UNIVERSIDADE ESTADUAL DE CAMPINAS
INSTITUTO DE BIOLOGIA

ALINE LUISA MANSUR

O PAPEL DAS CLAREIRAS DE DECIDUIDADE NA DINÂMICA DE COMUNIDADES ARBÓREAS EM FLORESTAS ESTACIONAIS SEMIDECÍDUAS

THE ROLE OF THE DECIDUOUSNESS GAPS IN THE DYNAMICS OF TREE COMMUNITIES IN SEASONAL SEMIDECIDUAL FORESTS

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Resumo

A Floresta Estacional Semidecídua (FES) é uma fitofisionomia da Mata Atlântica que tem como característica possuir 30 a 50 % das árvores que perdem total ou parcialmente suas folhas durante a estação seca, a qual pode estender-se entre abril e setembro. A queda foliar durante esse período faz com que os níveis de irradiância solar sob árvores decíduas sejam até 24 vezes maiores do que sob árvores sempre verdes, atingindo níveis de irradiância semelhantes aos encontrados em clareiras formadas pela queda de árvores, formando o que foi denominado de clareiras de deciduidade: áreas sob dossel decíduo onde os níveis de luz são maiores em relação a áreas sob dossel não decíduo. O presente estudo teve como objetivo investigar se clareiras de deciduidade são fatores determinantes da estrutura e composição da FES. Para verificar como a abertura de dossel varia ao longo do ano sob árvores decíduas e sempre verdes obtivemos fotos hemisféricas sob 24 árvores classificadas como decíduas, 55 como semidecíduas e 54 como sempre verdes. Para avaliar se clareiras de deciduidade afetam a estrutura e composição da vegetação, selecionamos árvores (árvores focais) cujas copas não eram encobertas por outras árvores como unidade amostral. Sob a copa de cada árvore focal, amostramos os indivíduos arbustivo-arbóreos a partir de 1 m de altura que cresciam sob 83 árvores decíduas (ou semidecíduas) e 59 sempre verdes e medimos a taxa de crescimento trimestral de 33 plantas sob árvores decíduas e 30 sob árvores perenes com diâmetro a altura do peito ≥ 5 cm. Não encontramos diferenças nos valores de abertura de dossel entre as árvores classificadas nos diferentes grupos fenológicos em nenhum período do ano. Os maiores valores de abertura de dossel ocorreram durante a estação seca para todas as fenologias, indicando que o incremento de luz no período das clareiras de deciduidade ocorre em todo o sub-bosque florestal e não somente em trechos diretamente sob a copa de árvores decíduas. Quanto à estrutura e composição de espécies de plantas sob a copa de árvores com diferentes fenologias, encontramos diferenças somente para plantas pequenas (Diâmetro a Altura do Solo < 5 cm). A densidade de plantas pequenas foi menor sob árvores decíduas do que sob árvores sempre verdes, o que pode estar relacionado a uma maior mortalidade ocasionada pela queda concentrada de serapilheira em sub-bosques decíduos. Não encontramos diferenças nas taxas de crescimento de árvores sob copas decíduas no período das clareiras de deciduidade, o que pode estar relacionado ao fato de que o incremento de luz é semelhante em sub-bosques decíduos e sempre-verdes no período da deciduidade. Concluímos que as diferenças que ocorreram na estrutura da vegetação de sub-bosques decíduos em comparação com sempre verdes são decorrentes de outras características associadas à queda concentrada de folhas sob árvores decíduas na estação seca que não o incremento de luz *per se*. Mesmo assim, estar sob copas decíduas ou sempre-verdes poderá afetar a dinâmica futura em FES.

Palavras-chave: Mata Atlântica, abertura do dossel, heterogeneidade ambiental, fenologia foliar, luz do sub-bosque, vegetação do sub-bosque.

Abstract

Seasonal Semideciduous Forests (SSF) is one of the phytophysiognomies of Atlantic Forest where 30 to 50 % of trees lose totally or partially their leaves during the dry season, which may extend from April to September. Leaf fall causes an increase in light availability under deciduous canopies and solar irradiance in these areas may be up to 24 times higher than under evergreen canopies. Solar irradiance under deciduous canopies in that period is similar to solar irradiance found in treefall gap areas and are called deciduousness gaps: understory regions where light levels are greater when compared to areas under evergreen canopies. This study aim to investigate if deciduousness gaps are key factors in determining structure and composition of SSF. In order to evaluate how canopy openness vary over the year under evergreen and deciduous canopies we took hemispherical photos under 24 trees classified as deciduous, 55 classified as semidecidous and 54 classified as evergreen. To assess whether deciduousness gaps affect vegetation structure and composition we used understories under overstory trees whose crowns were not covered by any other tree crown (focal tree) as sample unit. We sampled shrub and tree individuals from 1 m height under 83 deciduous canopies and 59 evergreen canopies. We also measured growth of 33 plants (Diameter at Breast Height > 5 cm) under deciduous canopies and 30 plants under evergreen canopies each three months. We did not find differences in canopy openness values under canopies classified in different phenological groups in all periods of the year. Regarding structure and composition of plants in deciduous and evergreen understories we found differences only for small plants (Diameter at Soil Height < 5 cm). Small plants density was lower under deciduous canopies when compared to evergreen canopies, which may be related to a greater mortality brought by concentrated litter fall in deciduous understory. We did not find differences in growth rate of trees under deciduous and evergreen canopies, which may be related to the fact the light increment is similar under deciduous and evergreen understories during the period of deciduousness or to the fact that water availability is lower in this period in SSF. We conclude that, even if light entrance is not different between understory of different phenological categories during the deciduousness period, another consequences of deciduousness for understory environment, like mechanical damage to saplings, may affect small plants community structure. In this way to be under deciduous or evergreen canopies in SSF may affect future dynamics in SSF.

Key-words: Atlantic Forest, canopy openness, environmental heterogeneity, leaf phenology, understory light, understory vegetation.

Sumário

Introdução Geral

A compreensão da dinâmica de florestas tropicais tem se mostrado crucial em um cenário de mudanças climáticas e mudanças no uso da terra. Não apenas por serem ambientes sujeitos a alterações (Pan et al. 2013) mas, principalmente, por serem potenciais protagonistas da mitigação de seus efeitos. Florestas tropicais respondem por metade da biodiversidade mundial, são fundamentais para a manutenção dos ciclos hidrológicos globais e fornecem alimento, combustível e água potável para milhões de pessoas (ver Wright 2010 para uma revisão). Identificar os fatores que promovem a permanência das espécies em determinados ambientes é essencial para a compreensão da estrutura e organização de comunidades florestais (Brown 1995). O reconhecimento de como esses fatores atuam em diversas escalas espaço-temporais auxiliam tanto a identificar padrões – como localizar espécies de plantas restritas a manchas dentro da vegetação (Antonovics et al. 1971), maior densidade de espécies sob algumas espécies de árvores (Sánchez-Velásquez et al. 2004) ou agregação espacial de plantas (Tirado & Pugnaire 2003) – como a compreender os processos responsáveis por esses padrões (Levin 1992). Em escalas mais amplas, ou em nível continental, fatores climáticos como precipitação e temperatura serão os filtros preponderantes à distribuição de espécies. Já em escalas locais, fatores edáficos, topográficos e diferenças na irradiância solar, além influenciarem a composição de espécies, serão determinantes das abundâncias e da ocorrência de determinados fenótipos (Bello et al. 2013, Pan et al. 2013). Todos esses filtros poderão atuar concomitantemente a processos neutros, podendo ser analisados em conjunto a fim de complementar o entendimento da montagem de comunidades (Chave 2004, Gravel et al. 2006).

Interações bióticas também têm papel importante na distribuição de espécies em escala local (Jones et al. 1997, George & Bazzaz 1999, Bello et al. 2013). Entre os exemplos mais bem documentados na literatura incluem-se o estudo das interações animal-planta, como os que relacionam o declínio de populações vegetais com a diminuição da fauna dispersora (Dirzo et al. 2014) ou com o desaparecimento de polinizadores (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services 2016) e interações microoganismo-planta, principalmente relacionados a associações micorrízicas e associações simbiônticas com bactérias fixadoras de nitrogênio (Reynolds et al. 2003, Bever et al. 2010). Além dessas, interações planta-planta também são consideradas importantes mecanismos moduladores da vegetação (Janzen 1970, Connell 1971, Callaway & Walker 1997, Hubbell 2001, Brooker 2006, McIntire & Fajardo 2009).

Interações negativas entre plantas, como competição e parasitismo, são consideradas processos fundamentais na distribuição de plantas observada em determinado ambiente (Berger et al. 2008). Plantas competem localmente por recursos, os quais podem ser esgotados (nutrientes, água) ou modificados (luz, temperatura) pelas plantas vizinhas, tornando seu desempenho extremamente dependente das competidoras ao redor, já que a única maneira de buscarem mais recursos é através do crescimento (Stoll & Weiner 2000). Mais recentemente, porém, estudos têm verificado interações positivas entre diferentes espécies de plantas, onde uma planta “enfermeira” gera alterações locais nos recursos que acabam por favorecer as condições de sobrevivência, crescimento e/ou reprodução das plantas ao redor, processo chamado de facilitação (Callaway 1995). Estudos avaliando o papel estruturador da facilitação tem demonstrado que este processo pode ser mais relevante ecologicamente em ambientes considerados extremos, submetidos, ao menos sazonalmente, a fatores limitantes como seca ou temperaturas muito altas ou muito baixas: zonas áridas, alpinas, desérticas e até mesmo savânicas (He et al. 2013). Porém, em ambientes mais amenos, com maior disponibilidade hídrica e temperaturas menos drásticas, como ocorre em florestas tropicais, a característica de algumas espécies de plantas também pode causar heterogeneidade ambiental suficiente para alterar a performance de plantas vizinhas (Ingwell et al. 2010, Souza et al. 2015).

Em ecossistemas florestais, onde árvores são o componente predominante na paisagem, a influência das condições físicas do ambiente sobre a assembleia de plantas do sub-bosque poderá ser alterada profundamente de acordo com as árvores que compõem o dossel (Souza et al. 2015). A ideia de "filtros de biodiversidade" apresenta-se como uma tentativa de explicar a coexistência do grande número de espécies em florestas tropicais e postula que cada árvore, com seu conjunto de particularidades (arquitetura da copa, estrutura e qualidade nutricional da serapilheira, associações simbióticas das raízes, acúmulo de elementos químicos, deciduidade), criará microssítios com certas especificidades (diferenças de irradiância que chega ao solo, presença ou não de alelopatia, danos mecânicos por queda de folhas) abaixo de suas copas promovendo a regeneração diferencial de espécies (Jones et al. 1997, Gandolfi et al. 2007, Souza et al. 2015). Entretanto, dada a justaposição de copas e o grande número de espécies de árvores em florestas tropicais, os efeitos de associações espécie-específicas poderão estar diluídos ou sobrepostos, tornando difícil detectar seus resultados, caso existam (Wilson & Keddy 1986, Goldenberg 1987, Mejía-Domínguez et al. 2011).

Na Floresta Estacional Semidecídua (FES) há uma dinâmica sazonal com a alternância de períodos com maior pluviosidade, entre o verão e a primavera, e períodos mais secos, no outono e inverno (Morellato 1995). Durante a estação seca, cerca de 30 a 50% das espécies arbóreas do dossel apresentam algum nível de deciduidade, o que pode ser uma estratégia de escape do estresse hídrico do período (Gandolfi et al. 2009, Martins & Batalha 2011) e também está relacionada à síndrome de dispersão anemocórica de algumas espécies arbustivo-arbóreas (Janzen 1967, Morellato et al. 1989, Griz & Machado 2001, Yamamoto et al. 2007). Os níveis de irradiância encontrados nos sub-bosques sob copas de árvores decíduas durante esse período aumentam, apresentando valores de irradiância similares àqueles encontrados em áreas de clareiras formadas pela queda de árvores (Gandolfi 1991). Enquanto isso, sob árvores sempre verdes, o regime de luz se mantém constante ao longo do ano (Gandolfi et al. 2007). Esse incremento de luz durante a estação seca no sub-bosque sob dossel decíduo foi denominado "clareiras de deciduidade" (Gandolfi 2000). Ao contrário das clareiras causadas pela queda de árvores, as clareiras de deciduidade são previsíveis no espaço - todos os anos no período seco árvores decíduas perderão suas folhas - e no tempo - o fenômeno é recorrente (Gandolfi 1991, Gandolfi et al. 2007).

Em florestas úmidas, sempre-verdes, foi demonstrado que a luz é o principal limitante para o desenvolvimento de árvores que ainda não atingiram o dossel ou que são típicas de sub-bosque em florestas tropicais (Nicotra et al. 1999). A competição por luz em ambientes florestais é um processo fundamental na determinação das taxas de crescimento, mortalidade e biomassa das árvores em pé (Purves et al. 2008). Em florestas semidecíduas, durante a estação seca, o aumento dos níveis de luz no sub-bosque, decorrente da deciduidade, pode favorecer o incremento em diâmetro de algumas espécies sob copas decíduas ao mesmo tempo em que pode causar fotoinibição em outras, dependendo da guilda ecológica à qual a espécie faz parte (plantas de sol ou de sombra), e da intensidade e duração da exposição à irradiância solar (Krause et al. 2001). Esta influência diferencial no crescimento, por sua vez, pode se tornar uma vantagem competitiva para algumas espécies, ou abrir uma "janela de oportunidade", o que poderá refletir em uma composição diferencial de espécies naquela área (Balke et al. 2014). Entretanto, o aumento de disponibilidade de luz em áreas sob dossel decíduo ocorre durante o inverno, um período do ano onde as temperaturas são menores e as condições de umidade são desfavoráveis ao crescimento de plantas em florestas tropicais, pois é a época de menores temperaturas e precipitações (Mulkey & Wright 1996). Esta característica pode restringir a potencial vantagem que plantas sob dosséis decíduos teriam durante o período das clareiras de deciduidade (Gandolfi 2000).

Nosso estudo tem como objetivo investigar o papel das clareiras de deciduidade na estruturação da comunidade arbórea em áreas de FES avaliando a estrutura e composição de espécies e o crescimento de indivíduos no sub-bosque sob dossel decíduo e sob dossel não decíduo. Uma vez que plantas de diferentes tamanhos podem ser afetadas diferencialmente por um mesmo conjunto de fatores bióticos e abióticos (Coomes & Grubb 2000, Wright 2002), neste estudo analisamos separadamente o efeito da abertura de dossel para plantas "pequenas" (diâmetro a altura do solo < 5 cm) e "grandes" (diâmetro a altura do solo ≥ 5 cm). A escolha deste critério para separar as plantas em classes de tamanho (5 cm) facilitará a comparação dos resultados deste estudo com outro estudo avaliando os efeitos das clareiras de deciduidade em uma FES (Souza et al. 2014).

Para alcançar nossos objetivos, essa dissertação foi dividida em três capítulos, cada um tentando responder a questões específicas, de modo que o conjunto de resultados nos permita entender o papel das clareiras de deciduidade na estrutura e composição das comunidades arbóreas na FES. No primeiro capítulo buscamos responder, através de medidas de abertura de dossel, quais são os valores de abertura do dossel que ocorrem sob as copas de árvores classificadas como decíduas até árvores consideradas não decíduas. Procuramos verificar se a classificação das espécies em grupos fenológicos com base na literatura corresponde a comportamentos distintos de abertura de dossel sob suas copas. Há diferenças na abertura de dossel ao longo do ano entre grupos fenológicos? Quais as variáveis ambientais são determinantes para a abertura do dossel de árvores em FES?

No segundo capítulo investigamos se clareiras de deciduidade causam alguma alteração na estrutura e composição da comunidade arbustivo-arbórea dos sub-bosques sob árvores de diferentes grupos fenológicos. Essas diferenças se estabelecem desde plantas pequenas (diâmetro a altura do solo < 5 cm) ou é consequência de mecanismos que atuam em etapas posteriores do ciclo de vida das espécies arbóreas (diâmetro a altura do solo ≥ 5 cm)?

No terceiro capítulo avaliamos as taxas de crescimento das árvores (com diâmetro a altura do peito, DAP, ≥ 5 cm) sob dossel com algum nível de deciduidade (decíduo ou semidecíduo) e sob dossel sempre verde ao longo das estações do ano. As taxas de crescimento dos indivíduos arbustivo-arbóreos difere entre plantas sob árvores decíduas ou semidecíduas e sempre verdes? Esse crescimento difere entre árvores pertencentes à diferentes categorias sucessionais? Quais os fatores determinantes para o crescimento de árvores do sub-bosque em FES?

A partir dos resultados obtidos nestes três capítulos pretendemos avaliar se o incremento diferencial de luz no sub-bosques sob copas de diferentes categorias de fenologia foliar causa alterações em alguma etapa do desenvolvimento de plantas em FES (plantas grandes e pequenas). Caso isso ocorra, esperamos encontrar seus reflexos na composição diferencial de espécies ou em estruturas distintas da comunidade arbustivo arbórea entre sub-bosques decíduos e sempre verdes. Por fim, avaliaremos se o crescimento de árvores com DAP ≥ 5 cm é o mecanismo responsável pelas possíveis diferenças observadas entre sub-bosques, o que nos ajudará a responder se as clareiras de deciduidade são determinantes para a dinâmica da comunidade de plantas em FES.

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Capítulo I - Canopy openness variation through the year among leaf phenological categories

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ABSTRACT

Tree phenophases reflect alterations on plant physiology due to changes in environmental conditions. In Seasonal Semideciduous Forests (SSF) of canopy tree species present some degree of deciduousness during the dry season. This synchronic leaf fall alters forest light regime allowing greater irradiance levels penetrating the understory of deciduous trees, a phenomenon called deciduousness gaps. However, between trees that can be classified as totally deciduous and totally evergreen, there are trees classified as semideciduous, which lose only part of their leaves but never stay totally leafless. We aimed to investigate whether there are differences the three main phenological categories recognized by most classification system: deciduous, semideciduous and evergreen plants. We expect that deciduous trees will present the greatest values of canopy openness, while evergreen trees will present the lowest and semideciduous will presente overlapping values with the other two categories. We placed hemispheric lenses under the canopy of selected trees and evaluated the light regime under 24 deciduous, 55 evergreen and 56 semideciduous individuals using those hemispherical photos. We didn't find differences in canopy openness among the three phenological categories. All phenological groups exhibited canopies with large values of canopy openness during the dry period. This result may be due to influence of surrounding trees in light that reaches the understory or due to phenological plasticity in leaf phenology of focal trees. Anyhow, it seems that light amount in the understory is not a differential factor bellow the canopy of deciduous, semideciduous and evergreen trees in any period of the year in SSF.

Key-words: Atlantic Forest, Brazil, Canopy openness, Leaf phenology, Understory light.

