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INSTITUTO DE BIOLOGIA

LUCIANA DE CAMPOS FRANCI

Estrutura populacional de *Astronium graveolens* Jacq. (Anacardiaceae) em uma Floresta Estacional Semidecídua no sudeste do Brasil

Este exemplar corresponde à redação final
da tese defendida pelo(a) candidato (a)
Luciana de Campos Franci
e aprovada pela Comissão Julgadora.

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

Fernando R. Martins
Orientador: Prof. Dr. Fernando Roberto Martins

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“Acho que na sociedade actual nos falta filosofia. Filosofia como espaço, lugar, método de reflexão, que pode não ter um objectivo determinado, como a ciência, que avança para satisfazer objectivos. Falta-nos reflexão, pensar, precisamos do trabalho de pensar, e parece-me que, sem ideias, não vamos a parte nenhuma.”

José Saramago, 2008

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Resumo geral

Investigamos nesse estudo a estrutura populacional da espécie arbórea emergente *Astronium graveolens* Jacq. (Anacardiaceae) em uma Floresta Estacional Semidecídua no Sudeste do Brasil. *Astronium graveolens* é uma espécie anemocórica de ampla distribuição na Mata Atlântica. Nossos objetivos principais foram: (1) investigar quais as adaptações quanto a arquitetura e morfologia da espécie para melhor interceptação de luz; (2) compreender as relações biomecânicas da espécie; (3) investigar as demandas conflitantes enfrentadas em cada estádio ontogenético na história de vida de *A. graveolens* relacionadas à sazonalidade de chuvas; (4) investigar os padrões de distribuição espacial de cada estádio ontogenético; (5) investigar se os fatores abióticos explicam as densidades de cada estádio ontogenético em cada parcela e (6) se os indivíduos de cada estádio ontogenético co-ocorrem com frequência maior que o esperado ao acaso com determinada espécie da comunidade. Realizamos a coleta de dados em um fragmento de Floresta Estacional Semidecídua localiza no município de Campinas, SP. Utilizamos 100 parcelas aleatórias de 10 x 10 m nas quais amostramos todos os indivíduos de *A. graveolens*. Medimos o diâmetro à altura do solo e altura total de todos os indivíduos. Dos indivíduos com até 1,5 metros medimos o comprimento da raque das folhas e contamos o número de folhas. Dos indivíduos com até 5 metros, contamos o número de ramificações. Identificamos todos os indivíduos arbóreos de todas as espécies com perímetro à altura do peito maior que 15 cm. Definimos os estádios ontogenéticos (plântula, infante, juvenil I, juvenil II, imaturo e adulto) utilizando marcadores macromorfológicos. A relação alométrica entre diâmetro e altura diferiu dos modelo teóricos isométrico, similaridade elásticas e similaridade de estresse. A espécie apresenta estratégias contra a seca, e sua arquitetura e características morfológicas sugerem que a luz pode ser um filtro importante na história de vida dos indivíduos. Para *A. graveolens* crescer rápido em altura e atingir o dossel parece ser a chave para a sobrevivência. Os indivíduos dos estádios infante, juvenil I e adulto apresentaram padrão agregado em pequena escala, enquanto os demais estádios, juvenil II e imaturo, apresentaram distribuição aleatória. A densidade dos estádios ontogenético não foi influenciada por fatores ambientais. A similaridade de densidade das parcelas diminuiu com a distância, o que indica que processos estocásticos podem atuar como fatores importantes na população. As co-ocorrências negativas se mostraram mais frequentes que as positivas e houve mudança nas freqüências de co-ocorrências ao longo da ontogenia. Aparentemente para *A. graveolens* processos estocásticos e determinísticos podem ser importantes para a população no local estudado.

Palavras-chave: ontogenia, história de vida, alometria, distribuição espacial, co-ocorrência.

Abstract

We investigated the population structure of the emergent tree species *Astronium graveolens* Jacq. (Anacardiaceae) in a Tropical Seasonal Semideciduous Forest, southeastern of Brazil. *Astronium graveolens* is an anemochorous species widely distributed in Atlantic Forest. Our main goals was: (1) to investigate which architectural and morphological characters of *A. graveolens* are adapted to better light interception; (2) to investigate the biomechanical relationship of the species ; (3) to investigate the trade-offs face by each ontogenetic stage in the life-history related to rain seasonality; (4) to investigate the patterns of spatial distribution of each ontogenetic stage; (5) to investigate whether the abiotic factors explain the density of each ontogenetic stage in each plot and (6) whether individuals of each ontogenetic stage co-occur with frequency greater than expected by chance with a given specie. We collected the data in a fragment of Seasonal Semideciduous Forest in Campinas, SP, municipality. We used 100 plots randomly arranged with 10 x 10 m each. We measured diameter at ground level and total height of each individual. From the individuals up to 1.5 m we measured leaf length and counted the number of leaves. From the individuals up to 5 m we counted the number of branches. We indentified every individual of each species in each plot with circumference at breast height higher than 15 cm. We indentified five ontogenetic stages (infant, juvenile I, juvenile II, immature and adult) using macromorphological characters. Allometric relationships differed from all the theoretical models of geometric, elastic similarity and stress similarity. The species have strategies against drought, and its architecture and morphological characteristics suggest that light may be an important filter in *A. graveolens* life-history. *Astronium graveolens* is a species that must grow quickly in height to reach the canopy, and it is the key for surviving. Individual of the stages infant, juvenile I and adult had aggregated pattern, while juvenile II and immature were randomly distributed. The density of the stages in each plot was not influenced by abiotic factors. Similarity of density of each plot decreased with distance, suggesting that stochastic processes are important factors in the population. The negative co-occurrences were more frequent than positive ones and the frequencies changed through the ontogeny. Apparently, this population of *A. graveolens* suffers influences of stochastic and deterministic processes.

Key-words: ontogeny, life-history, allometry, spatial distribution, co-occurrence.

Considerações iniciais

Com a intensa fragmentação da Mata Atlântica restaram apenas 7,5% da sua cobertura original (Myers et al. 2000), o que torna essencial a realização de estudos que auxiliem a compreender a dinâmica e a ecologia das formações vegetacionais desse domínio (Connell et al. 1984). Documentar padrões de abundância e distribuição dos organismos e desenvolver teorias para explicá-los é um tema de estudo central na ecologia (Schnitzer 2005). A Floresta estacional semidecídua é uma formação vegetacional da Floresta Atlântica, caracterizada pela sazonalidade de chuvas e sazonalidade de distribuição da precipitação (Veloso et al. 1991). No período de seca, que dura aproximadamente de março a outubro, cerca de 50% das espécies arbóreas perdem suas folhas, o que faz com que a luminosidade no interior da floresta seja maior nesse período. No período chuvoso, de novembro a fevereiro, as árvores tem as copas densas, com muitas folhas, sombreando o interior da floresta (Hernandes et al. 2004). Portanto, há correlação negativa entre disponibilidade de água e luz nas florestas estacionais semidecíduas (Valladares & Niinemets 2008). Assim, as plantas que vivem nessas formações vegetacionais podem enfrentar demanda conflitante entre tolerância à seca e à sombra.

Estudar a estrutura de uma população é essencial para entender a diversidade e os processos que regulam a dinâmica e a estrutura de comunidades naturais (Connell et al. 1984; Santos 2002). Estudos populacionais podem ser utilizados como bases de programas de manejo e conservação de espécies (Santos 2002; Marques & Joly 2000). Para compreender a estrutura de uma população é possível abordar aspectos de sua história de vida, distribuição espacial e suas relações com os meios bióticos e abióticos.

Neste trabalho estudamos a espécie de árvore emergente *Astronium graveolens* Jacq. (Anacardiaceae). A espécie tem ampla distribuição, desde a América Central até o Sul do Brasil

(Carvalho 2006; Silva-Luz and Pirani 2011). É uma espécie decídua que perde todas as folhas no período de seca (Marín and Flores 2002), apresenta resistência a seca (Pereira 2011), é anemocórica e considerada indicadora de solos pobres (Carvalho 2006).

No primeiro capítulo definimos os estádios ontogenéticos de *Astronium graveolens* e abordamos aspectos de sua história de vida considerando as demandas conflitantes relacionadas principalmente à sazonalidade de chuvas enfrentada pela população na floresta estacional semidecídua de *Astronium graveolens*. A história de vida de uma planta descreve, entre outros aspectos, a duração do tempo de vida, o crescimento, as fases reprodutivas e estratégias de sobrevivência e obtenção de luz (Silvertown and Doust 1993). Considerando a distribuição dos indivíduos segundo uma variável, como tamanho, idade ou distribuição espacial dos indivíduos, é possível levantar informações sobre padrões de mortalidade, crescimento e estabelecimento de novos indivíduos no espaço e no tempo, possibilitando compreender a história de vida e as respostas da espécie estudada a diferentes condições ambientais (Hutchings 1997).

Os estudos que descrevem a estrutura populacional de uma espécie, geralmente abordam estruturas de tamanho ou idade e distribuição espacial (Hutchings 1997). Alguns autores sugerem ser mais adequado utilizar estádios ontogenéticos para estudar uma população de plantas (Bernacci et al. 2008; Gatsuk et al. 1980; Smirnova et al. 2002; Zhukova and Glotov 2001), contornando, assim, o problema de determinar a idade cronológica da planta (Smirnova et al. 2002). Indivíduos diferentes podem atingir um determinado estádio ontogenético em tempos diferentes, mas a partir do momento que estão em um mesmo estádio, seus papéis na população são muito semelhantes (Smirnova et al. 2002). A ontogenia é o desenvolvimento do indivíduo desde seu nascimento até a morte. A duração de cada estádio ontogenéticos é determinada geneticamente em cada espécie, mas pode variar sob diferentes condições ambientais. Os estádios são definidos a partir de marcadores morfológicos e características fisiológicas (Gatsuk et al.

1980; Smirnova et al. 2002). O reconhecimento dos estádios é relevante na análise da estrutura e da dinâmica de populações (Gatsuk et al. 1980), pois fornece informações com significado ecológico a partir do desenvolvimento ontogenético dos indivíduos (Silvertown and Doust 1993).

Além de conhecer a ontogenia dos indivíduos, avaliamos as relações de forma e tamanho de cada estádio ontogenético. Para que o indivíduo atinja determinada altura é necessário crescimento mínimo em diâmetro que evite o tombamento da planta devido a seu próprio peso (McMahon 1973). Logo, crescer em diâmetro ou em altura representa demandas conflitantes na história de vida da planta (King 1990). No entanto, as relações alométricas não permanecem constantes ao longo da vida da planta (Alves & Santos 2002; Sterck & Bongers 1998), podendo ser diferentes em cada estádio ontogenético.

No segundo capítulo identificamos os padrões de distribuição espacial de cada estádio ontogenético. A distribuição espacial dos indivíduos é uma questão chave para se entender como os recursos são usados pelas populações e se relacionam ao sucesso reprodutivo dos indivíduos, evitando a extinção local (Condit et al. 2000; Götzenberger et al. 2011). Muitos fatores ambientais, bióticos e abióticos, influenciam a distribuição das espécies, como síndrome de dispersão, padrões históricos de especiação e migração e estocasticidade, os quais podem agir simultaneamente (Bell 2001; Chase 2003, 2007; Ejrnæs et al. 2006; Götzenberger et al. 2011; Urich 2004). Ainda, investigamos se os fatores ambientais estão relacionados à densidade de indivíduos por parcela e se os estádios ontogenéticos co-ocorrem com determinada espécie da comunidade mais que o esperado ao caso, para entender como é a relação de *A. graveolens* com as árvores vizinhas.

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CAPÍTULO 1

Life-history of a light-demanding emergent tree in the Tropical Seasonal Semideciduous Forest[1]

Luciana de Campos Franci e Fernando Roberto Martins

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Luciana de C. Franci[1] and Fernando R. Martins[2,3]

Life-history of a light-demanding emergent tree in the tropical seasonal semideciduous forest

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Abstract

The Tropical Seasonal Semideciduous Forest (TSSF) is characterized by rainfall seasonality and deciduousness of about 50% of the trees in the dry season, implying a trade-off between drought and shade tolerance. Species living under these conditions must have strategies against drought or dimness. We aimed to investigate how *Astronium graveolens* (Anacardiaceae) grows from the understory up to the canopy in order to understand life history and survival strategies of a light-demanding emergent tree of the TSSF. We analyzed height-diameter allometry and mechanical design across ontogenetic stages, which were distinguished according to external macromorphological traits. We analyzed scatterplots of these traits to infer about the existence of trade-offs whenever a variable increased and the other decreased or kept grossly constant. We recorded data of every individual of *A. graveolens* in random 100 plots of 10 x 10 m each in the Ribeirão Cachoeira Forest (22°49’50.5”S, 46°55’35.86” W), a well preserved 244.89 ha fragment of the Seasonal Semideciduous Forest, in Southeastern Brazil. We defined six ontogenetic stages (seedling, infant, juvenile-I, juvenile-II, immature, and adult) and inferred possible trade-offs between leaf length vs. leaf number or plant height or stem diameter at breast height (DBH), leaf number vs. plant height, branch number vs. plant height or DBH. In infants and the juvenile-I increasing height, diameter or leaf number implied smaller leaves, and if the plants grew in height they did not produce more leaves. If immature plants grew in height or diameter they did not produce more branches. DBH and height SMA regression (slope=1.19, intercept=0.01) fitted well (r^2=0.86) the population and differed from all the theoretical models of geometric, elastic similarity and stress similarity. Although safety factor decreased with height, biomechanical stability was achieved by a great wood density and by the absence of individuals below the safety limit. During ontogeny *Astronium graveolens* invests energy first in height then in diameter growth and overcomes trade-offs imposed by changes of water and light availability in the understory along the year.

