimmed the data, removing data from every second sampling point in each transect. In this way, a subsample of independent transect points was obtained, with points separated by distances ≥ 1.0 m ($N = 153$).

For the juvenile emergence experiment, we used split-plot analyses of variance to test for differences in juvenile emergence across canopy openness and soil water status treatments, using each bag as our observational unit (Sokal & Rholf 1995). To equalize variances for juvenile emergence, which are proportion data, this variable was arcsin-transformed before analysis. Whenever the result of a replicate was zero or 100% the relative values of $1/4n$ or $1 - 1/4n$ were used, respectively, to calculate proportions before transformation (n is the number of seeds per replicate; Zar 1996).

As our data on the spatial distribution of genets consisted of a map of points, we used edge-corrected spatial point pattern analyses based on Ripley's K-function (Ripley 1981; Diggle 1983) and its inter-type extension, the K_{12} function (Diggle 1983; Haase 2001). These methods consist of density functions using the second moment, i.e., they use all point-to-point distances for a statistical description of two-dimensional distribution patterns. They test the significance of the departure of observed samples from randomness (either regularity of clumping), and whether the relationship between two types of sampled points suggests spatial association, repulsion, or independence. The calculation of K for a range of distances allows for the study of spatial pattern at a range of scales, which is a very attractive feature of this test, since the degree of clumping in nature is frequently strongly influenced by the spatial scale considered (Hurlbert 1990). Bivariate analyses of the spatial interaction (association/repulsion) between two groups of points (e.g., two species) were based on the K_{12} test, where distances are computed between points of the two groups (1 and 2), instead of points within the same group. We used bivariate analyses to test for spatial association between solitary juvenile and reproductive genets.

The derived variable $L(d) = \sqrt{[K(d)/\pi]} - d$ (or $L_{12}(d) = \sqrt{[K_{12}(d)/\pi]} - d$ for the intertype analysis) enables the interpretation of the type of spatial pattern as a function of distance by plotting $L(d)$ against d. For a completely random pattern $L(d) = 0$; $L(d)$ becomes negative when the pattern is regular and positive when trees are clustered. Similarly, values of $L_{12}(d) = 0$ indicate independence of the two types of points; $L_{12}(d) < 0$ indicate repulsion effects, while $L_{12}(d) > 0$ indicate attraction effects (Haase 2001).

The ranges of scales were chosen after inspection of the results from spatial structure of soil relative moisture, which revealed fine-structuring of this variable at scales up to ca. 1.0 m. Thus, a 0.5 m step was used for both K and K_{12} functions, which were computed up to $d = 1.5$ m. From this scale up to 50 m, a step of 1.5 m was used, which corresponded to the average crown diameter of individual reproductive ramets, and thus was adequate to study interactions between individuals. Edge corrections were calculated using local weighting method (Haase 1995). Test significance was estimated through the Monte Carlo procedure to simulate randomly generated plots of the same density and dimensions as the observed plot. We used 1000 simulations of each of the univariate or bivariate patterns. In the bivariate analyses, new random coordinates were assigned to the juvenile genets only (the 'dependent' group). The means ± 1.96 standard deviation (2.5 % tails) of the 1000 simulations were used to construct a confidence envelope for the *L*-statistic (data) for each value of d (Haase 1995, 2001). To test whether the sample statistic deviated significantly from complete spatial randomness over specific ranges of d we used a Cramer-von Mises type of test (Haase 2001). This test integrates the squares of the deviations of the sample statistic from the expected value, which equals d. The result of the integration of the *L*-statistic was translated into significance probability according to Haase (2001), at the 5% significance level. Point pattern analyses were performed on SPPA software (Haase 2002).

RESULTS

Percent canopy openness ranged from 5.2 to 39.8% (mean = 14.3, SD = 7.0, N = 100) and showed strong positive skewness (Fig. 1). The majority of plots (57%) had 10 to 20% canopy openness. Soil moisture in the forest understorey ranged from 2 in the driest mounds to 10 in the flooded pits and channels (mean = 6.6, median = 6.0, N = 303). The frequency distribution of background soil relative moisture was bimodal, with one maximum around 6.0 and another at 10.0 (Fig. 2a). The distribution of soil moisture around these two most abundant classes, however, was not similar. Except for the completely flooded sites, there was a predominance of sites with intermediate values of soil moisture. As consequence, completely flooded sites (soil moisture degree = 10.0) were frequent, accounting for 17.2% of the sample points, while drier (soil moisture degree < 4) sites were scarce, corresponding to just 4.6% of the sample points. As a bimodal distribution, this distribution was platykurtic (Sokal & Rohlf 1995, Fig. 2a). However, excluding the flooded (moisture = 10.0) microsites, the distribution became mesokurtic (kurtosis not significantly different from a normal distribution, $g_2 = -0.46$).

Figs 1 & 2

All three correlograms calculated from the transect data (Fig. 3) were globally s The first value of spatial autocorrelation (distance class 1), which corresponds to pairs of neighbouring points on the transects, was positive and significant (P < 0.001) in all cases. Autocorrelated values at larger distances were rare and not consistent between transects. This means that the patch size was larger than 0.5 m, but generally smaller than 1 m. This reflects the fine-scale spatial structure of soil moisture, which was strongly influenced by a regular microtopographic pattern of flooded pits and channels delimited by drier mounds, both structures with ca. 1 m diameter. At larger scales soil moisture was unpredictable. Such unpredicta

Figure 3

shown in transect 2, where a weak ($P < 0.05$) negative autocorrelation pattern emerged at the scales from 4.5 to 6.5 m (Fig. 3).

Density of *G. brevispatha* genets was not correlated with canopy openness (Spearman's $r = 0.023$; $P > 0.05$). As expected, juvenile genets were not correlated with canopy openness ($r = 0.061$; $P > 0.05$), but the lack of correlation was present for reproductive genets as well ($r = -0.011$; $P > 0.05$). On the other hand, the distribution of individual genets of *G. brevispatha* with regard to soil moisture in all ontogenetic stages pooled, as well as solitary juveniles and reproductive genets, was significantly different from the background distribution of forest soil moisture (Fig. 2b - d). The majority of solitary juveniles (78.6%) occurred in microsites with soil moisture values between 6.0 and 8.0, which corresponded to 36.0% of the sample points; while 48.2% of reproductive genets occurred in microsites with moisture values between 6.0 and 7.0, which accounted for 28.1% of the sample points.

Two common features of the distribution of *G. brevispatha* with regard to soil moisture were the absence of genets in flooded sites (soil moisture = 10.0), and the concentration of the majority of genets around soil moisture values of ca. 6.0. Contrary to the distribution found for all genets pooled and for reproductive genets, the distribution of solitary juveniles was negatively skewed and concentrated in somewhat wetter microsites, with 46.4% of the individuals occurring in microsites between 7.0 and 8.0 degrees of soil moisture (Fig. 2c). Yet, juvenile distribution was less peaked (leptokurtic) in relation to the background soil moisture distribution than the distribution of reproductive genets, which was more symmetric but highly leptokurtic, with most genets occurring in microsites between 6.0 and 7.0 degrees of soil moisture (Fig. 2d).

Of 720 seeds sown in the juvenile emergence experiment, 75 (10.4%) had successfully developed into juveniles one year later. The number of juveniles developed was not related to

Table 1

canopy openness (Table 1). Juvenile emergence was zero in all flooded sub-plots, and a significant effect of location within soil water status was detected.

Overall, there were 576 *G. brevispatha* genets in the 1-ha study area (Fig. 4). Most genets (64.9%) were in the reproductive ontogenetic stage, while solitary juvenile genets comprised just 6.6% of the population. Genets were aggregated at all scales except 0.5 m (Fig. 5a). This pattern indicates that genets formed clumps, which concentrated in patches at intermediate scales, and were aggregated in some forest sectors but not in others at larger scales. In the study area the population of genets was largely restricted to the western sector (Fig. 4). Both reproductive and juvenile genets were randomly distributed at very local (< 1.0 m) scales (inset graphs in Figs. 5b and c). The spatial point pattern analysis of reproductive genets (Fig. 5b) followed closely that of the overall population, largely due to the numeric prevalence of reproducers in the population, and showed marked aggregation at all scales. Juvenile genets, however, showed an alternation of random and aggregated patterns up to a scale of 10.5 m (Fig. 5c), showing an aggregated pattern at scales up to 40 m, when the observed values of the $L(d)$ function were not significantly different from complete spatial randomness (Cramer-von Mises test P = 0.054, range 40.5 – 49.5 m). Analyses of spatial association between juvenile and reproductive genets showed values of the derived statistic $L_{12}(d)$ larger than the confidence envelope at all scales > 1.5 m (i.e., significant positive association, Fig. 5d).

Figures 4 & 5

DISCUSSION

Spatial structure of soil moisture

Our description of the Santa Genebra swamp forest physiography revealed that soil moisture was spatially structured, i.e., autocorrelated, at very local scales (< 1.0 m), but had a homogeneous (*i.e.*, with low autocorrelation, Li & Reynolds 1995) distribution at larger scales. These results reflect a nearly regular microtopographic pattern of flooded pits and channels delimited by drier mounds, repeated over the whole studied hectare. It is hard to say whether this picture is characteristic of other flood-prone forests. While it has been recognized that tropical wetlands have high spatial soil moisture variability (Lieberman *et al*. 1985; Scarano *et al.* 1997; Scarano 1998), few studies have quantified such variation at the scale of individual plants. Patterns analysed at coarser scales than ours have reported soil drainage types at scales of 10 m and coarser (Lieberman *et al*. 1985, Robertson *et al.* 1993, Daws *et al.* 2002). It is possible that the fine-grained structure of soil moisture we found at Santa Genebra be recurrent in the Brazilian Atlantic forest swamps, judging by the qualitative description of other authors (Scarano *et al.* 1997; Scarano 1998).

Canopy openness and palm density

Our first hypothesis, that the abundance of young individuals of *G. brevispatha* should occur independently of light conditions while adult palms should concentrate on more illuminated microsites, was partially rejected. Understorey and canopy palms have very diverse responses to canopy openness (Svenning 2001b), and the occurrence (Svenning 2000) and density (Svenning 2002) of many species do not show any significant relationship to canopy openness. Yet, the lack of a relationship between genet abundance and canopy openness by no means implies that the latter is not important to both individual performance and population growth, as has been shown for many understorey species (Chazdon 1986; Martínez-Ramos *et al.* 1988; Svenning 2001b, 2002). Percent canopy openness at any given point in space results from the number of leaf layers overtopping that point. However, leaf layers are dynamic in both time and space and are unlikely to be stable enough to leave a spatial signature in the spatial abundance of a slow-growing species like *G. brevispatha* (Souza *et al.* 2003). Furthermore, as the average canopy of the swamp forest we studied was considerably open in relation to other sites (*e.g.*, Denslow & Guzman 2000), severely light-limited genets growing in deep shade were probably absent or very rare at best, precluding any contrast between genet-rich brighter microsites and genet-poor darker microsites.

Structuring effects of soil moisture on the G. brevispatha population

The hypothesis that *G. brevispatha* would be restricted to the transitional zones between flooded and well-drained microsites was accepted based on the individual-oriented measurement of soil moisture and the juvenile emergence experiment. Such microhabitat specialization occurs along all the ontogenetic maturation process of the species, being detectable from seed germination (Gomes 2003), and juvenile emergence to reproductive genets. Thus, the regeneration of *G. brevispatha* is mostly restricted to the ca. 30% of soil microsites with intermediate moisture degree between flooded pits and channels and dry mounds. Such a pattern represents the outcome of the habitat choice process imposed on the species by its environment (Schupp 1995). Palm communities generally segregate relative to topography, with many species restricted to flood-prone bottomlands (Frangi & Lugo 1998; Scariot *et al.* 1989; Svenning 1999). Other plant groups also show microhabitat specialization with regard to soil factors at a range of scales (Clark *et al.* 1995; Duivenvoorden 1996; Miyamoto *et al.* 2003; Nagamatsu *et al.* 2002). These and other examples (reviewed in Svenning 2001b) emphasise the importance of topography-dependent soil moisture distribution for the regeneration of palm populations.

Juvenile emergence

The results from our juvenile emergence experiment are in agreement with the finding of Souza *et al.* (1999) and Marques and Joly (2000), that even species characteristic of seasonally flooded forests may not germinate under a water column of more than a few centimetres. They suggest that the habitat selection soil moisture imposes on *G. brevispatha* takes place through the early phases of seed germination and juvenile establishment. Recently-dispersed seeds of *G. brevispatha* are likely to germinate in most microsites present in the Santa Genebra swamp forest except the flooded ones. Flooding alters a number of soil properties, including soil structure, reduced dissolved oxygen, accumulated carbon dioxide and induced anaerobic decomposition of organic matter (Kozlowski 1997), and few species are able to cope with such conditions (Andrade *et al.* 1999; Nagamatsu *et al.* 2002; Kozlowski 1997; Scarano *et al.* 1997; Souza *et al.* 1999).

Since the rate of water supply to seeds varies with substrate composition (Dasberg & Mendel 1971), *G. brevispatha* seed germination may eventually be successful at higher topographic positions depending on variable soil texture and the presence and amount of water-retaining leaf litter (Molofsky & Augspurger 1992; Nagamatsu *et al.* 2002). This would explain the occurrence of a few juveniles on drier microsites, despite the fact that the germination of species from seasonally flooded or otherwise flood-prone forests is generally inhibited at even moderate levels of substrate desiccation (Souza *et al.* 1999). Juvenile survival on higher microsites, however, may be restricted by water shortage during the driest periods. Although in the Santa Genebra swamp forest the water table never falls far below the soil surface during the dry season (maximum water table depth is ca. 60 cm in the driest months, Lobo-Faria 1998), the short root systems of young palms located on the highest microsites are likely to fail reaching it.

Palm spatial distribution

Our third hypothesis, that individuals should aggregate at scales equal to or larger than that corresponding to the sizes of patches of soil moisture, but a random spatial pattern should emerge at smaller scales, was accepted. Both juvenile and reproductive genets are aggregated at the scale of 1.0 m, but occur randomly at smaller scales corresponding to the saturated zones around flooded pits and channels. This indicates that stochastic events acting on seed rain (e.g., disperser behaviour, perch availability and microhabitat selection, Nathan & Muller-Landau 2000) and microsite conditions (e.g., litter volume and composition, Molofski & Augspurger 1992) are likely major determinants of the exact position of newly emerged juveniles within intermediate soil moisture microsites. At the scale of soil moisture patches, however, individual genets aggregate on suitable patches, being excluded from flooded pits and occurring at low densities on drier mounds. Imbert *et al.* (2000) found the same pattern for *Pterocarpus officinalis* in swamp forests in the island of Guadeloupe.

However, if the distribution of *G. brevispatha* were to reflect the distribution of favourable waterlogged microsites, then a random distribution should emerge at all larger scales. At such scales, newly emerged juveniles occur in clumps always associated with reproductive genets, which are themselves clumped. This is a common phenomenon resulting from limited seed dispersal (Nathan & Muller-Landau 2000). In our study system, however, this effect is probably enhanced by scarcity of dispersal agents. Seeds of *Geonoma* are dispersed by small understorey birds (Zona & Henderson 1989), which are lacking or becoming rare in Santa Genebra, leading to the rupture of many seed dispersal systems in the Reserve (Pizo 1997). The spatial association between successive recruitment events and reproductive genets may lead to the aggregation of plants at many scales (Souza & Martins 2002). These results are in agreement with Chesson and Murdoch (1986), who argued that the scales of patterns might suggest the scales at which the processes responsible for such patterns operate.

The reasons for genet aggregation in the western sector of the study area, on its turn, are less evident. Although the eastern limit of our study area coincides with the transition from swamp to semideciduous forest, a plot-scale gradient in soil microtopography, *i.e.* an eastward change in the frequency or size of flooded channels and dryer mounds, does not occur (unpubl. data). Instead, the sharp decrease in *G. brevispatha* occurrence eastwards is likely due to the reduction of favourable microhabitat availability. With increasing relative altitude, soil erosion by water movement creates abrupt discontinuities between well-drained mounds and channels and flooded pits (pers. observation). This eliminates or greatly reduces the amount of waterlogged transitional zones between the two soil moisture microhabitats. This would restrict the establishment of large genets in this plot sector, which in turn could act as a sink of plants dispersing from the western sector.

Our results also support the growing body of evidence that many tropical species show microhabitat specialization within previously recognised patterns of habitat specialization at larger scales (Svenning 1999, 2001b). More specifically, they strengthen the view that palms divide swamps and floodplains into numerous microtopographic niches along the hydrological niche axes of flooding and drainage (Duivenvoorden 1996; Scariot *et al.* 1989; Svenning 1999, 2001b), as has been suggested for other plant groups (Silvertown *et al.* 1999; Meinzer *et al.* 1999; van den Berg & Oliveira-Filho 1999). The three palm species found in the Santa Genebra swamp forest also seem to partition the swamp into microtopographic niches: *Syagrus romanzoffiana* (Cham.) Glassman occurs on elevated patches, *Euterpe edulis* Mart. is widespread on wetter and lower areas, pers. obs., while *G. brevispatha* is restricted to waterlogged zones around flooded depressions in the lower areas. Such patterns support the hypothesis that coexistence by microhabitat specialization is important in maintaining the local species richness of these groups (Chesson 2000; Svenning 1999, 2001b).

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LEGENDS TO FIGURES

Fig. 1. Frequency distribution of percent canopy openness in a tropical swamp forest in southeastern Brazil.

Fig. 2. Frequency distribution of soil moisture degree in a tropical swamp forest in southeastern Brazil. a) Background distribution, measured along three 50-m transects, b) all genets of *Geonoma brevispatha*, c) solitary juvenile genets of *G. brevispatha* d) reproductive genets of *G. brevispatha*. D = Kolmogorov-Smirnov statistic for goodness of fit between each distribution and the forest background distribution shown in (a). g_2 = measure of kurtosis; values significantly smaller than 0 indicate a platykurtic (i.e., flatter than normal) distribution, while values larger than 0 indicate a leptokurtic (i.e., more centred than normal) distribution. * $P < 0.05$, ** $P < 0.001$, *** $P < 0.0001$.

Fig. 3. a) Soil relative moisture at 0.5-m intervals along three transects in a tropical swamp forest in southeastern Brazil. b) Correlograms of soil relative moisture. Distance classes correspond to 0.5-m intervals. ■ = Significant values at the $\alpha = 0.05$ level; □ = non-significant values. X axis: distance classes; the width of each distance class is 0.5 m. Y axis: Moran's *I* statistics. The resulting plot gives a measure of similarity between the values as a function of their separation distance.

Fig. 4. Map of the horizontal distribution of *Geonoma brevispatha* genets in a tropical swamp forest. △ = juvenile genets; ● = reproductive genets; ○ = other genet ontogenetic stages.