INTRODUCTION

The study of phenological events in plants consists in the observation of physiological and morphological changes that occurs on vegetation and their relation with biotic and abiotic variations in the environment (Lieth 2013). Changes on photoperiod (Matthes 1980), temperature (Matthes 1980, Polgar & Primack 2011), precipitation (Morellato et al. 1989, Reich & Borchert 1984) and soil nutrients availability (Nord et al. 2009) can signal or trigger phenological alterations on plants that includes reproductive events, periods with higher or lower metabolic activity, growth and senescence (Barr et al. 2009). Interactions with herbivores, seed dispersers, pollinators and with other plants also may modulate phenophases (Elzinga et al. 2007). Many of these seasonal changes reflect responses to the environment where the plant evolved, synchronizing phenophases with favorable periods of the year (Cleland et al. 2007, Vasconcelos et al. 2010, Weinig et al. 2014).

Vegetative phenology comprises senescence, abscission and leaf budding. Leaf senescence may represent an adaptation to water loss (Rizzini 1976), constituting an escape strategy to water stress (Levitt 1980a, b). Different tree species may present many patterns of leaf production and senescence under similar precipitation and temperature conditions, that is, there are several possible strategies to overcome adverse periods (Martins & Batalha 2011). These variety of strategies may be associated to trade-offs, such those related to the amount of nutrients in the soil. Plants have to find an optimum between lose lots of water by evapotranspiration in dry periods or lose leaves and resources in a poor nutrient environment (Beadle, 1953). Intraspecific variation in timing and intensity of leaf phenology may also occur and are related with internal physiological conditions like water status and nonstructural carbohydrate supply (Williams et al. 2008) and with different environmental conditions where plant established, such as soil water availability, vapor pressure deficit, etc. (Williams et al. 2008, Satake et al. 2013).

In Seasonal Semideciduous Forests (SSF) of São Paulo state, Brazil, it was observed that up to 50 % of canopy tree species may have some degree of deciduousness during the dry season (Gandolfi et al. 2009). This synchronic leaf fall alters the forest light regime allowing greater irradiance levels reaching the soil bellow deciduous trees (Gandolfi 2000). Gandolfi et al. (2007) showed that photosynthetic photon flux density levels (PPFD) reaching the understory under deciduous trees during the winter and beginning of spring (dry period) may be 24 times higher than PPFD levels found in understory of evergreen trees. Based on that data they proposed the idea of "deciduousness gaps", areas where solar irradiance levels during the winter time are similar to irradiance levels in treefall gaps areas (Gandolfi 2000).

However, in addition to trees classified as "deciduous", there are trees classified as "semideciduous" that undergo a period of intense leaf loss, but do not stay totally leafless

(Morellato et al. 1989). Comparable to gaps established by treefalls of different sizes and shapes that have distinct effects on understory plants composition (Denslow 1987), the amount of leaves lost by overstory trees may influence the structure of understory plant community bellow it. Thus, if canopy trees are deciduous, semideciduous or evergreen, this may influence light levels that reaches the soil and, consequently, alters the understory plant assemblage. So, in order to investigate biological effects of deciduouness gaps, its necessary to consider the influence of semidecidual canopy dynamics on understory light regime. A problem is that when trying to group SSF trees by phenological categories according to the literature, we observed a wide range of variation on phenological classifications among authors. More than reflecting subjectivity or different methods of phenological classification (Bencke & Morellato 2002), this variation may be demonstrating phenotipic plasticity among populations or among individuals of a single population.

Considering the semideciduous status attributed to some species and the plasticity in leaf phenology that may occur between individuals of the same species, our objective is to evaluate the variation of canopy openness through the year regarding understories of trees considered deciduous, semidecidous and evergreen according to the literature, answering the following questions: (1) Are there differences in canopy openness among phenological groups? (2) Which are the environmental variables that determine tree canopy openness in SSF? We expect that during the dry period, trees classified as deciduous will present the greatest values of canopy openness, evergreen trees will present the lowest values of canopy openness and semidecidous trees will present overlapping values to other categories. In the remaining months, we expect to find the same values of canopy openness for the three phenological categories evaluated, so the annual variation in canopy openness of deciduous trees will be the greatest, while for evergreen trees will be the lowest.

METHODS

STUDY AREAS - The study was conducted at the two largest fragments of Seasonal Semideciduous Forest that remained in Campinas municipality, São Paulo State, Brazil: the Santa Genebra Forest (22°49’22"S, 47°06’33"W), with 251.77 ha and the Ribeirão Cachoeira Forest (22°49'44"S, 46°55'25"W), with 233.7 ha (Fig. 1; Santin 1999, Santos 2006). Fragments are 18 km distant of each other. Both areas have Köppen's Cwa climate (Subtropical with Dry Winter), annual mean temperature is 15.6ºC and annual mean rainfall is 1372.0 mm (CEPAGRI 2016). Dry season occurs from April to September with average temperature about 20.3 ºC and precipitation about 298 mm; rainy season occurs during summer from October to March, with average temperature 24.1 ºC and precipitation about 1100 mm (CIIAGRO 2016). Altitude varies between 630 to 760 m at Ribeirão Cachoeira forest (SMMA CAMPINAS 2012), where predominant soil type is Chromic

Luvisol (FAO 1974, EMBRAPA 1999). At Santa Genebra forest, altitude varies between 580 and 610 m (Martins & Rodrigues 2001) with predominant soil type Rhodic Ferralsol (FAO 1974).

FOCAL TREES SELECTION - At SG forest we took photos of 74 focal trees, 13 deciduous (belonging to 3 species), 32 semidecidous (6 species) and 29 evergreen (10 species). We started the selection of trees to be photographed arbitrarily choosing trees along a trail about 3 km away. We chose canopy trees with no other canopy tree crowns above it. Then, in order to avoid bias, we continued to determine trees to be photographed by raffling a list of 100 m² plots already installed in both forest fragments (see Gandolfi 2000 for more details) and selecting the tallest tree of each plot that was not covered by any other tree crown (named from here as "focal tree"). In cases where there were two possible trees to be sampled, that is, two overstory trees whose crown do not touch each other, we sampled understories of both trees in the same plot. The plots here were used more like a guide to select focal trees, in order to avoid actively seek for them and possibly bring some kind of personal bias to that choice. At RC forest we took photos of 59 focal trees, 11 deciduous (belonging to 4 species), 23 semidecidous (9 species) and 25 evergreen (12 species). We selected trees to be photographed by shuffling a list of 100 m² plots already installed for a previous phytosociological study (see Cielo-Filho et al. 2007 for more details) using the "sample" function of R software (R Core Team 2015) and then proceeding as already described for SG forest.

After selecting focal trees, we classified them according to the literature in three phenological groups: deciduous, semidecidous and evergreen (Appendix 1). When we observed discrepancies in classification among authors we considered the classification (1st) of studies with focus on the species of interest and (2nd) the more frequent classification among the studies.

HEMISPHERICAL PHOTOS - We accompanied canopy openness of canopy trees through the collection and analysis of hemispherical photos, which provides indirect evaluations of several physical components of canopy structure (Jonckheere et al. 2004). In this study, we used hemispherical photos to describe temporal variations in canopy openness of tree species classified as deciduous, semideciduous and evergreen according to the literature (Appendix 1). Like in other studies, we are considering canopy openness as an indirect measure of the amount of light that reaches forest understory (Rich et al. 1993, Valverde & Silvertown 1997, Beaudet & Messier 2002). Canopy openness is the proportion of the sky hemisphere not obscured by vegetation when viewed from a single point measure and is directly related to local light behavior and microclimate (Jennings et al. 1999).

We took the photos from a distance of 10 cm from the focal tree trunks, in the North direction, 1 m height from soil, with a NIKON E 5000 camera, where we coupled fisheye lens FC-E8 0.21x with aperture 180°. During two years, from 2014 to 2016, photos were taken each three months (February, May, August and November) under focal trees at SG forest. At RC forest, photos were taken from 2015 February and thereafter each three months, always in the last week of the month (Available in https://figshare.com/s/047d0442665b68ebb06f). We used Gap Light Analizer software (GLA 1999) to perform photo analysis.

STATISTICAL ANALYSIS - In order to assess canopy openness variation over the year for deciduous, semideciduous and evergreen trees we constructed a canopy openness variation index according to the formula:

$$(COmax - COmin) / COmax ,$$

where COmax is the maximum canopy openness exhibited by a focal tree individual in all months analyzed and COmin is the minimum canopy openness exhibited by a focal tree individual in all months analyzed. We expect that trees classified as deciduous according to the literature will present the highest values of canopy openness variation index, evergreen trees, the lowest, and semidecidous trees will present intermediate values. In order to verify if size of focal tree crown influences the values of canopy openness obtained we performed a linear regression between crown size (see details of crown area calculation in Methods of Chapter 2) and the canopy openness variation index. Also, to evaluate the influence of understory vegetation density on the values of canopy openness obtained we performed a linear regression between the density of trees under each focal tree (see Methods in Chapter 2) and the canopy openness variation index. Since our indexes values are limited inside a range of values between 0 and 1, before performing regressions we transformed canopy openness variation index with probit, an analysis that transform binomial response variables so they can be analyzed by regression either through least squares or maximum likelihood (Bliss 1934).

To evaluate influence of climatic variables on canopy openness we used linear mixed models. As fixed effects we used intervals of three months representing the seasons and the climatic variables: accumulated precipitation, number of days without rain, mean minimum and mean maximum temperatures. The sampling years and each focal tree was considered as a repeated measure (random effect). The model with the lowest AIC (Akaike Information Criterion) was considered with maximum likelihood method (Pinheiro & Bates 2006). We performed the analysis using the packages "VGAM" (Yee 2010), "car" (Fox & Weisberg 2011), "lattice" (Deepayan 2008), "lme4” (Bates et al. 2015) and "bbmle" (Bolker & R Development Core Team 2016) inside the R software environment (R Core Team 2015).

RESULTS

Despite canopy openness vary throughout the year there were no differences among phenological categories (Fig. 1). Even for trees of a single species canopy openness variation was variable among individuals and trees belonging to different phenological categories presented overlapped values of canopy openness variation index (Fig. 2). So, contrary to our hypothesis, variation in canopy openness is the same among individuals classified in different leaf phenologies (ANOVA: $F_{2,129} = 0.852$; $p = 0.43$, Fig. 3). Individuals of all categories exhibited overlapping values of canopy openness in all months, ranging from 1.5 % (minimum measure) to 19.4 % (maximum measure), with mean values ranging from 6 % in the wet season to 9 % in dry season.

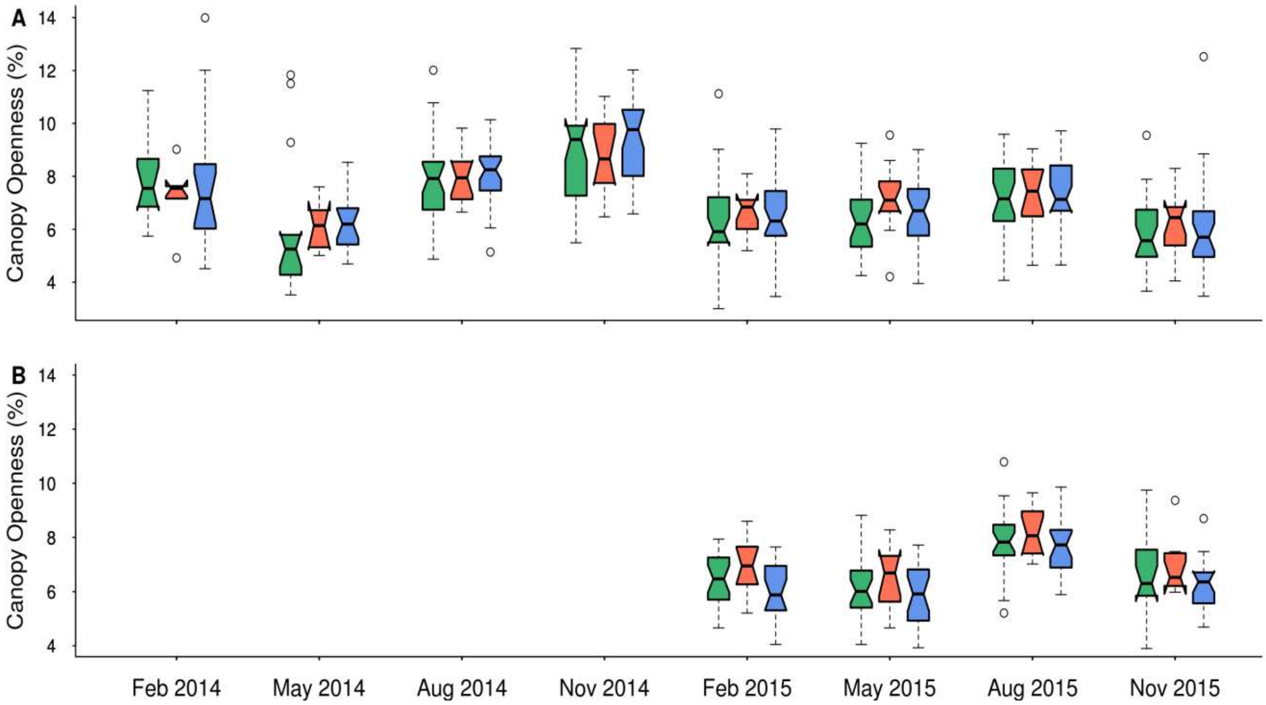

Figure 1: Distribution of the canopy openness (proportion of sky not covered by vegetation) values for SG forest (A) and RC forest (B). Deciduous (red boxes), evergreen (green boxes) and semideciduous trees (blue boxes). Boxes notches show the 95% confidence intervals.

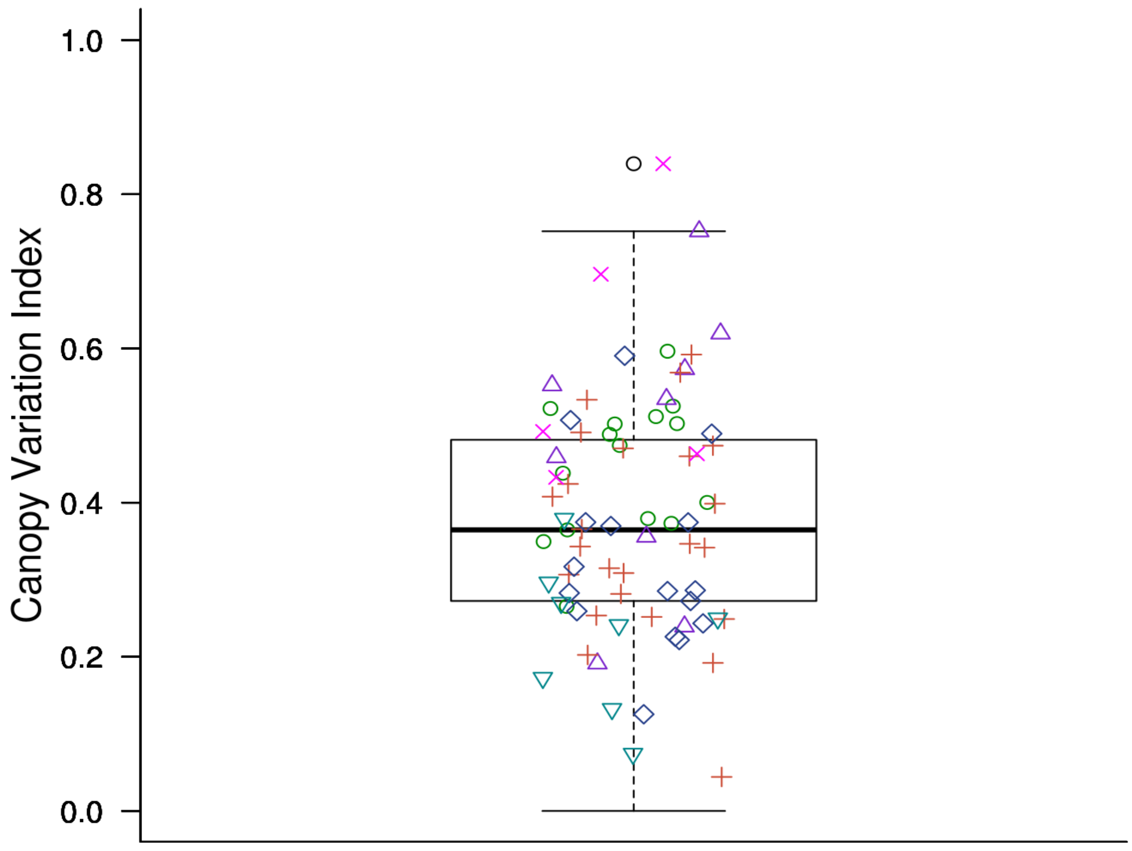

Figure 2: Distribution of Canopy Variation Index of focal trees individuals per species. Evergreen: *Aspidosperma polyneuron* Müll.Arg. (turquoise triangles), *Pachystroma longifolium* (Nees) I.M.Johnst. (green circles); Deciduous: *Croton piptocalyx* Müll.Arg. (purple triangles), *Esenbeckia leiocarpa* Engl. (orange plus signals), *Piptadenia gonoacantha* (Mart.) J.F.Macbr. (pink crosses) and *Astronium graveolens* Jacq. (blue diamonds).

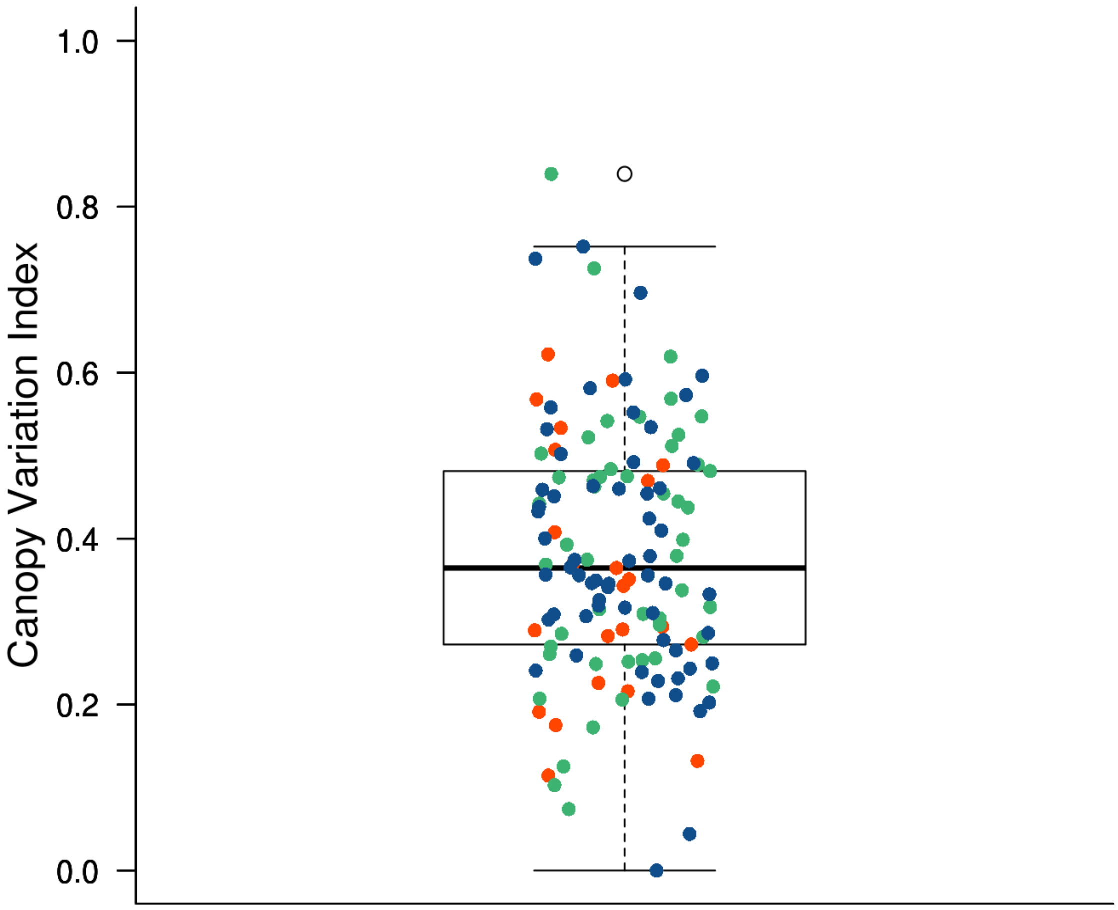

Figure 3: Distribution of Canopy Variation Index of all focal trees individuals classified by phenology groups. Deciduous (red dots), evergreen (green dots) and semideciduous trees (blue dots).