Keywords: allometry, life-history, mechanical design, ontogeny, seasonal semideciduous forest, shade-intolerance, trade-off.

INTRODUCTION

Overall, tropical forests are known by high rainfall throughout the year, but some forest formations suffer seasonal drought (Walsh 1996). Among the forest formations of the Brazilian Atlantic Forest, the Tropical Seasonal Semideciduous Forest is characterized by a wet-dry seasonality (Veloso et al. 1991). The dry season generally lasts from March/April to September/October, a period that includes the winter, when almost half of the trees, especially the canopy ones, shed leaves, increasing light penetration to the understory. During the summer (October – March), rainfall is plenty, and the trees are full of leaves, closing the canopy and shading the forest understory. In the dry season, light radiation in the understory can increase about 33% compared to the rainy season (Hernandes et al. 2004).

Light availability is directly related to carbon budget influencing tree growth and survival (Sterck et al. 2001, Montgomery and Chazdon 2002, van Gelder et al. 2006). Trees growing in the understory encounter increasing light gradients up to the canopy, and with height gain trees come to occupy sites with more light availability, until they reach the canopy and no longer compete for light (Sterck and Bongers 2001). In tropical forests, the irradiance varies from 1-2% of full light at the ground level to 100% above the canopy (Poorter et al. 2006), and no plant can perform optimally over the entire light gradient, because of its morphological and physiological adaptations (Valladares and Niinemets 2008). Considering macromorphological characters, trees have different strategies for improving light use and interception. Some species forage for light by optimizing leaf display (Valladares et al. 2002, Pearcy et al. 2004, Poorter et al. 2006, Poorter and Rozendaal 2008), including crown architecture (Aiba and Kohyama 1997, Sterck and Bongers 2001, Valladares et al. 2002, Kitajima et al. 2005), and some invest in height growth to quickly reach the canopy (Kohyama and Hotta 1990, Clark and Clark 1992, Bohlman and O'Brien 2006, King et al. 2006).

Water availability is one of the most important factors in tropical forests, and seasonality is an important key component related to its availability (Poorter and Markesteijn 2008), so that on macroscale tree α-diversity is limited by the dry season length (Steege et al. 2006). To understand the overall effects of drought, it is necessary to study its effects individually on microscale. Through the ontogeny, plants have different physiological and morphological drought-tolerance strategies, classified, respectively, as drought resistance and drought delay (Tyree et al. 2003, Markesteijn and Poorter 2009). Drought resistance mechanisms permit continued gas exchange, water transport, increased cell resistance to low water content and potentials, and increased resistance of xylem to embolism (Tyree et al. 2003). Drought delay traits include deep roots, early stomatal closure, low cuticular conductance, water storage in plant organs (Tyree et al. 2003), and deciduousness (Poorter and Markesteijn 2008).

In the Tropical Seasonal Semideciduous Forest, water and light are negatively correlated (Valladares and Niinemets 2008), leading plants to a trade-off between drought- and shade-tolerance. This trade-off can be directly associated with the trade-off between aboveground and underground biomass allocation (Smith and Huston 1989). In fact, species from dry environments have a trade-off between the biomass allocated to roots conferring a competitive advantage for water uptake and the biomass invested in shoots to take advantage in light foraging during the wet, shaded season (Poorter and Markesteijn 2008, Valladares and Niinemets 2008). In any trade-off, the energy allocated to one part of the plant is no longer available to invest in another part; thereby, for some species the trade-off between drought- and shade-tolerance can imply a trade-off between diameter and height growth.

In low light conditions, sapling of shade-intolerant species are smaller with higher mortality rates than shade-tolerant species (Clark and Clark 1992), and to survive they must escape from low light levels (Sterck and Bongers 1998). Canopy and emergent trees do this by growing up to the canopy as soon and fast as possible, but reaching the canopy quickly means great investment in height gain during the ontogeny to the detriment of diameter growth. For shade-intolerant species, investing in height is more important than growing in diameter, since the latter does not lead to a competitive advantage for light foraging (Henry and Aarssen 1999). However, height gain prerequires resource allocation to a minimum diameter, so that the tree does not bend due to its own weight (Niklas 1994). Biomechanical models predict that the diameter should increase faster than height for the trunk not to bend according to the constant stress model or the elastic similarity model (Henry and Aarssen 1999), the most common models found in wet tropical forests. However, for shade-intolerant trees in the Tropical Seasonal Semideciduous Forest, it may be more important to reach the canopy quickly because of the seasonality of light and water availability; so, maybe these species grow faster in height than in diameter, following an economic isometric model, such as the geometric model (Norberg 1988).

Tree architecture refers to the shape and the spatial position of the tree components (Poorter et al. 2006). Due to the different conditions found in the vertical gradient during growth (Poorter et al. 2005), tree architecture is related to light foraging, which can be optimized by leaf display (Poorter and Rozendaal 2008), carbon gain, and the optimization of the tree efficiency to reach the canopy (Iida et al. 2011). While thriving to reach the canopy, a tree can grow in only one way among 23 possible paths, which are the architectural models (Oldeman 1979). Although the architectural model is an inherited trait of the species (Oldeman 1979), the plant accomplishes architectural adjustments due to stresses it faces across ontogeny (Hallé et al. 1978). Because of this plasticity, tree architecture can change during the ontogeny although the architectural model does not change (Hallé et al. 1978, Sterck and Bongers 2001).

Plant architecture is also related to mechanical stability (Poorter et al. 2006), which can be analyzed by knowing the tree bending safety factor. The bending safety factor indicates the safety margin that trees maintain against dynamic loads, such as wind and bending for its own weight (van Gelder et al. 2006). The safety margin of pioneer and shade-intolerant species can diminish through the ontogeny (Sposito and Santos 2001). Investing in height gain rather than in diameter represents a trade-off, because the bending safety factor decreases as the plant grows in height. The priority to invest in an optimal shape to grow in height is appropriate to shade-intolerant species (King 1981). Light-demanding species grow with small safety margins, maximizing height growth for better competing for light (King 1981, Claussen and Maycock 1995, van Gelder et al. 2006).

Here we investigated life-history traits and trade-offs of a light-demanding emergent tree species to assess the strategies adopted across ontogeny with height gain for better light use. Faced with the negative correlation between light and water availability, as in the Tropical Seasonal Semideciduous Forest, young canopy trees are met with a trade-off between drought- and shade-tolerance (Valladares and Niinemets 2008). Hence, we expected light to be the main filter acting on the life-history of a shade-intolerant species. Our aim was to investigate (1) which architectural and morphological adaptations a light-demanding canopy tree has to better light interception; (2) whether the initial ontogenetic stages invest in height growth rather than in diameter to quickly reach the canopy; (3) whether there are changes in the allometric relationships through the ontogeny as a consequence of changes in the tree architecture; and (4) whether there are decrease in the bending safety margin along ontogeny as consequence of a greater investment in height than in diameter growth.

MATERIAL AND METHODS

Study site

We collected the data on a slope at the southern portion of the Ribeirão Cachoeira forest (22°50’ S, 46°55’ W), a fragment of the Tropical Seasonal Semideciduous Forest with 244.89 ha, located in an Environmental Protection Area in Campinas municipality, São Paulo state, southeastern Brazil. The regional climate is Koppen Cwa, with rainy, warm summer and dry, mild winter (CEPAGRI 2011). The annual average temperature is 22.4°C and precipitation is 1424.5 mm. The rainy season occurs from October to March, with a mean total precipitation of 1141.5 mm and average temperature of 24.48°C. The dry season lasts from April to September, with a mean total precipitation of 283 mm and average temperature of 20.44°C (CEPAGRI 2011 – data for the period of June 1988 to October 2008). The altitude varies between 630 to 760 m above sea level, and the soil of the slope makes a catena with sandy Red-Yellow Argisol (Alfisol) in the lower portion and Lytholic Neosol (Lythosol) in the upper portion (personal observation).

Species studied

Astronium graveolens Jacq. (Anacardiaceae) is an emergent tree, reaching up to 35 m in height, characteristic of the Neotropical Seasonal Semideciduous Forest (Carvalho 2006), and occurs from Central America to South America (Marín and Flores 2002). In Brazil it is found in the entire range of the Atlantic Forest (Lorenzi 2002, Carvalho 2006, Silva-Luz and Pirani 2011), in Amazon rainforest, savannas (Cerrado), semi-arid steppe savanna (Caatinga) and southern grassland (Pampas) (Silva-Luz and Pirani 2011). The species is deciduous, shedding the leaves during the dry season (Marín and Flores 2002). Flowering occurs in the dry season, from June to October, when the individuals are totally leafless (Carvalho 2006). The flowers are grouped into terminal panicles (Marín and Flores 2002), and the fruit is a pseudo-samara with an acrescent calyx (Carmello-Guerreiro and Paoli 2000), which renders it star-shaped (hence the genus name) facilitating the wind dispersal of the single seed (Marín and Flores 2002). Frequently *A.*

graveolens is found in rocky and alluvial soil (Lorenzi 2002, Marín and Flores 2002, Carvalho 2006) as an indicator of poor soils (Carvalho 2006), being classified as non-pioneer, early or late secondary (Würth et al. 2005, Carvalho 2006), drought-resistant species (Pereira, 2011).

Data collection

We carried out the study in a 6.5 ha area, where 100 plots with 10 x 10 m each were previously established (see Cielo-Filho, Gneri, and Martins 2007 for more details) according to the unrestricted randomization procedure (Greig-Smith 1983). We tagged every individual of *A. graveolens* within the 100 plots and measured their total height and diameter at the ground level (DGL). We used a telescopic ruler to measure the total height of the individuals over 1.8 m tall, and for the individuals up to this height we used a measuring tape. We measured the DGL with a caliper for small individuals and a measuring tape for large individuals. We recorded the presence of lianas and counted the number of branching of the individuals up to 5 m tall and the number and length of leaves of the individuals up to 1.5 m tall.

Data analysis

We classified the individuals into ontogenetic stages according to Gatsuk et al. (1980), Zhukova and Glotov (2001), Smirnova, Palenova, and Komarov (2002) and Bernacci, Martins and Santos (2008), considering the presence or absence of cotyledons, branches, flowers, fruits, the position of the leaves and the number of leaves and leaflets. We also considered architectural traits, such as axis orientation (plagiotropic or orthotropic), type of growth (monopodial or sympodial), meristem activity (rhythmic or continuous) and meristem differentiation (vegetative or sexual). To define the architectural model of *A. graveolens*, we based on the identification key proposed by Hallé, Oldeman and Tomlinson (1978). We characterized the seedling stage using pictures taken during a germination experiment in greenhouse (L. Pereira, unpublished data). All the other stages were recognized based on the external macromorphological characters observed in field.

To analyze the size variation in height, diameter and leaf number and length in each stage, we used Kruskall-Wallis analysis followed by *a posteriori* Dunn test using BioEstat version 5.0 software (Ayres et al. 2007). We constructed scatterplots of leaf length vs. leaf number, leaf number vs. stem height, leaf area proxy (total length of the leaves) vs. stem height, leaf area proxy vs. stem diameter, branch number vs. stem height and branch number vs. stem diameter. We made a visual analysis to know whether there was a trade-off between variables in each scatterplot. We considered the presence of a trade-off whenever one variable increased and the other variable decreased or did not change.

To analyze the allometric relationship between diameter and height of the whole *A. graveolens* population we used standardized major axis (SMA) regression slopes. We compared the regression slope of log diameter vs. log height with the regression slope of the theoretical allometric models: geometrical model (b = 1), elastic similarity (b = 1.5) and stress similarity (b = 2). We did this comparison by testing for correlation between residual and fitted values (Warton et al. 2006). The SMA is recommended to describe linear relationships on logarithmic scales and when neither variable is independent (Warton et al. 2006). We used the software SMATR (Falster et al. 2006).

To analyze the mechanical design, we considered the bending safety factor, i.e., the ratio between the observed diameter (D_{obs}) and the critical bending diameter (D_{crit}). The D_{crit} is calculated based on the modified McMahon (1973) bending equation $D_{crit} = 0.109H^{3/2}$. In this equation, we used the constant 0.109, which is a product of the constant proportionality (0.792) multiplied by the ratio between elastic modulus (E) and wood density (ρ), as suggested by

McMahon (1973), because values of elastic modulus are not available in the literature for *A. Graveolens*, and the methods to measure it are destructive. According to Niklas (1993), E. ρ^{-1} is a constant in gymnosperms and dicotyledon trees. Therefore, the safety factor we calculated is only an estimate. We plotted the safety factor against height in a scatterplot and constructed all the diagrams with aid of the R environment (R Development Core Team 2010).

RESULTS

We distinguished five ontogenetic stages in the field and the seedling stage in the greenhouse: 501 individuals in the infant stage, 286 individuals in the juvenile-I stage, 72 individuals in the juvenile-II stage, 25 individuals in the immature stage and 43 individuals in the adult stage. We did not find any seedling in the field.

Ontogenetic stages and architectural model

Astronium graveolens has epigeal germination and cryptocotylar seedlings (Marín and Flores 2002). The orthotropic stem axis in the seedling stage is green, not branched and bears a pair of cotyledons covered by the seed coat. Seedlings have a pair of opposite, ternate primary compound leaves (Fig. 1). In the infant stage, the individuals do not have cotyledons anymore, but keep the pair of primary opposite ternate leaves. The monopodial orthotropic axis is still green and, above the primary leaves, it may or not bear one or up to nine ternate leaves with spiral alternate disposition (Fig. 1). The individuals in the juvenile-I stage have no primary opposite ternate leaves anymore and have one to eight spiral alternate ternate leaves. The axis is monopodial orthotropic not branched and its base is not green anymore (Fig. 1). The juvenile-II stage has one to eleven alternate compound leaves, which are spirally arranged and have three or more leaflets. The monopodial orthotropic stem is woody and not branched (Fig. 1).