Fig. 5. Second-order spatial analysis of *Geonoma brevispatha* genets in a tropical swamp forest. a - c: univariate distribution of all genets (a); juvenile (b), and reproductive (c) genets. Insets show detailed results for small scales at 0.5 m steps. d: bivariate distributions of juvenile and reproductive genets. The sample statistic $L(d)$ or $L_{12}(d)$ is plotted against d (solid line). The dotted lines give a 95% confidence envelope for complete spatial randomness.

Table 1 Summary of split-plot analysis of variance on juvenile emergence of *Geonoma brevispatha*. Terms tested in the model include canopy openness, soil water status and location (plots) as a random variable.

Source of Variation	SS	df	MS	F
Canopy Openness	0.044	2	0.022	2.823 ns
Soil Water Status within Canopy Openness	1.190	1	1.190	153.672***
Plots within Soil Water Status	0.556	3	0.185	23.942***
Error	0.186	24	0.008	

ns – non significant, *** = $P < 0.0001$

Fig. 1. Souza, A. F. & Martins, F. R.

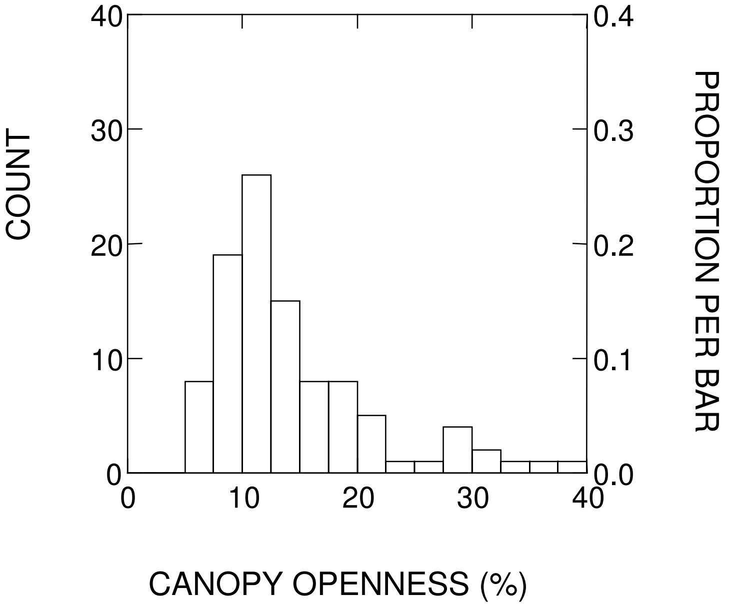


Fig. 2. Souza, A. F. & Martins, F. R.

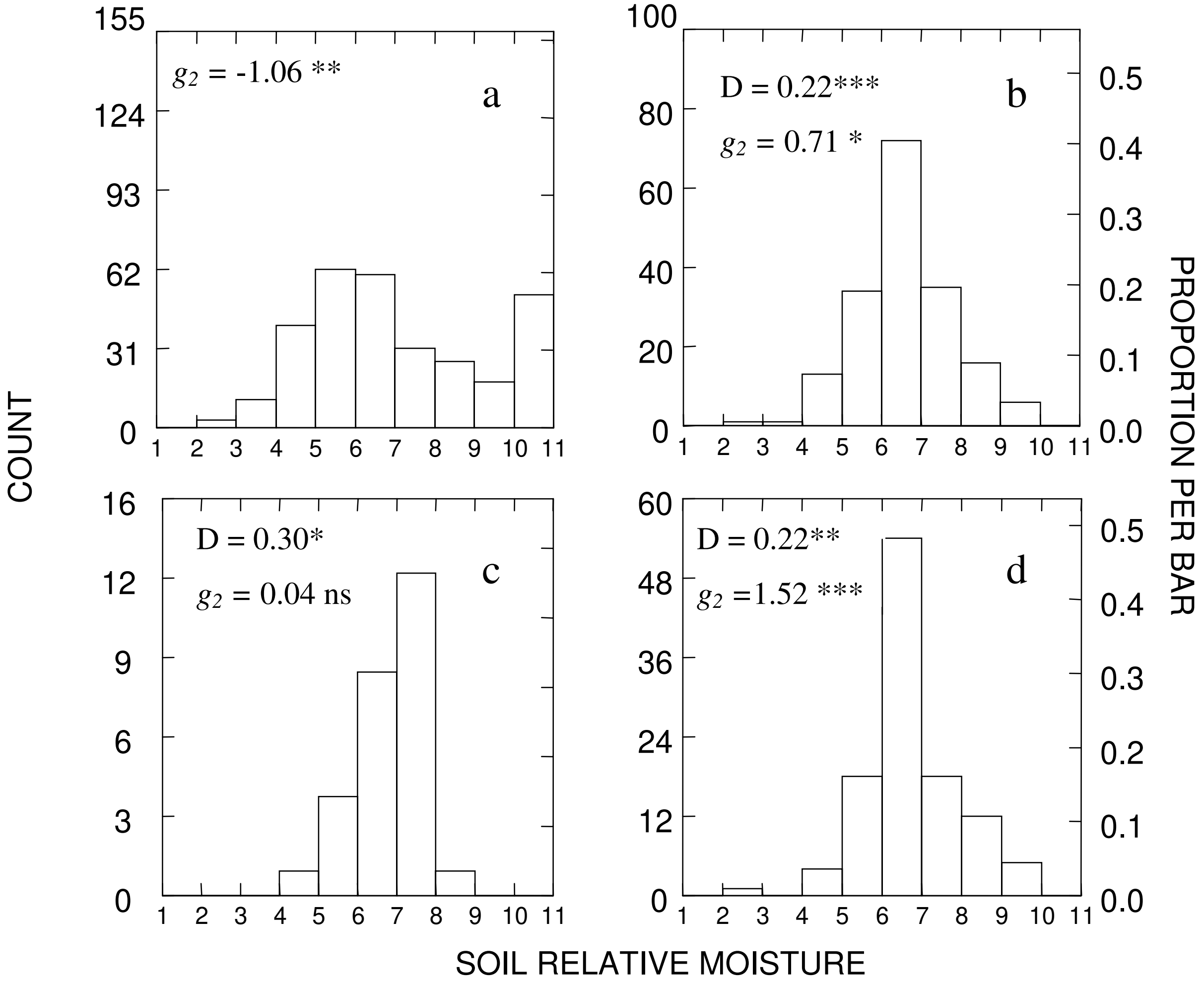


Fig. 3. Souza, A. F. & Martins, F. R.

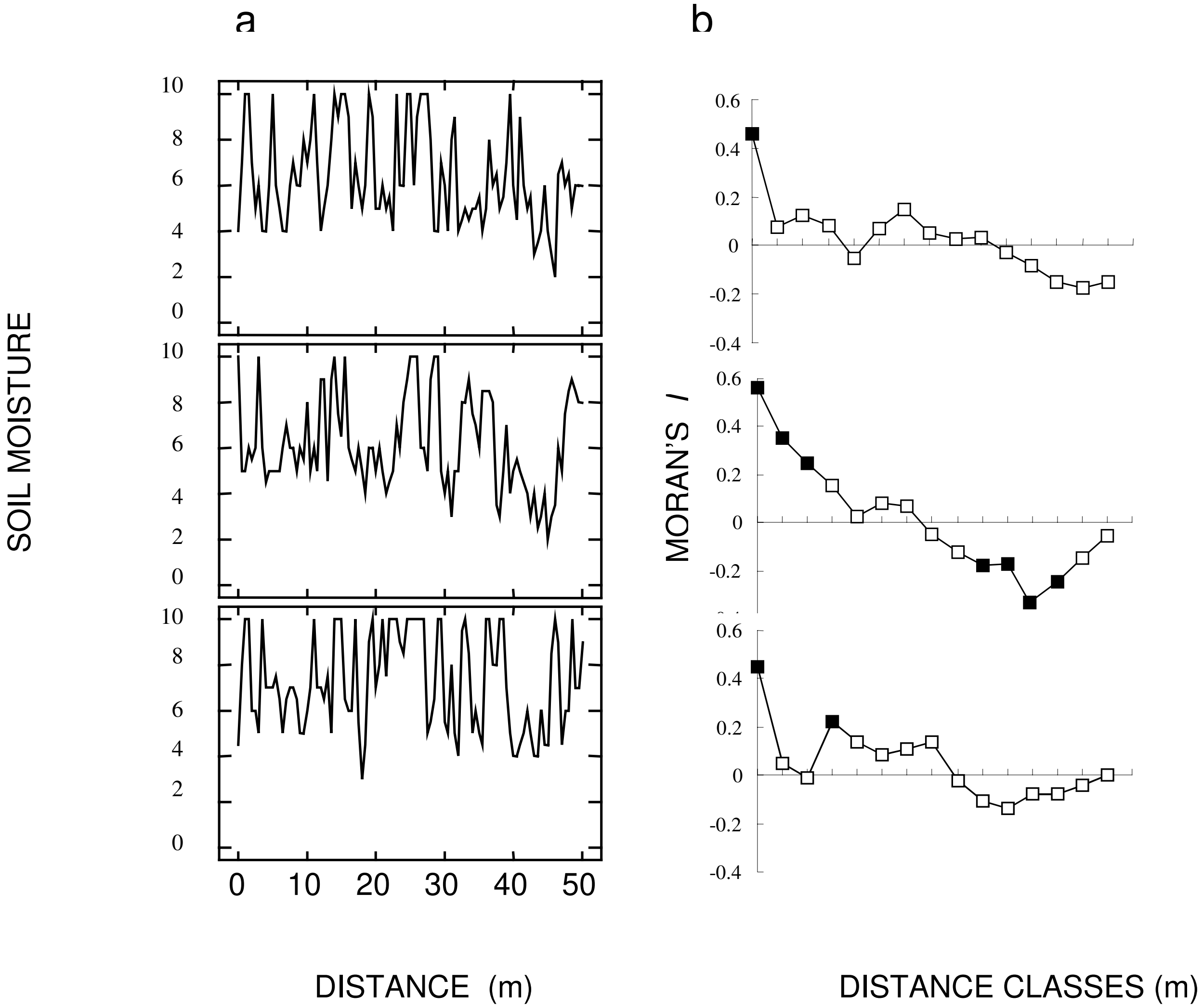


Fig. 4. Souza, A. F. & Martins, F. R.

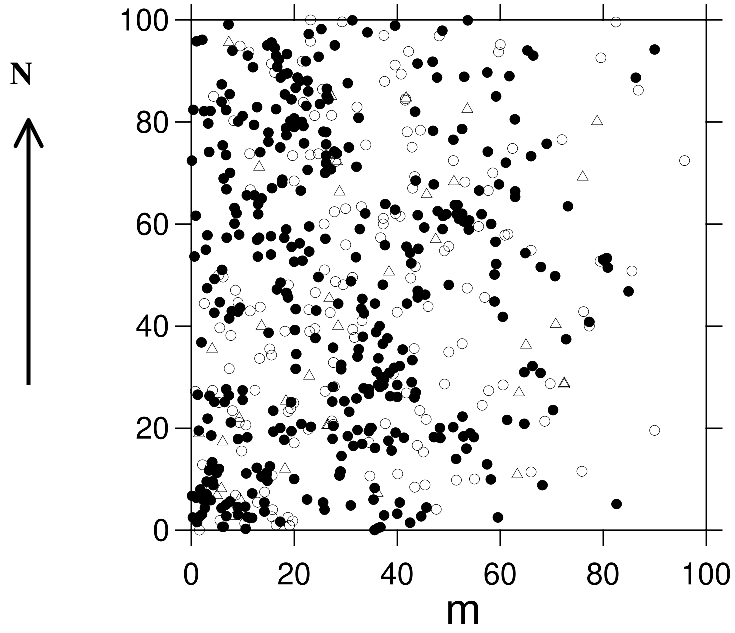
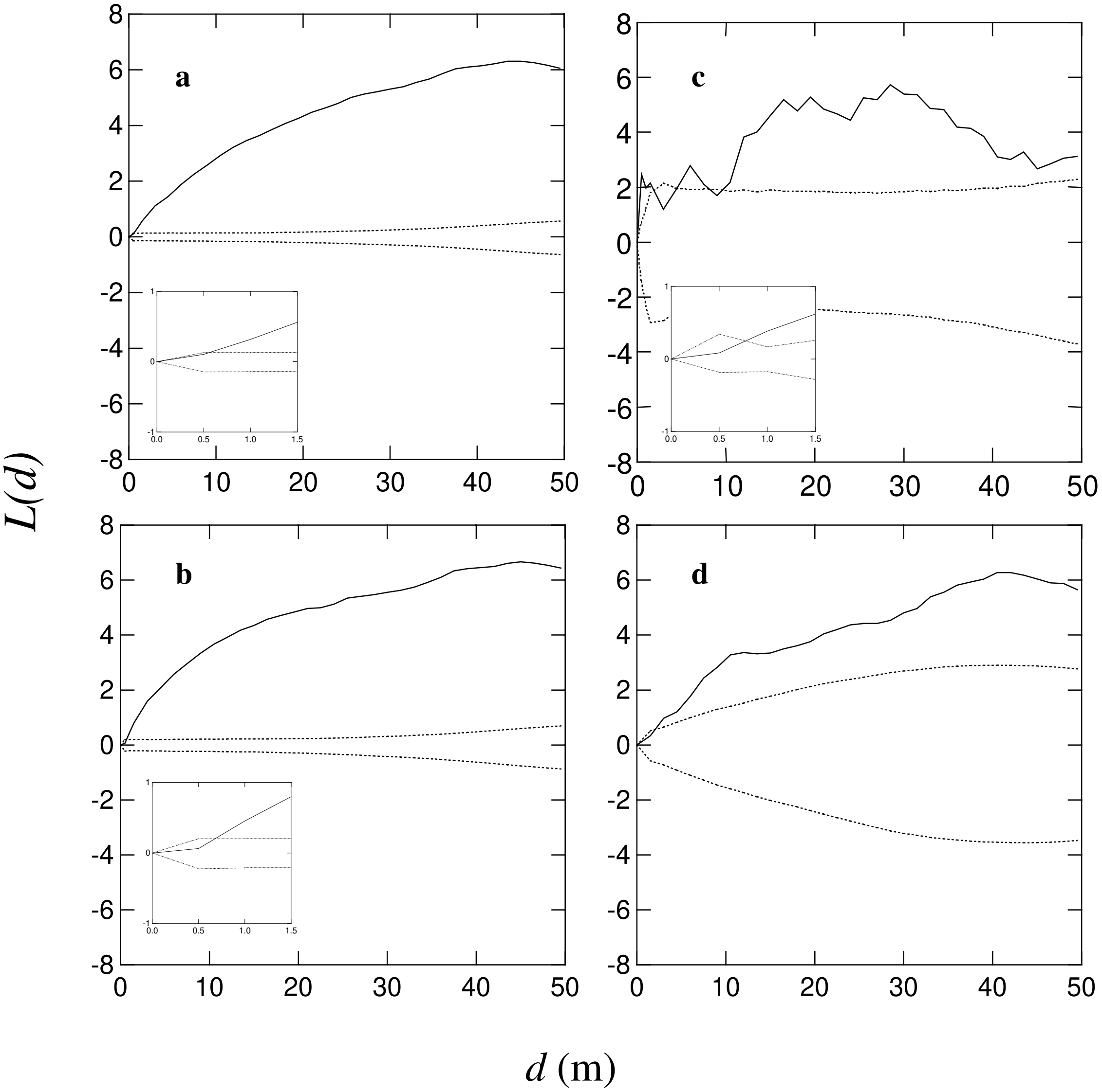


Fig. 5. Souza, A. F. & Martins, F. R.



CAPÍTULO 4. Demography of the understorey clonal palm *Geonoma brevispatha* in a Neotropical swamp forest.[1]

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1 – TrabTabelas e figuras no final do capítulo. Trabalho formatado segundo as regras da revista *Journal of Ecology.*

Resumo

A dinâmica de populações de plantas clonais tropicais é pouco conhecida, assim como o papel da heterogeneidade ambiental que ocorre em pequena escala em seus ambientes, e o papel que a variação temporal desempenha em suas taxas vitais. Neste trabalho, conduzimos um estudo demográfico com três anos de duração (dois intervalos demográficos), sobre a demografia da palmeira clonal *Geonoma brevispatha*. Quantificamos os efeitos demográficos da heterogeneidade na abertura de dossel, do tamanho do geneta, bem como da distancia e do tamanho do vizinho conspecífico e arbóreo (DAP ≥ 10 cm). A mortalidade de genetas estabelecidos foi < 2,0%, e foi concentrada em rametas solitários. As taxas demográficas no interior de cada geneta foram afetadas principalmente pelo tamanho do geneta, mais do que por fatores ambientais diretos. A sobrevivência de juvenis solitários (27,8%) foi muito menor do que a de juvenis produzidos vegetativamente (79,3%), indicando subsídios para o estabelecimento, através da integração fisiológica no interior dos genetas. As taxas de produção vegetativa de rametas foram positivamente relacionadas com o tamanho dos genetas em ambos os anos. No Segundo ano, houve uma redução importante na sobrevivência dos rametas reprodutivos, em grande parte devido a um aumento na pressão de predação por macacos da espécie *Cebus apella nigritus*. Modelos populacionais matriciais predisseram que a taxa de crescimento da população geral de rametas foi significativamente maior do que a unidade no primeiro ano de estudo, mas significativamente menor do que 1,0 no ano seguinte. As taxas de crescimento populacional de rametas no nível dos genetas individuais foram maiores do que 1,0 na maioria dos genetas no primeiro ano, mas no segundo ano genetas com taxas de crescimento menores do que 1,0 formaram a maioria da população. A predação maciça por macacos nas copas dos rametas reprodutivos e uma estação seca prolongada foram provavelmente responsáveis pela diminuição

populacional. Simulações periódicas e estocásticas indicaram que longas seqüências de anos desfavoráveis seriam necessárias para reduzir as taxas de crescimento populacionais.

Summary

1 The population dynamics of tropical clonal plants is poorly understood, as well as the role fine-scale environmental heterogeneity and temporal variation play in the variation of their vital rates.

2 We carried out a three-year (two intervals) demographic study on the forest understorey clonal palm *Geonoma brevispatha* in a disturbed swamp forest in southeastern Brazil. Data were collected in 100 5 × 5 m plots randomly distributed within 1 ha in the swamp forest. The demographic effects of heterogeneity in forest canopy openness, genet size, and distance and size of nearest conspecific and large tree (DBH ≥ 10 cm) were quantified.

3 Mortality of established genets was < 2.0%, and was concentrated on solitary ramets. Within-genet ramet vital rates were mainly affected by genet size, rather than by direct environmental factors. Solitary juvenile survivorship (27.8%) was much lower than the survivorship of juvenile ramets produced vegetatively (79.3%), indicating establishment support through physiological integration within genets. Rates of vegetative ramet production were positively related to genet size in both years. In the second year, there was a marked reduction in the survivorship of reproducer ramets, largely attributable to increased predation pressure by *Cebus apella nigritus* monkeys.

