UNIVERSIDADE ESTADUAL DE CAMPINAS

INSTITUTO DE BIOLOGIA

LIGIA PAULILLO SIMS

"Aspectos da história de vida da espécie de dossel *Savia dictyocarpa* Müll. Arg. (Phyllanthaceae) em um fragmento da Floresta Estacional Semidecídua no município de Campinas, SP"

Este exemplar corresponde à redação final
da tese defendida pelo(a) candidato (a)
LIGIA PAULILLO SIMS
e aprovada pela Comissão Julgadora.

Fernando R. Martins
04/08/2009

Dissertação apresentada ao Instituto de Biologia da Universidade Estadual de Campinas para obtenção do título de Mestre em Ecologia.

Orientador: Prof. Dr. Fernando Roberto Martins

Campinas, 2009

FICHA CATALOGRÁFICA ELABORADA PELA
BIBLIOTECA DO INSTITUTO DE BIOLOGIA – UNICAMP

Sims, Ligia Paulillo
Si58a Aspectos da história de vida da espécie de dossel *Savia dictyocarpa* Müll. Arg. (Phyllanthaceae) em um fragmento de floresta estacional semidecídua no município de Campinas, SP / Ligia Paulillo Sims. – Campinas, SP: [s.n.], 2009.

Orientador: Fernando Roberto Martins.
Dissertação (mestrado) – Universidade Estadual de Campinas, Instituto de Biologia.

1. Ontogenia. 2. Alometria. 3. Padrão espacial. I. Martins, Fernando Roberto, 1949-. II. Universidade Estadual de Campinas. Instituto de Biologia. III. Título.

Título em inglês: Life story aspects of the canopy species *Savia dictyocarpa* Müll. Arg. (Phyllanthaceae) in a seasonal semideciduous forest in Campinas municipallity, SP.
Palavras-chave em inglês: Ontogeny; Allometry; Spatial pattern.
Área de concentração: Ecologia.
Titulação: Mestre em Ecologia.
Banca examinadora: Fernando Roberto Martins, Kikyo Yamamoto, Tereza Cristina Souza Sposito.
Data da defesa: 04/08/2009.
Programa de Pós-Graduação: Ecologia.

Campinas, 04 de agosto de 2009

BANCA EXAMINADORA

Prof. Dr. Fernando Roberto Martins (Orientador)

Fernando R. Martins

Assinatura

Profa. Dra. Kikyo Yamamoto

K Yamamoto

Assinatura

Profa. Dra. Tereza Cristina Souza Sposito

Tereza Cristina Sposito

Assinatura

Prof. Dr. Flavio Antonio Mães dos Santos (Suplente)

Assinatura

Prof. Dr. Dalva da Silva Matos (Suplente)

Assinatura

Dedico

A quem lutou por uma vida melhor para
seus filhos e netos e que colherá esses
frutos por muitas gerações.
À minha avó, Celina Godoy Paulillo.

Agradecimentos

Principalmente à minha família (mãe, pai, irmãos, avós, tios e primos) que SEMPRE me apoiou e ajudou em todos os momentos de minha vida acadêmica e pessoal. Obrigado pela motivação, pelo amor e também pelo suporte financeiro (que foi essencial). Á vocês, Márcia (mammy), Amauri (pai), Luciana (irmãzinha), Luiz Fernando (irmão rebelde) e Celina (vovózinha do meu coração), eu devo mais do que imaginam.

Ao meu companheiro, amigo, confidente, Luiz, eu agradeço pelas horas e horas de conversas, pela ajuda com as figuras e fotos, por compreender a distância, por todo o carinho e por me dar conselhos que só uma pessoa sensata e consciente como você poderia dar. Eu te amo.

À família Aquino Dias, que sempre me motivou e torceu por mim.

Agradeço ao professor Fernando Roberto Martins, que me deu a oportunidade de integrar uma das melhores instituições de ensino do Brasil e que em todos os momentos me indicou o melhor caminho e ensinou uma nova maneira de pensar um problema, de levantar uma hipótese e de saber o que buscar. Muito obrigado.

Às pessoas que com muita dedicação, entusiasmo e bom humor me acompanharam ao campo e me ajudaram muito: Sandro Muniz (você foi essencial), Juliano van Melis, Fabíola Merendoni, Leandro Vieira, Júlia Sfair, Chaiene Lopes, Seu Valdivino, Nino Amazonas, Pedro Michelutti, Letícia Garcia, Arildo Dias, Vanessa Rosseto e a meus irmãos Fer e Lú - que muito bravamente enfrentaram seus medos e suaram comigo no campo. Os lanchinhos, as risadas, as descobertas e também os sustos foram momentos que adorei passar ao lado de vocês.

Devo um agradecimento especial ao Luciano Pereira que me ajudou na ‘caça a sementes de *Savia dictyocarpa*’, apesar de não ter sido bem sucedida. Ainda encontraremos!

Aos professores da Ecologia e Biologia Vegetal, que me ensinaram em disciplinas, bancas de qualificação e pelos corredores, e que acabaram

colaborando muito para minha formação: Flavio A. M. dos Santos, Eleonore Z. F. Setz, Marlies Sazima, Rafael S. Oliveira, Thomas M. Lewinsohn, Woodruff W. Benson, Arício X. Linhares, Paulo Inácio K. L. de Prado, José R. Trigo, Jorge Tamashiro, George Sheperd, Carlos Joly e Kikyo Yamamoto.

A todos os companheiros de disciplinas, de laboratório, de Cafés Ecológicos e de Biofórum: Fabíola, Cris, Xiris, Arildão, Pequeno, Bruno Aranha, Bruno Rosado, Carol Virillo, Carol Scultori, Carina, Érico, Mari Cruz, Pedro Cavalin, Pedro Eisenlohr, Júlia, Vivi, Nívea, Leandro, Léo Meirelles, Maíra, Larissão, Larissinha, Giseli, Helô, Ana Paula, Maíra, Felipe, Rafael, Letícia & Daniel, André, Cátia, Valéria, Maurício, Gabi, Déia, Camila, Claudinha, Léo, Ricardo, Tiago Aranha, Tiago Egídio, Antônio, Sandro Von Matter e Sandro Muniz. Vocês fizeram meus dias mais felizes e me ensinaram muito. Obrigado!

Em especial, agradeço ao Rafa, Xiris, Leandro e Arildo pela ajuda com programas estatísticos e análises. Ao Fer pela ajuda com as fotos hemisféricas.

À todos amigos que ficaram em Araraquara, torcendo pelo meu sucesso: Graziela & Lú, Tassi, Veri & Valmir, Aline Vidal, André e a galera, Carolzinha, Ana Racco, Melina, Lérida & Rô, Flavinha & Dú, Doug & Lê, Diego & Sú e Gica.

À Unicamp pela ótima infra-estrutura que fornece a seus alunos de graduação e pós-graduação.

Aos funcionários do IB, em especial à Célia que prontamente sempre esclareceu minhas dúvidas e aos motoristas, Joaquim e Carlinhos que nas inúmeras viagens à Mata Ribeirão Cachoeira foram uma ótima companhia e sempre deram um jeitinho de me levar.

Á administração do Condomínio Colinas do Atibaia, que permitiu a execução do trabalho de campo dentro de sua área.

Á FAPESP e a Fundação MB pelas bolsas concedidas.

Á FAEPEX pelo financiamento do trabalho de campo.

Índice

Capítulo 1: Life history of a tropical canopy tree species: ontogenetic stages, architectural analysis, allometric relationships and mechanical design.

Capítulo 2: Soil nutrients, light, and the spatial distribution of a tropical canopy tree

Resumo Geral

O presente estudo investigou a estrutura de estádios ontogenéticos e espacial da espécie *Savia dictyocarpa* (Phyllanthaceae) na Mata Ribeirão Cachoeira, Campinas, SP. Essa espécie dióica é comum ocupante do dossel de florestas estacionais da região sudeste do Brasil e dada sua importância resolveu-se levantar informações sobre sua história de vida. Para tanto foram feitas duas questões centrais: 1) é possível definir os estádios ontogenéticos de *S. dictyocarpa* a partir da variação morfométrica e arquitetural que ocorre longo da vida da espécie? 2) qual distribuição espacial dos indivíduos ao longo da ontogenia dessa espécie e quais os fatores ambientais que influem na distribuição? Nos 0,5 hectares amostrados encontramos 194 indivíduos distribuídos em 5 estádios ontogenéticos: infantil, jovem, imaturo, adulto e senil. Não encontramos plântulas ou adultos reprodutivos nas parcelas, mas encontramos algumas plântulas. Portanto a definição do estádio plântula foi feita sem considerações sobre caracteres morfométricos. Os frutos encontrados não possuíam sementes, o que pode ser indicativo de ausência de polinização de flores, seja pela baixa freqüência de indivíduos masculinos ou pela ausência de polinizador. O padrão de ramificação apresentado é próprio do modelo arquitetural de Massart, que é característico de espécies bem adaptadas às condições de pouca luz. Os estádios apresentaram diferenças significativas quanto à altura e diâmetro. Jovem e imaturo apresentaram menor aumento em diâmetro por incremento em altura, ocorrendo o inverso com o estádio adulto. O maior investimento em altura durante os estádios iniciais permite que os indivíduos alcancem rapidamente as boas condições de luminosidade próximas ao dossel, em detrimento da estabilidade mecânica. Encontramos que o investimento em altura da copa por unidade de aumento em diâmetro da copa tem tendência de aumentar ao longo da ontogenia, o que denota diferenciação entre estádios para aumento da eficiência na obtenção de luz. A infestação de lianas parece ter efeito sobre desenvolvimento da copa dos indivíduos adultos, pois indivíduos com lianas têm menor investimento em altura da copa. Todos os estádios apresentaram distribuição aleatória no espaço, sendo que imaturo e jovem possuem tendência de ocupar mesmos locais, possivelmente por necessitarem das mesmas condições ambientais para recrutamento e crescimento. Todas as correlações entre estádios e luz, solo e interferência interespecífica foram espúrias e/ou não significantes. É possível que o padrão aleatório possa ser explicado por características ambientais não consideradas nesse estudo ou por processos estocásticos. A distribuição da espécie pode também ser fortemente afetada pela distribuição de sementes, plântulas e infantes, que inexistiam na área amostrada. Os resultados encontrados sugerem que há variações nas estratégias de ocupação do ambiente e de uso dos recursos ao longo da vida de uma espécie de dossel, no entanto as características ambientais amostradas não foram capazes de explicar como esses caracteres determinam os padrões de recrutamento.

Palavras-chave: Ontogenia, Alometria, Padrão Espacial.

Abstract

The present study investigated the ontogenetic and spatial structure of the tree species *Savia dictyocarpa* (Phyllanthaceae) in the Mata Ribeirão Cachoeira, Campinas municipality, SP. This is a dioecious species that commonly occur on seasonal forest canopy from southeast region of Brazil, and because of its importance we decided to gather information about its life history. To do that, we ask two main questions: 1) Can we define *S. dictyocarpa* ontogenetic stages using morphometric and architectural variation along the species life? ; 2) Which is the spatial distribution of different ontogenetic stages and which are the environmental factors that influence this distribution? We sampled 0,5 hectares and found 194 individuals distributed in 5 ontogenetic stages: infant, juvenile, immature and adult and senile. We did not found seedlings or reproductive adults in the plots we sampled, but we found some fruits and seedlings on the trail. Thus, seedling stage was described with no consideration of morphometric characteristics. The fruits we found did not have seeds and this fact indicates the absence of flower pollination, which could be caused by low frequency of male individuals or by absence of pollinator. The ramification pattern showed by *S. dictyocarpa* is correspondent to Massart architectural model, which is common for species that grow under low light conditions. Stages presented significant differences in height and diameter. Juvenile and immature presented smaller diameter increment per unit of height, and adult stage had higher diameter increment per unit of height. This suggests that in early stages a greater investment in height allows then to quickly reach for good light conditions on the forest canopy, disregarding the mechanical stability. We also found that crown length investment per unit of crown width increase along ontogeny, what shows that there is differences between stages to increase the light absorption efficiency. Liana infestation seems to affect adult crown development because individuals with liana have smaller investment in crown length. All stages presented random spatial distribution and juvenile and immature showed the tendency to occupy the same places, probably because they have the same recruitment and growth requirements. All correlations between stages and abiotic and biotic factors (light, soil and interspecific competition) were spurious or nom significant. This random pattern could be explained by environmental characteristics that were not considered here or by stochastic processes. Species distribution could also be strongly affected by seed, seedling or infant distributions, which were not found in the sampled area. These results suggests that there are different environmental occupation and resource use strategies along a canopy species live, however the environmental characteristics sampled here were not able to explain how this strategies determinates recruitment patterns in the space. To understand the absence of seeds and seedlings in the area and to propose conservation and management plans for *S. dictyocarpa*, reproductive biology and population dynamic studies are required.

Key-words: Ontogeny, Allometry, Spatial Pattern.

Considerações Iniciais

Os estudos populacionais são considerados essenciais para o entendimento dos processos que regulam a dinâmica e a estrutura de comunidades naturais além de ser a base para programas de manejo e conservação de espécies (Santos 2002). Mais especificamente, os estudos da estrutura populacional que abordam a distribuição dos indivíduos segundo uma determinada variável, que pode ser tamanho, idade ou distribuição espacial dos indivíduos (Hutchings 1997), apresentam um modelo estático que permite levantar informações sobre padrões de mortalidade no espaço e no tempo bem como sobre a resposta de espécies a diferentes condições do ambiente.

Há alguns trabalhos sobre a estrutura populacional de espécies de Florestas Estacionais Semidecíduas do Estado de São Paulo. Esses se mostraram eficazes no entendimento de como os indivíduos de certas espécies se relacionam entre si, em relação a outras espécies e com o ambiente heterogêneo. Esses trabalhos levantaram informações sobre, por exemplo: existência de grupos de diferentes estratégias de regeneração (Martini 1996, Furtado 2005), a influência da heterogeneidade ambiental na distribuição espacial das espécies (Souza 2004, Rosseto 2008) e status de conservação da espécie a partir do tipo de distribuição dos indivíduos (Dacinger 1996, Conforti 2006). Nesse trabalho discutimos a estrutura ontogenética e espacial da espécie *Savia dictyocarpa* (Phyllanthaceae).

A estrutura é geralmente descrita através da distribuição de indivíduos em classes de tamanho (Santos 2002), no entanto hoje há vários trabalhos que dividem as populações em estádios ontogenéticos. Esses são definidos pela idade biológica dos indivíduos, isto é, por critérios biológicos que consideram características morfológicas e fisiológicas (Gatsuk *et al.* 1980, Zhukova & Glotov 2001, Smirnova *et al.* 2002). Várias características das plantas podem ser utilizadas para definir os estádios ontogenéticos e essas podem variar ao longo da ontogenia, como por exemplo, as relações alométricas (Clark & Clark 1992, Sterck & Bongers 1998). Os estádios ontogenéticos diferentes podem apresentar propriedades ecológicas distintas e exercer diferentes papéis dentro da população e da comunidade, o que resulta numa complexa utilização dos recursos ambientais no espaço e no tempo, promovendo a coexistência das espécies e contribuindo para a diversidade das comunidades (Grubb 1977).

Espécies arbóreas tropicais apresentam diferentes estratégias de ocupação do espaço ao longo da ontogenia (Clark & Clark 1992). De acordo com o modelo de diferenciação de nicho, espécies com requerimentos ecológicos diferentes ocupariam ou dominariam porções da comunidade com características abióticas distintas, sendo, portanto, a coexistência facultada pela heterogeneidade ambiental (Wright 2002, Wright *et al*. 2003). Heterogeneidade ambiental refere-se à ação conjunta de fatores abióticos (propriedades físicas e químicas do solo, microtopografia e microclima) e fatores bióticos (produtores, consumidores, decompositores, mutualistas, parasitas e patógenos) (Dale 1999, Hutchings *et al*. 2000). A distribuição não uniforme dos recursos ou condições produz assim áreas favoráveis ou desfavoráveis para o estabelecimento e recrutamento dos indivíduos, de acordo com as necessidades de cada espécie e/ou estádio.

Alguns autores defendem que a heterogeneidade nas condições do dossel é a principal fonte de variação microambiental nas florestas tropicais (Svenning 2000) e que é responsável por grande parte da diversidade de estratégias de ocupação do gradiente vertical da floresta (Wright *et al*. 2003). No entanto, há outros fatores ambientais que podem estar associados à distribuição das populações vegetais, como a composição do solo, que tem sido correlacionada à distribuição de espécies de florestas tropicais (Clark *et al*. 1998, Palmiotto *et al*. 2004). O solo de regiões tropicais não é homogêneo em escalas regionais e locais e descontinuidade abrupta nas condições edáficas são comuns, assim essas condições podem determinar um padrão distribuição espacial não aleatório das espécies.

A estrutura espacial, as relações alométricas e a arquitetura são aspectos fundamentais da história de vida das espécies, isto é, da maneira como os indivíduos percebem, respondem e ocupam o ambiente ao longo da ontogenia. O conhecimento de aspectos da história de vida pode dar uma idéia do estado da população no fragmento, bem como fundamentar a proposição de planos de manejo de suas populações e orientar plantios.

Objetivo

O presente estudo tem como objetivo avaliar o estado de uma população de *Savia dictyocarpa* Müll. Arg. (Phyllanthaceae) num fragmento florestal, a partir do conhecimento de sua estrutura ontogenética e de seu padrão espacial, bem como avaliar a influência das condições luminosas nesses aspectos da estrutura da população.

No primeiro capítulo foram definidos os estádios ontogenéticos da espécie a partir da arquitetura e relações alométricas, com considerações sobre as condições ambientais na qual os indivíduos crescem. No segundo capítulo foi discutido o papel da heterogeneidade luminosa, da composição do solo e da competição com outras espécies distribuição espacial da população de *S. dictyocarpa*.

Material e Métodos Geral

Floresta Estacional Semidecídua

A Floresta Atlântica originalmente cobria uma área de aproximadamente 1.100.000 km² (Siqueira 1994), estendendo-se do Rio Grande do Norte ao Rio Grande do Sul. É considerada um dos hotspots de diversidade do mundo (SOS Mata Atlântica 1993), mas levantamentos recentes mostram que restam apenas 7,6% de sua cobertura original. O estado de São Paulo apresentava cerca de 80% de sua área coberta por estas florestas chamadas de Mata Atlântica *sensu lato* (Joly *et al.* 1999), mas dados recentes (Kronka *et al.* 2003) mostram que restam apenas 12% dessa cobertura florestal, sendo os fragmentos remanescentes de diversos tamanhos e diferentes situações de conservação. A Mata Estacional Semidecídua é uma formação florestal da Mata Atlântica e distingui-se por ser composta por 20 e 50% de espécies que perdem parte das folhas na estação seca, pois ocorrem em locais em que o clima possui duas estações bem definidas: um inverno seco e frio e verão úmido e quente.

A Floresta Estacional Semidecídua já recebeu várias denominações, entre elas floresta pluvial estacional tropical do planalto centro-sul (Veloso 1962), floresta mesófila semidecidual Rizzini (1963), floresta semidecídua de planalto (Eiten1970), matas foliadas subtropicais (Hueck 1972), floresta estacional semidecídua submontana (Veloso e Goes Filho 1982), floresta latifólia semicaducifólia ou mata de planalto (Leitão Filho 1982). Sua expansão dentro das áreas de cerrado se dá junto às linhas de drenagem, e é popularmente conhecida como Floresta de Galeria. Atualmente, a denominação mais usada é Floresta Estacional Semidecídua (Veloso *et al.* 1991; IBGE 1993).

O município de Campinas possui uma área de cerca de 800 km², altitude em torno de 680 m, distante cerca de 100 km da capital. Através de imagens de satélite e trabalhos de campo, o Núcleo de Monitoramento Ambiental da Embrapa detectou, identificou e mapeou 98 remanescentes florestais no município, sendo a Mata de Santa Genebra e a Mata Ribeirão Cachoeira os maiores remanescentes, cada um com pouco mais de 200 ha de Mata Estacional Semidecídua.

***Savia dictyocarpa* (Phyllanthaceae)**

A família Phyllanthaceae tem distribuição pantropical, com aproximadamente 2.000 espécies divididas em 59 gêneros. É monofilética e dividida em dois grandes clados que se distinguem principalmente pela presença de células epidérmicas taníferas e inflorescências alongadas ou fasciculadas (Wurdack *et al*. 2004; Kathariarachchi *et al*. 2005). As espécies possuem flores diclamídias e não apresentam nectários extraflorais nem látex, razão pela qual o grupo foi retirado da família Euphorbiaceae (Souza & Lorenzi 2005).

O gênero *Savia* era freqüentemente citado como um grupo disjunto, presente na América e África. No entanto, análises moleculares recentes provaram que muitas espécies agrupadas no gênero *Savia* são na verdade clados não relacionados, cada um com uma distribuição coerente (Hoffmann 2008). Assim o gênero *Savia,* que já foi considerado o maior gênero da tribo Wielandieae, hoje está reduzido a duas seções: *Savia* e *Heterosavia* (Wurdack *et al*. 2004). A seção *Heterosavia* possui 5 espécies (Hoffmann 2008), enquanto a seção S*avia* está restrita a 2 espécies: *Savia dictyocarpa* Müll. Arg. e *Savia sessiliflora* (Sw.) Willd. (Wurdack *et al.* 2004; Hoffmann 2008).

A espécie arbórea *Savia dictyocarpa* Müll. Arg. (Phyllanthaceae) está entre as espécies arbóreas mais abundantes nos remanescentes da Floresta Estacional Semidecídua no município de Campinas, SP (Santos & Kinoshita 2003), porém não há dados sobre sua ecologia populacional. É uma espécie que atinge 25 metros e pode ocorrer também em Floresta Ombrófila Densa (Figura 3). Há poucos dados ecológicos sobre todas as espécies do gênero *Savia* (Samuel *et al.* 2005), mas na literatura recente há informações sobre a filogenia, taxonomia, palinologia, arquitetura e anatomia do gênero (Wurdack *et al.* 2004, Kathariarachchi *et al.* 2005, Hoffmann 2008).

Savia é um gênero de distribuição neotropical (Hoffman 2008) e no Brasil existem registros da espécie *S. dictyocarpa* nos seguintes estados brasileiros: São Paulo (Durigan 2000; Santos & Kinoshita 2003), Minas Gerais (Rocha *et al.* 2005, Pinto *et al*. 2005) and Paraná (Costa Filho *et al.* 2006, del Quiqui *et al.* 2007).

Área de Estudo

O estudo foi realizado na floresta Ribeirão Cachoeira (22°50'S, 46°55'W), um fragmento de Floresta Estacional Semidecídua, pertencente ao condomínio rural "Colinas do Atibaia" na Área de Proteção Ambiental dos distritos de Sousas e Joaquim Egídio, no nordeste do município de Campinas, interior do estado de São Paulo (Figura 1). A reserva florestal do Ribeirão Cachoeira tem área de 233,7 ha, com 2584 m de comprimento no sentido leste-oeste e 1360 m no sentido norte-sul (Miranda 1996). Na porção meridional da maior extensão da mata, corre o ribeirão Cachoeira, um dos afluentes do rio Atibaia, o maior abastecedor do município de Campinas e um dos principais formadores da bacia do rio Piracicaba. Esse fragmento florestal também recebe os nomes de Mata da Fazenda Embaúba, Mata das Três Pontes, Mata da Fazendinha e Japizinho (Santos & Kinoshita 2003).

A Mata Ribeirão Cachoeira tem em seu entorno o Condomínio Colinas do Atibaia que é composto por lotes de área mínima de 20.000 m², na maioria ocupada por chácaras de lazer. O acesso ao condomínio é restrito bem como é vedada a entrada de moradores no fragmento florestal. Além disso, o fragmento representa 4,9% dos 223km² de área total da APA em que está inserido (Miranda 1996). A APA possui industrialização restrita, baixo nível de tráfego de veículos automotores devido à existência de poucas pequenas estradas e em sua maioria é composta por áreas de pastos, reflorestamento comercial e fragmentos florestais de diferentes graus de perturbação (Miranda 1996). Todos esses elementos colaboram para que a Mata Ribeirão Cachoeira seja o fragmento florestal mais bem conservado do município de Campinas.

As altitudes variam de 630 a 760 m. O relevo é composto por morros e morrotes paralelos com declividades de 13 a 40% (Instituto Geológico 1993). O solo predominante é do tipo Luvissolo Crômico, com pedaços de rochas e areia (Embrapa 1999). A vegetação é densa, com altura de dossel variando entre 15 a 25 m e árvores emergentes com mais de 30 m e não há sinais evidentes de atividade humana como corte seletivo, produção de carvão ou deposição de lixo.

O clima é Cwa de Köppen, temperado macrotérmico com inverno seco não rigoroso, com pluviosidade média anual de 1409 mm (Mello *et al*. 1994). O período seco dura de Abril a Setembro e tem média de 273 mm de precipitação e temperaturas que variam entre 19-23 °C; já no período chuvoso, que corresponde ao período de Outubro a Março, a precipitação média é de 1.143mm e temperaturas que variam de 23-24° (CIIAGRO 2007 – período de observação: 1993-2006)

Amostragem

A área amostral é de 6,474 ha e encontra-se na porção norte da mata, na margem esquerda do Ribeirão Cachoeira (Figura 2). A amostragem foi realizada em 50 parcelas de 10 x 10 m, totalizando 0,5 ha. As parcelas foram instaladas por Cielo-Filho (2000), de acordo com a técnica de aleatorização irrestrita (Greig-Smith 1983). Em cada parcela foram marcados e amostrados todos os indivíduos de *S. dictyocarpa*.