We found no relation between size of focal tree crown and canopy openness variation index

(Linear Regression: $R^2 = -0.06$, $p < 0.67$; Fig. 4) and we found negative relation between density of trees under focal tree and the canopy openness variation index (Linear Regression: $R^2 = 0.05$, $p < 0.01$; Fig. 5).

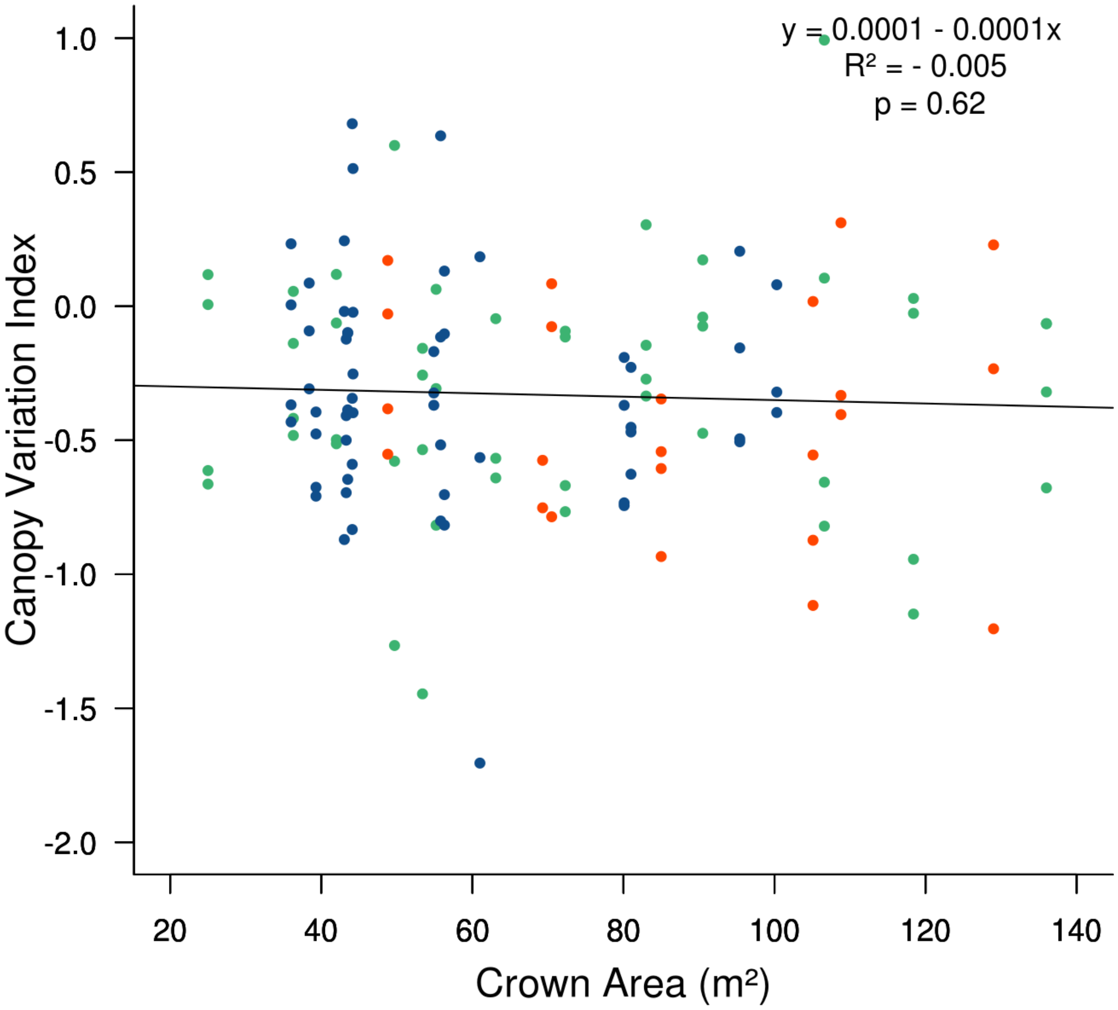

Figure 4: Linear regression between canopy area (m²) and the the probits transformed values of Canopy Variation Index, (COmax - COmin) / COmax, of each focal tree individual. Black line represents the adjusted linear model.

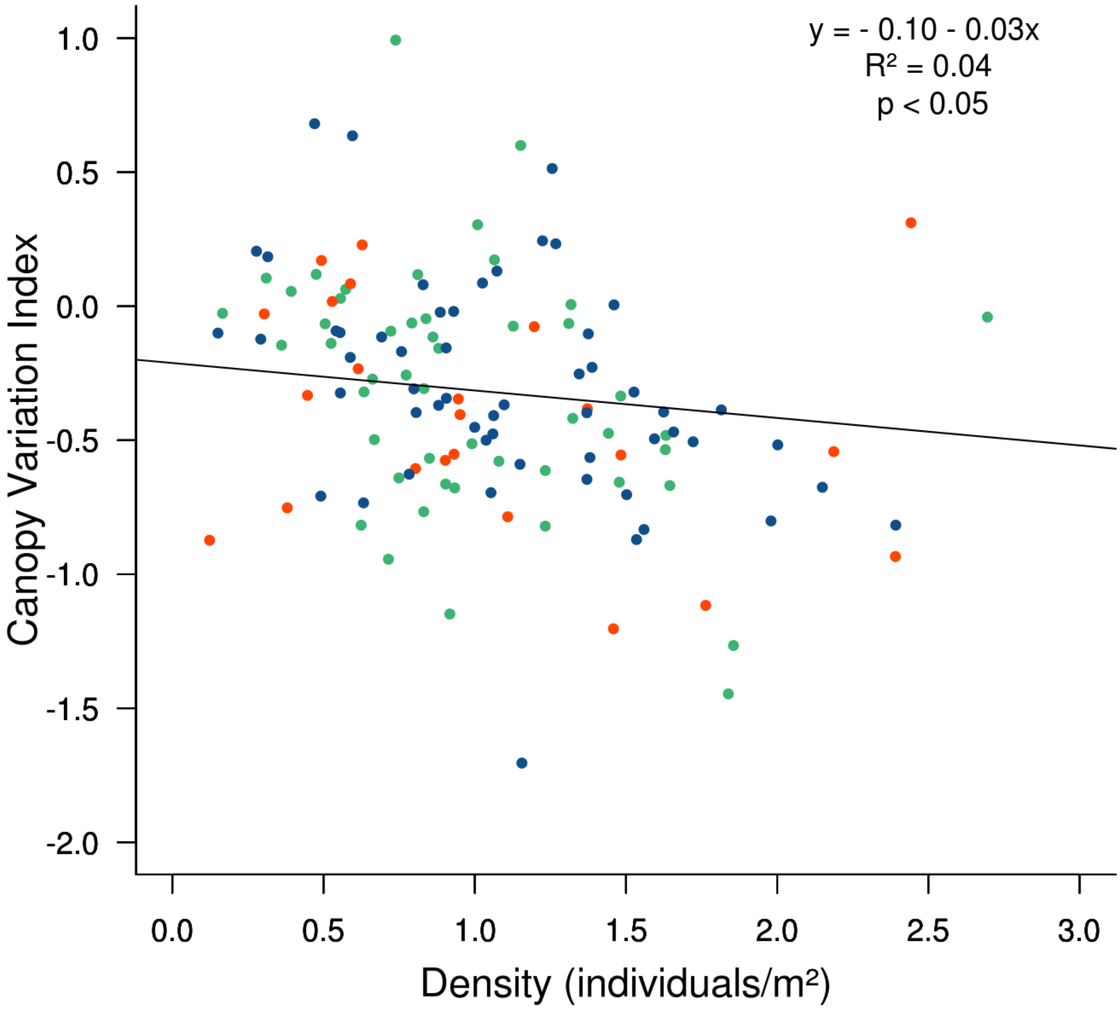

Figure 5: Linear regression between the density of understory individuals and the probits transformed values of Canopy Variation Index, (COmax - COmin) / COmax, of each focal tree individual. Black line represents the adjusted linear model.

At SG forest, canopy openness in 2014 reached the highest values in November and not in August as occurred in 2015 in both forests. The model that best explained canopy openness considered the seasons of the year as fixed factor (Appendix 2).

DISCUSSION

We were not able to detect greater variation in the canopy openness between deciduous, semideciduous and evergreen trees during the dry season, which may be related to several factors. First, because this study was conducted in two isolated and fragmented forest areas (Santin 1999, Farah 2009) one can imagine that the canopy of these forests is unstructured and they do not represent the canopy characteristics of undisturbed SSFs. However, we are convinced that this is not the case, since values of canopy openness we found are similar to values obtained in other SSF from Brazil and the world during the dry season, between 8 and 13% (Holdridge et al. 1971, Santos 2003, Vieira 2008). In contrast, at totally deciduous forests in Central Brazil, canopy openness during dry season vary between 30 and 80 % (Nascimento et al. 2007).

It is known that vegetation surrounding focal tree influences understory light regime and that light that reaches the forest floor is the final result of light filtering through a mosaic of crowns, branches and lianas (Lieberman & Lieberman 1989). Our results show that greater density of individuals under a focal tree results in lower canopy openness variation index of this focal tree, although the relation is weak ($R^2 = 0.04$). That weak relation may be indicating that other factors are important to determine canopy openness variation. For example, we wondered if deciduous focal trees support greater proportion of deciduous trees in their understory, the same for evergreen and semideciduous, but there were no differences in the proportions betweeen phenologies (data not shown). Another possibility is that crown size is influencing our canopy openness measures. Since hemispherical photos capture a wide viewing angle, photos taken of small crowns may be composed also by surrounding tree crowns while bigger crowns would fill the entire space of the picture and all vegetation observed will belong to the crown of that focal tree individual. However our results show that crown size does not influence our measures of canopy openness variation through the year.

Another explanation why we did not see differences in canopy openness may be related to an ecological compound, an internal regulation in which trees with a particular phenological strategy have their metabolism altered depending on local weather variation (Schlichting 1986). Plants and other organisms may use resources in an opportunistic way according to their spatiotemporal availability, exhibiting a deviation from the mean species phenotype (Hubbell

2001). Some trees of SSF, for instance, may present leaf loss more than once in the same year due to atypical dry months or present more pronounced leaf fall in drier than usual seasons (Morellato 1991). Therefore, even for species unanimously classified within a phenological category, there is variation among tree populations across geographic regions or even inside a single forest fragment. Since 2014 and 2015 years showed greater drought periods when compared climatic means (Appendix 3) it is possible that this has affected trees leaf phenology. Then, as a result of phenotypic plasticity, we were no able to detect differences in canopy openness among phenological categories. This explanation is corroborated by our results of canopy openness variation per individuals (Fig. 2), where it is possible to observe that canopy openness variation index of individuals of a single species present overlapping values to species classified in another phenological category.

The model that best explained canopy openness at both forests took into account the period of three months (season) as fixed factor. Rather than only one environmental variable driving leaf phenology, our results suggest that a range of environmental signals, like precipitation, photoperiod and temperature, plus internal regulation of each plant act together triggering trees phenophases (Reich & Borchert 1984, Williams et al. 2008), therefore season was the best tree growth predictor. Studies conducted in others phytophysiognomies of Atlantic Forest, the Araucaria Forest (Marques et al. 2004) and Ombrophilous Atlantic Forest (Cardoso 2006) - found that photoperiod and temperature are major factors influencing leaf phenology. When the dry season extended until the spring, like in 2014, we observed the highest values of canopy openness in November and not during the winter time, as ocurred in 2015. These high values of canopy openness may be related to a delay in leaf production by trees due to water stress (Aide 1993, Morellato 2016).

Our results show that not only semideciduous trees presented overlapping values of canopy openness with both deciduous and semideciduous phenological categories, but canopy openness values in all categories overlap. As noticed by (Morelato 1991), we observed that even evergreen trees reach greater canopy openness values as dry season becomes severe (personal observation). In this way, it is possible that tree classification in phenological categories is not appropriate, because it did not take into account phenological plasticity of individuals, and most species may exhibit all leaf phenologies according to weather conditions. Another possibility is that hemispherical photos are not the best procedure to assess leaf phenology, because they capture phenology of surrounding focal trees and their influence on canopy openness. We conclude that phenology attributed to the species whose focal tree individual belongs will not have major influence on light that reaches understory, otherwise, even with the influence of vegetation under the focal tree, their leaf phenology would determine light regime below it. So, from the point of view of understory vegetation, to be under species classified as deciduous, semideciduous or evergreen do not determine the light regime under which plants will be submitted in SSF. Therefore, we will expect that, if deciduousness gaps have biological effects on understory vegetation, these effects will not be so contrasting between canopy types and may be more related to other canopy characteristics rather than light input through tree crown. For instance, fertility islands may occur under deciduous trees due intense leaf fall, which may cause higher decomposition rates and nutrients liberation in the soil (Stahlheber et al. 2015, Rhoades 1997).

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Capítulo II - Deciduousness gaps determine the structure and composition of Seasonal Semideciduous Forests?

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ABSTRACT

Gaps are important components of tropical forests dynamics, promoting seedlings establishment, tree development and reproduction. Seasonal Semideciduous Forests (SSF) are characterized by presenting an annual cycle with two seasons: a rainy season when leaves flush and the trees have their canopies closed, and a dry season when some trees lose its leaves, generating the so-called "deciduousness gaps". If we consider light as a limiting factor on forest understory we will expect that some plant species on Seasonal Semideciduous Forests will be favored by increase in light amount during the leaf fall, and possibly by nutrients input from those leaves, created by deciduousness gaps. However, most of deciduousness gaps occur in a dry period with unfavorable conditions of water availability, which may restrict species that could possibly be favored by light increment. The goal of this work was to investigate the role of the deciduousness gaps in the dynamics of Seasonal Semideciduous Forests. We sampled 4429 individuals up to 1 m height growing under 83 deciduous (belonging to 24 species) and 59 evergreen (15 species) focal trees in two Seasonal Semideciduous Forests fragments. We found differences on structure and composition of vegetation community across canopy phenologies only when we considered small plants (Diameter at Soil Height < 5 cm). Even so, since seedling recruitment and survival play central roles in shifts species distributions even if these patterns disappear through the time we conclude that be under deciduous or evergreen canopies in SSF may affect future dynamics in SSF.

Key-words: Atlantic Forest, biological filters, Brazil, environmental heterogeneity, light variation, tree phenology, understory vegetation.

INTRODUCTION

Tropical forests dynamics is the result of the interaction among biotic and abiotic factors that occurs in a cyclic or stochastic way determining the structure, species composition and function of forest communities (Ghazoul & Sheil 2010). Some factors like seed dispersal (Howe 1985), proximity to other forest fragments (Jordano et al. 2006), topography and soil characteristics, altitude, latitude and precipitation are fundamental to the maintenance of tree species diversity in neotropical forests (Gentry 1988). One component of the tropical forests dynamics is the occurrence of gaps, which may be formed naturally by treefall and liana tangles fall, break of tree branches and trees inclination, causing higher light levels in these areas (Whitmore 1996). Among the benefits brought by higher brightness in gaps areas, effects on seedlings establishment (Carvalho et al. 1999, Nicotra 1999), tree growth rate (Uhl et al. 1988, Turner 2001) and the individuals entrance on reproductive stage (Hartshorn 1980, Zuidema & Boot 2002) are some of the results reported.

In spite being one of the most threatened formations in the world, having nowadays about 12.5 % of its original cover (Ribeiro et al. 2009, SOS Mata Atlântica & INPE 2014), knowledge about the dynamics of forests inside the Atlantic Forest domain are far from being understood (Silva & Casteleti 2005, Farah 2009). The Atlantic Forest includes the Seasonal Semideciduous Forest (SSF), that have a marked dry season (Oliveira-Filho & Fontes 2000). These forests are fragmented in small remnants, some of them in conditions of deterioration due to the isolation and the urban pressure, while others were exploited, managed and abandoned in the past, being today in different stages of regenaration (Santos 2006, Rezende et al. 2015).

In SSF, due to the annual cycle formed by the seasonal alternation between a dry and a moist season, some trees lose their leaves total or partially in the winter time, that corresponds to the dry season (Morellato 1991). Some studies have reported that this seasonal opening beneath deciduous canopies will bring higher brightness during the dry season in these areas, with light intensity presenting values of photosynthetic photon flux density (PPFD) similar to treefall gaps areas (Gandolfi 1991, Gandolfi et al. 2007). Those places were called "virtual gaps" or "deciduousness gaps", whose main feature is the annual recurrence of periods with more light, during the dry season, alternating with periods with less light, in the wet season (Gandolfi 2000). According to Gandolfi (2000) the increase of light in the dry season at SSF may last about five months (from April to August) showing diffuse irradiance levels up to three times higher during the deciduousness period (Gandolfi 2000, Gandolfi et al. 2007).

However, when trying to detect differences in understory light under canopies belonging to different leaf phenologies we were not able to find greater values of canopy openness under deciduous canopies during the dry season (Chapter 1). Even so, recently, Souza et al. (2014) found higher proportion of light-demanding species and individuals beneath deciduous canopies in a SSF fragment and attributed that result to greater light under deciduous trees during the period of deciduousness. Their findings support that there are differences in understory plants community attributes between canopies phenologies, even though we believe that these differences are not related to differential light under deciduous and evergreen canopies in our study areas (Chapter 1). In this way, in this study we aim to evaluate how multiple canopy tree species, joined by similar phenology, affect the plant community growing below them.