4 Matrix models predicted that the growth rate of the overall ramet population was significantly greater than unity in the first study year, but it was significantly smaller than 1.0 in the next. Ramet population growth rates at the level of individual genets were greater than unity in the majority of genets in the first year, but in the second year genets with growth rates smaller than unity prevailed. Massive predation by monkeys on the crowns of reproductive ramets and prolonged dry season were probably responsible for population decrease. Periodic and stochastic simulations indicated that long sequences of unfavourable years would be necessary to reduce population growth rates.

5 Disturbed forest conditions in the study site seems to be favourable to *G. brevispatha*, while clonal growth spreads mortality risk in the genet among ramets, and provides support to increased predation pressure episodes. However, frequent elevated predation pressure by food-limited vertebrate predators may threaten the persistence of clonal palms in tropical understoreys.

Keywords: *Cebus apella apella,* clonal growth, environmental stochasticity, *Geonoma brevispatha*, herbivory, matrix models, population dynamics, ramet vs. genet mortality, swamp forest, tropical forests.

Introduction

In recent years, a growing number of studies focused on aspects of the demography of tropical plants (reviewed by Alvarez-Buylla *et al.* 1996). These studies have largely focused on solitary trees and palms (Alvarez-Buylla 1994; Ratsirarson *et al.* 1996; Silva Matos *et al*. 1999; Svenning 2002; Souza & Martins in press). In most cases, results revealed populations at equilibrium, capable of self-maintenance but not growth (Alvarez-Buylla *et al.* 1996). Another common finding is that many species depend on localised canopy openings to promote increases in vital rates and thus maintain population viability (Chazdon 1986; Horvitz & Schemske 1995; Alvarez-Buylla 1994; Pascarella & Horvitz 1998; Svenning 2002).

The demography of tropical species in forest fragments is, however, less well known. Although the above-cited results point to increased population growth in disturbed vegetation due to increased light penetration (De Steven 1989; Alvarez-Buylla 1994; Souza & Martins in press), there is some evidence that hyperdisturbed habitats may be unfavourable to the persistence of understory species (Souza & Martins 2002). In this paper we address the population dynamics of *Geonoma brevispatha* Barb. Rodr. (Arecaceae), an understory palm with clonal growth. We used demographic analyses at the two levels of biological organisation present in clonal plants (the genet level and the ramet level), to investigate the demographic patterns of the species and infer the suitability of its habitat, a swamp forest embedded in a tropical forest fragment.

Although clonal plants represent an important component of understory tropical forest communities, frequently achieving high densities (De Steven 1989; Henderson *et al.* 1995; Kimura & Simbolon 2002), only a few studies have addressed their demography in the tropics (De Steven 1989; Chazdon 1992; Horvitz & Schemske 1995; Cirne & Scarano 2001; Sánchez-

Velásquez *et al*. 2002). Most population studies of clonal species concern temperate herbaceous species (e.g., Barkham 1992; Silvertown & Lovett-Doust 1993; Damman & Cain 1998; Valverde & Silvertown 1998), and it is not clear the extent to which theoretical predictions (e.g., Eriksson 1993) based on these data apply to tropical palm species. Combined with data on clonal palm architecture and growth strategies (Chazdon 1992; Mendoza & Franco 1998; Kimura & Simbolon 2002; Souza *et al*. 2003), the few demographic studies on clonal palms indicate that the production of multiple ramets by each genet results in increased genet survivorship and spreading of important mortality risk among ramets, and that vegetatively-produced juveniles benefit from physiological integration with older ramets (Bullock 1980; De Steven 1989; Chazdon 1992).

Tropical swamp forests occur on permanently flooded soils and represent a poorly studied vegetation type within tropical forest landscapes. They possess high microsite heterogeneity, created by the interaction between microtopography and flooding. In the present study we analyse the demography of *G. brevispatha* based on genet size and ramet ontogenetic stages (Souza *et al*. 2003) in relation to a number of environmental variables, including canopy openness and neighbourhood effects. Specifically, we asked the following questions: (1) Does the population have frequent recruitment events from seed (Repeated Seedling Recruitment, Eriksson 1993), or the replacement of individuals depends entirely on the vegetative production of new ramets? (2) Are ramet stage-specific vital rates related to environmental variables? (3) Is the swamp forest fragment suitable to population growth at both genet and ramet levels?

Materials and methods

STUDY SITE AND STUDY SPECIES

The study was conducted at the Santa Genebra Municipal Reserve (SGMR; 22°44'S, 47°06'W), municipality of Campinas, state of São Paulo, south-eastern Brazil. SGMR is a 250-ha urban reserve of semideciduous tropical forest. Mean annual temperature is 20.6°C (Leitão Filho 1995), and the mean annual rainfall of 1377.5 mm (1961 - 1990) is unevenly distributed along the year, with a wet season extending from November to April. Fieldwork was carried out in an evergreen swampy forest of ca. 10 ha, where the water table never falls far below the soil surface, even in the dry season (maximum water table depth is ca. 60 cm in the driest months, Lobo-Faria 1998). Previous analyses revealed that soil water status (classified as flooded, waterlogged or well-drained) was unpredictably distributed at scales larger than 2.5 m, and that the forest shows signs of increasing tree mortality and canopy openness, probably due to edge effects (A.F. Souza, unpublished data).

Geonoma brevispatha is a monoecious, ornitochoric understorey palm with clonal growth. It is restricted to swampy areas at stream edges, gallery forest or lowland rain forest in central and south-eastern South America (Henderson *et al.* 1995). The scant information available indicates that *G. brevispatha*, as most species of the genus *Geonoma* (Chazdon 1986; Henderson *et al.* 1995), is moisture-loving and non-pioneer (Henderson *et al.* 1995; Souza *et al*. 2003). A *G. brevispatha* genet emerging from seed first establishes as a solitary juvenile and grows by adding new leaves to a vertical stem. A clumped arrangement of ramets is produced because vegetative ramets develop from basal axillary buds, rooting next to the parent ramet. The successive production of new ramets by each daughter ramet results in a tight clump of varying-aged ramets representing a single genet. Genets are not connected and are easily distinguished in the field as individualized tufts separated in the space. Ramets pass through four ontogenetic stages (bifid-leafed juveniles, pinnatifid-leafed stemless immatures, stemmed non-reproductive virgins, and reproducers; Souza *et al.* 2003). Static analyses showed that clonal fecundity (vegetative production of new ramets) precedes sexual fecundity, and that sexual and clonal fecundity increase continuously with genet size, although both kinds of fecundity seem not to be related (Souza *et al.* 2003). In this work, the stage of individual genets was classified by the stage of its most mature ramet, as this defines how the genet is functioning within the population (i.e., whether as juvenile, immature, virgin or reproducer, De Steven 1989). Here we use the term 'established ramets' to refer collectively to immature, virgin or reproductive ramets, and 'established genets' to genets represented by at least one established ramet.

FIELD MEASUREMENTS

The data were collected in 100 permanent 5 × 5 m plots randomly distributed within 1 ha of the swampy forest (sampled area = 0.25 ha). Within each 5 x 5 m plot, all ramets were numbered and tagged from March to July 2001, and the fates of the plants were subsequently monitored in April and May 2002 and 2003, when all new plants were also tagged. In 2001, each ramet was assigned to one of the four above-mentioned ontogenetic stages, according to Souza *et al.* (2003). In subsequent years, each ramet could be dead or found in the same or in a later ontogenetic stage. In May 2001, basal area of all trees $5 \leq \text{DBH} < 10$ cm, hereafter referred to as small trees, was measured in the same 100 5 x 5 m plots mentioned above. In the same year, all genets ($N = 576$) and trees with $\text{DBH} \geq 10$ cm ($N = 844$), hereafter referred to as large trees, present in the 1 ha study area were mapped. Polar coordinates within the 100 x 100 m plot were measured relative to a reference 10 x 10 m grid delimited by pegs.

In 2001 and 2002, we assigned each 5 x 5 m plot to one of five classes of soil flooding, based on the number of 2.5 x 2.5 m flooded subplots. Hence, soil water status of each plot ranged from 0 (no apparent flooding) to 4 (entirely flooded). A subplot was regarded as flooded in the presence of a water column of at least 1 cm. We assessed forest light environment by measuring percent canopy openness with a spherical densiometer, a concave mirror with an engraved grid system (Lemmon 1957). In May 2001 and 2002, four readings of canopy openness were made in the centre of each 100 random 5 x 5 m plots. The densiometer was hand-held at elbow height (ca 1.30 m), and the average of the four readings was used as a measure of canopy openness in each plot. Canopy openness has been shown to be related to microclimate, and is regarded as a better measure of the local environment plants face than physical gap size (Whitmore *et al.* 1993). Although indirect methods may not yield accurate enough estimates of light conditions at a single site, needed for example for detailed ecophysiological studies (Engelbrecht & Herz 2001; Whitmore *et al.* 1993), they are well suited to rank understory light conditions among a large number of sites (Engelbrecht & Herz 2001). In particular, densiometer measurements are correlated with total site factor and weighted-canopy openness estimates derived from hemispherical photographs (Englund *et al.* 2000, but see Engelbrecht & Herz 2001).

STATISTICAL ANALYSES

Analyses were carried out at three scales: the plot-scale, the ramet-scale and the genet-scale. (1) Plot-scale analyses: the effects of canopy openness, basal area of small and large trees, and flooding on genet and established ramet density were analysed by stepwise standard least-squares multiple regression analysis with significance levels of 0.05 and 0.10 to enter or leave, respectively (Sokal & Rohlf 1995). Continuous and count variables were $\log_{10}$- and square-root transformed, respectively (Zar 1996), due to strong positive skewness. (2) Ramet-scale analyses: data related to ramets of all established genets were pooled and analysed for ontogenetic stage-structured population dynamics (see *Transition matrix analyses* below). (3) Genet-scale analyses: we used stepwise multiple regression to assess the effects of canopy openness, basal area of small trees, flooding, genet size, distance and size of the nearest genet and large tree neighbours, and reproductive ramet survivorship on the total annual number of new ramets produced per genet (asexual recruitment), and the proportional ramet survivorship and progression (transition to a later stage). In each genet, ramet survivorship and progression were considered separately for each ontogenetic stage. Cases where only one ramet was found in a given ontogenetic stage were not considered. The proportional survivorship and progression data were arcsine-transformed (Zar 1996). Whenever one of these proportions was zero or 100% the relative values of $1/4n$ or $1 - 1/4n$ were used, respectively, to calculate proportions before transformation (n is the number of ramets; Zar 1996). Genet size was measured as the number of established (i.e., immature, virgin and reproducer ramets combined) ramets, and large tree size was measured as bole volume (m^3) obtained from diameter and height measurements of each tree. Note that canopy openness, flooding and basal area of small trees are plot-specific measures, while genet size, distance and size of nearest genet and tree neighbours are genet-specific measures. In order to account for edge effects regarding nearest neighbour measurements, the largest distance between one genet and its nearest neighbour (3.85 m) was obtained, and all genets closer to the limits of the 1 ha area than this distance were excluded from the analyses.

TRANSITION MATRIX ANALYSES

Ramet population dynamics and its dependence on microenvironmental heterogeneity were analysed by means of the asymptotic ramet population growth rates predicted by transition matrix population models (Caswell 2001). The ontogenetic stages described above were used to build square stage-classified transition matrices. Transition probabilities were calculated directly from counts of individuals involved in each transition. The three annual censuses yielded two years of transition data. Transitions among ontogenetic stages were grouped into three categories (Fig. 1): *Vegetative reproduction* is the production of new individuals from basal axillary buds of immature, virgin and reproducer ramets. *Stasis* is persistence within the same stage. *Progression* is transition to a later stage. As noted by Caswell (2001), the measurement of fecundity is frequently complicated by the difficulty of tracing offspring to parents. This was true for *G. brevispatha*, since vegetatively-produced juveniles arise from the genet's base (Souza *et al.* 2003); thus no single ramet can be identified as the "parent" of a new juvenile. To express juvenile production on a per-ramet basis at the genet level, we assumed that all established ramets contributed to juvenile production, and that the contribution of an established ramet was proportional to its stem length. This is reasonable, because in *G. brevispatha* vegetative fecundity occurs mainly from the immature ramet stage on, stem length is significantly larger at each successive stage, and the probability of ramet production is positively dependent on stem length of adult ramets (Souza *et al.* 2003). Following Huenneke & Marks (1987), the number of juveniles produced by a genet (or by all genets, in the case of the whole-population model, see below) during the study interval was divided by the sum of stem lengths of established ramets present at the beginning of the interval. For genet-specific models, the average stem lengths of each ramet established stage was used. This yielded an estimate of "per-length" (in cm) contribution to vegetative juvenile production, which was used to estimate the collective contribution of each established stage to vegetative fecundity. Dividing this contribution by the number of ramets in the corresponding stage yielded the mean vegetative production by a ramet in a given stage in each genet.

Analyses were carried out at two scales. At the whole-population scale, the study unit was comprised by all ramets sampled in the study area, regardless of genet identity. This population was modelled by one transition matrix in each time interval, each one yielding a single population growth rate (λ_r). At this scale, newly produced juvenile ramets came from one of two possible sources: sexual (from seed) or vegetative. Juveniles from both sources were pooled to estimate juvenile survivorship probability, but solitary plants emerging from seed were excluded from the data used to calculate vegetative fecundities. Instead, the number of sexually-produced recruits divided by the number of reproducer ramets present at the beginning of the interval (an estimate of sexual fecundity) was added to the vegetative fecundity of reproducer ramets in the matrix. Thus, in the whole-population models, reproducers contribute to juvenile recruitment by both sexual and asexual ways. We opted for not separating sexually-produced juveniles from the vegetatively-produced ones in the matrices because they represented only 0.31% of the overall ramet population, and because we had incomplete data on survivorship and progression of this stage class (i.e., survivorship based on only the second study year, when no progression occurred). In these models, the fruit category was omitted because from one year to the following, all seeds either germinate or die.

At the genet scale, a separate transition matrix was built for each individual genet, yielding genet-specific ramet dynamics and population growth rates (λ_g). Here, fecundity estimates represented vegetative juvenile production only, since sexually-produced juveniles do not contribute to changes in ramet number. Only genets with 10 or more ramets were included in these analyses (N = 93 for the 2001-2002 interval, and N = 95 for the 2002-2003 interval). Due to varying sample sizes among genets, specific stages were absent in some genets. As this was due to small ramet population size rather than biology, the transition matrices were corrected for these problems. If zero individuals in a given genet represented a stage, it was assigned the transition rates estimated by pooling the data from all ramets, regardless of genet affiliation (global matrices, Horvitz & Schemske 1995; Hal Caswell, *pers. communication*, Table 1). If a stasis rate was unity, it was replaced by 0.998, in order to allow for both mortality and progression, while if a progression rate was unity, it was replaced by 0.999. If a progression rate was zero, it was replaced by 0.001, while the same value was subtracted from the corresponding stasis rate (Piñero *et al.* 1984; Svenning 2002).

We used the power method to calculate the dominant eigenvalue of each projection matrix, which corresponds to the finite rate of increase (λ) of the ramet population (Caswell 2001). We estimated confidence intervals for λ by drawing 1000 bootstrap samples from the original data, building a life table and a matrix for each, and solving it for λ (Alvarez-Buylla & Slatkin 1991). We classified genets into three categories of ramet population growth (stasis, growth or reduction), based on whether the 95% confidence interval of λ included unity or not. Differences between the distribution of genets among these categories in the two study intervals were evaluated using the log-likelihood ratio, *G*, which is a more robust test than χ^2 to evaluate goodness-of-fit (Sokal & Rohlf 1995). Finally, the effects of canopy openness, basal area of small trees, flooding, genet size, distance and size of the nearest genet, and large tree neighbours on λ_g were analysed by stepwise multiple regression analysis, as explained above.

Elasticity analyses were performed on projection matrices at the whole-population scale, to study the relative importance of different phases of the life cycle on population dynamics (de

Kroon *et al.* 1986, 2000; Caswell 2001). Elasticity measures the proportional change in λ resulting from a proportional change in a matrix element a_{ij}, and is defined by de Kroon *et al.* (1986) as $e_{ij} = a_{ij}/\lambda s_{ij}$, where s_{ij} is the sensitivity of λ to changes in the matrix element a_{ij}, holding all other matrix elements constant. The elasticity of a matrix element can be interpreted as the contribution of this element to the population growth rate (de Kroon *et al.* 1986). The sum of all the elasticities of a matrix equals unity, and allows for comparison among different species or populations of the same species (de Kroon *et al.* 1986; Caswell 2001).

Demographic differences between populations at different times may be ascertained by comparing entire transition matrices using log-linear analyses of contingency tables to evaluate the degree of interdependence between the explanatory and response factors involved (Caswell 2001; Horvitz & Schemske 1995; Valverde & Silvertown 1998). Here we determined the significance of year on global transition matrices. A log-linear analysis of three-way contingency tables was performed to compare entire global transition matrices. Explanatory factors were year and initial ontogenetic stage, and the fate of individuals was the response variable (Sokal & Rohlf 1995).

TIME-VARYING MODELS

Given the demographic differences between the two time intervals (see *Results: transition matrix analyses: time-invariant models*), and because the future trajectory of a population will depend on the frequency, magnitude and sequence of demographic rates occurring, a series of time-varying models incorporating temporal variation in demographic rates were built. Time-varying models provide insights into the future size or behavior of the population studied (Silva *et al.* 1991). In these models, temporal variation in demographic rates was considered to occur because of the alternation of favourable and unfavourable years, represented by the 2001-2002 and 2002-2003 transition matrices, respectively. Two types of models were used: deterministic (periodic) models and stochastic models.

In deterministic matrix models, favourable and unfavourable years occur in a fixed sequence, and the matrices **F** and **U** (standing for favourable and unfavourable years, respectively) were used to simulate the different sequences that characterized distinct periods. For example, to simulate population dynamics during a 5-yr period in which two unfavourable years followed three favourable years, we can use

$$\mathbf{N}_5 = \mathbf{U}\cdot\mathbf{U}\cdot\mathbf{F}\cdot\mathbf{F}\cdot\mathbf{F}\cdot\mathbf{N}_0$$

$\mathbf{N}_5$ and $\mathbf{N}_0$ are the population vectors at year 5 and year 0, respectively (Caswell 2001). These models can be written as (Silva *et al.* 1991)

$$\mathbf{N}_{(t+m)} = \mathrm{U}^x\mathrm{F}^{m-x}\mathbf{N}_t$$

where m is the period of the complete cycle and x is the number of unfavourable years in the cycle (x/m being the frequency of unfavourable years). The unfavourable-phase return time interval $T = m - x$ is defined as the number of years between unfavourable phases. The dominant eigenvalue of the matrix product $\mathrm{U}^x\mathrm{F}^{m-x}$ is the population growth rate over a period of m years, which can be transformed to an annual growth rate by taking the m-th root. Periodic population growth rates were determined for return times of up to 50 years, with the number of unfavourable years in each cycle increasing at 1-yr steps until periodic growth rate was less than unity.