De cada indivíduo foi registrado o diâmetro do caule à altura do solo (DAS), o diâmetro do caule à altura do peito (DAP), duas medidas perpendiculares do diâmetro da copa, a altura total, a altura do ponto de inversão morfológica (fuste), presença de cotilédones, ramificações, estruturas de reprodução como flores e frutos, rebrotas e infestação por lianas.

Nessas parcelas também foram coletadas amostras de solo para análise física e química. Amostras de solo foram retiradas do centro de cada parcela, a 0-20 cm de profundidade, e foram submetidas à análise química e física realizada pelo Instituto Agronômico de Campinas. Foram obtidas as concentrações de MO (Matéria Orgânica), pH, P, K, Ca, Mg, Al, H+Al (Acidez Potencial), S.B. (Soma de Bases), C.T.C. (Capacidade de Troca Catiônica), V (Saturação de Bases), proporções de areia fina, areia grossa, areia total, argila, silte e a classificação textural.

A composição da comunidade arbórea das 50 parcelas foi levantada. Todas as árvores com PAP > 15 cm foram re-medidas e as ingressantes em relação ao último censo (Roque Cielo Filho 2000) foram marcadas.

Referências Bibliográficas

CIIAGRO 2007. **Boletim Climático: Campinas**. Centro integrado de informações agrometereológicas. Instituto Agronômico de Campinas, Campinas, Brasil.

CIELO FILHO, R. 2000**. Estrutura de abundância de um trecho da floresta estacional semidecídua no município de Campinas, estado de São Paulo: Mata Ribeirão Cachoeira**. Tese de Mestrado. Universidade Estadual de Campinas, Brasil.

CLARK, D. A.; CLARK, D. B. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. **Ecological Monographs** 62 (3): 315-344.

CLARK, D. B.; READ, J. M.; CLARK, D. A. 1998. Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. **Journal of Ecology** 86: 101-112.

CONFORTI, T. B. 2006. **Ecologia populacional de *Solanum erianthum* D. Dom**. Tese de mestrado. Escola Superior de Agricultura Luiz de Queiroz, Universidade de São Paulo, Brasil.

COSTA FILHO, L. V.; NANNI, M. R.; CAMPOS, J. B. 2006. Floristic and phytosociological description of a riparian forest and the relationship with the edaphic environment in Caiuá Ecological Station, Paraná, Brazil. **Brazilian Archives of Biology and Technology** 49 (5): 785-798.

DANCIGUER, L. 1996. **Aspectos da regeneração de duas espécies arbóreas em um fragmento florestal do Sudeste Brasileiro**. Tese de mestrado. Universidade Estadual de Campinas, Brasil.

DALE, M. R. T. 1999**. Spatial pattern analysis in plant ecology**. Cambridge University Press, London, England.

DEL QUIQUI, E. M.; MARTINS, S. S.; BROGHI, W. A.; SILVA, O. H.; SAKURAGUI, C. M.; PACHECO, R. B. 2007. Estudo fitossociológico de um trecho da floresta estacional semidecidual em Diamante do Norte, Estado do Paraná, Brasil. **Acta Scientia Agronômica** 29 (2): 283 - 290.

DURIGAN, G.; FRANCO, G. A. D.; SAITO, M.; BAITELLO, J. B. 2000. Estrutura e diversidade do componente arbóreo da floresta na Estação Ecológica dos Caetetus, Gália, SP. **Revista Brasileira de Botânica** 23 (4): 371-383.

EITEN, G. A vegetação do Estado de São Paulo. 1970. **Boletim do Instituto de Botânica** 7: 1- 147.

EMBRAPA. 1999. **Sistema brasileiro de classificação dos solos**. Empresa Brasileira de Pesquisa Agropecuária – Centro Nacional de Pesquisas do Solo. Brasília, Brasil.

FURTADO, A. G. 2005. **Estrutura de uma população de *Esenbeckia leiocarpa* Engl. (Rutaceae) numa floresta estacional semidecídua no sudeste do Brasil.** Tese de Mestrado. Universidade Estadual de Campinas, Brasil.

GATSUK, L. E.; SMIRNOVA, O. V.; VORONTZOVA, L. I.; ZAUGOLNOVA, L. B.; ZHUKOVA, L. A. 1980. Age states of plants of various growth forms: a review. **Journal of Ecology** 68: 675-696.

GRUBB, P. J. 1977. Maintenance of species-richness in plant communities: the importance of regeneration niche. **Biological Reviews of the Cambridge Philosophical Society** 52: 107-145.

HOFFMANN, P. 2008. Revision of *Heterosavia*, stat. nov., with notes on *Gonatogyne* and *Savia* (Phyllanthaceae). **Brittonia** 60 (2): 136-166.

HUECK, K. 1972. **As florestas da América do Sul**. Editora Polígono, São Paulo, Brasil.

HUTCHINGS, M.J. 1997. The structure of plant populations. *In*: Crawley, M.J. **Plant Ecology**. 2ª ed. Blackwell Science, London, England. 342-348 pp.

HUTCHINGS, M. J.; JOHN, E.; STEWART, A. J. A. 2000. **The ecological consequences of environmental heterogeneity**. Cambridge University Press.

IBGE - Instituto Brasileiro De Geografia e Estatística. 1993. **Mapa de vegetação do Brasil**. Rio de Janeiro, Brasil.

INSTITUTO GEOLÓGICO. 1993. **Subsídios do meio físico e geológico ao planejamento do município de Campinas**. Secretaria de Planejamento e meio Ambiente, Prefeitura Municipal de Campinas, Campinas, São Paulo, Brasil.

JOLY, C. A.; AIDAR, M. P. M.; KLINK, C. A.; MCGRATH, D. G.; MOREIRA, A. G.; MOUTINHO, P.; NEPSTAD, D. C.; OLIVEIRA, A. A.; POTT, A.; RODAL, M. J. N.; SAMPAIO, E. V. S. B. 1999. Evolution of the Brazilian phytogeography classification systems: implications for biodiversity conservation. **Ciência e Cultura** 51 (5/6): 331-348

KATHRIARACHCHIA, H.; HOFFMANN, P.; SAMUEL, R.; WURDACK, K. J. CHASE, M. W. 2005 Molecular phylogenetics of Phyllanthaceae inferred from Wve genes (plastid *atpB*, *matK*, *3'ndhF*, *rbcL*, and nuclear *PHYC*). **Molecular Phylogenetics and Evolution** 36: 112-134.

KRONKA, F. J. N.; NALON, M. A.; MATSUKUMA, C. K.; PAVÃO, M.; YWANE, M. S. S.; KANASHIRO, M. M.; LIMA, L. M. P. R.; PIRES, A. S.; SHIDA. C. N.; FUKUDA, J. C.; GUILLAUMON, J. R.; BARBOSA, O.; BARRADAS, A. M. F.; BORGO, S. C.; MONTEIRO, C. H. B.; PONTINHAS, A. A. S.; ANDRADE, G. G.; JOLY, C. A.; COUTO, H. T. Z.; BAITELLO, J. B. 2003. O verde em São Paulo. **Pesquisa FAPESP** 91: 48-53.

LEITÃO-FILHO, H. F. 1982. Aspectos taxonômicos das florestas do Estado de São Paulo. **Silvicultura em São Paulo** 16: 197-206.

MARTINI, A. M. Z. 1996. **Estrutura e dinâmica populacional de três espécies arbóreas tropicais**. Tese de mestrado. Universidade Estadual de Campinas, Brasil.

MELLO, M. H. A.; PEDRO JUNIOR, M. J.; ORTOLANI, A. A.; ALFONSI, R. R. 1994. Chuva e temperatura: cem anos de observações em Campinas. **Boletim Técnico do Instituto Agronômico de Campinas** 154: 1-48.

PALMIOTTO, P. A.; DAVIES, S. J.; VOGT, K. A.; ASHTON, M. A.; VOGT, D. J.; ASHTON, P. S. 2004. Soil- related habitat specialization in dipterocarp rain forest tree species in Borneo. **Journal of Ecology** 92: 609 - 623.

PINTO, L. V. A; BOTELHO, S. A.; OLIVEIRA-FILHO, A. T.; DAVID, A. C. 2005. Estudo da vegetação como subsídios para propostas de recuperação das nascentes da bacia hidrográfica Ribeirão das Cruzes, Lavras, MG. **Revista Árvore** 29 (5): 775-794.

RIZZINI, C. T. 1963. Nota prévia sobre a divisão fitogeográfica do Brasil. **Revista Brasileira de Geografia** 25: 3-64.

ROCHA, C. T. V.; CARVALHO, D. A.; FONTES, M. A.; OLIVEIRA-FILHO, A. T.; VAN DER BERG, E.; MARQUES, J. J. 2005. Comunidade arbórea de um continuum entre floresta paludosa e de encosta em Coqueiral, Minas Gerais, Brasil. **Revista Brasileira de Botânica** 28 (2): 203-218.

ROSSETO, V. 2007. **Aspectos da história de vida de quatro espécies de *Trichilia* (Meliaceae) na Reserva de Santa Genebra, Campinas**. Tese de Mestrado. Universidade Estadual de Campinas, Brasil.

SAMUEL, R.; KATHRIARACHCHI, H.; HOFFMANN, P.; BARFUSS, M. H. J.; WURDACK, K. J.; DAVIS, C. C.; CHASE, M. W. 2005. Molecular phylogenetics of Phyllanthaceae: evidence from plasticid matK and nuclear PHYC sequences. **American Journal of Botany** 92 (1): 132-141.

SANTOS, F. A. M. 2002. Ecologia de populações de plantas – Região Sudeste do Brasil. *In*: Araújo, E. L. *et al*. **Biodiversidade, Conservação e uso sustentável da flora do Brasil**. Sociedade Botânica do Brasil, Recife, Pernambuco, Brasil.

SANTOS, K.; KINOSHITA, L. S. 2003. Flora arbustivo-arbórea do fragmento de floresta Estacional Semidecídua Ribeirão Cachoeira, município de Campinas, SP. **Acta Botanica Brasilica**, 17 (3): 325-341.

SIQUEIRA, M. F. 1994. **Análise florística e ordenação de espécies arbóreas da Mata Atlântica através de dados binários**. Dissertação de Mestrado. Universidade Estadual de Campinas, Campinas, Brasil

SMIRNOVA, O. V.; PALENOVA, M. M.; KOMAROV, A. S. 2002. Ontogeny of different life forms of plants and specific features of age and spatial structure of their populations. **Russian Journal of Developmental Biology** 33:1-10.

SOS MATA ATLÂNTICA. 1993. **Evolução dos remanescentes florestais e ecossistemas associados do domínio da Mata Atlântica no período 1985-1990**. Fundação SOS Mata Atlântica e Instituto Nacional de Pesquisas Espaciais, São Paulo, Brasil.

SOUZA, A. F. 2004. **Aspectos da dinâmica populacional de uma palmeira clonal na floresta paludícola da Reserva Municipal de Santa Genebra (Campinas, SP).** Tese de Doutorado. Universidade Estadual de Campinas, Brasil.

SOUZA, V. C.; LORENZI, H. 2005**. Botânica Sistemática: Guia para identificação das famílias de Angiospermas da flora brasileira, segundo APG II**. Plantarum, Nova Odessa, Brazil.

STERCK, F. J.; BONGERS, F. 1998. Ontogenetic changes in size, allometry, and mechanical design of tropical rain forest trees. **American Journal of Botany** 85: 266-272.

SVENNING, J. C. 2000. Small canopy gaps influence plant distributions in the rain forest understory. **Biotropica** 32: 252-261.

VELOSO, H. P. 1962. Os grandes clímaces do Brasil: 1- considerações sobre os tipos vegetativos da região sul. **Memórias do Instituto Oswaldo Cruz** 60: 175-194.

VELOSO, H. P.; RANGEL FILHO, A. L. R.; LIMA, J. C. A. 1991. **A classificação da vegetação brasileira adaptada a um sistema universal**. IBGE, Rio de Janeiro.

VELOSO, H. P.; GOES FILHO, L. 1982. Fitogeografia brasileira: classificação fisionômica ecológica da vegetação neotropical. **Boletim Técnico Radam-Brasil: Série vegetação** 1: 1-80.

VIEIRA, L. 2008. **Padrões geográficos e estrutura da comunidade do estrato herbáceo da Mata Atlântica Meridional**. Tese de Mestrado. Universidade Estadual de Campinas, Brasil.

WRIGHT, S. J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. **Oecologia** 130: 1-14.

WRIGHT, S. J.; MULLER-LANDAU, H. C.; CONDIT, R.; HUBBELL, S. P. 2003 Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. **Ecology 84** (12): 3174-3185.

WURDACK, K. J.; HOFFMANN, P.; SAMUEL, R.; BRUIJN, A.; VAN DER BANK, M.; CHASE, M. 2004. Molecular phylogenetic analysis of Phyllanthaceae (Phyllanthoideae pro parte Euphorbiaceae *sensu lato*) using plastid *rbcL* DNA sequences. **American Journal of Botany** 91 (11): 1882-1900.

ZHUKOVA, L. A.; GLOTOV, N. V. 2001. Morphological polyvariance of ontogeny in natural plant populations. **Russian Journal of Developmental Biology** 32: 381-387.

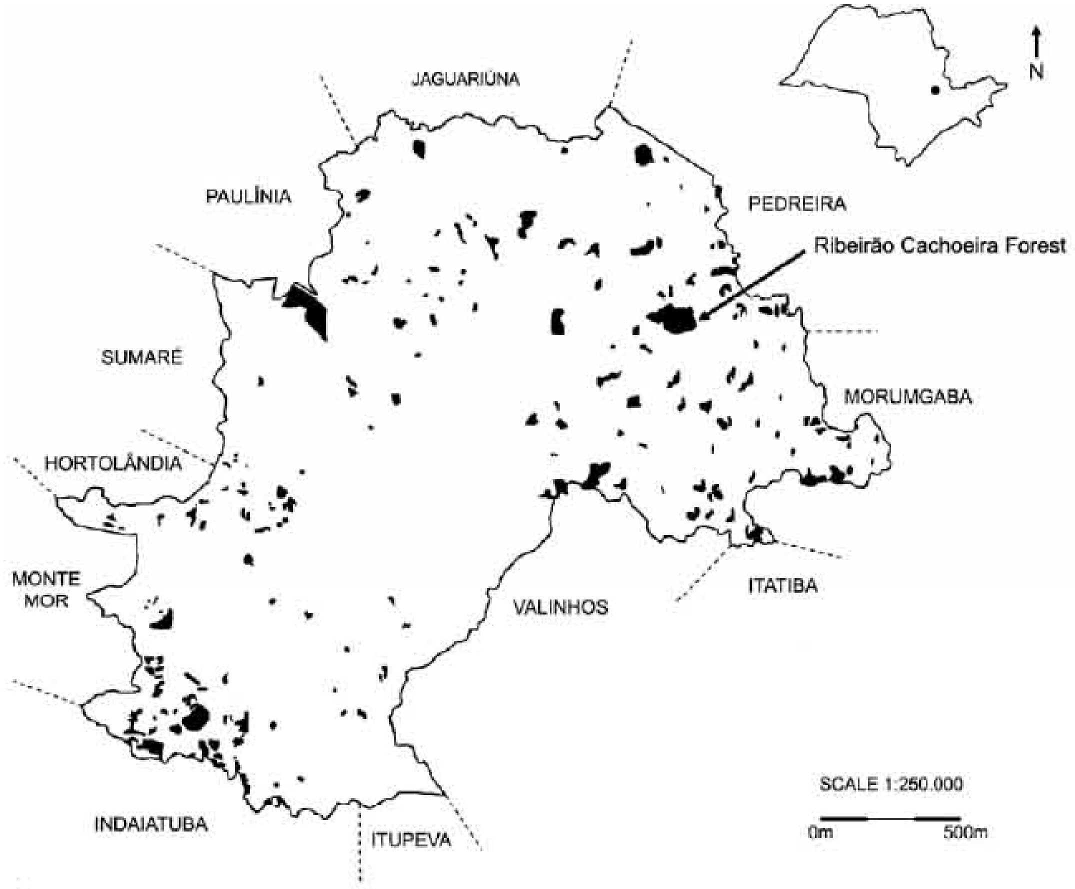

Figura 1. Mapa da cobertura vegetal do município de Campinas, destacando a Mata Ribeirão Cachoeira. Extraído de Vieira (2008).

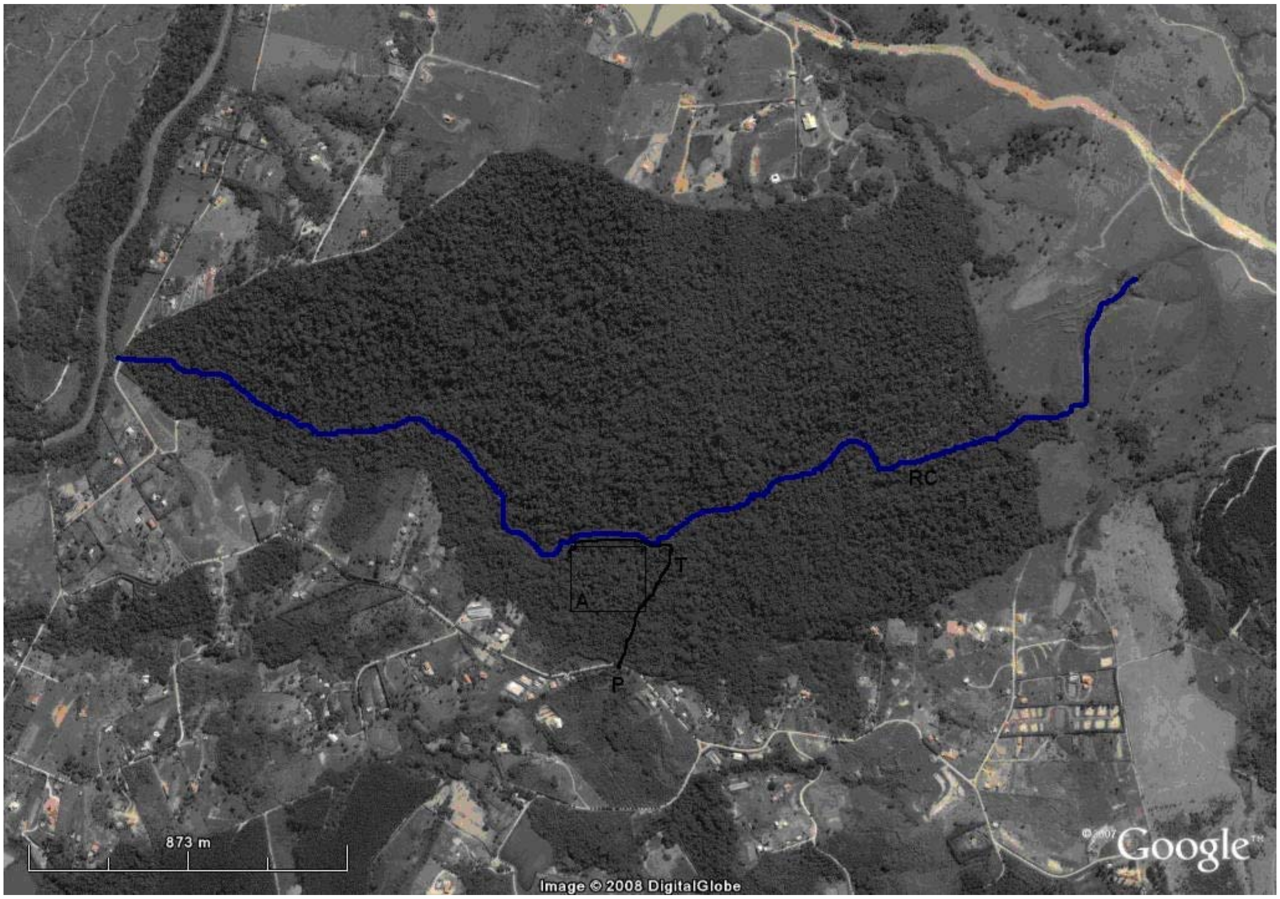

Figura 2. Imagem de satélite da Mata Ribeirão Cachoeira. Imagem extraída e alterada do site www.google.maps.com. Em destaque RC= Ribeirão Cachoeira, P= Porta de acesso a trilha, T= Trilha, A= Área Amostral.

Figura 3. Indivíduos da espécie *Savia dictyocarpa* pertencentes a diferentes estádios ontogenéticos. Destaque para as plaquetas de identificação utilizadas.

Capítulo 1

Life history of a tropical canopy tree species: ontogenetic stages, architectural analysis, allometric relationships and mechanical design.

Ligia Paulillo Sims [1], Fernando R. Martins [2]

1. Ecology Graduate Course, Institute of Biology, P. O. Box 6109, University of Campinas – UNICAMP, 13083-970 Campinas, SP, Brazil.

2. Department of Plant Biology, Institute of Biology, P.O. Box 6109, University of Campinas – UNICAMP, 13083-970 Campinas, SP, Brazil. Corresponding author: fmartins@unicamp.br

Abstract

Gatsuk *et al.* (1980) created a classification scheme that indicates the state of development of a plant using several quantitative and qualitative features that appear or are lost in the transition between stages. Each ontogenetic stage has unique ecological properties and plays a different role in the ecological community, promoting species coexistence by differential use of environment resources in time and space. We choose to use architectural and morphometric characteristics to define the ontogenetic stages. In the present article we discuss some aspects of life history of the shade-tolerant canopy specie *Savia dictyocarpa*. We sampled this species in 50 plots of 100 m² in Ribeirão Cachoeira forest, a 233,7 ha fragment of Seasonal Semideciduous Forest in Campinas municipality, SE, Brazil. We expect its initial ontogenetic stages to invest in optimization of light foraging and diameter growth, thus resisting fallen debris and supporting the crown expansion at cost of height growth; and in latter stages to invest in height growth rather than in diameter, thus reaching the forest canopy and then to grow in diameter and in crown length to enhance the light absorption, thus maintaining mechanical stability. We defined 5 ontogenetic stages well characterized by morphological characteristics. Seedlings were not found in plot area and we observed that out of the plots some trees of *S. dictyocarpa* were fruiting, but did not produce seeds. This could be caused by the absence of flower pollinator. In the immature stage the plant conforms to Massart architectural model. All ontogenetic stages had significantly differences in height and diameter, except for senile stage. For the juvenile, immature and senile the regression slope conformed to geometric similarity model. Adults significantly conformed to the elastic similarity model so they had greater diameter investment per unit of height than other stages. The safety factor changed throughout the ontogeny: juvenile and immature safety factor decreased with height, suggesting a larger investment in height per unit diameter. In adults the safety factor maintained stable with a slight increase, suggesting a change in growth strategy with a larger investment in diameter. The slopes of crown width vs. crown length regressions showed that there is a tendency of increase in crown length investment as the plant grows in height. Overall, we could explain differences of each ontogenetic stage by plants architecture and allometry. This demonstrated that the ecological role of each stage can be specific and may affect the surrounding environment in different ways. Although the plant didn't presented mechanical stability expected from shade-tolerant specie, other factors could allow this specie to occupy this niche, like its wood density. Also, the liana effect in crown architectures demonstrated that biomass partitioning patterns can influenced by environmental conditions.

Key-words: Ontogeny, Allometry, Tree Architecture, Ontogenetic trade-off, Light Partitioning.

Introduction

A review of literature can provide a variety of definitions of plant life stages, but all authors agree that a basic knowledge of this subject is necessary to improve the understanding of how individuals are distributed in the space, how they interact with each other or how natural selection works upon them (Carvalho *et al.* 1999, Souza *et al.* 2000, 2003, Boege 2005, Miranda-Mello *et al.* 2007, Bernacci *et al.* 2008, Knight *et al.* 2008, Octavio-Aguilar *et al.* 2008). Gatsuk *et al.* (1980) created a classification scheme that indicates the state of development of a plant (e.g., seeds, seedlings, juveniles, adults) using several quantitative and qualitative features that are achieved or lost in the transition between ontogenetic stages (Zhukova *et al.* 2001, Smirnova *et al.* 2002). These stages are not related with plant chronological age, but present unique ecological properties and play a different role in the ecological community, promoting species coexistence by differential use of environment resources in time and space (Grubb 1977).

There is much confusion among different authors who do not follow Gatsuk *et al*. (1980) and call size classes by stages (Fischer *et al.* 2001, Lehtilä *et al.* 2006). The incorrect identification of the ontogenetic stages can have negative implications on the results of analysis, such as matrix models that calculate demographic rates and make projections on future alterations. The study of the dynamics of a stage-structured plant population through prospective analysis, such as elasticity, predicts how population growth rate varies as a function of transition rates (Horvitz *et al.* 1997) and indicates which transition rates are good candidates for management targets (Caswell 2001). Therefore, the way we define stages will influence the calculated transition from a stage to another and so the whole proposition of the analysis. Size can't always be a good predictor of other important characteristics. In the case of *Trillium grandiflorum* (Melanthiaceae), a perennial herb, the annual appearance of different types of leaves and the flowering period are the characteristics that define their stages and are not related to size (Knight *et al.* 2008).

