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COMPREENDENDO O ESTABELECIMENTO INICIAL DE SEIS ESPÉCIES FLORESTAIS SOB GRADIENTE DE IRRADIÂNCIA EM SISTEMA SILVICULTURAL DE ENRIQUECIMENTO DE FLORESTA SECUNDÁRIA

VICTOR ALEXANDRE HARDT FERREIRA DOS SANTOS

Manaus, Amazonas
Setembro, 2019

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Sinopse:
Foram investigados, durante dois anos, os efeitos de tratamentos silviculturais sobre o estabelecimento inicial de seis espécies florestais em um plantio de enriquecimento de floresta secundária na Amazônia Central. Os efeitos foram estudados no que concerne o microclima da floresta secundária, estabelecimento inicial (crescimento, mortalidade e susceptibilidade à praga) e características fotossintéticas foliares.

Palavras chave: *Cedrela fissilis*, características funcionais, *Tabebuia rosea*, *Swietenia macrophylla*, broca das meliáceas, *Hymenaea courbaril*, crescimento de mudas de árvores tropicais, *Carapa guianensis*, *Bertholletia excelsa.*

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Resumo geral

Tratamentos silviculturais são críticos para o adequado estabelecimento inicial de espécies arbóreas plantadas em sistemas silviculturais de enriquecimento de floresta secundária. Entretanto, o nível ótimo de irradiância – obtido com intervenções silviculturais que promovem a abertura do dossel (*e.g.* refinamento) – depende das espécies que serão introduzidas. Além dos tratamentos aplicados em árvores no dossel, tratamentos no sub-bosque (*e.g.* corte do sub-bosque) reduzem a competição entre a vegetação nativa e as espécies plantadas, podendo aprimorar os efeitos da abertura do dossel. A plasticidade fenotípica é crucial para a compreensão das respostas interespecíficas à abertura do dossel durante os anos iniciais que seguem o plantio de enriquecimento. O objetivo geral neste estudo de doutoramento é compreender o estabelecimento inicial de seis espécies florestais sob gradiente de irradiância em sistema silvicultural de enriquecimento de floresta secundária. Para tanto, em março de 2017, um plantio de enriquecimento de floresta secundária foi estabelecido na Fazenda Experimental da Universidade Federal do Amazonas (FAEXP-UFAM). O experimento foi conduzido em um delineamento experimental fatorial com parcelas subdivididas (seis níveis de refinamento das árvores do dossel x dois tratamentos de corte do sub-bosque). Entre setembro e dezembro de 2016, foram aplicados seis níveis de redução de área basal via refinamento (0, 20, 40, 60, 80 e 100%) em parcelas principais de 2318 m^2 replicadas em cinco blocos. Cada parcela principal foi dividida em duas subparcelas (com e sem corte do sub-bosque), onde foram plantadas seis espécies arbóreas comerciais (*Cedrela fissilis*, *Tabebuia rosea*, *Swietenia macrophylla*, *Hymenaea courbaril*, *Carapa guianensis* e *Bertholletia excelsa*). Tratamentos silviculturais afetaram o microclima, em especial a disponibilidade de irradiância, da floresta secundária (*Capítulo 1*), e, consequentemente, o crescimento, sobrevivência e a susceptibilidade ao ataque de pragas das seis espécies (*Capítulo 2*). A variação no crescimento das espécies teve boa relação com a plasticidade das características fotossintéticas foliares (morfológicas e fisiológicas) e, portanto, pode ajudar a nossa compreensão sobre os principais mecanismos responsáveis pelas respostas de crescimento de mudas de árvores tropicais a tratamentos silviculturais no enriquecimento de florestas secundárias (*Capítulo 3*).

Palavras chave: *Cedrela fissilis*, características funcionais, *Tabebuia rosea*, *Swietenia macrophylla*, broca das meliáceas, *Hymenaea courbaril*, crescimento de mudas de árvores tropicais, *Carapa guianensis*, *Bertholletia excelsa.*

Abstract

Silvicultural treatments are critical for the suitable initial establishment of the planted tree species in secondary forest enrichment planting. However, the optimum irradiance level – obtained with silvicultural interventions that promote canopy openness (*e.g.* thinning) – rely on the introduced species. Besides silvicultural treatments at the canopy level, understory treatment (*e.g.* slashing) reduce the competition between natural and planted species and can improve canopy openness effect. The phenotypic plasticity is crucial to understand the interspecific responses to canopy openness during the early years following the planting. The principal objective in this doctoral study is to understand the initial establishment of six commercial tree species under a gradient of canopy openness in a secondary forest enrichment planting. Therefore, in March 2017, a secondary forest enrichment planting was implemented at Experimental Farm of Amazonas Federal University (FAEXP-UFAM). The experiment was conducted in a full factorial design in split-plots (canopy refinement x understory treatments). Between September and December 2016, were applied six levels of basal area reduction by canopy refinement (0, 20, 40, 60, 80 and 100%) in main plots of 2318 m^2 replicated in five blocks. Each main plot was divided into two sub-plots (with and without understory slashing) where were planted six tree species of recognized economic value (*Cedrela fissilis*, *Tabebuia rosea*, *Swietenia macrophylla*, *Hymenaea courbaril*, *Carapa guianensis* and *Bertholletia excelsa*). Silvicultural treatments affected the secondary forest microclimate, mainly light environment (*Chapter* 1), and, consequently, the growth, survival and pest attack susceptibility of the six species (*Chapter 2*). The variation in species growth had a good relationship with the plasticity of leaf photosynthetic characteristics (morphological and physiological) and, therefore can to help our understanding about the main mechanisms responsible to growth responses of tropical tree seedlings to silvicultural treatments in secondary forest enrichment planting (*Chapter 3*).

Keywords: *Cedrela fissilis*, functional traits, *Tabebuia rosea*, *Swietenia macrophylla*, Hypsipyla shoot borer, *Hymenaea courbaril*, tropical seedling growth, *Carapa guianensis*, *Bertholletia excelsa.*

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1. Introdução Geral

Nos últimos 25 anos, 195 milhões de hectares de florestas tropicais foram substituídos por outras formas de uso da terra (Keenan et al., 2015). Considerando esse cenário de degradação florestal, estima-se que metade das florestas tropicais está regenerando naturalmente em áreas que foram desflorestadas, utilizadas para determinada finalidade econômica e abandonadas na sequência (FAO, 2010; Chazdon, 2014). No Brasil, país com tendência de redução das taxas de desflorestamento, cerca de 23% da área desflorestada na Amazônia Legal até o ano de 2014 (~173.000 km^2) encontrava-se em estágio avançado de regeneração da vegetação arbórea e arbustiva, constituindo a classe de uso e cobertura do solo denominada florestas secundárias (Hansen et al., 2013; INPE, 2016).

Diante do aumento da representatividade das florestas secundárias na paisagem tropical, nas últimas décadas grande esforço de pesquisa tem sido empregado na compreensão do papel dessas florestas em fornecer serviços e bens (ITTO, 2002; Wiener, 2010; Chazdon, 2014; Schwartz et al., 2015; Bongers et al., 2015; Poorter et al., 2016). Florestas secundárias crescem rapidamente e, assim, possuem reconhecido potencial em acumular carbono na biomassa e mitigar os efeitos das elevadas concentrações de carbono atmosférico (Poorter et al., 2016). Ao mesmo tempo em que protegem o solo contra agentes erosivos, florestas secundárias são fonte de matéria orgânica e nutrientes, aprimoram a infiltração da água no solo, e reestabelecem a evapotranspiração, fundamental ao ciclo hidrológico (Guariguata e Ostertag, 2001; Sommer et al., 2003; Bruijnzeel, 2004; Zimmermann et al., 2006; Chazdon, 2014). Apesar de já ter sido definida como uma paisagem degradada (Pereira e Vieira, 2001), quando adequadamente manejadas mediante a implementação dos sistemas silviculturais, produtos florestais madeireiros podem ser explorados e produzidos em florestas secundárias (Schwartz et al., 2015; Fantini et al., 2019), com rentabilidade econômica ao silvicultor (Keefe et al., 2012).

A adoção do sistema silvicultural de enriquecimento no manejo de florestas secundárias possibilita a introdução de espécies arbóreas com reconhecido valor econômico, ecológico e social sob o dossel da floresta remanescente (Lamprecht, 1990). Nesse sistema, a abertura do dossel é fundamental para o estabelecimento inicial das espécies plantadas (ITTO, 2002; Peña-Claros et al., 2002; Romell et al., 2008; Wiener, 2010; Jakovac et al., 2012), pois, a ausência de grandes clareiras, reduz a quantidade de micro-sítios com maior disponibilidade de irradiância em florestas secundárias quando comparadas com florestas maduras (Nicotra et al., 1999; Montgomery e Chazdon, 2001; Numata et al., 2006). Geralmente, níveis intermediários de abertura do dossel, em plantios realizados em linhas ou clareiras com desbaste uniforme, são suficientes para o máximo crescimento e sobrevivência das espécies florestais plantadas, não sendo necessária a abertura de linhas com ampla largura ou desbaste excessivo (Ådjers et al., 1995; ITTO, 2002; Peña-Claros et al., 2002; Wiener, 2010; Jakovac et al., 2012; Gustafsson et al., 2016). Adicionalmente à abertura do dossel, a remoção da vegetação no sub-bosque por meio da aplicação de tratos silviculturais aumenta a disponibilidade de irradiância, reduz a competição por recursos primários e também afeta positivamente o estabelecimento das espécies (Lamprecht, 1990; Ådjers et al., 1995; Romell et al., 2008; Duclos et al., 2013). Além dos tratamentos silviculturais, aplicados no dossel ou sub-bosque, a variação sazonal da disponibilidade da irradiância também deve ser considerada no planejamento de um sistema silvicultural de enriquecimento, pois, conforme registrado por alguns autores (Chazdon e Fetcher, 1984; Rich et al., 1993), a variação intra-anual desse recurso pode divergir entre diferentes ambientes florestais (e.g. dossel, clareiras, sub-bosque).

Embora seja reconhecido o efeito positivo da abertura do dossel sobre o estabelecimento, as respostas aos tratamentos silviculturais podem variar entre as espécies (Ådjers et al., 1995; Wiener, 2010). O grau de tolerância à sombra, observado entre os grupos ecológicos, ao longo da sucessão florestal pode ajudar na seleção das espécies e níveis de abertura do dossel empregados em sistemas de enriquecimento de florestas secundárias (Bazzaz e Pickett, 1980; Swaine e Witmore, 1988). No entanto, Wiener (2010) demonstrou haver diversos padrões de resposta a um gradiente de abertura do dossel, independente do grupo ecológico da espécie, em plantio de enriquecimento na Amazônia Peruana. O melhor entendimento das respostas de sobrevivência e crescimento das plantas à abertura do dossel pode ser obtido com a divisão das espécies em grupos de plasticidade fisiológica, considerando a estreita relação entre as características funcionais e o crescimento de espécies arbóreas tropicais (Poorter e Bongers, 2006; Dos Anjos et al., 2015; Guimarães et al., 2018). As características funcionais afetam indiretamente o desempenho por meio dos seus efeitos sobre a sobrevivência, crescimento e reprodução (Violle et al., 2007) e, por isso, poderiam ser fundamentais na seleção de espécies e níveis de intervenções silviculturais em sistemas de enriquecimento.

A presente tese está estruturada em forma de três artigos científicos, apresentados, conforme as normas dos periódicos científicos aos quais foram submetidos, em três capítulos. Os capítulos contemplam, em sequência, os efeitos de tratamentos silviculturais sobre o microclima (Capítulo 1), estabelecimento inicial de seis espécies florestais comerciais (Capítulo 2) e a relação do crescimento com características fotossintéticas foliares, para subsidiar a seleção de espécies (Capítulo 3), em um plantio de enriquecimento de floresta secundária na Amazônia Central.

No Capítulo 1, foram avaliadas as alterações no microclima de uma floresta secundária submetida a tratamentos silviculturais aplicados no dossel e sub-bosque. Foi demonstrado o potencial dos tratamentos silviculturais em manipular o microclima, principalmente a disponibilidade de luz.

No Capítulo 2, foi testado como as alterações no microclima, promovidas pelos tratamentos silviculturais, influenciam o estabelecimento de seis espécies florestais de reconhecido valor econômico plantadas em um sistema silvicultural de enriquecimento de floresta secundária. Foi comprovado que os tratamentos silviculturais determinam o sucesso do estabelecimento de um plantio de enriquecimento, pois afetam diretamente o crescimento, sobrevivência e susceptibilidade das mudas ao ataque de pragas.

No Capítulo 3, foi avaliada a plasticidade das características fotossintéticas foliares em resposta aos tratamentos silviculturais e como essas respostas se associam ao crescimento das seis espécies plantadas. Foi evidenciado que características fotossintéticas, que representam a interceptação e uso eficiente da luz, possuem potencial para auxiliar na seleção de espécies em plantios de enriquecimento na Amazônia Central.

2. Objetivos

O objetivo desse estudo é compreender o estabelecimento inicial de seis espécies florestais em um plantio de enriquecimento de floresta secundária na Amazônia Central. Para tanto, a tese foi escrita em três capítulos com objetivos específicos:

Capítulo 1. Investigar como tratamentos silviculturais afetam o microclima de uma floresta secundária na Amazônia Central.

Capítulo 2. Testar se o estabelecimento inicial (crescimento, mortalidade e susceptibilidade ao ataque de pragas) de seis espécies florestais, em plantio de enriquecimento de floresta secundária, depende do refinamento das árvores do dossel e corte do sub-bosque.

Capítulo3. Avaliar a relação entre as plasticidades do crescimento e características fotossintéticas foliares que foram induzidas pelos tratamentos silviculturais.

Capítulo 1

Santos, V.A.H.F; Modolo, G.S., Ferreira, M.J. 2019. How do silvicultural treatments alter the microclimate in a Central Amazon secondary forest? A focus on light changes. Journal of Environment Management. *Under review*.

How do silvicultural treatments alter the microclimate in a Central Amazon secondary forest? A focus on light changes

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Abstract

Silvicultural treatments can change the microclimate inside tropical secondary forests and thus enable the artificial regeneration of ecologically and economically important tree species. Increasing levels of canopy tree refinement (diameter at breast height, DBH > 5 cm) were applied and combined with understory slashing to investigate how these silvicultural treatments affect the microclimate of a Central Amazon secondary forest. The refinement treatment was performed in six levels of basal area reduction (0, 20, 40, 60, 80, and 100%) in rectangular plots (2318 m^2) and was equally divided in two subplots that did (understory slashed) or did not (control) receive the application of understory slashing. Canopy openness was estimated using hemispherical photography before treatment implementation and periodically over 26 months. Light transmittance, total daily irradiance, air temperature, air humidity and soil moisture were measured during two climatic seasons (Dry and Wet season) of the two years following the application of the treatments. Understory slashing doubled the canopy openness before the refinement and had an effective and persistent effect on canopy openness, light transmittance and total daily irradiance for the 26 months. Refinement increased canopy openness, light transmittance and total daily irradiance; however, after one year of treatment application, the effect was greater in understory slashed than in control subplots. In plots with higher basal area reduction (> 60%), the understory slashed subplots total daily irradiance was 19% and 60% higher than control subplots after nine and 26 months, respectively. Refinement increased air temperature and reduced air humidity and soil moisture. The refinement of canopy trees and understory slashing change the microclimate (particularly light availability) in secondary forests and performed best when applied together. Silvicultural implications for sustainable secondary forest management and productive objectives are discussed.

Keywords: tropical silvicultural systems, canopy openness, photosynthetic photon flux density, sustainable forest management

1. Introduction

During the last quarter-century, there has been a 3% decline in global forest area (Keenan et al., 2015). In some climatic domains (*e.g.*, temperate forests), the area occupied by forests has increased; however, in the tropics, a 3.6 ratio of loss to gain supports the predominance of deforestation (Hansen et al., 2013). In this scenario, it is estimated that half of the tropical forests are not mature forests but secondary forests in regeneration (Chazdon, 2014; FAO, 2010). In the Brazilian Amazon, for example, approximately 23% of the deforested area (~ 751,000 km^2) is in an advanced stage of regeneration (INPE, 2016).