As we have no reason to suspect that unfavourable years do occur in strict cyclic pattern through time, the use of periodic models may lead to unrealistic projections of population dynamics. Stochastically time-varying models overcome this problem by randomly choosing year-types in each time step. Following the approach used by Damman and Cain (1998, see also

Caswell 2001), we simulated environmental stochasticity by randomly selecting one of the two matrices observed in the field to provide the probabilities that ramets would reproduce or survive from one year to the next. For the subsequent transition, a matrix would again be selected randomly from one of the two matrices. A constant probability of occurrence of an unfavourable year was used, regardless of year-types in previous years. In this case, the probability of occurrence of an unfavourable year in any year is 1/*T*, where *T* is the average unfavourable-phase return interval.

These models have the property that the probability distribution of stage structures eventually converges to a stationary distribution (Caswell 2001), so that final stage distributions are independent from initial population structures. The observed initial population was used as the starting vector in the simulations, which were iterated for 6000 yr. The first 1000 yr were omitted from the calculation of λ. The population growth rates for these long-term runs were estimated from the projected population size as suggested by Heyde & Cohen (1985):

$$\ln\lambda = \frac{\ln N(T) - \ln N(1)}{T - 1}$$

where N(T) is the sum of the individuals in all ontogenetic stages at time T. It should be noted that in this case λ is not the eigenvalue of a projection matrix but is used to represent conveniently the population growth rate.

Results

POPULATION DENSITY AND STRUCTURE

Geonoma brevispatha was abundant in the swamp forest. Average genet density (including juveniles recently emerged from seed) ranged from 1.7 to 2.0 genets per 5 x 5 m plot (676 - 804 ha^{-1}), and was constant along the study years (ANOVA on square-root transformed values: F = 0.38, df = 2, P = 0.69). The only environmental variable significantly related to genet density was the basal area of large trees (2001 data: coefficient = 0.401, r^2 = 0.084, P = 0.003, N = 100). This positive, but weak, relationship was also found in 2002 and 2003 (results not shown), largely due to the constant density of genets. The mean density of established ramets ranged from 8.1 to 10.1 plants per 5 x 5 m plot (*i.e.*, 3228 - 4044 ha^{-1}), and was also constant between the study years (ANOVA on square-root transformed values: F = 0.25, df = 2, P = 0.78). Densities of genets and established ramets were strongly correlated (Pearson correlation coefficients: 2001 = 0.84, 2002 = 0.84, 2003 = 0.82, P < 0.001 in all cases).

The stage structure of the population (i.e., the relative densities of ontogenetic stages) was dependent on year (two-way contingency table, G^2 = 20.73, df = 6, P = 0.002, Fig. 2). Generally, genets with reproducer ramets were the most abundant, representing more than 50.0% of the plants in both years, while the virgins were the least abundant stage. Population structure changed along time due to an increase in the number of juvenile genets (representing new individuals emerging from seed) in 2002 (G^2 = 34.41, df = 2, P < 0.001), while the relative proportion of the other stages remained stable (G^2 = 8.60, df = 4, P = 0.072).

GENET DYNAMICS

Survivorship of established genets, i.e., those represented by at least one established ramet, was 98.0% and 98.1% in the 2001-2002 and 2002-2003 intervals, respectively. Five out of the six established genets that died in the study period were represented by solitary ramets. Two of the dead genets were killed by fallen tree crowns near or at recently formed gaps. Genet recruitment occurred in 2002 and 2003, but the number of newly-emerged juvenile genets in 2002 (N = 36; 144 recruits ha^{-1}) was nearly twice the number of recruits in 2003 (N = 16; 64 recruits ha^{-1}). The first-year survivorship of the 2002 cohort (27.8%) was much lower than the survivorship of juvenile ramets produced vegetatively by established genets in the same period (pooled data from all established genets: 79.3%, $G = 10.3$, df = 1, $P = 0.001$). Although for most cases the causes of mortality of new recruits could not be identified, fallen leaves of the arborescent palm *Euterpe edulis* accounted for 11.5% of deaths. No juvenile genet of the 2002 cohort progressed to the immature stage in the study period.

RAMET DYNAMICS

The rate of vegetative ramet production by established genets varied from 0 to 15 juvenile ramets genet $^{-1}$ year $^{-1}$, and was higher in the 2001-2002 interval (average ± SD = 2.54 ± 2.89 juveniles $genet^{-1}$) than in the 2002-2003 interval (1.93 ± 2.37 juveniles $genet^{-1}$, paired *t* test, $t = 2.66$, df = 166, $P = 0.010$, N = 167). In both study years, ramet production was positively related to genet size, as measured by the number of established ramets in a genet (Table 2), but a positive relationship with canopy openness and the distance to the nearest large tree also appeared in the second year. The effects were additive, but genet size contributed more to the model than canopy openness and distance to the nearest tree, as seen by the values of the standardised regression coefficients (Table 2).

The log-linear analysis of general ramet survivorship in the entire population (survivorship data summarised in Table 1) indicated that the effects of both ontogenetic stage and year were significant (Table 3). Moreover, the two-way interaction term was significant, i.e. the explanatory factors were not independent of each other in their effect on the fate of individuals (Table 3). This reflects a reduction in the survivorship values in the second study interval, as well as a change in their distribution among stages. In such cases, it is only meaningful to look at the effects of a factor within each level of the other (Sokal & Rohlf 1995). In the 2001-2002 interval, survivorship was lowest (87.9%) in reproducer and highest (97.1%) in immature ramets (Table 1). In the following interval, there was a marked reduction in the overall survivorship of reproducer (reduction = 23.3%) and juvenile (reduction = 10.9%) ramets, accompanied by a raise to unity in the survivorship of virgins (Table 1). Most clonal juveniles that died during the study period were overtopped by leaf litter accumulating at the genet centre or submerged by lateral contact with flooded microsites.

The main cause of increased reproducer mortality in the 2002-2003 interval was increased predation pressure by capuchin monkeys (*Cebus apella nigritus*, Cebidae). Capuchin monkeys tore away expanded leaves of reproducer ramets, and destroyed completely or partially new leaves and the apical meristem, frequently extirpating all plant parts above the last exposed node on stem. This was revealed by both tooth marks left on destroyed leaf parts at or near individual palms and direct observation. Sixteen out of the 256 reproducer ramets marked in 2001 (6.3%) had signs of predation by capuchin monkeys, and only two had died one year later. This corresponded to 6.5% of reproducer ramet deaths in the period. In 2002, the number of reproducers attacked raised to 66 (28.0%), 60 of which were dead one year later. This corresponded to 71.4% of reproducer deaths in the period.

TRANSITION MATRIX ANALYSES: TIME-INVARIANT MODELS

The log-linear analysis performed with whole-population transition matrices indicated significant effects of year conditional on initial stage on the fate of individuals, with a significant interaction term (Table 4). Inspection of year-specific matrices (Table 1) reveal noticeable changes in the strength of distinct demographic routes between years. In the 2002-2003 interval there was an increase in the progression of virgins to the reproducer stage, as well as a lack of direct progression of juveniles to the virgin stage, present in the previous period. Furthermore, vegetative ramet production per established ramet (fecundity) decreased from 0.53 juveniles established ramet $^{-1}$ year $^{-1}$ to 0.36 established ramet $^{-1}$ year $^{-1}$. Asymptotic population growth rates for the entire ramet population (λ_r) were higher than unity in the 2001-2002 interval, but smaller than unity in in 2002-2003 (Table 1).

Apart from the evident effect of monkey predation on reproducer ramet survivorship, intraspecific factors were more prominent on ramet survivorship and progression to later ontogenetic stages than environmental factors. In the 2001-2002 interval, genet size and the size of the nearest large tree had a negative effect on juvenile ramet progression to the immature stage (Table 5). Genet size increased immature ramet survivorship (Table 6) at the same time that decreased its progression to the virgin stage (Table 5). This progression was positively related to the size of the nearest large tree and to the survivorship of reproducer ramets in the same genet. Survivorship of reproducers was negatively related to the distance to the nearest conspecific neighbour (Table 6).

These relationships were changed in the following year, when genet size had a negative effect on juvenile ramet survival, and a weak positive effect of the distance to the nearest large tree on the survivorship of reproducers was detected (Table 6). Additionally, a negative effect of genet size on the juvenile stage was detected on survivorship (Table 6), but not on progression. An inhibition of immature progression by genet size, however, was found in this period. In this period, virgin progression was significantly and strongly (as measured by the r^2 value) affected by the survivorship of reproducers in the same genet (negative effect), and canopy openness (positive effect, Table 5). A weak positive relationship between reproducer survivorship and the distance to the nearest large tree was also found (Table 6).

The genet-specific asymptotic ramet population growth rates (i.e., genet growth, λ_g) varied from 0.33 to 1.81 ($\bar{x} \pm SD = 1.05 \pm 0.16$, N = 93) in the 2001-2002 interval, and from 0.31 to 1.36 (0.98 ± 0.16, N = 95) in the 2002-2003 interval. A significant decrease in λ_g occurred in the second study year (paired *t* test, $t = 6.01$, df = 91, $P < 0.0001$). In the first study year, λ_g was not related to any of the microenvironmental factors measured, but in the second year they were weakly and negatively correlated to the distance to the nearest genet (coefficient = - 0.259, $r^2 = 0.10$, df = 1, F = 10.48, P = 0.002). Classification of genets in categories of growth by means of the 95% bootstrap confidence interval of λ_g revealed that genets with positive growth (lower confidence limit > 1.0) constituted the majority (75.27%) of the individuals in the first year of study, followed by genets with negative growth (upper confidence limit < 1.0, 21.51%, Fig. 3). These proportions showed a significant inverse tendency in the next year, when genets with negative growth outnumbered those with positive growth ($G = 16.13$, df = 2, $P < 0.001$).

Elasticity values varied over two orders of magnitude between ontogenetic stages and different kinds of transition (Table 7). In both intervals, population growth rate was most sensitive to stasis of ramets, which accounted for 78.4 – 80.7% of total elasticities, followed by progression (12.5 – 14.1%). High elasticity values tended to concentrate in the entries that corresponded to young/smaller individuals, mainly immature ramets surviving and staying in the same stage. This pattern was reinforced in the second year, when the relative contribution of stasis and progression increased at the expense of fecundities, and the contribution of immature stasis became 4.7 times greater than the second greatest value.

TRANSITION MATRIX ANALYSES: TIME-VARYING MODELS

Whole-population growth rates (λ_r) showed to be very resistant to both stochastic and periodic unfavourable phases. The time-varying stochastic models produced similar results to the periodic models in terms of the direction and rate of change in population size. The population is predicted to increase under the occurrence of alternating favourable and unfavourable years, and growth rates asymptotically approach the growth rate of fixed favourable time (λ_r for 2001-2002) as return time increases (Fig. 4). Increasing the duration of the unfavourable phase increases the return time needed for periodic growth rates to approach the growth rate of fixed favourable time. The minimum duration of the unfavourable phase capable of lowering λ_r below unity with a 1-yr return time is 5 yr. On the other hand, the minimum duration of the unfavourable phase needed to keep $\lambda_r \leq 1.0$ under return times as long as 50 yr was 265 yr.

Discussion

The population dynamics of clonal understorey species has been poorly studied in the tropics, despite their ubiquitous presence in tropical forests. This makes it difficult to assess their response to the numerous environmental changes taking place in tropical landscapes. In this study, we used matrix population models to evaluate the response of *Geonoma brevispatha*, a clonal palm endemic to swamp forests, to spatial and temporal variability in its environment. Results showed that recruitment from seed is frequent, clonal ramets benefit from higher survivorship rates than solitary ramets, and that genet size has strong influence on ramet production and growth. Furthermore, yearly variation in demographic vital rates, largely due to monkey predation pressure, resulted in significant variation in population growth rates.

GENET DYNAMICS

Genet recruitment from seed occurred in both study intervals, fitting Eriksson's (1993) 'repeated seedling recruitment' pattern for clonal plants. In this pattern, seedling recruitment occurs within patches of established genets. This was also true for the clonal palm *Oenocarpus mapora* (De Steven 1989), and leads to the formation of populations comprised of mixtures of genet cohorts. Successful genet establishment could not be followed due to the limited duration of our study, but it can be inferred by the presence of older solitary juvenile and immature ramets. This suggests that genet recruitment has been recurrent in the population studied. Plant populations in small forest fragments generally suffer from disrupted seed dispersal systems (Pizo 1997; Silva Matos & Watkinson 1998; Silva & Tabarelli 2000) and depressed seedling recruitment (Bruna 2003;

Souza & Martins *in press*), restraints that are believed to threaten their ability to maintain viable populations. Indeed, a one-year *G. brevispatha* seed rain experiment conducted in the same forest revealed almost no seedfall, while point pattern analysis of genet spatial distribution showed that solitary juveniles are closely associated with reproductive genets at various scales (A.F. Souza, unpublished data). Since Santa Genebra is an isolated small forest fragment embedded in an urban and agricultural landscape, supporting an impoverished avian fauna (Aleixo & Vielliard 1995; Pizo 1997), avian-mediated seed rain is probably severely reduced.

Recurrent genet recruitment in *G. brevispatha* is likely to result from the interactions between microsite specialisation and small-scale spatial heterogeneity of soil moisture. *Geonoma brevispatha* juvenile emergence and establishment are limited to soil moisture conditions restricted to the transitional zones between flooded and well-drained microsites (A.F. Souza, unpublished data). In the swamp forest studied, soil moisture is spatially autocorrelated at a very fine scale (ca. 1 m), and thus favourable microsites for *G. brevispatha* establishment are available in the close vicinity of most reproductive genets. This allows recruitment to occur despite very short presumed dispersal distances and dependency on specific soil moisture conditions. Thus, differently from what has been found for other tropical species (Hubbell *et al*. 1999; Dalling *et al*. 2002), dispersal limitation and microsite specialization are not restricting *G. brevispatha* population growth. Furthermore, the density of conspecifics seems not to have achieved sufficiently high levels to inhibit juvenile recruitment.

RAMET DYNAMICS AT THE GENET SCALE

Our data indicate that physiological integration plays an important role in the growth and survival of clonal genets along their developmental process. Physiological integration refers to the translocation of resources from larger ramets to developing smaller ramets by means of anatomical connections, and plays an important role in the demographic and foraging strategies of many clonal plant species (Caraco & Kelly 1991; Chazdon 1992; Silvertown & Lovett-Doust 1993; Hutchings & Wijesinghe 1997). Similarly to results found for other clonal plants (De Steven 1989; Barkham 1992), vegetatively-produced juveniles of *G. brevispatha* have greater growth rates (Souza *et al.* 2003) and increased survival relative to juveniles emerging from seed. This reinforces the view that physiological integration would support growth and survival of the deeply shaded juvenile ramets of tropical palms, which do not receive enough light intensity for daily carbon balance in most cases (Chazdon 1986).

The high survivorship of established ramets agrees with data for other tropical forest species, in which mortality decreases after the initial establishment stage (Piñero *et al.* 1984; Olmsted & Alvarez-Buylla 1995; Silva Matos *et al.* 1999; Souza & Martins *in press*). High survivorship may also result from physiological integration equalising carbon balances in ramets experiencing vertical microsites of distinct light quality (Hutchings & Wijesinghe 1997). Ramets at the reproductive stage, however, had lower survivorship than younger stages. This can be attributed to the senescence of older ramets, which have reduced leaf number and sexual fecundity (Souza *et al.* 2003), as well as to mechanical instability of longer stems, which have continuous length growth but limited diameter increase (Chazdon 1991b; Souza *et al.* 2003) and frequent leaning (Chazdon 1992; Souza *et al.* 2003). These architectural characteristics make palms susceptible to breakage (Martinez-Ramos *et al.* 1988; Chazdon 1986, 1992). Most dead reproductive ramets were found smashed down by falling debris, indicating that mechanical factors may frequently kill longer ramets before physiological death from senescence effects.

Cloning in tropical palms is regarded as a strategy directed to growth and persistence rather than propagation (De Steven 1989; Chazdon 1992; Mendoza & Franco 1998; Svenning 2000;

Souza *et al*. 2003). In *G. brevispatha*, such a space consolidation strategy (*sensu* van Groenendael *et al*. 1997) consists of mortality risk spreading among the ramets of each genet, and increased clonal reproduction and immature ramet survivorship with genet size. Thus, our results confirm the view that clonal growth confers high survivorship to established genets (De Steven 1989; Chazdon 1992; Silvertown & Lovett-Doust 1993; Svenning 2000). During the study period no clonal genet died, despite the death of many ramets in all ontogenetic stages and the fall of canopy trees over some genets. On the other hand, five out of the six non-juvenile genets dead in the study period were solitary, and the only dead clonal genet comprised a single immature ramet with a few daughter juveniles. Larger genets also produced more clonal juveniles, in agreement with previous analyses for this (Souza *et al*. 2003) and other clonal palm species (Bullock 1980; De Steven 1989; Chazdon 1992; Mendoza & Franco 1998; Svenning 2000). Eriksson (1993) argued that some inherent mechanism preventing genets to achieve high ramet densities should be present in clonal plants, as self-thinning seems not to be a common phenomenon among ramets of each genet (but see Cirne & Scarano 2001). Indeed, in *G. brevispatha* the density of established ramets had a negative effect on the progression of juveniles and immatures to later stages (Table 5). This makes younger stages a sort of ramet reservoir from which established ramets are recruited in face of the mortality of reproductive ramets.

The negative relationship between survivorship of reproducer ramets and distance to the nearest conspecific genet in the first study year indicates that (a) genets benefit from aggregation on favourable microsites, (b) favourable conditions are spatially autocorrelated (*i.e.,* conditions farther from genet aggregates become increasingly unfavourable), and (c) current genet densities within genet aggregates are not sufficiently high to counterbalance the increased resource levels or improved conditions that generate the aggregates.

POPULATION GROWTH AND FOREST STRUCTURE

Time-invariant population matrix models revealed a significant change in population growth rates from one study year to the next. The population of *G. brevispatha* was growing at the Santa Genebra swamp forest from 2001 to 2002. Positive population growth occurred at both genet and ramet scales and resulted from abundant juvenile recruitment from both seed and vegetative ramets and high survivorship of established genets and established ramets. Positive population growth was found in the same forest by Silva Matos *et. al.* (1999) for the arborescent solitary palm *Euterpe edulis*. These results suggest that the Santa Genebra swamp forest currently represents a favourable environment for a subset of both understory and canopy species. The higher densities of both genets and ramets of *G. brevispatha* than densities reported for most clonal palm populations (De Steven 1989; Siebert 2000; Svenning 2002) strengthen this idea. Most tropical plant populations studied to date in mature forests were found to be stable, self-maintaining, but not growing (Alvarez-Buylla *et al.* 1996; Svenning 2002; Pascarella e Horvitz 1998), suggesting the presence of density-dependent mechanisms (Alvarez-Buylla *et al.* 1996). Understorey plant populations are frequently light-limited, relying on localised canopy openings to compensate for negative carbon balance that suppress individuals in deep shadow (De Steven 1989; Chazdon 1986; Alvarez-Buylla 1994; Valverde & Silvertown 1998; Svenning 2002; Sánchez-Velásquez *et al*. 2002; Pascarella e Horvitz 1998).