Each plant or group of plants has their own traits and ways to relate with the environment, so different tools and approaches can be used in the definition of the ontogenetic stages. In this article we choose to use architectural and morphometric characteristics to define the ontogenetic stages. The architectural analysis aims to identify and describe the inherited branching pattern of species, such as the direction of branch growth, meristem activity in time and destiny (Enriquez *et al.* 2008; Barthélémy *et al.* 2007; Hallé *et al.* 1978). It is important to notice that architectural features can change during life as the plant faces different environments. For example, in the early stages, a tree has just an orthotropic axis that bears the leaves, but in late stages the plant has orthotropic or plagiotropic branches that grow in a sympodial or monopodial way to increase light absorption efficiency (Miranda-Mello 2007). The definition of the architectural model is also important because it is useful to phylogenetic studies since one can get an idea of how the architecture evolved within a family or genus (Enriquez *et al.* 2008). Very few studies have compared the phylogeny of a group with the prevailing architectural models, since there is no information concerning a great number of families and genera (Enriquez *et al.* 2008).

Tropical forest species can also change their morphometric characteristics during ontogeny (Sterck & Bongers 1998, Bohlman & O´Brien 2006) depending on the life history of each species. These changes are related with differential resource allocation during ontogeny, such as horizontal expansion of the crown and photosynthetic organs, growth in height, or development of reproductive structures. Light is thought to be the most limiting factor for plant growth and survival because it’s related to the plant carbon budget (Sterck *et al.* 2001). So, for a canopy specie the morphometric characteristics can change along life stages (O’Brien *et al.* 1995; Sterck & Bongers 1998) due to trade-offs associated mainly with the light environment (Koyama & Hotta1990). Light availability increases horizontally from the understorey to gap centers, and vertically from the forest floor to the canopy (van Gelder *et al.* 2006), thus this variation would cause changes in plant architecture to achieve higher net carbon budget (Sterck *et al.* 2001).

There are different levels of shade tolerance: shade-tolerant species that can regenerate and grow under the canopy layer, and gap-dependent species that only germinate and grow in open sites with direct light above then (Clark & Clark 1992). Shade tolerance is a continuum rather than a disrupted relation among species in tropical forests and a well-defined life history axis that contributes to the coexistence of different tree species (Wright *et al.* 2003). Trees of shade-tolerant species grow slower and can survive low light intensities through: a) enhancing survival in the understory by means of longer leaf life spans (King 1994), higher allocation of biomass to the leaves (King 1991), dense and tough wood (van Gelder *et al.* 2006); b) developing a greater surface and decreasing self-shading, thus being able to capture light more efficiently by means of high investment in horizontal crown expansion (Kohyama & Hotta, 1990, Baker *et al.* 2006). Horizontal crown investment in low light environment would increase the light assimilation surface as well the investments in crown length when the plant reaches the canopy, where space competition is higher (Sterck *et al.* 2001).

Since growing in diameter or height is a trade-off, greater investments in diameter and crown shape implies in smaller investments in height growth (Sterck & Bongers 1998). Shade tolerant species can adjust to light conditions along their ontogeny by changing allocation to height versus crown development (Bohlman & O´Brien 2006). However, we should be cautious about these expectations because some studies that considered allometry as an evidence of life history trade-offs within functional groups focused a particular stage instead of analyzing the whole ontogeny (Bohlman & O´Brien 2006). Also, some results indicates that differential investments in crown shape *vs*. height throughout ontogeny may not exist, and that in fact there is a opportunist behavior, that plants under the canopy would take advantage of unpredictable canopy disturb (Alves & Santos 2002).

The buckling safety factor is the ratio of the buckling height to the observed height, and indicates the safety margins that trees maintain against dynamic loads such as wind, rain and falling debris. On the one hand, shade-tolerant species are thought to grow with large safety margins in the understorey, thus resisting dynamic loads by falling debris, increasing survival in the understorey and supporting crown expansion at the expenses of height growth; on the other hand, pioneer species are thought to grow with small safety margins, thus maximizing height gain and effectively competing with neighbor trees for light and space in gaps (King 1996, Sterck & Bongers 1998, van Gelder *et al.* 2006). When trees grow taller they attain higher light availability and so they can acquire more carbon and invest in their mechanical safety, which allows them to resist stronger winds high in the canopy (Sterck & Bongers 1998).

Following these information, we hypothesized that in its early ontogenetic stages, a shade tolerant canopy tree species should thrive in the forest understorey. If so, we expect its initial ontogenetic stages to be characterized by investment in a) photosynthetic tissues thus optimizing light foraging (showed by higher investment in crown width), and b) diameter growth, thus resisting fallen debris and supporting the crown expansion at cost of height growth. In late stages a shade tolerant canopy tree species should attain the forest canopy and resist stronger winds. If so, we expect that late ontogenetic stages: c) first, to invest in height growth rather than in diameter, thus reaching the forest canopy, and d) then to grow in diameter and in crown length to enhance the light absorption, thus maintaining mechanical stability, so that e) the safety margins for self-loading and wind force increase with ontogeny. Besides investigating the above expectations, our aim was to identify the ontogenetic stages of a shade tolerant canopy tree species through different approaches, in order to investigate how it responds to different environment conditions during its ontogeny.

Materials and methods

Study area

This study was developed in the Ribeirão Cachoeira forest (22°50’S, 46°55’W), a 233,7 ha fragment of Seasonal Semideciduous Forest in the Sousas-Joaquim Egídio Environmental Protection Area in Campinas municipality, São Paulo State, SE Brazil. The altitude varies from 630 to 760 m and the relief is hilly with 13-40% steepness (Instituto Geológico 1993). The predominant soil is Red-Yellow Argisol (Alfisol) with sandy texture and sparse rock outcrops (Embrapa 1999). The canopy height varies between 15 and 25 m, with emergent trees reaching 30 m. In the area there are no signs of recent human disturbances such as logging, charcoal or garbage (personal observation).

The climate is Köppen's Cwa with a dry season from April to September, with average total precipitation of 273 mm and temperatures between 19°C and 23°C. The rainy season lasts from October to March, with temperatures between 23°C and 24°C and average total precipitation of 1.143 mm (CIIAGRO 2007 – period of observation: 1993-2006)

Savia dictyocarpa Müll. Arg. **(Phyllanthaceae)**

The Phyllanthaceae is a pantropical monophyletic family with about 2000 species in 59 genera with a wide variety of habits (large trees, xeromorphic shrubs, small herbs and aquatic plants), and has monoecious or dioecious species with different morphology of flowers and fruits (Kathariarachchi *et al.* 2005; Samuel *et al.* 2005). Most of the Phyllanthaceae have architectural models with indeterminate growth, monopodial axes, and axillary inflorescences such as the models of Attims and Rauh (Enriquez *et al.* 2008).

Savia genera there are dioecious species that have simple, petiolate leaves with penninerved brochidodromous venation, and symmetrical, glabrous or simple-indumented blade without glandules (Hoffmann 2008). The pistillate or staminate flowers are different from each other: the pistillate have thicker and longer petals relatively to the sepals and the staminate have petals and sepals shorter than the pistillate. The staminate flower in *S. dictyocarpa* lacks petals (Hoffmann 2008).

Savia dictyocarpa is a canopy tree that reaches 25 meter in height and in Brazil it occurs in the Dense Ombrophilous Forest and mainly in the Seasonal Semideciduos Forest of the Southeast Region (Lorenzi 1992). *Savia* is a neotropical genus (Hoffman 2008) and in Brazil we found records of *S. dictyocarpa* in the following states: São Paulo (Durigan 2000; Santos & Kinoshita 2003), Minas

Gerais (Rocha *et al.* 2005, Pinto *et al*. 2005) and Paraná (Costa Filho *et al.* 2006, del Quiqui *et al.* 2007). We could not find ecological studies for the genus *Savia* or for the specie *Savia dictyocarpa*, because they have been poorly known (Samuel *et al.* 2005)*,* but there is a recent literature that discusses some phylogenetic, taxonomic, palynological, morphological and anatomical aspects of the genus (Wurdack *et al.* 2004; Kathariarachchi *et al.* 2005; Samuel *et al.* 2005; Hoffmann 2008; Enriquez *et al.* 2008).

Savia fruit is a dehiscent capsule that explosively frees the seeds (Souza & Lorenzi 2005). So, *S*. *dictyocarpa* has autochorous dispersal and probably does not have secondary dispersal by ants because the seeds do not have elaiosome or caruncule (Wurdack *et al.* 2004; Souza & Lorenzi 2005; Hoffmann 2008). There is no consensus in the literature about the phenodynamics of *S. dictyocarpa*: Lorenzi (1992) described it as an evergreen species, but Hoffmann (2008) stated that *Savia* is deciduous. In Ribeirão Cachoeira forest, we observed that the trees shed most of their leaves in the winter (dry season) and flush new leaves in the beginning of spring (first rains). From August 2007 to October 2008 we observed that flowering and fruiting were asynchronic and irregular: just some adults produced flowers and then produced fruits without seeds. This is probably the reason for the absence of seedlings in the plots we surveyed. *Savia dictyocarpa* wood is used to make simple objects and mostly in charcoal production (Lorenzi 1992). However, the major impact on *S*. *dictyocarpa* populations might be the lost of habitat by fragmentation since the Seasonal Semideciduos Forests has been almost completely devastated in São Paulo state (Ribeiro *et al.* 2009).

Data Collection

The sampling area of 6,5 ha are located in the south portion of the fragment, to the left of the Cachoeira stream. Aerial photographs (1:25,000) were used to choose the sampling area (Cielo Filho *et al.* 2007), which is in a slope with approximately 270 m in length, and 40 m of difference between the up and low ends (Cielo Filho *et al.* 2007). In this area Cielo Filho *et al*. (2007) set down 100 random 10 x 10 m plots according to Greig-Smith's (1983) unrestricted randomization procedure. Individuals of *Savia dictyocarpa* (Phyllanthaceae) were more abundant in the 50 plots on the lower slope (Cielo Filho *et al.* 2007), where we collected our data.

We tagged and measured all individuals of *S. dictyocarpa* in the plots. We identified the ontogenetic stages following Gatsuk *et al.* (1980) and by using architectural traits, such as axis orientation (plagiotropic or orthotropic), meristem differentiation (vegetative or sexual), type of growth (sympodial or monopodial branching), presence of reiteration and conformation to an architectural model (Hallé *et al.* 1978; Barthélémy & Caraglio 2007). The age states were first defined by Gatsuk *et al.* (1980), who classified plant life through biological criteria. The use of the term "age" represents a false relation between chronological and biological age (Wellington *et al.* 1985); hence many authors prefer the term stage. Following Carvalho *et al*. (1999), we use the term "ontogenetic stage" to refer to a specific time interval in the ontogeny of an individual plant in which the plant body has a characteristic shape associated with characteristic qualitative and quantitative traits.

We characterized the seedling stage observing only seven seedlings that we found outside the plots below a *S. dictyocarpa* crown that had fell on the ground, of which we could not make measurements.

For each individual we recorded total height, stem diameter at the ground level, crown width, crown length (the difference between the total height and the height of the lowest branch), the presence or absence of liana, and the crown illumination index (CII). Total height and branching height of each tree were measured with a telescopic ruler for the trees more than 2 m tall, and with a tape otherwise. The crown illumination index (CII, Clark & Clark 1992) is a modification of Dawkins and Field's (1978) crown position index. CII is a measure of light exposure of the crown based on observations of the number and size of canopy openings, i.e., the index scores the source and relative amount of crown lighting (Table 1). We used arithmetic mean of CII recorded from two observers.

Data analysis

We used total height and diameter at ground level to check whether the ontogenetic groups were consistent. These measures were used in a notched box plot analysis, which gave us median confidence intervals, with which we could test whether there were significant differences among the stages (McGill *et al.* 1978; Wilkinson 2007). Box plot analyses of CII and canopy openness were also used to characterize habitat preferences of each ontogenetic stage. For this analysis we used the program Systat 12.0.

We analyzed the allometric relationships between height and diameter of each ontogenetic stage with the power function equation (O´Brien *et al.* 1995): log y = log a + b log x, where y is stem diameter (cm), **x** is plant height (m), **a** is the intercept and **b** is the slope. Dimensional relationships for crown shape and height were determined by least square regressions of crown width (m) against height (m), and crown width (m) against crown length (m). We choose not to make crown length and tree total height regression because these two variables are dependent, which violates the premise of independence. Crown width of a tree was estimated by the arithmetic mean of two perpendicular directions, including the widest projection. Crown length was defined as the difference between the tree total height and the height of the lowest living branch or lowest petiole base for nom branched plants (Alves & Santos 2002, Baker *et al.* 2006, Yamada *et al.* 2006). To plot and analyze the regressions we used log-transformed (log10) values (Alves & Santos 2002, Osunkoya *et al*. 2007). Plant height was used as the independent trait in all regressions (Osunkoya *et al.* 2007) because height influences the light environment and the space available for plant growth (King 1996).

We performed a covariance analysis (Ancova, Zar 1999) to compare the regression line coefficients among ontogenetic stages. Ancova is commonly used to compare allometric relationships (Kohyama & Hotta 1990, Yamada *et al.* 2006). A global analysis, with all ontogenetic stages was performed to test whether the slopes of the regression lines are all the same. If at least one pair of coefficients was different, then the null hypothesis was rejected and we performed a Scheffé multiple comparison test to calculate the differences between slope pairs (Zar 1999). If the null hypothesis was not rejected, meaning that the slopes were not significantly different, we proceeded to test the second hypothesis that the Y-intercepts of the regression lines were all the same. Species with a steeper slope (b) show larger unit increase of Y per unit increment of X, and for lines with the same slope, species with a larger Y-intercept (a) have a larger Y for any particular value of X (Abe & Yamada 2008).

Each regression slope (b) of log trunk diameter vs. log total tree height was compared with proposed coefficients from elastic similarity (b= 1,5; McMahon 1973), geometric similarity (b= 1,0), and stress similarity (b= 2,0; Dean & Long 1986) through a t-test (Zar 1999) on the program ANCOVA33 (Santos 1997).

We calculated the safety factor against elastic bending, which is based on the critical bending diameter under which a stem suspended on one extremity would break under its own load (van Gelder *et al.* 2006). Tree bending moments originate mainly from an inclined stem, wind loads and/or asymmetrical weight distribution of the crown due to crown asymmetry and/or epiphyte/liana loads. The bending safety factor is the ratio between the observed diameter (D_{obs}) and the critical bending diameter (D_{crit}). Stem safety factors decrease with height, and a power function can well describe the relationship between H_{obs} and D_{obs}/D_{min} (Sposito & Santos 2001). The critical diameter is calculated from the following equation:

$$D_{min} = 0{,}109\ H^{3/2}$$

This is a measure of the degree of safety against bending based on stem dimensions and McMahon's (1973) buckling equation:

$$H_{crit} = C\ (E/\rho)^{1/3}.D^{2/3})$$

Where C is the constant of proportionality (0,792), E is the modulus of elasticity, ρ is the wood density, and D is the trunk diameter. Accordingly to Niklas (1993), E/ρ is a constant in gymnosperms and dicotyledonous woody tree. The formula assumes the shape of an untapered cylinder with its weight evenly distributed along the column height. It also assumes that the weight of leaves and branches equals the additional weight of the stem, by considering it a cylinder rather than a tapered stem (Holbrook & Putz 1989).

So, the safety factor we calculated is an approach estimate, since dry density of wood, one of the predictors of stem mechanical properties, is not available for *Savia dictyocarpa*. Instead we used the values ρ value used by McMahon (1973). The minimum stem diameter (D_{min}) was calculated for diameter at ground level (cm) and the safety factor was plotted against observed total height (m). Since we could not properly measure the seedlings and infants, we did not consider this ontogenetic stage in our analyses.

Results

Ontogenetic Stages

Seedlings (Se) – The germination is epigeal, and the seedlings have two fleshy cotyledons. The seedling functional morphology classification (*sensu* Ressel *et al.* 2004) is phanero-epigeal-reserve, with circular shape and truncated apex cotyledons that present sparse trichomes at the basis of the adaxial surface. (Figure 1). The seedling stage is characterized by the presence of embryonic structure, such as cotyledons, it is not branched, and can bear primary leaves with shape similar to adult leaves, although smaller, distributed spirally in the axis.

Infant (In) – The infant stage has no cotyledons neither branches (Figure 1). The herbaceous monopodial orthotropic axis bears two or more leaves with spiral alternate disposition above the primary leaves. We defined this intermediary stage between seedling and juvenile following Carvalho *et al.* (1999).

Juvenile (Jv) – The aerial body is constituted by a woody monopodial, orthotropic axis with two or more monopodial, orthotropic lateral branches (Figure 1). The lateral branches bear new leaves with spiral alternate disposition near the top and scars from old, fallen leaves below.

Immature (Im) – This stage has a well defined trunk with a finely-cracking bark. The plants have a well branched crown, in which the branches have monopodial growth and orthotropic or plagiotropic orientation. The branches have rhythmic growth, starting the grow season at the spring. In this stage the plant conforms to Massart architectural model.

<u>Adults (Ad) – </u>In this stage the plants have a thick cracking bark and the trunk has expansions resembling tabular roots or buttresses at the base. In adult stage *S. dictyocarpa* reiterate its architectural unit and therefore expand its crown by repeating the architectural model. Reiteration is a morphogenetic process through which the organism duplicates its own elementary architecture (Barthélémy & Caraglio 2007) by activation of some resting meristems caused by events like canopy openness or a mechanical injure. The formed reiterated trunk differs from others (Oldeman 1990): more vertical position than other branches; live longer; larger diameter; and faster growth. We could not found reproductive adults in the plots, so this stage comprises all the adults without differentiating vegetative or reproductive stages.

<u>Senile (Sn) – </u>This stage comprised plants that were alive but presented great injuries such as broken trunks and fallen crowns, with adventitious resprouting.

Size variation

In the box plot analysis, if the notch intervals of two medians do not overlap, the medians are considered significantly different at a 95% confidence level (McGill 1978). All ontogenetic stages had significantly different heights, except the senile that overlapped with immature and adult (Figure 2). This was probably due to frequent crown damages suffered by immature and adult that originated the senile individuals.

The stages were progressively higher from infant to adults (Table 2). The height in infant stage ranged from 10 to 20 cm and in the juvenile from 10 to 79 cm. The overlap in height between these two stages was probably an outcome of frequent breaking of branches of the juvenile due to falling debris (personal observation). In the immature height ranged from 51 cm to 5 meters. The shorter individuals overlapped with the juvenile also due to branch breakage and trunk bending caused mostly by fallen debris. The adult height ranged from 4,5 to 28 m with little overlap with the immature.

Except in the senile and immature, stem diameter was statistically different among the stages, which were progressively thicker (Figure 3). In the infant diameter ranged from 0,06 to 0,4 cm and in the juvenile, from 0,12 to 2,10 cm. The stem diameter of the immature varied from 0,30 to 9,20 cm, overlapping with the juvenile in the smallest diameters. This overlap is also an outcome of branch breakage because some immature can suffer injuries and became smaller or return to juvenile stage. In adults the trunk diameter ranged between 3,47 and 67 cm and the senile, between 2,90 and 16,90 cm.

Allometric Relationships

Height and Diameter

All regression lines were highly significant ($P < 0,005$) (Table 3) with good adjustment, meaning that around 50-70% of diameter variation was explained by variation of height. Considering the whole population, we found a significant relation between diameter and height represented by a high coefficient of determination ($r^2 = 0,92$).

For the juvenile, immature and senile the regression slope was not different from that expected by the geometric similarity model ($b = 1$), although only for the immature this relation was significant on the 95% confidence interval (Table 4 and Figure 5). Adults significantly conformed to the elastic similarity model ($b=1,30$; $r^2=0,58$; $p= < 0,01$), so they had greater investment in diameter per unit height than other stages. The slope of the regression line of infant was different from the expected for all allometric relationship models. Considering the whole population, the slope of the regression was not different from the geometric similarity model. The safety factor changed throughout the ontogeny (Figure 9) in an expected manner, since the juvenile and immature stages the safety factor decreased with height, suggesting a larger investment in height per unit diameter and in adults the safety factor maintained stable with a slight increase, suggesting a change in growth strategy with a larger investment in diameter.

This change in growth strategy was also indicated by significant differences of regression slopes (Ancova; $F_{3,182} = 6,78$; $p < 0,01$) and intercepts (Ancova; $F_{2,119} = 31,32$; $p < 0,01$). The juvenile ($a = 0,08$; $b = 0,92$ $p < 0,01$) and the immature ($a = 0,06$; $b = 0,73$; $p < 0,01$) had similar slope and intercept, indicating that these two stages are closely related, which is plausible because they occupy forest understorey and may grow in the same light conditions. The immature and senile had a significantly smaller regression slope than the adults ($b = 1,30$; $p < 0,01$). This is consistent with the result we found for the allometric models and with the expectation that in late ontogenetic stages a shade-tolerant canopy species would develop a larger mechanical stability, thus being able to resist larger crown weights and strong winds.

Crown allometry

Relations between crown width (m) and height (m) were significant for Juvenile, Immature and Adult stages (Figure 6). For the two latter stages more than 55% of the variation of crown width was explained by variation in crown height (Table 5). For the juvenile, the coefficient of determination was smaller ($r^2 = 0,29$; $p= < 0,01$), indicating a poor relation between crown width and height in this stage. For the immature and adult stages crown width was better explained by height increase (Immature: $b = 0,82$; $r^2 = 0,64$; $p < 0,01$; Adult: $b = 0,70$; $r^2 = 0,53$; $p < 0,01$). For the whole population, height explained a great amount of the variation in crown width ($r^2 = 0,86$; $p < 0,01$). To test for differences of the regression among stages we performed Ancova and found that all slopes were statistically similar ($F_{(3,181)} = 1,93$; $p = 0,124$), but the intercepts of the juvenile and adults were distinct. The regression of log crown length (m) vs. log crown width (m) was significant for all stages, except for senile ($p = 0,21$), but the amount of crown length variation explained by crown width was higher then 50% only for immature stage (Figure 7). Nevertheless, the slope of these regressions showed a tendency to be consecutively higher along ontogeny, although they was not significant different in Ancova test ($F_{(3,179)}$ = 0,59; p=0,63). This represents a tendency of higher crown length investment per unit of crown width as tree grows old.

Liana Effect on Adult Allometry

We performed separate regression analyses of diameter vs. height for 39 adults with and 28 without lianas (Table 6 and Figure 8). Then we applied Ancova to test for differences and found no significant difference of slope ($F_{(1,63)}$ = 3,18; p = 0,075) or intercept ($F_{(1,64)}$ = 0,04; p = 0,81). Also, we found no difference in crown width/height regressions of plants with or without lianas (Slope: $F_{(1,63)}$ = 0,12; p = 0,72; Intercept: F $_{(1,64)}$ = 0,28; p = 0,60).

Nevertheless we were able to find significant difference between slopes of crown length vs. crown width regression (Ancova $F_{(1,\ 58)}$ = 3,84, $p < 0,05$). Without lianas the slope were higher meaning that in this case there is more increase in crown length as the plant grows in crown width.

In all lines the height explained more than 50 per cent of the variation of the dependent variable, except for crown length of adults without lianas.

Light Environment

The Crown Illumination Index significantly differed among the ontogenetic stages (Figure 4), an expected result, since exposure to light could be related to plant height. Infant, juvenile and immature stages had the smallest CII, around level 2, meaning that the crown was exposed to some small and medium openings in the canopy and received a medium level of lateral light. This means that mostly the plants of these stages were found under the canopy and not in gaps, where the canopy is open and exposure to light is higher. In the adult stage median CII was 3 and showed a great variation because some plants were exposed to lateral light and some others had full exposure to direct light.

Discussion

Ontogenetic Structure

We did not include seedlings and the infant stage in our numerical analyses due to the small number of individuals we found. The lack of seedlings and saplings in the understorey of tropical forest has been seen as an indicator of population decline (Feeley *et al.* 2007; Souza 2007). Species that are suffering a process of elimination from the community through natural process of succession or human activity fail to reproduce and thus lack sufficient initial regeneration. However this is a controversial hypothesis that has received negative (Condit *et al.* 1999) as well as positive backup (Wright *et al.* 2003) when species are treated separately accordingly to their life history. Shade-tolerant species establish widely and persist in the understory despite deep shade and often intense root competition, so the population structure should be characterized by a high number of small plants in the understorey and a long tail of larger plants that have already reached the canopy. This population structure is supported by low rates of growth, mortality and recruitment (Nascimento *et al.* 2005). Juvenile and immature stages were found under low light conditions indicating that the species have some degree of tolerance to shady environments.

Absence of seedlings and presence of only few juvenile and infant in the plot area on this two year study could be explained to supra-annual reproduction phenology, like suggested Rocha *et al*. (2006) for a tree population from Costa Rica. This reproductive strategy is expected to be common under late successional species (Kang & Bawa 2003) and could be related to microenvironment variation or to intrinsic traits (Janzen 1978; Engel & Martins 2005; Rojas-Robles & Stiles 2009). Tropical species reproductive event can vary under an interval of two or three years but in some cases this interval could take more than 20 years (Kang & Bawa 2003). So, *S. dictyocarpa* could present a long interval between reproduction events, like other seasonal semideciduous forest tree species (Dias & Oliveira-Filho 1996), that lead to the absence of young stages.