Historically, secondary forests have been less studied compared to the prominence given to mature forests in the tropics (Bongers et al., 2015). However, in the last few decades, secondary growth forests have become the focus of several studies that demonstrate the potential of these forests for providing ecosystem services (Barlow et al., 2007; Bruijnzeel, 2004; Chazdon, 2014; Guariguata and Ostertag, 2001; Poorter et al., 2016; Schwartz et al., 2015; Sommer et al., 2003; Zimmermann et al., 2006; Wiener, 2010). Moreover, secondary forests can play a substantial economic role when considering the goods and services that can be exploited and produced (Fantini and Siminski, 2016; Fantini et al., 2019; Finegan, 1992; Schwartz et al., 2015). Sustainable management of tropical secondary forests with economic profitability and maintenance of ecosystem services could be achieved through silvicultural systems that ensure the availability of primary resources essential for the production of timber and nontimber products (*e.g.,* timber, fruits, seeds and medicinal plants) but which maintain the structure and diversity of the forest (ITTO, 2002). Among tropical silvicultural systems, enrichment plantations are a crucial silvicultural strategy for reintroducing secondary forests to productive land uses and simultaneously protecting this vulnerable vegetation from transformation to pastures or industrial agriculture lands (Jakovac et al., 2012; Peña-Claros et al. 2002; Wiener, 2010).

The canopy of secondary forests is more homogeneous and occupied by narrow-crowded trees than mature forests and thus has infrequent large canopy gaps, resulting in a scarcity of microsites with high light availability (Montgomery and Chazdon, 2001; Nicotra et al., 1999; Numata et al., 2006). Based on the production ecology equation (Binkley et al., 2004; Montheit, 1977), increasing tree and stand growth is related to increasing resource availability, resource uptake and/or resource use-efficiency (Forrester, 2017). Therefore, the introduction of important ecological and commercial species to secondary forests by enrichment planting requires initial silvicultural treatments that increase the canopy openness and, consequently, light availability (named irradiance here) at the forest floor (Schwartz et al., 2015). The objective of this intervention is to reduce interspecific competition and increase the availability of resources, mainly irradiance, fundamental to the survival and growth of arboreal species regenerating naturally in the area, as well as those introduced artificially in enrichment plantations (Kuijk et al., 2014; Mesquita, 2000; Romell et al., 2009; Schwartz et al., 2015).

Manipulation of the light environment in secondary forests can be achieved by different technics, such as cutting lines (Peña-Claros et al., 2002), localized canopy gaps (Balderrama and Chazdon, 2005) and basal area reduction by the thinning of upper-canopy trees, named canopy tree refinement (Romell et al., 2009; Wiener, 2010). These silvicultural technics have been successfully studied in tropical secondary forests, but few studies have investigated the application of these technics over a wide range of levels, which comprise the poor understory light environment in intact forests, for intense interventions that cause a close to full-sun condition (Dupuy and Chazdon, 2008). Therefore, the first objective of this study was to investigate the microclimate changes—with a focus on irradiance—inside a Central Amazon secondary forest subjected to a wide range of basal area reduction by the refinement of canopy trees.

In addition to the artificial opening of the canopy, removal of vegetation in the understory (understory slashing) can increase the availability of irradiance, reduce competition for primary resources (water and nutrients), and thus positively affect the establishment of species introduced at enrichment plantations (Ådjers et al., 1995; Duclos et al., 2013; Lamprecht, 1990; Romell et al., 2008). However, it has not yet been shown whether removal of the understory can enhance the effects on the light environment provided by treatments applied to canopy trees. Thus, the second objective of this work was to investigate whether understory slashing alters the microclimates in a Central Amazon secondary forest and, furthermore, whether refinement effects are improved when understory slashing is also applied.

2. Materials and Methods

2.1. Study site description

The study was conducted in a Central Amazon secondary forest located at Fazenda Experimental da Universidade Federal do Amazonas (02°38'S, 60°03.5'W), 38 km north of Manaus, Brazil. The Central Amazon region is characterized by annual precipitation of 2350 mm, monthly air temperature ranging from 26.4°C to 28.5°C and air humidity reaching an average value of 75% in the dry season and 85% in the wet season (data from 1988-2018; INMET, 2019). The precipitation seasonality is generally moderate with dry season lengths from August to September (Sombroek, 2001).

The mature forest was mostly clear-cut, burned in 1986 and then abandoned (Fig. S1). Eleven years later (1997), a secondary forest that had regrown was cut and burned; a crop of cupuaçu tree (*Theobroma gradiflorum* (Willd. ex Spreng.) K. Schum.) was planted, but the area was once more abandoned. Therefore, the silvicultural treatments of this study were applied to a 19-year-old secondary forest. The secondary forest was established in a well-drained clayed oxisol (Chauvel, 1982) with acid reaction (pH 4.2 ± 0.05), low cation exchange capacity (1.6 ± 0.11 cmolc kg^{-1}), high exchangeable aluminum saturation (1.4 ± 0.08 cmolc kg^{-1}), extremely poor phosphorus concentration (1.4 ± 0.76 mg kg^{-1}) and medium concentration of organic matter (3.27%). According to the inventory within the experimental plots, the secondary forest structure is characterized by a density of 1200±180 trees ha^{-1} (DBH > 5 cm) and basal area of 12±3.6 m^{2} ha^{-1}, and the dominance of the genera were ordered *Bellucia* sp. > *Goupia* sp. > *Vismia* sp. > *Cecropia* sp. The secondary forest covers 17 hectares and is neighbored by a wide mature forest along approximately 80% of the edges (Fig. S1).

2.2. Silvicultural treatments and experimental design

Two silvicultural treatments for light management were applied in the secondary forest during the last quarter of 2016. The first applied treatment was understory slashing, which consisted of removing all herbaceous plants and small trees (DBH < 5 cm) with a machete—hereafter termed understory slashing. All understory regrowth was cut again during two maintenance visits per year. The second treatment, which occurred soon after understory treatment, consisted of thinning the trees (DBH > 5 cm) occupying the forest canopy and subcanopy in progressive levels of basal area reduction (0, 20, 40, 60, 80 and 100%) by felling with a chainsaw—hereafter termed canopy refinement. The trees selected to be felled ranged from smallest to greatest until the targeted level of basal area reduction of each treatment was reached. We chose this criterion, taking into consideration that the removal of large trees could create localized and wide gaps. Moreover, felling big trees could damage other trees and decrease the level of control for canopy openness. Each level of canopy refinement was applied to a plot of 2318 m^2 (61 x 38 m), and understory slashing was applied in a subplot within half of the main canopy refinement plot (Fig. 1). The treatment combinations were applied in five repetitions (blocks). Six tree species (*Bertholletia excelsa*, *Carapa guianensis*, *Cedrela fissilis*, *Hymenaea courbaril*, *Tabebuia rosea* and *Swietenia macrophylla*) were planted in these plots in March 2017, configuring a silvicultural system of enrichment planting.

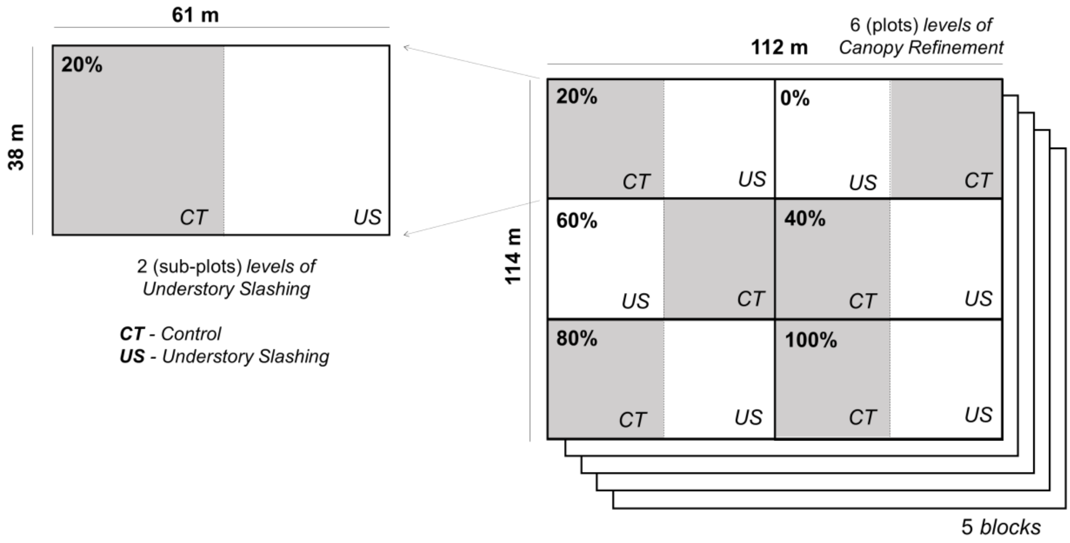

Fig 1. Experimental design showing the experimental plots which the silvicultural treatments (understory slashing and canopy refinement) were applied. Two levels of understory slashing (control and understory slashed) and six levels of canopy

refinement (0, 20, 40, 60, 80 and 100% basal area reduction) were applied in five blocks.

2.3. Canopy openness

Canopy openness was calculated from hemispherical photography using a Digital Plant Canopy Imager (CI-110, CID Bio-Science, Camas, WA, USA). The hemispherical photos were taken nine times: before the understory treatment (October 2016); before canopy treatment (December 2016); and three (March 2017), six (June 2017), nine (September 2017), fifteen (March 2018), eighteen (June 2018), twenty-one (September 2018) and twenty-six (February 2019) months after the canopy treatment. At the center of each subplot (avoiding the 10 meters from the plot edges and between subplots) nine systematically spaced hemispherical photos were taken (Fig. S2) from 1.3 m above the ground. The photos were taken on 2-3 cloudy days per season in the early morning (06:00 – 07:30 h) or late afternoon (17:00 – 18:00 h). The photos were analyzed using the Plant Canopy Analyses System Software (CID Bio-Science, Camas, WA, USA) following a protocol for adjusting the color (brightness, contrast and gamma), applying sky and leaf filters (indicating the pictures that were sky and vegetation) and manually adjusting the canopy fraction threshold. The average value of canopy fraction in each plot was registered and utilized for canopy openness.

2.4. Irradiance measurements and transmittance calculations

For irradiance measurements and transmittance calculations, two photosynthetic photons flux density (PPFD; µmol m^{-2} s^{-1}) sensors were used: one for measurements inside the plots subjected to silvicultural treatments and a second for measurements in a full sun area. Measurements in plots were taken by using a line sensor (MQ-301: Line quantum with 10 sensors and handheld meter, Apogee, USA) during six-hour intervals (06:30-07:00 h; 08:30-09:00 h; 10:30-11:00 h; 12:30-13:00 h; 14:30-15:00 h; 16:30-17:00 h). Irradiance measurements were carried out following the same sampling scheme used in hemispherical photography with the exception that the height of the irradiance was recorded. PPFD values were recorded above each planted seedling in irregular heights. The second PPFD sensor (MQS B/ULM-500 logger, Heinz Walz, Germany) was installed in a full-sun area (100 m from the secondary forest), and PPFD values were recorded every 30 seconds for 5-14 days. The values of irradiance in the plots and full-sun area were measured during four periods: 2017 dry season (September), 2018 wet season (April), 2018 dry season (September) and 2019 wet season (February).

The daily transmittance was obtained from the average of hourly transmittance values recorded during the day (Rich et al., 1993). Hourly transmittance was calculated as the ratio of PPFD measured at the plots in each hour interval and the average values recorded during the same hour interval in the full-sun area. Total daily irradiance (mol m^{-2}) in the full sun area was calculated by the product of mean daily values and photoperiod (Chazdon and Fetcher, 1984). Total daily irradiance (mol m^{-2}) in the plots subjected to silvicultural treatments in each analyzed season was calculated by multiplying the daily transmittance and full sun total daily irradiance.

2.5. Air temperature and humidity measurements

The temperature and humidity of the air were measured on the same irradiance measurement days with two digital thermo hygrometers (7666.02.0.00, INCOTERM, Brazil) that were protected from direct solar radiation by a protective tube made of white polychloroethene (1 mm thick) and an inner layer of styrofoam (5 cm thick). The values were recorded manually after thermo hygrometers stabilization (~10 min) in the center of each subplot at 1.3 m of height. The two subplots of each plot were measured at the same time, and the measurements started at 06:30 h and finished at 17:00 h.

2.6. Soil moisture

Soil moisture surveys were made during the 2017 dry season and 2018 wet season in the first year after silvicultural treatments. Composite soil samples (three subsamples distributed within a subplot) were collected to a depth of 10 cm and packed in impermeable containers. An aliquot of 5 g of soil was weighed on a precision scale (wet mass) and then oven-dried to constant mass (dry mass). Gravimetric moisture was obtained by the ratio between the water mass in the soil sample (wet mass - dry mass) and the dry mass of soil sample (Gardner, 1986).

2.7. Statistical analyses

The effect of understory slashing on canopy openness was tested by a one-tailed, paired t-test ($P < 0.05$). The refinement effect on canopy openness over the time was analyzed comparing the canopy openness at three months with six subsequent times (six, nine, fifteen, eighteen, twenty–one and twenty-six months) after treatments for each understory slashing condition (slashed and control) by two-tailed, paired t-test ($P < 0.05$). The effects of refinement, understory slashing and the interaction factors of light transmittance, total daily irradiance, soil moisture, air temperature and humidity were tested by an analysis of covariance (ANCOVA). Soil moisture, air temperature and humidity data were grouped in relation to the seasons. The data of light transmittance and total daily irradiance were Log10 transformed to meet the assumptions of linearity and normality. All analyses were performed using the statistical program R version 3.5.1 (R Core Team, 2018).

3. Results

3.1. Canopy openness

Understory slashing, applied before canopy refinement, doubled the canopy openness (6% before and 12% after the understory slashing, Fig. 2). Canopy openness reduced during over time in both understory slashed and control subplots, but the effects varied depending on the refinement level (Fig. 3). Canopy openness decreases with intermediary levels of refinement (40% and 60%) were observed for both understory slashed and controls by the sixth month after the application of the treatments. However, canopy closure of 37% at the highest level of refinement (100%) eighteen months after treatments was observed only in control subplots.

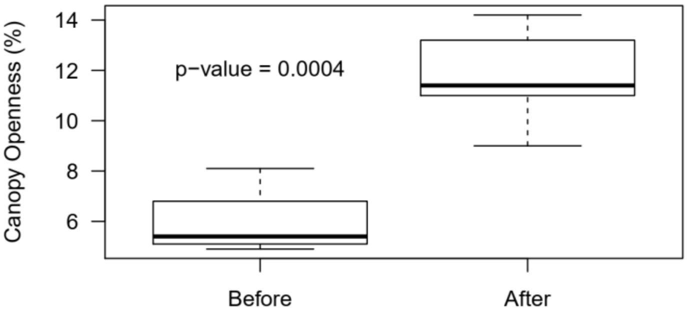

Fig. 2. Box-plot of canopy openness before and after understory slashing. *P-value* is the result of one-tailed, paired t-test (n = 30). The line inside the box is the median, the top and bottom ends of the box are the 75 and 25 percentiles, and the whiskers the minimum and maximum values.