Several studies have found that trees with distinct sizes may present differential responses under several environmental pressures, like drought or temperature variation (Condit et al. 1995, Nepstad et al. 2007). In this study we evaluated tree community attributes for small and large plants separately, in order to understand if focal tree leaf phenology affect them in different ways. We expect to infer about facilitation or competition mechanisms involving canopy deciduous species structuring plant communities and possible inversions of action of these mechanisms in differents sizes of plants life cycle (small and large plants). Our questions are: (1) Are there differences in structure and composition of plant community under deciduous and evergreen canopies? (2) Such differences are established on plants since they are small (DAS < 5 cm) or they are consequences of mechanisms that act in subsequent steps of life cycle of tree species (DAS ≥ 5cm)? We expect that, if we find differences in structure and composition of understory plants between deciduous and evergreen canopies, that differences may be explained by others factors related to distinct focal tree leaf dynamics that not light contrasts between understories.

METHODS

STUDY AREAS — The study was conducted in the two largest fragments of Seasonal Semideciduous Forest in the municipality of Campinas, São Paulo State, Brazil (Santin 1999): the Santa Genebra Forest (22°49’22"S, 47°06’33"W), with 251.77 ha and the Ribeirão Cachoeira Forest (22°49'44"S, 46°55'25"W), with 233.7 ha (Fig. 1). Fragments are 18 km distant of each other. Both areas have Köppen's Cwa climate (Subtropical with Dry Winter) with annual mean temperature 15.6ºC and annual mean rainfall 1,372 mm. Dry season occurs from April to September with average temperature about 24.1 ºC and precipitation about 298 mm; rainy and warm season occurs from October to March, with average temperature 20.3 ºC and precipitation about 1,100 mm (CIIAGRO 2016). Altitude varies between 630 and 760 m at Ribeirão Cachoeira forest (SMMA CAMPINAS 2012), where predominant soil type is Chromic Luvisol (FAO 1974, Embrapa 1999). At Santa Genebra forest, altitude varies between 580 and 610 m (Martins & Rodrigues 2002), where predominant soil type is Rhodic Ferralsol (FAO 1974).

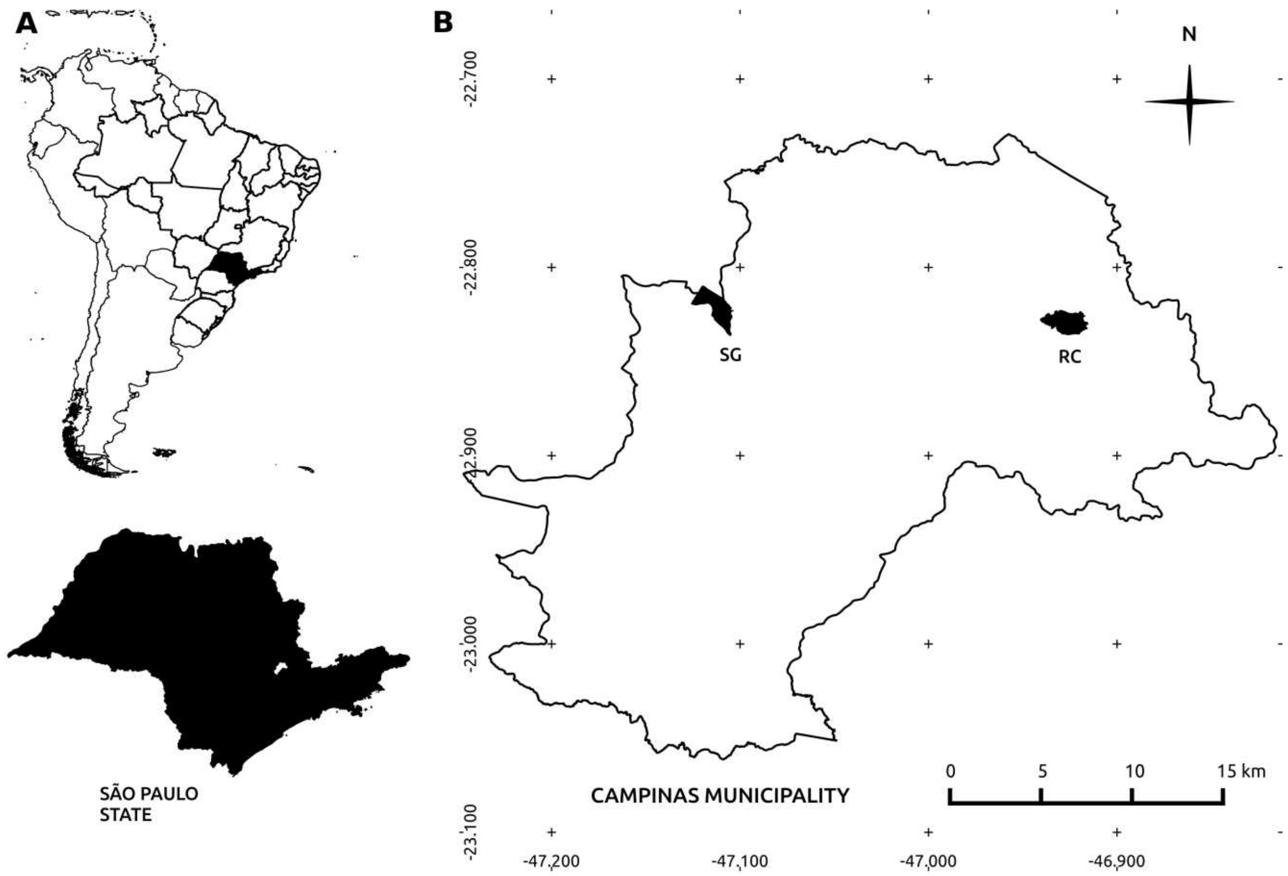

Figure 1: Campinas Municipality located in the State of São Paulo - Brazil (A). Forest fragments studied at Campinas Municipality: Santa Genebra Forest - SG and Ribeirão Cachoeira Forest - RC (B).

FLORISTIC SURVEY AND PHENOLOGY CLASSIFICATION — We started the field work arbitrarily choosing trees whose understories would be sampled along a trail about 3 km away. We preferred canopy trees with no other tree crowns above it. Then, in order to avoid bias, we continued to determine trees to be sampled by shuffling a list of 100 m² plots already installed in both forest fragments (see Cielo-Filho et al. 2007 for RC forest and Gandolfi 2000 for SG forest for more details) using the "sample" function of R software (R Core Team 2015). Then, the tallest tree of each plot that was not covered by any other tree crown (named from here as "focal tree") was chosen, identified and classified according its leaf phenology. In cases when there was two possible trees to be sampled, that is, two canopy trees whose crown do not touch each other, we sampled both trees in the same plot. The plots were used as a guide to select focal trees in order to avoid actively seek for them and possibly bring some kind of personal bias to that choice. The understory was considered as the projection of tree crown on the ground, calculated from the distance between the trunk and the border of the crown, measured every 45° from North (Fig. 2). Total area was obtained from the geometric figure formed (octagon). Then, we sampled all trees and shrubs higher than 1 m and measured the Diameter at Soil Height (DSH) of all sampled individuals.

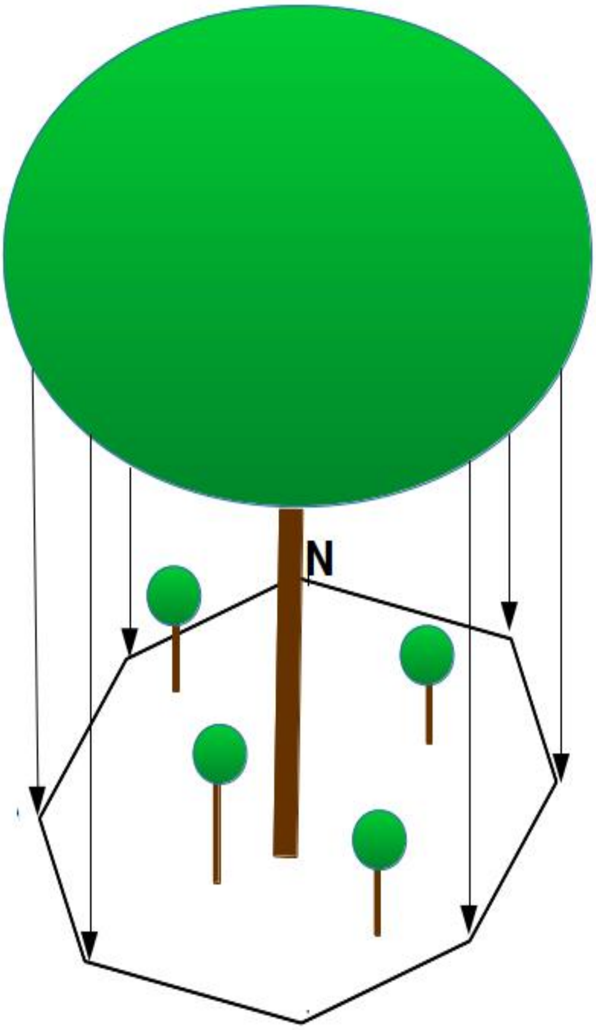

Figure 2: Understory area under focal tree, delimited by the crown projection on the ground, indicating the sample area under each focal tree (octagon). North direction (N).

We identified each focal tree to species level and classified each species in one phenology category (deciduous, semideciduous and evergreen) based on references in the botanical literature about that species. To make the analysis we grouped as "deciduous" both totally deciduous species and semideciduous species, since most of them have concentrated leaf fall in dry season (Morellato 1991). When we observed discrepancy of the phenological classification for a particular species among authors in the literature we prioritized (1st) studies with focus on the species of interest and (2nd) the more frequent classification among the studies. The list of focal trees and the studies were we found support is available in Appendix 1.

COMMUNITY STRUCTURE AND COMPOSITION — The species richness of the plant communities growing under deciduous and evergreen canopies was estimated through individual based rarefaction curves, allowing us to analyze if the annual variation in abiotic conditions under deciduous canopies create sites more or less favorable to the development of a higher number of species. We made an abundance-based rarefaction (Magurran 2004, Gotelli & Colwell 2001) because our sample units, that is, the projected crown areas, have different sizes (Fig. 3), and a sample based rarefaction could bring an error regarding the size of sample area. We use iNEXT package for R environment (Chao et al. 2014) to perform this analysis.

The Simpson dominance index (1- D) was used to compare the dominance of species between the understories according to the formula:

$$D = [\sum n(n-1)] / [N(N-1)],$$

where n is the relative abundance of individuals from species "i" in the sample, N is the total number of individuals of all species in the sample and $\sum$ represents the sum of all species in the sample (Simpson 1949). Average values of Simpson index were estimated separately for each phenological group of focal trees and we compared the averages differences with confidence intervals (95%) constructed by means of Monte Carlo resampling techniques (1000 iterations).

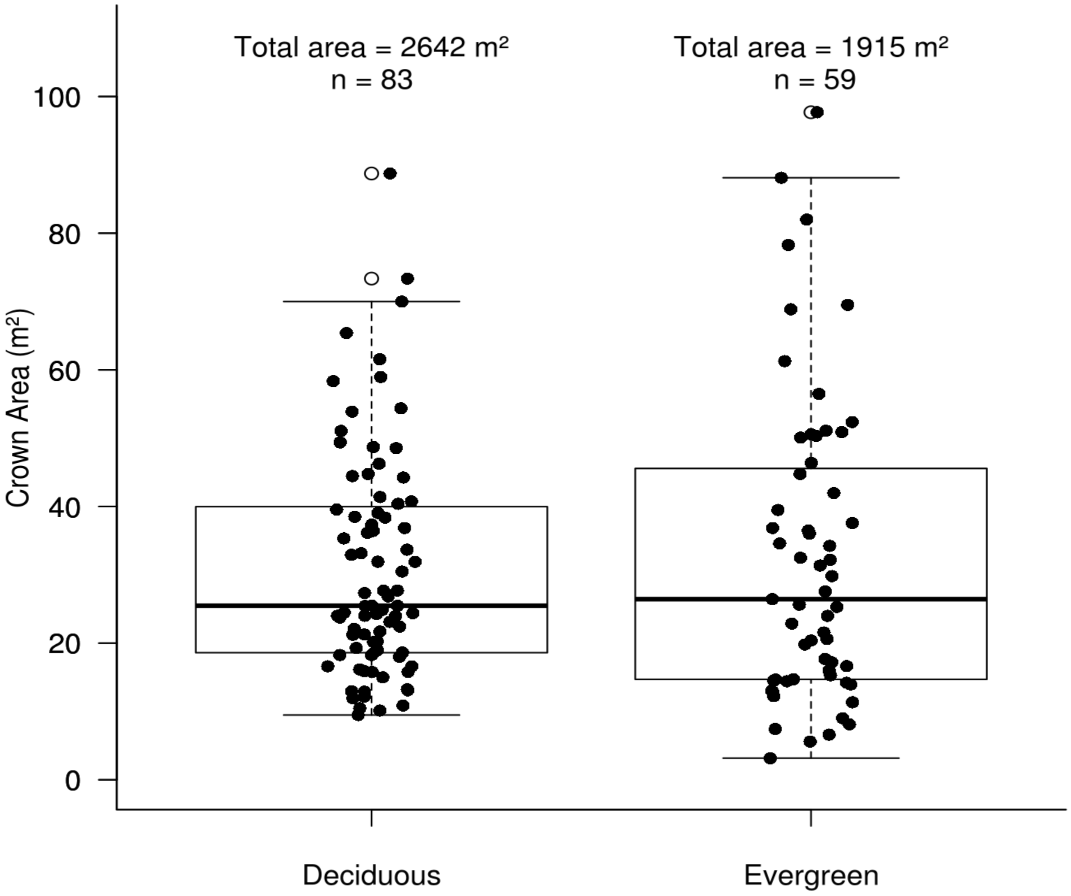

Figure 3: Crown areas distribution for deciduous and evergreen focal trees. Black dots represent each one of focal trees (n). Boxes include second and third quartiles, inner and outer fences are defined by interquartile ranges and circles represent outliers.

Analysis of dissimilarity were performed using non metric multidimensional scaling (NMDS) to visualize differences in species composition and abundance between canopies phenologies. Bray-Curtis index was adopted as our distance matrix measure. Differences in Bray-Curtis index between canopies phenologies was tested with a PERMANOVA analysis (ADONIS; Anderson 2001, Oksanen et al. 2008) using the "vegan" package (Oksanen et al. 2015) on R software (R Core Team 2015). With this analysis we will be able to answer if species that occur under evergreen canopies belong to the same group of species that occur under deciduous canopies.

In order to compare the proportion of light-demanding species present in the understories of deciduous and evergreen focal trees we performed comparisons of average proportion values for each phenological group and compared the averages differences with confidence intervals (95%) constructed by means of Monte Carlo resampling techniques, since data did not follow assumptions for parametric tests. We adopted the successional category classification of understories plants - light-demanding or shade-tolerant - used by Gandolfi (1991, 2000) and Souza & Valio (2001) in order to compare our results with the study about deciduousness gaps made by Souza et al. (2014). This comparison will enable us to verify if higher proportion of light-demanding species and individuals occur in other SSF and can be a further step towards generalizing deciduousness gaps effects to all SSF. Species that was not included those studies was classified according to other authors (Appendix 1). To obtain the Density of Species per phenological category (individuals/m²) we calculated the ratio between the number of understory individuals and the area for each focal tree.

We did all analysis separately for individuals with DSH < 5 cm, hereinafter referred as "small plants", and individuals with DSH ≥ 5 cm, hereinafter referred as "large plants", always for trees from 1 m height. We did this separation because it is known that size is related to differential performance of trees under several biotic and abiotic conditions. For instance, when compared to small plants, large plants may present lower mortality rates caused by desiccation in low rainfall levels periods, due to their well developed root system (Coomes & Grubb 2000, Wright 2002). We chose this 5 cm cutoff criterion to separate the sizes of plants in order to compare our results with another study that assessed deciduousness gaps effects in a SSF (Souza et al. 2014).

We used R software (R Core Team 2015) to perform all analysis in this study.

RESULTS

We sampled the understories of 59 evergreen focal trees belonging to 25 species and 83 deciduous and semideciduous focal trees belonging to 16 species. We measured a total of 4,429 understory individuals of 141 species: 2029 individuals belonging to 106 species under evergreen canopies and 2401 individuals belonging to 118 species under deciduous canopies (Appendix 1).

Density of small plants (individuals) was lower under deciduous canopies than under evergreen canopies (Monte Carlo, $p < 0.025$) and density of large plants was the same between canopies of different phenologies (Monte Carlo, $p > 0.975$; Fig. 4).

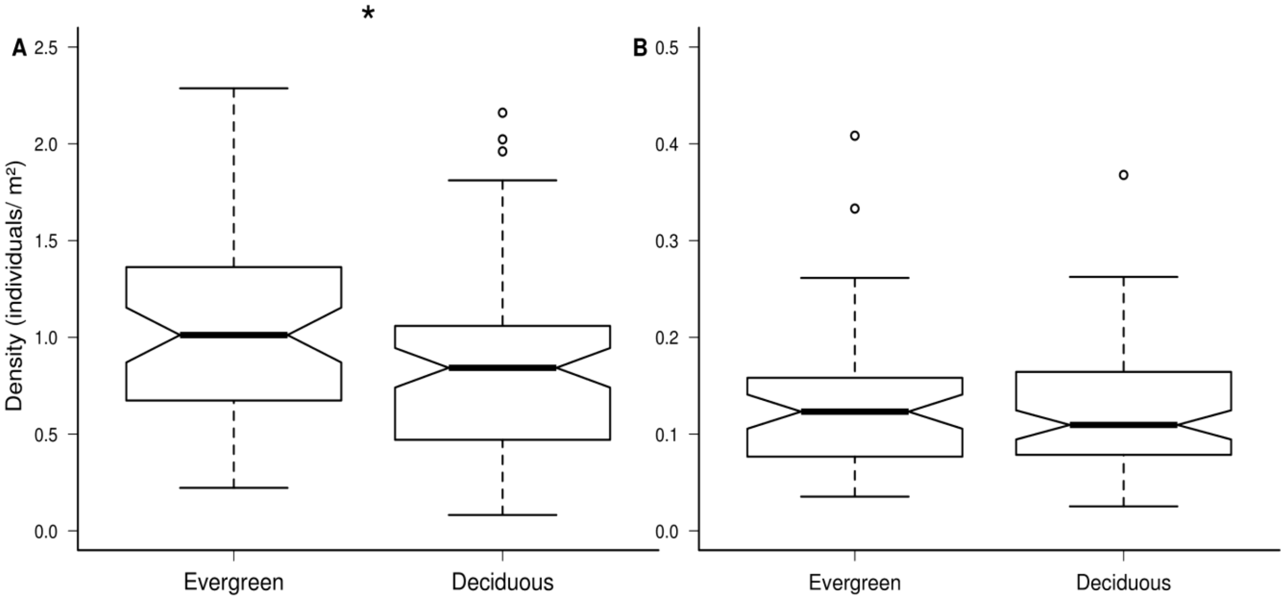

Figure 4: Plant densities (Individuals/m²) for small (A) and large plants (B). Boxes include second and third quartiles, inner and outer fences are defined by interquartile ranges, circles represent outliers and the asterisk represents difference between phenologies. Note that the y-axis scales are different.