Besides, we observed that out of the plots some trees of *S. dictyocarpa* were fruiting, but in the fruits there were no seeds. The absence of seeds could also explain this lack of seedlings, which could be caused by the absence of flower pollinator. Recent articles show that in Phyllanthaceae family, in tribe Phyllanthus, there is an obligatory pollination mutualism with *Epicephala* moths in some dioecious species whereas other species are pollinated by various nectar-seeking insects (Kawakita & Kato 2009). Although the phylogenetic classification of Phyllantheae has been the subject of previous investigations (Kathriarachchi *et al.* 2005), virtually nothing is known about the pollination biology of the remaining groups of Phyllanthaceae (Kawakita & Kato 2009). We suppose that in Ribeirão Cachoeira fragment the population of the specialized pollinators of *S. dictyocarpa* could be somehow recently reduced or having large fluctuations along time, so that present adults are not able to produce seeds, seedlings and so on. We suggest that specific studies on pollination of this species should be carried on, since *S. dictyocarpa* is important canopy tree specie in seasonal Atlantic Forest.

Tree Architecture and Allometry

Although some of the biomechanical characteristics did not significantly differ between the juvenile and immature, probably because they occupied similar niches in the vertical stratification of the forest, these stages differed in their architecture, which could indicate the use of different strategies of carbon allocation.

Branching in *S. dictyocarpa* begins in the juvenile stage, which has branches with plagiotropic orientation bearing leaves in a horizontal plane. A branching growth habit could expand crown area more widely than a monoaxial growth habit. Also, a widely distributed crown with leaves borne by multistoreyed branches often diminishes self shading (Sterck *et al.* 2003). Diminishing self shading is important mainly for the initial ontogenetic stages, which thrive in the understorey of closed canopy and need to maximize light absorption.

In the immature stage plants conformed to Massart´s model. Hallé *et al.* (1978) provided a set of 23 architectural models that can describe the different architectural structure of tree species, thus indicating that many trees from unrelated families have similar overall organization. Massart´s model has an orthotropic monopodial trunk with a rhythmic growth that produces tiered plagiotropic branches (Hallé *et al.* 1978), which may minimize self-shading (Tomlinson 1987). This rhythmic growth is endogen, but its cycle can be influenced by external factors, such as seasonality, affecting light or water availability (Hallé *et al.* 1978). *S. dictyocarpa* flushes new leaves in early spring season and cease the growth in the winter, following climatic seasonality as predicted. In the adult stage plants present reiteration, which is a mechanism whereby a tree duplicates its architectural unit to increase its photosynthetic structure or to respond to some environmental stress (Begin & Filion 1999).

Architectural models are not usually defined by variables related to photosynthetic efficiency (Osada *et al.* 2004), although leaf display seems important in the ecological strategy of most species. In *S. dictyocarpa* the realization of the architectural model occurs in the immature, while the plants are still in the understorey, and the reiteration realized in the adult stage can both increase light absorption and take over a position in the forest canopy, since these processes promote the horizontal and vertical growth of the crown.

Indeed, architecture can vary during ontogeny because taller trees have different requirements for mechanical support, respiratory loads, and carbon investments in reproduction, and experience different environmental conditions in the forest canopy (Poorter *et al.* 2005). These shifts could be expressed in some of the differences we found among the ontogenetic stages. We observed that the stages were well defined by height and diameter, thus indicating that they are progressively taller and thicker (Figure 5). In the understorey, juvenile and the immature presented a small investment in diameter per unit of height than the adults, and conformed to the geometric similarity model. However, adults that occupy the canopy level had a greater investment in diameter and conformed to elastic similarity model.

The geometric self-similarity model is based on the notion that, whenever wind load is not the dominant controlling factor in tree biomechanical design, stem length will scale in direct proportion to stem diameter ($H \alpha D$) (Osunkoya *et al.* 2007). In fact, this model predicts shorter increase in diameter related to height when compared to the other two biomechanical models. We expected that initial ontogenetic stages of a shade tolerant tree would invest in stem diameter growth to resist fallen debris and support crown expansion, but our findings pointed to greater investment in height, thus suggesting that reaching upper levels in the forest profile is important in the struggle for light.

Juvenile and immature had also a small safety factor, indicating that the plants were close to the mechanical bending limit. This could be explained by a greater investment in crown width because shade-tolerant species may be exposed to very low light in early stages, and thus continue to invest in crown expansion at the cost of safety margins. Consequently, the safety margins would be small in early stages and only start to increase when the plants get brighter light in later stages (Sterck & Bongers 1998). We can see that adults have a tendency to increase the safety margins; however this non significant change may indicate a lack of relation between crown width investments and stem mechanical stability.

Wood properties could compensate for the proximity to the buckling limit and to the conformation to geometric model we found in the initial stages of *S. dictyocarpa*. We did not record wood density, but some authors found that seedling and sampling survival is positively related to stem density and “toughness” and that wood density is the best predictor of survival (van Gelder *et al.* 2006; Muller-Landau 2004). Wood density could provide a better resistance against physical damage, such as fallen debris and trampling. Trees may also ricochet off their neighbors, relying on then for support, which could prevent them from swaying, and thus from buckling or tipping up (Holbrook & Putz 1989; O´Brien *et al.* 1995).

Niklas (1995) suggested that geometric self-similarity might occur early in the ontogeny of a tree, whereas elastic or stress similarity would be reached toward the end of a tree's life. Adults of *S. dictyocarpa* conformed to the elastic similarity model and showed a tendency to increase safety margins against bending. The elastic similarity model assumes that for trees to resist buckling under their own mass, longer stems need to be proportionally thicker than shorter ones (Osunkoya *et al.* 2007), and hence diameter should scale at 3/2 to the power of trunk height. The increase in stability with tree height found in canopy-sized trees is expected given the rapid increase in wind speed with height in the middle and upper canopy (King 1996) and possibly due to increased weight promoted by epiphyte and liana infestation, the latter more important in seasonal tropical forests. Bearing fruits also represents a periodic or sporadic weight load that demands increased mechanical stability of canopy tree species.

As well as some species studied by Sterck & Bongers (1998), *S. dictyocarpa* crown width: tree height didn't change throughout the ontogeny. Moreover, crown width: tree height and crown width: crown length relations for juvenile stage had lowest coefficient of determination, showing that their crown shape varies more than expected. This plasticity of crown shape in smaller trees could be advantageous in situations of unpredictable canopy disturbance: a less expensive crown form would allow suppressed trees to survive until adequate light conditions become available (Alves & Santos 2002). However, we can see a tendency to increase crown length, in despite the fact that slope regression for each ontogenetic stage was not significant different (Figure 7). Alves & Santos (2002) also found this greater investment in crown length in 2 canopy trees from Atlantic Forest. The investment in vertical crown dimensions seems to be associated with some degree of shade intolerance in larger trees or reflecting the effect of interspecific branch competition on the canopy layer. Crown shape is expected to change in a plants life depending on the species life history or the maximum height (Sterck *et al.* 2001). This result evidences that there may be restrict ontogenetic shifts in this height: crown relation and, in fact, there should be different strategies of resource allocation in tropical species (Baker *et al.* 2006).

Other environmental factors can influence these changes in crown shape. For example, Martinez & López-Portillo (2003) found that on soil texture and long-term water availability affects the height growth and production of branches in semi-arid environment. In seasonal tropical forests this factors is frequently neglected and we don't really know its real influence in allometric changes during ontogeny.

Another factor that can interfere in allometric relations is the infestation of lianas but they don't seem to have a direct effect on diameter or crown width growth that could be expected by the additional weight and sunlight blocking that these climbing plants can practice. *S. dictyocarpa* adults have their crown development affected by lianas since tree that didn't presented lianas had a greater crown length increment by unit of crown width increment (Figure 8) probably because of the added weight of lianas on the saplings as well as a combination of mechanical stress or damage and the casting of dense shade. Schnitzer *et al.* (2005) found, through an experimental approach, a similar result for samplings: below-ground and above-ground competition between lianas and tree samplings has an effect in accumulation of biomass of 3 species samplings in disturbed forests and in treefall gaps. Competition with lianas caused saplings to invest a higher proportion of their above-ground biomass into stem construction and less in leaf and branch biomass (Schnitzer *et al.* 2005).

Overall, we could explain differences of each ontogenetic stage by plants architecture and allometry. This demonstrated that the ecological role of each stage can be specific and may affect the surrounding environment in different ways. Plants allocate carbon to stems to support their photosynthetic tissues and elevate their leaves above competitors and into the sunlight, so in the understorey who wins or loses the competition for light are determined largely by "who shades whom" (O´Brien *et al.* 1995). *S. dictyocarpa* has a plagiotropic architecture that enables it to capture low light in the understorey to grow to the canopy. Although the plant didn't presented mechanical stability expected from shade-tolerant specie, other factors could be allowing this specie to occupy this niche, like its wood density. Our results are evidence that shade-tolerant and pioneer are extremes and that there are species able to live in shaded environments without conforming to expected trade-offs. Also, the liana effect in crown architectures demonstrated that biomass partitioning patterns can influenced by environmental conditions.

There must be other studies to analyze specifically the conservation status of this population to evidence the factors that influence the population structure and that are causing the reproduction failure.

References

ABE, N.; YAMADA, T. 2008. Variation in allometry and tree architecture among *Symplocos* species in a Japanese warm-temperate forest. **Journal of Plant Research** 121:155-162.

APG II. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. **Botanical Journal of the Linnean Society** 141: 399-436.

ALVES, L. F.; SANTOS, F. A. M. 2002. Tree allometry and crown shape of four tree species in Atlantic rain forest, south-east Brazil. **Journal of Tropical Ecology** 18: 245-260.

BAKER, M. G.; PINARD, M.; NILUS, R. A. 2006. Allometry and shade tolerance in pole-sized trees of two contrasting dipterocarp species in Sabah, Malaysia. **Biotropica** 38 (3): 437-440.

BERNACCI, L. C.; MARTINS, F. R.; SANTOS, F. A. M. 2008. Estrutura de estádios ontogenéticos em população nativa da palmeira *Syagrus romanzoffiana* (Cham.) Glassman (Arecaceae). **Acta Botânica Brasílica** 22 (1): 119-30.

BEGIN, C.; FILION, L. 1999. Black spruce (*Picea mariana*) architecture. **Canadian Journal of Botany** 77 (5): 664-672.

BARTHÉLÉMY, D.; CARAGLIO, Y. 2007. Plant architecture: a dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. **Annals of Botany** 99: 375-407.

BOEGE, K. 2005. Herbivore attack in *Casearia nitida* influenced by plant ontogenetic variation in foliage quality and plant architecture. **Oecologia** 143: 117-25.

BOHLMAN, S.; O´BRIEN, S. 2006. Allometry, adult stature and regeneration requirement of 65 tree species on Barro Colorado Island, Panama. **Journal of Tropical Ecology** 22: 123-136.

CARVALHO, R. M.; MARTINS, F. R.; SANTOS, F. A. M. 1999. Leaf ecology of pre-reproductive ontogenetic stages of the palm tree *Euterpe edulis* Mart. (Arecaceae). **Annals of Botany** 83: 225-233.

CASWELL, H. 2001. **Matrix population models**. Sinauer, Sunderland, Massachusetts, USA.

CIELO FILHO, R.; GNERI, M. A.; MARTINS, F. R. 2007. Position on slope, disturbance, and tree species coexistence in a Seasonal Semideciduous Forest in SE Brazil. **Plant Ecology** 190:189-203.

CIIAGRO 2007. **Boletim Climático: Campinas**. Centro integrado de informações agrometereológicas. Instituto Agronômico de Campinas, Campinas, Brazil.

CLARK, D. A.; CLARK, D. B. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. **Ecological Monographs** 62 (3): 315-344.

CONDIT, R.; SUKUMAR, R.; HUBBELL, S. P.; FOSTER, R. B. 1998 Predicting population trends from size distributions: a direct test in a tropical tree community. **American Naturalist** 152 (4): 495- 509.

COSTA FILHO, L. V.; NANNI, M. R.; CAMPOS, J. B. 2006. Floristic and phytosociological description of a riparian forest and the relationship with the edaphic environment in Caiuá Ecological Station, Paraná, Brazil. **Brazilian Archives of Biology and Technology** 49 (5): 785-798.

DAWKINS, H. C.; FIELD, D. R. B. 1978. **A long-term surveillance system for British woodland vegetation**. Oxford University, Oxford, England.

DEAN, T.; LONG, J. N. 1986. Validity of constant-stress and elastic instability principles of stem formation in *Pinus contorta* and *Trifolium pratense*. **Annals of Botany** 58: 833-840.

DEL QUIQUI, E. M.; MARTINS, S. S.; BROGHI, W. A.; SILVA, O. H.; SAKURAGUI, C. M.; PACHECO, R. B. 2007. Estudo fitossociológico de um trecho da floresta estacional semidecidual em Diamante do Norte, Estado do Paraná, Brasil. **Acta Scientia Agronômica** 29 (2): 283-290.

DIAS, H. C. T.; OLIVERIA-FILHO, A. T. 1996. Fenologia de quatro espécies arbóreas de uma floresta estacional semidecídua montana em Lavras, MG. **Revista CERNE** 2 (1): 66-68.

DURIGAN, G.; FRANCO, G. A. D.; SAITO, M.; BAITELLO, J. B. 2000. Estrutura e diversidade do componente arbóreo da floresta na Estação Ecológica dos Caetetus, Gália, SP. **Revista Brasileira de Botânica** 23 (4): 371-383.

EMBRAPA. 1999. **Sistema brasileiro de classificação dos solos**. Empresa Brasileira de Pesquisa Agropecuária – Centro Nacional de Pesquisas do Solo. Brasília, Brasil.

ENGEL, V. L.; MARTINS, F. R. 2005. Reproductive phenology of Atlantic forest tree species in Brazil: an eleven year study. **Tropical Ecology** 46 (1): 1-16.

ENRIQUEZ, B. L. L.; VESTER, H. F. M.; HALLÉ, F. 2008. The architecture of *Phyllanthus acuminatus* Vahl: a prelude to understanding the architectural evolution in the Phyllanthaceae. **Adansonia** 30 (1): 137-149.

FEELEY, K. J.; DAVIES, S. J.; NOOR, S. M.; KASSIM, A. R.; TAN, S. 2007. Do current stem size distributions predict future population changes? An empirical test of intraspecific patterns in tropical trees at two spatial scales. **Journal of Tropical Ecology** 23: 191-198.

FISCHER, E.; SANTOS, F. A. M. 2001. Demography, phenology and sex of *Calophyllum brasiliense* (Clusiaceae) trees in the Atlantic forest. **Journal of Tropical Ecology** 17:903-909.

GAP LIGHT ANALIZER version 2.0. 1990. Simon Frasier University, Burnabe, Canada.

GATSUK, L. E.; SMIRNOVA, O. V.; VORONTZOVA, L. I.; ZAUGOLNOVA, L. B.; ZHUKOVA, L. A. 1980. Age states of plants of various growth forms: a review. **Journal of Ecology** 68: 675-696.

GREIG-SMITH, P. 1983. **Quantitative plant ecology**. University of California, Berkeley, USA.

GRUBB, P. J. 1997. Maintenance of species-richness in plant communities: the importance of regeneration niche. **Biological Reviews of the Cambridge Philosophical Society** 52: 107-145.

HALLÉ, F.; OLDEMAN, R. A. A.; TOMLINSON, P. B. 1978. **Tropical trees and forests: an architectural analysis**. Springer-Verlag, New York, USA.

HOFFMANN, P. 2008. Revision of *Heterosavia*, stat. nov., with notes on *Gonatogyne* and *Savia* (Phyllanthaceae). **Brittonia** 60 (2): 136-166.

HOLBROOK, N. M.; PUTZ, F. E. 1989. Influence of neighbors on tree form: effects of lateral shade and prevention of sway on the allometry of *Liquidambar styraciflua* (Sweet Gum). **American Journal of Botany** 76 (12): 1740-1749.

HORVITZ, C. C., SCHEMSKE, D. W.; CASWELL, H. 1997. The relative importance of life-history stages to population growth: prospective and retrospective analyses. *In*: Tuljapurkar S.; Caswell H. **Structured-population models in marine, terrestrial and freshwater systems**. Chapman & Hall, New York, USA. 247–272 pp.

INSTITUTO GEOLÓGICO. 1993. **Subsídios do meio físico e geológico ao planejamento do município de Campinas**. Secretaria de Planejamento e meio Ambiente, Prefeitura Municipal de Campinas, Campinas, São Paulo, Brasil.

JANZEN, D. H. 1978. Seeding patterns of tropical trees. *In*: Tomlinson, P.B.; Zimmermann, M.H. **Tropical Trees as Living Systems**. Cambridge University Press, Cambridge. 83-127 pp.

KANG, H.; BAWA, K. S. 2003. Effects of successional status, habitat, sexual systems, and pollinators on the flowering patterns in tropical rain forest trees. **American Journal of Botany** 90 (6): 865–876.

KATHRIARACHCHIA, H.; HOFFMANN, P.; SAMUEL, R.; WURDACK, K. J. CHASE, M.W. 2005 Molecular phylogenetics of Phyllanthaceae inferred from Wve genes (plastid *atpB*, *matK*, *3'ndhF*, *rbcL*, and nuclear *PHYC*). **Molecular Phylogenetics and Evolution** 36: 112-134.

KAWAKITA, A.; KATO, M. 2009. Repeated independent evolution of obligate pollination mutualism in the Phyllantheae-*Epicephala* association. **Proceedings of the Royal Society B** 276: 417-426.

KING, D. A. 1991. Correlations between biomass allocation, relative growth rate and light environment in tropical forest saplings. **Functional Ecology** 5 (4): 485-492.

KING, D. A. 1994. Influence of light level on the growth and morphology of saplings in a Panamanian forest. **American Journal of Botany** 81 (8): 948-957.

KING, D. A. 1996. Allometry and life history of tropical trees. **Journal of Tropical Ecology** 12 (1): 25-44.

KNIGHT, T. M.; BARFIELD, M.; HOLTH, R. D. 2008. Evolutionary dynamics as a component of stage-structured matrix-models: an example using *Trillium grandiflorum*. **American Naturalist** 172 (3): 375-392.

KOHYAMA, T.; HOTTA, M. 1990. Significance of allometry in tropical saplings. **Functional Ecology** 4 (4): 515-521.

LEHTILÄ, K.; SYRJÄNEN, K.; LEIMU, R.; GARCIA, M. B.; EHRLÉN, J. 2006. Habitat change and demography of *Primula veris*: identification of management targets. **Conservation Biology** 20 (3): 833-843

LORENZI, H. 1992. **Árvores brasileiras: manual de identificação e cultivo de plantas arbóreas nativas do Brasil**. Plantarum, Nova Odessa.

MARTÍNEZ, A. J.; LÓPEZ-PORTILLO, J. 2003. Allometry of *Prosopis glandulosa* var. *torreyana* along a topographic gradient in the Chihuahuan desert. **Journal of Vegetation Science** 14: 111-120.

MCGILL, R.; TUKEY, J. W.; LARSEN, W. A. 1978. Variations of box plots. **American Statistician** 32: 12-16.

MCMAHON, T. A. Size and shape in biology. 1973. **Science** 179: 1201-1204.

MIRANDA-MELO, A. A.; MARTINS, F. R.; SANTOS, F. A. M. 2007. Estrutura populacional de *Xylopia aromatica* (Lam.) Mart. e de *Roupala montana* Aubl. em fragmentos de cerrado no Estado de São Paulo. **Revista Brasileira de Botânica** 30 (3): 501-507.

MOORA, M.; KOSE, M.; JÕGAR, Ü. 2007. Optimal management of the rare *Gladiolus imbricatus* in Estonian coastal meadows indicated by its population structure. **Applied Vegetation Science** 10: 161-168.

MULLER-LANDAU, H. C. 2004. Interspecific and inter-site variation in wood specific gravity of tropical trees. **Biotropica** 36: 20-32.

NASCIMENTO, H. E. M.; LAURENCE, W. F.; CONDIT, R.; LAURENCE, S. G.; D'ANGELO, S.; ANDRADE, A. C. 2005. Demographic and life-history correlates for Amazonian trees. **Journal of Vegetation Science** 16: 625-634.

NIKLAS, K. J. 1995. Size-dependent allometry of tree height, diameter and trunk taper. **Annals of Botany** 75: 217-227.

O'BRIEN, S. T.; HUBBELL, S. P.; SPIRO, P.; CONDIT, R.; FOSTER, R. B. R. B. 1995. Diameter, height, crown, and age relationship in eight neotropical tree species. **Ecology** 76 (6): 1926-1939.

OCTAVIO-AGUILAR, P.; GONZÁLEZ-ASTORGA, J.; VOVIDES, A. P 2008. Population dynamics of the Mexican cycad *Dioon edule* Lindl. (Zamiaceae):

life history stages and management impact. **Journal of Linnean Society** 157: 381-391.

OLDEMAN, R.A.A. 1990. **Forest: elements of silvology**. Springer-Verlag, Berlin, Germany.

OSADA, N.; TATENO, R.; HYODO, F.; TAKEDA, H. 2004 Changes in crown architecture with tree height in two deciduous tree species: developmental constraints or plastic response to the competition for light? **Forest Ecology and Management** 188: 337-347.

OSUNKOYA, O. O.; OMAR-ALI, K.; AMIT, N.; DAYAN, J.; DAUD, D. S.; SHENG, T. K. 2007. Comparative height-crown allometry and mechanical design in 22 tree species of Kuala Belalong rainforest, Brunei, Borneo. **American Journal of Botany** 94 (12): 1951-1962.

PINTO, L. V. A; BOTELHO, S. A.; OLIVEIRA-FILHO, A. T.; DAVID, A. C. 2005. Estudo da vegetação como subsídios para propostas de recuperação das nascentes da bacia hidrográfica Ribeirão das Cruzes, Lavras, MG. **Revista Árvore** 29 (5): 775-794.

POORTER, L.; BONGERS, F.; STERCK, F. J.; WÖLL, H. 2005. Beyond the regeneration phase: differentiation of height–light trajectories among tropical tree species. **Journal of Ecology** 93: 256-267.

RESSEL, K.; GUILHERME, F. A. G.; SCHIAVINI, I.; OLIVEIRA, P. E. 2004. Functional morphology and ecology of tree species seedlings of the Ecological Station of Panga, Uberlândia, Minas Gerais. **Revista Brasileira de Botânica** 27 (2): 311-323.

RIBEIRO, M. C.; METZGER, J. P.; MARTESEN, A. C.; PONZONI, F. J.; HIROTA, M. M. 2009. The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? **Biological Conservation** 142: 1141-1153.

ROCHA, C. T. V.; CARVALHO, D. A.; FONTES, M. A.; OLIVEIRA-FILHO, A. T.; VAN DER BERG, E.; MARQUES, J. J. 2005. Comunidade arbórea de um continuum entre floresta paludosa e de encosta em Coqueiral, Minas Gerais, Brasil. **Revista Brasileira de Botânica** 28 (2): 203-218.

ROCHA, O. J.; VÍLCHEZ, B.; ANCHETTA, A. L. A. 2006.A mast fruiting episode of the tropical tree *Peltogyne purpúrea* (Caesalpinaceae) in the Osa Peninsula, Costa Rica. **Revista de Biologia Tropical** 54 (4): 1151-1155.

ROJAS-ROBLES, R.; STILES, F. G. 2009. Analysis of a supra-annual cycle: reproductive phenology of the palm *Oenocarpus bataua* in a forest of the Colombian Andes. **Journal of Tropical Ecology** 25: 41-51.

ROSSETO, V. **Aspectos da história de vida de quatro espécies de *Trichillia* (Meliaceae) na Reserva de Santa Genebra, Campinas**. 2007. Master Thesis. Universidade Estadual de Campinas, Campinas, São Paulo, Brazil.

SAMUEL, R.; KATHRIARACHCHI, H.; HOFFMANN, P.; BARFUSS, M. H. J.; WURDACK, K. J.; DAVIS, C. C.; CHASE, M. W. 2005. Molecular phylogenetics of Phyllanthaceae: evidence from plasticid *matK* and nuclear *PHYC* sequences. **American Journal of Botany** 92 (1): 132-141.

SANTOS, F. A. M. 1997. **Ancova33: Programa para cálculo de regressão e covariância. Versão 3.3**. Departamento de Botânica. Universidade Estadual de Campinas, Campinas, Brasil.

SCHNITZER, S.A.; KUZEE, M. E.; BONGERS, F. 2005. Disentangling above- and below-ground competition between lianas and trees in a tropical forest. **Journal of Ecology** 93: 1115-1125.

SMIRNOVA, O. V.; PALENOVA, M. M.; KOMAROV, A. S. 2002. Ontogeny of different life forms of plants and specific features of age and spatial structure of their populations. **Russian Journal of Developmental Biology** 33: 1-10.

SOUZA, A. F. 2007. Ecological interpretation of multiple population size structures in trees: The case of *Araucaria angustifolia* in South America. **Austral Ecology** 32: 524-533.

SOUZA, A. F.; MARTINS, F. R. 2005. Spatial variation and dynamics of flooding, canopy openness, and structure in a Neotropical swamp forest. **Plant Ecology** 180: 161-173.