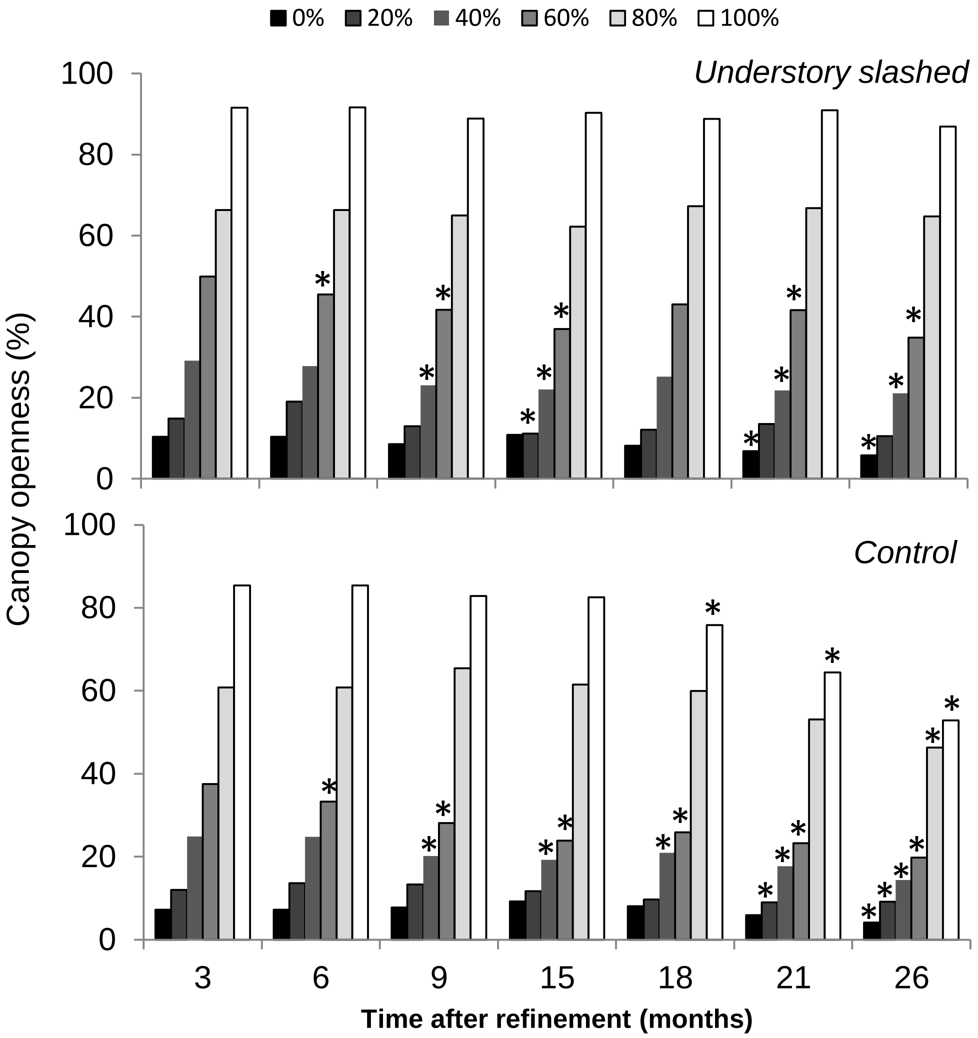

Fig. 3. Canopy openness over the time in understory slashed and control subplots subject to increasing levels of refinement (basal area reduction: 0%, 20% 40% 60%, 80% and 100%). * indicates the time effect (two-tailed, paired t-test, $P < 0.05$) on canopy openness for each level of basal area reduction. Canopy openness at three months was compared with six subsequent times.

3.2. Irradiance transmittance and total daily irradiance

Silvicultural treatments affected the secondary forest irradiance transmittance in different ways during the two analyzed years (Fig. 4). During the first year (Dry 2017 and Wet 2018), understory slashing and canopy refinement increased the transmittance, but the effect of basal area reduction on transmittance was the same in understory slashed and control subplots. In contrast, during the two seasons analyzed in the second year (Dry 2018 and Wet 2019), the increase of transmittance with basal area reduction was greater in conditions where the understory was removed. During the second year, the difference between the increased rates of transmittance with the basal area reduction can be attributed to the large contrast between the control subplots and understory slashed plots with 80 and 100% basal area reduction. In the first year (considering only the 80% and 100% plots), the transmittance was 1.25 times greater in understory slashed subplots than in control plots, while in the second year, this difference was 1.54 times.

The values for full-sun total daily irradiance (mol m^{-2}) and instantaneous mean daily irradiance (µmol m^{-2} s^{-1}) at two seasons during each of the two years investigated are summarized as average, minimum and maximum in Table 1. The average values of full-sun total daily irradiance were utilized to derive the total daily irradiance in the plots (the product of transmittance and total daily irradiance in full-sun) and were 41.5% higher in the dry season than in the wet season. Comparing the two years, dry season values were quite similar, and the Wet 2019 value was slightly higher (19%) than the Wet 2018 value.

Understory slashing and canopy refinement increased total daily PPFD (Table 2). The increase in PPFD according to the basal area reduction (canopy refinement) was independent of understory slashing during the first year but not during the second year for both analyzed seasons. The effect of canopy refinement on PPFD improved during the second year in the slashed subplot. The significant interaction of canopy refinement and understory slashing during the second year was attributed to a greater difference between slashed and control subplots in the plots with 60, 80 and 100% basal area reduction. Therefore, the average PPFD in slashed subplots with the higher basal area reduction (60, 80 and 100%) was just 19% higher than control subplots after nine months (Dry 2017) but 60% higher after 26 months (Wet 2019).

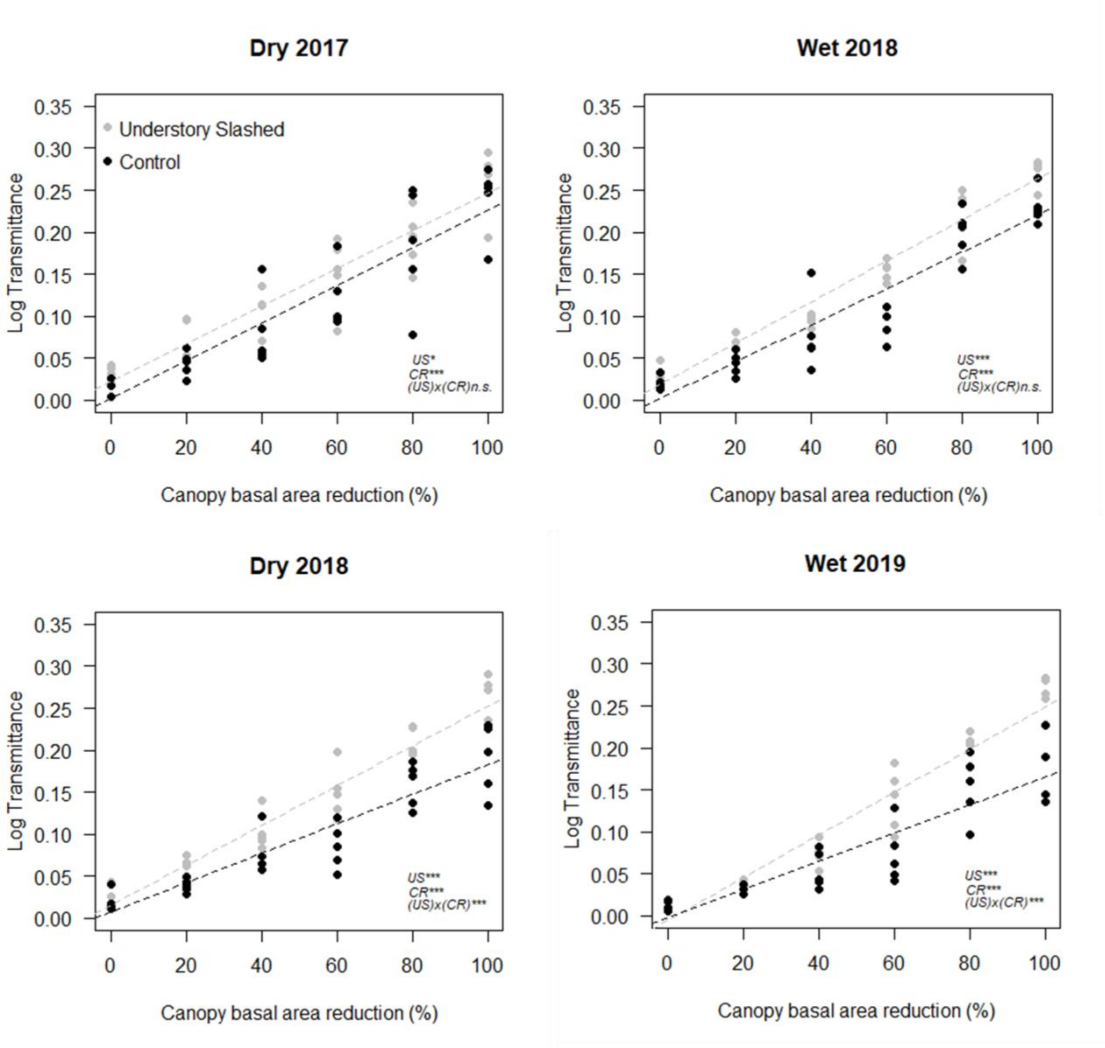

Fig. 4. Scatterplot of transmittance (Log$_{10}$ values) and canopy refinement intensity (basal area reduction) in plots with understory slashed (gray) and control (black) during two seasons in each of two years in a Central Amazonian secondary forest. ANCOVA p-values are inserted as: * < 0.05; *** < 0.001; n.s. ≥ 0.05. US – Understory Slashing; CR – Canopy Refinement; (US) x (CR) interaction.

Table 1

Average, minimum and maximum total daily PPFD and the instantaneous daily mean PPFD values in a Central Amazon site during two seasons in two years.

		Total daily (mol m^{-2})			**Daily average (µmol m^{-2} s^{-1})**		
	n (days)	*average*	*minimum*	*maximum*	*average*	*minimum*	*Maximum*
Dry 2017	13	43.72	33.65	57.75	1012.13	779.03	1336.75
Wet 2018	14	28.11	13.46	48.85	650.64	311.51	1130.73
Dry 2018	6	43.40	35.28	46.53	1004.64	816.65	1077.01
Wet 2019	5	33.45	25.93	39.71	774.32	600.28	919.10

Table 2

Effects of understory slashing, canopy refinement and interaction (US vs CR) on total daily photosynthetic photon flux density (PPFD, µmol m^{-2} s^{-1}) during two seasons of each of two years in a Central Amazonian secondary forest.

Canopy basal area reduction (%)	**Dry 2017**	**Wet 2018**	**Dry 2018**	**Wet 2019**
	Understory slashed			
0	3.3 ± 0.4	1.9 ± 0.4	2.8 ± 0.5	1.3 ± 0.2
20	7.8 ± 1.2	4.5 ± 0.4	6.3 ± 0.7	3.1 ± 0.2
40	11.3 ± 1.8	7.8 ± 1.0	11.6 ± 1.3	6.2 ± 0.6
60	18.5 ± 2.6	12.0 ± 0.5	18.0 ± 2.0	12.6 ± 1.7
80	24.3 ± 2.4	18.6 ± 1.6	26.1 ± 1.7	19.7 ± 0.9
100	36.6 ± 3.1	24.2 ± 0.8	35.9 ± 2.2	27.9 ± 1.4
	Control			
0	1.7 ± 0.4	1.4 ± 0.2	2.0 ± 0.6	0.9 ± 0.2
20	4.6 ± 0.7	2.9 ± 0.4	4.1 ± 0.4	2.4 ± 0.2
40	9.2 ± 2.5	5.6 ± 1.6	8.3 ± 1.5	4.5 ± 0.9
60	14.2 ± 2.4	6.6 ± 0.7	9.5 ± 1.4	6.2 ± 1.5
80	23.7 ± 4.7	16.4 ± 1.4	19.3 ± 1.7	14.3 ± 1.9
100	32.5 ± 3.1	19.7 ± 1.1	24.0 ± 2.8	16.0 ± 2.0
Understory slashing (US)	**	***	***	***
Canopy refinement (CR)	***	***	***	***
US vs CR	n.s.	n.s.	*	***

ANCOVA p-values (* < 0.05; ***<0.001; n.s. ≥ 0.05)

3.3. Air temperature and humidity

Air temperature and humidity in the Central Amazon secondary forest were dependent on silvicultural treatments (Fig. 5). The air temperature increased with both canopy refinement and understory slashing, while air humidity reduced with only canopy refinement. An interaction effect between the two silvicultural treatments was not observed. In plots with understory slashed, the air temperature was slightly higher (1.01%) than control subplots but increased 0.24°C for each 10% of increase in basal area reduction. Therefore, in plots with wide canopy openness (100% basal area reduction), the air temperature was 2.4°C higher and air humidity 4% drier than in the untouched forest (0% basal area reduction).

The amplitude of air temperature and air humidity was wider according to basal area reduction (Fig. 6). Air temperature varied 1.76 fold (23.4 - 41.3°C) and 1.66 fold (21.8 - 36.2°C) in plots with 100% and 0% of basal area reduction, respectively. Air humidity varied 2.79 fold (34 - 95%) and 1.82 fold (52 - 95%) in plots with 80% and 0% of basal area reduction, respectively. Concerning slashed and control subplots, the amplitudes in air temperature and air humidity were quite similar (Fig. 6). Air temperature ranged from 22.5°C to 41.1°C in slashed and from 21.8°C to 41.3°C in control subplots. Air humidity varied from 37% to 95% in slashed and from 34% to 95% in control subplots. Soil moisture was slightly affected by refinement, with a 3% (43% to 40%) drop in moisture between plots with 0% and 100% basal area reduction.

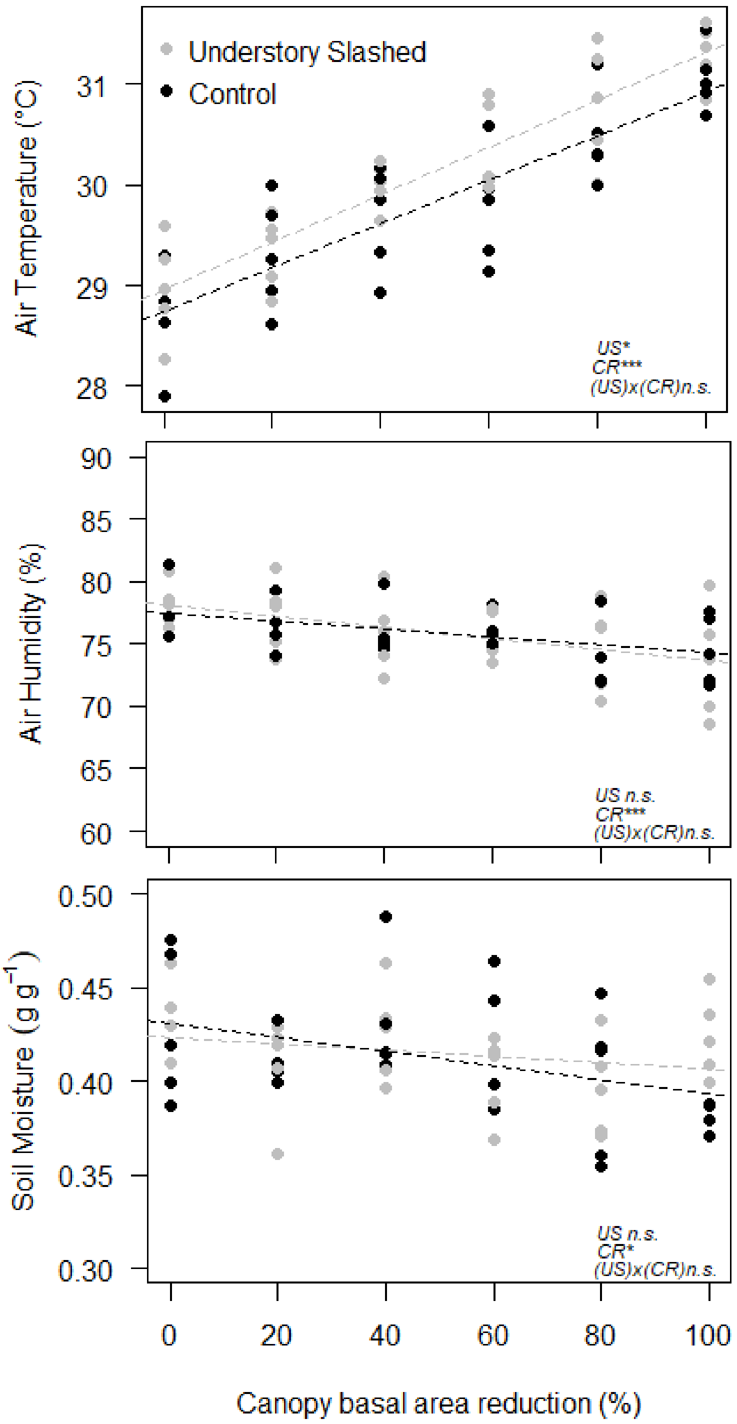

Fig. 5. Scatterplot of silvicultural treatment effects on air temperature, air humidity and soil moisture in a Central Amazon secondary forest. ANCOVA p-values are inserted as: * < 0.05; *** < 0.001; n.s. ≥ 0.05. US – Understory Slashing; CR – Canopy Refinement; (US) x (CR) interaction.