Small tropical 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 (Oliveira-Filho *et al*. 1997; Tabanez & Viana 2000). Spatial analyses of the Santa Genebra forest structure pointed to the occurrence of widespread forest degradation, which seems to be particularly advanced in some forest sectors (A.F. Souza, unpublished data).

Although our study of *G. brevispatha* was not a long-term analysis of population dynamics during the whole process of gap formation and closure, our results support the idea that forest degradation at Santa Genebra, leading to more open canopy conditions, may release the population of *G. brevispatha* from light limitation and allow for population growth at both ramet and genet levels. Indeed, a number of recent studies suggest that understory palm populations may be benefiting from moderate forest degradation (Pascarella e Horvitz 1998; Silva Matos *et al.* 1999; Siebert 2000; Souza & Martins 2002 and *in press*).

These results confirm that even understorey palm species morphologically adapted to tolerate low light levels may benefit from increased canopy openness conditions (De Steven 1989; Svenning 2002; Svenning & Macía 2002). Furthermore, our results correspond with the hyperdinamism hypothesis of Laurance (2002), according to which increased amplitude of biological processes including recruitment and mortality rates should be expected in forest fragments due to disturbed conditions such as edge effects and increased canopy openness.

Stasis was the kind of transition that most contributed to population growth, summing up most of total elasticity. Population growth rate of long-lived organisms rely mostly on adult survivorship (Gotelli 1991). However, in *G. brevispatha* the largest elasticity values concentrate in the survivorship of immature ramets. Silva *et al.* (1991) proposed that in short-lived species, like annuals and grasses, transitions to larger size classes should be the most important parameter determining population growth rate. It is thus possible that, in long-lived clonal plants like *G. brevispatha*, an intermediate condition occurs, and population growth relies mostly on survivorship of smaller ramets.

THE IMPACT OF AN UNFAVOURABLE YEAR ON PALM DEMOGRAPHY

The relatively small elasticities of reproducer ramet survivorship and fecundity help explain why population growth became < 1, but remained close to unity despite extensive reproducer ramet mortality in the second study interval. Increased predation pressure by *Cebus apella* monkeys on the crowns of reproducer ramets of *G. brevispatha* led to a significant increase in this stage's mortality rate. Solitary understorey palms also show reduced survivorship under leaf harvesting (Mendoza *et al*. 1987; Pinard 1993). This implies that *G. brevispatha* reproducers act as resource sources for younger ramets, but might not act as sinks in face of leaf tissue loss. This picture agrees with the suggestion that dependence upon vegetative regeneration is an adaptive strategy to high rates of crown damage by herbivorous animals in rainforest tree palms (De Steven & Putz 1985).

Most monkey species of the genus *Cebus* includes some green plant material in their diet (Freese & Oppenheimer 1981; Galetti & Pedroni 1994). However, the diet of *Cebus apella* in undisturbed forests is based on ripe fruit pulp, to which they add invertebrates (Peres 1994; Simmen & Sabatier 1996). Capuchins respond to seasonal fruit shortage by relying mostly on immature seed, flowers and nectar (Galetti & Pedroni 1994; Peres 1994). However, climatic-driven episodes of low community-level fruit production may lead frugivorous mammals to experience famine events, with increased mortality (Wright *et al*. 1999). During such extreme famine episodes capuchins may rely on alternative, energy-poor food items such as *G. brevispatha* shoots, since they cannot migrate from the Santa Genebra fragment. Heavy monkey predation on palm green tissues seems not to be uncommon (Rowe 1996; Siebert 2000).

However, the negative population growth rates observed at the whole-ramet population scale and in almost half of the individual genets are not attributable solely to primate predation.

Contrary to 2001 (Alfonsi & Camargo 2001), 2002 was a dry year, receiving less total rainfall than the local long-term average (Alfonsi *et al.* 2002). Furthermore, rainfall was exceptionally heterogeneous in 2002, producing an unusually long, dry and hot winter (Alfonsi *et al.* 2002). At our study plot, this dry period was accompanied by a significant reduction in the proportion of flooded areas, with consequent retraction of transition microsites between flooded and well-drained sites (A.F. Souza, *unpublished data*), and probable lowering of the soil water table. Hence, the observed negative population growth rates are likely to result from combined effects of adverse climatic conditions and increased predation pressure.

The unfavourable moisture conditions and increased monkey predation pressure on reproductive ramets evoked distinct responses among ontogenetic stages. Genets tended to allocate resources to replace dead reproductive ramets. Increased reproductive ramet mortality released previously suppressed virgin ramets to grow to the reproductive stage (Table 5). Reduced production and survivorship of clonal juvenile and lack of direct progression to the virgin stage indicate that genets reduced resource transfer to juveniles. This agrees with the theoretical prediction that, although larger clonal plants should share resources with daughter ramets (favourable year), smaller plants (i.e., genets reduced by ramet predation) should often abandon daughter ramets and allocate all its available resources to growth of older ramets (Caraco & Kelly 1991).

IMPLICATIONS FOR CONSERVATION

It is worth remembering that our models, both time-fixed and time-varying, are tools used in *projection*, in which the hypothetical consequences of maintaining current environment are explored, in contrast to *prediction*, in which one is interested in the actual population dynamics in the future (Caswell 2001). Due to the time scale of our study, it is not possible to estimate the frequency of increased predation pressure events. Abnormally dry years, on the other hand, seem not to be a tendency in the local climate, judging by analyses of the last 100 years (Mello *et al.* 1994). Whatever the relative importance of predation pressure and climate, their combined effects on the overall population growth were sufficiently strong to reduce λ_r to declining (< 1.0) levels. Both periodic and stochastic simulations indicated that unfavourable years should be very frequent in order to threaten the persistence of *G. brevispatha* in the Santa Genebra swamp forest. Frequent episodes of high monkey predation pressure are not improbable. Reduced fragment size and forest degradation at Santa Genebra may reduce food availability to *Cebus apella*. Predation of *G. brevispatha* crowns was not common a few years ago (Galetti & Pedroni 1994), although the *Cebus apella* population already used alternative food sources external to the reserve, such as surrounding corn and sugar cane plantations (Galetti & Pedroni 1994, pers. observation). In this context, massive monkey use of *G. brevispatha* crowns is indicative of severe food shortage (M. Galetti and E.Z.F. Setz, *personal communication*). If the killing of reproducer ramets continues, severe population reductions are possible, since subsided growth and survivorship of pre-reproductive ramets may be reduced due to depleted stored reserves. Thus, although the clonal habit appears to buffer individual genets against the short-term traumatic effects of ramet and leaf removal (Chazdon 1991a), it is possible that frequent mass predation events threaten the persistence of *G. brevispatha*. In this case, management plans should be directed towards increasing food availability to *Cebus apella*. This scenario highlights that even species favoured by forest degradation-induced increases in light availability may be threatened by disturbance-mediated biotic interactions.

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Table 1 Whole-population transition matrices estimated for the *Geonoma brevispatha* population in Santa Genebra swamp forest. Transitions were estimated by pooling all ramets, regardless of genet affiliation. Average population growth rates (λ) with 95% confidence interval is given for each year.

Stage at time $t + 1$	Stage at time t			
	Juvenile	Immature	Virgin	Reproducer
2001-2002				
λ_r: 1.092 (1.090 - 1.0947)				
Juvenile	0.741	0.151	0.371	1.428
Immature	0.156	0.909	0	0
Virgin	0.004	0.038	0.855	0
Reproducer	0	0.012	0.091	0.879
$\sum$	0.902	0.960	0.945	0.879
2002-2003				
λr: 0.987; (0.986 - 0.989)				
Juvenile	0.630	0.115	0.281	1.043
Immature	0.163	0.879	0	0
Virgin	0	0.024	0.676	0
Reproducer	0	0.005	0.324	0.644
$\sum$	0.793	0.907	1	0.644

Note: $\sum$ values are the survival rates for each ontogenetic stage.

Table 2 Factors influencing genet-specific ramet production of *G. brevispatha* (final models shown).

Parameter	Standardized Coefficient	Coefficient
2001-2002		
Constant		0.78**
Square root (number of established ramets[1])	0.63	0.53***
N = 136, df = 1, F = 86.75***, r^2 = 0.39		
2002-2003		
Constant		-1.82**
Square root (number of established ramets[1])	0.63	0.43***
Canopy Openness	0.23	4.39**
Log_{10}(distance to the nearest tree)	0.14	1.55*
N = 135, df = 3, F = 33.66***, r^2 = 0.42		

1 – Measured as the number of established ramets (immatures, virginiles and reproductives), * $P < 0.05$, ** $P < 0.01$, *** $P < 0.0001$.

Table 3 Results of the log-linear analysis for the models built with survivorship data from a *G. brevispatha* population for the periods 2001-2002 and 2002-2003. Frequency tables (including death or survival as fates) were used for the analysis. A constant 0.5 was added to all cells prior to analysis. The explanatory variable is Y = year, and the response variable is F = fate (death or survival), conditional on I = initial category (juvenile, immature, etc.). The significance of the explanatory variable is analysed by examining the increase in χ^2 (i.e., $\Delta\chi^2$) when it is excluded from a model that included it.

Model	Effect	df	χ^2	$\Delta\chi^2$	P
IY,FY		6	31.48		0.00002
IY,F		19	122.17		< 0.0001
	Year	1		90.69	< 0.0001

Table 4 Results of the log-linear analysis for the models built with entire transition matrices from a *G. brevispatha* population for the periods 2001-2002 and 2002-2003. Frequency matrices (including death as a fate, and excluding fecundities) were used for the analysis. A constant 0.5 was added to all cells prior to analysis. The explanatory variable is Y = year, and the response variable is F = fate (death, juvenile, immature, etc.), conditional on I = initial category (juvenile, immature, etc.). The significance of the explanatory variable is analysed by examining the increase in χ^2 (i.e., $\Delta\chi^2$) when it is excluded from a model that included it.

Model	Effect	df	χ^2	$\Delta\chi^2$	P
IY,FY		15	29.87		0.01239
IY,F		19	43.02		< 0.0001
	Year	4		113.15	< 0.0001

Table 5 Factors influencing genet-specific ramet progression to later ontogenetic stages of *G. brevispatha* (final models shown).

Parameter	Standardized Coefficient	Coefficient
2001-2002		
Juveniles		
Constant		
Log_{10}(size of the nearest tree^1)	0.25	1.68*
Square root (number of established ramets^2)	-0.22	-46.66*
N = 96, df = 2, F = 4.92**, r^2 = 0.08		
Immatures		
Constant		4.00 ns
Log_{10}(size of the nearest tree^1)	0.62	68.53***
Survivorship of reproducer ramets	0.38	0.20*
Square root (number of established ramets^2)	-0.28	-1.09*
N = 39, df = 3, F = 8.28***, r^2 = 0.37		

Table 5 Continued

Parameter	Standardized Coefficient	Coefficient
2002-2003		
Immatures		
Constant		23.09***
Square root (number of established ramets^2)	-0.61	-1.55***
N = 75, df = 1, F = 42.35***, $r^2 = 0.37$		
Virginiles		
Constant		35.95 ns
Survivorhip of reproductive ramets	-0.69	-1.12**
Canopy openness	0.43	146.16*
N = 8, df = 2, F = 25.88**, $r^2 = 0.88$		

1 – Measured as the bole volume (m^3); 2 – Measured as the number of established ramets (immatures, virginiles and reproductives), * $P < 0.05$, ** $P < 0.01$, *** $P < 0.0001$.

Table 6 Factors influencing genet-specific ramet survivorship of *G. brevispatha* (final models shown).

Parameter	Standardized Coefficient	Coefficient
2001-2002		
Immatures		
Constant		59.60***
Square root (number of established ramets[1])	0.48	2.43***
N = 70, df = 1, F = 19.84***, r^2 = 0.23		
Reproductives		
Constant		74.00***
Log_{10}(distance to the nearest genet)	-0.34	-14.83**
N = 51, df = 1, F = 6.41**, r^2 = 0.12		

1 – Measured as the number of established ramets (immatures, virginiles and reproductives), * P < 0.05, ** P < 0.01, *** P < 0.0001.

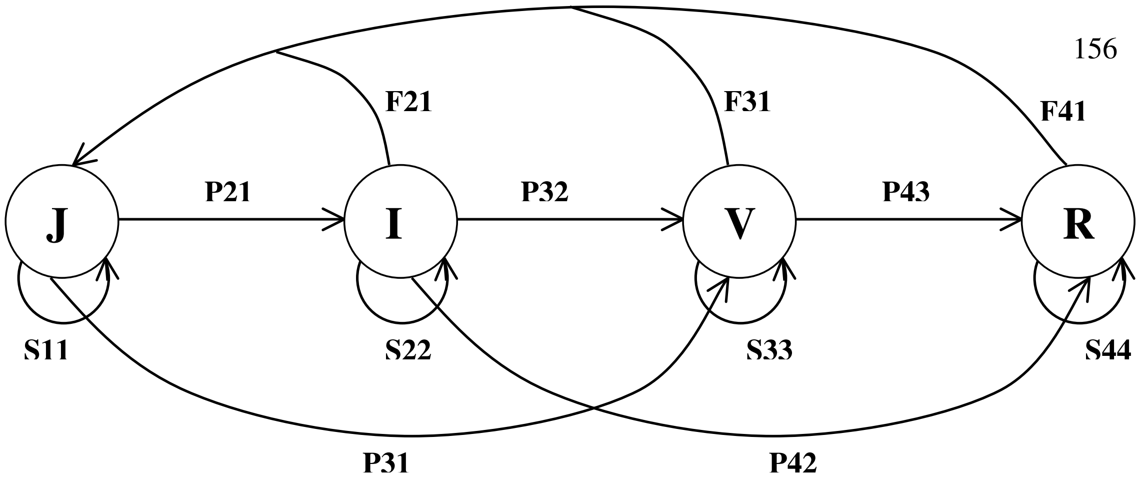
Table 6 Continued.

Parameter	Standardized Coefficient	Coefficient
2002-2003		
Juveniles		
Constant		77.98***
Square root (number of established ramets[1])	-0.42	-2.21***
N = 100, df = 1, F = 21.06***, $r^2 = 0.18$		
Reproductives		
Constant		34.49***
Log_{10}(distance to the nearest tree)	0.317	47.22*
N = 50, df = 1, F = 5.37*, $r^2 = 0.10$		

1 – Measured as the number of established ramets (immatures, virginiles and reproductives), * P < 0.05, ** P < 0.01, *** P < 0.0001.

Table 7 Whole-population elasticity matrices for the *Geonoma brevispatha* population in Santa Genebra swamp forest for two consecutive periods. The highest value is bold and the smallest is underlined in each matrix.

Stage at time $t + 1$	Stage at time t			
	Juvenile	Immature	Virgin	Reproducer
2001-2002				
Juvenile	0.160	0.028	0.012	0.035
Immature	0.072	**0.359**	0	0
Virgin	<u>0.004</u>	0.029	0.119	0
Reproducer	0	0.015	0.020	0.146
2002-2003				
Juvenile	0.121	0.034	0.007	0.028
Immature	0.068	**0.569**	0	0
Virgin	0	0.029	0.065	0
Reproducer	0	<u>0.005</u>	0.023	0.052



Stage at time *t*

Stage at time *t* + *1*

$$\begin{array}{cc} & \begin{array}{cccc} J & I & V & R \end{array} \\ \begin{array}{c} J \\ I \\ V \\ R \end{array} & \begin{bmatrix} S_{11} & F_{12} & F_{13} & F_{14} \\ P_{21} & S_{22} & 0 & 0 \\ P_{31} & P_{32} & S_{33} & 0 \\ 0 & P_{42} & P_{43} & S_{44} \end{bmatrix} \end{array}$$

Fig. 1 Life-cycle graph of *Geonoma brevispatha* and its correspondence with the basic population projection matrix. Circles correspond to plant ontogenetic stages (J = juveniles, I = immatures, V = virgins, and R = reproducers), arrows represent the possible transitions between stages, and letters show the connection between each transition and its corresponding matrix entry. Note that some transitions (i.e., P_{31}) may not occur every year. Matrix entries are subdivided into stasis (S, i.e. persistence within the same stage), progression (P, i.e. is transition to a later stage), and fecundity (F, i.e. juvenile ramet production). At the genet scale, fecundity represent vegetative juvenile production only, but at the whole-population scale, it combines both sexual and vegetative juvenile production.

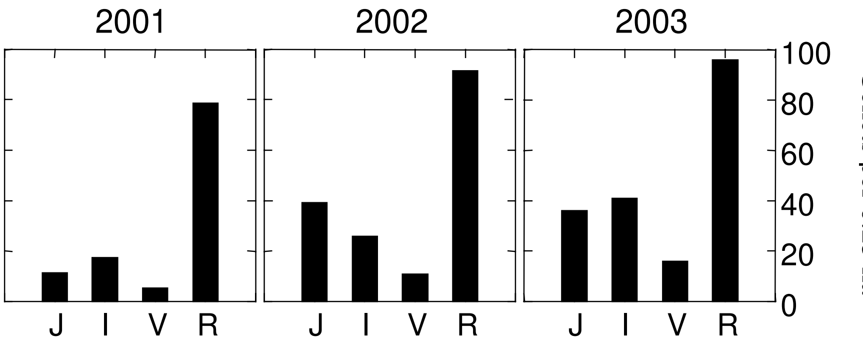


Fig. 2 *Geonoma brevispatha* genet ontogenetic stage structure. J = juveniles, I = immatures, V = virgins, and R = reproducers. The stage of individual genets was classified by the stage of its most mature ramet.

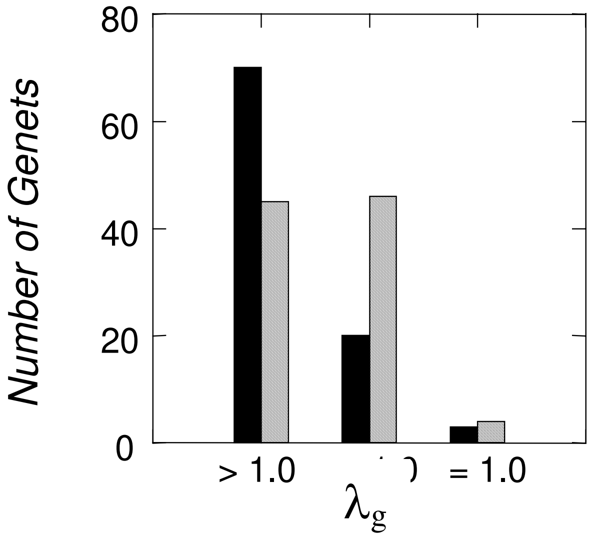


Fig. 3 Distribution of genets across genet-specific ramet population growth rate (λ_g) categories. Genet classification was done according to 95% confidence interval of λ_g. Solid bars = 2001-2002; Hatched bars = 2002-2003.