From the immature stage on, all the individuals are branched and have imparipinnate spiral alternate leaves (Fig. 1). The monopodial orthotropic axis produces orthotropic branches rhythmically. Secondary branches have rhythmic growth, which have orthotropic orientation. The individuals in the adult stage have monopodial trunk with light-grey bark (Fig. 1). The orthotropic branches have sympodial growth, conforming to Scarrone architectural model. The crown consists of expansions of the branches reiterating the architectural model. We could not distinguish between vegetative and reproductive adults, because during the study no individual of *A. graveolens* produced flowers and fruits.

Size variation

Although the stages became significantly larger in height and diameter during the progression from infant to adult (Fig. 2), the size ranges overlapped partially between consecutive stages (Tables 1 and 2). Almost the entire height ranges of the infants (0.010 – 1.27 m) and juvenile I (0.035 – 1.25 m) overlapped, the tallest juvenile-I being a little shorter than the tallest infant (Table 1). Likewise, the diameter ranges of the infants (0.010 – 1.46 cm) and juvenile-I (0.010 – 1.37 cm) overlapped almost entirely, the juvenile-I with the largest diameter being slenderer than the infant with the largest diameter (Table 2). However, height and diameter medians of these three stages were different (Tables 1 and 2). The height ranges of the juvenile-II (0.20 – 3.60 m) and immature (0.15 – 7.50 m) overlapped, the shortest immature being a little shorter than the shortest juvenile-II (Table 1). The height ranges of the immature (0.15 – 7.50 m) and adults (5.00 – 27.00 m) overlapped very narrowly (Table 1). Likewise, the diameter ranges of the immature (0.252 – 17.507 cm) and adults (8.594 – 63.662 cm) overlapped to some extent (Table 2). Height and diameter medians of juvenile-II, immature and adults did not differed (Table 1 and 2). In general, size ranges overlapped progressively less from the initial to the final ontogenetic stages. The wide overlapping of size ranges between consecutive stages indicates that recruitment from a stage to the next does not depend on the individual size.

Leaf number (median ± semi-amplitude of the confidence interval at 95%) of the infants (3 ± 0.06) was different from the juvenile-I (4 ± 0.08) and juvenile-II (4 ± 0.24) (Kruskal-Wallis with *a posteriori* Dunn test, $P < 0.05$). Leaf length (median ± semi-amplitude of the confidence interval at 95%) was different among all the three early stages, infant (0.75 ± 2.23), juvenile-I (1.3 ± 0.07) and juvenile-II (12.23 ± 0.55) (Kruskal-Wallis with *a posteriori* Dunn test, $P < 0.05$).

In infants and the juvenile-I the increase of leaf number was associated with smaller leaves (Fig. 3 A). In infants and the juvenile-I and II increasing stem height did not increase leaf number (Fig. 3 B), but growing in height (Fig 3 C) or in diameter (Fig. 3 D) diminished the plant total leaf area. In the immature branch number did not increase as stem height (Fig. 3 E) or stem diameter (Fig 3 F) increased.

Size-shape relationships and mechanical design

The regression between diameter and height was significant (ANOVA, $p < 0.05$). The regression line slope value was 1.19 and the intercept value was 0.01. The coefficient of determination (r^2) indicated a good adjustment for the population ($r^2 = 0.86$). The regression line was different from any theoretical model ($p < 0.05$).

The safety factor decreased with height gain; the immature and adults had values closer to the safety limit (Fig. 4). However, neither adult nor immature individuals had values below the safety limit. Hence, we could assume that individuals got stability across the ontogeny.

DISCUSSION

Architecture model and the trade-offs in each ontogenetic stage

Astronium graveolens conformed to Scarrone architectural model, characterized by an orthotropic rhythmically growing trunk with active terminal meristem. The trunk bears rhythmic orthotropic branch-complexes, from which each orthotropic branch grows sympodially resulting in hapaxanthic, terminal flowers (Hallé et al. 1978). The rhythmic growth, a characteristic of Scarrone model, allows dicotyledonous trees to have dense crown and reach up the canopy or even surpass it as emergent trees (Hallé et al. 1978). In canopy species, the arrangement of branches seems to be more important for light capture than the position of the leaves (Kitajima et al. 2005). In Scarrone model, the presence of orthotropic terminal branches contributes to more efficient light interception, rendering the tree a better light competitor (Kitajima et al. 2005). In addition to the arrangement of the branches, the spiral alternate leaf display diminishes self-shading, optimizing light interception. In *A. graveolens* Scarrone model is possible to be identified only in the adult stage.

The earliest ontogenetic stage we observed in the field – infant – had few and small leaves, but the individuals overlapped in height and diameter ranges with the juvenile-I, although the medians were significantly different. Compared to infants, the juvenile-I had significantly larger leaf size and number. We found a trade-off between height and number of leaves in infants and juvenile-I and II, as expected in face of the need to get up to the canopy and improve light assimilation, which can be accomplished by the orthotropic stem assuring an efficient growth in height (Poorter et al. 2006). Infant and the juvenile-I seemed to invest in height in detriment of the plant total leaf area, as observed by Kohyama and Hotta (1990) for the emergent tree *Swintonia schwenkii* Teijsm. & Binn. ex Hook f. (Anacardiaceae), in a tropical seasonal forest: in the first stages of life individuals invested in height rather than in expansion of assimilative area. Therefore, for emergent, shade-intolerant tree species, investing in height during early life to reach upper levels in the forest profile light gradient seems to be more important than enlarging light-assimilative area.

In the forest understory, many species increase light interception by making larger leaves instead of making larger branches (Poorter et al. 2006). This seems to be the strategy adopted by the juvenile-I and II, which were not branched but had leaves larger than infants. Infants had significantly less leaves than juvenile-I and II, whereas leaf number did not differ between juvenile-I and II. The common trade-off between leaf number and size (e.g., Westoby and Wright 2003, Kleiman and Aarssen 2007, Yang et al. 2008) holds for *A. Graveolens*, since in infants and the juvenile-I we observed an inverse tendency between leaf length and number: the greater the leaf number the smaller the leaf length. Depending on the environmental conditions, for a determined amount of biomass allocation plants have many small leaves or a few large ones (Yang et al. 2008, Nicotra et al. 2011). However, it has been suggested that this relationship can be more than a trade-off between leaf size and number, being possibly related to plant investment in hydraulics or biomechanics (Nicotra et al. 2011).

Juvenile-II was the first stage to produce pinnate leaves, which are more efficient for light interception than the ternate leaves found in the previous stages. Compound leaves enhance light interception and work as a cheaper twig (Malhado et al. 2010). Also, in juvenile-II stage there were larger and more numerous leaves compared to earlier stages. So, in this stage light interception begins to increase indicating that juvenile-II may be a key stage in the life history of *A. graveolens*.

Branching starts in the immature stage, but these individuals could grow only up to 7.5 m tall, not enough to reach the canopy. Individuals in this stage grew in height without increasing the number of branches; hence it is likely to exist a trade-off between branching and growing in height in the immature stage. Branching requires biomass allocation (Sun et al. 2010), which would no longer be available for investment in growth. Only the adults of *A. graveolens* were able to reach the canopy, and they did this by performing four steps: first, they conformed to Scarrone model; second, they grew in both height and diameter; third, they reiterated Scarrone model; and finally they reached the canopy. Only after being positioned in the forest canopy, *A. graveolens* can reproduce. The early stages of large-statured trees often construct small crowns with thin stems; once they reach the canopy, they start reiterating the architectural model to maximize carbon gain and reproduction (Iida et al. 2011). In this way, our finding leads us to suggest that there would possibly be a trade-off between vegetative growth and early reproduction (Iida et al. 2011), a relevant trait in the life history of trees. In addition, *A. graveolens* is wind-dispersed, so starting reproduction after reaching the canopy optimizes seed dispersal.

Height-diameter allometry and mechanical design

Seedlings of *A. graveolens* had the lowest photosynthetic rates when compared to other three abundant tree species from the same forest fragment (Pereira 2011). Although *A. graveolens* demands high light intensity for photosynthesis and further growth, young plants occur scattered in the understory and not only in treefall gaps (personal observation); hence the species would be better classified as a light-demander rather than a shade-intolerant. Growing isometrically is the most economic manner to get taller, and since *A. graveolens* has low photosynthetic rates, ascending to the canopy as quickly as possible is a good way to overcome the understory dimness.

Light availability seems to be one of the most important filters acting on *A. graveolens*, so the individuals with the most appropriate architecture – that improving height gain and light interception – would be recruited. The slope of the regression line did not fit any theoretical model, but remained between the geometric and the elasticity similarity models, thus encompassing characteristics of both pioneer and canopy species. In the geometrical model the stem length scales in direct proportion to the stem diameter (Norberg 1988, Osunkoya et al. 2007). The geometric model is expected to occur in understory species and saplings of canopy and emergent species (King 1990, 1996), whereas canopy and emergent adult trees fit the elasticity similarity model or the constant stress model (e.g., Alves and Santos 2002, Osunkoya et al. 2007). Both of these latter models predict more investment in diameter growth, maintaining large safety factor and avoiding bending for own weight (McMahon 1973). Since *A. graveolens* is a light-demanding emergent tree, it is important to have a mechanical design allowing for fast height growth to get the canopy as soon as possible and concomitantly resisting mechanical loads through diameter growth.

Growth rate influences the probability of an individual to reach the canopy, but it is constrained by the wood efficiency in supporting the crown without buckling (King 1986). Although *A. graveolens* adults were close to the safety limit, they maintained a reasonable safety margin to not bend. In addition to the investment in diameter growth, *A. graveolens* has high woody density, about $0.97 g.cm^{-3}$ (Carvalho 2006). The woody density is strongly positively related to wood flexibility and breaking strength (Niklas 1992, van Gelder et al. 2006). Most emergent trees are expected to have smaller safety factors as they get closer to the upper canopy, mainly because of the wind effect (King and Clark 2011).Although storm winds have been associated with high mortality rates when trees reach the canopy (King 1986), *A. graveolens* is a deciduous tree and can decrease tree buckling chances in the dry season, when the wind usually acts strongly in the canopy.

Life-history traits and trade-offs: strategies of a light demanding emergent tree to survive in the Tropical Seasonal Semideciduous Forest

Seedlings of deciduous tree species have higher survival rates than evergreen species in seasonally dry tropical forests (Poorter and Markesteijn 2008). Their survival strategies include dense stems, compound leaves, increased belowground biomass with deep roots, maximized resource capture during the limited growing season, and reduced transpiration (Poorter and Markesteijn 2008, Markesteijn and Poorter 2009). *Astronium graveolens* occurs in an environment where light and water availability is alternately restricted in the rainy and dry seasons, respectively, meaning that restrictive conditions prevail over the entire year long. Survival strategies of *A. graveolens* are manifested through its allometric, architectural, physiological, and macromorphological traits. Water shortage is a limiting of carbon investment (Würth et al. 2005), and the low photosynthetic rates of *A. graveolens* saplings submitted to drought (Pereira 2011) confirm this issue. The tree species we studied has deciduousness and high wood density, which are strategies related to drought delay (Poorter and Markesteijn 2008). Heavy wood provides better resistance to drought-induced embolism (Hacke et al. 2001), and adults of deciduous species can have low embolism degree during the dry season (Sobrado 1997, Brodribb and Holbrook 2003). Also, deciduousness is an important character to avoid water loss by transpiration. Moreover, in dry conditions *A. graveolens* seedlings have low transpiration rates (Pereira 2011), which is facilitated by the small length and number of leaves implying small transpiration surfaces in the early ontogenetic stages. Provided that *A. graveolens* has strategies to overcome water shortage in the dry season, light availability seems to be the main abiotic factor influencing its growth and survival.

The rapid decrease of the safety factor through the ontogeny is a characteristic of pioneer and shade-intolerant species in tropical rainforests (Alvarez-Buylla and Martinez-Ramos 1992, Claussen and Maycock 1995, Sposito and Santos 2001). In general, the small safety factor of the taller individuals is compensated by a great wood density (Claussen and Maycock 1995, van Gelder et al. 2006). Nevertheless, Sterck and Bongers (1998) found greater safety factors in older individuals and suggested that because of the greater light availability in the canopy the species may acquire more carbon and invest it in their mechanical safety. This is not the case of *A. graveolens*, for which we suggest that because of heavy wood, deciduousness, and mechanical design that invests both in height and diameter growth, its individuals are resistant against bending under its own weight or dynamic loads, in spite of getting close to the bending safety limit. Great wood density helps canopy species not to bend (van Gelder et al. 2006), because heavy wood may provide the best combination of flexibility and strength to support strong winds (King 1986). Despite the low values of the safety factor of *A. graveolens* adults, they acquire stability by not having values under the safety limit. Low photosynthetic rates due to drought can compromise gain in height, and in addition to the need to reach the canopy, *A. graveolens* individuals have to survive water shortening and benefit from increased light availability during the dry season rather than to acquire greater safety factors. Reaching quickly the canopy while keeping the safety factor above the limit, even with a low safety margin, seems to be an efficient strategy of a drought-resistant, light-demanding species with low photosynthetic rate to survive, grow and reproduce in an environment with alternating intra-annual water and light shortening like the Tropical Seasonal Semideciduous Forest.