SOUZA, A. F.; MARTINS, F. R.; BERNACCI, L. C. 2003. Clonal growth and reproductive strategies of the understory tropical palm *Geonoma brevispatha*:

an ontogenetic approach. **Canadian Journal of Botany** 81: 101-112.

SOUZA, A. F.; MARTINS, F. R.; MATOS, D. M. S. 2000. Detecting ontogenetic stages of the palm *Attalea humilis* in fragments of the Brazilian Atlantic forest. **Canadian Journal of Botany** 78: 1227-1237.

SOUZA, V. C.; LORENZI, H. 2005. **Botânica Sistemática: Guia para identificação das famílias de Angiospermas da flora brasileira, segundo APG II**. Plantarum, Nova Odessa, Brasil.

SPOSITO, T. C.; SANTOS, F. A. M. 2001. Scaling of stem and crown in eight *Cecropia* (Cecropiaceae) species of Brazil. **American Journal of Botany** 88: 939–949.

STERCK, F. J.; BONGERS, F. 1998. Ontogenetic changes in size, allometry, and mechanical design of tropical rain forest trees. **American Journal of Botany** 85 (2): 266-272.

STERCK, F. J.; BONGERS, F.; NEWBERY, D. M. 2001. Tree architecture in a Bornean lowland rain forest: intraspecific and interspecific patterns. **Plant Ecology** 153: 279-292.

STERCK, F. J.; MARTÍNEZ-RAMOS, M.; DYER-LEAL, G.; RODRÍGUEZ-VELAZQUEZ, J.; POORTER, L. 2003. The consequences of crown traits for the growth and survival of tree saplings in a Mexican lowland rainforest. **Functional Ecology** 17: 194-200.

TOMLINSON, P. B. 1987. Architecture of tropical trees. **Annual Review in Ecology and Systematics** 18: 1-21.

VAN GELDER, H. A.; POORTER, L.; STERCK, F. J. 2006. Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community. **New Phytologist** 171: 367-378.

WELLINGTON, A.B.; NOBLE, I.R. 1985. Post-fire recruitment and mortality in a population of the mallee *Euclyptus incrassata* in semi-arid, south-eastern **Australian Journal of Ecology** 73: 645-656

WILKINSON, L. 2007. **Systat 12: Graphics**. Systat Software Inc. San Jose, California, USA.

WRIGHT, S. J.; MULLER-LANDAU, H. C.; CONDIT, R.; HUBBELL, S. P. 2003 Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. **Ecology** 84 (12): 3174-3185

WURDACK, K. J.; HOFFMANN, P.; SAMUEL, R.; BRUIJN, A.; VAN DER BANK, M.; CHASE, M. 2004. Molecular phylogenetic analysis of Phyllanthaceae (Phyllanthoideae pro parte Euphorbiaceae *sensu lato*) using plastid *rbcL* DNA sequences. **American Journal of Botany** 91 (11): 1882-1900.

YAMADA, T.; TAN, S.; YAMAKURA, T. 2006. Interspecific patterns underlying variations in allometric relationship of sympatric Sterculiaceae species in a Bornean rainforest. **Trends in Ecology and Evolution** 20: 186-195.

ZAR, J. H.1996. **Biostatistical analysis**. Prentice-Hall, New Jersey, USA.

ZHUKOVA, L. A.; GLOTOV, N. V. 2001. Morphological polyvariance of ontogeny in natural plant populations. **Russian Journal of Developmental Biology** 32: 381-387.

Table 1. Definition of levels of Crown Illumination Index, proposed by Clark & Clark 1992.

Level	Definition
5	Crown completely exposed (to vertical light and to lateral light within the 90° inverted cone encompassing the crown)
4	Full overhead light (≥ 90% of the vertical projection of the crown exposed to vertical light; lateral light blocked within some or all of the 90° inverted cone encompassing the crown)
3	Some overhead light (10-90% of the vertical projection of the crown exposed to vertical light). Lateral light (<10% of the vertical projection of the crown exposed to vertical light; crown lit)
2,5	High lateral light
2	Medium lateral light
1,5	Low lateral light
1	No direct light (crown not lit directly either vertically or laterally)

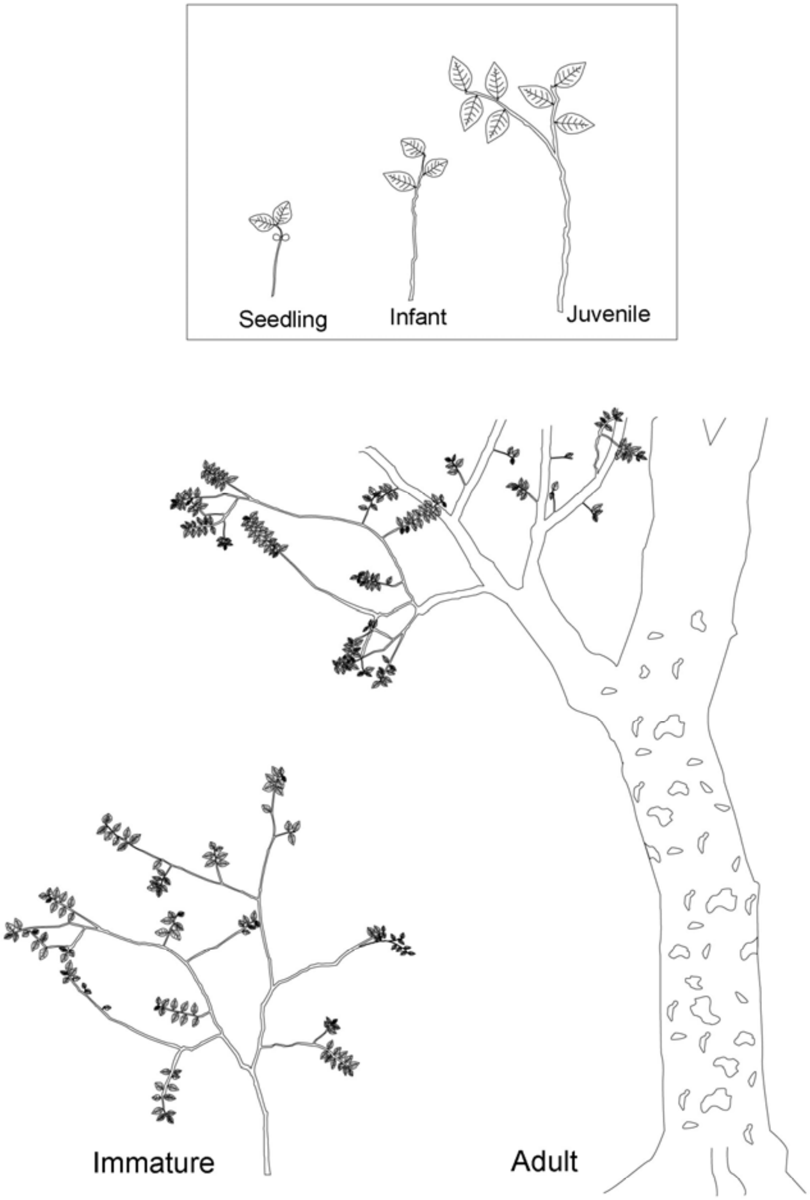

Figure 1. Ontogenetic Stages of *Savia dictyocarpa* (Phyllanthaceae) by Ligia Sims & Luiz Dias.

Table 2. Size variables of each ontogenetic stage of *Savia dictyocarpa* species. Min.= minimum, Max.= maximum, Med.= median, A. Me. = arithmetic mean, S. D. = standard deviation, N = number of individuals.

Stages	Min.	Max.	Med.	A. Me.	S. D.	N
Grown level diameter (cm)						
Infant	0,10	0,80	0,50	0,50	0,30	4
Juvenile	0,10	2,20	0,50	0,60	0,30	51
Immature	0,30	10,80	1,60	2,10	1,70	69
Adult	1,20	67,00	10,60	14,00	12,00	67
Senile	2,90	16,90	7,70	9,50	5,70	7
Height (m)						
Infant	0,07	0,10	0,10	0,09	0,01	4
Juvenile	0,12	0,79	0,39	0,41	0,20	51
Immature	0,51	5,00	1,55	1,93	1,21	69
Adult	4,50	28,00	10,00	10,6	4,54	67
Senile	0,90	10,00	3,80	4,27	3,08	7
Crown Width (m)						
Infant	0,04	0,06	0,05	0,05	0,01	4
Juvenile	0,03	0,55	0,21	0,21	0,12	51
Immature	0,20	2,45	0,69	0,87	0,55	69
Adult	1,47	12,5	4,00	4,00	1,67	67
Senile	0,38	6,81	1,92	2,56	2,04	7
Crown Length (m)						
Infant	0,00	0,10	0,08	0,07	0,05	4
Juvenile	0,02	0,68	0,12	0,20	0,17	51
Immature	0,05	3,90	0,60	0,80	0,66	69
Adult	0,50	12,00	4,50	4,56	2,73	67
Senile	0,20	5,00	1,60	2,27	1,84	7

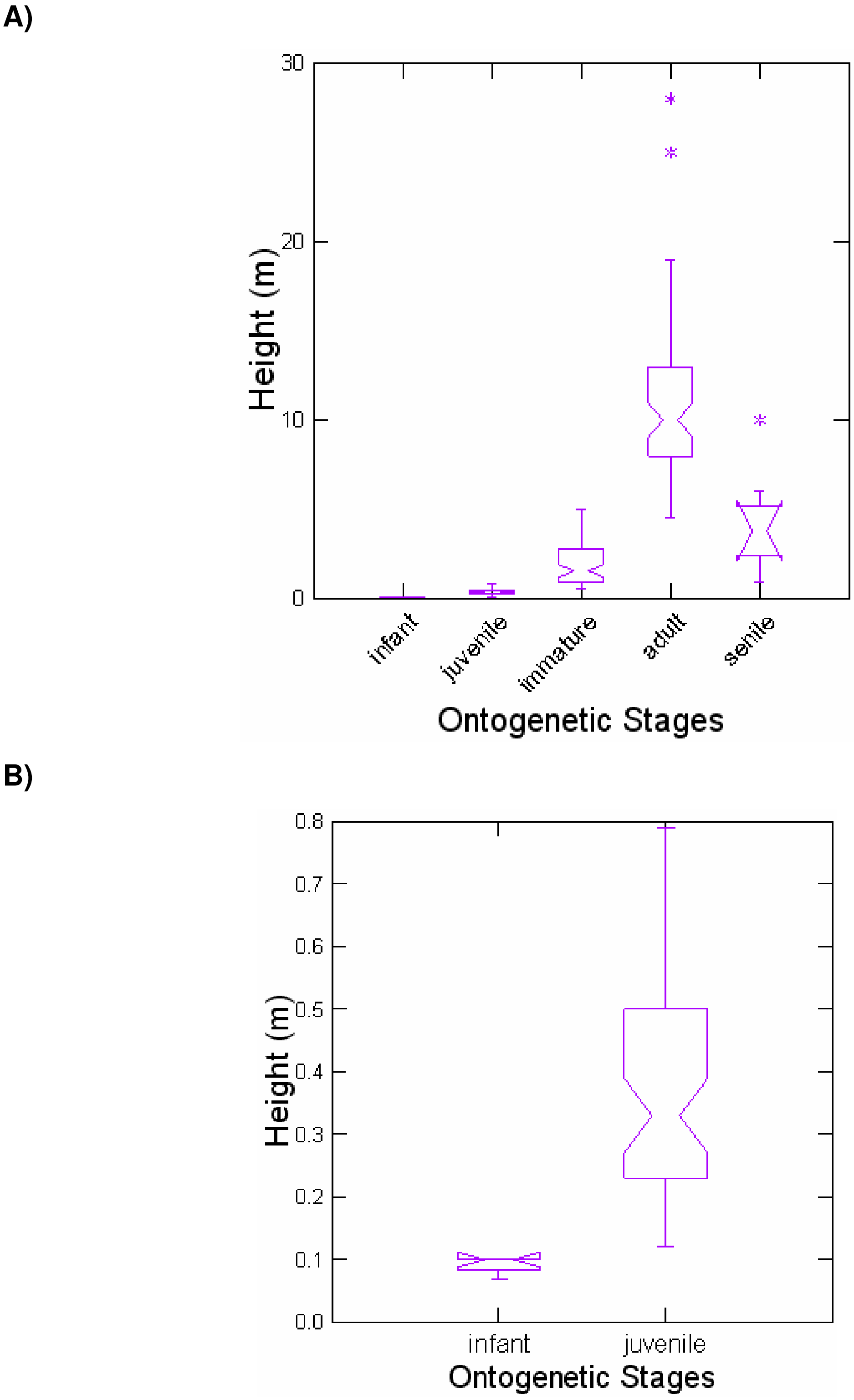

Figure 2. A. Box plot of height (m) of ontogenetic stages of *Savia dictyocarpa*, excepting Seedling. B. Box Plot of Infant and Juvenile stages, highlighting the difference between these two stages of *Savia dictyocarpa*.

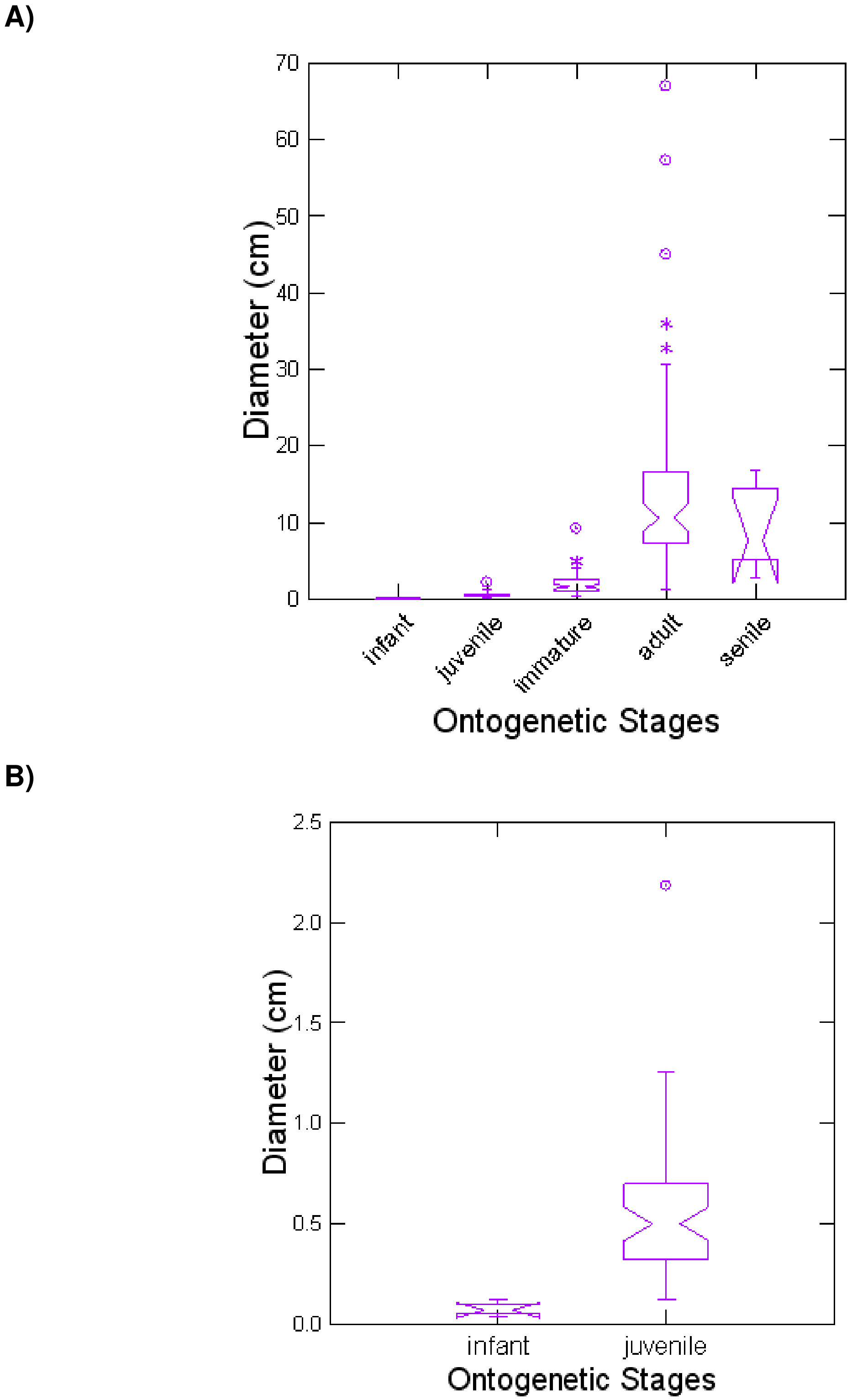

Figure 3. A. Box plot of diameter (cm) of ontogenetic stages of *Savia dictyocarpa*, excepting Seedling. B. Box Plot of diameter (cm) of Infant and Juvenile stages, highlighting the difference between these two stages of *Savia dictyocarpa*.

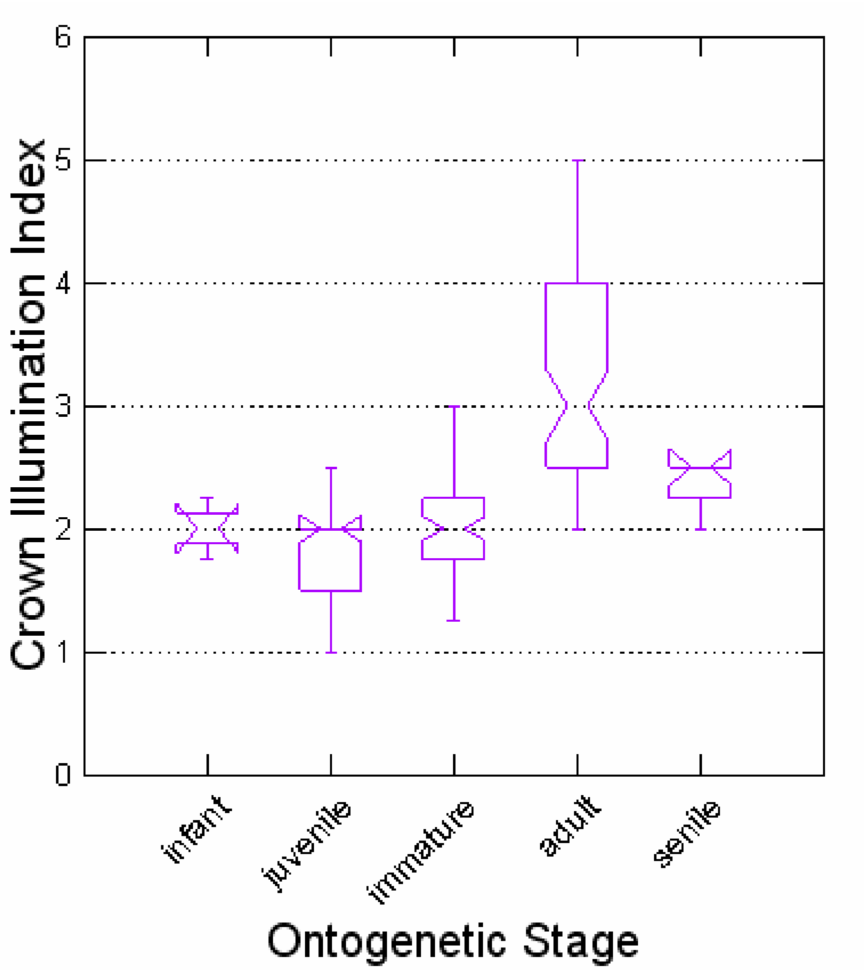

Figure 4. A. Box plot of Crown Illumination Index (CII) of ontogenetic stages of *Savia dictyocarpa*, excepting Seedling. B.

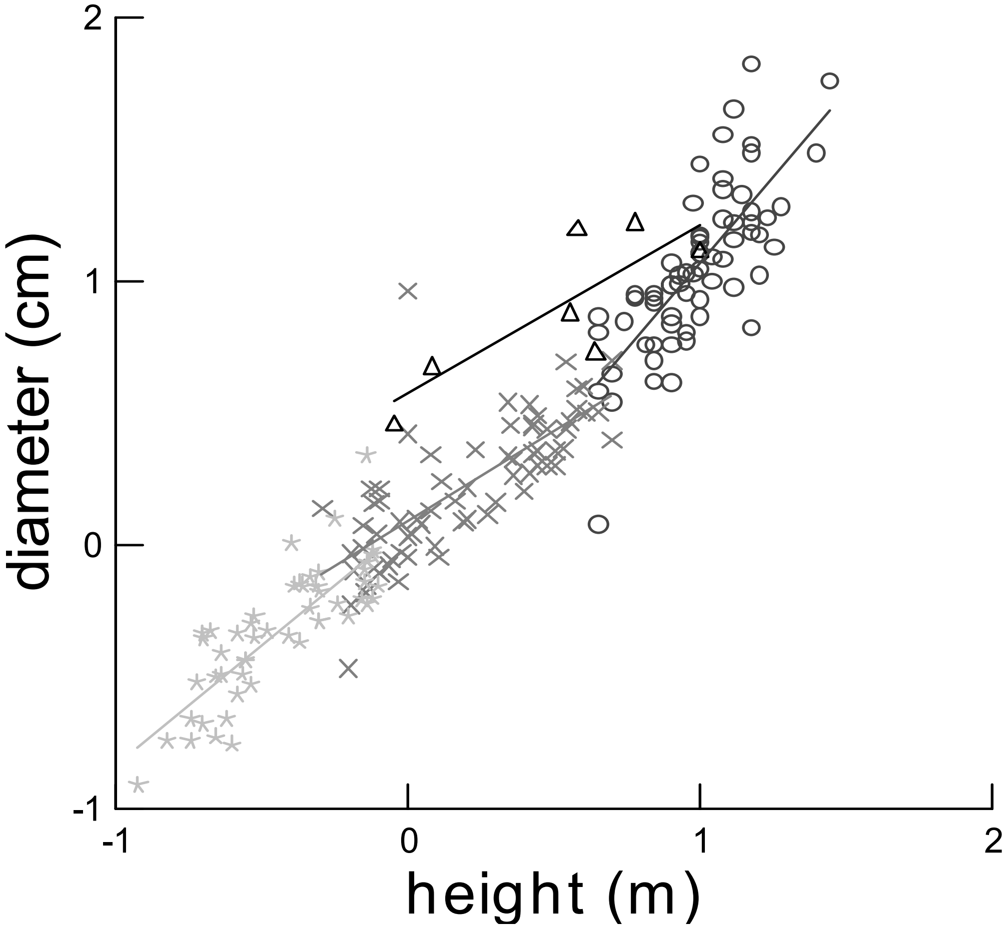

Figure 5. Regressions of log10 stem diameter (cm) vs. log10 height (m) for each ontogenetic stage of *Savia dictyocarpa* in a tropical semideciduous forest (SE/Brazil). Jv = Juvenile (★), Im= Immature (x), Ad= Adult (o), Sn= Senile (Δ).

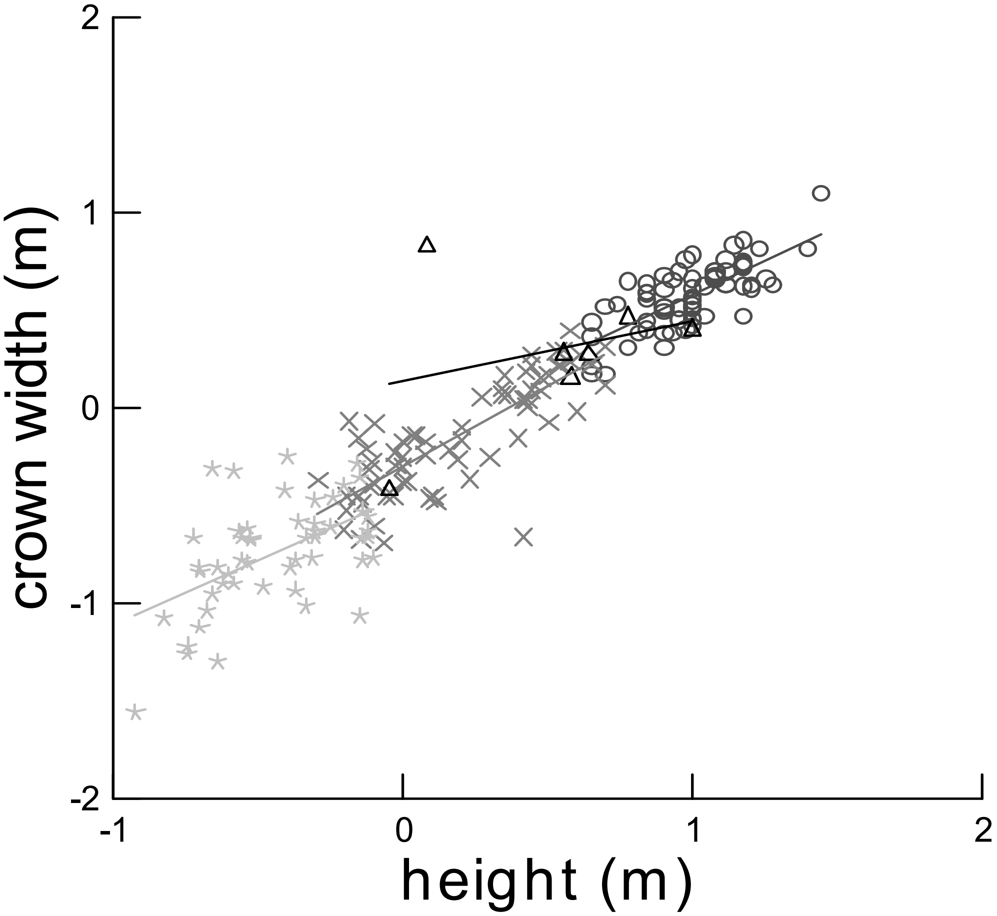

Figure 6. Regressions of log10 crown width (m) vs. log10 height (m) for each ontogenetic stage of *Savia dictyocarpa* in a tropical semideciduous forest (SE/Brazil). Jv = Juvenile (★), Im= Immature (x), Ad= Adult (o), Sn= Senile (Δ).