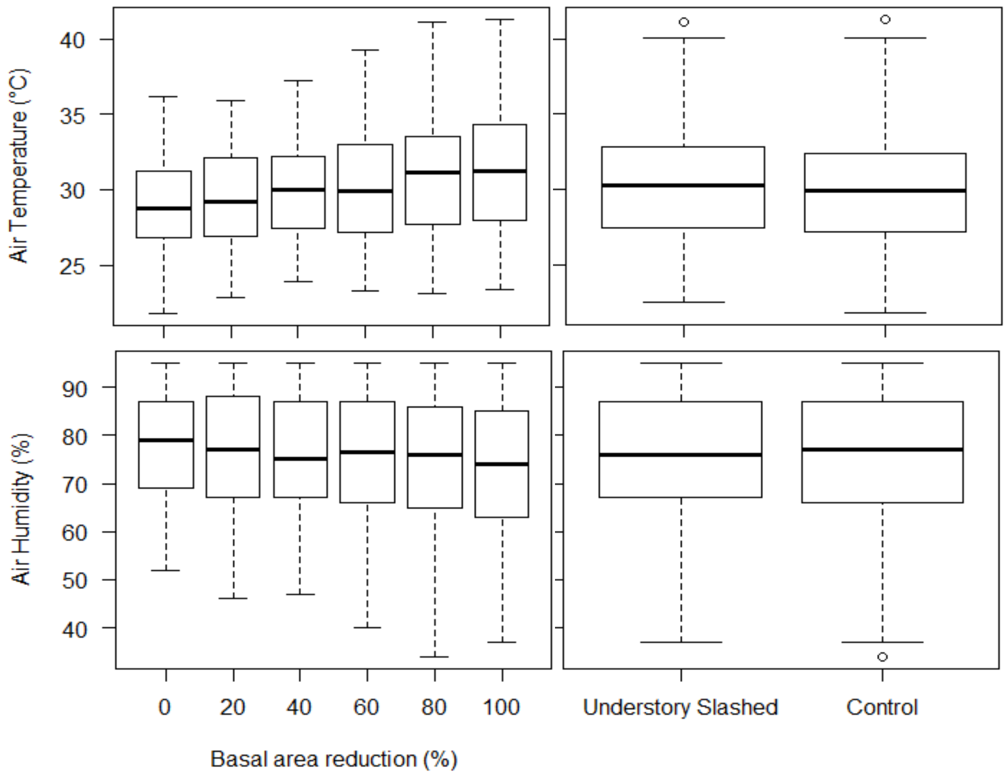

Fig. 6. Boxplot of air temperature and air humidity of a Central Amazon secondary forest subject to silvicultural treatments of basal area reduction (canopy refinement) and understory slashing. The line inside the box is the median, the top and bottom end of the box are the 75 and 25 percentiles, the whiskers are the minimum and maximum value, and the circles indicate the outliers.

4. Discussion

In the Brazilian Amazon, approximately 23% of deforested areas are secondary forests (INPE, 2016). Considering the relevance of these landscapes in Amazonia, the use of these ecosystems for protective and/or productive objectives is emergent. Here, we show significant findings regarding the effects of rigorously controlled silvicultural interventions for the sustainable management of secondary forests. First, understory slashing alone can enhance the light supply on the forest floor. Second, canopy refinement treatments, applied to result in a wide range of canopy openness, create specific microclimate conditions to improve the establishment of seedlings from natural regeneration and/or enrichment planting.

4.1. Understory slashing in Central Amazon secondary forests enhances light availability in an effective and persistent way

Understory slashing in a secondary forest in the Central Amazon, before and combined with canopy refinement, increased irradiance (Fig. 2 and Table 2) but only had a minor effect on air temperature and humidity (Fig. 5). Understory vegetation can impair natural regeneration and growth of artificially established seedlings in enrichment plantings in tropical forests (Duclos et al., 2013; Dupuy and Chazdon, 2006; Romel et al., 2008). The negative effects have been attributed to competition for light (Romel et al., 2008) and underground resources (Duclos et al., 2013). There is evidence indicating that understory slashing is an efficient silvicultural intervention for enhancing environmental light (Dupuy and Chazdon, 2006; Romel et al., 2009). Without light stimulation for aggressive pioneer trees, lianas and shrubs species and, consequently, understory regrowth, the effects of understory slashing can persist for at least 30 months in a *Macaranga* spp. dominated secondary tropical rain forest in northern Borneo (Romel et al., 2009). However, with large canopy gaps in a secondary tropical forest in Costa Rica, the enhanced recruitment of shrubs, lianas and large-leafed herbaceous plants resulted in a canopy closure 13 months after treatments (Dupuy and Chazdon, 2006). The present study observed a canopy closure eighteen months after refinement in conditions of wide canopy openness (100% basal area reduction) that were not controlled for understory vegetation regrowth (Fig. 3). Therefore, periodic understory slashing has an effective and persistent effect on irradiance, principally in conditions with strong refinement of the canopy trees.

4.2. Changes in secondary forest microclimate along with a wide range of basal area reduction by canopy refinement

Some studies have investigated light availability in secondary tropical forests subjected to silvicultural treatments (Ådjers et al., 1995; Mesquita, 2000; Peña-Claros et al., 2002; Romell et al., 2009, Wiener, 2010), but only a few studies were based on a wide range (gradient) of canopy openness (Dupuy and Chazdon, 2008). Here, the canopy openness ranged from 7.4% to 91% soon after the silvicultural intervention and from 5.9% to 86.9% after 26 months. In this wide range of canopy openness, the daily irradiance availability varied between 0.9 and 36.6 mol m^{-2} (Table 2). Compared with a Sri Lanka rainforest valley (Ashton, 1992), the understory values were similar (0.92 mol m^{-2}) to observed in plots with 0% basal area reduction; however, the maximum value registered in a large gap of 454 m^2 (21.8 mol m^{-2}) was lower than the average value observed in plots with 100% basal area reduction (27.1 mol m^{-2}).

Along with the different levels of canopy refinement (0% to 100%), air temperature increased 1.09 times, and air humidity reduced 1.07 times (Fig. 5); irradiance increased 21.05 times when comparing the average of all seasons and understory slashing (Table 2). The discrepancies between the increase of irradiance versus air temperature and humidity variations were demonstrated in early studies comparing canopy gaps and understory environments in mature tropical forests (Chazdon and Fetcher, 1984; Denslow, 1980; Fetcher et al., 1985). Comparing forest understory and large clearings, Denslow (1980) found that air temperature was 1.12 times warmer and air humidity 1.25 times drier than the understory, while Chazdon and Fetcher (1984) reported that in large clearings, the light availability was 26 times higher than in understory. These results reinforce the pivotal role of light availability on artificial and natural forest regeneration, principally regarding light manipulation by silvicultural treatments (Finegan, 1992; Finegan, 2016).

Despite the small effects of silvicultural treatments on average values of air temperature and humidity, the differences observed in the amplitudes of the values should be carefully analyzed (Fig. 6) since high temperature peaks and low air humidity can induce stress to the established seedlings during enrichment planting (Dünisch et al., 2003; Gerhardt, 1996). The maximum air temperature values registered in plots with a higher proportion of basal area reduction (80 and 100%) reached 40°C and were high enough to impair photosynthetic processes (Slot and Winter, 2017). In large gaps, leaf-to-bulk air vapor pressure deficit (VPD) is higher than in the understory because of high air temperatures and low air humidity (Fetcher et al., 1985). Moreover, during heat waves, the amplitude of air temperature could be even higher in open-site conditions. (Renaud and Rebetez, 2009). Therefore, the higher VPD, such as in conditions of intensive silvicultural treatments applications (wide canopy openness), can induce stomatal closure and photosynthesis reduction, principally during droughts, at midday and in leaves exposed to high irradiance (Brodribb and Holbrook, 2004; Santos et al., 2018). Soil moisture was negatively affected by refinement, but all values were above the permanent wilting point (0.28 g g^{-1}) when considering the gravimetric soil moisture at -1500 kPa in clay Ferralsols in Central Amazon (Marques et al., 2004).

4.3. Implications for sustainable secondary forest management: the importance of silvicultural treatments

The canopy of secondary forests is homogeneous and dominated by narrow-crowned trees, which create small gaps when they fall and, consequently, microsites with low availability of irradiance compared with wider gaps found in mature forests

(Montgomery and Chazdon, 2001; Nicotra et al., 1999; Numata et al., 2006). Moreover, an early gap closure succeeds the tree fall because of high regrowth of natural regeneration and quickly reduces the irradiance on the forest floor (Dupuy and Chazdon, 2008; Romell et al., 2009). The production ecology theory states that resource supply (light, water and nutrients) is one of the factors affecting the growth (Binkley et al., 2004; Montheit, 1977). Thus, the recruitment of naturally regenerated seedlings, as well as the survival and growth of artificially introduced seedlings (*e.g.*, enrichment planting), can be hampered by the poor light environment in secondary forest (Mesquita, 2000; Wiener, 2010). Silvicultural systems applied for the management of secondary forests have to focus on silvicultural treatments that improve the light conditions in the understory (Guariguata, 2000, Schwartz et al., 2015). In the present study, the light environment was altered by the applications of silvicultural treatments on the canopy and understory trees, and it was demonstrated that both were effective.

The light environment can be manipulated in the secondary forest by different techniques; the most common are cutting lines (Peña-Claros et al., 2002), localized canopy gaps (Dupuy and Chazdon, 2008) and basal area reduction by the refinement of upper-canopy trees (Romell et al., 2009; Wiener, 2010). Canopy gaps, localized or spread in refinement, have been suggested as a better way to create an appropriated light environment in the understory of the secondary forest when considering the uniformity and availability of irradiance (Bebber et al., 2002, Sovu et al. 2010). In the present study, the high capacity of the treatments to control the availability of irradiance on the forest floor was demonstrated for application of a wide range of refinement levels (the strong relationship between basal area reduction and total daily PPFD; Table S1). Therefore, basal area reduction could be applied in a secondary forest as a way to manipulate the light environment because it has the advantage of high control of canopy openness and daily irradiance available to the seedlings. In Central Amazon secondary forests similar in structure and composition (Mesquita et al., 2001), stakeholders can easily apply the refinement and estimate the light availability using the proportion of basal area reduction. However, additional refinements need to be planned to keep a favorable level of canopy openness over time, particularly for intermediary levels of refinement (40% and 60%) that reduce the values of canopy openness six months after treatments (Fig. 3). A combination of felling and girdling (removing a strip of bark along the entire circumference of the trunk) the canopy trees could be advantageous for keeping canopy openness constant over time (Romell et al., 2009).

Although modest, the effect of understory slashing on irradiance availability should be carefully considered, as it may interfere with the effects that are achieved by refinement. In the present study, it was observed that light availability reduced considerably in plots with wide canopy openings when the understory slashing had not been applied periodically. Other studies have demonstrated a persistent effect of understory slashing under conditions of lower canopy opening and consequently, a lower incentive for aggressive pioneer vegetation growth (Romell et al., 2009). Even if light availability were not improved, removal of the understory vegetation should still be analyzed for reduction in interspecific competition for other resources, in this case, those below ground, which may also compromise the establishment and growth of the seedlings that are regenerating (Duclos et al., 2013). The maintenance of light conditions through the establishment years of the enrichment plantations, both in mature and secondary forests, is one of the causes of the failure in this silvicultural system (ITTO, 2002), and it is imperative to include periodic understory slashing in the agenda of silvicultural systems for the enrichment of secondary forests that begin with high canopy openness. However, in some situations, one must consider only the removal of the vegetation that is competing directly with the seedlings. First, costs could be reduced because maintenance activities can reach 58% of total costs in enrichment plantings (Schwartz et al., 2016). Second, maintenance of an auxiliary stand will improve the shape of the tree trunk during the growth by lateral shade and will aid in the control of some specific pests, such as Hypsipyla shoot bores in Meliaceae (Catinot and Bossanyi, 2018; Lamprecht, 1990; Newton et al., 1993).

5. Conclusion

The refinement of canopy trees is an effective silvicultural treatment to manipulate the light environment in secondary forests. Understory slashing can further increase the availability of light and enhances the effects of refinement when it is applied periodically. Light manipulation is a central pivot in the secondary forest management. Finally, sustainable management of secondary forests by the silvicultural systems (i.e., enrichment planting) that valorize the vital role of this sometimes-neglected vegetation is crucial for tropical forest conservation as a whole.

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Appendix A. Supplementary material

Fig. S1. Temporal changes in the forest cover at Fazenda experimental da Universidade Federal do Amazonas. The secondary forest area is red highlighted in 2017 image. The images were obtained from CNES/Astrium satellite on Google earth and Landsat – 5 were downloaded from http://www.dgi.inpe.br/CDSR/.

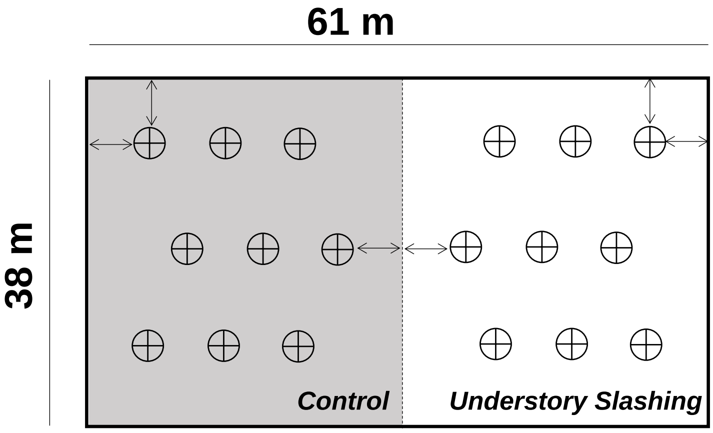

Fig. S2. Hemispherical photography and irradiance sampling at a plot containing two sub-plots (Understory Slashing and Control). The cross-circles are representing the sampling points and the 10 m edges are represented by the arrows

Table S1

Parameters and coefficient of determination of the relationship between total daily irradiance and basal area reduction in a Central Amazon secondary forest.