We found indirect evidences of different trade-offs operating at different ontogenetic stages of a light-demanding canopy tree species of the Tropical Seasonal Semideciduous Forest: there is an overall trade-off between drought- and shade-tolerance that manifests itself in stage-specific trade-offs. The overall trade-off requires high investment in height growth in life beginning as a way to attain the forest canopy as fast as possible while overcoming the recurrent understory dimness during the rainy season and the periodical water shortage in the dry season. During the ontogeny this overall trade-off manifests itself in different stage-specific trade-offs, such as those between growing and producing new leaves in the infant/juvenile-I transition, between branching and growing in height and diameter in the juvenile-II/immature transition, or between vegetative growth and early reproduction in the immature/adult transition. The existence of these stage-specific trade-offs is in agreement with Gatsuk et al. (1980), Zhukova and Glotov (2001), Smirnova, Palenova, and Komarov (2002), who stated that each ontogenetic stage is faced with different environmental conditions and performs different roles in the population and in the community. These trade-offs imply in the development of strategies related to improve light interception, such as architectural model and leaf display, as well as to overcome drought through physiological and morphological characters, such as low photosynthetic and transpiration rates, deciduousness and heavy wood.

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Table 1. Height (m) variables of each ontogenetic stage of *Astronium graveolens* in a Tropical Seasonal Semideciduous Forest (SE, Brazil). N = number of individuals; $IC.2^{-1}$ = semi-amplitude of the confidence interval at 95%; Min. = minimum height; Max. = maximum height. Values of median sharing different letter differ significantly (Kruskall-Wallis and *a posteriori* Dunn test, $P < 0.05$).

Ontogenetic Stage	N	Median	$IC.2^{-1}$	Min.	Max.
Infant	501	0.070^{a}	0.005	0.01	1.27
Juvenile-I	286	0.09^{b}	0.007	0.03	1.25
Juvenile-I	72	0.57^{c}	0.065	0.2	3.6
Immature	25	3.03^{c}	0.489	0.15	7.5
Adult	43	14.00^{c}	0.588	5	27

Table 2. Diameter (cm) variables of each ontogenetic stage of *Astronium graveolens* in a Tropical Seasonal Semideciduous Forest (SE, Brazil). N = number of individuals; $IC.2^{-1}$ = semi-amplitude of the confidence interval at 95%; Min. = minimum diameter; Max. = maximum diameter. Values of median sharing different letter differ significantly (Kruskall-Wallis and *a posteriori* Dunn test, $P < 0.05$).

Ontogenetic Stage	**N**	**Median**	**$IC.2^{-1}$**	**Min.**	**Max.**
Infant	501	0.05^{a}	0.004	0.01	1.46
Juvenile-I	286	0.06^{b}	0.007	0.01	1.37
Juvenile-II	72	0.57^{c}	0.081	0.15	5.04
Immature	25	5.12^{c}	1.073	0.25	17.51
Adult	43	21.64^{c}	1.735	8.60	63.66

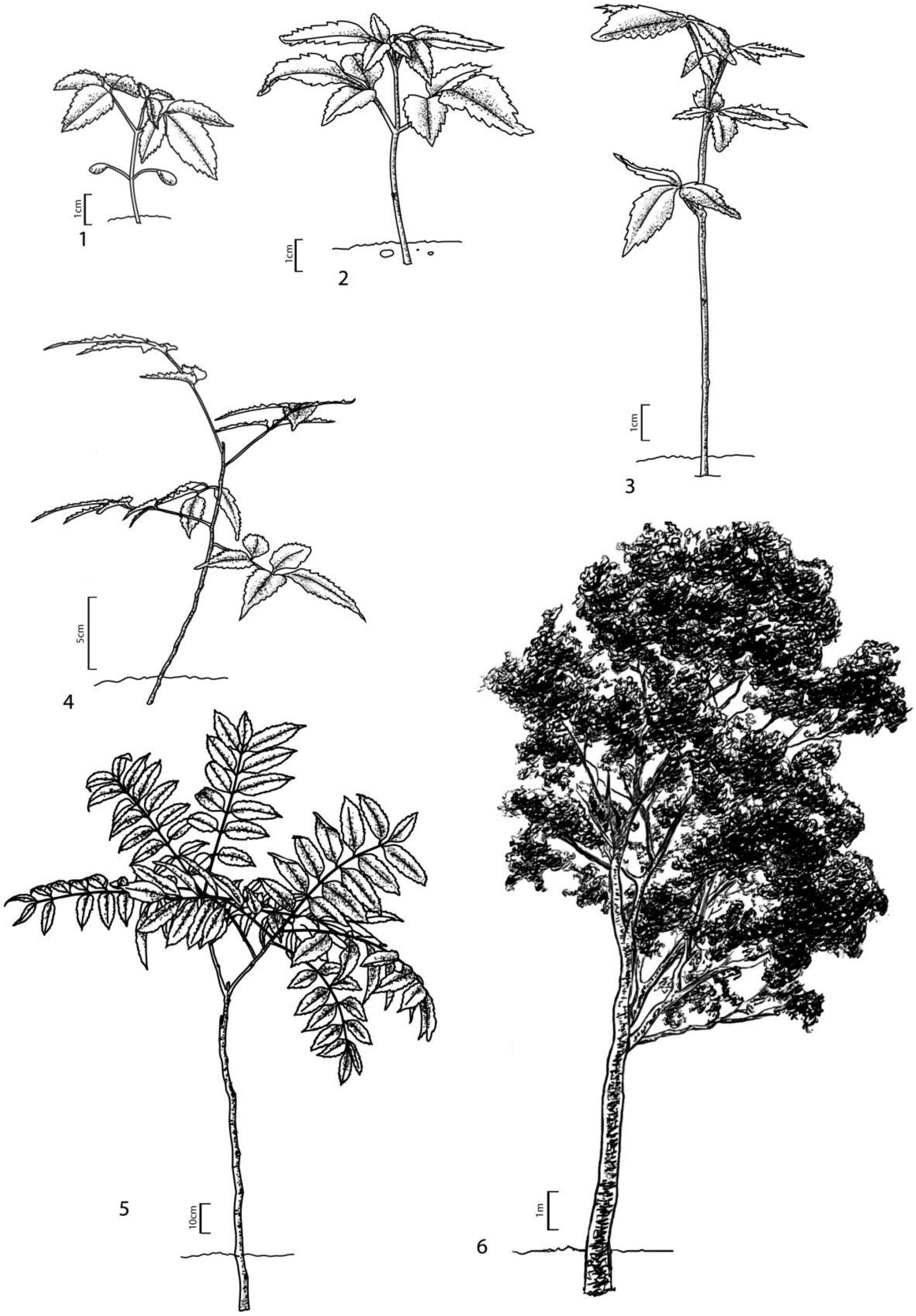

Fig 1. Ontogenetic stages of *Astronium graveolens*. 1 = Seedling; 2 = Infant; 3 = Juvenile-I; 4 = Juvenile-II; 5 = Immature; 6 = Adult.

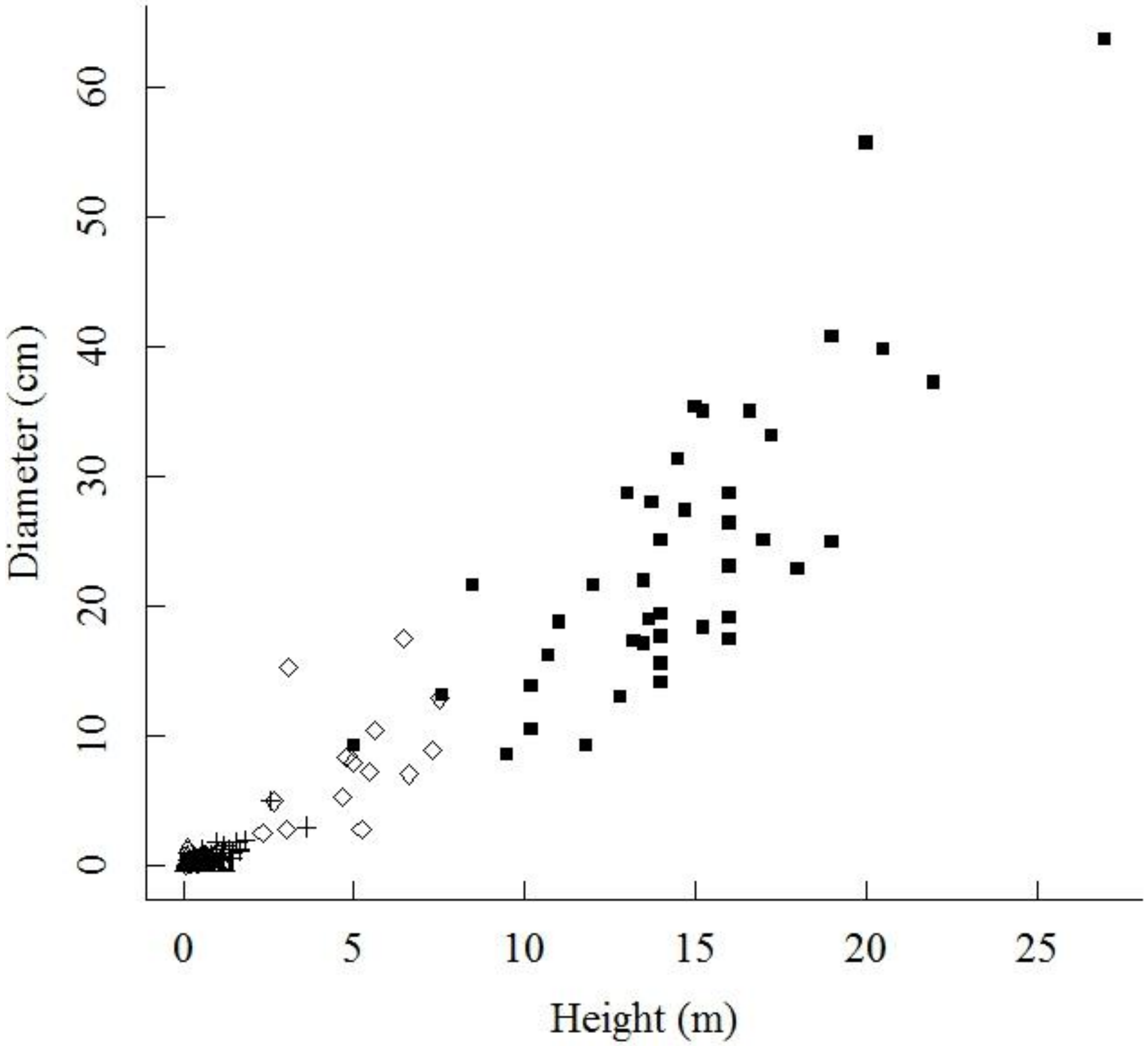

Fig. 2. Relationship between diameter at the ground level (cm) and height (m) of the tree *Astronium graveolens* in a Tropical Seasonal Semideciduous Forest (SE, Brazil). ○ = infant; Δ = juvenile-I; + = juvenile-II; ◊ = immature; ■ = adult.

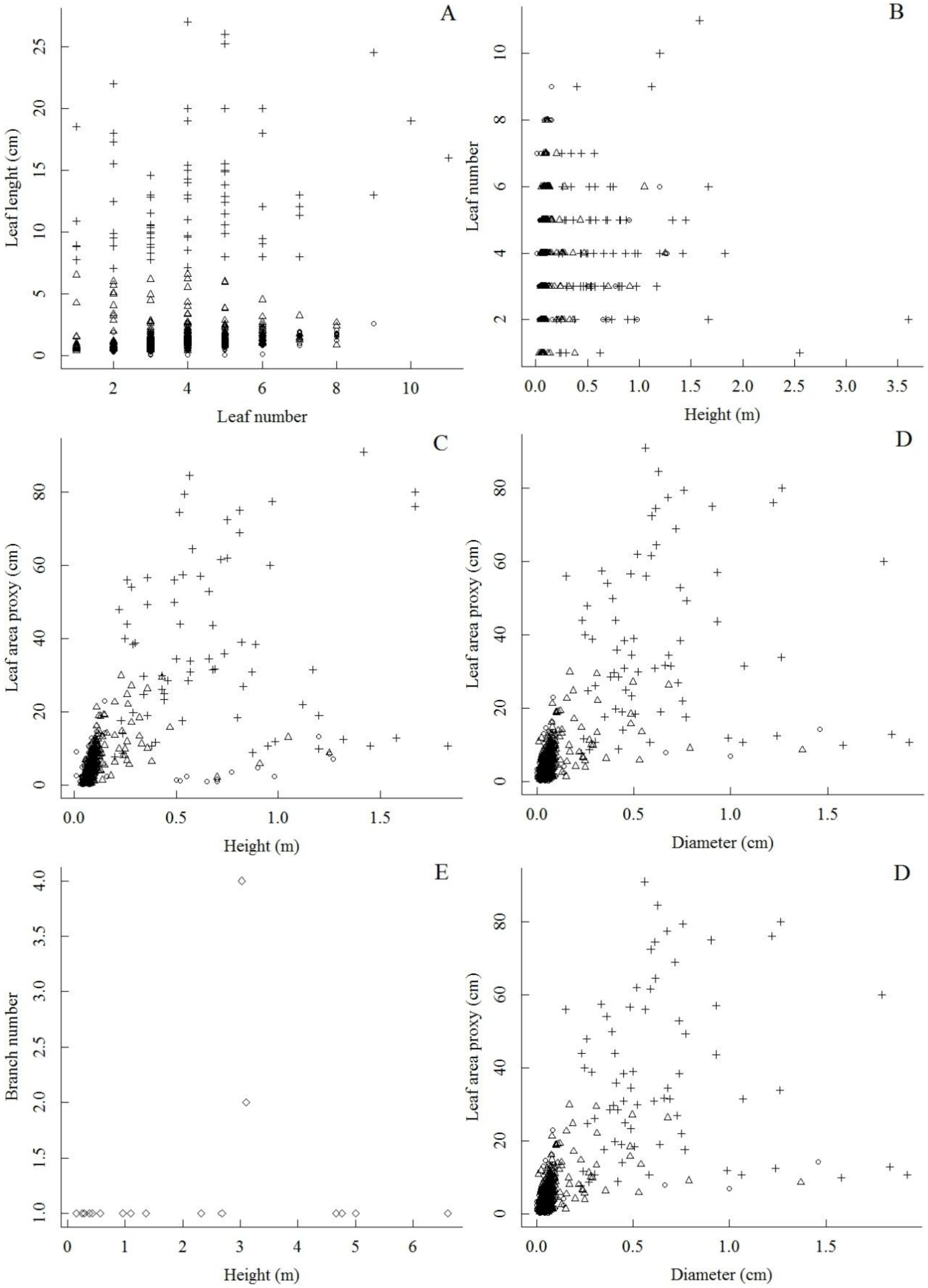

Fig. 3. Scatterplots of leaf length and leaf number (A), leaf number and height (B), leaf area proxy and height (C) and diameter (D), branches number and height (E) and diameter (F) of the tree *Astronium graveolens* in a Tropical Seasonal Semideciduous Forest (SE, Brazil). ○ = infant; Δ = juvenile-I; + = juvenile-II; ◊ = immature.