The species richness of the community under deciduous and evergreen canopies was the same for both DSH categories evaluated (Fig. 5). However, the Simpson index of small plants under deciduous canopies was greater than under evergreen canopies (Monte Carlo, $p < 0.05$; Tab. 1). For large plants, Simpson indexes were the same under deciduous and evergreen canopies (Monte Carlo, $p > 0.05$).

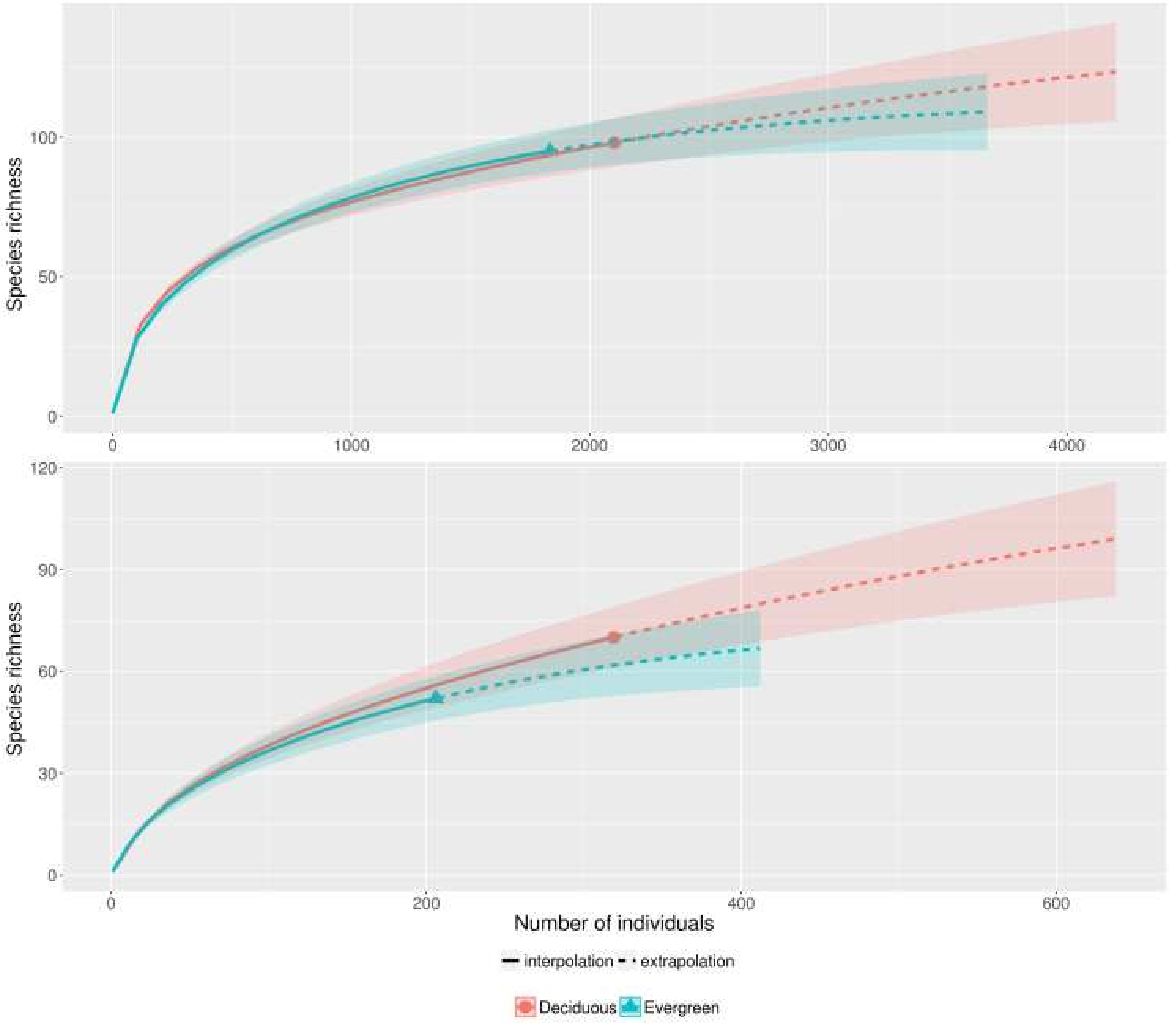

Figure 5: Rarefaction curve for the understory community under deciduous (red) and evergreen (blue) canopies. Solid lines represent the mean species richness (interpolation) and dashed lines represent extrapolation. Shadows represent the 95 % confidence interval. Small plants (A) and large plants (B).

Table1: Simpson index calculated for small plant community (DSH < 5) cm and large plant community (DSH ≥ 5 cm) under deciduous and evergreen canopies. Letters in the same column indicate differences or similarities in Monte Carlo indexes.

	DSH < 5 cm	DSH ≥ 5 cm
Deciduous	0.907^{a}	0.953^{a}
Evergreen	0.866^{b}	0.944^{a}

Once species richness is the same for both canopy groups, the component of diversity that differs between understories vegetation when considering small plants is dominance. So, under evergreen canopies there are greater dominance of species. We seek for positive influence of focal trees conspecifics on understory trees abundance, that is, the possibility of more individuals from species "A" in the understory of focal tree "A", but we found no relations (data not shown). In this way we are confident that the results obtained on species composition are not related to focal tree identity.

Dissimilarity of species between phenologies was not different both for small plants (stress = 28.4, ADONIS r^2= 0.023, p = 0.009 Fig. 6A) and large plants (stress = 11.7, ADONIS r^2= 0.005, p = 0.779; Fig. 6B).

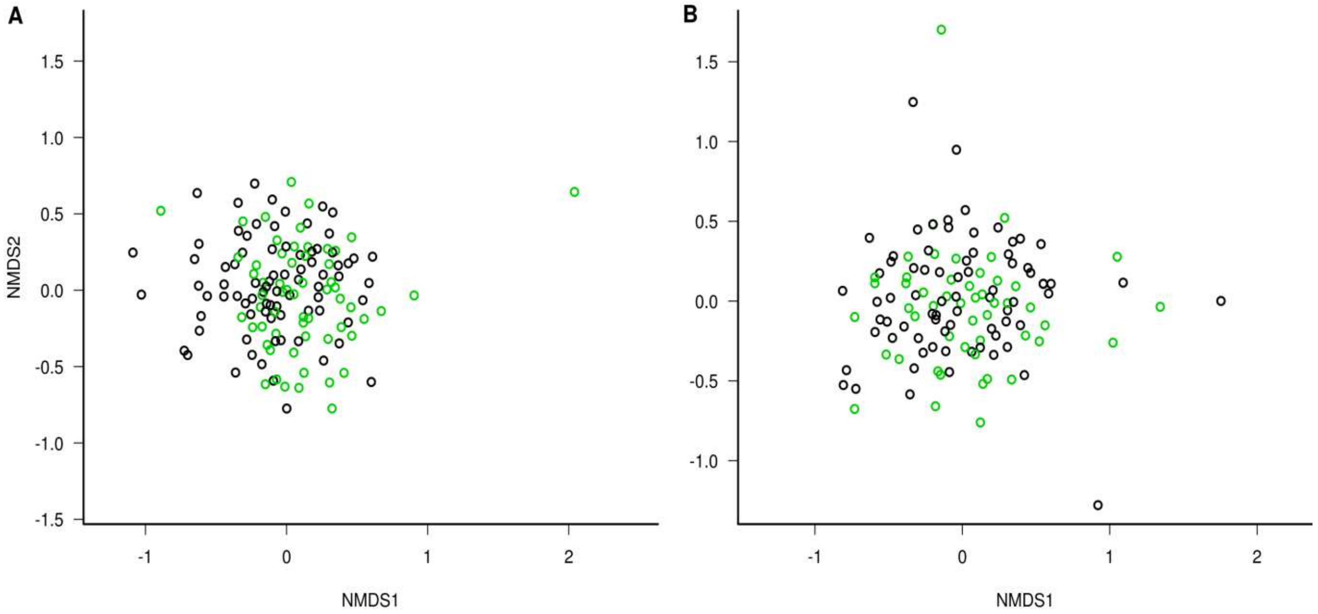

Figure 6: Non-metric multidimensional scaling of vegetation under evergreen (green circles) and deciduous (black circles) canopies using Bray-Curtis distance matrix as our dissimilarity measure plots. Small plants (A) and large plants (B) showed no dissimilarity between canopy phenologies.

The proportion of light-demanding individuals and species (Fig. 7) beneath evergreen and deciduous canopies was the same both considering small and large plants (Monte Carlo; $p > 0.05$).

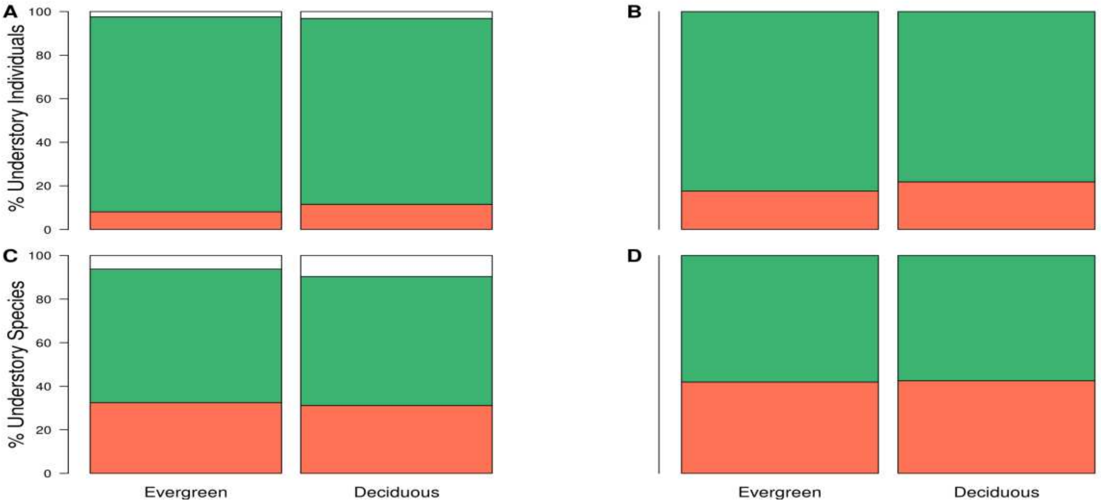

Figure 7: Proportion of light-demanding (orange), shade-tolerant (green) and unclassified (white) understory individuals (A for small plants and B for large plants) and species (C for small plants and D for large plants) under evergreen and deciduous canopies. For discrepancies in successional categories and classification see Methods. Unclassified species belong to understory specialized trees, treelets and shrubs (Appendix 1). There was no difference on proportions in all situations (Monte Carlo, $p > 0.05$).

DISCUSSION

The five families with the largest number of species in the understory were Rubiaceae, Myrtaceae, Rutaceae, Fabaceae and Euphorbiaceae, which are among the most common families reported for SSF (Oliveira-Filho & Fontes 2000). The lower density of small plants under deciduous canopies may result from greater sapling or seedling mortality in these areas due to concentrated litter deposition under deciduous and semidecidous trees (Morellato 1991). Litter deposition may cause mechanical damage on seedlings and saplings (Clark & Clark 1991) or inhibit germination through the release of toxic or allelopathic compounds (Facelli & Picket 2001) and interception of light (Vázquez-Yanes et al. 1990). In gap environments, for instance, litter may prevent light to reach seeds in the soil disturbing germination of light-sensitive seeds (Eriksson 1995, Scariot 2000). Alternatively, if litter layer under deciduous trees increase soil humidity (Sayer 2006, Xu et al. 2013) this could enhance saplings survival rather than decrease, and we would expect to find greater density of plants under deciduous canopies, not under evergreen as we found. In this way our results are in agreement with the idea that, despite a possible positive effect of litter deposition on plant development - due to greater nutrient input, attenuating extreme changes in temperature and humidity or keeping soil moisture for longer - in most cases they are negative effects (Xiong & Nilsson 1999). Indeed, in studies carried in this same forest and in others SSFs, harmful effects of litter to plant regeneration was recorded and emergence of seedlings was enhanced when the litter layer was removed (Santos & Válio 2002, Portela & Santos 2009). The fact that we did not find greater density under evergreen trees for large plants as well, seems to indicate that, as plants grow, this pattern (greater density under evergreen trees) disappears through the time, as occur in environments where facilitative effects of nurse trees stop and understory plants start to compete with focal or surrounding trees (Valiente-Banuet et al. 2001).

Some studies show that the way that treefall gaps contribute to species diversity is through the "density effect" and not because they are favorable regions for regeneration of species with different light requirements (Denslow 1995, Hubbell et al. 1999). This idea postulates that, since there is greater juvenile density on gap areas when compared to closed canopy understories, there are more chance of these plants belong to a higher number of species, so richness is higher (Hubbell et al. 1999). That greater vegetation density is possible due to higher light entrance in treefall gaps. Deciduousness gaps, however, did not show higher plant density, instead, these areas have lower plant density when considering only small plants and present the same density of evergreen when considering large plants. Then, the way that deciduousness gaps contributes to species diversity in SSF is different from how treefall gaps do. The fact of species richness between canopies be the same for all DSH categories but the Simpson index under deciduous canopies be higher when considering small plants, means that the effects of canopy phenology on understory plant community is on abundance distribution of species, not on the total number of species that can inhabit these two types of understories. So, it is possible that the way that canopy gaps contribute with maintenance of diversity in SSF is reducing the dominance of some species.

Observing Fig. 5 we can also see that, after a defined value, about 250 individuals, species richness of small plants still increase, while for large plants richness reaches the asymptote. This may be explained by the fact that among small plants there are individuals that belong to species that never will reach overstory forest, resident species, and also there are saplings of overstory trees, transient species (Gilliam et al. 1994, Polisel et al. 2014). On the other hand, among large plants, most of trees belong only to adult transient species, then, potential species richness of small plants are greater than potential species richness of large plants. Still comparing small plants with large plants, it is possible to observe that individuals density of small plants is greater than individuals density of large plants (Fig. 4). This characteristc may be related to smaller trunk diameter of small trees, allowing a greater number of individuals per area. Also, many understory species (resident species) from SSFs exhibit vegetative propagation (Castellani 1986, Martins et al. 2002, Rodrigues et al. 2004), which may increase their aggregation potential.

The fact that dissimilarity of species is the same between understories indicates that there is no group of species that occur exclusively or in greater abundance under deciduous canopies than in evergreen canopies. It is possible that others features of focal and surrounding trees, such as different crown architectures (Montgomery & Chazdon 2001), leaf chemical compounds (Kraus et al. 2003) and root structure (Oliveira et al. 2005) also impact the environment where understory plants are developing. Then, seems like focal tree leaf phenology is not a predominant factor and do not impact SSF species composition.

Different from expected according to deciduousness gaps hypothesis, light-demanding species and individuals proportion is not greater under deciduous canopies both for small and large trees. This is in agreement with our data of hemispherical photos, that supports that canopy openness is the same under all phenological categories (Chapter 1). Souza et al. (2014), studying a SSF fragment, found greater proportion of light-demanding species (≈ 40 %) and individuals (≈ 30 %) in comparison to shade-tolerant species (≈ 25 %) and individuals (≈ 15 %) under deciduous canopies for large plants. In contrast, our results show similar proportion of light-demanding species (≈ 40 %) and individuals (≈ 20 %) for large plants under deciduous and evergreen canopies. This result may be explained by several, not exclusive, reasons. For instance, differences on successional category classification are expected among SSFs since trees may exhibit several ecological behaviors depending on the site analyzed and belowground resources availability

(Walters and Reich 1997, Gandolfi 1995). This characteristic is related to the fact that trees must survive to a variety of light regimes during their broad life time (Lieberman et al. 1989), allowing that light-demanding and shade-tolerant trees, even if not in optimal conditions, are able to develop along a variety of light regimes (Wright et al. 2003, Silvestrini et al. 2007). Another consideration is that Souza et al. (2014) did not measured light in their study area, so we can not affirm that in their area there are light increment under deciduous canopies.

All differences on plant structure between canopies phenology detected here, Simpson index and understory individuals density, were significant only when we considered small plants. For large plants we did not find differences on Simpson index, understory individuals density, proportion of light-demanding species and species dissimilarity across canopies phenologies. In this way, we conclude that current canopy do not affect composition and structure of large plants. Even so, our results indicate that focal tree leaf phenology affect plant community structure in SSF: there is lower density and dominance of small plants under deciduous cenopies. A temporal monitoring of the understory individuals would allow us to understand if we do not see the response observed for small plants on large plants because those patterns gradually disappear as plants grow and reach high portions of forest canopy; or if when current large plants established, canopy composition was different and now we can not detect the patterns. Anyway, since germination, seedling recruitment and survival are critical bottlenecks for tree population dynamics and play central roles in shifts in species distributions (Gerhardt 1996, Grubb 1977), even if these patterns observed for small plants disappear through the time, they may impact chances of plant establishment and development, then changing future structure of SSFs.

Plant-plant interactions can be modified by external drivers like climate change (Soliveres et al. 2015) and land use change (Sala et al. 2000). Since there is strong relation between leaf phenology and climate on seasonal environments (Reich et al. 2004), if one type of leaf phenology strategy be favored, as already considered for others ecosystems (Aerts 1995, Bonan 2008), this shift may modify structure and composition of understory plants, altering SSF dynamics.

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Capítulo III - Deciduousness gaps affect diameter increment of understory trees in Seasonal Semideciduous Forests?

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ABSTRACT

Understanding patterns of tree growth rate and their relation with variation in light availability is a crucial approach to comprehend forest dynamics. Seasonal Semideciduous Forests (SSF) are characterized by the alternation of a moist and a dry season, the latter resulting in about 30 to 50 % of canopy trees losing their leaves. Deciduousness gaps generated by the leaf loss may modify the understory light conditions under deciduous trees, which will present increased levels of diffuse irradiance at soil level, very similar to the increase obtained by treefall gaps. However, most of deciduousness gaps occur during the dry season, when moisture conditions is unfavorable to the growth of tropical trees, resulting in a trade off, where light at soil level is increased, but only during the dry season when water is limiting. We expect that light increment brought by deciduousness gaps will favor growth of tree species able to deal with drought. We also expect that light-demanding trees will be favored by light increment under deciduous trees and will present greater growth rates in this period compared to shade-tolerant trees. We installed dendrometers bands on 63 woody individuals growing under the canopy of deciduous and evergreen trees and measured their growth for two years each three months. We did not find differences in tree growth rate of trees under deciduous and evergreen canopies even when we separated them by successional categories. This result may be due to deciduousness occur during the dry season, when light increment occurs during water supply shortage, resulting in unfavorable conditions for plants growth in tropical forests. We conclude that deciduousness does not affect growth of understory trees in SSF.