Season	b	a	R^2
Understory Slashed			
Dry 2017	3.969	0.023	0.862
Wet 2018	2.331	0.025	0.904
Dry 2018	3.366	0.025	0.913
Wet 2019	1.537	0.031	0.942
Control			
Dry 2017	1.983	0.030	0.817
Wet 2018	1.474	0.027	0.883
Dry 2018	2.184	0.025	0.862
Wet 2019	1.082	0.029	0.850

$Y = b + e^{aX}$; *Y: total daily irradiance (mol* m^{-2}*); X: basal area reduction (%)*

Capítulo 2

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Initial establishment of commercial tree species under enrichment planting in a Central Amazon secondary forest: Effects of silvicultural treatments

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Abstract

Enrichment planting has the potential to conserve wide areas of secondary forest in the Amazon. Therefore, it is necessary to understand the effects of silvicultural treatments applied to secondary forest management on the initial establishment of planted species. Enrichment planting was performed in a Central Amazon secondary forest to test whether the growth, mortality and presence of shoot borer attacks of six commercial trees species - in the first two years after planting - depend on canopy trees refinement and understory slashing. Six commercial tree species were planted under a gradient of light transmittance that was created by canopy trees refinement applied in six levels of basal area reduction (0; 20; 40; 60; 80 and 100%) and combined with two understory slashing levels (control and understory slashed). The effects of silvicultural treatments on root collar diameter and height growth (realized and relative), mortality and shoot borer attack were evaluated during the first and second year after planting. The relationships between realized growth and light transmittance were different among the species, but maximum growth was observed at intermediary to high light transmittance (>50%) values for all species. Understory slashing slightly increased the response of realized growth to light transmittance. Species relative growth was strongly affected by light transmittance, but there was a reduced response in the second year after planting, particularly in the light-demanding pioneer species (*Cedrela fissilis*, *Tabebuia rosea* and *Swietenia macrophylla*). Pioneer species mortality was higher in deep shade (lowest transmittance) and was related to fast growth at full sun (highest transmittance) during the first, but not the second, year after planting. Shade-tolerant species (*Hymenaea courbaril*, *Carapa guianensis* and *Bertholletia excelsa*) have slower growth in full sun than pioneers, but only during the first year. Shoot borer attacks in Meliaceae species (*C. fissilis*, *S. macrophylla* and *C. guianensis*) occurred more frequently in high light transmittance and understory slashed environments (60% of *S. macrophylla* seedlings) but were absent in intermediary to low light transmittance and untreated understory. Thus, silvicultural treatments improve the initial establishment of commercial tree species in secondary forest enrichment planting sites. However, such findings should be analyzed considering the effects on growth, mortality and pest attacks during the seedling to juvenile tree development stages after planting.

Keywords: tropical silvicultural systems, tropical seedlings growth, sustainable forest management, ontogeny, *Hypsipyla* sp.

1. Introduction

Secondary forests represent a significant portion (~23%) of the area that has been deforested in the Legal Amazon (INPE, 2016). Developing alternatives to maintain these growing forests is critical to the conservation of ecosystem services and the production of timber, medicinal plants and food by stakeholders (Chazdon, 2014; Guariguata e Ostertag, 2001; Mesquita, 2000; Poorter et al., 2016). These objectives can be achieved through sustainable forest management, which includes an adequate silvicultural system for forest harvesting, regeneration and tending (Finegan, 1992; Lamprecht, 1990; Schwartz et al., 2015). Because secondary forests are scarce in tree species of high commercial value, enrichment planting can be a good silvicultural system alternative since the main objective of this system is to increase the proportion of species of high commercial value in a forest (Peña-Claros et al., 2002, Wiener, 2010).

The initial seedlings growth in enrichment planting in a secondary forest is highly dependent on the light availability (Jakovac et al., 2012; Kuijk et al., 2014; Wiener, 2010). Likewise, the proportion of full sunlight that is transmitted by the secondary forest stand that reaches the planted seedlings is determined by the forest structure, floristic composition and the silvicultural treatments (Jakovac et al., 2012; Romell et al., 2008). In the Central Amazon, for example, *Cecropia*-dominated secondary forests are characterized by a dense vertical stratum that intercepts a high fraction of the light, whereas *Vismia*-dominated stands allow more light transmittance (Jakovac et al., 2012). As a response, regeneration under a *Vismia* canopy is dominated by *Vismia* individuals, whereas regeneration is more diverse in *Cecropia* (Mesquita et al., 2001). Thus, the creation of artificial gaps by partial canopy removal in secondary forests can be critical for species establishment (Mesquita, 2000). Refinement is a silvicultural treatment in which a proportion of the canopy trees are thinned; this improves the forest light transmittance due to canopy openness (Lamprecht, 1990; Wiener, 2010). Consequently, refinement can improve the growth of regenerating seedlings until a maximum level that is dependent on the species (Wiener, 2010). Intermediate canopy opening levels have been shown to be sufficient for the maximum growth and survival of planted forest species, and no excessive opening is required (Ådjers et al., 1995; Peña-Claros et al., 2002; Ramos and del Amo, 1992; Wiener, 2010). In addition to canopy tree thinning, understory slashing increases irradiance availability, reduces competition for primary resources and positively affects the establishment of planted species in enrichment plantings (Duclos et al., 2013; Balderrama and Chazdon, 2005; Romell et al., 2008). In a secondary forest enrichment system in Malaysia, Romell et al. (2008) demonstrated that the removal of understory vegetation near the seedlings had a long-term positive effect on the irradiance availability, survival and growth of dipterocarp species.

During seedling development to a juvenile tree, ontogenetic changes lead to shifts in the balance between photosynthetic and nonphotosynthetic tissues with consequences for plant carbon balance and light requirements (Delagrange et al., 2004; Machado and Reich, 2006). Therefore, new evidence has shown that light-demanding tropical tree species reduce your net daily carbon gain and relative growth according to the size of the saplings, whereas a minimal ontogenetic shift has been observed in shade-tolerant tree species (Sendal et al., 2018). In view of the above discussion, seedling growth responses to silvicultural treatments that increase light at the forest floor can be dependent on the time after planting.

In addition to the effects on growth, silvicultural treatments applied to enrichment plantations can contribute to the initial establishment via reducing seedling mortality and pest attacks in particular species, such as shoot bores in Meliaceae (*Hypsipyla sp.*). According to the growth-survival trade-off, the species that grow faster in high light conditions (pioneers) also have high mortality rates in low light conditions, whereas nonpioneer species have a high survival in low light and moderate growth in full sun (Kitajima et al., 1994, Sendal et al., 2015). Shoot borers have been considered the main pest that prevents the commercial planting of Meliaceae species, and among the various methods proposed for the control of this pest, the silvicultural method via enrichment planting in secondary forests has shown satisfactory results (Newton et al., 1993; Opuni-Frimpong et al., 2008, Yared and Carpanezzi, 1981). In the enrichment planting by *Recrú* method tested in the Brazilian Amazon, lateral shade – promoted by forest regrowth after clear-cutting – and the maintaining of high species diversity were the main causes responsible for the absence of shoot borer attacks in mahogany (*Swietenia macrophylla* King) seedlings planted (Yared and Carpanezzi, 1981).

Enrichment planting was performed in a Central Amazon secondary forest to address the following specific objectives: to investigate whether the growth response (establishment) of six commercial tropical tree seedlings to (under a) the light transmittance gradient is affected by understory slashing and the time after the planting. Additionally, this study aimed to report the seedlings mortality and Meliaceae shoot borer attacks under the different conditions created by silvicultural treatments.

2. Materials and Methods

2.1. Site

The study site was a Central Amazon secondary forest located at Fazenda Experimental da Universidade Federal do Amazonas (02°38’S, 60°03.5’W), 38 km north of Manaus, Brazil. The site history can be described by two events of clear-cutting and burning. The mature forest was clear-cut and burned first in 1986 and then abandoned (Fig. S1, Chapter 1). Eleven years later (1997), a secondary forest that had regrown was again cut and burned. At first, a crop of cupuaçu trees (*Theobroma gradiflorum* (Willd. ex Spreng.) K. Schum.) was planted in the recently opened area, but it was once more abandoned, allowing secondary forest regrowth. Therefore, at the beginning of the silvicultural treatments (2016), the secondary forest was 19 years old, covered an area of 17 ha and was surrounded by an extensive mature forest preserved area (Fig S1).

The secondary forest is located in a region characterized by moderate precipitation seasonality with a dry season lasting from August to September (Sombroek, 2001), an annual precipitation of 2350 mm, a mensal average air temperature ranging from 26.4°C to 28.5°C and air humidity reaching an average of 75% in the dry season and 85% in the wet season (data from 1988-2018; INMET, 2019). The secondary forest was established in a well-drained clayed oxisol (Chauvel, 1982) with acid reaction, low cation exchange capacity, high exchangeable aluminum saturation and extremely poor phosphorus concentrations (Table 1). According to a floristic and structural inventory performed within the experimental plots before the silvicultural treatments, the secondary forest is characterized by a density of 1200±180 trees ha^{-1} (inclusion diameter at the breast height, DBH > 5 cm) and a basal area of 12±3.6 m^2 ha^{-1}. The dominant individuals belong to the genera as follows: *Bellucia* sp. > *Goupia* sp. > *Vismia* sp. > *Cecropia* sp.

Table 1.

Chemistry and fertility soil characterization in a Central Amazon secondary forest.

pH		Ca^{2+}	Mg^{2+}	Al^{3+}	K^+	t	SB	P	C/N	M
H_2O	KCl	cmolc kg^{-1}						mg kg^{-1}	%	
4.19 ± 0.05	3.85 ± 0.02	0.035 ± 0.03	0.084 ± 0.01	1.43 ± 0.08	0.043 ± 0.01	1.6 ± 0.11	0.16 ± 0.05	1.43 ± 0.76	12.32 ± 0.79	89.85 ± 2.24

Values are means ± standard deviation. Soil samples were collected at a depth of 0-20 cm. **Ca^{2+}** exchangeable calcium; **Mg^{2+}** exchangeable magnesium; **Al^{3+}** exchangeable aluminum; **K+** exchangeable potassium; **t** effective cation exchange capacity; **SB** sum of bases; **P** available phosphorus; **C/N** carbon and nitrogen ratio; **m** aluminum saturation.

2.2. Experimental design

The secondary forest was subjected to two silvicultural treatments during the last quarter of 2016. In a split-plot design, six levels of basal area reduction (0, 20, 40, 60, 80 and 100%) were randomly applied in main plots with 2,318 m^2 (61 x 38 m). The understory slashing was conducted in two subplots within each main plot (Fig. 1). The basal area reduction – hereafter termed canopy refinement – consisted of felling canopy trees (DBH > 5 cm) until reaching the desired basal area level, whereas the understory slashing consisted in cutting all herbaceous plants and small trees (DBH < 5 cm). The treatment combinations were replicated in five repetitions (blocks).

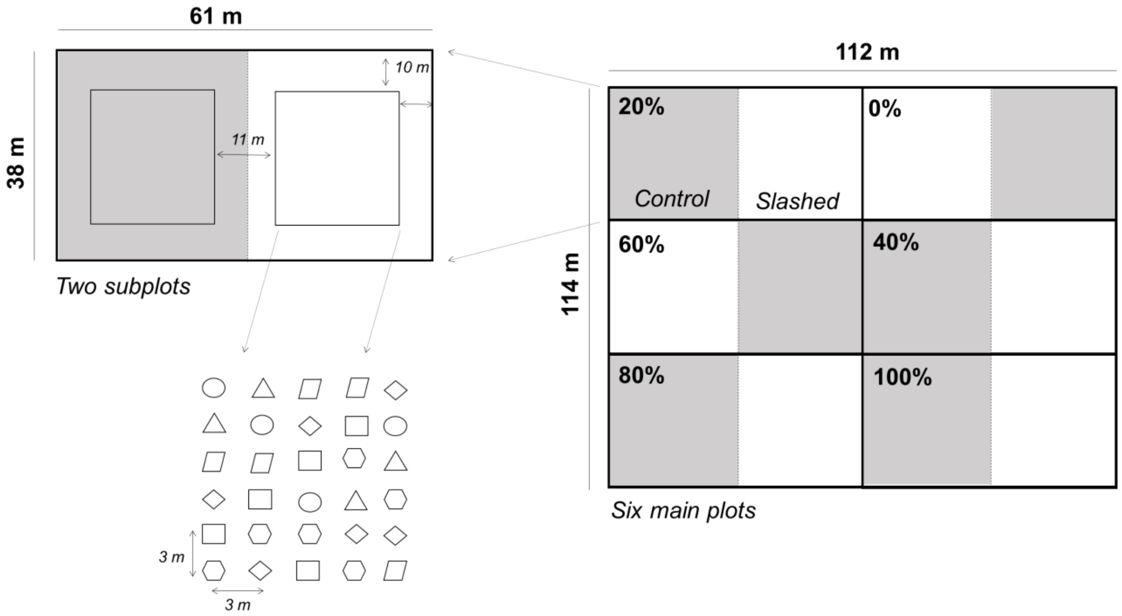

Fig. 1. Plot and subplot design where silvicultural treatments were applied and the six tropical species were planted in an enrichment planting silvicultural system. The different symbols at the lower left are a representation of the six species.

2.3. Enrichment planting

Six tree species were planted in March 2017 under the treated secondary forest configuring a silvicultural system of enrichment planting (Table 2). In each subplot, five seedlings of each species were planted, 3 x 3 m spaced, with an edge of 10 m between plots and 11 m between subplots (Fig 1).

The seedlings were grown at Viveiro Florestal da Universidade do Amazonas (3°6'S, 59°58'W) during the second semester of 2016 from seeds collected in mother trees (at least six trees) planted (*S. macrophylla, T. rosea, B. excelsa, C. guianensis*) or present in native forest fragments (*H. courbaril* and *C. fissilis*). After germination, the seedlings were transplanted in plastic containers (1 dm^3) filled with clayed soil (20 cm superficial forest soil layer) conditioned with limestone (500 g m^{-3}), P_2O_5 (700 g m^{-3}), KCl (150 g m^{-3}), N (200 g m^{-3}) and micronutrients (200 g m^{-3} of FTE-BR12: 1.8% B;

0.8% Cu; 3.0% Fe; 2.0% Mn; 0.1% Mo; 9.0% Zn). The growing media were fertilized twice (40 ml per seedlings of 10 g l^{-1} P_2O_5; 2.5 g l^{-1} N; 3 g l^{-1} KCl solution) during the six months in the nursery. During the two months prior to the field planting, the seedlings were acclimated under intermediate to high levels of photosynthetic irradiance flux (~ 25 mol m^{-2} day $^{-1}$).

Table 2.

Scientific name, botanical family and ecological group of the six tropical tree species utilized for the secondary forest enrichment planting.

Specie	Botanical family	Ecological group*
Cedrela fissilis Vell.	Meliaceae	Pioneer (LLP)
Tabebuia rosea (Bertol.) Bertero ex A.DC.	Bignoniaceae	Pioneer (LLP)
Swietenia macrophylla King	Meliaceae	Pioneer (LLP)
Hymenaea courbaril L.	Fabaceae	Non-Pioneer (PST)
Carapa guianensis Aubl.	Meliaceae	Non-Pioneer (PST)
Bertholletia excelsa Bonpl.	Lecythidaceae	Non-Pioneer (PST)

*Ecological group according to Swaine and Whitmore, 1988; Finegan 1992, Poorter et al., 2006; Chazdon, 2014. LLP (long-lived pioneer), PST (partial shade-tolerant).

The seedlings were planted in 30 x 30 x 30 cm planting holes in which the soil had been conditioned with limestone (65 g per planting hole) one month prior to planting. During the planting, the soil surrounding each seedling was fertilized with P_2O_5 (46 g), N (11.6 g), KCl (12 g) and micronutrients (10 g of FTE-BR12: 1.8% B; 0.8% Cu; 3.0% Fe; 2.0% Mn; 0.1% Mo; 9.0% Zn). The phosphate fertilizer was applied concentrated in two holes 15 cm away from the seedling whereas nitrogen, potassium and micronutrients were applied in a circle 15 cm away from the seedling. Additional nitrogen and potassium fertilization were performed one and two months following the planting with the same dosage and application method utilized during the planting. The dosages and methods that ensure the minimal nutrient requirements of tropical trees were obtained from a literature review (Furtini Neto, 2000; Resende et al., 2005; Campoe et al., 2014, Alvarado, 2015).

2.4. Relative growth

The relative growth in root collar diameter (5 cm above the soil) and total height were calculated according to Hunt (1990).

$$RG_X = \frac{lnX_2 - lnX_1}{T_2 - T_1}$$

In which RG_x = relative growth in height or diameter, $\ln X_2 - \ln X_2$ = increment of logarithmic height or diameter between two measurements and $t_2 - t_1$ = interval between measurements.