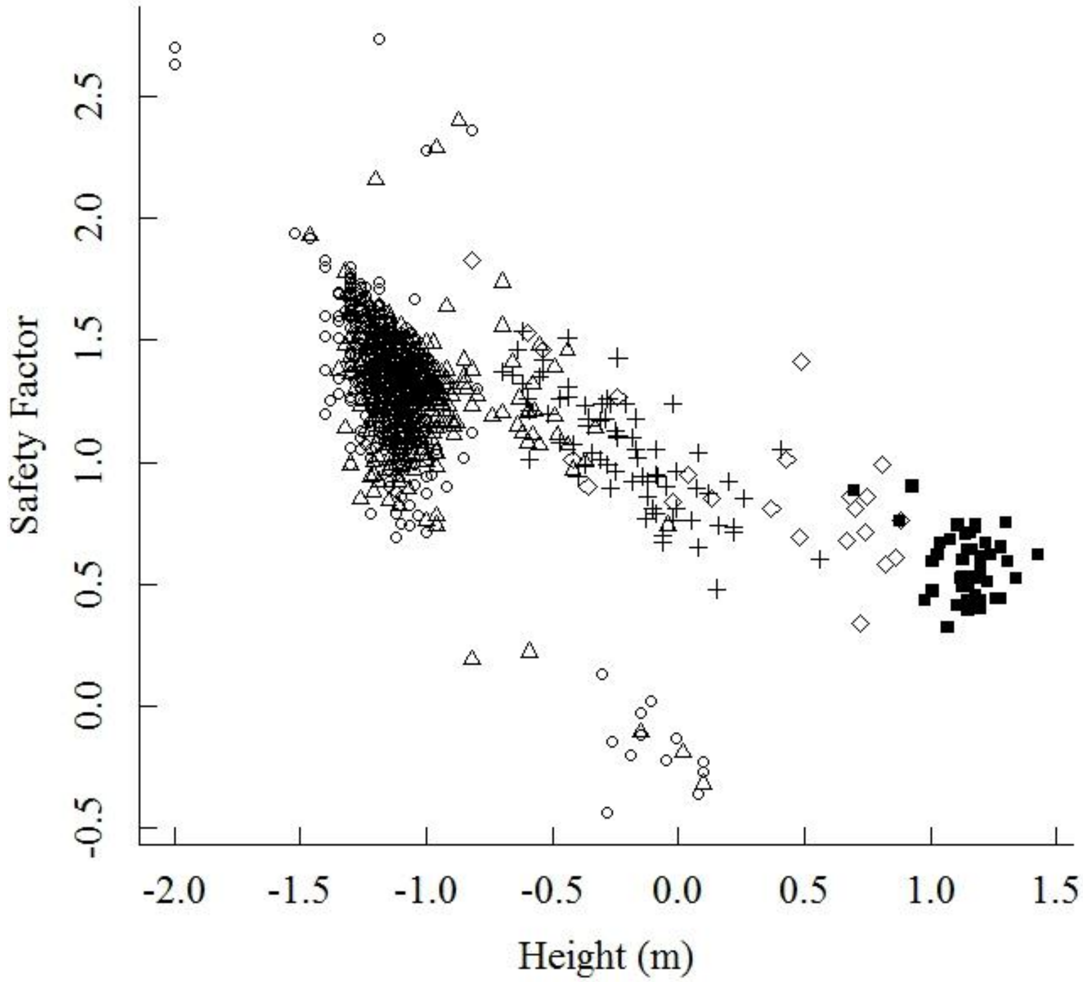

Fig. 4. Function of $\log_{10}$ bending safety factor vs. $\log_{10}$ height (m) for *Astronium graveolens* in a Tropical Seasonal Semideciduous Forest (SE Brazil). The bending safety factor is the ratio between the observed diameter and the critical bending diameter. ○ = infant; Δ = juvenile-I; + = juvenile-II; ◊ = immature; ■ = adult.

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Species interactions and stochasticity affect the spatial distribution of the emergent tropical tree *Astronium graveolens* Jacq. (Anacardiaceae) at fine scale

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Abstract

We evaluated the spatial distribution of the emergent tree *Astronium graveolens* on a fine scale in a fragment of the semideciduous seasonal forest in SE Brazil. We tested whether the abiotic variables, species interactions or stochasticity predominantly predict the distribution of *A. graveolens* population in space. We sought relationships between the spatial distribution of the population and both environmental filters and neighborhood species. We tried to answer whether (1) the ontogenetic stages are spatially autocorrelated; (2) the spatial distribution of the ontogenetic stages correlates to each other; (3) the similarity of the population structure among plots decreases with distance; (4) the density of *A. graveolens* is explained by abiotic variables, and (5) the individuals of *A. graveolens* co-occur with a given species more often than expected by chance. We used Moran's I coefficient to answer the first question, cross-correlograms to answer the second question, and Mantel test to answer the third question. To answer the fourth question we built minimum adequate models, choosing the best model using ordinary least squares model selection sorted by Akaike information criterion, and to answer the last question we used null models. In life beginning, the individuals were spatially aggregated, in the middle of life, they were randomly distributed, and in the adult stage, they were aggregated again. The distribution of each ontogenetic stage was not influenced by the abiotic factors we analysed. However, we found evidence of dispersal limitation and negative interactions with neighborhood species were more frequent than positive interactions. We argued that biotic factors and stochastic processes are more important than abiotic factors in determining the spatial distribution of *A. graveolens* on fine scale.

Keywords: clustered spatial distribution, environmental constraint, Neutral theory, ontogenetic stages, species co-occurrence, tropical forest.

Introduction

In ecological theory, the spatial heterogeneity of populations has received a growing attention, not only because of the potential nuisance for sampling or statistical testing, but also because of its functional implications for biodiversity (Legendre and Fortin 1989, Murrell et al. 2001, Stoll and Prati 2001, Lieberman and Lieberman 2007). The spatial distribution of individuals is the key to understand how resources are used by the population and how they assure the reproductive success, avoiding local extinction (Condit et al. 2000, Götzenberger et al. 2011). The spatial distribution of populations may result from several factors, such as dispersal, historical patterns of speciation and migration, biotic and abiotic factors, and chance, which could act simultaneously (Bell 2001, Chase 2003, Urich 2004, Ejrnæs et al. 2006, Chase 2007, Götzenberger et al. 2011). Thus, non-random spatial distributions of contemporary populations may have different causes.

Environmental filters, mainly those related to edaphic factors, are important determinants of the spatial distribution of plant populations (Clark et al. 1999, Hall et al. 2004, Russo et al. 2005), even influencing the distribution of individuals in different life stages (Clark and Clark 1992, Clark et al. 1998, Condit et al. 2000, Comita et al. 2007). Niche processes seem to be more important in later stages of life (Dalling et al. 2001); thereby, established trees may be more associated with edaphic factors than individuals in early stages of life (Paoli et al. 2006). Niche shifts during ontogeny are associated with energetic costs for morphological and physiological changes and their trade-offs imposed during lifespan (Dalling et al. 2001, Comita et al. 2007). Moreover, environmental heterogeneity may lead to density-dependent mortality and changes in plant population dynamics (Getzin et al. 2008). Niche differentiation implies the existence of favourable microsites for plant recruitment and establishment, but the number of niche space available is different within habitats (Terborgh 1973). Thus, favourableness can directly influence individual distribution. Although many authors have described associations between plant distribution and habitat variables (e.g., Clark and Clark 1992, Clark et al. 1999, Hall et al. 2004, Russo et al. 2005, Paoli et al. 2006, Comita et al. 2007, Getzin et al. 2008), it is difficult to distinguish the importance of niche and dispersal process acting on species distribution at fine spatial scale (John et al. 2007).

Biotic-assembly takes into account the contingent of species present in the local assemblage as well the historical contingent, i.e., the arrival order of species (Chase 2003, Ejrnæs et al. 2006). It predicts that interactions among species, i.e. competition and facilitation, influence the species co-occurrence, which may leave a spatial signature (Bolker et al. 2003, Perry et al. 2009, Silva et al. 2010a). In this case, the spatial contingence of a population is commonly attributed to an asymmetric competition among species (Ejrnæs et al. 2006, Perry et al. 2009). However, not only negative interactions influence species coexistence; positive interactions, such as facilitation, also may influence the spatial distribution of population and permit coexistence (Callaway 1995, Bruno et al. 2003). Facilitation, for example, may lead to spatial aggregation of the population; this positive interaction is frequently found between seedling of one species and adults of another species (Callaway and Walker 1997).

According to the neutral theory (Hubbell 2001), limited dispersal can also lead to a spatial aggregation of the individuals and therefore is an important mechanism in the generation of non-random spatial distributions. Dispersal-assembly is a consequence of the ecological drift (Bell 2001, Urich 2004, Chase 2007), and assumes that every individual has the same probabilities of giving birth, dying and dispersing (Hubbell 2001). According to Hubbell (2001), dispersal limitation is more limiting for the distribution of a population in space than resource limitation. Conversely, niche-assembly theory (MacArthur 1965, MacArthur and Levins 1967) implies that environmental conditions (environmental filtering) is crucial for the establishment of the individuals of a population (John et al. 2007), so that each species is a better competitor in its own niche (Wright 2002). According to the niche-assembly theory, environmental variation, including resource availability, may be the main limitation for the spatial distribution of tropical trees (Russo et al. 2005).

In this study, we assessed the relative influence of (1) environmental filters, (2) species interactions, and (3) stochastic processes on the fine-scale spatial distribution of a population of *Astronium graveolens* Jacq., a common emergent tree species in neotropical forests. We evaluated the general role that dispersal limitation plays in the spatial distribution of *A. graveolens* with spatial autocorrelation and similarity tests. We expected to find (1) a spatial autocorrelation in the early ontogenetic stages and a random distribution in adult stage, and (2) a decrease of similarity of the population structure with the increase of distance. We tested whether the spatial distribution of each ontogenetic stage was associated with abiotic factors (i.e. light availability and soil characteristics), with the occurrence of neighbor species, and whether the similarity in the population structure decreased with the distance among plots. We built minimum adequate models using ordinary least squares model selection to evaluate the role of abiotic factors. We expected that abiotic filters would have little influence on early stages distribution and more influence on later stages. At last, we evaluated the role of species interactions by comparing the observed co-occurrence between the individuals of *A. graveolens* and other species to a null distribution of co-occurrence pairs. We expected that positive co-occurrences with other species were more frequent in early stages and negative co-occurrences were more frequent in later stages.

In summary, we addressed the following question: (1) Is each ontogenetic stage spatially autocorrelated? (2) Is the spatial distribution of the ontogenetic stages correlated with each other? (3) Does the similarity of the structure of *A. graveolens* population among plots decrease with distance? (4) Do the abiotic variables explain the density of the *A. graveolens* population? (5) Do *A. graveolens* individuals associate to a given species more often than expected by chance in each plot?

Methods

Study site

We collected the data in the Ribeirão Cachoeira forest (22°50' S, 46°55' W), a fragment of the Tropical Seasonal Semideciduous Forest with 244.89 ha, located in an Environmental Protection Area in Campinas municipality, southeastern Brazil. The Semideciduous Seasonal Forest is characterized by a seasonal drought in which 20-50% of trees, especially the canopy ones, shed leaves in the dry season (Veloso et al. 1991). The regional climate is humid subtropical, with rainy summers and dry winters (Cwa, Peel et al. 2007). The annual average temperature is 22.4°C and total precipitation is 1,424 mm. The rainy season occurs from October to March, when the total precipitation average is 1141.5 mm and the average temperature is 24°C; the dry season lasts from April to September, when the average total precipitation is 283 mm and average temperature is 20°C (CEPAGRI 2011 - data for the period of June 1988 to October 2008). The altitude varies between 630 to 760 m a.s.l., and the predominant soil is Acrisol (FAO nomenclature).