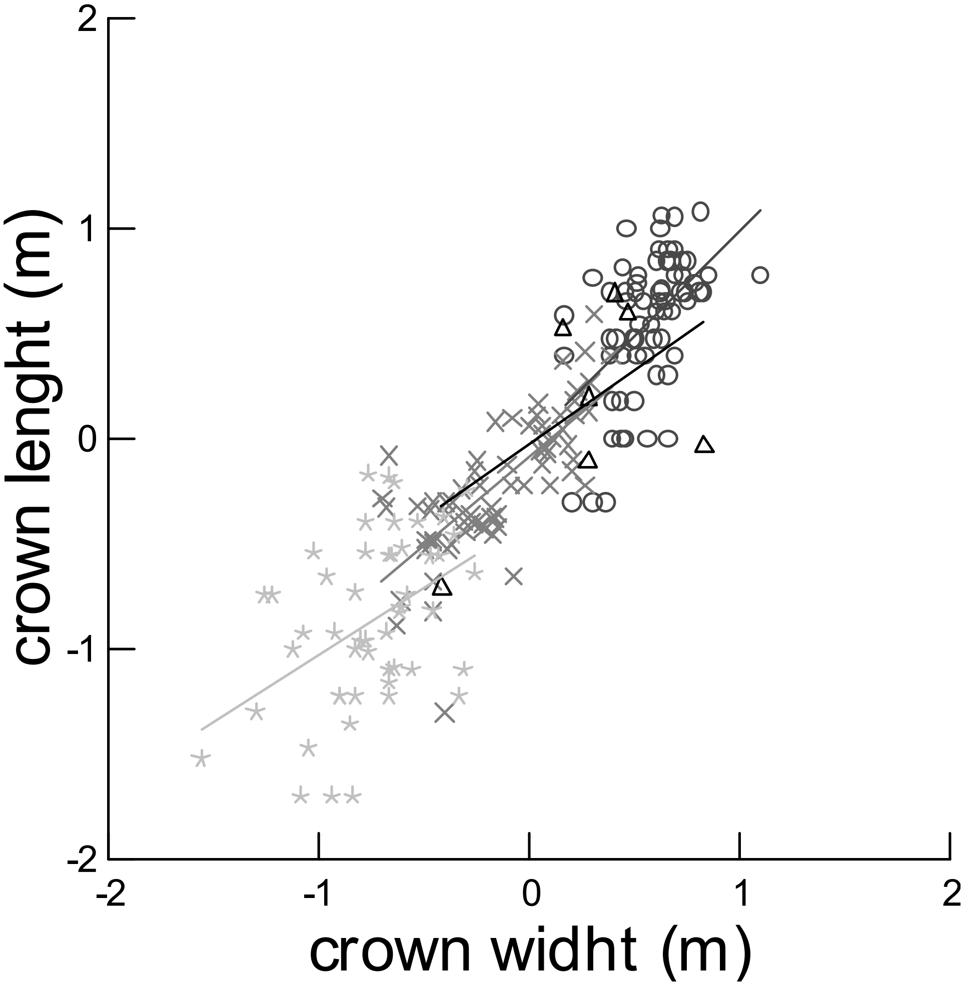

Figure 7. Regressions of log10 crown length (m) vs. log10 crown width (m) for each ontogenetic stage of *Savia dictyocarpa* in a tropical semideciduous forest (SE/Brazil). Jv = Juvenile (★), Im= Immature (x), Ad= Adult (o), Sn= Senile (Δ).

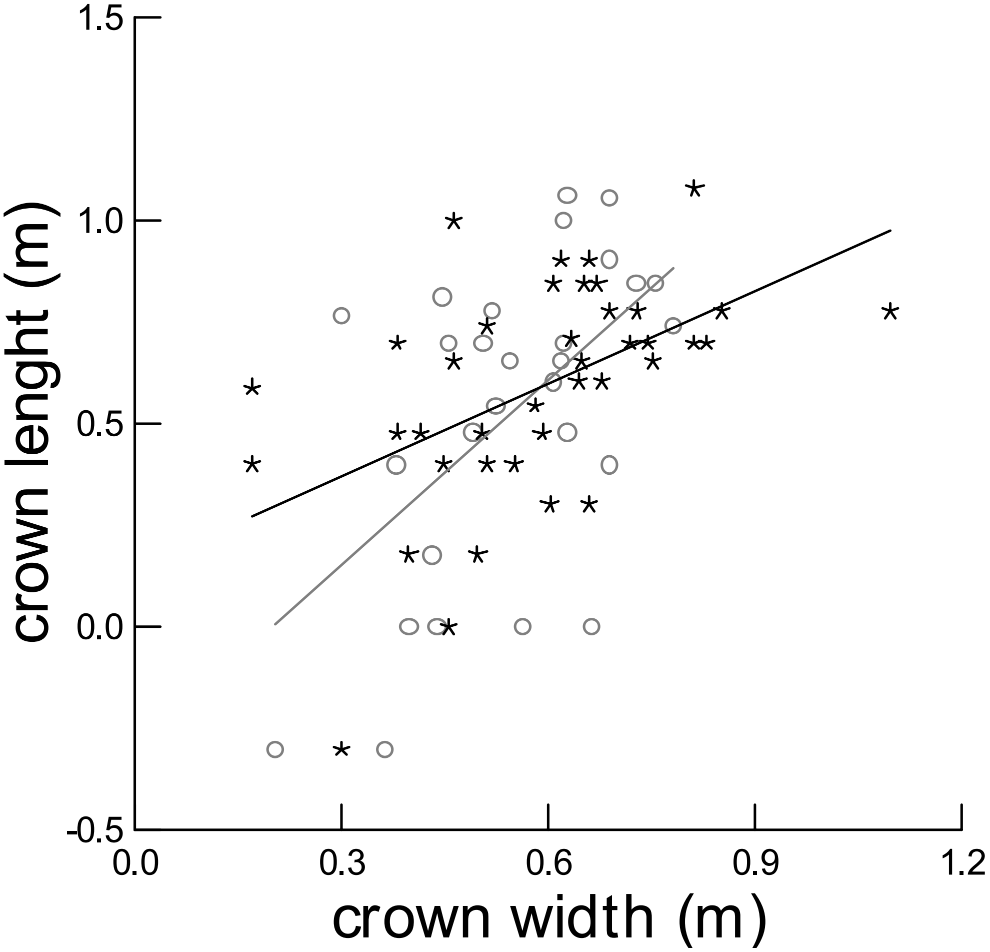

Figure 8. Regressions of log10 crown length (m) vs. log10 crown width (m) for each adult stage of *Savia dictyocarpa* with (⋆) or without (o) liana infestation in a tropical semideciduous forest (SE/Brazil). N with liana = 39, N without liana = 28.

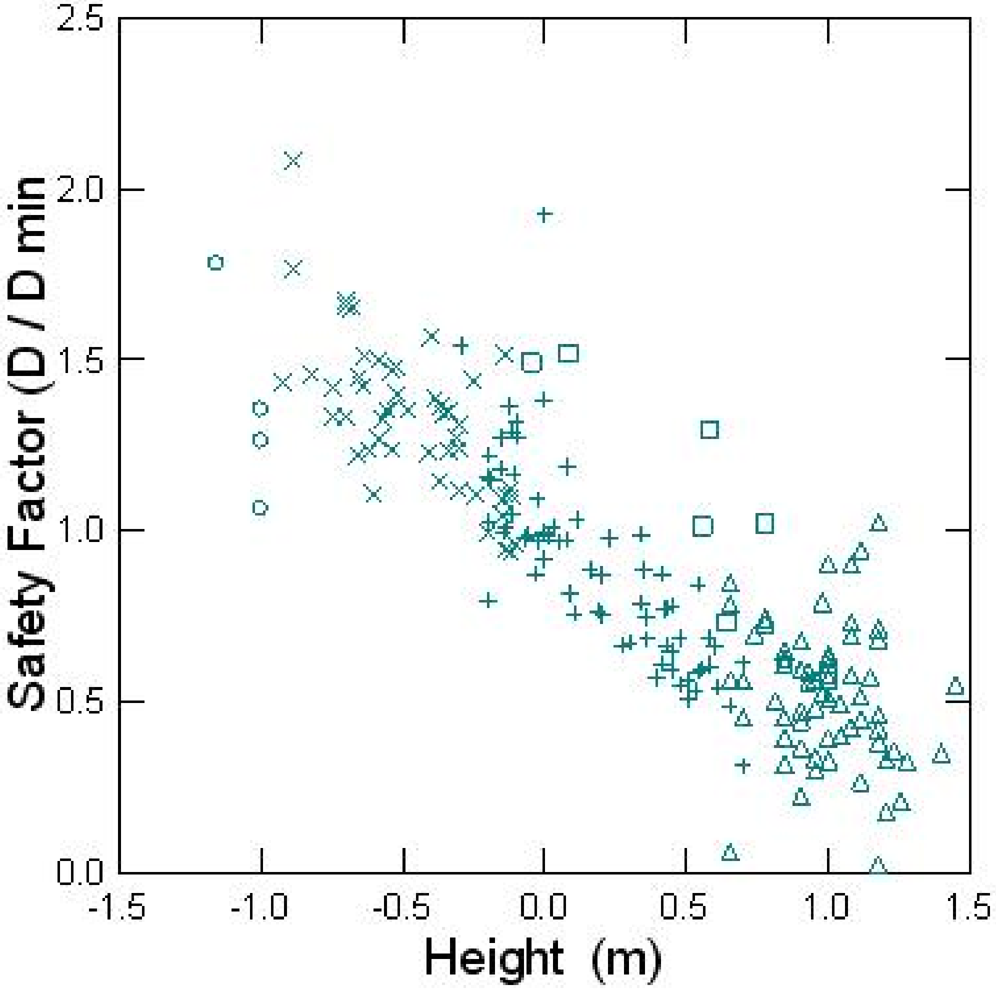

Figure 9. Function of log10 Stability Safety Factor (D/Dmin) vs. log10 Height (m) for *Savia dictyocarpa* in a tropical semideciduous forest (SE, Brazil). D is the observed diameter and D min is the minimum diameter that a plant should have to maintain its own weight (Dmin = 0.109 $h^{3/2}$) (McMahon 1973). In= Infant (o), Jv = Juvenile (x), Im= Immature (+), Ad= Adult (Δ), Sn= Senile (□).

Table 3. Linear regression coefficients of $\log_{10}$ diameter (cm) and $\log_{10}$ height (m), for each ontogenetic stage of *Savia dictyocarpa*. N= sample size; a= intercept; b = slope; r^2 = coefficient of determination; P = confidence intervals. Values within a column for intercept and slope sharing a different letter differ significantly (ANCOVA and Scheffé test, $P < 0,005$, except for Population).

Ontogenetic Stages	**N**	**A**	**b**	**R^2**	**P**
Juvenile	51	0,08 ^{a}	0,92 ^{b,c}	0,68	<0,01
Immature	69	0,06 ^{a}	0,73 ^{b}	0,72	<0,01
Adult	67	-0,24	1,30 ^{c}	0,58	<0,01
Senile	6	0,66	0,55 ^{b}	0,57	<0,05
Population	198	0,07	0,98	0,92	<0,01

Table 4. T test for the slope (b) of linear regression of each stages of *Savia dictyocarpa* and the slope of each allometric relationship models: b=1 (geometric similarity), b=1,5 (elastic similarity), b=2 (stress). We just show the results for best fitting relations.

Ontogenetic Stages	**N**	**b**	**Models**	**P**
Juvenile	51	0,92	geometric similarity	0,35
Immature	69	0,73	geometric similarity	< 0,01
Adult	67	1,22	elastic similarity	0,15
Senile	6	0,64	geometric similarity	0,19
Population	198	0,98	geometric similarity	0,31

Table 5. Linear regressions coefficients of $\log_{10}$ crown width (m) vs. $\log_{10}$ height (m) and $\log_{10}$ crown width (m) vs. $\log_{10}$ length (m) for *Savia dictyocarpa*. N= sample size; a= intercept; b = slope; r^2 = coefficient of determination; P = confidence intervals. Values within a column for intercept and slope sharing a different letter differ significantly (ANCOVA and Scheffé test, $P < 0,005$, except for Population).

Ontogenetic Stages	N	a	b	R^2	P
Crown Width (m) vs. Height (m)					
Juvenile	51	-0,45 ^{a}	0,67	0,29	< 0,01
Immature	69	-0,31	0,82	0,64	< 0,01
Adult	67	-0,13 ^{b}	0,70	0,53	< 0,01
Senile	6	0,13	0,31	0,09	0,51
Population	198	-0,32	0,88	0,88	< 0,01
Crown Length (m) vs. Crown Width (m)					
Juvenile	51	-0,40	0,63	0,18	< 0,01
Immature	69	-0,09	0,84	0,52	< 0,01
Adult	67	-0,07	0,91	0,28	< 0,01
Senile	6	-0,03	0,70	0,28	0,21
Population	194	-0,04	1,05	0,81	< 0,01

Table 6. Allometric differences in diameter, crown width and crown length were tested within *S. dictyocarpa* Adult stage for plants with or without Lianas. Linear regression coefficients of $\log_{10}$ diameter (cm) and $\log_{10}$ height (m), $\log_{10}$ crown width (m) vs. $\log_{10}$ height (m) and $\log_{10}$ crown width (m) vs. $\log_{10}$ crown length (m) were performed for each situation. N= sample size; a= intercept; b = slope; r^2 = coefficient of determination; P = confidence intervals. Values within a column for intercept and slope sharing a different letter differ significantly (ANCOVA and Scheffé test, $P < 0,005$).

Adult Stage	N	a	b	R^2	P
Tree Diameter vs.Tree Height					
With Liana	39	0,06	1,12	0,63	< 0,01
Without Liana	28	0,55	1,63	0,57	< 0,01
Crown Width vs. Tree Height					
With Liana	39	0,13	0,72	0,51	< 0,01
Without Liana	28	0,09	0,66	0,57	< 0,01
Crown Length vs. Crown Width					
With Liana	39	0,18	0,70 ^{a}	0,25	< 0,01
Without Liana	28	0,22	1,50 ^{b}	0,40	< 0,01

Capítulo 2

Soil nutrients, light, and the spatial distribution of a tropical canopy tree

Ligia Paulillo Sims [1], Fernando R. Martins [2]

1. Ecology Graduate Program, Institute of Biology, P.O.Box 6109, University of Campinas – UNICAMP, 13083-970 Campinas, SP, Brazil.

2. Department of Plant Biology, Institute of Biology, P.O.Box 6109, University of Campinas – UNICAMP, 13083-970 Campinas, SP, Brazil.

Abstract

In tropical forests variation of resources, factors, and biotic interactions generate great environmental heterogeneity in space and time, thus creating a patchy environment, in which microsites have different conditions that change along time. This heterogeneity influences plant distribution in space and time, so that recruitment can be highly influenced by favorable spots, especially by light and soil. Soils variables are important determinants of plant growth and influence plant spatial distribution. Canopy heterogeneity in tropical forests creates many different light conditions so it is hypothesized that different tree species specialize to thrive in different light conditions and then coexist in this highly competitive habitat. The effect of each environmental filter changes during plant ontogeny, generating a specific spatial pattern. One way to assess which microsite is preferred by a species is to analyze the population spatial distribution. Our major goal was to investigate the expectations that the spatial pattern of *Savia dictyocarpa* population changes along ontogeny and that established ontogenetic stages are associated with environmental variables. We sampled this species in 50 plots of 100 m^2 in a 233,7 ha fragment of Seasonal Semideciduous Forest in Campinas municipality, SE, Brazil. We took one hemispherical photograph of the canopy from the center of each plot and collected a surface soil sample from the center of each plot. From each stage and environmental factor we tested the spatial autocorrelation with Moran's I coefficient and correlograms. Total and Partial Mantel were performed to analyze the relation between each ontogenetic stage and the environmental characteristics. We sampled 51 juveniles, 69 immatures, 67 adults and 6 seniles. Seedlings were not found and infants were few. All the correlograms were not globally significant, except for fine sand, indicating the objects were randomly distributed in space. Correlations were spurious and non significant for ontogenetic stages and all light, soil and biotic characteristics except for positive relation between juvenile and immature; immature and senile; clay and senile; fine sand and senile. This lack of shift from random pattern throughout the ontogeny is not usual in tropical tree species and could not be explained by the variables we measured. It is possible that the random pattern of ontogenetic stages is related to other factors that we did not consider here. Also, it is possible that the spatial distribution of all stages is strongly related to seed, seedling and infant establishment and mortality. Seedling survival could have been affected by random spatial distribution of some biotic or abiotic factor, leading to random distribution, and this pattern would be kept in later stages, suggesting that the definitive spatial pattern of the individuals is printed early in the ontogeny. The positive spatial association between juvenile and immature could indicate that these stages are recruited and grow in the same environment. Immature and senile correlation indicates that immatures have higher risk to suffer injuries on the understorey. The absence of correlations between the stages and biotic and abiotic variables indicate that mortality, survival, and recruitment of individuals in the population of *S. dictyocarpa* could rely on processes that are totally stochastic in space and time.

Key-words: Environmental Heterogeneity, Seasonal Semideciduous Forest, Environmental Filter.

Introduction

A tropical forest is a mosaic of different successional stages in degradation and regeneration, caused by total or partial death of trees, and constituted by eco-units of reorganization, development, maturity, and degeneration (Oldeman 1990). The silvatic mosaic and the variation of resources, factors, and biotic interactions generate great environmental heterogeneity in space and time, thus creating a patchy environment, in which microsites have different conditions that change along time. In the last decades, this environmental heterogeneity has been associated with the existence of different plant regeneration niches and promotion of high tree species diversity in tropical forests (Grubb 1977, Denslow 1980, 1987). The regeneration niche or the life history of a tree population encompasses all the processes involved in the replacement of adults by others in the next generation (Grubb 1977). Forest environmental heterogeneity influences plant distribution in space and time, so that recruitment of young stages can be highly influenced by favorable spots, especially by light and soil characteristics (Comita *et al*. 2007).

Soils can exhibit significant heterogeneity on intermediate and fine spatial scales, and relatively minor differences in soil properties can be important determinants of plant growth (Hall *et al*. 2004). A variety of soil variables have been related to the spatial distribution of tropical trees, such as phosphorus, calcium, magnesium, potassium, and aluminum contents, soil porosity, and water availability (Sollins 1998, Hall *et al*. 2004, Palmiotto *et al*. 2004, Paoli *et al*. 2005). Clark & Clark (1999) found that almost 30% of the species of their studied area showed to be edaphically biased on a mesoscale landscape. Comita *et al.* (2007) also found an association of species distribution with soil variables and pointed that habitat associations of large trees typically do not form when they are young; rather, many species appear to exhibit different ecological habitat preferences across life stages.

Canopy heterogeneity in tropical forests creates many different light conditions, which affect forest lower layers (Svenning 2001). This spatial heterogeneity of light can be related to gaps, structural complexity and/or deciduousness of the canopy (Bianchini *et al.* 2001). When compared to other tropical forests, the Seasonal Semideciduous Forest, such as the fragments scattered in the hinterland of southeastern Brazil, has a higher rate of gap disturbances due to tree uprooting and branch fall (Martini *et al.* 2008). Moreover, about 30% of the trees in the canopy of the Seasonal Semideciduous Forest shed their leaves in the dry season, creating periodical deciduousness gaps and enlarging light heterogeneity in the understory (Gandolfi 2003).

Due to this heterogeneity of light environments in the forest, different tree species specialize to thrive in different conditions and coexist in this highly competitive habitat (Wright *et al.* 2003). Tropical forest trees are thought to be different regeneration strategists that are specialized in different light levels: 1) pioneers that need high light levels and normally are gap colonizers; 2) secondary species that are able to exploit intermediate light levels such as small canopy gaps; 3) and climax species that recruit seedlings only under closed canopy (Swaine & Whitmore 1988, Whitmore 1996). This classification is a simplification of a species specialization gradient between light and dark (Wright *et al.* 2003) that emerged from studies demonstrating shifts in tree species light requirements from seedling to adult stage (Clark & Clark 1992; Dalling *et al*. 2001). The changing light requirements along ontogeny affect mortality, growth and recruitment rates and, hence, influence spatial distribution of plants. Therefore, due to the existence of a variety of life histories, different species occupy and/or prefer distinct microsites in the forest. One way to assess which microsite is preferred by a species is to analyze the population spatial distribution.

The spatial distribution of tropical forest trees has been investigated in many ways, and there are several hypotheses aiming to explain the patterns of resource use in plant communities (Condit *et al.* 2000). The spatial distribution of individuals depends on environmental heterogeneity, species dispersal process, and successive mortality events throughout ontogeny (Hutchings 1997, Peres & Baider 1997, Clark *et al.* 1998, Barot *et al.* 1999, Fonseca *et al.* 2004, Guzmán *et al*. 2008). On the population level, environmental filters, *i.e.*, the combination of factors locally affecting the specific number of individuals of a given cohort as time progresses, are most often spatially heterogeneous. In general, three kinds of filters are considered to act consecutively and/or simultaneously (Garcia & Houle 2005): the dispersal filter prevents seeds of a species to spread over all available sites; the abiotic filter prevents dispersed seeds to meet suitable conditions to germinate and establish; the biotic filter prevents established plants to survive competition and other negative biotic interactions. The spatial pattern of different populations can vary from random through uniform to aggregate with many aggregation degrees and depends on scale (Fonseca *et al.* 2004). The environmental filters affect the recruitment and mortality and can cause different spatial patterns among ontogenetic stages. That is why some authors argue that to understand life history variation and its role in the maintenance of high diversity in tropical rainforests we must perform detailed analyses of species responses to the full spectrum of resource heterogeneity throughout their life cycles (Clark & Clark 1992, Comita *et al.* 2007).

Given this background, it is important to understand how distinct ontogenetic stages of tree species interact with environmental heterogeneity (Comita *et al*. 2007) because there is often a lack of significant relationship among the spatial patterns of successive life stages (Herrera *et al.*1994). Different species of tropical trees frequently show an aggregated pattern in the early stages of life and a gradual decrease of aggregation in later stages (Hubbel 1979, Henriques & Souza 1989, Oliveira-Filho *et al.* 1996, Barot *et al.* 1999, Lopes 2007). In the early ontogenetic stages, mortality is generally related to density-dependent factors, such as competition with siblings and other individuals of different ontogenetic stages and pressure of natural enemies, which is stronger when young plants are close to their genitors (Janzen 1970, Connel 1971, Clark & Clark 1984). Therefore, recruitment to older stages should be higher at a certain distance of the genitor, thus leading to less aggregation throughout ontogeny and to spatial segregation among different ontogenetic stages (Oliveira-Filho *et al.* 1996). However, some positive spatial associations between seedlings of one species and sheltering adults of another species are common, and have been widely referred to as the nurse plant syndrome (Niering *et al.* 1963). These facilitator plants can lead to an aggregated spatial pattern.

To understand the regeneration processes of a tree species population, it is necessary to describe how the spatial distribution of its ontogenetic stages changes along ontogeny and investigate which factors are associated with shifts of the space pattern. One way to perform this investigation is through the longitudinal approach, in which a population cohort is followed along time while the individuals develop from seedling to reproductive adults. Clearly, this approach is unviable for long-living tree species. Another way is through the transversal approach, which assumes that the ontogeny proceeds in consecutive ontogenetic stages, none of which can be skipped. In the transversal approach all the ontogenetic stages are investigated at the same time and the data about each consecutive stage are treated as referring to different time intervals. The transversal approach has been successfully used for the study of the spatial dynamics of many tree species (Henriques & Souza 1989, Oliveira-Filho *et al.* 1996, Yamada & Suzuki 1997, Fonseca *et al.* 2004, Lopes 2007, Miranda-Mello *et al*. 2007).

Our major goal is to investigate the expectations that the spatial pattern of a canopy tree species population changes along ontogeny and that established ontogenetic stages are associated with environmental variables. If we pick a species with self dispersal and without secondary dispersers, and if we assume only density-dependent mortality to occur, we expect the spatial pattern to be aggregated in all ontogenetic stages, although density can lessen as ontogeny proceeds. However, if the spatial pattern changes along ontogeny, we may assume density-independent mortality factors to be important and expect association of the established ontogenetic stages with environmental variables. If the abiotic filter is important, we expect established ontogenetic stages to correlate with light and soil variables. On the other hand, if the biotic filter exerted by plants of other species is important, we expect some significant correlations of established ontogenetic stages with trees of other species. Through investigating these expectations, our subsidiary goal is to provide a background for the knowledge of the regeneration niche and life history of a tropical tree species population of *Savia dictyocarpa* (Phyllanthaceae). This knowledge is necessary to evaluate the conservation status of tree populations and plan management actions.