The seedlings were measured every two months, and the relative growth was calculated for the first (t_1 = planting; t_2 = one year after planting) and second (t_1 = one year after planting; t_2 = two years after planting) years after planting. Every two months, measurements were performed to observe any damage (cut or broken accidentally or by insects) to the realized growth in the seedlings and therefore to exclude them from the analysis. Concerning the relative growth during the first and second years, 111 (0.06%) and 50 (0.03%) observations were excluded from growth analysis, respectively. Moreover, all seedlings that died and were attacked by the Meliaceae shoot borer (*Hypsipyla grandella* Zeller) were counted during the measurement campaigns.

2.5. Data analysis

The root collar diameter and height of the six species – two years after planting – were evaluated by plotting the relationship between realized growth variables (root collar diameter and height) and light transmittance (two years average) for each understory slashing condition (control and understory slashed). Therefore, we tested polynomial (linear and quadratic) and exponential growth rise to maximum equations, and those that best represented root collar diameter and height responses to light transmittance were used (R^2 and parameters significance). The response shape indicates whether the diameter and height reach a maximum in an intermediary level of light transmittance and remain constant (exponential growth rise to maximum, $f = a*[1-\exp[-b*x]]$); whether they reach an optimum maximum and then decrease (polynomial quadratic, $f = y0+a*x+b*x^2$); or whether they increase consistently until 100% transmittance (polynomial linear, $f = y0+a*x$).

To evaluate how silvicultural treatments affected the seedling growth during the first and second years following the planting, a mixed-model nested ANCOVA was performed for each of the six species. The light transmittance of the secondary forest estimated for each level of canopy refinement (Text S1) was utilized as a continuous predictive variable (covariate); understory slashing was used as a categorical predictive variable and the year of growth analysis was used as a categorical predictive variable nested within understory slashing. The relative growth (root collar diameter and height) and transmittance values were natural logarithmic (ln) transformed to meet the assumptions of linearity. To test how the growth-survival trade-off is affected by silvicultural treatment and the time after planting, mortality at low light (0% of basal area reduction) was related to growth at full sun (100% of basal area reduction) in the control and understory slashed subplots for the first and second year after planting.

Shoot borer attacks were interpreted descriptively. All analyses were performed using the statistical program R version 3.5.1 (R Core Team, 2018).

3. Results

3.1. Realized root collar diameter and height two years after planting

The realized growth (root collar diameter and height) and light transmittance relationships differed between species and understory slashing (Table 3, Fig. 2 and 3). The diameter and height of *C. fissilis*, *T. rosea* and *S. macrophylla* showed a curvilinear (polynomial quadratic) response to light transmittance, whereas a linear relationship was observed for *H. courbaril* and *B. excelsa* – except for root collar diameter in control subplots – in the most cases. The *C. guianensis* responses were in most cases curvilinear quadratic, but the relationship was exponential for height in control subplots.

S. macrophylla, *T. rosea* and *C. guianensis* reached a maximum root collar diameter and height at high light transmittance (>0.74) when refinement was combined with understory slashing, whereas in the untreated understory, the maximum values were observed in intermediary transmittance levels between 0.64 (*T. rosea*, root diameter collar) and 0.48 (*C. guianensis*, height). The maximum height and diameter of *C. fissilis* was observed at high light, independent of understory slashing and of *H. courbaril* and *B. excelsa* at the highest transmittance experimented. An exception was observed for *B. excelsa* for height in untreated understory conditions in which the maximum value of root collar diameter was observed at low transmittance (0.33) and remained constant throughout the light gradient.

Table 3.

Equation summary of the relationship between realized growth (root collar growth and height) and light transmittance for six commercial tree species in a secondary forest enrichment planting site.

Specie	Equation	R^2	*a*	*b*	*intercept*
Root collar diameter					
Understory Slashed					
C. fissilis	Polynomial quadratic	0.88	176.51	-119.44	6.70
T. rosea	Polynomial quadratic	0.90	97.12	-48.78	16.38
S. macrophylla	Polynomial quadratic	0.85	85.84	-43.56	11.16
H. courbaril	Polynomial linear	0.95	56.8		5.13
C. guianensis	Polynomial quadratic	0.84	80.31	-47.80	12.4
B. excelsa	Polynomial linear	0.86	40.28		8.23
Control					
C. fissilis	Polynomial quadratic	0.91	169.01	-111.4	4.60
T. rosea	Polynomial quadratic	0.87	100.85	-78.94	13.26
S. macrophylla	Polynomial quadratic	0.88	115.30	-101.72	6.04
H. courbaril	Polynomial linear	0.71	29.82		7.58
C. guianensis	Polynomial quadratic	0.91	100.88	-101.27	7.54
B. excelsa	Exponential rise to maximum	0.66	18.89	8.91	
Height					
Understory Slashed					
C. fissilis	Polynomial quadratic	0.90	755.23	-525.47	15.32
T. rosea	Polynomial quadratic	0.85	688.00	-464.36	54.14
S. macrophylla	Polynomial quadratic	0.73	495.56	-304.17	43.79
H. courbaril	Polynomial linear	0.85	229.82		86.10
C. guianensis	Exponential rise to maximum	0.71	260.66	8.50	
B. excelsa	Polynomial linear	0.79	197.74		68.32
Control					
C. fissilis	Polynomial quadratic	0.84	626.63	-461.83	23.24
T. rosea	Polynomial quadratic	0.76	585.37	-483.54	73.66
S. macrophylla	Polynomial quadratic	0.78	807.00	-715.20	22.52
H. courbaril	Polynomial linear	0.66	291.12		79.47
C. guianensis	Polynomial quadratic	0.85	958.22	-1001.1	48.03
B. excelsa	Polynomial linear	0.65	152.34		73.27

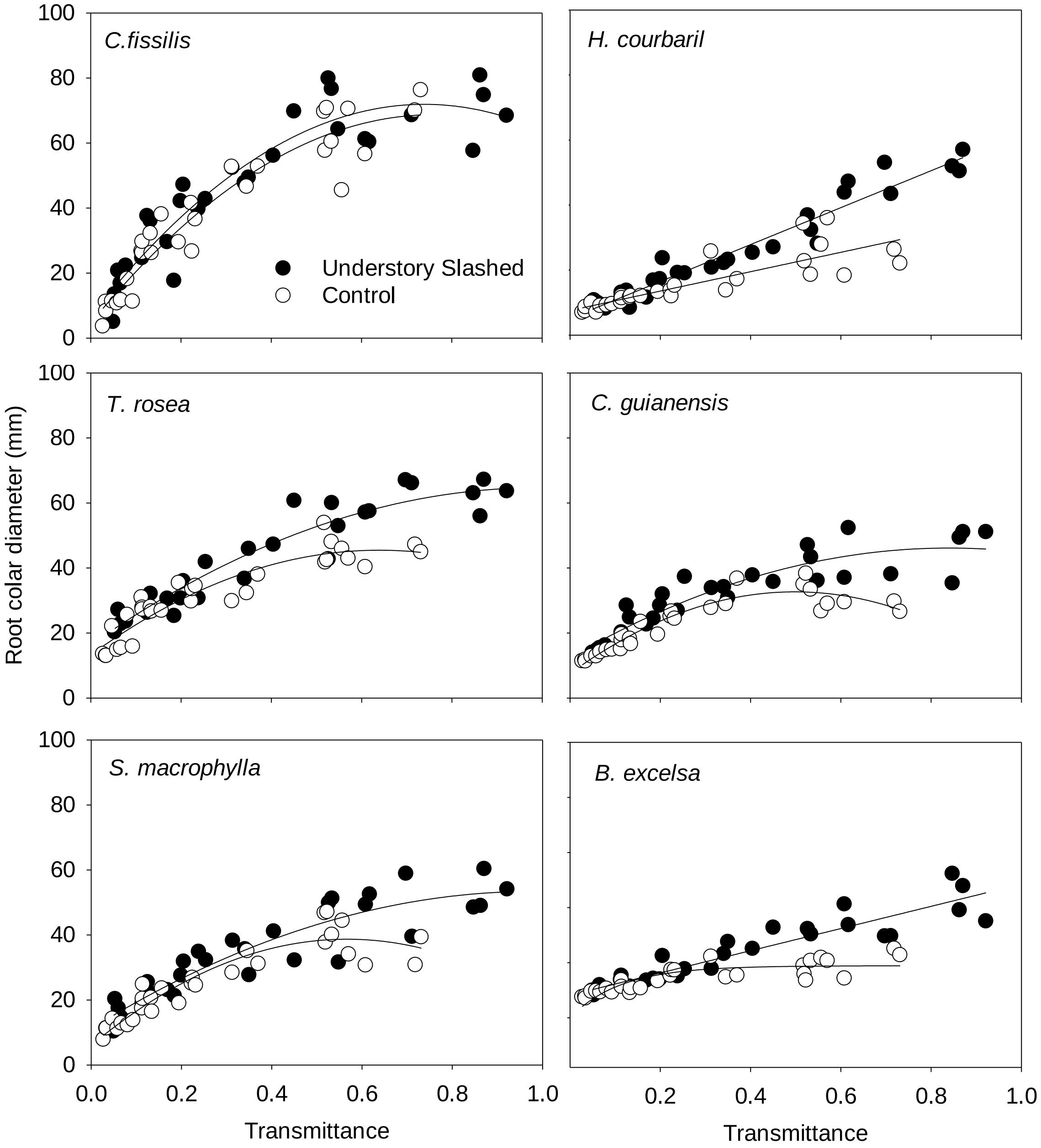

Fig. 2. Scatter plot of the relationship between root collar diameter and light transmittance for six tropical tree species in a secondary forest enrichment planting site two years after planting. The summary of equations parameters are presented in Table 3.

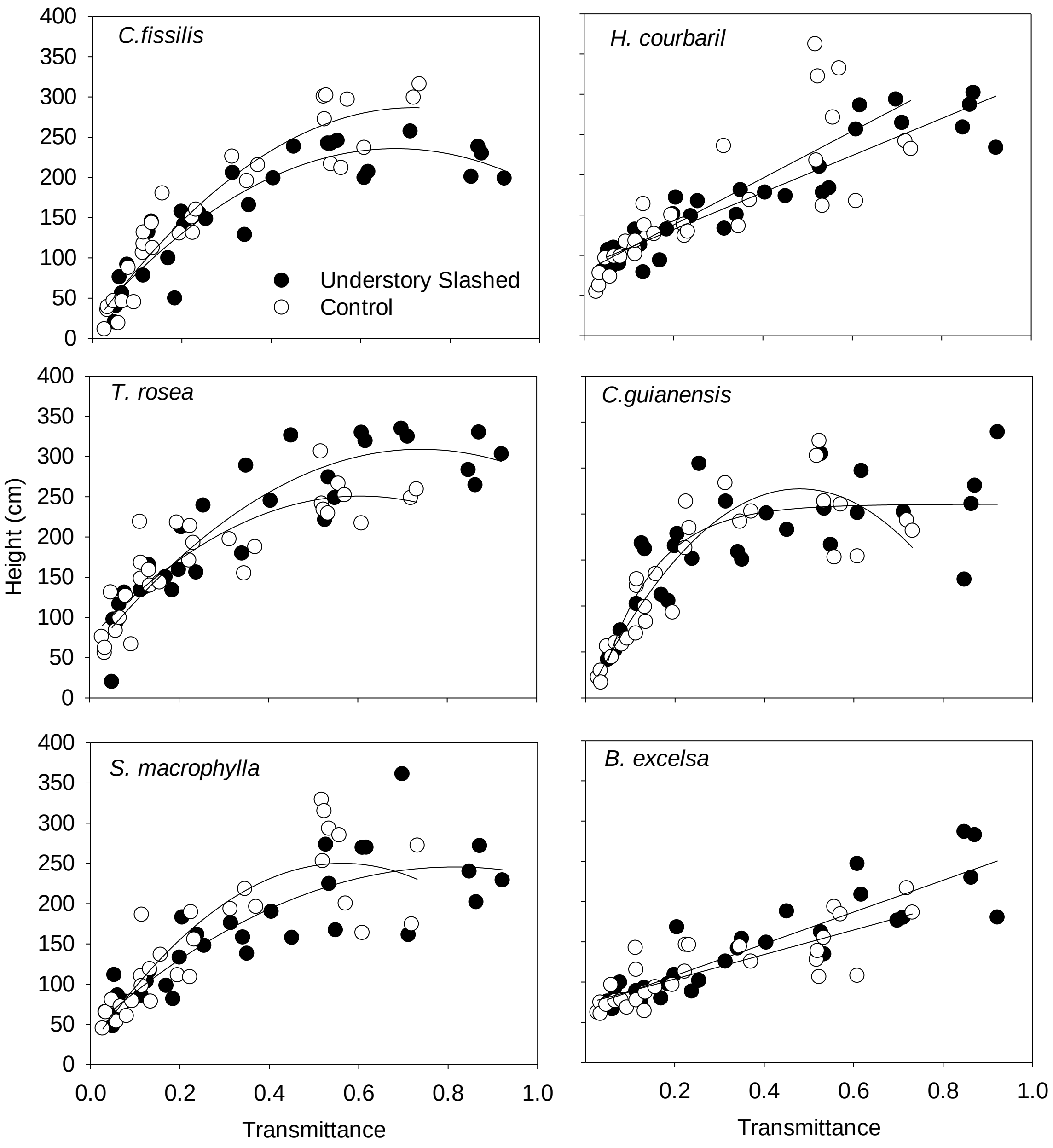

Fig. 3. Scatter plot of the relationship between root collar diameter and light transmittance for six tropical tree species in a secondary forest enrichment planting site two years after planting. The summary of equations parameters are presented in Table 3.

3.2. Root collar diameter relative growth

The root collar diameter growth of all species, except *C. fissilis*, was strongly affected by light transmittance and the year (Table 4). During the first year after planting, the growth was higher than during the second year for all species (Fig. 4). The year after planting also affected the relationship between transmittance and diameter growth of *C. fissilis* and *T. rosea* (Table 4). The *C. fissilis* and *T. rosea* growth responses to light transmittance were more pronounced during the first year after planting (Fig. 4). Only *C. guianensis* growth was directly sensitive to understory slashing; however, understory slashing changed the *C. fissilis* and *T. rosea* diameter growth responses to light transmittance (Table 4). *C. guianensis* grew faster in the understory slashed plots than in the control plots (Fig. 4). The *T. rosea* diameter growth response to light transmittance was steeper in understory slashed subplots only during the second year after planting (three-factor interaction, Table 4 and Fig. 4).

3.3. Height relative growth

The height growth of all species, except *C. fissilis* and *C. guianensis,* was strongly affected by light transmittance and the year (Table 5). Similar to that observed for root collar diameter, height relative growth was higher for the first year than the second year (Fig. 5). The relationships between transmittance and diameter growth of *C. fissilis* and *T. rosea* were year-dependent (Table 5). In the first year, the growth response to transmittance was steeper for *T. rosea*, whereas the *C. fissilis* height growth at intermediary and low levels of light transmittance was greater during the second year (Fig. 5). Understory slashing did not directly affect the height growth of any species but changed the response to light transmittance for *T. rosea*, *C. fissilis* and *C. guianensis* (Table 5). For these three species, the height response to transmittance was steeper in the control subplots (Fig. 5). A tree-factor interaction was observed in *T. rosea* and shows that the height response to transmittance was steeper in the control subplots only in the second year (Table 5 and Fig. 5).

Table 4.

Summary of transmittance (T), understory slashing (US), year (Y) and interaction effects on root collar diameter relative growth of six tree species planted in a secondary forest enrichment planting site.

Factors	*C. fissilis*	*T. rosea*	*S. macrophylla*	*C. guianensis*	*H. courbaril*	*B. excelsa*
(T)	***	***	***	***	***	***
(US)	n.s.	n.s.	n.s.	***	n.s.	n.s.
(Y)	n.s.	***	***	***	***	***
(T) x (US)	***	**	n.s.	n.s.	n.s.	n.s.
(T) x (Y)	***	**	n.s.	n.s.	n.s.	n.s.
(US) x (Y)	*	n.s.	n.s.	n.s.	n.s.	n.s.
(T) x (US) x (Y)	n.s.	*	n.s.	n.s.	n.s.	n.s.