Key-words: Atlantic Forest, Brazil, Canopy openings, Growth patterns, Light-demanding trees, Seasonal drought, Shade-tolerant trees.

INTRODUCTION

Tropical forest geographical extent is decreasing quickly due to intense land use change (Ribeiro et al. 2009) and may be even more threatened with global climate change (IPCC 2014). The Atlantic Forest is a biodiversity hotspot ecosystem now with less than 15% of its vegetation cover remaining (Mittermeier et al. 1999, SOS Mata Atlântica & INPE 2015) and the majority of the remaining fragments (number of fragments) are located at private areas, not public nature reserves (Brancalion et al. 2015). Seasonal Semideciduous Forest (SSF) is a phytophysiognomy of the Atlantic Forest Domain that is located in areas not close to the coast (Oliveira-Filho & Fontes 2000). They receive less annual rainfall and are submitted to an annual cycle of a dry season and a moist season (Oliveira-Filho & Fontes 2000). During the dry season, about 30 to 50 % of SSF trees lose their leaves total or partially and may remain leafless from one to twenty weeks, depending on the species (Gandolfi et al. 1999).

In evaluating canopy openness of deciduous, semideciduous and evergreen canopies, an indirect measure of sunlight that reach forest understory, we did not find differences in understory light regime among phenological groups (Chapter 1). However, because we took photos at 1 m height, plants taller than that may be exposed to deciduousness gaps light regime not captured by our method. Deciduousness gaps hypothesis states that leaf loss of deciduous plants during the unfavorable season causes a canopy openness beneath some trees generating higher light incidence on the soil during the unfavorable season (Gandolfi 1991), with values of photosynthetic photon flux density (PPFD) similar to areas of treefall gaps and are named "deciduousness gaps" (Gandolfi et al. 2007, Gandolfi et al. 2009). The annual recurrence of periods with more light, alternate with periods with less light is the main characteristic of the deciduousness gaps (Gandolfi 2000).

Light is a very restrictive resource for plants inside the shaded understory of tropical umid forests, limiting the maximum potential metabolic rates of understory plants (Chazdon et al. 1996). Canopy and height-structured competition for light also are considered the most important process determining forest dynamics by affecting tree development and mortality (Purves et al. 2008). From seedlings to saplings and adult trees, low light levels strongly reduces plant development (Clark & Clark 1999; Brienen & Zuidema 2005, Clark & Clark 1999). Decreasing of red to far-red light ratio, especially in light-demanding trees, may affect morphological features, like stem elongation and root–shoot ratios (Turnbull 1991). Greater light availability in areas under deciduous canopies could be a window of opportunity to understory plants. This condition, however, occurs during the winter time, a period of the year where temperatures are lower and the moisture conditions are unfavorable for the growth of plants in tropical seasonal forests (Mulkey & Wright 1996). This characteristic may restrict the potential advantage of light increment for plants under deciduous canopies, restricting the favorability of canopy openness in this period in SSF. Thus we expect that species that will be potentially favored by light increment of deciduouness gaps will be able to cope with reduced rainfall.

Intra-annual stem radius variation is a crucial measure to understand tree's behavior related to changes in environmental conditions throughout the year, specially in seasonal ecosystems (Bouriaud et al. 2005, Deslauriers et al. 2007). We address here several objectives related to seasonality and the role of canopy phenology on tree growth. We expect that if an ecological group within the trees of SSF can cope with the water shortage and are not affected by reduced rainfall and temperatures during the winter time in SSF, this group will present greater growth rates under deciduous canopies when compared to this same group of species growing under evergreen canopies. Also, although we expect that some species will present an increase in growth rates due to light availability under deciduous trees, we expect that the greatest increase in growth rates for all trees will occur during the rainy season, as shown by other studies that found positive relations between precipitation and tree growth (Borchert 1998, Vieira et al. 2004). Finally, once tropical rainforest trees can be grouped into functional groups that explain their growth performance in different light conditions (Silva et al. 1995, Clark & Clark 1999, Poorter et al. 2010), we will try to determine if light-demanding and shade-tolerant trees of SSF have different growth rates during the period of deciduousness gaps. We expect that light-demanding trees will present a greater growth rate under deciduous canopies when compared to shade-tolerant trees, due to higher light availability in these places (Gandolfi et al. 2007). The goals of this study are: (1) To investigate if tree growth rates differ throughout the seasons of the year under evergreen and deciduous canopies; (2) To compare if tree growth rate differs between light-demanding and shade-tolerant trees in different periods of the year; (3) To assess which factors are crucial for tree growth in SSF understory trees.

METHODS

STUDY SITE - The study was conducted at Santa Genebra Forest (22°49’22"S, 47°06’33"W), a Seasonal Semideciduous Forest with 251.77 ha located at Campinas Municipality, São Paulo State, Brazil. Climate classification is Köppen's Cwa (Subtropical with Dry Winter) with annual mean temperature 15.6ºC and annual mean rainfall 1372.0 mm. Dry season occurs from April to September with average temperature about 20.3 ºC and precipitation about 298 mm; rainy and warm season occurs from October to March, with average temperature 24.1 ºC and precipitation about 1100 mm (CEPAGRI 2016). Altitude varies between 580 and 610 m (Martins & Rodrigues 2001) with predominant soil type Rhodic Ferralsol (FAO 1974).

FOCAL TREES SELECTION - We installed the dendrometers bands in understory trees under focal trees selected as follows. First, we started the selection of focal trees arbitrarily choosing trees along a trail about 3 km away. We preferred canopy trees with no other tree crowns above it. Then, in order to avoid bias, we continued the selection of trees by shuffling a list of 100 m² plots already installed in both forest fragments (see Gandolfi 2000, A area, for more details) and selecting the tallest tree of each plot that was not covered by any other tree crown (named from here as "focal tree"). In cases when there were two possible trees to be sampled, that is, two canopy trees whose crown do not touch each other, we selected both trees in the same plot. The plots here were used more like a guide to select focal trees, in order to avoid actively seek for them and possibly bring some kind of personal bias to that choice.

DENDROMETER MEASUREMENTS - The dendrometer bands was made using the method of Liming (1957). We attached the bands in understory trees under focal trees selected as described above in all understory trees > 5 cm DBH (Diameter at Breast Height) at 1.30 m height of the stem regarding to the soil. Dendrometer bands are an useful tool to make frequent and consistent measurements of tree growth, providing a good measure of individuals performance under distinct environmental conditions (Rossi et al. 2006, Keeland & Young 2014). Among its advantages, multiple measurements made through the time (days, months or years) will be always made at exactly the same position of the trunk (Keeland & Young 2014). Also, they are easy to install, have low costs and cause no damage to the tree trunk and cambium (Keeland and Sharitz, 1993).

Tree growth rate of understory trees was measured each three months always in the last week of the selected month (February, May, August and November) during two years using a digital caliper. After installing the dendrometers we wait three months to do the first measure, period for dendrometer fitting (Keeland and Sharitz 1993, Silva et al. 2003). We took measures from May 2014 to February 2016. All measurements in tree diameter were calculated as change in the circumference divided by π.

Throughout the months some dendrometers were broken or warped due to branches fall and other unkown causes. Another sources of sampling loss was the natural death of trees, mainly due to strong winds and storms in the summer, and the "absorption" (growth of wood over the bands) of the dendrometers by two of our trees (*Alchornea glandulosa* Poepp. and *Pombalia atropurpurea* (A.St.-Hil.) Paula-Souza) turning them worthless.

CLIMATIC CONDITIONS - Weather variability was high during the two years of our study. To characterize local conditions we used data from an institution of the state government São Paulo, CIIAGRO Automatic Weather Station -22º49'07.40" - 47º03'43.64", (CIIAGRO 2016; Appendix 3).

DATA ANALYSIS - In spite of the fact that deciduousness in SSF may extend over six months, from May to October, leaf loss in the studied forests are mostly concentrated between the months of June and August (Morellato 1991). So, we defined the deciduousness gaps phase as the time between June and August and performed a Monte Carlo test to compare tree growth rate of trees under deciduous and evergreen canopies during this period. We also used Monte Carlo analysis to compare annual growth of trees separated by successional categories and canopy leaf phenology.

In order to compare the relative contribution of predictor variables on the tree growth rate (perimeter growth each three months), linear models were fitted to the data (Appendix 1, Table 2). We used seasons (intervals of three months), canopy phenology, successional categories of understory trees, accumulated precipitation, number of days without rain, mean minimal and mean maximum temperatures as our predict variables and year and individuals as repeated measures (random effect). We choose the most parsimonious model through stepwise algorithm using the Akaike Information Criterion analysis (Legendre & Legendre 1998). The simple model was subsequently complicated by step-wise addition of variables and the model with the lowest Akaike’s information criterion (AIC) value was selected (Zuur et al. 2009). Models were fitted using maximum likelihood (Pinheiro & Bates 2006) using the packages "*car*" (Fox & Weisberg 2011), "*lattice*" (Deepayan 2008), "*lme4*” (Bates et al. 2015) and "bbmle" (Bolker & R Development Core Team 2016). Monte Carlo tests were made using "asbio" package (Aho 2016). All analyses were made using R environment for statistical computing (R Core Team 2015).

RESULTS

We measured 29 understory trees growing under deciduous canopies belonging to 19 species; and 30 understory trees growing under evergreen canopies belonging to 15 species (Figure 1, Appendix 1). Species that show highest growth values in diameter (> 0.3 mm per quarter) was *Actinostemon klotzchii* (Spreng.) Müll.Arg., *Alchornea glandulosa* Poepp., *Cecropia hololeuca*

Miq., *Esenbeckia leiocarpa* Engl., *Pachystroma longifolium* (Nees) I.M.Johnst, *Piptadenia gonoacantha* (Mart.) J.F.Macbr. and *Urera baccifera* (L.) Gaudich ex. Wedd.

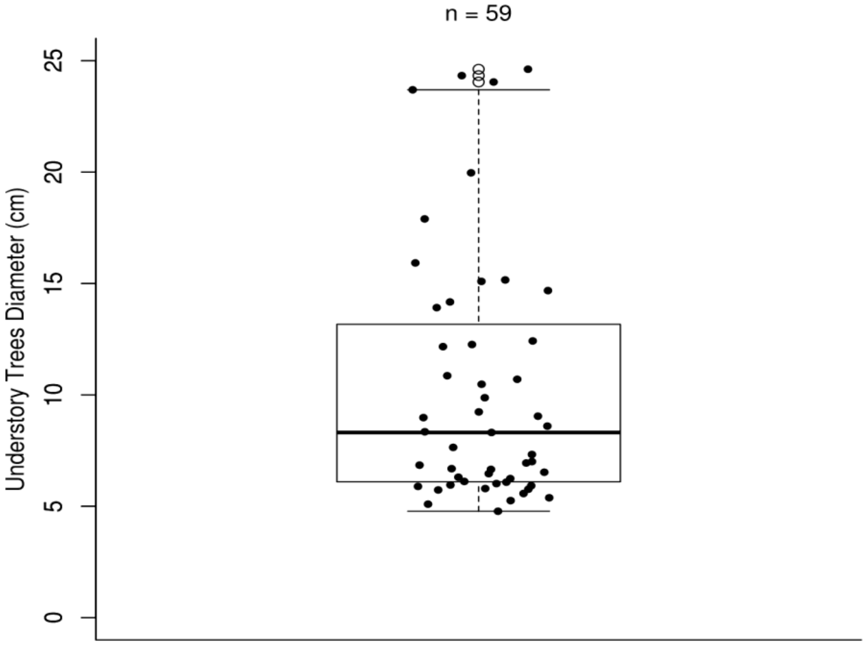

Figure 1: Initial understory trees diameter distribution (first measure in February 2014). Black dots represent each one of understory trees (n). Boxes include second and third quartiles, inner and outer fences are defined by interquartile ranges and circles represent outliers.

Trees under deciduous canopies do not exhibited differences in growth rates when compared to trees under evergreen canopies during the period of deciduousness gaps (Monte Carlo, $p = 0.24$). The models that best explained tree growth took into account tree successional category, accumulated rainfall and mean minimum temperature separately (Appendix 2, Table 2). The greatest growth rates occurred during the wet season, represented by February (Fig 1). We also performed a model that took into account the identity of understory and canopy species in order to verify if species-specific relations would be influencing tree growth, but we did not find relations (data not shown).

Annual growth rates were the same for trees under evergreen and deciduous canopies in both years (Monte Carlo, $p > 0.05$, Fig. 3A), but when we separated trees by different successional categories, light-demanding trees presented higher annual diameter increment than shade-tolerant trees in 2015 under the two canopy categories (Monte Carlo, $p < 0.05$, Fig. 3B). In 2014 annual growth was the same for light-demanding and shade-tolerant trees. Also, when we compared growth between years, both light-demanding and shade-tolerant exhibited greater growth rates in 2015 compared to 2014 under both canopy categories (Monte Carlo, $p < 0.05$).

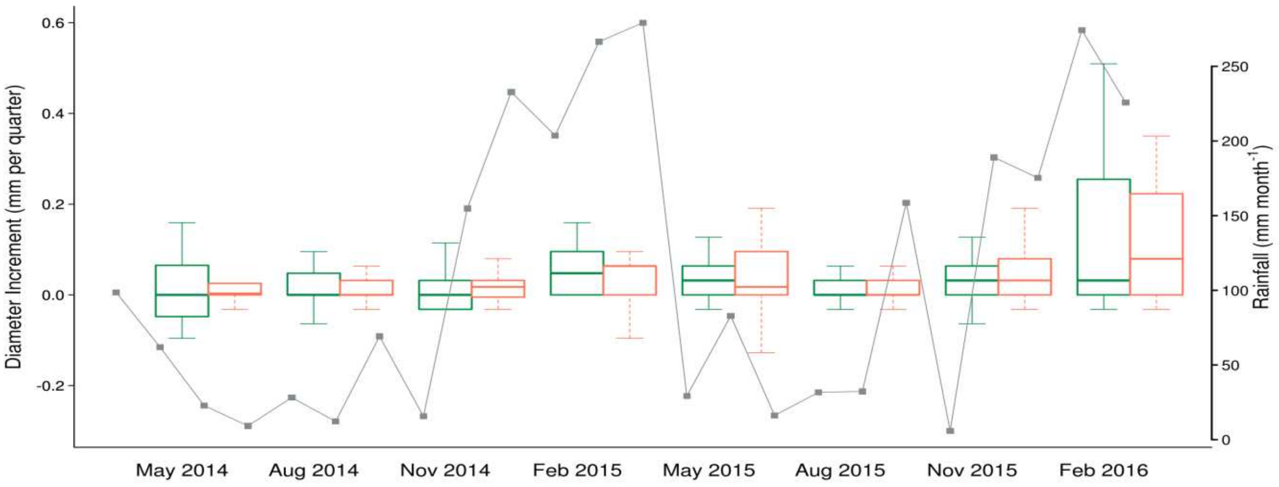

Figure 2: Distribution of diameter increment (mm per quarter) for trees under evergreen (green boxes) and deciduous (orange boxes) canopies. Grey lines and squares show the accumulated precipitation per month. Boxes include second and third quartiles, inner and outer fences are defined by interquartile ranges and thick solid black lines represent median.

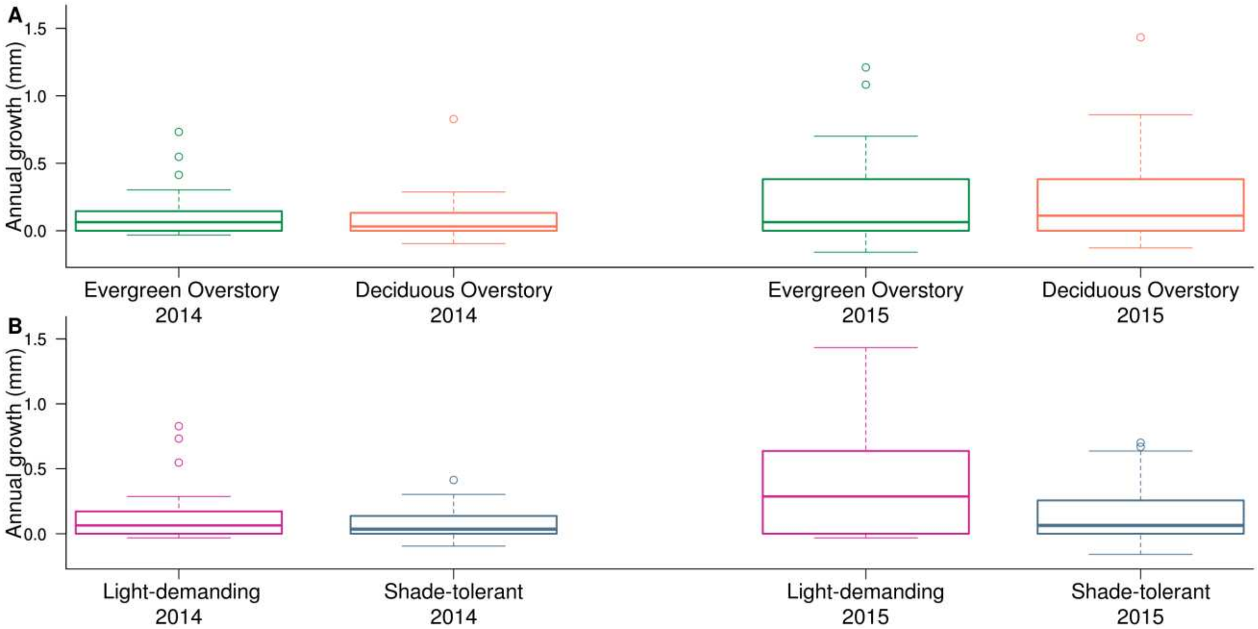

Figure 3: Annual diameter increment (mm) of understory trees separated by canopy phenology (A) and annual diameter increment (mm) of understory trees separated by successional categories (B). Boxes include second and third quartiles, lower vertical lines represent first quartile, upper vertical lines represent the fourth quartile, thick solid black lines represent median and circles represent outliers.

DISCUSSION

Tree growth rate during the deciduousness gaps was the same under evergreen and deciduous canopies and, even when we separated trees by successional categories, we found similar growth values in this period. Annual growth of trees under evergreen and deciduous canopies was the same in both years and supports the fact that there is no period when trees present differential growth growing under one or another type of canopy phenology. These results may indicate that, as observed for trees up to 1 m height (Chapter 1), light availability in upper layer understory is the same under evergreen and under deciduous focal trees. Another explanation is related with reduced temperatures and rainfall during the period of deciduousness gaps, which may prevent trees from benefiting from greater light availability in deciduous understories. Deciduousness occurs during a period of the year where temperatures and moisture conditions are unfavorable for plant's growth in tropical forests (Mulkey & Wright 1996, Bréda et al. 2006).