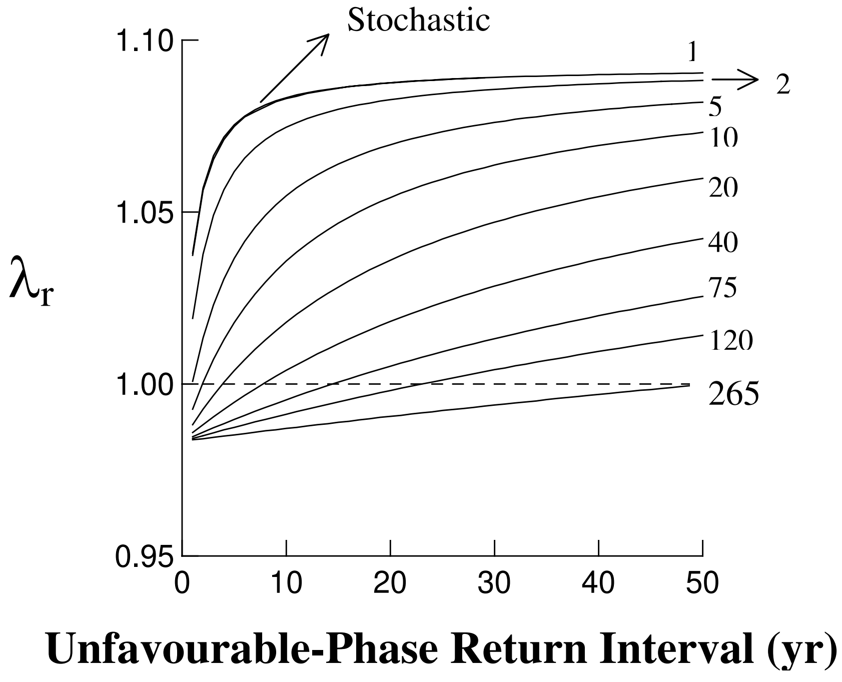


Fig. 4 The effect of unfavourable-phase return interval upon the whole-ramet population growth rate (λ_r), as simulated by the time-invariant and stochastic matrix models. The fixed interval was simulated by maintaining a constant number of favourable years between sequences of unfavourable years. Each line represents a simulation made with a distinct duration of the unfavourable phase (indicated by the numbers at right of each line, in yr). The random interval was simulated by maintaining a fixed probability of occurrence of an unfavourable year, regardless of population history. For the random regime, each λ_r is the λ equivalent of mean population growth rate (ln λ) over 30 runs with 5000 yr each.

CONCLUSÃO GERAL

Como disse na *Introdução Geral*, os quatro trabalhos aqui reunidos abordaram aspectos da ecologia de populações de Geonoma brevispatha visando à detecção de padrões e tendências populacionais. Sendo assim, na maior parte dos casos não pudemos aqui elucidar as causas geradoras dos padrões observados nem prever exatamente em que condições poderão repetir-se no futuro. Porém, através das análises apresentadas e das informações disponíveis na literatura, posso delinear algumas conclusões gerais:

(1) A floresta paludícola de Santa Genebra apresenta grande variação espacial de seus elementos estruturais em microescalas, constituindo um ambiente com baixa previsibiliade.

(2) Em escalas relativamente maiores, há diversos sinais de degradação florestal, que merecem atenção do ponto de vista conservacionista.

(3) Os rametas de *Geonoma brevispatha* passam por quarto estádios ontogenéticos (juvenis de folhas bífidas, imaturos de folhas pinatissectas, imaturos acaulescentes, virgens com estipe e reprodutivos).

(4) A fecundidade clonal precede a sexual, e ambas aumentam continuamente com o tamanho do geneta. Entretanto, aparentemente os dois tipos de reprodução não estão relacionados.

(5) As estratégias de crescimento e sobrevivência de *G. brevispatha* são consistentes com os padrões encontrados para outras espécies clonais. A fecundidade sexual e clonal aprecem ser dois processo integrados

favorecidos pelas condições ambientais que também subsidiam o crescimento dos rametas.

(6) A espécie estudada tem nicho de regeneração restrito a micro-habitats do solo com teor de umidade alto, que ocorrem às margens dos canais e poças que constituem o substrato das florestas paludícolas atlânticas.

(7) A população estudada parece responder favoravelmente as condições ambientais vigentes no fragmento estudado, tendendo a aumentar em abundancia em anos favoráveis. Entretanto, períodos de pluviosidade reduzida e com pressão de predação por macacos-prego aumentada têm potencial para reduzir o crescimento populacional, e ameaçar a persistência da espécie na Reserva de Santa Genebra.

Um dos principais resultados que emergiram deste trabalho dizem respeito às implicações demográficas do hábito clonal de *G. brevispatha*. De maneira geral, esta estratégia de crescimento e consolidação do espaço ocupado parece funcionar como tampão demográfico, amenizando os efeitos negativos de fatores bióticos e abióticos sobre as taxas demográficas (crescimento, sobrevivência e fecundidade). Pela mesma razão, tornou-se mais difícil detectar padrões definidos que relacionem estas taxas às variáveis ambientais medidas.

Sendo assim, uma linha de pesquisa promissora e necessária a ser desenvolvida no futuro da pesquisa das plantas clonais seria a investigação dos mecanismos de integração fisiológica entre os rametas de um mesmo geneta. Conhecer os mecanismos internos de regulação de produção vegetativa de juvenis, sua mortalidade em função das condições enfrentadas pelos rametas reprodutivos e a definição do papel dos rametas em estádios ontogenéticos intermediários entre juvenis e reprodutivos (*i.e.*, imaturos e virgens agem predominantemente como juvenis, sendo abandonados em face a condições adversas, ou tem seu crescimento estimulado nestas circunstâncias?) estão entre as questões gerais que poderiam lançar luz sobre os mecanismos através dos quais a clonalidade aumenta a sobrevivência dos genetas diante das flutuações ambientais.

APÊNDICE

SOUZA, A. F., MARTINS, F. R. e BERNACCI, L.C. 2003. Clonal growth and reproductive strategies of the understory tropical palm *Geonoma brevispatha*: an ontogenetic approach. *Canadian Journal of Botany* 81(2): 101-112.

Clonal growth and reproductive strategies of the understory tropical palm *Geonoma brevispatha*: an ontogenetic approach

Alexandre F. Souza, Fernando R. Martins, and Luis Carlos Bernacci

Abstract: We investigated the patterns of growth and reproduction of the understory clonal palm *Geonoma brevispatha* based on the identification of post-germinative ontogenetic stages, over a 3-year period. Genets were monitored in 100 5 × 5 m plots and 100 2 × 2 m subplots, in a 1-ha area of swamp forest in São Paulo state, southeastern Brazil. Ramets pass through four ontogenetic stages (bifid-leafed juveniles, pinnatifid-leafed stemless immatures, stemmed nonreproductive virgins, and reproducers). Leaf size, leaf number, and leaf production rate increased during ontogeny, but diameter growth rate was higher among immatures. Stem length, number of nodes, and leaf rachis length were positively correlated across ontogenetic stages, but crown height was smaller than stem length in adult palms because of frequent leaning. Leaf number and sexual fecundity increased with ramet size, but declined in larger, senescent ramets. Clonal fecundity preceded sexual fecundity, and sexual and clonal fecundity increased continuously with genet size. No relationship was found between sexual and clonal fecundity. Growth and survival strategies of *G. brevispatha* were consistent with the patterns found in other tropical clonal palm species. Sexual fecundity and cloning seem to be two integrated processes favored by environmental conditions that also support the growth of existing ramets.

Key words: stage-structured populations, ontogenetic stages, swamp forest, Brazil, Atlantic forest, senescence.

Résumé : Les auteurs ont examiné les patrons de croissance et de reproduction du *Geonoma brevispatha,* un palmier de sous bois à croissance clonale, en se basant sur l'identification des étapes ontogénétiques post-germinales, pendant 3 ans. Ils ont suivi les genets dans 100 parcelles de 5 × 5 m et 100 sous-parcelles de 2 × 2 m, sur une surface d'un hectare, dans un marécage forestier de l'état de Sao Paulo, du sud-est du Brésil. Les ramettes passent par quatre stades ontogénétiques (juvéniles à feuilles bifides, immatures sans tige à feuilles pinnatifides, vierges non-reproductifs avec tige, et reproducteurs). La grandeur des feuilles, le nombre de feuilles et le taux de production des feuilles augmentent au cours de l'ontogenèse, mais le taux de croissance en diamètre est plus rapide chez les immatures. La longueur de la tige, le nombre de nœuds et la longueur du rachis foliaire montrent une corrélation positive à travers les stades ontogénétiques, mais la hauteur du houppier est plus petite que la longueur de la tige chez les palmiers adultes, par chute fréquente de feuilles. Le nombre de feuilles et la fécondité sexuelle augmentent avec la dimension des ramettes, mais diminuent chez les ramettes plus grosses et sénescentes. La fécondité clonale précède la fécondité sexuelle, et les fécondités, sexuelle et clonale, augmentent de façon continue avec la dimension du genet. Aucune relation n'a pu être observée entre la fécondité clonale et la fécondité sexuelle. Les stratégies de croissance et de survie du *G. brevispatha* sont congruentes avec les patrons observés chez d'autres espèces de palmiers tropicaux clonaux. La fécondité sexuelle et le clonage semblent être deux processus intégrés favorisés par les conditions environnementales, qui supportent également la croissance des ramettes déjà existantes.

Mots clés : structure de stade des populations, stades ontogénétiques, marécage forestier, Brésil, forêt atlantique, sénescence.

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Introduction

The modular structure of plants makes them especially suited to clonal growth. Indeed, clonal growth is regarded as evolutionarily ancient and is widespread among plant taxa (Mogie and Hutchings 1990; Van Groenendael et al. 1997). In tropical forests, clonal plants are particularly abundant in the understory (Sagers 1993; Richards 1996, Van Groenendael et al. 1997; Kammesheidt 1999). This corresponds to a broader pattern of distribution of clonality, according to which clonal plants are more frequent under wet and resource-poor circumstances (Van Groenendael et al. 1997). The tropical forest understory is regarded as such an environment, receiving only a small fraction (0.5–5%) of the solar radiation incident above the canopy (Chazdon and Pearcy 1991; Richards 1996), but having high air and soil humidity (Brown 1993; Richards 1996).

An understanding of the population biology of tropical clonal species depends on previous knowledge of the ecological consequences of clonal growth. At the individual level, clonal growth is thought to enable plants to forage for resource-rich microsites through a division of labor among ramets, which may become specialized in acquiring different resources (de Kroon and Hutchings 1995; Hutchings and Wijesinghe 1997). Moreover, clonal growth may increase adult persistence through the spread of mortality risk among ramets (Bullock 1980; De Steven 1989; Chazdon 1992). Cloning may also represent a way of escaping biomechanical size constraints and potentially reaching large sizes, thus increasing size-related sexual fecundity (Watkinson 1988). In species with persistent connections among ramets, these advantages seem to be mediated by physiological integration, allowing the redistribution of resources from sites of acquisition to clone parts sited where the same resources are scarce (Chazdon 1991*a*; Silvertown and Lovett-Doust 1993; Hutchings and Wijesinghe 1997).

In tropical forests, the abundance of palms in the community and their simple architectural characteristics have made them a focus of quantitative studies on plant growth and survival strategies (Bullock 1980; Ash 1988; Martínez-Ramos et al. 1988; De Steven 1989; Oyama 1990; Ataroff and Schwarzkopf 1992; Chazdon 1992; Bernal 1998; Mendoza and Franco 1998; Barot and Gignoux 1999; Svenning 2000). Although a full understanding of the role of clonal growth in the maintenance of palm populations in tropical forests is far from complete, a number of generalizations on the size, growth, and reproduction of tropical palms (clonal and nonclonal) have been advanced. These generalizations are tentative, but they provide a general model of the main external macromorphological changes shown by tropical clonal palms during their ontogeny. We investigated whether this model applies to a species occurring in a different habitat (swamp forests) and region (Brazilian Atlantic Forest) from the majority of related studies. We studied the understory palm *Geonoma brevispatha* Barb. Rodr. over a 3-year period.

As the ecological interactions of a species with its environment change markedly with its phase of development (Werner and Gilliam 1984), we adopted the ontogenetic stage approach, according to Gatsuk et al. (1980). These authors advanced a comprehensive classification scheme for the ontogeny of higher plants, which has been used recently to show the spatial and temporal stability of morphometrical characteristics of palm ontogenetic stages in forest fragments (Souza et al. 2000). Gatsuk et al. (1980) divide the ontogeny of plants into pre-reproductive, reproductive, and post-reproductive periods based on the rise and extinction of the reproductive function. The process of formation and development of plant structures, their change and death, and the correlation of these processes in an organism lead to a more detailed division of the ontogenetic sequence in ontogenetic stages (seed, seedling, juvenile, immature, virgin, and others). Each succeeding stage is characterized by the appearance of new structures that were lacking in earlier stages of development, and by the loss of previous ones (Gatsuk et al. 1980).

Specifically, we tested the validity of the following predictions:

1. Leaf size and number increase through ontogeny, as has been showed for many palm species (Tomlinson 1990; Chazdon 1991*b*; Carvalho et al. 1999; Souza et al. 2000). Accordingly, the rates of leaf production, diameter growth, and stem length growth also increase in later ontogenetic stages (Bullock 1980; Piñero et al. 1986; Ash 1988; De Steven 1989; Ataroff and Schwarzkopf 1992).
2. Morphological traits such as stem diameter, stem length, number of nodes, and leaf rachis length are positively correlated across ontogenetic stages (Chazdon 1991*b*). However, in adult palms, crown height is smaller than stem length because of frequent bending or otherwise leaning (Chazdon 1992).
3. At the ramet level, leaf number and sexual fecundity increase with size and then reach a plateau, declining in the oldest stems, which enter a senescence period (Chazdon 1992; Enright 1992; Enright and Watson 1992; Barot and Gignoux 1999).
4. Clonal fecundity precedes sexual fecundity (Bullock 1980; De Steven 1989; Tomlinson 1990; Chazdon 1992; Sun et al. 2001).
5. At the genet level, sexual and clonal fecundity increases continuously with genet size, i.e., the number of large ramets or the size of the largest ramet (Bullock 1980; De Steven 1989; Oyama 1990; Chazdon 1992; Cunningham 1997; Mendoza and Franco 1998; Svenning 2000).
6. Sexual and clonal fecundity are positively correlated at the genet level (De Steven 1989; Lord 1998; Svenning 2000), but are negatively correlated at the ramet level (Svenning 2000).

Materials and methods

Study site and species

The study was conducted at the Santa Genebra municipal reserve (22°44′S, 47°06′W; 670 m a.s.l.), municipality of Campinas, state of São Paulo, southeastern Brazil. Santa Genebra is a 250 ha urban reserve, and its predominant vegetation is classified as semideciduous tropical forest, in a climate with mean annual temperature of 20.6°C and annual precipitation of 1360 mm (Leitão Filho 1995). The study was carried out in a swampy area of ca. 10 ha where the water table never falls far below the soil surface, even in the dry season. *Geonoma brevispatha* (Arecaceae) is a monoecious understory palm with clonal growth. It is restricted to swampy areas at stream edges, gallery forest, or lowland rain forest through central and southeastern South America (Henderson et al. 1995).

Sampling method and data analysis

In March 1993, all ramets of *G. brevispatha* higher than 1 m were numbered and tagged in 100 5 × 5 m plots randomly distributed within 1 ha of the swampy forest. Within each 5 × 5 m plot, one area of 2 × 2 m was demarcated at the northeastern corner. In this area, all ramets of any size of each *G. brevispatha* genet were also numbered and tagged. For each ramet, we measured the diameter at soil level, stem length and height from the ground to midcrown, the number of exposed nodes, the number of leaves, the length of the two newly expanded leaf rachis, and the number of inflorescences and infructescences. Additionally, we recorded the leaf morphology of the most recently expanded leaf of each individual as bifid or pinnate. We recorded the shape of the newly opened leaf because the series of leaf forms that characterize the transition to the adult vegetative stage in palms is highly constant and characteristic for each species (Tomlinson 1990). Dead leaves were not included, and a leaf was considered alive if at least 75% of its blade carried green segments. When adventitious roots were present, we measured the diameter of the first exposed node. For 128 randomly chosen individual ramets, the most recently expanded leaf was marked and the number of new leaves produced was recorded monthly for periods varying from 12 to 22 months. Measurements were repeated in April 1994 and April 2001 (except for leaf rachis length and leaf production), including the new ramets recruited to the population. In 2001, sampling was extended to include ramets of all sizes in the 5 × 5 m plots. In 2001, most tags used in 1993–1994 could not be found, and thus growth estimates are restricted to the 1993–1994 period.

Ontogenetic stages were distinguished according to Gatsuk et al. (1980), and minimum reproductive size was defined as the minimum height at which flowering was observed. The ontogenetic stages were tested for differences in leaf size and number, leaf production rate, stem diameter growth rate, and stem length growth rate (prediction 1) by analysis of variance. Individuals with signs of crown damage, especially meristem predation, were excluded from the analyses involving leaf number, size, or production rate. Variables were checked for normality and $\log_{10}$ or square root transformed when necessary (Zar 1996). Significance of differences between ontogenetic stages was assessed by notched box plots (McGill et al. 1978). Mean growth rates were estimated for each individual on an annual basis through the number of new leaves produced or size difference in each recording period. Values of $\log_{10}$-transformed measures of stem diameter, number of nodes, and leaf rachis length were linear-regressed against stem length to test the allometric patterns expected in prediction 2. Logit regression was used to analyze the relationship between probability of sexual and clonal reproduction and year, taking genet size as a covariate (Steinberg and Colla 2000). These probabilities were simply the proportion of genets in each size category that produced fruits and ramets, respectively. All covariance analyses (for morphometric measures, sexual and clonal fecundity, Sokal and Rholf 1995) were performed with the general linear model (GLM, Wilkinson and Coward 2000) procedure of Systat 10.0 software (SPSS 2000). Finally, the data were tested for correlation between sexual and clonal fecundity at genet level and between the average ramet fecundity and the ratio of small to large ramets (an estimate of clonal fecundity per large ramet, Svenning 2000) by Spearman's coefficient of rank correlation.

Results

Definition of ontogenetic stages

The qualitative observations on the external macromorphological structures allowed the distinction of three prereproductive stages and one reproductive ontogenetic stage (Fig. 1). These four stages were characterized as follows:

Juvenile

Juveniles are stemless palms producing bifid leaves, which are similar to the first expanded leaves or eophylls (sensu Tomlinson 1960) (Fig. 1A). Diameter (0.83 ± 0.60 cm) of outer leaf sheaths is small, but very variable because of the accumulation of basal parts of dead leaves.

Immature

The immature stage is a transitional stage characterized by incomplete segmentation of the leaf blade and an increase in meristematic activity, which leads to the enlargement of stem bases (2.4 ± 1.2 cm) and some vertical growth that exposes the basal sheaths of outer leaves (Fig. 1B). Immature plants are still stemless and may present both entire and transitional leaves.