Species studied

Astronium graveolens Jacq. (Anacardiaceae) is a Neotropical emergent tree often found in seasonal semideciduous forests (Carvalho 2006). It can reach up to 35 m in height and occurs from Central America to South America (Marín and Flores 2002). In Brazil, *A. graveolens* can be found in almost all phytogeographical domains, i.e. Amazon rainforest, Atlantic forest, Cerrado, Caatinga and southern grassland (Silva-Luz and Pirani 2011). Frequently *A. graveolens* is found in rocky and alluvial soils (Lorenzi 2002, Marín and Flores 2002, Carvalho 2006) and is considered an indicator of nutrient-poor soils (Carvalho 2006). The species has allelopathy potential (Silva et al. 2010b) and is classified as early or late secondary in the ecological succession of neotropical forests (Würth et al. 2005, Carvalho 2006). The species is deciduous, shedding all leaves during the dry season (Marín and Flores 2002), when flowering occurs, from June to October (Carvalho 2006). The star-shaped dehiscent fruit facilitates the wind dispersal of a single seed (Marín and Flores 2002).

Experimental design

We carried out our study in the southern portion of the fragment, where 100 plots of 10 m x 10 m each were randomly placed. A system of coordinated X-Y axes with 400 m and 200 m in length, respectively, was used to draw random number pairs, one number corresponding to the plot position in the X axis and other in the Y axis (see Cielo-Filho et al. 2007 for more details). For each plot, we estimated the forest canopy cover index using a spherical convex densitometer at the breast height (Lemmon 1956). In each plot, we collected one sample of 500 g of soil using an auger. In the laboratory, analytical procedures measured the amount of Al, P, Ca, Mg, K, organic matter, pH, potential acidity, cation exchange capacity, sum of bases, base saturation, and total sand. We sampled and identified every tree individual with circumference at breast height equal to or greater than 15 cm.

We tagged and measured the total height and diameter at the ground level of every individual of *A. graveolens* found in the 100 plots. We used macromorphological characters to classify the individuals in ontogenetic stages, according to Gatsuk et al. (1980). We chose to use ontogenetic stages to get a better description of the role of each individual in the population, because individuals at the same stage have similar roles in the population (Smirnova et al. 2002). For each individual, we recorded macromorphological characters, such as axis orientation, meristem activity, and order of ramification. For those individuals up to 5 m tall, we counted the number of branching. For those individuals up to 1.5 m tall, we recorded the length and number of leaves.

Since we did not find seedlings, we classified the individuals into five ontogenetic stages: infant, juvenile I, juvenile II, immature, and adult. The (1) infants were those individuals with primary opposite ternate leaves, with green monopodial orthotropic axis that could bear, above the primary leaves, ternate leaves with spiral alternate disposition. The (2) juveniles I had no primary opposite leaves; the monopodial orthotropic axis was still green and not branched and bore spiral alternate ternate leaves. The (3) juveniles II had alternate compound leaves spirally arranged, the monopodial orthotropic stem was woody and not branched. The (4) immature had imparipinnate spiral alternate and the monopodial orthotropic axis bore orthotropic branches in regular intervals. The (5) adults had monopodial trunk with light-grey bark, a morphological inversion point, orthotropic, sympodial branches, and conformed to Scarrone architectural model (Hallé et al. 1978).

Data analysis

Spatial autocorrelation and dispersal limitation analysis

To answer our first question, we calculated Moran’s I coefficient (Legendre and Fortin 1989) for a series of eleven distance classes, being 293 m the limit class. Moran’s I coefficient varies between +1 and -1, positive values indicating positive autocorrelation and spatial aggregation, whereas negative values indicate negative autocorrelation (Legendre and Legendre 1998). Negative autocorrelation may indicate either avoidance at short distance, i.e. individuals are regularly spaced, or spatial gradient at long distance if there is also a positive autocorrelation at short distance (Legendre and Fortin 1989). Because of the lack of independence among the distance classes, we tested the global significance of each correlogram with a Bonferroni-corrected significance level (Legendre and Legendre 1998). We did the autocorrelation analyses with the SAM 4.0 software (Rangel et al. 2010). We plotted the Moran's I values against the distance classes in correlograms.

To test whether the spatial distribution of the ontogenetic stages was correlated with each other, we constructed a geographical matrix with plot coordinates, and for each ontogenetic stage, we built a matrix with the abundance of individuals in each plot. Then we used cross-correlograms with Pearson correlation coefficient and Dutilleul correction (Dutilleul 1993) to test the correlation between each pair of ontogenetic stage matrices. Then to answer the third question, we constructed (1) a matrix with the Sørensen similarity among plots, considering the densities of each ontogenetic stage in each plot, and (2) a matrix of distance. We applied a Mantel test with 999 randomizations to evaluate the correlation between the two matrices.

Selection of the abiotic variables

To answer our fourth question, we built minimum adequate models (MAMs). We chose the best model using ordinary least squares OLS model selection sorted by Akaike information criterion (AIC; Diniz-Filho et al. 2008). The response variables were the ontogenetic stages, and the explanatory variables were Al, P, Ca, Mg, K, organic matter, pH, potential acidity, cation exchange capacity, sum of bases, base saturation, total sand, and canopy openness. Since autocorrelations in explanatory variables violates the assumption of data independence (Legendre 1993), our first step was to test the spatial autocorrelation of the variables before beginning to selected the MAMs. The presence of spatial autocorrelation in the residuals is also a problem in model selection. It may strongly inflate Type 1 error, because, in this case, the standard errors of the regression coefficients are usually underestimated (Diniz-Filho et al. 2003, Diniz-Filho and Bini 2005). In this regard, we first did a correspondence analysis (CA) with the density of each ontogenetic stage. We constructed a matrix with the geographic matrix (the plot coordinates), response variable (the first axis scores of the CA) and explanatory variables (the environmental variables). Then, we did a multiple regression with the response and explanatory variables and obtained the residuals. We tested the autocorrelation of the variables and of the residuals by constructing a spatial correlogram with Moran's I coefficient for 11 distance classes and 999 permutations. We tested the correlogram significance with Bonferroni corrections (Legendre and Legendre 1998).

Given that the residuals were autocorrelated, our next step was to incorporate the spatial structure of the data into the model, to estimate better and test the MAM parameters. In this regard, we used an approach that has been called eigenvector-based spatial filtering or the principal coordinate of neighbour matrices (PCNM), which extracts eigenvectors from a connectivity matrix expressing the spatial relationship among plots (Borcard and Legendre 2002, Diniz-Filho and Bini 2005). These eigenvectors (i.e. the spatial filters) express the relationships among plots at decreasing spatial scales, so that the first eigenvectors (i.e., those related to large eigenvalues) tend to describe broad-scale spatial patterns, whereas eigenvectors with small eigenvalues tend to describe local patterns (i.e. the spatial structure of the regression; (Borcard and Legendre 2002, Diniz-Filho and Bini 2005). They were therefore used as additional predictors of the response variables in the MAM, in an attempt to reduce the autocorrelation in the residuals (Diniz-Filho and Bini 2005). Then, we parsimoniously selected two filters (i.e. the smallest number of eigenvectors) that ensured a minimum desirable level of spatial autocorrelation in residuals.

Finally, by fitting OLS, we tested whether the abiotic variables and the two spatial filters predicted the biotic variables. The best models are generally those with the lowest AIC values. However, the MAM is that in which the difference between the AIC value of the model and the minimum AIC value of all models considered (Δ_i) is lower than 2 (Richards 2005, Diniz-Filho et al. 2008). We found three models with $\Delta_i < 2$. Then, we tested the collinearity of the variables in those three models with the variance inflation factor (VIF). Values of VIF greater than 10 indicate collinearity between variables (Borcard et al. 2011). We also tested for autocorrelation in the residuals of these models by constructing correlogramas with Moran's I coefficient. After that, we selected the MAM, the final model, which best adjusted to the assumptions of spatial independence and lack of collinearity among the explanatory variables.

To test whether there was correlation between each ontogenetic stage and the environmental variables selected by the MAM, we did a canonical correspondence analysis (CCA) with the density of each ontogenetic stage in the biotic matrix and the environmental variables of the selected model plus the two spatial filters selected by the PCNM in the abiotic matrix. We did 999 permutations and used a Monte Carlo procedure to evaluate whether the correlation between biotic and abiotic matrices was different than the expected by chance. We did the CA and CCA using the PC-ORD 6.0 software (McCune and Mefford 2011) and the spatial correlograms, PCNM and model selection using the SAM 4.0 software (Rangel et al. 2010).

Species interaction analysis

To answer our last question, we generated a distribution of expected frequencies for each potential pair of *A. graveolens* and all the sampled species. We followed the null model proposed by Lieberman and Lieberman (2007), in which the combination of possible pairs between individuals of *A. graveolens* and other species in a plot reflects a process of random sampling from the community. We picked two individuals at random, with replacement, from the complete list of individuals of the 100 plots, being one individual of *A. graveolens* and other of any other species. We recorded the pair identity and repeated these steps until the number of pairs drawn was equal to the number of possible pairs in the plot. We repeated this procedure 1,000 times, producing a null distribution of 1,000 expected counts for a given combination between *A. graveolens* and other species for each plot.

We used a Monte Carlo procedure to evaluate whether the observed number of pairs of *A. graveolens* and other species was different than expected by chance. We used the following procedure: (1) we computed the observed number of *A. graveolens* and other species pairs in each plot; (2) we randomised the individuals in the plots and recorded the number of random pairs; (3) we repeated these steps 1,000 times and estimated a random mean and SD for the null species assemblages; and (4) we compared the observed number of *A. graveolens* and other species pairs to those expected by chance and computed *P* values. We did this analysis considering individuals of *A. graveolens* in each ontogenetic stage.

Results

We sampled 927 individuals distributed in total of 76 plots, of which 501 individuals were infants, 286 juveniles I, 72 juveniles II, 25 immature, and 43 adults.

Spatial structure

Correlograms of infants, juveniles I and adults were globally significant according to Bonferroni correction ($P < 0.05$). These stages were spatially structured at small distance (Figure 1). Infants formed clumps up to 58 m of distance (Figure 1a), whereas juveniles I and adults were clumped up to 29 m of distance (Figure 1b and e). Juveniles II and the immature were distributed at random (Figure 1c and d) and were the only stages that correlated with each other (Table 1). We found a negative correlation (Pearson $r = - 0.1004$, $P < 0.001$) between similarity of densities and distance matrices. Thus, dispersal limitation may structure the spatial distribution of the *A. graveolens* population.

Model selection

The AIC sorted a total of 8,191 OLS models, from which three had $\Delta_i < 2$ (Table 2). The final model, the one with independence among data, without collinearity among variables, and the smallest Δ_i, included the explanatory variables potassium, total sand, and the two filters selected by PCNM (Table 3), resulting in the following OLS final equation:

$$Y = 0.682 - 0.277\text{potassium} - 0.014\text{total sand} - 4.279\text{filter 1} - 3.035\text{filter 2}.$$

However, no correlation was found between the ontogenetic stages of *A. graveolens* and the environmental variables in the canonical correspondence analysis (Monte Carlo test, $P = 0.11$) and hence abiotic factors seem not to explain the spatial distribution of the population.

Species interactions

We found 335 possible pairs of *A. graveolens* and other 62 species, of which 31 pairs (9.25 % of the total pairs) had observed frequency greater than expected by chance (hereafter positive co-occurrence) and 41 pairs (12.24% of total of pairs) had observed frequency lower than expected by chance (hereafter negative co-occurrence, Table 4). Juveniles I had more possible pairs than the other stages (23.58% of total pairs), whereas the immature was the stage with the least possible pairs (14.03% of total pairs). Infant was the stage with the greatest proportion of negative co-occurrences (80.77% of the total pairs in this stage), whereas adults had the lowest proportion of negative co-occurrences (16.67% of the total pairs in this stage). We found the contrary for positive co-occurrences: among all the stages adult had the greatest proportion (83.33% of the total pairs in this stage) and infant had the lowest proportion (19.23% of the total pairs in this stage) (Table 4).

The early ontogenetic stages infant and juvenile I had more negative than positive co-occurrences. The opposite was found for the later stages juvenile II, immature and adult, which had more positive than negative co-occurrences (Table 4). Most co-occurrences remained negative in several ontogenetic stages of *A. graveolens* (57.7% of pairs occurred in more than one stage). *Savia dyctiocarpa*, *Ocotea beulahiae* and *Rudgea jasminoides* were the species with negative co-occurrences in more than two stages (Table 4). In general, most positive co-occurrences were exclusive to each stage. Only *Cryptocarya aschersoniana* and *Urera baccifera* had positive co-occurrences in two ontogenetic stages (Table 4). However, the co-occurrence frequency of some species pairs changed from negative to positive along the ontogeny. We observed these changes with the pairs formed between *A. graveolens* and *Celtis tala*, *Esenbeckia leiocarpa*, *Rapanea balansae, Trichilia claussenii* and *Urera baccifera*. These five species had negative co-occurrence with infant and positive in some later stage. *Rapanea balansae* and *U. baccifera* also had negative co-occurrence with juvenile II and juvenile I, respectively. Thus, the interaction with neighbour species may play also an important role in structuring the spatial distribution of *A. graveolens* population.

Discussion

We evaluated the relative influence of environmental filters, species interactions, and stochastic processes on the spatial distribution of the emergent tree *A. graveolens*. Our results support that the stochasticity and species interactions determine predominantly the spatial distribution of the population. The young and adult individuals were spatially autocorrelated and the population structure was more similar among close than distant plots. The species interactions were also important and negative interactions with neighbour species were more frequent than positive interactions. However, we did not find evidence of environmental filtering in the spatial distribution of the *A. graveolens.* We argue that the stochastic population dynamics and limited dispersal, allelopathic potential of *A. graveolens* as well as competition interactions with neighbour species are more important than environmental filtering in spatial distribution of the population at fine scale.