In agreement with this result, we found that accumulated precipitation in each quarter is one of the best predictors of understory tree growth in SSFs (Appendix 2, Table 2). Several studies also found positive relation between stem increment and water supply in tropical forests with some degree of seasonality (Vieira et al. 2004, Brienen & Zuidema 2005, Vlam et al. 2014, Wagner et al. 2014). Evolutionary history of species living in seasonal environments may have selected species that grow in the period of water availability, otherwise they could die due to causes related to water stress, like embolism (Sperry & Tyree 1988). Therefore, our results support that tree growth patterns in SSFs have positive relationships with periods with greater levels of precipitation, as reported for others tropical forests (Lisi et al. 2008, Rozendaal & Zuidema 2011, Vlam et al. 2014, Blagitz et al. 2016). In this way, water availability, and not light, is the primary limiting factor for SSF tree growth.

Among the variables that best explained understory tree growth in SSF, successional categories had the highest weight, followed by mean minimum temperature and accumulated rainfall. Tree classification in light-demanding and shade-tolerant are related to species performance under different light conditions. This classification predicts that pioneer or light-demanding trees are related to functional traits like greater growth rates when young, low wood density, small seeds and shade intolerance, as opposed to shade-tolerant species that present lower growth rates, high wood densities and investment in durable structures that allows them to survive longer periods (Muller-Landau et al. 2004, Sánchez-Gomez et al. 2006, Poorter et al. 2010). In this study we were able to detect greater total annual growth rates of species classified as light-demanding under both types of canopy phenology. In this way, greater tree growth for light-demanding understory species in SSF are not related to the phenology of the canopy tree under which they grow. In other words, we did not find support to the deciduousness gap hypothesis. Also, the greatest growth rates obtained for all species, including both light- and shade-demanding species, occurred during the moist season, when overstory trees are full of leaves and canopy openness values are the lowest (Chapter 1). Our results are in agreement with studies that support that light-demanding trees grow faster than shade-tolerant trees both under deep shade and high light environments (Bloor & Grubb 2003, Sánchez-Gomez et al. 2006).

Meanwhile, it should be noted that annual growth of light-demanding trees was higher than annual growth of shade-tolerant trees only in 2015, when drought period was less intense than 2014 (Appendix 3). In 2014, when dry season lasted longer, total annual rainfall was low and a drought has occurred in February, annual growth of light-demanding and shade-tolerant trees were similar. So, potentially, light-demanding species may present greater growth rates than shade-tolerant species, as found by other studies in SSF (Lisi et al. 2008, Blagitz et al. 2016), but this will happen only if water supply is not imposed as a limiting factor, as in 2015. This result indicates that if changes on rainfall patterns materialize and dry seasons at tropical forests become more frequent and durable (IPCC 2014), trees growth will be affected and, as a consequence, the role of SSF in carbon storage may decline.

Temperature is also an important driver of tree growth rate (Way & Oren 2010). We found greater growth rates in the period of greatest month mean minimum temperatures. Other studies found negative correlation between tree growth and increment in annual daily mean minimal temperatures (Feeley et al. 2007) or increasing nighttime air temperatures (Clark et al. 2003). Trees respond positively to increasing temperatures until it exceeds their thermal optimum growth (Doughty & Goulden 2008). If temperatures continuing to rise this may lead to a reduced tree growth in the future (Clark 2004, Way & Oren 2010).

In this study we found that phenology of canopy trees do not affect growth of understory trees. Also, we found that mean minimum temperature, successional categories and rainfall are among the main drivers of tree growth in SSF. When water intake is regular, as in 2015, trees can grow twice the amount of dry years. However, when water supply is insufficient, division into successional categories makes differences between guilds irrelevant, since shade-tolerant and light-demanding trees do not differ in annual growth due to water shortage. Although we have not found greater growth rates for understory trees with DBH ≥ 5 cm under deciduous trees, future studies may evaluate growth dynamics of seedlings and saplings under both types of understories. This may be important to assess because even a small period of fast growth of a set of young trees may disproportionately contribute to the population growth of these species (Zuidema et al. 2009) and, consequently, affect trees community dynamics.

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Considerações Finais

A dinâmica sazonal da fenologia foliar das árvores na Floresta Estacional Semidecídua promove um incremento de luz generalizado no sub-bosque florestal durante a estação seca. Esse aumento da luz no sub-bosque não ocorre somente sob árvores decíduas ou semidecíduas, mas também sob a copa de árvores sempre verdes. Este resultado pode ser decorrente da plasticidade fenotípica apresentada por indivíduos de uma mesma espécie ou, como observado neste estudo, ainda que com baixo poder de explicação, devido à influência da densidade de árvores sob a árvore focal. Mesmo sem observar diferenças na abertura de dossel entre fenologias, encontramos diferenças na estrutura da comunidade arbustivo-arbórea de plantas pequenas (DAS < 5 cm). A menor densidade de plantas pequenas nas áreas de clareiras de deciduidade pode ser decorrente da intensa queda foliar que ocorre sob dosseis decíduos na estação seca, o que pode causar danos mecânicos às plântulas e plantas jovens (Santos & Válio 2002, Portela & Santos 2009) e uma maior mortalidade, acarretando em uma menor densidade de plantas pequenas nesses locais. A menor dominância de espécies observada sob dosseis decíduos (calculada pelo Índice de Simpson), por sua vez, pode ser consequência da menor densidade de plantas nessas áreas. Por fim, não encontramos maior proporção de indivíduos e espécies pioneiras sob copas decíduas quando comparado às copas sempre verdes, o que seria esperado caso essas áreas contassem com períodos recorrentes de maior quantidade de luz.

Em relação às taxas de incremento em diâmetro para árvores em sub-bosques sob dosseis decíduos em comparação com sempre verdes, não encontramos diferenças nem mesmo quando consideramos somente árvores heliófilas. Este resultado parece corroborar nossas observações de que o incremento de luminosidade em FES não ocorre somente sob árvores decíduas, pois nesse caso esperaríamos que algumas espécies de árvores apresentassem maior incremento em diâmetro sob árvores decíduas na estação seca, pois se beneficiariam deste incremento de luminosidade. Por outro lado, é possível que, mesmo com maiores níveis de luminosidade, a restrição hídrica durante o período de deciduidade não permita que plantas se beneficiem do incremento de luz, uma vez que a precipitação é uma das variáveis que mais explicam o incremento em diâmetro de árvores de sub-bosque em FES, de acordo com nossos resultados do terceiro capítulo.

As clareiras de deciduidade só foram espaços onde a estrutura da comunidade arbustivo-arbórea ocorre de modo diferente em relação a sub-bosques sob dossel sempre verde quando consideramos as árvores pequenas (DAS < 5 cm). Mesmo assim, uma vez que germinação e estabelecimento são fatores chave na montagem de comunidades de plantas (Grubb 1977), a maior quantidade de plantas estabelecidas em sub-bosques sempre verdes poderá alterar as chances de desenvolvimento das plantas nesses locais alterando a dinâmica das Florestas Estacionais Semidecíduas. Já foi sugerido que mudanças globais climáticas e no uso da terra poderão favorecer um tipo de estratégia fenológica em plantas em detrimento de outras (Aerts 1995, Reich 1995, Bonan 2008). Além do que isso possa acarretar em termos das chances das próprias espécies de dossel se estabelecerem, alterações na proporção de árvores pertencentes a cada tipo de fenologia foliar poderão impactar a estrutura futura das plantas do sub-bosque em FES.

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Appendix 1. References used to determine leaf fenology of tree species at SG and RC forests fragments, located in **Campinas Municipality, São Paulo State, Brazil.** Deciduous species = D, semideciduous species = S, evergreen species = E, non-classified species = NC.

Family/Species	**Leaf Phenology Considered**	**Deciduous**	**Semideciduous**	**Evergreen**	**Voucher used by this study as a taxonomic reference for each species**
ACANTHACEAE					
Ruellia brevifolia (Pohl) C.Ezcurra.	E			1	UEC30401
ANACARDIACEAE					
Astronium graveolens Jacq.	D	2			UEC066793
ANNONACEAE					
Annona sylvatica A.St.-Hil.	E		3	2	UEC136905
Guatteria australis A.St.-Hil.	E			2,4	UEC149097
APOCYNACEAE					
Aspidosperma polyneuron Müll.Arg.	E			1,2	UEC78273
Aspidosperma ramiflorum Müll.Arg.	S	2	1	4	UEC136981
ARECACEAE					
Syagrus romanzoffiana (Cham.) Glassman	E			2,5	UEC118340

ASTERACEAE					
Eupatorium sp	NC				
Vernonanthura divaricata Less.	D	1,4	2		UEC136938
BORAGINACEAE					
Cordia ecalyculata Vell.	E			1,2	UEC172306
Cordia sellowiana Cham.	S		2		UEC097816
CANNABACEAE					
Celtis iguanaea (Jacq.) Sarg.	D	1	2		UEC168891
CARDIOPTERIDACEAE					
Citronella paniculata (Mart.) Howard	NC				UEC62736
CARICACEAE					
Jacaratia spinosa (Aubl.) DC.	D	1,2			UEC154005
CELASTRACEAE					
Maytenus aquifolia Mart.	E			1,6	UEC45528
Maytenus floribunda	NC				
Maytenus gonoclada Mart.	D	5			UEC88165
CHRYSOBALANACEAE					

Hirtella hebeclada Moric. ex DC.	E			1,5	UEC118341
COMBRETACEAE					
Terminalia glabrescens Mart.	D	7			UEC126557
CONNARACEAE					
Connarus regnellii G.Schellenb.	NC				UEC176767
ELAEOCARPACEAE					
Sloanea hirsuta (Schott) Planch. ex Benth.	E			2,5	UEC071383
EUPHORBIACEAE					
Actinostemon concolor (Spreng.) Müll.Arg.	E			8	UEC115490
Actinostemon klotszchii *(Didr.) Pax*	E			8	UEC46741
Alchornea glandulosa Poepp.	D	4		2	UEC173086
Croton floribundus Spreng.	S		1,2		UEC108502
Croton piptocalyx Müll.Arg.	D	4	2		UEC110368
Gymnanthes edwalliana Pax & K.Hoffm.	S		8		UEC78268
Gymnanthes serrata Baill. ex Müll.Arg.	D	9,4			UEC79041
Pachystroma longifolium	E			1,2	UEC4945

(Nees) I.M.Johnst.					
Philyra brasiliensis Klotzsch	S		8		UEC115029
FABACEAE					
Calliandra foliolosa Benth.	E			8	UEC115492
Centrolobium tomentosum Benth.	D	2,4			UEC168924
Holocalyx balansae Michx.	E			4	UEC61799
Hymenaea courbaril L.	S	1	2,6		UEC115049
Inga marginata Willd.	E		2	1,4	UEC47038
Inga vera subsp. Affinis (DC.) T.D.Penn.	E			10	UEC93355
Luetzelburgia guaissara Toledo.	D	1			UEC155241
Machaerium nyctitans (Benth.) Rudd.	S		1,2		UEC061531
Machaerium stipitatum Vogel	D	4	2		UEC177902
Piptadenia gonoacantha (Mart.) J.F.Macbr.	D	1,4	2		UEC170316
Senegalia polyphylla DC.) Britton & Rose.	D	1,2			UEC168923
Senegalia riparia Kunth	S		8		UEC168767
Sweetia fruticosa Spreng.	D	2			UEC177897
LAURACEAE					
Cryptocarya aschersoniana Mez	E			2	UEC155270

Endlicheria paniculata (Spreng.) J.F.Macbr.	E			4,5	UEC155247
Nectandra grandiflora Nees & Mart. ex Nees	E			2,5	UEC155251
Nectandra oppositifolia Nees	E			5,11	UEC126545
Ocotea beulahiae Baitello	E			4	UEC62096
Ocotea bicolor	E			8	
Ocotea corymbosa (Meisn.) Mez	E			1,4	UEC156103
Ocotea odorifera (Vell.) Rohwer.	E			8	UEC155190
LECYTHIDACEAE					
Cariniana estrellensis (Raddi) Kuntze.	D	1,4			UEC169005
Cariniana legalis (Mart.) Kunt.	D	1,4			UEC169004
MALVACEAE					
Callianthe fluviatilis (Vell.) Donnel	NC				UEC28769
Ceiba speciosa (A.St.-Hil., A.Juss. & Cambess.) Ravenna	D	1			UEC063071
Guazuma ulmifolia Lam.	D	1,4	2		UEC52487
Helicteres ovata Lam.	D	1			UEC14818
MARANTACEAE					
Ctenanthe sp	NC				

MELASTOMATACEAE					
Miconia discolor DC.	E			1	UEC77980
Miconia pusilliflora (DC.) Naudin.	E			8	UEC114935
Mouriri glazioviana Cogn.	S		2		UEC115042
MELIACEAE					
Cedrela fissilis Vell.	D	1,2			UEC060856
Guarea kunthiana A.Juss.	E			4	UEC99564
Guarea macrophylla Vahl	E			1,2	UEC155137
Trichilia casaretti C.DC.	E			2	UEC155139
Trichilia catigua A.Juss.	E			1,2	UEC155297
Trichilia claussenii C.DC.	E		2	1,4	UEC155279
Trichilia elegans A.Juss.	E			1	UEC155304
Trichilia pallida Sw.	E		2	1,4	UEC11312
MONIMIACEAE					
Mollinedia elegans Tul.	E			12	UEC108580
Mollinedia widgrenii A.DC.	E		2	4	UEC168871
MORACEAE					
Brosimum glaziovii Taub.	E			2	UEC115474
Ficus guaranitica Chodat.	S		6	2	UEC99584
Maclura tinctoria (L.) D.Don ex Steud.	D	1,2			UEC149072
Sorocea bonplandii (Baill.) Bürger, Lanj. & Wess.Boer	E			2,3	UEC173106

MYRTACEAE					
Calyptranthes lucida Mart. ex DC.	E			13	UEC47468
Campomanesia guaviroba	E	2		4	
Eugenia acutata Miq.	S		2		UEC168948
Eugenia excelsa O.Berg.	NC				UEC169292
Eugenia involucrata DC.	E	2		14	UEC127286
Eugenia leptoclada O.Berg.	E			8	UEC115483
Eugenia ligustrina (Sw.) Willd.	NC				UEC60522
Eugenia neoverrucosa Sobral	NC				UEC11751
Eugenia pyriformis Cambess.	S		2		UEC115471
Eugenia sulcata Spring.	E			2	UEC71524
Myrciaria floribunda (West ex Willd.) O.Berg.	E	2		13,4	UEC168920
Myrcia splendens (Sw.) DC.	S		7		UEC168946
Plinia cauliflora (Mart.) Kausel.	E			2	UEC126983
NYCTAGINACEAE					
Guapira opposita (Vell.) Reitz	E			1,2	UEC176949
OXALIDACEAE					
Oxalis rhombeo-ovata A.St.-Hil.	NC				UEC172332
PERACEAE					

Pera glabrata (Schott) Poepp. ex Baill.	E			2,5	UEC31082
PHYLLANTHACEAE					
Savia dictyocarpa Müll.Arg.	S		6	2	UEC118344
PHYTOLACCACEAE					
Gallesia integrifolia (Spreng.) Harms	E	1		2,4	UEC177880
Seguieria langsdorfii Moq.	D	4	2		UEC177875
PICRAMNIACEAE					
Picramnia ramiflora G.Planch.	E			7	UEC108399
PIPERACEAE					
Piper aduncum L.	E			15	UEC105860
Piper amalago L.	E			9	UEC168837
Piper glabratum Kunth	NC				UEC065606
Piper mollicomum Kunth	E			16	UEC062732
Piper ovatum Vahl.	NC				UEC168913
POLYGALACEAE					
Acanthocladus brasiliensis (A.St.-Hil.) Klotzsch ex Hassk.	NC				UEC168914
PRIMULACEAE					
Myrsine balansae (Mez)	E			8	UEC172373

Otegui					
Myrsine coriacea (Sw.) R.Br. ex Roem. & Schult.	S		7		UEC126569
Myrsine umbellata Mart.	E			2,4	UEC168939
Stylogyne pauciflora	NC				
Stylogyni warmingii Mez.	NC				UEC168961
PROTEACEAE					
Roupala montana var. brasiliensis (Klotzsch) K.S.Edwards	D	2			UEC177914
RHAMNACEAE					
Colubrina glandulosa Perkins	D	1,2			UEC169631
RUBIACEAE					
Alseis floribunda Schott.	E			8	UEC170518
Amaioua intermedia Mart.	E			5,7	UEC114937
Coffea arabica L.	E			8	UEC060654
Cordiera myrciifolia (K.Schum.) C.H.Pers. & Delprete	E			5	UEC168957
Ixora gardneriana Benth.	E			2	UEC171310
Ixora venulosa Benth.	E			1	UEC114972
Margaritopsis cephalantha Müll.Arg.) C.M.Taylor	NC				UEC65302
Psychotria carthagenensis Jacq.	E			2	UEC168952

Psychotria hastisepala Müll.Arg.	NC				UEC170520
Psychotria leiocarpa Cham. & Schltdl.	S		17		UEC170523
Psychotria myriantha Müll.Arg.	S		16		UEC168979
Rudgea jasminoides (Cham.) Müll.Arg.	E			18	UEC170507
Rudgea nodosa (Cham.) Benth.	NC				UEC170515
Randia armata (Sw.) DC.	D	9			UEC162559
RUTACEAE					
Balfourodendron riedelianum (Engl.) Engl.	D	1,4	2		UEC171081
Conchocarpus lilacinus (A. St.-Hil.) Bruniera & Groppo	E			8	UEC150743
Conchocarpus pentandrus (A.St.-Hil.) Kallunki & Pirani	NC				UEC97674
Esenbeckia febrifuga (A.St.-Hil.) A.Juss. ex Mart.	E		2	4	UEC46507
Esenbeckia leiocarpa Engl.	D	1,4	2		UEC168788
Galipea jasminiflora (A.St.-Hil.) Engl.	E			2,4	UEC97676
Metrodorea nigra A.St.-Hil.	E			2,4	UEC172218
Metrodorea stipularis Mart.	E			2,4	UEC105896
Zanthoxylum acuminatum (Sw.) Sw.	NC				UEC172188
Zanthoxylum monogynum A.St.-Hil.	NC				UEC149096

SALICACEAE					
Casearia decandra Jacq.	D	1,2			UEC154078
Casearia gossypiosperma Briq.	D	1,2			UEC173309
Casearia sylvestris Sw.	E			1,2	UEC144727
SAPINDACEAE					
Cupania vernalis Cambess.	S		2		UEC168990
Diatenopteryx sorbifolia Radlk.	D	1,4	2		UEC47258
Matayba elaeagnoides Radlk.	S		2		UEC115030
SAPOTACEAE					
Chrysophyllum gonocarpum (Mart. & Eichler) Engl.	E		2	1,4	UEC177879
SOLANACEAE					
Acnistus arborescens L.	NC				UEC188574
Solanum gnaphalocarpum Vell.	NC				UEC64740
Solanum pseudoquina A.St.-Hil.	S		2		UEC145070
Solanum swartzianum Roem. & Schult.	E		4	1	UEC060738
SYMPLOCACEAE					
Symplocos estrellensis Casar.	NC				UEC105249

URTICACEAE				
Cecropia glaziovii Snethl.	E		1,2	UEC177261
Cecropia hololeuca Miq.	E		1,2	UEC149946
Urera baccifera (L.) Gaudich. ex Wedd.	D	1,4		UEC63899
VERBENACEAE				
Lantana camara L.	NC			UEC141374
VIOLACEAE				
Pombalia atropurpurea (A.St.-Hil.) Paula-Souza	D	1		UEC55035
Schweiggeria fruticosa Spreng.	NC			UEC172621

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References used to determine successional category of tree species at SG and RC forests fragments, located at Campinas Municipality, São Paulo State, Brazil. Late secondary = LS, early secondary = ES, pioneer = P, and non-classified species = NC.