Virgin

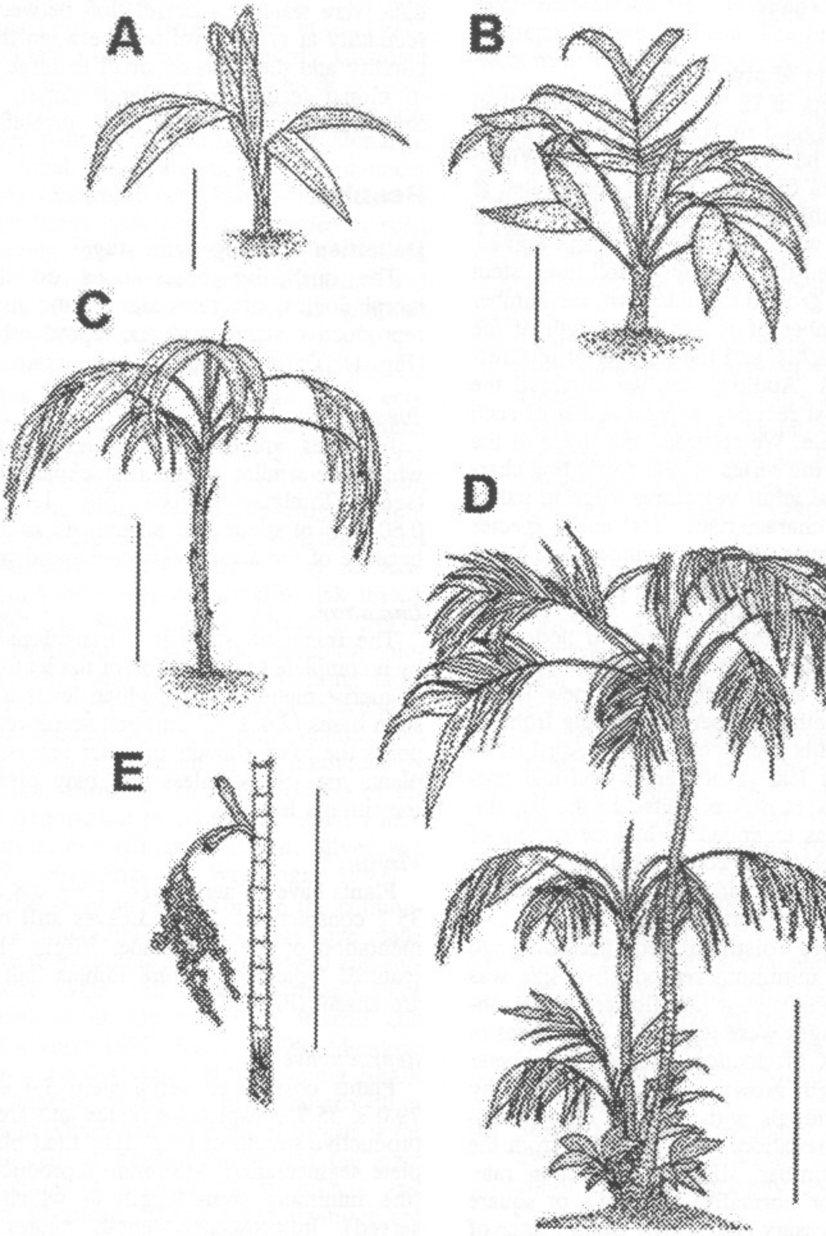
Plants have an aerial stem 3.5 ± 0.8 cm thick with 34.1 ± 35.2 conspicuous nodes. Leaves still have incomplete segmentation of the leaf blade. Virgin plants show the main features typical of mature ramets, but reproductive organs are absent (Fig. 1C).

Reproductive

Plants possess an aerial stem 3.4 ± 0.6 cm thick with 79.0 ± 35.7 conspicuous nodes and are able to produce reproductive structures (Fig. 1D). Leaf blades may show complete segmentation. Minimum reproductive size was 1.10 m (the minimum stem length at which flowering was observed). Inflorescence length ranges from only 2.5 to 65.0 cm (mean = 29.4 ± 16.2 cm, $N = 170$). Infructescences are reddish and bear small (ca. 1 cm diameter) dark blue (blackish) fruits (bacca sensu Spjut 1994, Fig. 1E).

A *G. brevispatha* genet first establishes as a solitary juvenile and grows vertically by adding new leaves to a vertical stem. According to Gatsuk et al. (1980) and Tomlinson (1990), the seedling stage precedes the juvenile stage and is characterized by partial heterotrophic nutrition from seed reserves. In fact, some of the few smaller solitary juvenile ramets we found could still be attached to seed remains, but this could not be checked nondestructively in the field. Thus, we opted for not using the term "seedling" for *G. brevispatha*.

Fig. 1. Ontogenetic stages of *Geonoma brevispatha* ramets. (A) juvenile; (B) immature, with transitional, but still distichous leaves; (C) virgin, with aerial stem and conspicuous nodes; (D) mature genet with a reproductive ramet (tallest plant), a virgin, an immature (lower left) and a number of juveniles (bifid-leafed); (E) mature infructescence. Scale bars = 5 cm for Fig. 1A, 30 cm for Fig. 3B, and 50 cm for Figs. 3C–3E.



A clumped arrangement of ramets is produced because the vegetative ramets develop from basal axillary buds, rooting next to the parent ramet (Tomlinson's architectural model, Hallé et al. 1978). The successive production of new ramets by each daughter ramet results in the tight clump of varying-aged ramets representing a single genet of up to 1.95 m of total clone basal diameter.

Morphometric comparisons between ontogenetic stages

Leaf size and leaf number increased through ontogeny (Fig. 2, Table 1), but the relationship between stage and leaf number varied between years (the interaction between stage and year was significant; Table 1). Leaves are produced one at time, each leaf leaving an exposed node when it is shed at senescence. The monthly leaf production rate (mean ± SD) increased from the juvenile (0.18 ± 0.10) to the immature stage (0.28 ± 0.10), remained stable in virgins (0.31 ± 0.10), and showed a further increase among reproducers (0.39 ± 0.14) (Fig. 2). Diameter growth rate was higher in immature ramets, but stem length growth rate did not show significant differences between stages (Table 1). Considering the 95% confidence interval of the mean stem length growth rate (pooled data from all stages), the largest juvenile would be between 14.7 and 20.4 years old, while the mean juvenile age would be 2.1–3.0 years old. Accordingly, the age at first reproduction (110 cm length) would be between 11.2 and

Fig. 2. Box-plots of size and growth characteristics for ontogenetic stages of *Geonoma brevispatha* ramets. In each graph, each box comprises 50% of data. Boxes are notched (narrowed) at the median and return to full width at the lower and upper 95% confidence interval values. Inner and outer fences are defined by interquartile ranges. Asterisks and circles are outliers. When confidence intervals do not overlap, the median of the stages are different (McGill et al. 1978). J, juvenile; I, immature; V, virgin; R, reproductive.

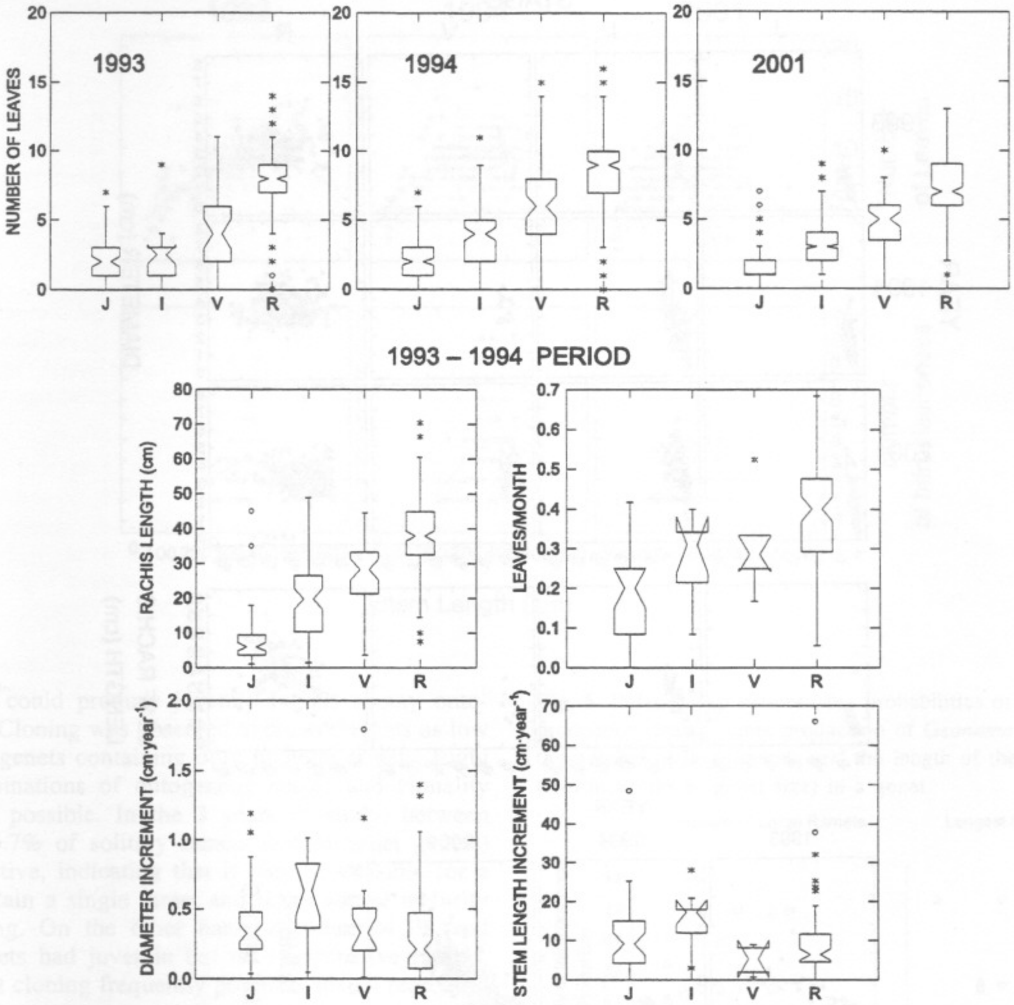


Table 1. Analysis of variance for the effects of ontogenetic stage and year on the number of leaves, leaf rachis length, leaf production rate, and diameter and stem length growth rates of *Geonoma brevispatha* ramets.

Source	df	F	P
Number of leaves*			
Stage	3	710.368	<0.0001‡
Year	2	16.761	<0.0001‡
Stage × year	6	4.626	<0.0001‡
Leaf rachis length†			
Stage	3	208.678	<0.0001‡
Leaves per year			
Stage	3	18.545	<0.0001‡
Diameter growth rate			
Stage	3	4.187	0.007‡
Stem length growth rate			
Stage	3	1.503	0.218

*Square-root-transformed variable.
†Log_{10}-transformed variable.
‡Significant effects.

15.5 years, and the oldest ramet (length = 530 cm) would be between 53.7 and 74.5 years old. Note that this is also the age estimate of the oldest genet in the population.

Ramet diameter, number of nodes, and leaf rachis length tended to increase linearly with stem length (Fig. 3). The relationship between ramet diameter and stem length was linear until the reproductive stage, when no clear relation between the variables could be found (Fig. 3). The slope of the regression line representing this relation was different between ontogenetic stages (Table 2). A significant interaction between stage, stem length, and year indicates that small differences in diameter and stem length from one year to another are sufficient to affect the slope of the regression line in each stage. The slope of the regression line between leaf rachis length and stem length was also different between stages (ANCOVA, between slopes: $F = 2.636$, df = 3, $P = 0.050$). The slope of the regression line between the number of exposed nodes and stem length (stemless ramets not considered) differed between years (between slopes: $F = 26.187$, df = 2, $P < 0.0001$). In 2001, 34.4% of ramets with exposed nodes were bent or otherwise leaning. Thus, for virgin and

Fig. 3. The relationship between ramet stem diameter, leaf rachis length, and number of exposed nodes and stem length of *Geonoma brevispatha* at different ontogenetic stages in 3 years. J, juvenile; I, immature; V, virgin; R, reproductive.

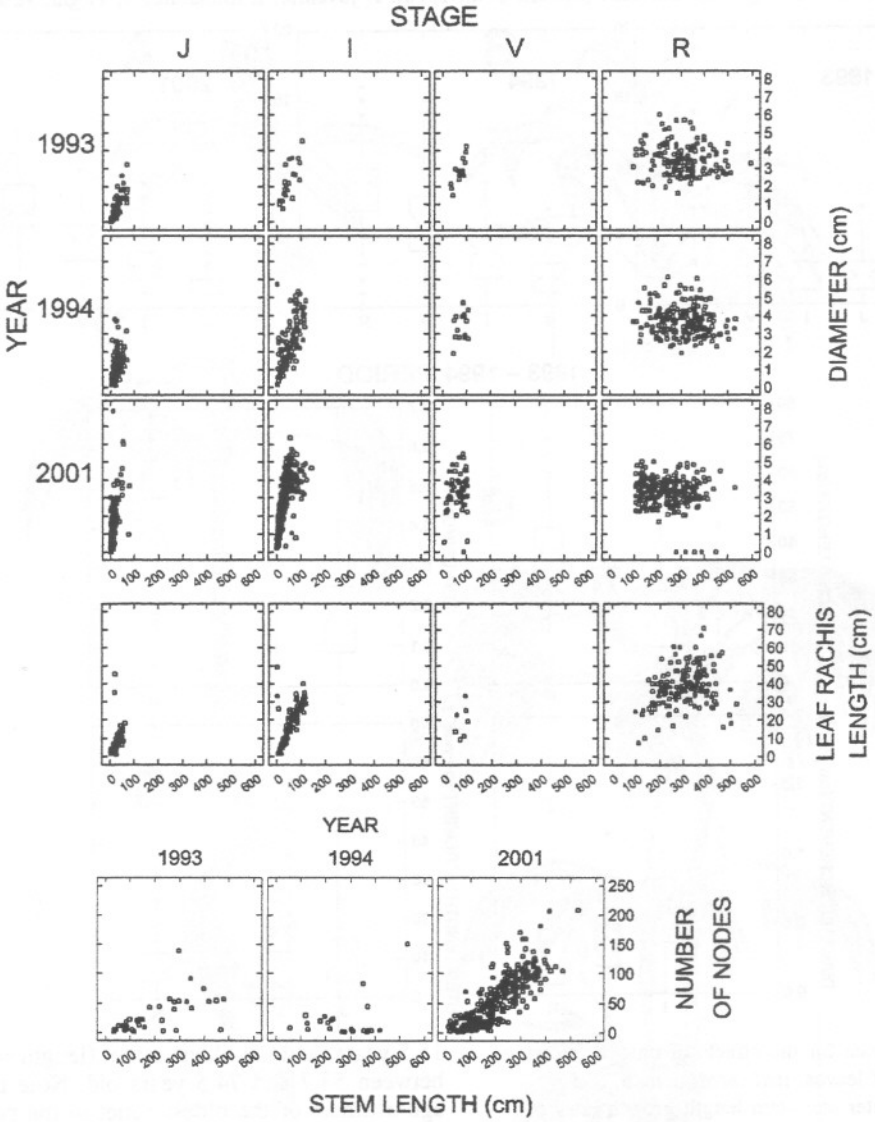


Table 2. Covariance analysis of *Geonoma brevispatha* ramet stem diameter (dependent variable) as a function of ontogenetic stage, stem length, and year and their interactions.

Source	df	*F*	*P*
Stage	3	6.680	<0.0001*
Stem length	1	1.379	0.240
Year	1	5.307	0.021*
Stage × year	3	6.685	<0.0001*
Stage × stem length	3	6.804	<0.0001*
Stem length × year	1	1.328	0.249
Stage × stem length × year	3	6.865	<0.0001*

Note: Logarithm of stem length and diameter was used.
*Significant effects.

reproductive ramets (pooled data) crown height was smaller than stem length (t = 3.269, df = 607.853, $P < 0.002$).

The number of leaves and the number of infructescences were not constant in ramets with different aerial stem lengths (Fig. 4). Both variables increased with stem length until intermediate values, suffering a decline in the longer, older ramets. This parabolic relationship was marked by high variance and a constant shape in time for each variable (between slopes: F = 1.15, df = 2, P = 0.318 for the number of leaves, and F = 0.89, df = 2, P = 0.412 for the number of infructescences), but changed in magnitude between years (between intercepts: F = 11.701, df = 2, $P < 0.0001$ for the number of leaves, and F = 7.196, df = 2, P = 0.001 for the number of infructescences).

Clonal fecundity generally preceded sexual fecundity. However, the timing of occurrence of clonal fecundity in the maturation process of *G. brevispatha* was flexible, and indi-

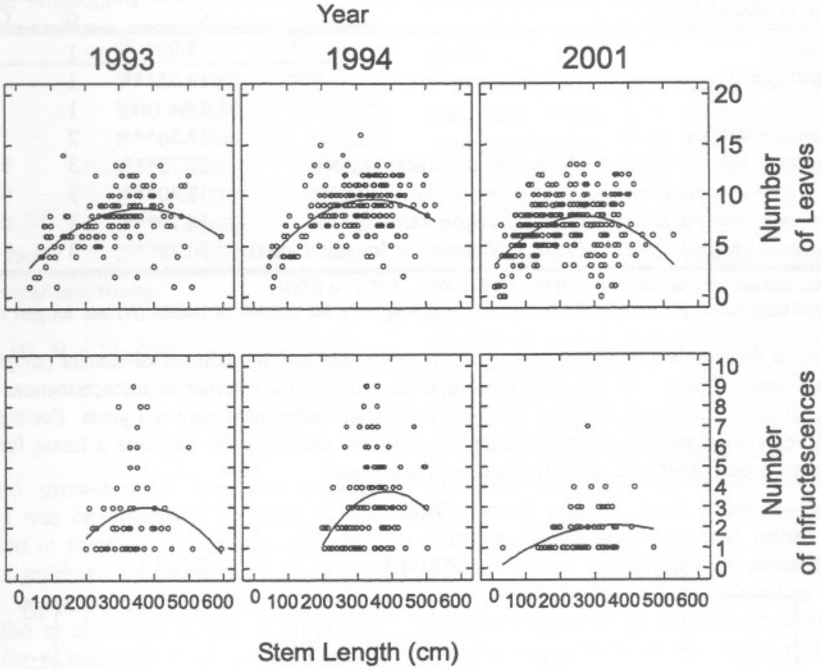


Fig. 4. The relationship between the number of leaves and the number of infructescences and stem length of *Geonoma brevispatha* in 3 years. The solid line represents the quadratic regression curve.

vidual ramets could produce juvenile ramets at any ontogenetic stage. Cloning was observed at crown heights as low as 7.0 cm, in genets containing only juvenile ramets. Eight possible combinations of ontogenetic stages and clonality state are thus possible. In the 3 years of study, between 13.3% and 16.7% of solitary ramets (single-ramet genets) were reproductive, indicating that it may be possible for a genet to maintain a single ramet and reach sexual maturity without cloning. On the other hand, between 24.3% and 36.4% of genets had juvenile but no reproductive ramets, suggesting that cloning frequently precedes sexual reproduction.