ANCOVA p-values (* < 0.05; **<0.01; ***<0.001; n.s. ≥ 0.05)

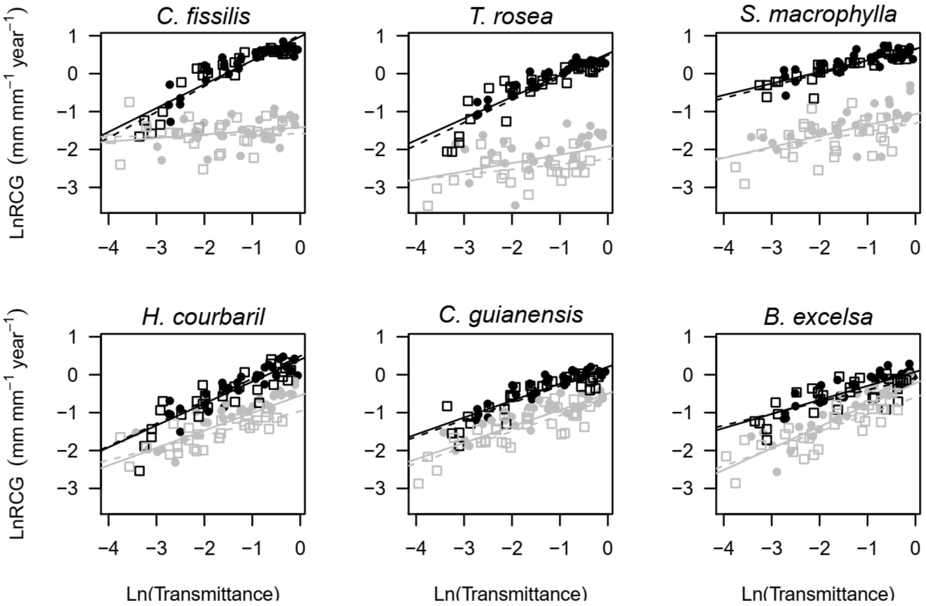

Fig. 4. Scatterplot of the relationship between light transmittance (Ln values) and root collar diameter relative growth (LnRCG, Ln values) of six commercial species in plots with understory slashing (circle) and control (square) during the first (black) and second (gray) years of enrichment planting in a Central Amazonian secondary forest.

Table 5.

Summary of transmittance (T), understory slashing (US), year (Y) and interaction effects on height relative growth of six tree species planted in a secondary forest enrichment planting site.

Factors	*C. fissilis*	*T. rosea*	*S. macrophylla*	*C. guianensis*	*H. courbaril*	*B. excelsa*
(T)	***	***	***	***	***	***
(US)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
(Y)	n.s.	***	***	.	***	***
(T) x (US)	***	**	n.s.	*	n.s.	n.s.
(T) x (Y)	***	**	n.s.	n.s.	n.s.	n.s.
(US) x (Y)	*	n.s.	n.s.	*	.	n.s.
(T) x (US) x (Y)	n.s.	*	n.s.	n.s.	n.s.	n.s.

ANCOVA p-values (.<0.10; * < 0.05; **<0.01; ***<0.001; n.s. ≥ 0.05)

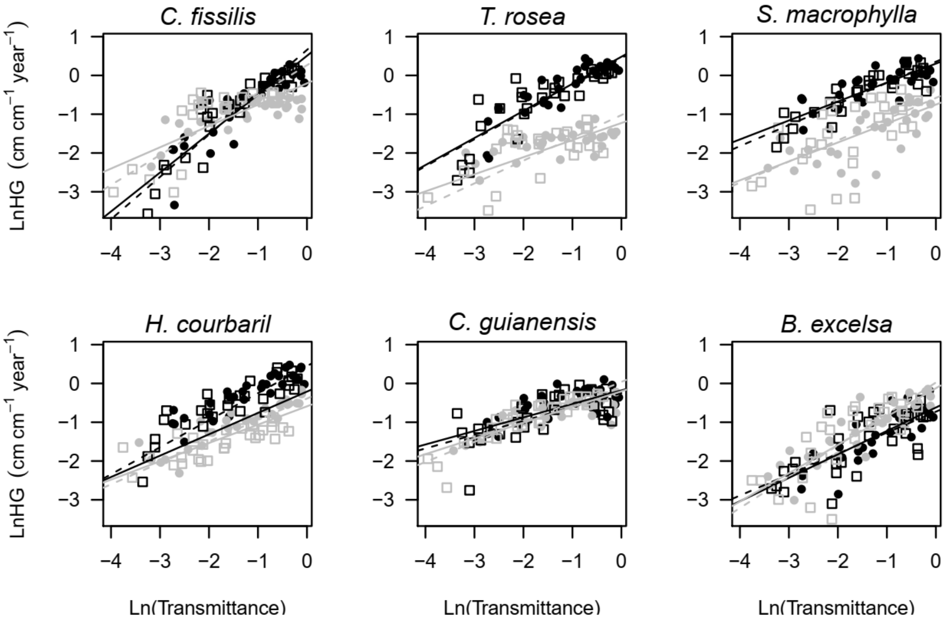

Fig. 5. Scatterplot of the relationship between light transmittance (Ln values) and height relative growth (LnHG, Ln values) of six commercial species in plots with understory slashing (circle) and control (square) during the first (black) and second (gray) years of enrichment planting in a Central Amazonian secondary forest.

3.4. Mortality and shoot borer attack

The average mortality (%) was the highest for *C. fissilis*, *T. rosea* and *S. macrophylla*, whereas the lowest values were observed for *C. guianensis* and *B. excelsa* (Table S1). Mortality decreased with basal area reduction and was the highest at low light levels in plots where no canopy trees were felled (Table S1). The consistent mortality at plots without refinement demonstrates the trade-off between growth and mortality. During the first year – in both the control and slashed understory subplots – a clear trade-off pattern between fast growth in high light and low survival in deep shade was observed (Fig. 6). The only exception was the root collar diameter growth in understory slashed subplots. Conversely, a significant trade-off pattern was not observed during the second year.

Shoot borer attacks were strongly dependent on understory slashing. Shoot borer attacks were only observed in two seedlings in control subplots whereas in understory slashed conditions, the attacks increased according to basal area reduction and reached values of 56%, 32% and 24% for *S. macrophylla*, *C. fissilis* and *C. guianensis*, respectively, during the experimental period (Fig. 7).

4. Discussion

4.1. Realized root collar diameter and height growth as affected by light transmittance two years after planting

Two years after enrichment planting, the root collar diameter and height responses to light transmittance were different in terms of species and understory slashing (Table 3, Fig 2 and 3). A species-specific growth response to light has been shown in secondary forest enrichment planting that manipulated the light environment by cutting line width (Ådjers et al., 1995) and refinement intensity (Wiener, 2010). The present study, in addition to corroborating previous evidence, showed that understory slashing as supplementary silvicultural treatment to canopy openness treatment (*e.g.*, refinement) is effective in improving the maximum height and diameter attained by some species. Both the diameter and height reached were the result of seedling growth planted under different conditions. Therefore, we will next discuss the relative growth responses of the species to the silvicultural treatments in the first and second years after planting.

4.2. Relative growth as affected by silvicultural treatments and the time after planting

The relative growth of the root collar diameter and height were directly and indirectly affected by the year after planting but were less dependent on understory slashing. The direct effect showed the highest growth during the first year – with exceptions for the heights of *C. fissilis* and *B. excelsa* – and the indirect effect was the less steep root collar diameter (*C. fissilis* and *T. rosea*) and height growth (*T. rosea*) in response to light transmittance in the second year after planting. Growth reductions of seedlings in enrichment planting over the years can be a result of technical and biological factors. Technical factors are maintenance practices, which control the light availability during the initial establishment period and nutritional status (Catinot and Bossanyi, 2018; ITTO, 2002; Lamprecht, 1990). However, technical factors do not seem to have been the main factors responsible for the reduction in seedling growth during the second year, given that growth was reduced even in plots where the understory was periodically controlled and in plots where all canopy trees were felled (Fig. 4 and 5). Moreover, no visual nutrient symptom deficiency was observed during the period of study.

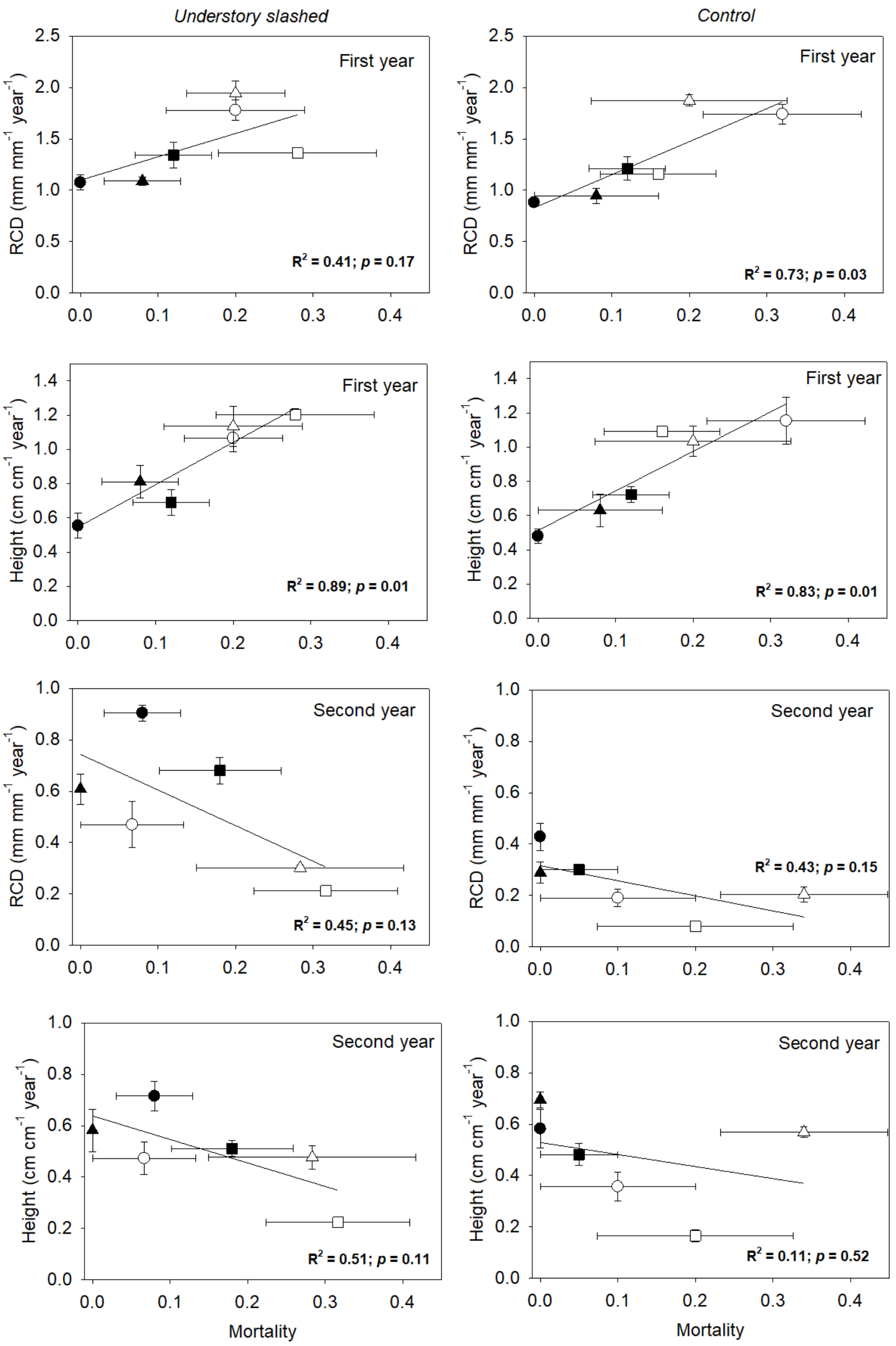

Fig. 6. Scatter plot of the relationship between mortality at low light and relative growth (root collar diameter [RCD] and height) at high light of six tree species in a secondary forest enrichment planting. *C. fissilis* (open triangle); *T. rosea* (open square); *S. macrophylla* (open circle); *H. courbaril* (closed square); *C. guianensis* (closed triangle); *B. excelsa* (closed circle).

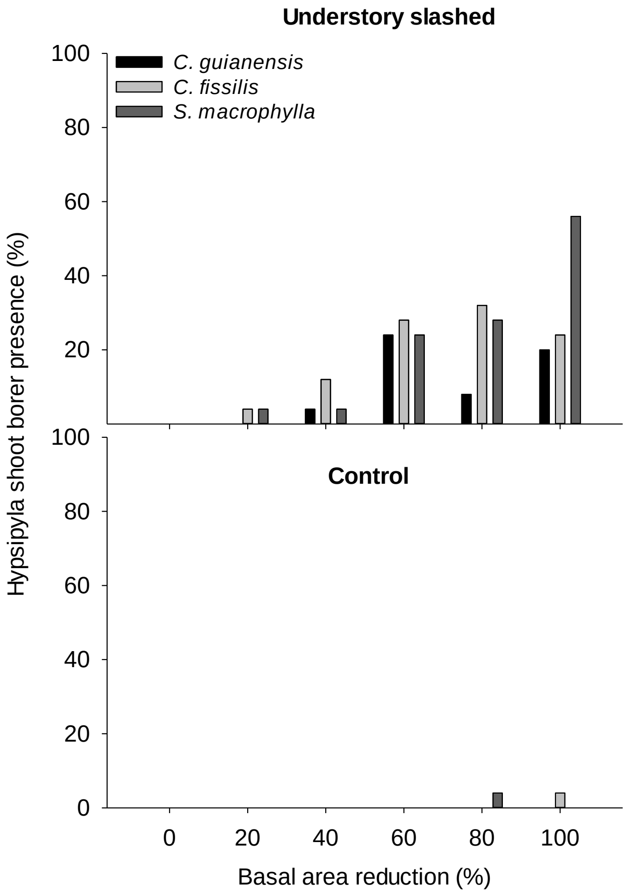

Fig. 7. Bar plot of shoot borer presence in the control and understory slashed subplots along a gradient of basal area reduction created by refinement in a secondary forest enrichment planting site.

Biological factors are the ontogenetic changes during the seedling development to juvenile tree stages (Delagrange et al., 2004; Machado and Reich, 2006). The growth drop during the second year was the greatest for the long-lived pioneers (*C. fissilis, T. rosea* and *S. macrophylla*) and those growing in high light conditions (Fig. 2 and 3). In a subtropical Australian rainforest, the magnitude of ontogenetic changes in growth response to light was higher for light-demander than shade-tolerant species (Sendal et al., 2018). As a seedling grows, the changes in the proportion of photosynthetic and nonphotosynthetic tissues, self-shading and functional traits affect the plant growth (Delagrange et al., 2004; Machado and Reich, 2006, Sendal et al., 2015; Sendal et al., 2018) and seem to be more pronounced in light-demander tree species. Unlike the other species, *B. excelsa* height growth was highest during the second year whereas it did not change in *C. fissilis*. The *B. excelsa* seedlings that were 1 m high grew faster than smaller (< 70 cm) seedlings in two natural populations in Northern Bolivia (Zuidema, 2003); this height threshold was followed by lateral branching in the present study (field observations). As a result, *B. excelsa* needs more time than the other tested species to acclimate in the field, and the mechanisms (*e.g.*, root development, branching, seed reserves depletion) should be better investigated.

Understory slashing treatment directly affected only the root collar diameter of *C. guianensis* (understory slashed > control) and indirectly changed the light transmittance effect on height and diameter growth of *C. fissilis* and *T. rosea*. The native understory plants compete with planted seedlings for above and below ground primary resources, hampering the growth in enrichment plantings (Ådjers et al., 1995; Duclos et al., 2013; Gerhardt, 1996; Romell et al., 2008), as shown for *C. guianensis*. However, an untreated understory can stimulate the height growth of some species by lateral shading (Catinot and Bossanyi, 2018), according to that observed for *C. fissilis* and *T. rosea* growing in intermediary to high light levels (transmittance 0.3 - 0.9, Fig. 5). Both former species are pioneer light-demanders that grow faster in open areas (*e.g.*, large canopy gaps and clear cutting) and have higher height growth investment to overcome competitors' growth and stay in good light conditions (Swaine and Whitmore, 1988). Moreover, the ecological characteristics of *C. fissilis* also explain the absence of the year effect on height growth.