Family/Species	Successional Category Considered	Late Secondary	Early Secondary	Pioneer	Unclassified
ACANTHACEAE					
Ruellia brevifolia (Pohl) C.Ezcurra.	LS	1			
ANACARDIACEAE					
Astronium graveolens Jacq.	ES		2		
ANNONACEAE					
Annona sylvatica A.St.-Hil.	ES		2		
Guatteria australis A.St.-Hil.	LS	2			
APOCYNACEAE					
Aspidosperma polyneuron Müll.Arg.	LS	2			
Aspidosperma ramiflorum Müll.Arg.	LS	2			
ARECACEAE					
Syagrus romanzoffiana (Cham.) Glassman	ES		2		
ASTERACEAE					
Eupatorium sp	NC				

Vernonanthura divaricata Less.	P			2
BORAGINACEAE				
Cordia ecalyculata Vell.	LS	2		
Cordia sellowiana Cham.	ES		2	
CANNABACEAE				
Celtis iguanaea (Jacq.) Sarg.	P			1
CARDIOPTERIDACEAE				
Citronella paniculata (Mart.) Howard	NC			
CARICACEAE				
Jacaratia spinosa (Aubl.) DC.	P			2
CELASTRACEAE				
Maytenus aquifolia Mart.	ES		3	
Maytenus floribunda	LS	4		
Maytenus gonoclada Mart.	LS	2		
CHRYSOBALANACEAE				
Hirtella hebeclada Moric. ex DC.	LS	3		

COMBRETACEAE			
Terminalia glabrescens Mart.	P		5
CONNARACEAE			
Connarus regnellii G.Schellenb.	NC		
ELAEOCARPACEAE			
Sloanea hirsuta (Schott) Planch. ex Benth.	LS	2	
EUPHORBIACEAE			
Actinostemon concolor (Spreng.) Müll.Arg.	LS	2	
Actinostemon klotszchii *(Didr.) Pax*	LS	2	
Alchornea glandulosa Poepp.	P		2
Croton floribundus Spreng.	P		2
Croton piptocalyx Müll.Arg.	P		2
Gymnanthes edwalliana Pax & K.Hoffm.	LS	2	
Gymnanthes serrata Baill. ex Müll.Arg.	LS	2	
Pachystroma longifolium	LS	2	

(Nees) I.M.Johnst.				
Philyra brasiliensis Klotzsch	LS	6		
FABACEAE				
Calliandra foliolosa Benth.	ES		6	
Centrolobium tomentosum Benth.	ES		2	
Holocalyx balansae Michx.	LS	2		
Hymenaea courbaril L.	LS	7		
Inga marginata Willd.	LS	2		
Inga vera subsp. Affinis (DC.) T.D.Penn.	ES		1	
Luetzelburgia guaissara Toledo.	ES		2	
Machaerium nyctitans (Benth.) Rudd.	LS	2		
Machaerium stipitatum Vogel	ES		2	
Piptadenia gonoacantha (Mart.) J.F.Macbr.	ES		2	
Senegalia polyphylla DC.) Britton & Rose.	ES		1	
Senegalia riparia Kunth	P			6
Sweetia fruticosa Spreng.	LS	2		
LAURACEAE				
Cryptocarya aschersoniana Mez	ES		2	

Endlicheria paniculata (Spreng.) J.F.Macbr.	LS	2		
Nectandra grandiflora Nees & Mart. ex Nees	LS	8		
Nectandra oppositifolia Nees	LS	2		
Ocotea beulahiae Baitello	LS	1		
Ocotea bicolor	LS	7		
Ocotea corymbosa (Meisn.) Mez	ES		2	
Ocotea odorifera (Vell.) Rohwer.	LS	2		
LECYTHIDACEAE				
Cariniana estrellensis (Raddi) Kuntze.	LS	2		
Cariniana legalis (Mart.) Kunt.	LS	2		
MALVACEAE				
Callianthe fluviatilis (Vell.) Donnel	LS	1		
Ceiba speciosa (A.St.-Hil., A.Juss. & Cambess.) Ravenna	ES		9	
Guazuma ulmifolia Lam.	P			2
Helicteres ovata Lam.	P			7
MARANTACEAE				

Ctenanthe sp	NC		
MELASTOMATACEAE			
Miconia discolor DC.	LS	2	
Miconia pusilliflora (DC.) Naudin.	LS	2	
Mouriri glazioviana Cogn.	LS	10	
MELIACEAE			
Cedrela fissilis Vell.	ES		2
Guarea kunthiana A.Juss.	LS	2	
Guarea macrophylla Vahl	LS	8	
Trichilia casaretti C.DC.	LS	7	
Trichilia catigua A.Juss.	LS	2	
Trichilia claussenii C.DC.	LS	2	
Trichilia elegans A.Juss.	LS	3	
Trichilia pallida Sw.	LS	2	
MONIMIACEAE			
Mollinedia elegans Tul.	LS	7	
Mollinedia widgrenii A.DC.	LS	1	
MORACEAE			
Brosimum glaziovii Taub.	ES		4
Ficus guaranitica Chodat.	LS	9	
Maclura tinctoria (L.) D.Don ex Steud.	ES		1
Sorocea bonplandii (Baill.)	LS	7	

Bürger, Lanj. & Wess.Boer			
MYRTACEAE			
Calyptranthes lucida Mart. ex DC.	LS	11	
Campomanesia guaviroba	LS	2	
Eugenia acutata Miq.	LS	2	
Eugenia excelsa O.Berg.	LS	2	
Eugenia involucrata DC.	LS	7	
Eugenia leptoclada O.Berg.	LS	4	
Eugenia ligustrina (Sw.) Willd.	LS	1	
Eugenia neoverrucosa Sobral	LS	2	
Eugenia pyriformis Cambess.	LS	2	
Eugenia sulcata Spring.	LS	10	
Myrciaria floribunda (West ex Willd.) O.Berg.	LS	2	
Myrcia splendens (Sw.) DC.	ES		10
Plinia cauliflora (Mart.) Kausel.	LS	7	
NYCTAGINACEAE			
Guapira opposita (Vell.) Reitz	ES		2

OXALIDACEAE				
Oxalis rhombeo-ovata A.St.-Hil.	NC			
PERACEAE				
Pera glabrata (Schott) Poepp. ex Baill.	LS	4		
PHYLLANTHACEAE				
Savia dictyocarpa Müll.Arg.	LS	2		
PHYTOLACCACEAE				
Gallesia integrifolia (Spreng.) Harms	LS	2		
Seguieria langsdorfii Moq.	ES		2	
PICRAMNIACEAE				
Picramnia ramiflora G.Planch.	LS	12		
PIPERACEAE				
Piper aduncum L.	P			8
Piper amalago L.	P			2
Piper glabratum Kunth	NC			
Piper mollicomum Kunth	P			13
Piper ovatum Vahl.	NC			
POLYGALACEAE				

Acanthocladus brasiliensis (A.St.-Hil.) Klotzsch ex Hassk.	LS	1		
PRIMULACEAE				
Myrsine balansae (Mez) Otegui	ES		6	
Myrsine coriacea (Sw.) R.Br. ex Roem. & Schult.	P			10
Myrsine umbellata Mart.	ES		2	
Stylogyne pauciflora	NC			
Stylogyne warmingii Mez.	NC			
PROTEACEAE				
Roupala montana var. brasiliensis (Klotzsch) K.S.Edwards	LS	3		
RHAMNACEAE				
Colubrina glandulosa Perkins	ES		2	
RUBIACEAE				
Alseis floribunda Schott.	LS	7		
Amaioua intermedia Mart.	ES		2	
Coffea arabica L.	LS	6		
Cordiera myrciifolia (K.Schum.) C.H.Pers. & Delprete	LS	14		

Ixora gardneriana Benth.	LS	2	
Ixora venulosa Benth.	LS	2	
Margaritopsis cephalantha Müll.Arg.) C.M.Taylor	LS	1	
Psychotria carthagenensis Jacq.	LS	1	
Psychotria hastisepala Müll.Arg.	LS	15	
Psychotria leiocarpa Cham. & Schltdl.	LS	1	
Psychotria myriantha Müll.Arg.	LS	1	
Rudgea jasminoides (Cham.) Müll.Arg.	ES		3
Rudgea nodosa (Cham.) Benth.	NC		
Randia armata (Sw.) DC.	ES		10
RUTACEAE			
Balfourodendron riedelianum (Engl.) Engl.	ES		2
Conchocarpus lilacinus (A. St.-Hil.) Bruniera & Groppo	ES		1
Conchocarpus pentandrus (A.St.-Hil.) Kallunki & Pirani	LS	1	
Esenbeckia febrifuga (A.St.-Hil.) A.Juss. ex Mart.	LS	2	

Esenbeckia leiocarpa Engl.	LS	2		
Galipea jasminiflora (A.St.-Hil.) Engl.	LS	2		
Metrodorea nigra A.St.-Hil.	LS	2		
Metrodorea stipularis Mart.	LS	2		
Zanthoxylum acuminatum (Sw.) Sw.	ES		2	
Zanthoxylum monogynum A.St.-Hil.	ES		2	
SALICACEAE				
Casearia decandra Jacq.	LS	1		
Casearia gossypiosperma Briq.	LS	1		
Casearia sylvestris Sw.	P			1
SAPINDACEAE				
Cupania vernalis Cambess.	ES		2	
Diatenopteryx sorbifolia Radlk.	ES		2	
Matayba elaeagnoides Radlk.	ES		3	
SAPOTACEAE				
Chrysophyllum gonocarpum (Mart. &	ES		2	

Eichler) Engl.				
SOLANACEAE				
Acnistus arborescens L.	P			7
Solanum gnaphalocarpum Vell.	LS	1		
Solanum pseudoquina A.St.-Hil.	P			16
Solanum swartzianum Roem. & Schult.	P			2
SYMPLOCACEAE				
Symplocos estrellensis Casar.	ES		17	
URTICACEAE				
Cecropia glaziovii Snethl.	P			2
Cecropia hololeuca Miq.	P			2
Urera baccifera (L.) Gaudich. ex Wedd.	P			2
VERBENACEAE				
Lantana camara L.	P			13
VIOLACEAE				
Pombalia atropurpurea (A.St.-Hil.) Paula-Souza	LS	1		
Schweiggeria fruticosa	NC			

Spreng.

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Number of understory trees with dendrometer bands in the understory and number of focal trees at SG forest.

Family/Species	Nº of understory individuals	Nº of focal trees
ANACARDIACEAE		
Astronium graveolens Jacq.	2	5
ANNONACEAE		
Guatteria australis A.St.-Hil.	1	0
APOCYNACEAE		
Aspidosperma polyneuron Müll.Arg.	2	0
Aspidosperma ramiflorum Müll.Arg.	1	0

ASTERACEAE		
Vernonanthura divaricata Less.	1	3
CANNABACEAE		
Celtis iguanaea (Jacq.) Sarg.	1	0
CARICACEAE		
Jacaratia spinosa (Aubl.) DC.	2	1
MYRTACEAE		
Eugenia leptoclada O.Berg.	1	0
Myrciaria floribunda (West ex Willd.) O.Berg.	0	1
EUPHORBIACEAE		
Actinostemon klotzschii (Didr.) Pax	2	0
Alchornea glandulosa Poepp	4	0
Croton piptocalyx Müll.Arg.	1	6
Gymnanthes serrata Baill. ex Müll.Arg.	2	0
Pachystroma longifolium (Nees) I.M.Johnst.	8	7
FABACEAE		
Inga vera subsp. Affinis (DC.) T.D.Penn.	0	1
Luetzelburgia guaissara Toledo.	1	0
Piptadenia gonoacantha (Mart.) J.F.Macbr.	1	1
LAURACEAE		
Nectandra grandiflora Nees & Mart. ex Nees	0	1

MELIACEAE		
Guarea kunthiana A.Juss.	0	1
PHYLLANTHACEAE		
Savia dictyocarpa Müll.Arg.	1	1
PHYTOLACCACEAE		
Seguieria langsdorffii Moq.	2	1
PICRAMNIACEAE		
Picramnia ramiflora G.Planch.	3	1
RUTACEAE		
Balfourodendron riedelianum (Engl.) Engl.	1	0
Esenbeckia leiocarpa Engl.	7	7
Galipea jasminiflora (A.St.-Hil.) Engl.	10	0
Metrodorea nigra A.St.-Hil.	1	0
Metrodorea stipularis Mart.	0	2
URTICACEAE		
Cecropia glaziovii Snethl.	1	1
Cecropia hololeuca Miq.	1	0
Urera baccifera (L.) Gaudich. ex Wedd.	4	0
VIOLACEAE		
Pombalia atropurpurea (A.St.-Hil.) Paula-Souza	1	0

Appendix 2. Delta akaike's information criterion (dAICC) of the linear models.

Table 1. Delta akaike's information criterion (dAICC) of the linear models of canopy openness of trees classified as deciduous, semidecidous and evergreen across intervals of three months for both forests. Models with seasons (three months intervals), rainfall (accumulated three months), number of days without rain (without rain), mean minimum temperature (temp_min), mean maximum temperature (temp_max), phenology (phenol: deciduous, semideciduous and evergreen) and dichotomized phenology (phenol_dicot: in deciduous and evergreen).

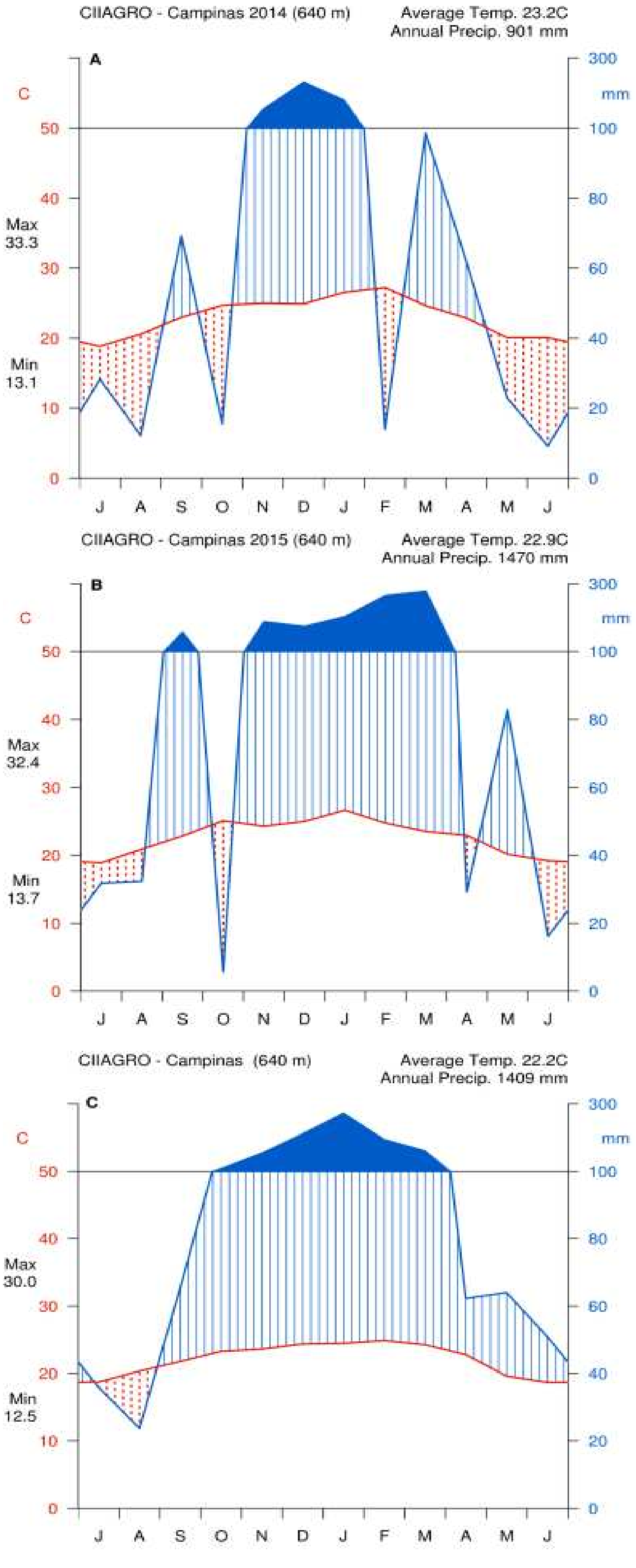
Model	**dAICc**	**df**	**Weight**
season	0.0	7	0.99
rainfall	0.0	5	< 0.001
temp_min	0.0	5	< 0.001
temp_max	0.0	5	< 0.001
without_rain	109.6	5	< 0.001
null	116.1	4	< 0.001
phenol_dicot	121.5	5	< 0.001
phenol	172.2	6	< 0.001

Table 2. Delta akaike's information criterion (dAICC) of the linear models of tree growth rate each three months at SG forest. Models with rainfall (accumulated three months), mean minimum temperature (temp_min), mean maximum temperature (temp_max) and successional categories (light-demanding and shade-tolerant).

Model	dAICc	df	Weight
succession	0.0	5	0.327
temp_min	0.3	5	0.280
rainfall	0.5	11	0.259
rainfall*temp_min	2.5	12	0.093
null	4.2	4	0.040
succession*temp_min	228.2	7	<0.001
succession*rainfall	234.2	19	<0.001

Appendix 3. Walter-Lieth climate diagrams of Campinas Municipality.

Walter-Lieth climate diagrams. Monthly average temperature (red solid line) and precipitation



(blue solid line) of Campinas Municipality based on CIIAGRO database for 2014 (A), 2015 (B) and twenty years climatic means (C).

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