At the genet level, the probability of infructescence production increased linearly with the length of the largest ramet as well as with the number of large ramets, i.e., ramets with an aerial stem (Fig. 5, Table 3). Neither year alone nor the interactions between year, ramet length, and ramet number were significant. The number of infructescences produced per genet was also positively related to both the length of the largest ramet and the number of large ramets, with no significant changes between years (Fig. 6, Table 4). Logit regression of the probability of ramet production versus genet size in 3 years showed a pattern similar to that found for sexual fecundity. The chance of producing new ramets increased with both the number of large ramets and the length of the largest ramet, but the magnitude of this relationship differed between years (Fig. 5, Table 5). The interactions between the two measures of genet size and year were not significant. The number of juvenile ramets per genet, however, was positively related to the number of large ramets in a genet but not to the length of the largest ramet (Fig. 6, Table 6).

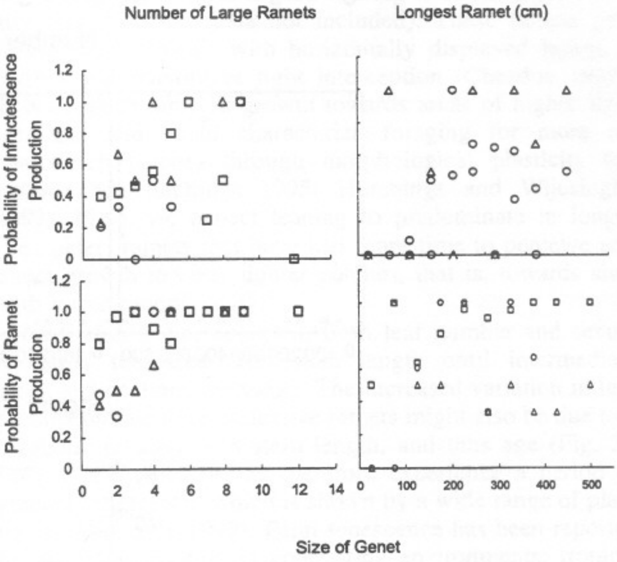


Fig. 5. Relationship between the probabilities of infructescence production and of ramet production of *Geonoma brevispatha* and the number of large ramets and the length of the largest ramet (two measures of genet size) in a genet.

Sexual and clonal fecundity were not correlated at the genet level (1993: $r_s = 0.135$, $P < 0.50$, $N = 30$; 1994: $r_s = 0.031$, $P > 0.50$, $N = 31$; 2001: $r_s = 0.077$, $P < 0.50$, $N = 125$). Similarly, the average sexual fecundity of large ramets and the ratio of small to large ramets were not correlated in any one year of study (1993: $r_s = 0.244$, $P < 0.20$, $N = 30$;

Table 3. Logit regression (G) between the probability of fruit production and genet size of *Geonoma brevispatha* in a swamp forest in southeastern Brazil in a 3-year period.

Terms in model	G	df	$G^{\dagger}$	df
N ramets	5.99*	1		
Longest ramet	17.35***	1		
Year	1.84 (ns)	1		
N ramets + longest ramet	17.36***	2		
N ramets + longest ramet + (N ramets × longest ramet)	20.73***	3	3.37	1
N ramets + longest ramet + (year × N ramets)	17.40***	3	0.02	1
N ramets + longest ramet + (year × longest ramet)	18.10***	3	0.37	1
N ramets + longest ramet + (year × N ramets × longest ramet)	20.75***	3	3.39	1

Note: ns, not significant. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

[†] Likelihood-ratio test relative to the model containing only the number of ramets (N) and longest ramet.

Fig. 6. Relationship between the number of infructescences and genet size and the number of ramets per genet and genet size of *Geonoma brevispatha* in 3 years. The model that best described the data for the number of infructescences was a linear function with significant effects of two different measures of genet size and significant differences between years. For the number of juvenile ramets per genet, data for the 3 years were pooled, because the model that best describes the data was a linear function with significant effect of the number of large ramets per genet and no difference between years.

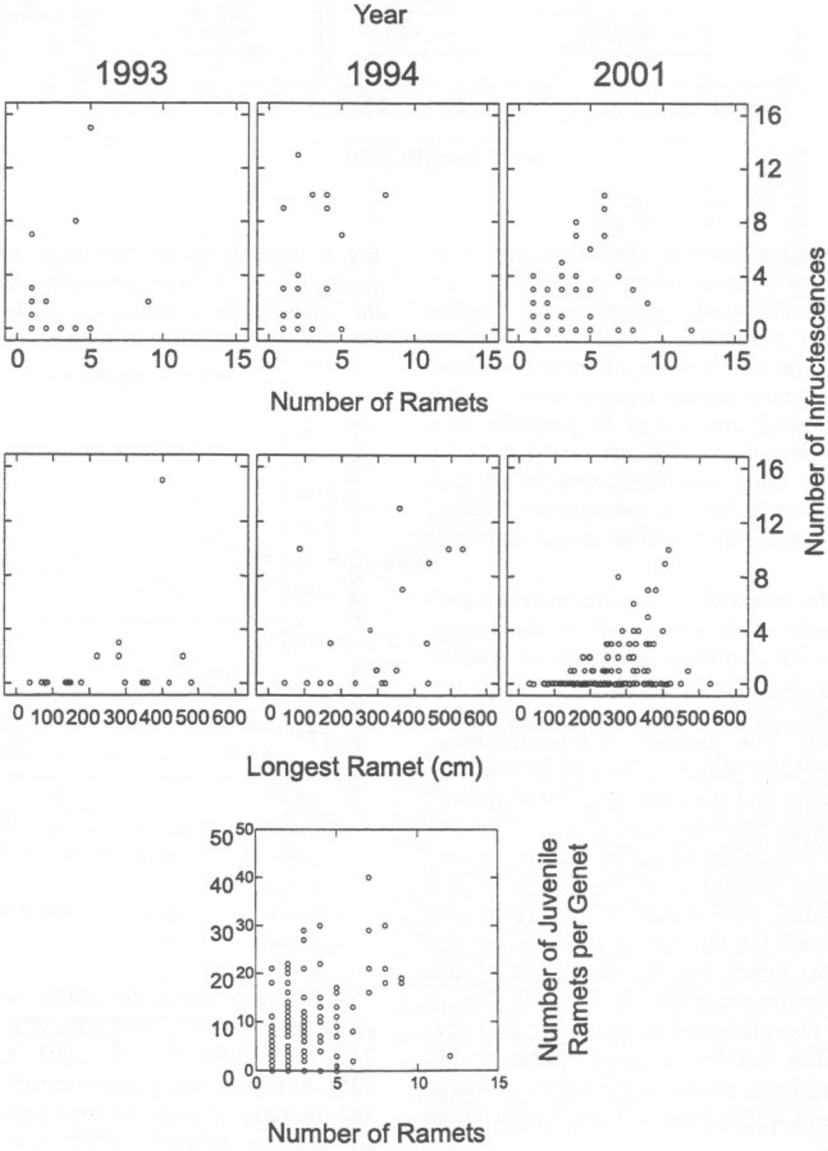


Table 4. Covariance analysis of *Geonoma brevispatha* infructescence production (dependent variable) as a function of genet size and year and their interactions.

Terms in Model	df	F	P
Year	2	0.252	778
N ramets	1	3.850	0.052*
Longest ramet	1	5.436	0.021*
Year × N ramets	2	0.831	0.438
Year × longest ramet	2	0.323	0.724
Longest ramet × N ramets	1	0.488	0.486
Year × N ramets × longest ramet	2	0.005	0.995

*Significant and marginally significant effects.

1994: $r_s = -0.312$, $P < 0.10$, $N = 31$; 2001: $r_s = -0.008$, $P > 0.50$, $N = 125$).

Discussion

Prediction 1 (size and growth rates increase through *G. brevispatha* ontogeny) was confirmed in relation to leaf characteristics, but rejected in relation to diameter and stem length growth rates. The increase in crown and stem size through ontogeny is a common phenomenon in palms (Tomlinson 1990; Carvalho et al. 1999; Souza et al. 2000), and has been recorded for a number of *Geonoma* species (Chazdon 1991*b*). Increased diameter growth of the immature ramets, however, may correspond to the morphometric changes that take place during the establishment period of palm ontogeny (Tomlinson 1990). In this period, there is a gradual expansion of the palm axis below ground, accompanied by transition of leaf morphology to the characteristic form of the adult vegetative stage (Tomlinson 1990). The transition from bifid to pinnatifid leaf morphology and stem base thickening shown by immature *G. brevispatha* ramets seem to provide biomechanical support to continuing stem length increase (Tomlinson 1990). Lugo and Batlle (1987) also reported higher diameter growth rate in young individuals of the arboreal palm *Prestoea montana*.

Prediction 2 was confirmed. Along with the confirmation of prediction 1 for leaf traits, prediction 2 fits well for the general development of *Geonoma* (Chazdon 1991*b*): crown development occurs gradually during ontogeny; increase in the number of leaves in the crown is accompanied by increase in leaf size, leaf production rate, and primary thickening of the stem. The relationship between the number of nodes and stem length (Fig. 3) arises from the direct relationship between stem length growth and leaf production, since each leaf produces one internode. Stem length growth, however, was constant along the ontogeny and similar to the height growth of the understory palm *Chamaedorea tepejilote* (Oyama 1990). Although the extent of physiological integration among ramets within a genet was not investigated here, the constant stem length growth of ramets is consistent with the hypothesis that growth of small ramets may be sustained by the translocation of resources from larger ramets of the same genet (Caraco and Kelly 1991; Chazdon 1992; Silvertown and Lovett-Doust 1993; Hutchings and Wijesinghe 1997). This view is also supported by the fact that most species with permanent connections between ramets show physiological integration (Silvertown and Lovett-Doust 1993). Physiological integration would support growth and survival of the deeply shaded juvenile ramets of tropical palms, which do not receive enough light intensity for daily carbon balance (Chazdon 1986).

Geonoma brevispatha produces relatively large leaves at low rates, which is a characteristic of tropical understory species (Bentley 1979; Ash 1988; De Steven 1989; Oyama 1990; Chazdon 1992; Ataroff and Schwarzkopf 1992) and young individuals of tall palm species (e.g., Carvalho et al. 1999). Mathematical models related to water-use efficiency predict that large leaves should be selected for in warm environments with low radiation such as tropical forest understories (Parkhurst and Loucks 1972). Increased leaf production rate in later ontogenetic stages has been observed in other palm species (Piñero et al. 1986; De Steven et al. 1987; Ash 1988; De Steven 1989; Ataroff and Schwarzkopf 1992). Increased leaf production but constant stem length growth rate with ontogenetic stage in *G. brevispatha* implies that internode length shortens in later stages. This indicates that small ramets invest most resources in vertical growth through internode elongation rather than through leaf production. Since light levels increase significantly with height in tropical understories (Chazdon 1986) and the translocation of resources from large ramets to small ramets may reduce the growth of the large ramets (Caraco and Kelly 1991), this strategy seems to reduce the time taken for new ramets to become independent of large ones.

A few ramets of *G. brevispatha* were felled by fallen trees but were still alive, with turned stem apex. This is a common characteristic of understory palms (Martínez-Ramos et al. 1988; Watkinson 1988; Chazdon 1992). However, most non-erect ramets were, in fact, leaning to some degree, usually less than 45° (data not included). These ramets possessed erect crowns, with horizontally displayed leaves, a pattern that maximizes light interception (Chazdon 1985). This suggests directed growth towards areas of higher light intensity, and could characterize foraging for more resource-rich patches through morphological plasticity (de Kroon and Hutchings 1995; Hutchings and Wijesinghe 1997). If so, we expect leaning to predominate in longer (i.e., older) ramets that have had more time to perceive and direct growth towards lighter patches, that is, towards sites with lower canopy cover.

Prediction 3 was accepted. Both leaf number and sexual fecundity increased with stem length until intermediate sizes, and declined thereafter. The increased variation in leaf production rate in reproductive ramets might also be due to a parabolic relation with stem length, and thus age (Fig. 2). Longer and older ramets therefore experience a period of gradual senescence, which is shown by a wide range of plant types (Watkinson 1992). Palm senescence has been reported for species occurring in contrasting environments: tropical savanna (Barot and Gignoux 1999), New Zealand temperate forest (Enright 1992; Enright and Watson 1992), and understory tropical forest (a *Geonoma* species; Chazdon 1992). Our results agree with the hypothesis that the fecundity of trees with a single apical meristem, such as palms, is restricted by the number of leaves these plants can produce (Watkinson and White 1986; Watkinson 1988). However, our data and the results of Barot and Gignoux (1999) also

Table 5. Logit regression (*G*) between the probability of ramet production and genet size of *Geonoma brevispatha* in a swamp forest in southeastern Brazil in a 3-year period.

Terms in Model	*G*	df	*G*[†]	df
N ramets	17.38***	1		
Longest ramet	7.47**	1		
Year	25.56***	1		
N ramets + longest ramet + year	40.45***	3		
N ramets + longest ramet + year + (*N* ramets × year)	40.85***	4	0.40	1
N ramets + longest ramet + year + (longest ramet × year)	41.50***	4	1.05	1
N ramets + longest ramet + year + (*N* ramets × longest ramet)	41.94***	4	1.49	1
N ramets + longest ramet + year + (year × *N* ramets × longest ramet)	41.95***	4	1.50	1

** $P < 0.01$, *** $P < 0.001$.

[†] Likelihood-ratio test relative to the model with no interactions.

Table 6. Covariance analysis of *Geonoma brevispatha* ramet production (dependent variable) as a function of genet size and year and their interactions.

Terms in Model	df	*F*	*P*
Year	2	0.357	0.700
N ramets	1	7.676	0.006*
Longest ramet	1	0.470	0.494
Year × *N* ramets	2	0.440	0.645
Year × longest ramet	2	2.382	0.096
Longest ramet × *N* ramets	1	1.361	0.245
Year × *N* ramets × Longest ramet	2	0.983	0.376

*Significant effects.

contradict the view that leaf number of palms remains constant as size increases (Watkinson 1988). Senescence signs, such as reduced fecundity, may result from increasing burden of respiratory tissue and vascular transport problems as the plant gets taller (Watkinson 1988). It is worth noting, however, that no sign of reduced fecundity was found in larger genets (Fig. 6). This agrees with the notion that clonal plants would have negligible or very gradual senescence, despite the senescence, death, and decay of individual constituent ramets (Watkinson and White 1986; Watkinson 1992).

Prediction 4 was accepted as a general tendency instead of a fixed rule. Most genets had juvenile ramets sprouting from basal vegetative buds, regardless of the ontogenetic stage of the largest ramet in a genet. That clonal fecundity precedes sexual fecundity is a common finding in tropical palms (Bullock 1980; De Steven 1989; Chazdon 1992) and other clonal plants (e.g., Sun et al. 2001), and has been considered a feature of the early establishment phase of clonal palms (Tomlinson 1990). The solitary ramets in the reproductive stage we found may have not skipped ramet formation, but may represent individuals that survived past disturbance, which rarely kill whole genets (De Steven 1989; Chazdon 1992; Silvertown and Lovett-Doust 1993), or genets occupying resource-poor sites, a situation in which large ramets are predicted to abandon (i.e., stop sharing resources with) small ramets (Caraco and Kelly 1991). Cloning before producing large ramets also increases the probability of survival of a genet (De Steven 1989), since long and slender-stemmed palms show high mechanical instability (Chazdon 1991*b*, 1992; Svenning 2000). Thus, our results for *G. brevispatha* agree with the hypothesis that resources are preferentially and simultaneously allocated to developing a storage system and to vegetative growth during the first stages of the life cycle (Cheplick 1995; Mendoza and Franco 1998). Once a critical size or physiological state is reached, then the genet would start flowering, as denoted by the dependency of reproductive probability on genet size.

This idea is reinforced by prediction 5, which was confirmed. Both sexual and asexual fecundity increased continuously with the number of large ramets and the size of the largest ramet in a genet. According to Svenning (2000), size-dependency in sexual fecundity is the rule in palms, and has been found in a number of clonal and solitary species (Bullock 1980; De Steven 1989; Oyama 1990; Chazdon 1992; Cunningham 1997; Mendoza and Franco 1998; Svenning 2000). Size-dependency in clonal reproduction, however, has been found in some clonal palms (Bullock 1980; De Steven 1989; Chazdon 1992; Svenning 2000), but not in others (Mendoza and Franco 1998). That both the number of large ramets and the length of the largest ramet are important determinants of the number of infructescences a genet produces indicates that large genets forage resources more efficiently in space both in the vertical (lengthy ramets access lighter forest strata, Chazdon 1986) and in the horizontal (many large ramets have higher chances of intercepting sunflecks)(de Kroon and Hutchings 1995; Hutchings and Wijesinghe 1997).

Prediction 6, that sexual and clonal fecundity are positively correlated at the genet level, but are negatively correlated at the ramet level (Svenning 2000) was rejected. Instead, sexual and clonal fecundities were not related. Until recently, a trade-off between the two modes of reproduction was expected in understory palms, since it has been found in other clonal plants (Silvertown and Lovett-Doust 1993; Sun et al. 2001), and because reproduction may reduce stored carbohydrates (Cunningham 1997; but see Cheplick 1995). However, our results agree with recent evidence for clonal palms (De Steven 1989; Mendoza and Franco 1998; Svenning 2000) and for *Festuca novaezelandiae* (Lord 1998), that the resource costs of reproduction are not high enough to result in a trade-off between the two modes of reproduction in understory palms (Svenning 2000).

Our results agree with the idea that cloning in tropical forest palms is a strategy directed to growth and persistence, rather than propagation (space consolidation strategy, sensu Van Groenendael et al. 1997; Bullock 1980; De Steven 1989; Chazdon 1992; Mendoza and Franco 1998; Svenning 2000). Sexual fecundity and cloning would not be antagonistic processes (Mendoza and Franco 1998). Instead, both would be favored by environmental conditions that also support the growth of existing ramets (De Steven 1989). Through cloning, these species also escape the limitation that a single apical meristem poses to reproduction (i.e., senescence), and achieve a continuous increase in sexual fecundity and vegetative growth with size and age, as found in branching plants with many meristems (Watkinson and White 1986; Franco and Silvertown 1996; Mendoza and Franco 1998).

Geonoma brevispatha occupies swampy and light-restricted tropical forest understories of central and southeastern South America, a combination of habitat type and geographical location that is poorly studied. The consistency of *G. brevispatha* growth and survival strategies with the patterns found in other clonal palms species confirms that the basic rules of clonal palm growth are becoming clear, and the functional relationships underlying such patterns must receive increasing attention in the future (Van Groenendael et al. 1997).

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