Spatial distribution and environmental filters

Overall, tree species in tropical forests are non-randomly distributed (Condit et al. 2000). Often tropical trees have some aggregation degree in life beginning and adults spatially distributed by chance (Hubbel 1979, Oliveira-Filho et al. 1996, Lopes 2007). Decrease in the aggregation pattern through the ontogeny is expected when there is density-dependent mortality (Janzen 1970, Connell 1971, Hubbel 1979). For that reason, we expected that *A. graveolens* had individuals aggregated in early stages of life and distributed by chance in later stages. However, the spatial distribution of adults were also aggregated.

Although clumping is the most commonly found pattern, it is not a rule, since tropical trees may be hyperdispersed or randomly dispersed (Lieberman and Lieberman 1994). A small aggregation degree may be caused by seed wind-dispersal, which is directly influenced by wind speed and seed shape (Seidler and Plotkin 2006), and is also expected for well-dispersed species, such as canopy trees (Condit et al. 2000). Wind-dispersal seed can achieve long-distance dispersal if they are caught in rare updrafts (Greene and Johnson 1995, Nathan and Muller-Landau 2000, Horn et al. 2001). Since *A. graveolens* is an emergent tree, its crown raises above the forest canopy, thus facilitating the wind-dispersal of its seeds, which are produced in the dry season, when up to half of the canopy trees shed their leaves, making it easier for the seed to be caught in updrafts. As a consequence, an aggregation pattern may occur. Once updrafts are rare (Greene and Johnson 1995, Nathan and Muller-Landau 2000, Horn et al. 2001), the limited dispersal range predominates in the population, as suggested by the similarity decrease with the increase of geographical distance. Wind direction changes randomly, although there is a prevailing direction, so seed may be dispersed in many directions, promoting small aggregated patterns.

The aggregation of adults at small distances suggests habitat-related patchiness, meaning that adults grew in more favourable sites (Condit et al. 2000). Environmental favourableness is not constant in space; hence the number of niches available in the plant community changes across the space (Terborgh 1973). *Astronium graveolens* did not have any correlation with the environmental variables we measured. Although spatial distribution of tropical trees often correlates with environmental variation (Clark et al. 1998, Russo et al. 2005), tropical trees may be randomly distributed in relation to edaphic factors at landscape scale (Clark et al. 1999, Paoli et al. 2006). Favorableness could be given by non measured variables, explaining the lack of correlation between *A. graveolens* distribution and environmental variables we found. The aggregation at small-scale we found for adults and the lack of correlation between adults and others stages, may suggest that the factors that allowed immature to be recruited to adult represent favorableness only to adult stage.

As we predicted, habitat associations did not occur in young *A. graveolens*. Niche shifts may occur across ontogeny, hence different stages may be associated with different habitats (Clark and Clark 1992, Clark et al. 1998, Dalling et al. 2001, Comita et al. 2007). Changes in habitat association occur because favourable sites for the establishment of early stages are not necessarily suitable for the continual survival at later stages (Comita et al. 2007). Also, species in life beginning may be strongly related to geographical distance rather than edaphic factors, but the conversely occurs with later stages, thus indicating increased importance of niche through the ontogeny (Paoli et al. 2006). Although the niche might explain the pattern we found for *A. graveolens* adults, the negative correlation we found between similarity and distance suggests that stochastic processes could also be important in that population (Hubbell 2001).

Only the juveniles II and the immature were correlated to each other in space. Juvenile II is a key stage in *A. graveolens* life-history: individuals allocate energy to height growth in detriment of leaf production, although they produce larger leaves and in greater number than earlier stages, increasing light interception (Franci and Martins 2012). The correlation between the juveniles II and the immature might indicate that the individuals of juvenile II recruited to immature were those in the microsites with conditions to increase light interception, once favorableness is very important in life beginning (Fowler 1988).

Astronium graveolens had aggregated pattern in early stages what can indicate density-dependent mortality. The spatial shift from juvenile I to juvenile II and immature could be related to the probability to die and survive. If this probability was related only to individuals density, it would not found spatial distribution shifts through the ontogeny, i.e., the individuals would be aggregated in spite of the ontogenetic stage. However, we found changes in the spatial pattern, suggesting that there are others factors beyond the density. Therefore, some variation in local environmental factors may influence the spatial distribution of the population. The intensity of these factors depends on the site, leading to a higher or lower individual survivor probability. As the mortality probability changes in the space, the probability of recruitment is no constant in space, thus, the juvenile I individuals that did not die and were in favourable sites could be recruited to juvenile II. The same favourable sites for juvenile II recruitment remain favourable to the recruitment of juvenile II to immature, as indicated by the correlation of these stages in space.

Astronium graveolens and near neighborhood

Neutral models predict non-random patterns of species co-occurrence (Bell 2005). Also, species autocorrelation may promote co-occurrence in the community (Stoll and Prati 2001). However, for *A. graveolens* negative co-occurrences were more frequent and they seemed to be more important than positive co-occurrences. Through the ontogeny the nearest neighborhood around *A. graveolens* changed, and whereas negative co-occurrences remained along more than one stage, most positive co-occurrences were exclusive to one stage. Only two species formed pairs with more than one stage of *A. graveolens*, both with early stages. Frequently, individuals in life beginning have positive co-occurrences with a certain species, characterizing the “nurse-plant syndrome”, in which the benefactor is eventually often eliminated by the beneficiary (Callaway 1995). If this were true for *A. graveolens*, positive co-occurrences would have become negative along the ontogeny. However, we found the opposite and some negative co-occurrences became positive. Thus, the same site can be favourable to the establishment of different species. In fact, neighborhood may be important to plant growth and survival, and its effects change in different spatial scales and abiotic conditions (Escudero et al. 2005). In addition, the transition of negative to positive co-occurrences along the ontogeny may be related to the different patterns of aggregation of *A. graveolens* population.

We observed a greater frequency of positive co-occurrences in the later stages of *A. graveolens*, reinforcing the idea that maybe favourableness is common for the co-occurring species and, therefore, individuals in later stages are recruited and persist mainly in these favorable microsites. The availability of favorable microsites, including safe sites, in the environment around the individuals has in important role in seed germination and establishment (Fowler 1988, Eriksson and Ehrlén 1992). Since *A. graveolens* has allelopathy potential (Silva et al. 2010b), trees living in the neighborhood would be those not affected by the allelopathic compounds. Conversely, other species of the community may have allelopathy potential and jeopardize the establishment of *A. graveolens*, thus explaining the great number of negative co-occurrences in its life beginning. If this occurs, competition may be an important issue to be considered to understand the spatial distribution of *A. graveolens*.

Neutral and deterministic processes

Deterministic and stochastic processes have been described to act simultaneously in plants communities (Weiher and Keddy 1995). *Astronium graveolens* seems to be influenced by both groups of processes. As stochastic processes, neutral models could be important to describe spatial patterns of the different ontogenetic stages. However, the distribution of *A. graveolens* could not be totally described by stochasticity, since also neighbourhood seemed to be important. For some species, constraints in the availability of safe sites are more important for seedling establishment than seed dispersal distance (Uriarte et al. 2010). For *A. graveolens*, both processes seemed to restrict its recruitment and persistence across the ontogeny. Once negative co-occurrences were more frequent in the early stages of life, and most positive co-occurrences did not remain through the ontogeny, we found that nurse-plant relationship is not common in *A. graveolens* life-history. We suppose that stochastic and deterministic processes, such as positive and negative relationships, may influence *A. graveolens*. The success of establishment of *A. graveolens* might be influenced by the near neighborhood through the ontogeny, and its spatial distribution might be strongly related to dispersal syndrome and stochasticity, although often for tropical plants abiotic factors seem to be more important, at least in seedling establishment (Uriarte et al. 2010). The spatial patterns found for *A. graveolens* seem to be related to favourableness, including safe sites, combined with the effect of the neighborhood, which seems to have low competitive influence due to the great frequency of negative co-occurrences.

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Table 1. Correlation tests among the abundance of ontogenetic stages of *Astronium graveolens*. Matrices 1 and 2 are ontogenetic stages and matrix 3 is the coordinates of each plot. We used Pearson's correlation coefficient at the significance level of 5%. Significant values are in bold.

Matrix 1	Matrix 2	Matrix 3	Correlation	*P*
Infant	Immature	Coordinates	-0.03	0.8
	Juvenile I	Coordinates	0.1	0.33
	Juvenile II	Coordinates	-0.07	0.53
	Adult	Coordinates	-0.02	0.88
Juvenile I	Immature	Coordinates	-0.05	0.66
	Juvenile II	Coordinates	-0.03	0.78
	Adult	Coordinates	0.01	0.91
Juvenile II	Immature	Coordinates	0.24	**0.02**
	Adult	Coordinates	-0.11	0.26
Immature	Adult	Coordinates	0.01	0.95

Table 2. Ordinary least squares (OLS) model selection, sorted by Akaike information criterion (AIC), coefficient of determination (r^2) and minimum AIC value (Δ_i) of soil variables and the two spatial filters selected by PCNM.

OLS Models	Variables	r^2	AIC	Δ_i
Model 1	K, Filter 1, Filter 2	0.339	231.89	0
Model 2	K, Total sand, Filter 1, Filter 2	0.346	233.463	1.573
Model 3	Organic matter, K, Filter 1, Filter 2	0.342	233.863	1.973

Table 3. Nonstandard coefficients of the explanatory variables selected by ordinary least squares model selection, sorted by Akaike information criterion and the respective variance inflation factors (VIF). (T test, $P < 0.05$)

Explanatory variable	**Coefficient**	**VIF**	**Standard error**	**t**	***P***
Potassium	0.277	1.059	0.087	3.198	0.002
Total sand	-0.014	1.056	0.016	-0.86	0.393
Filter 1	-4.279	1.04	1.987	-3.935	0.001
Filter 2	-3.035	1.012	1.072	-2.83	0.006

Table 4. Observed *Astronium graveolens* and other species pairs for which the null hypothesis was rejected (α = 0.05). The names of the species i for each pair is shown, followed by the number of individuals of each species in all plots sampled, n(*A. graveolens*), n(i); f(obs) = observed number of times *A. graveolens* and species i occurred as a near neighbor pair; f(exp) = expected number based on the null model. Positive co-occurrence: observed frequency greater than expected by chance, negative frequency: observed frequency lower than expected by chance.

A. graveolens	**Species *i***	**n (*A. graveolens*)**	**n (i)**	**f (obs)**	**f (exp)**	**p**
Positive co-occurrence						
Infant	*Cryptocarya aschersoniana* Mez	501	5	154	50.81	0.02
	Endlicheria paniculataa (Spreng.) J. F. Macbr.	501	3	143	31.03	0
	Guazuma cf. ulmifolia Lam.	501	1	143	10.42	0
	Hymenaea courbaril L.	501	8	188	84.91	0.04
	Prockia crucis P. Browne ex L.	501	1	143	10.25	0
Juvenile I	*Centrolobium tomentosum* Guillem. ex Benth.	286	6	118	28.86	0
	Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.) Engl.	286	9	141	43.3	0
	Cryptocarya aschersoniana Mez	286	5	125	24.37	0
	Eugenia dodonaeifolia Cambess.	286	1	65	4.73	0
	Trichilia claussenii C. DC.	286	36	311	175.26	0.01
	Trichilia pallida Sw.	286	7	122	34.06	0
Juvenile II	*Casearia sylvestris* Sw.	72	2	5	1.5	0.05
	Celtis tala Gillet ex Planch.	72	4	14	3.09	0
	Esenbeckia leiocarpa Engl.	72	179	200	136.06	0.01
	Eugenia leptoclada O. Berg	72	1	4	0.7	0.03
	Ocotea odorifera (Vell.) Rohwer	72	4	11	3.04	0.01
	Picramnia ramiflora Planch.	72	1	4	0.76	0.02

	Pseudobombax grandiflorum (Cav.) A. Robyns	72	3	16	2.29	0
	Urera baccifera (L.) Gaudich. ex Wedd.	72	35	52	26.54	0
Immature	*Cordia ecalyculata* Vell.	25	2	2	0.52	0.05
	Inga vera subsp. *affinis* (DC.) T. D. Penn.	25	4	4	1.07	0.03
	Jacaratia spinosa (Aubl.) A. DC.	25	12	9	3.17	0.01
	Machaerium stipitatum (DC.) Vogel	25	4	4	1.09	0.02
	Prunus myrtifolia (L.) Urb.	25	1	2	0.27	0.01
	Simira sampaioana (Standl.) Steyerm.	25	3	4	0.77	0.01
	Urera baccifera (L.) Gaudich. ex Wedd.	25	35	22	9.19	0.01
Adult	*Cecropia hololeuca* Miq.	43	4	6	1.84	0.02
	Lauraceae sp.4	43	1	3	0.45	0.02
	Rapanea balansae Mez	43	14	15	6.24	0.02
	Schinus terebinthifolius Raddi	43	1	3	0.46	0.02
	Trichilia casaretti C. DC.	43	1	2	0.42	0.04
Negative co-ocurrence						
Infant	*Ceiba speciosa* (A. St.-Hil.) Ravenna	501	9	12	94.28	0.02
	Celtis tala Gillet ex Planch.	501	4	2	41.9	0.05
	Croton floribundus Spreng.	501	28	54	298.69	0
	Esenbeckia leiocarpa Engl.	501	179	832	1889.77	0
	Eugenia sp.2	501	5	3	52.63	0.03
	Ficus guaranitica Chodat	501	4	2	41.63	0.05
	Gallesia integrifolia (Spreng.) Harms	501	4	3	42.68	0.05
	Holocalyx balansae Micheli	501	38	210	402.29	0.04
	Lonchocarpus muehlbergianus Hassl.	501	5	2	51.46	0.02
	Metrodorea nigra A. St.-Hil	501	89	495	935.33	0
	Mouriri glasioviana Cogn.	501	6	9	63.98	0.05
	Myrciaria floribunda (H. West ex Willd.) O. Berg	501	28	70	292.49	0
	Ocotea beulahiae Baitello	501	22	18	229.42	0