Material and Methods

Study area

Our field data were surveyed in a 233.7-ha fragment of the Seasonal Semideciduous Forest called Mata Ribeirão Cachoeira (22°50'S, 46°55'W) in the Sousas - Joaquim Egídio Environmental Protection Area of Campinas municipality, São Paulo State, southeastern Brazil. The forest canopy varies between 15 and 25 m with emergent trees reaching up to 30 m in height, and there are no signs of recent human disturbances, such as logging, charcoal or garbage. In the east-west direction the fragment is crossed by the Cachoeira stream, a tributary of the Atibaia River, which is the main water source in Campinas municipality. The altitude varies from 630 to 760 m, and the relief is hilly with 13-40% steepness (Instituto Geológico 1993). The soil is predominantly Red Yellow Argisol (Alfisol) with loamy-sandy texture and rock fragments. The climate is Köppen’s Cwa hot temperate with summer rain and mild dry winter. The normal dry season lasts from April to September (autumn and winter) with 273 mm average rainfall and 19 - 23°C temperatures; the normal rainy season includes October to March (spring and summer) with 23 - 24°C temperatures and 1,143 mm average rainfall (CIIAGRO 2007 – period of observation: 1993-2006)

Data Collection

Our sampling area had 6,5 ha on the left of Ribeirão Cachoeira stream in the south portion of the fragment. Aerial photographs were used to choose the sampling area (Cielo Filho *et al.* 2007), which is on a slope with approximately 270 m in length, and 40 m of elevation difference between the up and low ends (Cielo Filho *et al* 2007). In the area 50 plots of 10 x 10 m were set according to Greig-Smith’s (1963) unrestricted randomization procedure, in which we sampled all the individuals of *Savia dictyocarpa* (Phyllanthaceae).

We took one hemispherical photograph of the canopy from the center of each plot, one in the summer and another in the winter at 1,3 m from the ground in the center of each plot. These photographs were analyzed with the software Gap

Light Analyzer to calculate canopy openness in each plot. We collected a surface (0-20 cm) soil sample from the center of each plot, which was analyzed in IAC soil laboratories (for methods see Camargo *et al.*1986).

Savia dictyocarpa Müll. Arg. **(Phyllanthaceae)**

In the family Phyllanthaceae, the genus *Savia* has fruits of the dehiscent capsule type, which explosively disperses the seeds (Souza & Lorenzi 2005). Very little is known about species of the genus *Savia* (Samuel *et al.* 2005). The seed in *Savia dictyocarpa* has no elaiosome or caruncle, and probably has no secondary disperser (Wurdack *et al.* 2004; Souza & Lorenzi 2005; Hoffmann 2008), implying that the seed dispersal is limited to the genitor's proximity. *Savia dictyocarpa* trunks present a seasonal secondary growth, with higher increment in the wet months, starting in December, and with a reduction of growth from April on (Ferreira 2002). There is no consensus concerning leaf phenodynamics: Lorenzi (1992) considered *S. dictyocarpa* evergreen, but Hoffmann (2008) and Ferreira (2002) stated that the whole section *Savia* of the genus *Savia* is semideciduous. Ferreira (2002) observed leaf fall in *S. dictyocarpa* from June to September, when new leaves started to flush. In Mata Ribeirão Cachoeira, we observed leaf shedding in the dry season (April-September), leaf flushing in September, and full-leafed crown in the rainy season (October-March). Flowers and fruits were irregularly produced by only some adults from November to January. The fruits had no seeds, implying the absence of seedlings in the plots we sampled.

Savia dictyocarpa is an endemic species in the Atlantic forest, a shade tolerant (Viana 1989) canopy tree that reaches 25 m high in the Dense Ombrophilous Forest and is especially abundant in the Seasonal Semideciduous Forest of southeastern Brazil (Lorenzi 1992). Its wood is used for constructing simple objects and mostly for producing charcoal (Lorenzi 1992). However, the major impact on *S. dictyocarpa* populations comes from habitat fragmentation by the replacement of Seasonal Semideciduous Forest areas with agriculture in the last century.

Data analysis

In our analysis we considered the ontogenetic stages of Juvenile, Immature, Adult, and Senile, as characterized by Sims & Martins (2008 unpublished results). All plants found in the area were tagged and some characteristics were registered to identify each ontogenetic stage. There were not seedlings on sampled area and infant were excluded from the analysis because there were only four individuals. Juvenile stage is constituted by a woody monopodial, orthotropic axis with two or more orthotropic and has 0,40 m of average height and 0,5 cm mean diameter at ground level (dgl). Immature stage has a well defined trunk with a finely-cracking bark and with average height of 1,93 m and average dgl of 2,0 cm, and also has a well branched crown conforming to Massart architectural model. The adults have trunks with expansions resembling tabular roots or buttresses at the base and with thick cracking bark, which have average height of 10,66 m and average dgl of 14,39 cm; the crown reiterate the architectural unit. Senile stage comprised plants that are alive but present great injuries such as broken trunks and fallen crowns, with adventitious resprouting; their average height is 4,27 m and average dgl is 9,55 cm

Firstly, we tested for spatial autocorrelation in each ontogenetic stage and environmental characteristic considering Moran's I coefficient, which varies between -1 and + 1, indicating positive or negative autocorrelation in the data (Legendre & Legendre 1998). A variable is considered to be spatially autocorrelated when its value at some point of space can be predicted by its value at another point of known position (Legendre & Fortin 1989). The presence of spatial patterning in the data violates the assumption of many standard statistical tests (Legendre & Fortin 1989; Legendre & Legendre 1998). We calculated Moran's I coefficients for a series of 15 distance classes of 22 m interval, representing successively larger distances until the limit of the last class of 366 m. We chose binary weight and assumed that data had been sampled from a randomly distributed population (Rosenberg 2001).

We plotted the results of I against distance classes in a series of correlograms. The variable is structured in space if the correlogram is significant and it is randomly distributed in space if the correlogram is not significant. A correlogram is considered globally significant only if at least one of the I values is significant at the Bonferroni-corrected significance level ($\alpha' = \alpha/n$, where α is the chosen overall significance level, and n is the number of distance classes considered – Legendre & Legendre 1998). This procedure is necessary to deal with the lack of independence among the distance classes (Rosenberg 2001). Autocorrelation analyses were performed with Passage 11 package (Rosenberg 2001).

Then, we tested for correlation among the ontogenetic stages to assess whether different ontogenetic stages would tend to occur in the same patch. We analyzed the significance of correlations between the density of different ontogenetic stages in space using Total and Partial Mantel tests. Total Mantel test calculates the correlation between two matrices of distances or similarities among objects and tests for the independence of the objects between the two matrices (Dale *et al.* 2002). Partial Mantel test assesses spatial autocorrelation by computing matrices of residuals of the linear regression of two variables (two matrices of distances, one for each variable) over the values of a third variable (a matrix of distances of a third variable, *e.g.*, location in space; Oden, 1992). We performed the tests with the randomization mode of the program Passage (Rosenberg 2001), followed by the sequential correction of Bonferroni. We applied a randomization procedure with 1000 iterations to test for the significance of the correlation (Legendre & Fortin 1989).

Finally, we used the correlograms and the Total and Partial Mantel tests to investigate the influence of environment heterogeneity on the ontogenetic stages of

S. dictyocarpa. Considering the abiotic filter, we expected that light and soil variables would influence the spatial distribution of the established ontogenetic stages. To investigate this expectation we tested for significance of the correlation between the number of individuals of each ontogenetic stage per plot and canopy openness or soil variables (Table 4). Since canopy openness was expressed in percentage, we transformed the data x in the arcsine of the square root of the proportions p, which is appropriate to percentages and proportion data (Sokal & Rohlf 1981): $x = \arcsin\sqrt{p}$. Considering the biotic filter, we expected the density of trees, especially the most abundant species, to positively or negatively influence spatial distribution of the ontogenetic stages of *S. dictyocarpa*. To investigate this expectation, we tested for significance of the correlation between the number of individuals in each ontogenetic stage per plot and the total number of trees per plot or the number of individuals of some chosen species per plot. We chose the most abundant canopy and subcanopy species in the community (Cielo Filho *et al.* 2007, Table 3): *Almeidea lilacina*, *Esenbeckia leiocarpa*, *Galipea jasminiflora*, *Metrodorea nigra* (all Rutaceae), *Actinostemon klotzchii* (Euphorbiaceae), *Aspidosperma polyneuron* (Apocynaceae), and *Trichillia catigua* (Meliaceae).

Results

We sampled 51 juveniles, 69 immatures, 67 adults and 6 seniles. We found no seedling and very few infants in the plots, a fact related to the absence of reproductive events in the two-year period in which we followed this population.

All the correlograms were not globally significant, except for fine sand, indicating that all ontogenetic stages and almost all measured environmental variables were not spatially structured, that is, they were randomly distributed in space. In this article we show only the correlograms of the ontogenetic stages (Figure 1). When investigating whether ontogenetic stages were associated with each other, we found that Juvenile and Immature had significant positive correlation along with Juvenile and Senile stages (Table 1), meaning that these stages overlapped in space.

The canopy openness changed significantly between the dry and rainy seasons (Wilcoxon test, $z = -6{,}15$, $p \leq 0{,}01$). In the dry season canopy openness range from 5 to 25 percent, with median of 10 percent; and in the rainy season openness range from 3 to 15 percent, with median of 5,4 percent. Mean annual canopy openness was 8 percent, ranging from 5 to 20 percent. If the canopy openness varies significantly during the year, light during the rainy season (growth season) could have a more important effect than during the dry season, but the average annual canopy openness could also exert a role in printing spatial pattern. Therefore, we tested for significant correlation between each ontogenetic stage and canopy openness in the rainy season, in the dry season, and in the whole year. However, all results were not significant or showed spurious negative correlations (Table 2).

The correlations between the early ontogenetic stages and some of the commonest species were not significant either (Table 3), showing that the presence of adult trees in the neighborhood apparently did not influence the early ontogenetic stages of *S. dictyocarpa*.

When looking for a relation between soil variables and distribution of each ontogenetic stage we also found just few significant positive relations between:1) clay and senile; 2) fine sand and senile (Table 4).

Discussion

All established ontogenetic stages had random distribution in space. This lack of shift in the spatial pattern throughout the ontogeny is not usual in tropical tree species and could not be explained by the variables we measured. Also, no environmental variable was spatially structured. We can only speculate about the lack of both spatial shift along ontogeny and overall significant correlations between the established ontogenetic stages and environmental variables. It is possible that the random pattern of all established ontogenetic stages is related to other factors that we did not consider here, such as soil water content, deciduousness gaps, or allelopathy. Also, it is possible that the spatial distribution of all ontogenetic stages is strongly related to seed, seedling and infant establishment and mortality.

The spatial pattern of a population is a consequence of the spatial pattern of recruitment and mortality. It is possible that *S. dictyocarpa* population suffers a high impact of seedling mortality influencing its whole life history. In the two years we observed the individuals we could not find viable seeds, seedlings, infants, and reproductive adults in the plots. The absence of viable seeds could be an outcome of a breakage of the pollination system, a common phenomenon in forest fragments (Ghazoul & Satake 2009). The absence of viable seeds implied in the absence of seedlings and infants; hence we could not assess the spatial pattern of the initial, non-established ontogenetic stages. Considering the autochorous dispersal and the absence of secondary dispersers in *S. dictyocarpa*, we assumed the initial, non-established ontogenetic stages to be aggregated and if there were a spatial shift, this would indicate non-random mortality in space. Since we could not find the initial, non-established ontogenetic stages, we had no element to conclude that a spatial shift had happened.

The random spatial pattern and the absence of correlation with environmental variables are not common findings for trees of tropical forests. Studies of seed rain and seedling survival have shown that early seedling recruitment can be spatially correlated with seed rain, although this relationship may disappear as the seedlings age and become saplings (Herrera *et al*. 1994) due to environmental elements that influence seedling survival and growth (Yamada & Suzuki 1997, Ramos *et al.* 2005). Yamada & Suzuki (1997) hypothesized that small and large saplings negatively associated with adults might be a result of seedling mortality that occurred just after seed germination. This expected aggregation decrease along ontogeny was observed in some species of the Brazilian Atlantic forest (Henriques & Sousa 1989, Souza & Martins 2002, Fonseca *et al.* 2004). Different habitat associations among life stages suggest that sites that are initially beneficial for establishment and survival can turn to be unsuitable for continued survival at later stages, and vice versa (Comita *et al*. 2007). Thus, *S. dictyocarpa* seedling survival could have been affected by random spatial distribution of some biotic or abiotic factor, leading to random distribution, and this pattern would be kept in later stages, suggesting that the definitive spatial pattern of the individuals is printed early in the ontogeny.

Seedling survival is affected by a great range of factors that can eventually lead to a regular or a random spatial pattern of the individuals. Density-dependent factors (Janzen 1970) could cause the segregation of seedlings and lead to segregation among life stages (Harper 1977). Yamada & Suzuki (1997) found that 96% of the fallen fruits of *Scaphium macropodum* (Meliaceae) under the crown had died one month after dispersal and the density of 1 month-old seedlings peaked 14 m from the parent tree. Although we did not detect any effect of intra- or interspecific competition in juvenile, immature and adult, it could affect seedling and infant stages of *S. dictyocarpa*. The litter layer depth is related to species composition of neighborhood; therefore, its effects could be species specific. Litter fall can cause seedling mortality by physically preventing the roots of seedlings from reaching the mineral soil surface (Yamada & Suzuki 1997). Seedling survival could also be affected by abiotic environment, such as soil moisture, which is correlated with spatial heterogeneity of slope and soil physical composition. Daws *et al.* (2005) reported great mortality of new seedlings in the wet season, potentially due to damage from water flow or to higher pathogen activity in the wetter environment, as predicted by Wright (1992). On the other hand, Paine *et al.* (2009) found that supplementary water supply had a positive effect on growth and survival of seedling of nine species. They evidenced as well that sapling survival and growth were less influenced by water availability.

The positive spatial association between juvenile and immature could indicate that individuals of these stages are recruited in the same environment, meaning that they need similar environmental conditions for growth. On the other hand, adults were associated nor with juvenile neither immature stages. When in the adult stage, individuals of *S. dictyocarpa* have already reached the forest canopy. We suppose that the recruitment of immature to adult depends on canopy openness larger than the one we measured here. Since we measured canopy openness at 1,3 m from ground, we could not detect canopy gaps that could be above a small individual with a crown higher than 1,3 m. Lima *et al*. (2008) showed that Atlantic seasonal forests have more canopy disturbances than other tropical forests. The recruitment of adults of *S. dictyocarpa* may dependent on canopy dynamics: adults would be recruited when there was an opening of the top canopy that is large enough for an individual to expand its crown. Top canopy opening is a random process in space and time (Gandolfi. 2003), which could explain the random spatial pattern of adults of *S. dictyocarpa* and their segregation from the previous immature and juvenile stages.

The spatial association of immature and senile individuals and the smaller size (diameter and height) of the senile than adults indicate that senility is cause by injuries in the population we studied. Probably the frequent damage of immature individuals by fallen debris prevents some of them to be recruited to adult and so they become senile with continued damage along time. Therefore, it is likely that immature mortality is related to fallen branches from canopy, a process that decreases aggregation and can lead to spatial segregation between immature and adult. On the other hand, the only soil variables significantly associated with the senile were clay and fine sand. Since clay and sand have contrasting properties and roles in the soil, we think this could be a spurious correlation.

Significant correlations between the distribution of tropical tree species and soil components are not an overall rule (Clark *et al.* 1999; Comita *et al*. 2007). Paoli *et al.* (2005) found that the most common Dipterocarp species were indifferent to substrate variation. On the other hand, the absence of relation between *S. dictyocarpa* distribution and canopy openness can be an outcome of the method we used. Hemispherical photography can detect only the overall canopy openness above a previously chosen level, in our case 1,3 m from the ground. This way, this technique can be suitable for studies dealing with plants that are below the level in which the photographs are taken. For plants with their canopies above that level this technique may not be appropriate. Moreover, hemispherical photographs represent just an instant of canopy openness during the whole season. Temporal variation of light in semideciduous forests leads to variations of the photon flux density through canopy, sunfleck distribution and levels of radiation in the vicinity of deciduous trees (Gandolfi 2003). The spatial arrangement of the plants, their crown architecture and leaf area determine the light penetration through the forest canopy, and several factors can interfere in canopy characteristics (Bianchini *et al.* 2001). Thus, sunflecks and small spatio-temporal variations of canopy are not considered in hemispherical photographs, but their spatial distribution could be highly related to plant physiological response to light and mortality and growth pattern (Chazdon & Pearcy 1991). Therefore, light spatial and temporal dynamics in semideciduous forests is far more complex, with smooth variation between light and dark environments (Gandolfi 2003), and should be taken into account in studies of spatial distribution of trees species.

Some other environmental elements can influence patterns of mortality and recruitment. For example, discontinuities in soil drainage cause changes in species composition of lowland tropical tree communities and promote the coexistence of species adapted to contrasting edaphic environments (Lieberman *et al*. 1985). The trade-off hypothesis (Smith & Huston 1989) predicts that drought has stronger impacts on individuals of a species grown in deep shade because generally they have a larger specific leaf area and invest more biomass to leaves but less to roots for efficient light capture (Poorter 1999), thus decreasing their ability to resist drought. Since younger stages occurred in the understorey, water availability could affect *S. dictyocarpa* distribution and should be considered in future studies.

We found a random spatial pattern in the juvenile, immature, adult, and senile stages of *Savia dictyocarpa*, and since we could not sample any seedling and infant, we were not able to know whether a shift occurs in the spatial pattern of the population we studied. The absence of viable seeds, seedlings, infants and reproductive adults could indicate both a serious breakage in the pollination system of the population as a consequence of fragmentation and disturbance. Like the juvenile, immature and senile, adults had also a random spatial pattern, but were segregated from the other stages. This segregation could be explained by several factors but since *S. dictyocarpa* is described as a shade-tolerant tree, the recruitment from immature to adult could be related to openings in the top canopy, large enough to allow crown expansion or to fallen debris that have a major impact in understorey individuals like immatures, causing then to skip to senile stage. The association of juvenile and immature may indicate that recruitment from the former to the latter stage seems to occur in the same environment. The absence of significant correlation with light and soil variables and with the most abundant tree species seems to show that the transition from juvenile to immature is autogenic. Senility seems to be caused by continuous damage of the immature in the population. The absence of consistent correlations between the ontogenetic stages and biotic and abiotic variables indicate that mortality, survival, and recruitment of individuals in the population of *S. dictyocarpa* could rely on processes that are totally stochastic in space and time.

References

BAROT, S.; GIGNOUX, J.; MENAUT, J. 1999. Demography of a savanna palm tree: predictions from comprehensive spatial pattern analysis. **Ecology** 80 (6): 1987-2005.

BIANCHINI, E.; PIMENTA, J. A.; SANTOS, F. A. M. 2001. Spatial and temporal variation in the canopy cover in a tropical semi-deciduous forest. **Brazilian Archives of Biology and Technology** 44 (3): 269-276.

CAMARGO, O. A.; MONIZ, A. C.; JORGE, J. A.; VALADARES, J. M. A. 1986. Métodos de análise química e física de solos do IAC. **Boletim Técnico do Instituto Agronômico de Campinas** 106.

CHAZDON, R. L.; PEARCY, R. W. 1991. The importance of sunflecks for forest understory. **BioScience** 41 (11): 760-766.

CIELO FILHO, R.; GNERI, M. A.; MARTINS, F. R. 2007. Position on slope, disturbance, and tree species coexistence in a seasonal semideciduous forest in SE, Brazil. **Plant Ecology** 190: 189-203.

CIIAGRO 2007. **Boletim Climático: Campinas**. Centro integrado de informações agrometereológicas, Instituto Agronômico de Campinas, Campinas, Brasil.

CLARK, D. A.; CLARK, D. B. 1984. Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. **American Naturalist** 124: 769-788.

CLARK, D. A.; CLARK, D. B. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. **Ecological Monographs** 62 (3): 315-344.

CLARK, D. A.; PALMER, M. W.; CLARK, D. B. 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. **Ecology** 80 (8): 2662-2075.

CLARK, D. B.; READ, J. M.; CLARK, D. A. 1998. Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. **Journal of Ecology** 86: 101-112.

COMITA L. S., L. S.; CONDIT, R.; HUBBELL, S. P. 2007. Developmental changes in habitat associations of tropical trees. **Journal of Ecology** 95: 482-492.

CONDIT, R.; ASHTON, P. S.; BAKER, P.; BUNYAVEJCHEWIN, S.; GUNATILLEKE, S.; GUNATILLEKE, N.; HUBBEL, S. P.; FOSTER, R. B.; ITOH, A.; LAFRANKIE, J. V.; LEE, H. S.; LOSOS, E.; MANOKARAN, N.; SUKUMAR, R.; YAMAKURA, T. 2000. Spatial patterns in the distribution of tropical tree species. **Science** 288: 1414-1418.

CONNEL, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *In*: den Boer, P. J.; Gradwell, G. R. (Eds.). **Dynamics of number in populations**. Centre for Agricultural Publishing and Documentation, Wageningen, Holanda, 298-312 pp.

DALE, M. R. T.; DIXON, P.; FROTIN, M.; LEGENDRE, P.; MYERS, D. E.; ROSEMBERG, M. S. 2002. Conceptual and mathematical relationships among methods for spatial analysis. **Ecography** 25: 558 - 577.

DALLING, J. W.; WINTER, K.; NASON, J. D.; HUBBELL, S. P.; MURAWSKI, D. A.; HAMRICK, J. L. 2001. The unusual life history of *Alseis blackiana*: a shade-persistent pioneer tree? **Ecology** 82 (4): 933-945.

DAWS, M. I.; PARSON, T. R. H.; BURSLEM, D.; MULLINS, C. E.; DALLING, J. W. 2005. Effects of topographic position, leaf litter and seed size on seedling demography in a semideciduous tropical forest in Panama. **Plant Ecology** 179: 93-105.

DENSLOW, J. S. 1980. Gap partitioning among tropical rainforest trees. **Biotropica** 12: 47-55.

DENSLOW, J. S. 1987. Tropical rainforest gaps and tree species diversity. **Annual Review of Ecology and Systematics** 18: 431-451.

FERREIRA, L. 2002. **Periodicidade do crescimento e formação da madeira de algumas espécies arbóreas de florestas estacionais semidecíduas da região sudeste do estado de São Paulo**. Master thesis. Escola Superior de Agricultura Luiz de Queiroz, São Paulo University, Piracicaba, Brazil.

FONSECA, M. G.; MARTINI, A. M. Z.; SANTOS, F. A. M. 2004. Spatial structure of *Aspidosperma polyneuron* in two semi-deciduous forests in Southeast Brazil. **Journal of Vegetation Science** 15: 41-48.

GANDOLFI, S. 2003. Regimes de luz em Florestas Estacionais Semideciduais e suas possíveis conseqüências. *In*: Claudino-Sales, V. (Ed.). **Ecossistemas Brasileiros: Manejo e Conservação**. Expressão Gráfica e Editora, Fortaleza, Brasil, 305-311pp.

GARCIA, D.; HOULE, G. 2005. Fine-scale spatial patterns of recruitment in red oak (*Quercus rubra*): what matters most, abiotic or biotic factors? **EcoScience** 12 (2): 223-235.

GHAZOUL, J.; SATAKE, A. 2009. Nonviable seed set enhances plant fitness: the sacrificial sibling hypothesis. **Ecology** 90 (2): 369-377.

GREIG-SMITH, P. 1983, **Quantitative plant ecology**. University of California, Berkeley, USA.

GRUBB, P. J. 1977 Maintenance of species-richness in plant communities – importance of regeneration niche. **Biology Reviews of the Cambridge Philosophical Society** 52: 107-145.

GUZMÁM, R. C.; MOYA E. G.; GARCÍA, J. A. V.; LÓPEZ, N. M. N. 2008. Estructura poblacional y relaciones ambientales del árbol tropical *Nectandra rudis* (Lauraceae), una especie rara en el occidente de México. **Revista de Biologia Tropical** 56 (1): 247-256.

HALL, J. S.; MCKENNA, J. J.; ASHTON, P. M. S.; GREGOIRE, T. G. 2004. Habitat characterizations underestimate the role of edaphic factors controlling the distribution of *Entandrophragma*. **Ecology** 85 (8): 2171-2183.

HARPER, J. L. 1977. **Population biology of plants**. Academic Press, London, England.

HENRIQUES, R. P. B.; SOUSA, E. C. E. G. 1989. Population structure, dispersion and microhabitat regeneration of *Carapa guianensis* in northeastern Brazil. **Biotropica** 21 (3): 204-209.

HERRERA, C. M.; JORDANO, P.; LOPEZ-SORIA, L. 1994 Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. **Ecological Monographs** 64: 315-344.

HOFFMANN, P. 2008. Revision of *Heterosavia*, stat. nov., with notes on *Gonatogyne* and *Savia* (Phyllanthaceae). **Brittonia** 60 (2) 136-166.

HUBBEL, S. P. 1979. Tree dispersion, abundance and diversity in a tropical dry forest. **Science** 213: 1299-1309.