	Ormosia arborea (Vell.) Harms	501	4	1	42.78	0.04
	Rapanea balansae Mez	501	14	12	146.03	0
	Rudgea jasminoides (Cham.) Müll. Arg.	501	10	3	105.79	0
	Savia dictyocarpa Müll. Arg.	501	95	355	1006.64	0
	Sebastiania edwalliana Pax & K. Hoffm.	501	26	98	267.91	0.01
	Trichilia catigua A. Juss.	501	53	276	563.8	0
	Trichilia claussenii C. DC.	501	36	178	381.22	0.01
	Urera baccifera (L.) Gaudich. ex Wedd.	501	35	116	371.54	0
Juvenile I	*Ceiba speciosa* (A. St.-Hil.) Ravenna	286	9	1	43.2	0
	Croton floribundus Spreng.	286	28	27	136.76	0
	Eugenia sp.2	286	5	1	23.98	0.01
	Galipea jasminiflora (A. St.-Hil.) Engl.	286	40	58	190.31	0
	Gallesia integrifolia (Spreng.) Harms	286	4	1	19.1	0.05
	Holocalyx balansae Micheli	286	38	35	181.78	0
	Machaerium nyctitans (Vell.) Benth.	286	6	4	28.77	0.04
	Metrodorea nigra A. St.-Hil	286	89	161	429.39	0
	Myrciaria floribunda (H. West ex Willd.) O. Berg	286	28	28	134.79	0
	Ocotea beulahiae Baitello	286	22	13	106.45	0
	Ocotea indecora (Schott) Mez	286	13	10	63.46	0
	Rudgea jasminoides (Cham.) Müll. Arg.	286	10	3	47.38	0
	Savia dictyocarpa Müll. Arg.	286	95	51	456.55	0
	Seguieria langsdorfii Moq.	286	16	12	76.85	0
	Trichilia elegans A. Juss.	286	7	2	35.19	0
	Urera baccifera (L.) Gaudich. ex Wedd.	286	35	47	168.57	0
Juvenile II	*Galipea jasminiflora* (A. St.-Hil.) Engl.	72	40	11	30.37	0
	Rapanea balansae Mez	72	14	3	10.62	0.03
	Savia dictyocarpa Müll. Arg.	72	95	29	71.56	0
	Trichilia catigua A. Juss.	72	53	25	40.22	0.05
Immature	*Ocotea beulahiae* Baitello	25	22	1	5.75	0.02

	Savia dictyocarpa Müll. Arg.	25	95	11	25.08	0.01
	Sebastiania edwalliana Pax & K. Hoffm.	25	26	1	6.85	0.01
Adult	*Rudgea jasminoides* (Cham.) Müll. Arg.	43	10	1	4.51	0.04

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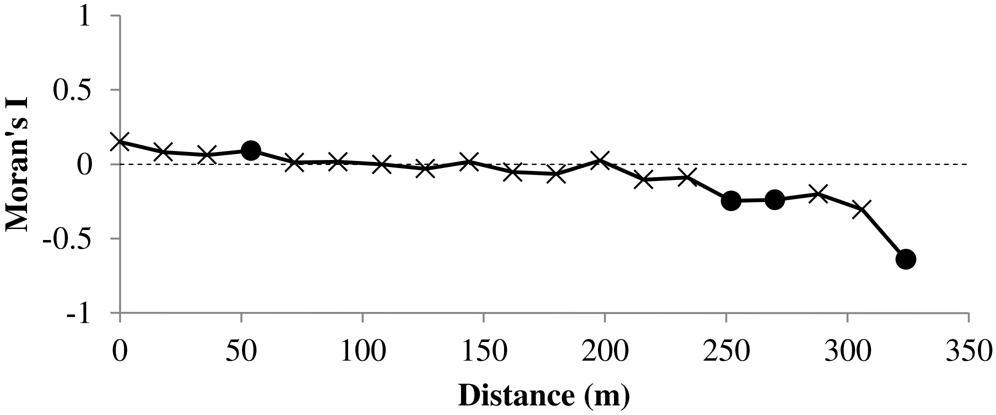
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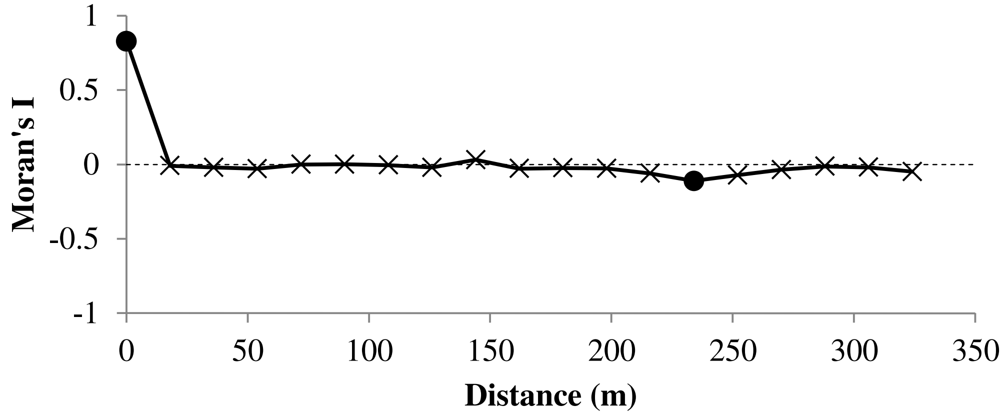
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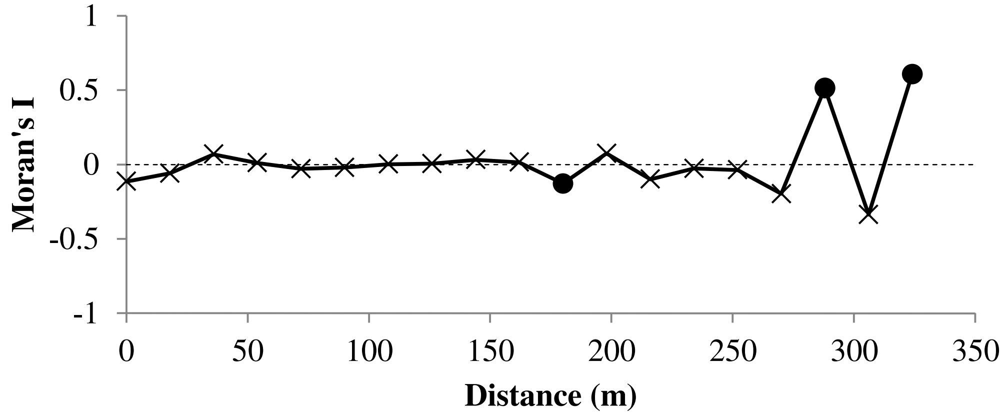
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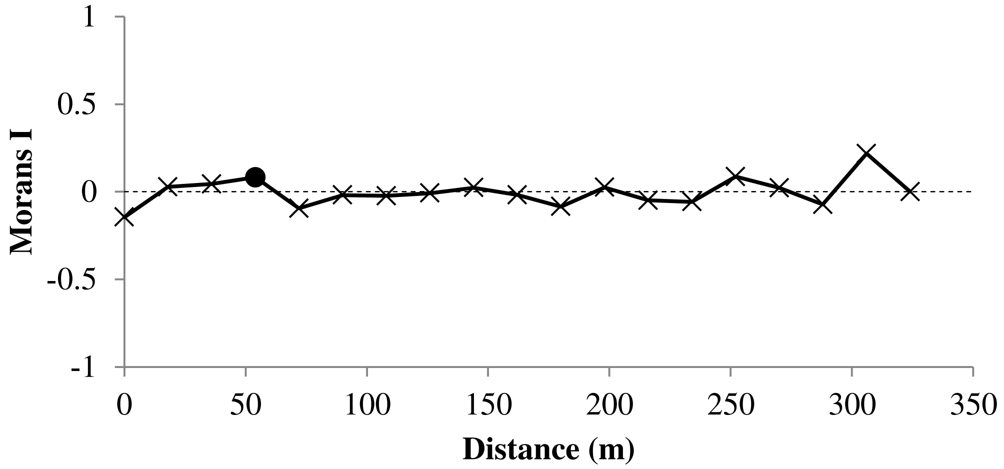

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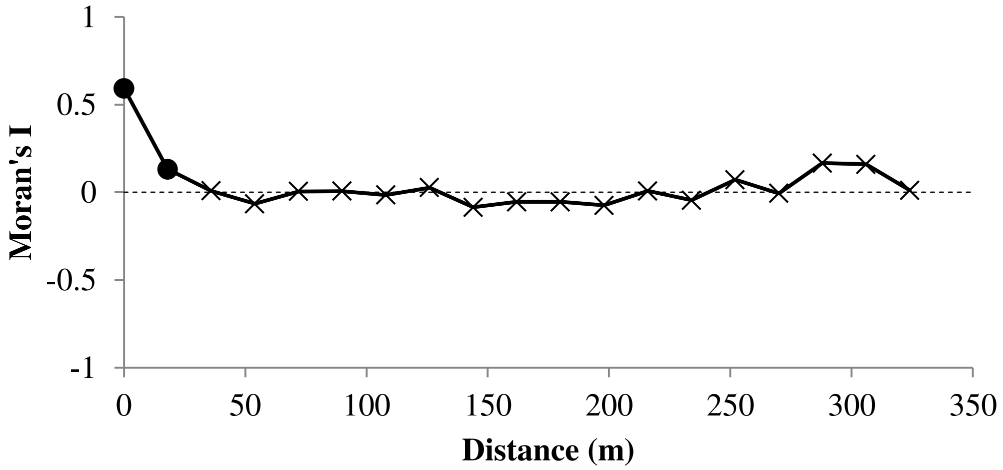

Figure 1. Spatial correlograms for ontogenetic stages of *Astronium graveolens*: infant (a), juvenile I (b), juvenile II (c), immature (d) and adult (e). The Moran's I coefficient was calculated for a series of eleven classes. Circles indicate significant Moran's I values ($P \leq 0.05$) and crosses indicate un-significant values ($P \geq 0.05$). Correlograms of infant, juvenile I and adult were globally significant according to Bonferroni correction ($P \leq 0.05$).

CONSIDERAÇÕES FINAIS

Com base nos cinco estádios ontogenéticos identificados em campo, infante, juvenil I, juvenil II, imaturo e adulto, a partir de estruturas macromorfológicas, pudemos inferir sobre aspectos importantes da estrutura populacional da espécie arbórea *Astronium graveolens*. Encontramos que sua história de vida, considerando as demandas conflitantes e a alometria entre altura e diâmetro, está intimamente relacionada à sazonalidade de chuvas e à necessidade de atingir o dossel o mais rápido possível. Os indivíduos investem muito em altura em detrimento do diâmetro. O pequeno diâmetro em relação à altura é compensado pela alta densidade da madeira, evitando que a planta tombe pelo seu próprio peso ou por forças externas, como o vento.

Os diferentes estádios ontogenéticos apresentaram diferentes demandas conflitantes. Em geral, as demandas conflitantes estão relacionadas ao investimento em altura e maior interceptação de luz, o que implica no modelo arquitetural de similaridade geométrica e na disposição das folhas e ramificações. O estádio juvenil II se mostrou um estádio chave na ontogenia da espécie, pois nesse estádio as folhas são maiores e mais numerosas, aumentando a interceptação de luz.

O grau de agregação dos indivíduos no espaço não se manteve ao longo da ontogenia. Os estádios infante, juvenil I e adulto apresentaram padrão agregado, enquanto juvenil II e imaturo estiveram distribuídos ao acaso. Nenhum estádio apresentou densidade correlacionada aos fatores abióticos analisados. A dispersão de *A. graveolens* é limitada pela distância, indicando que possivelmente processos estocásticos são importantes para a população de *A. graveolens* nesse local.

O grande número de co-ocorrências negativas encontrado pode estar relacionado ao potencial alelopático de *A. graveolens* e interações negativas como competição, embora não tenhamos subsídios suficientes para comprovar. As co-ocorrências positivas foram pouco frequentes nos estádios iniciais de vida e nenhum par se manteve por mais de dois estádios, o que pode indicar ausência de “nursery-relationship”. O número de co-ocorrências positivas foi maior nos estádios finais de vida. Nós sugerimos que isso está relacionado aos sítios favoráveis de desenvolvimento. Os fatores que determinam a favorabilidade para o *A. graveolens* podem ser comuns às espécies vizinhas, portanto, elas estabelecem próximas.

A espécie emergente *A. graveolens* enfrenta muitas demandas conflitantes durante sua ontogenia, a fim de atingir o dossel rapidamente e aumentar a interceptação de luz. Processos estocásticos e determinísticos podem influenciar a distribuição dos indivíduos, embora os processos estocásticos pareçam ser mais importantes para essa espécie.