HUTCHINGS, M. J. 1997. The structure of plant populations. *In*: Crawley, M. J. (Ed.). **Plant ecology**. Blackwell Scientific Publications, Oxford, England, 325-358 pp.

INSTITUTO GEOLÓGICO. 1993. **Subsídios do meio físico e geológico ao planejamento do município de Campinas**. Secretaria de Planejamento e Meio Ambiente, Prefeitura Municipal de Campinas, Campinas, Brasil.

JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. **American Naturalist** 104: 501-528.

KATHRIARACHCHIA, H.; HOFFMANN, P.; SAMUEL, R.; WURDACK, K. J. CHASE, M.W. 2005 Molecular phylogenetics of Phyllanthaceae inferred from Wve genes (plastid *atpB*, *matK*, *3'ndhF*, *rbcL*, and nuclear *PHYC*). **Molecular Phylogenetics and Evolution** 36: 112-134.

LEGENDRE, P.; FORTIN, M. J. 1989. Spatial pattern and ecological analysis. **Vegetatio** 80: 107-138.

LEGENDRE, P.; LEGENDRE, L. 1998. **Numerical ecology**. Elsevier, Amsterdam, Holland.

LIEBERMAN, D.; LIEBERMAN, M.; HARTSHORN, G. S.; PERALTA, R. 1985 Small-scale altitudinal variation in lowland tropical forest vegetation. **Journal of Ecology** 73: 505-516.

LIMA, R. A. F.; MOURA, L. C. 2008. Gap disturbance regime and composition in the atlantic montane rain forest: the influence of topography. **Plant Ecology** 197: 239-253.

LOPES, M. A. 2007. Population structure of *Eschweilera coriacea* (DC.) S. A. Mori in forest fragments in eastern Brazilian Amazonia. **Revista Brasileira de Botânica** 30 (3): 509-519.

LORENZI, H. 1992. **Árvores brasileiras: manual de identificação e cultivo de plantas arbóreas nativas do Brasil**. Plantarum, Nova Odessa, Brasil.

MARTINI, A. M. Z.; LIMA, R. A. F.; FRANCO, G. A. D. C.; RODRIGUES, R. R. 2008. The need for full inventories of tree modes of disturbance to improve forest dynamics comprehension: an example from a semideciduous forest in Brazil. **Forest Ecology and Management** 255: 1479-1488.

MIRANDA-MELLO, A. A.; MARTINS, F. R.; SANTOS, F. A. M. 2007. Estrutura populacional de *Xylopia aromatica* (Lam.) Mart. e de *Roupala montana* Aubl. em fragmentos de cerrado no estado de São Paulo. **Revista Brasileira de Botânica** 30 (3): 501-507.

NIERING, W. A.; WHITTAKER, R. H.; LOWE, C. H. 1963. The saguaro: a population in relation to environment. **Science** 142: 15-23.

OLDEMAN, R. A. A. 1990. **Forests: elements of silvology**. Springer-Verlag, Berlin, Germany.

ODEN, N. L. 1992. An investigation of three-matrix permutation tests. **Journal of Classification** 9: 275-290.

OLIVEIRA-FILHO, A. T.; CAMISAO-NETO, A. A.; VOLPATO, M. M. L. 1996. Structure and dispersion of four tree populations in an area of montane semideciduous forest in southeastern Brazil. **Biotropica** 28: 762-769.

PAINE, C. E. T.; HARMS, K. E.; RAMOS, J. 2009. Supplemental irrigation increases seedling performance and diversity in a tropical forest. **Journal of Tropical Ecology** 25: 171 - 180.

PAOLI, G. D.; CURRAN, L. M.; ZAK, D. R. 2006. Soil nutrients and beta diversity in the Bornean Dipterocarpaceae: evidence for niche partitioning by tropical rain forest trees. **Journal of Ecology** 94: 157-170.

PALMIOTTO, P. A.; DAVIES, S. J.; VOGT, K. A.; ASHTON, M. A.; VOGT, D. J.; ASHTON, P. S. 2004. Soil- related habitat specialization in dipterocarp rain forest tree species in Borneo. **Journal of Ecology** 92: 609-623.

PERES, C. A.; BAIDER, C. 1997. Seed dispersal, spatial distribution and population structure of brazilnut trees (*Bertholletia excelsa*) in southeastern Amazonia. **Journal of Tropical Ecology** 13 (4): 595-616.

POORTER, L. 1999. Growth responses of 15 rainforest tree species to a light gradient the relative importance of morphological and physiological traits. **Functional Ecology** 13: 396-410.

RAMOS, F. N.; MATOS, D. M. S.; SANTOS, F. A. M. 2005. Spatial distribution of seeds and juveniles of *Enterolobium glaziovii* Bentham (Leguminosae, Mimosoideae) in the atlantic forest, Brazil. **Acta Botanica Brasilica** 19 (3): 609-614.

ROSEMBERG, M. S. 2001. **PASSAGE: Pattern analysis, spatial statistics and geographic Exegesis**. Version 1.1. Department of Biology, Arizona State University, Tempe, USA.

SAMUEL, R.; KATHRIARACHCHI, H.; HOFFMANN, P.; BARFUSS, M. H. J.; WURDACK, K. J.; DAVIS, C. C.; CHASE, M. W. 2005. Molecular phylogenetics of Phyllanthaceae: evidence from plasticid *matK* and nuclear *PHYC* sequences. **American Journal of Botany** 92 (1): 132-141.

SMITH, T.; HUSTON, M. 1989. A theory of the spatial and temporal dynamics of plant-communities. **Vegetation** 83: 49-69.

SOKAL, R. R.; ROHLF, F. J. 1995. **Biometry: the principles and practice of statistics in biological research**. W.H. Freeman Publishing, New York, USA.

SOLLINS, P. 1998. Factors influencing species composition in tropical lowland rain forest: does soil matter? **Ecology** 79 (1): 23-30.

SOUZA, V. C.; LORENZI, H. 2005. **Botânica Sistemática: Guia para identificação das famílias de Angiospermas da flora brasileira, segundo APG II**. Plantarum, Nova Odessa, Brasil.

SOUZA, A. F.; MARTINS, F. R. 2002. Spatial distribution of an undergrowth palm in fragments of the Brazilian atlantic forest. **Plant Ecology** 164: 141-155.

SVENNING, G, J. C. 2001. On the role of microenvironmental heterogeneity in the ecology and diversification of Neotropical rain-forest palms (Arecaceae). **Botanical Review** 67: 1-53.

SWAINE, M. D.; WHITMORE, T. C. 1988. On the definition of ecological species groups in Tropical rain forests. **Vegetatio** 75: 81-86.

VIANA, V. M., 1989, **Seed dispersal and gap regeneration: the case of three Amazonia tree species**. Doctoral Thesis. Harvard University, Cambridge, USA.

YAMADA, T.; SUZUKI, E. 1997 Changes in spatial distribution during the life history of a tropical tree, *Scaphiurn macropodurn* (Sterculiaceae) in Borneo. **Journal of Plant Research** 110: 179-186.

WHITMORE. T.C. 1996. A review of some aspects of tropical rain forest seedlings ecology with suggestions for further enquiry. *In*: Swaine, M.D. (Ed.). **The ecology of tropical forest tree seedlings**. (Man & Biosphere Series; Vol. 18). UNESCO and Parthenon Publishing, France. 3-39 pp.

WRIGHT, S. J. 1992. Seasonal drought, soil fertility and the species density of tropical forest plant-communities. **Trends in Ecology and Evolution** 7: 260-263.

WRIGHT, S. J.; MULLER-LANDAU, H. C.; CONDIT, R.; HUBBELL, S. P. 2003. Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. **Ecology** 84: 3174 -3185.

WURDACK, K. J.; HOFFMANN, P.; SAMUEL, R.; BRUIJN, A.; VAN DER BANK, M.; CHASE, M. 2004. Molecular phylogenetic analysis of Phyllanthaceae (Phyllanthoideae pro parte Euphorbiaceae *sensu lato*) using plastid *rbcL* DNA sequences. **American Journal of Botany** 91 (11): 1882-1900.

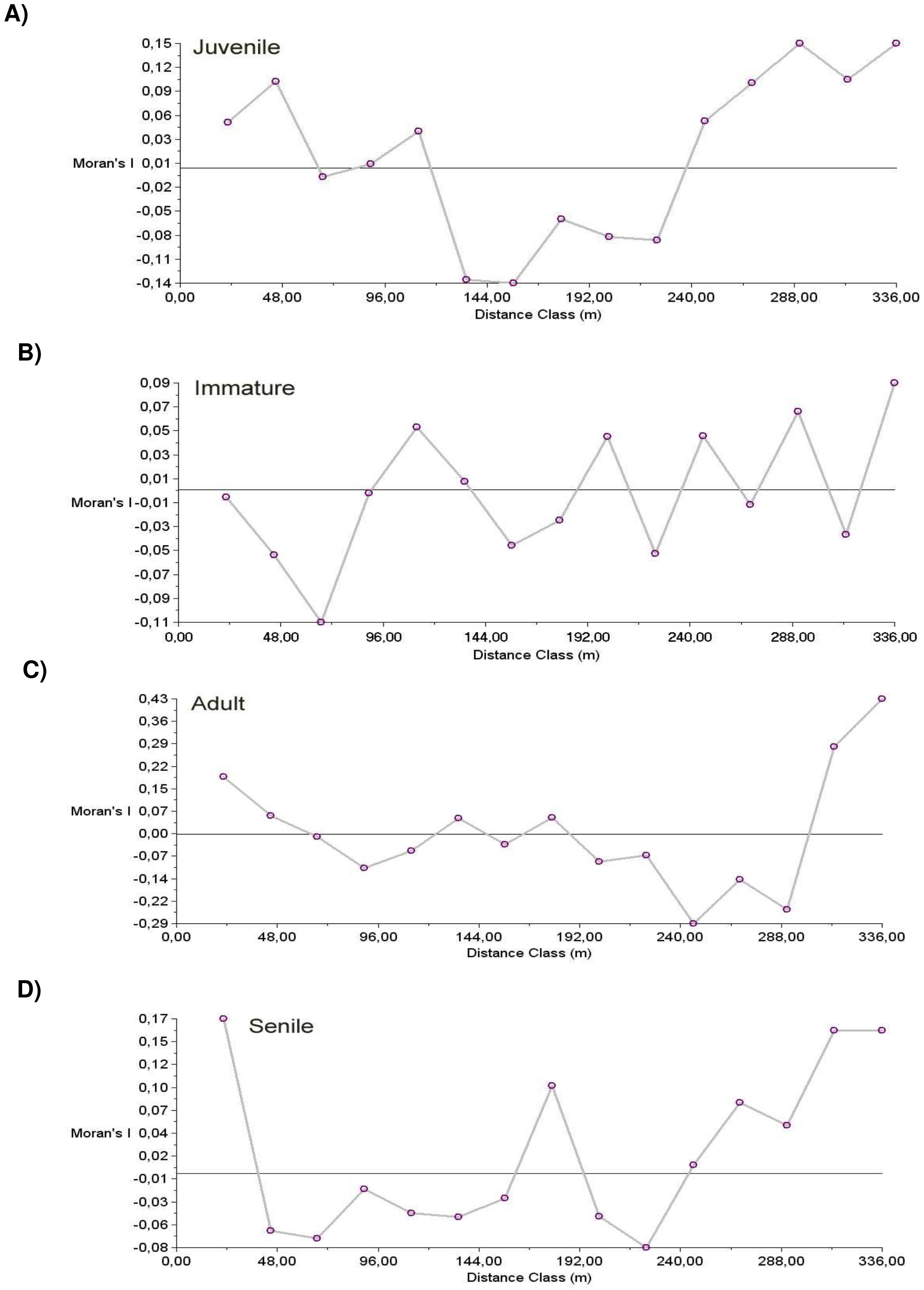

Figure 1. Spatial correlograms for ontogenetic stages of *Savia dictyocarpa*: Juvenile (a), Immature (b), Adult (c), and Senile (d). Moran's I autocorrelation values were plotted on the ordinate (y axis) against distance classes. Values on the x axis correspond to the upper limit (m) of each distance class. Open circles indicate non-significant Moran's I values ạt = 5% level. No correlogram was globally significant.

Table 1. Results of total Mantel test evaluating the correlation among densities of ontogenetic stage of *Savia dictyocarpa*. The r values probabilities (**: P ≤ 0,01; *: P ≤ 0,05) were obtained after 999 permutations.

Ontogenetic stages	Correlation	r
Juvenile and Immature	0,93	0,00 **
Juvenile and Adult	-0,02	0,29
Juvenile and Senile	0,39	0,00 **
Immature and Adult	-0,03	0,32
Immature and Senile	0,32	0,01 **
Adult and Senile	-0,05	0,53

Table 2. Total Mantel test evaluating the correlation between the density of ontogenetic stage of *Savia dictyocarpa* and the canopy openness in wet, rainy season and annual average found in the plots. The r values probabilities (**: P ≤ 0,01; *: P ≤ 0,05) were obtained after 999 permutations.

Stages	Season	Plot Distances	Correlation	p
Immature	Dry		-0,12	0,97
	Dry	Coordinate	-0,12	0,16
	Rainy		-0,08	0,79
	Rainy	Coordinate	-0,08	0,40
	Average		-0,11	0,97
	Average	Coordinate	-0,11	0,15
Adult	Dry		0,02	0,33
	Dry	Coordinate	0,02	0,84
	Rainy		-0,03	0,54
	Rainy	Coordinate	-0,04	0,69
	Average		-0,01	0,43
	Average	Coordinate	-0,01	0,90
Senile	Dry		-0,06	0,68
	Dry	Coordinate	-0,06	0,54
	Rainy		-0,01	0,44
	Rainy	Coordinate	-0,02	0,87
	Average		-0,04	0,56
	Average	Coordinate	-0,05	0,65
Population	Dry		-0,10	0,90
	Dry	Coordinate	-0,10	0,22
	Rainy		-0,06	0,66
	Rainy	Coordinate	-0,06	0,50
	Average		-0,09	0,88
	Average	Coordinate	-0,09	0,22

Table 3. Total Mantel test evaluating the correlation between the density of early ontogenetic stage of *Savia dictyocarpa* and the density of some abundant species found in the plots. The r values probabilities (**: P ≤ 0,01; *: P ≤ 0,05) were obtained after 999 permutations.

Stages	Species	Correlation	p
Juvenile	all species	-0,02	0,87
	Actinostemon klotzchii	-0,01	0,92

	Almeidea lilacina	0,12	0,11
	Aspidosperma polyneuron	0,01	0,94
	Astronium graveolens	0,06	0,55
	Esenbeckia leiocarpa	0,00	0,99
	Galipea jasminiflora	-0,10	0,32
	Metrodorea nigra	-0,03	0,62
	Trichilia catigua	-0,03	0,80
Immature	all species	-0,06	0,49
	Actinostemon klotzchii	-0,06	0,54
	Almeidea lilacina	-0,01	0,95
	Aspidosperma polyneuron	-0,03	0,79
	Astronium graveolens	0,04	0,65
	Esenbeckia leiocarpa	0,06	0,46
	Galipea jasminiflora	-0,09	0,32
	Metrodorea nigra	-0,10	0,15
	Trichilia catigua	-0,02	0,81

Table 4. Total and Partial Mantel tests evaluating the correlation between soil variables and the density of each ontogenetic stage of *Savia dictyocarpa*. The r values probabilities (**: P ≤ 0,01; *: P ≤ 0,05) were obtained after 999 permutations.

Matrix 1	**Matrix 2**	**Matrix 3**	**Correlation**	**P**
Juvenile	Aluminum		-0,06	0,61
	Aluminum	Coordinates	-0,05	0,65
	Phosphorus		-0,09	0,87
	Phosphorus	Coordinates	-0,08	0,28
	Calcium		-0,10	0,92
	Calcium	Coordinates	-0,09	0,21
	Magnesium		-0,12	0,96
	Magnesium	Coordinates	-0,12	0,16
	Organic Matter		-0,10	0,88
	Organic Matter	Coordinates	-0,10	0,27
	pH		-0,07	0,83
	pH	Coordinates	-0,07	0,31
	Potassium		-0,10	0,96
	Potassium	Coordinates	-0,10	0,16
	Potential Acidity		-0,02	0,59
	Potential Acidity	Coordinates	-0,02	0,75
	Cation Exchange Capacity		-0,10	0,92
	Cation Exchange Capacity	Coordinates	-0,10	0,21
	Sum of Bases		-0,02	0,58
	Sum of Bases	Coordinates	-0,02	0,72
	Base Saturation		-0,10	0,93
	Base Saturation	Coordinates	-0,10	0,22
	Silt		-0,04	0,54
	Silt	Coordinates	-0,04	0,76

	Clay		0,05	0,22
	Clay	Coordinates	0,05	0,52
	Fine Sand		0,01	0,34
	Fine Sand	Coordinates	0,02	0,84
	Coarse Sand		-0,06	0,74
	Coarse Sand	Coordinates	-0,06	0,48
	Total Sand		-0,08	0,80
	Total Sand	Coordinates	-0,08	0,38
Immature	Aluminum		-0,07	0,61
	Aluminum	Coordinates	-0,07	0,57
	Phosphorus		0,01	0,37
	Phosphorus	Coordinates	0,01	0,95
	Calcium		0,04	0,24
	Calcium	Coordinates	0,05	0,61
	Magnesium		-0,01	0,45
	Magnesium	Coordinates	-0,01	0,93
	Organic Matter		0,01	0,33
	Organic Matter	Coordinates	0,01	0,89
	pH		0,03	0,27
	pH	Coordinates	0,03	0,69
	Potassium		-0,04	0,61
	Potassium	Coordinates	-0,04	0,62
	Potential Acidity		0,00	0,41
	Potential Acidity	Coordinates	0,00	0,99
	Cation Exchange Capacity		0,08	0,13
	Cation Exchange Capacity	Coordinates	0,08	0,28
	Sum of Bases		0,02	0,33
	Sum of Bases	Coordinates	0,02	0,84
	Base Saturation		0,07	0,11
	Base Saturation	Coordinates	0,08	0,36
	Silt		-0,07	0,69
	Silt	Coordinates	-0,07	0,57
	Clay		0,00	0,44
	Clay	Coordinates	0,00	1,00
	Fine Sand		-0,02	0,42
	Fine Sand	Coordinates	-0,02	0,89
	Coarse Sand		-0,10	0,91
	Coarse Sand	Coordinates	-0,10	0,22
	Total Sand		-0,09	0,84
	Total Sand	Coordinates	-0,08	0,29
Adult	Aluminum		0,01	0,41
	Aluminum	Coordinates	0,01	0,92
	Phosphorus		0,00	0,48
	Phosphorus	Coordinates	0,00	0,99
	Calcium		-0,05	0,72
	Calcium	Coordinates	-0,04	0,54

	Magnesium		-0,02	0,53
	Magnesium	Coordinates	-0,01	0,88
	Organic Matter		-0,03	0,58
	Organic Matter	Coordinates	-0,03	0,77
	pH		-0,02	0,65
	pH	Coordinates	-0,03	0,70
	Potassium		-0,05	0,63
	Potassium	Coordinates	-0,05	0,53
	Potential Acidity		-0,07	0,91
	Potential Acidity	Coordinates	-0,07	0,91
	Cation Exchange Capacity		-0,05	0,73
	Cation Exchange Capacity	Coordinates	-0,05	0,56
	Sum of Bases		-0,02	0,58
	Sum of Bases	Coordinates	-0,02	0,81
	Base Saturation		-0,04	0,66
	Base Saturation	Coordinates	-0,04	0,57
	Silt		-0,10	0,90
	Silt	Coordinates	-0,10	0,24
	Clay		0,01	0,39
	Clay	Coordinates	0,01	0,92
	Fine Sand		0,11	0,10
	Fine Sand	Coordinates	0,11	0,14
	Coarse Sand		-0,08	0,81
	Coarse Sand	Coordinates	-0,08	0,37
	Total Sand		-0,07	0,79
	Total Sand	Coordinates	-0,07	0,40
Senile	Aluminum		0,03	0,35
	Aluminum	Coordinates	0,03	0,78
	Phosphorus		0,00	0,45
	Phosphorus	Coordinates	0,00	0,99
	Calcium		-0,02	0,52
	Calcium	Coordinates	-0,02	0,82
	Magnesium		-0,04	0,65
	Magnesium	Coordinates	-0,04	0,64
	Organic Matter		-0,03	0,57
	Organic Matter	Coordinates	-0,03	0,77
	pH		-0,03	0,68
	pH	Coordinates	-0,04	0,59
	Potassium		-0,06	0,74
	Potassium	Coordinates	-0,06	0,48
	Potential Acidity		-0,04	0,66
	Potential Acidity	Coordinates	-0,04	0,55
	Cation Exchange Capacity		-0,05	0,70
	Cation Exchange Capacity	Coordinates	-0,05	0,56
	Sum of Bases		-0,02	0,54
	Sum of Bases	Coordinates	-0,02	0,84
	Base Saturation		-0,05	0,71

	Base Saturation	Coordinates	-0,05	0,57
	Silt		-0,11	0,88
	Silt	Coordinates	-0,11	0,24
	Clay		0,28	**0,00***
	Clay	Coordinates	0,28	**0,00***
	Fine Sand		0,14	**0,07***
	Fine Sand	Coordinates	0,15	**0,05***
	Coarse Sand		0,37	0,92
	Coarse Sand	Coordinates	-0,11	0,22
	Total Sand		-0,10	0,90
	Total Sand	Coordinates	-0,10	0,28
Population	Aluminum		-0,06	0,60
	Aluminum	Coordinates	-0,06	0,60
	Phosphorus		-0,04	0,62
	Phosphorus	Coordinates	-0,04	0,64
	Calcium		-0,05	0,65
	Calcium	Coordinates	-0,05	0,58
	Magnesium		-0,08	0,83
	Magnesium	Coordinates	-0,08	0,37
	Organic Matter		-0,06	0,66
	Organic Matter	Coordinates	-0,05	0,57
	pH		-0,04	0,64
	pH	Coordinates	-0,04	0,59
	Potassium		-0,07	0,81
	Potassium	Coordinates	-0,07	0,34
	Potential Acidity		-0,03	0,59
	Potential Acidity	Coordinates	-0,03	0,68
	Cation Exchange Capacity		-0,03	0,57
	Cation Exchange Capacity	Coordinates	-0,03	0,68
	Sum of Bases		-0,06	0,69
	Sum of Bases	Coordinates	-0,06	0,50
	Base Saturation		-0,04	0,57
	Base Saturation	Coordinates	-0,03	0,65
	Silt		-0,05	0,60
	Silt	Coordinates	-0,05	0,71
	Clay		0,02	0,34
	Clay	Coordinates	0,02	0,87
	Fine Sand		0,01	0,29
	Fine Sand	Coordinates	0,02	0,88
	Coarse Sand		-0,07	0,77
	Coarse Sand	Coordinates	-0,07	0,38
	Total Sand		-0,06	0,68
	Total Sand	Coordinates	-0,06	0,49

Considerações Finais

Os critérios macromorfológicos utilizados neste estudo permitiram distinguir seis estádios ontogenéticos na população de *Savia dictyocarpa* – plântula, Infante, Jovem, Imaturo, Adulto e Senil – que, por sua vez, forneceram uma boa base para as análises alométricas e da estrutura da população. A pouca sobreposição de tamanho entre os estádios sugere que tanto a altura quanto o diâmetro podem auxiliar na identificação dos estádios ontogenéticos desta espécie, sendo que o surgimento de certas estruturas parece só ocorrer após a planta atingir um tamanho mínimo. A separação dos estádios quanto à altura e diâmetro também sugere que as características escolhidas para definição de estádios refletem as diferentes pressões que a espécie sofre ao longo da ontogenia.

As relações alométricas da espécie indicam que, apesar da grande variação de luminosidade devido à deciduidade da floresta, há mudanças nas estratégias de ocupação vertical da floresta. É interessante ressaltar as evidências da interferência de lianas na arquitetura da copa já que há poucos estudos que abordam essa questão.

A ausência de plântulas e de sementes viáveis levanta questões sobre o status de conservação da área de estudo. A ausência de polinizadores é uma das hipóteses que justifica a interrupção na produção de sementes. Alguns autores afirmam que a falta de produção de sementes em parte dos frutos produzidos por uma planta seria uma estratégia contra efeito de predação de sementes. No entanto, esse não parece ser o caso de *S. dictyocarpa* já que todos os frutos coletados não possuíam nenhuma semente. A ausência de polinizadores pode estar relacionada com a fragmentação de hábitat, que apesar de contida atualmente na área, já atuou na região de Campinas e transformou a paisagem natural em pequenos fragmentos espalhados pela APA.

Além disso, na escala estudada a distribuição espacial da espécie parece não estar correlacionada com características que comumente relacionam-se com padrões de mortalidade e recrutamento de plantas tropicais, como exposição à luz e nutrientes do solo. Com a distribuição aleatória da espécie não é possível propor medidas de manejo da espécie, pois não se sabe ainda qual micro habitat é propício para seu crescimento e recrutamento.

Assim, são necessários estudos de biologia reprodutiva e de dinâmica populacional para entender a ausência de indivíduos jovens na área e também para que sejam propostas medidas de conservação e manejo para *S. dictyocarpa*.