4.3. Mortality and shoot borer attack

The effect of the time after planting was also significant for the trade-off between growth and survival of the species (Fig. 6). During the first year after planting, there was a strong relationship between growth in high light and mortality of species under deep shading conditions. For species with pioneer characteristics (*C. fissilis, T. rosea* and *S. macrophylla*), higher mortality rates were observed under shade and high growth under full sun, whereas species with shade tolerance (*H. courbaril, C. guianensis* and *B. excelsa*) characteristics showed lower growth under full light conditions but low mortality values under accentuated shading. The growth-survival trade-off has been demonstrated in tropical tree species (Kitajima et al., 1994, Kobe, 1999, Sendal et al., 2015), but it is still the subject of much debate. The present study demonstrated that the growth-survival trade-off was absent two years after planting (Fig 6). The growth reduction of light-demander species was the main cause of this decoupling. Moreover, a shift in the rank growth was observed between pioneers and shade-tolerant species even though the pioneer species still had a higher mortality (Fig 6).

A high mortality at intermediary to high light levels (basal area reduction > 40%) was observed for *T. rosea* and *S. macrophylla* (Table S1). The seedlings of *T. rosea* were attacked by termites, which eventually led to high mortality under conditions of higher light availability, whereas the *S. macrophylla* species was affected by the shoot borer attack. All Meliaceae species experienced the terminal shoot borer attack under conditions of high light availability and with the understory cut (Fig. 7). However, only the young trees of *C. fissilis* and *C. guianensis* were able to sprout and recover from the attack most of the time, whereas *S. macrophylla* plants died in most cases after the attack. Planting in a highly diverse system has been demonstrated be an effective silvicultural control of shoot borers (Newton et al., 1993) and, therefore, the establishment of enrichment planting under secondary forests appears a good alternative for this purpose.

4.4. Silvicultural implications

Sustainable management of secondary forests for productive and protective objectives is a critical process for conservation of this vegetation in tropical landscapes and, as a consequence, its ecosystem provision, regulation and cultural services (Chazdon et al., 2016; Guariguata and Ostertag, 2001; Finegan, 1992; Poorter et al., 2016). Proper management of secondary forests must include the choice of an adequate silvicultural system; thus, enrichment planting has proven to be an appropriate alternative (ITTO, 2002; Peña-Claros et al., 2002; Wiener, 2010). However, for the initial establishment of the species planted in enrichment planting to be satisfactory, prior silvicultural treatments and periodic maintenance during the development of the plantation is necessary, which will create favorable conditions for the seedlings (Ådjers et al., 1995; Duclos et al., 2013; Lamprecht, 1990; Romell et al., 2008). Among the available silvicultural treatments, canopy tree refinement and understory slashing were tested in the present study. Recommendations of silvicultural treatments should be made with caution and in studies that assess medium and long-term responses of commercial species (ITTO, 2002; Neves et al., 2019). However, some generalizations can be made regarding the initial establishment of the six commercial tree species tested in the present study over two years.

The choice of the best silvicultural treatment and the intensity of application that will guarantee the initial establishment should be analyzed in relation to the effects on the growth, mortality and attack of pests for each tree species or group (*e.g.*, *pioneer* *and nonpioneer*). From a growth point of view, all species reached higher height and diameter values under larger canopy openings, where the refinement of the canopy trees was of high intensity and where the understory was removed (Table 3, Fig. 2 and 3). However, the direct effect of understory cutting was minimal compared to the effect of refinement and should be carefully analyzed because it strongly influences the attack of shoot borers on Meliaceas species (Fig. 7). Thus, particularly under conditions of larger canopy openness, localized control of understory competition (0.5 - 1 m radius around the seedling) can be seen as a preventive measure against shoot borer attack and still ensures reduced competition (Catinot and Bossanyi, 2018; Schwartz et al., 2013). Regarding mortality, the planting of light-demanding species in conditions of high shading should be avoided and the planting of shade-tolerant species viewed with caution, in cases where the objective is production, as they will present reduced growth. Finally, to improve our understanding about the mechanisms behind the interspecific growth variation in response to light availability as affected by silvicultural treatments, future studies should explore the link between functional traits, with more detailed morphological and physiological measurements, and tree demography (survival and growth).

5. Conclusion

Silvicultural treatments improve the initial establishment of commercial tree species in Amazon secondary forest enrichment planting. Seedlings grow faster under a higher light transmittance promoted by canopy trees refinement, but the effects depend on species, understory slashing and the year after planting. Understory slashing has a minor positive consequence on growth and a consistent negative effect on shoot borer attacks. In the second year after planting, the seedling growth is reduced and the silvicultural treatment effects on growth are limited, principally due to light-demanders species. As a result, the growth response analyses of tropical tree species to silvicultural treatments in enrichment planting should consider the tree development stages.

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Conflicts of interest

None.

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Appendix A. Supplementary material

Text S1

For irradiance measurements and transmittance calculations, two photosynthetic photon flux density (PPFD; µmol m^{-2} s^{-1}) sensors were used: one for measurements inside the plots subjected to the silvicultural treatments and a second for measurements in a full sun area. The measurements in the plots were obtained using a line sensor (MQ-301: Line quantum with 10 sensors and handheld meter, Apogee, USA) during six-hour intervals (06:30-07:00 h; 08:30-09:00 h; 10:30-11:00 h; 12:30-13:00 h; 14:30-15:00 h; 16:30-17:00 h). Irradiance measurements were obtained above nine systematically spaced planted seedlings per subplot. The second PPFD sensor (MQS B/ULM-500 logger, Heinz Walz, Germany) was installed in a full-sun area (100 m from the secondary forest), and PPFD values were recorded every 30 seconds for 5-14 days. The values of irradiance in the plots and full-sun area were measured during four periods: 2017 dry season (September), 2018 wet season (April), 2018 dry season (September) and 2019 wet season (February).

The daily transmittance was obtained from the average of the hourly transmittance values recorded during the day (Rich et al., 1993). Hourly transmittance was calculated as the ratio of PPFD measured at the plots in each hour interval and the average values recorded during the same hour interval in the full-sun area. Total daily irradiance (mol m^{-2}) in the full sun area was calculated by the product of mean daily values and photoperiod (Chazdon and Fetcher, 1984).

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Appendix A. Supplementary material

Fig. S1. Temporal changes in the forest cover at Fazenda experimental da Universidade Federal do Amazonas. The secondary forest area is red highlighted in 2017 image. The images were obtained from CNES/Astrium satellite on Google earth and Landsat – 5 were downloaded from http://www.dgi.inpe.br/CDSR/.

Table S1. Mortality (%) of six tree species along a gradient of basal area reduction (BAR) in a secondary forest enrichment planting site with understory slashed and control.

Understory slashed

BAR (%)	*C. fissilis*	*T. rosea*	*S. macrophylla*	*H. courbaril*	*C. guianensis*	*B. excelsa*
0	40%	48%	24%	28%	8%	8%
20	4%	36%	12%	12%	4%	16%
40	0%	16%	20%	4%	4%	4%
60	0%	20%	32%	0%	0%	0%
80	0%	4%	40%	4%	8%	0%
100	8%	16%	16%	0%	0%	0%

Control

BAR (%)	*C. fissilis*	*T. rosea*	*S. macrophylla*	*H. courbaril*	*C. guianensis*	*B. excelsa*
0	48%	36%	36%	16%	8%	0%
20	24%	12%	36%	16%	12%	8%
40	0%	8%	16%	12%	4%	4%
60	4%	20%	12%	4%	4%	8%
80	0%	16%	24%	12%	0%	16%
100	0%	20%	28%	4%	8%	0%

Capítulo 3

Santos, V.A.H.F; Ferreira, M.J. 2019. Are photosynthetic leaf traits related to first-year growth of tropical tree seedlings? A light-induced plasticity test in a secondary forest enrichment planting. Environmental and Experimental Botany. *Submitted*.

Are photosynthetic leaf traits related to first-year growth of tropical tree seedlings? A light-induced plasticity test in a secondary forest enrichment planting

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Abstract

Understanding light-induced plasticity of growth and your relationship with photosynthetic traits plasticity is central to the identification of the mechanisms associated with tropical tree seedlings establishment in enrichment plantings. In a secondary forest submitted to silvicultural treatments and enriched with six tropical tree species, we tested the hypothesis that growth is related to photosynthetic leaf traits; there is a relationship between light-induced plasticity of growth and photosynthetic leaf traits; and that growth plasticity is a subjacent mechanism of growth-survival trade-off. Growth was analyzed as a biomass index that gets together collar and height growth. Photosynthetic leaf traits were selected considering your significance in the photosynthetic process: biochemical (light-saturated CO_2 assimilation, A_{sat}), diffusive limitations (stomatal conductance, g_{s}), light interception (specific leaf area, *SLA*), light absorption (chlorophyll *a* and *b* ratio, $Chl_{\mathrm{a/b}}$) and light use (fluorescence parameters, $F_{\mathrm{v}}/F_{\mathrm{m}}$; PI_{abs}, PI_{total}). The plasticity was represented by the slope of the relationship between canopy light transmittance and growth, and photosynthetic leaf traits. At the end of the first year after planting, growth was related to almost all photosynthetic leaf traits and the strongest relationships (high slope and $R^2 > 0.50$) were observed with A_{sat}, *SLA* and PI_{total}. Light-induced growth plasticity varied three times between species. The interspecific growth plasticity was related to *SLA* and $F_{\mathrm{v}}/F_{\mathrm{m}}$ plasticity, which varied 4.9 and 2.4 times between species, respectively. Seedling mortality in the shaded understory and the growth at high light environment were associated with growth plasticity. Photosynthetic leaf traits effectively represent the growth response mechanisms to silvicultural treatments that manipulate the light environment in enrichment plantings and the subjacent mechanism of growth plasticity has an intrinsic effect on the growth-survival trade-off.

Keywords: growth-survival trade-off, Amazon, silvicultural treatments, photosynthesis, JIP-test

1. Introduction

Enrichment plantings are a suitable alternative to conserve the broad area of tropical secondary forests (ITTO, 2002). Generally, silvicultural treatments are applied in the secondary forest before the enrichment planting to manipulate the light conditions to the seedlings planted (Ådjers et al., 1995; Gustafsson et al., 2016; Romell et al., 2009; Peña-Claros et al., 2002). The seedlings growth response to light in enrichment planting is dependent on the species selected (Ådjers et al., 1995; Gustafsson et al., 2016; Wiener et al., 2010). For example, in an enrichment planting with 17 native tree species in a Northeastern Peru secondary forest were observed three main patterns of growth response to irradiance: a linear response, curvilinear response and non-response (Wiener, 2010). Hence, generalizations about the best silvicultural intervention intensity are generally not applied but could be facilitated by grouping the species with similar functional traits.

Functional traits are those measured at individual-level and which impact fitness indirectly via their effects on growth, reproduction and survival (Violle et al., 2007) and, recently, the functional trait approach has been experienced in the field with the objective of to test whether functional traits can predict tropical tree growth (Guimarães et al., 2018; Falster et al., 2018; Finegan et al., 2015; Li et al., 2017; Poorter et al., 2018). Two of these tests were realized at Central Amazon and your opposing results concluded that functional characteristics measure at individual-level are poor predictors of saplings growth in a rainforest (Poorter et al., 2018), but was recommended as growth predictors of tree seedlings planted in a disturbed area

(Guimarães et al., 2018). The growth-trait relationships inconsistencies between studies can be attributed to the level of approach (*e.g.*, individual or species), the lack of an appropriate set of characteristics used to represent relevant dimensions of function (*e.g.*, photosynthetic process) and the temporal and spatial variation of environmental conditions (Yang et al., 2018). Thus, considering the set of characteristics analyzed, a set of photosynthetic leaf characteristics can be promising because they represent the main biological process that affects plant growth. Besides, the environmental consideration - including testing for environmental effects - also can improve the growth-traits relationships, since both may interact with the abiotic environment (*e.g.* light).

Photosynthetic leaf traits can be divided into the main steps of the photosynthesis process. Therefore, for each step of the photosynthetic process - from interception (specific leaf area) and absorption (chlorophyll concentration) to the use of light (fluorescence parameters) - there are characteristics that represent a fundamental mechanism of growth responses to environmental variation and therefore could be good predictors of growth. Fluorescence parameters, for instance, have been shown as a good proxy of CO_2 assimilations for Amazonian trees under a gradient of light (Santos et al., 2019) and photosynthetic efficiency in ecological studies (Bussotti et al., 2020). Hence, the first objective of this work was to test the hypothesis that photosynthetic leaf traits are related to tree seedlings growth.

The diversity of tropical seedling growth response to light has been attributed to the plant's colonization strategies to the different light microhabitats into the forest (Asanok et al., 2013; Dalling et al., 2004; Denslow, 1980; Swaine and Whitmore, 1998). Light-demanding species (pioneers and long-lived pioneers) needs direct light to seed germination and fast seedling growth during the firsts years, whereas shade-tolerant species germinate in shaded understory and require (partial shade-tolerant) or does not require (total shade-tolerant) an increase in light available to growth (Chazdon 2014; Finegan, 1992; Swaine and Whitmore, 1998; Turner, 2001). In addition to growth, photosynthetic leaf traits also change with light availably in a species-dependent way (Chazdon et al., 1996; Kitajima, 1994; Rozendall et al., 2006; Strauss-Debenedetti and Bazzaz, 1991). As a result, tropical tree species have different light-induced growth and photosynthesis plasticity. Therefore, in the present study the growth and photosynthetic leaf traits - of six tropical tree species - responses to a canopy light transmittance were utilized to test the hypothesis that light-induced growth plasticity is related to the photosynthesis plasticity, and so indicate the major traits that could be used in species screening to enrichment planting. Further than growth, have been demonstrated that full-sun fast-growing species suffer high mortality in shaded environments during the first year after germination, while shade-tolerant species acquire conservative strategies to survival in understory but with consequences to growth (Kitajima, 1994). As a result, species niche partitioning is also related to growth-survival trade-off (Sterck et al., 2006). Since plasticity requires energy costs, these costs of plasticity may be a mechanism underlying the trade-off between growth and survival (DeWitt et al., 1998; Oguchi et al., 2017). Hence, the third objective of this study was to test the hypothesis that interspecific light-induced growth plasticity is related to fast growth in high light environments and mortality in the shaded understory. The confirmation of this hypothesis will add evidence that growth plasticity and underlying photosynthetic processes are fundamental to niche partitioning and, consequently, to recommendations of silvicultural treatments in enrichment plantings.

2. Materials and Methods

2.1. Experiment description

This study was realized in a secondary forest enrichment planting located at Manaus, Amazonas, Brazil (02°38'S, 60°03.5'W). Seedlings of six tree species were planted in a secondary forest that had received silvicultural treatments to promote a wide canopy opening gradient (Table 1). These treatments consisted of six levels of basal area thinning (0, 20, 40, 60, 80 and 100%) by direct cutting of canopy trees and two levels of understory cutting (cut and uncut). Silvicultural treatments promoted a canopy light transmittance gradient that varied 27 times (3.4% to 94.8%) and, consequently, total daily photosynthetic photon flux density ranged between 1.7 and 36.6 (PPFD, μmol m^{-2} s^{-1}). Further information about the planting methods and light transmittance measurements are described in Text S1.

Table 1.

The six tree species studied with the ecological group, average first-year root collar diameter relative growth at the full sun (RCRG, mm mm^{-1} year), average first-year height relative growth at full sun (HRG, cm cm^{-1} year) and first-year mortality (%) at shaded understory.

Species	Ecological group*	RCRG	HRG	Mortality
Cedrela fissilis Vell.	Pioneer (LLP)	55.91	156	20
Tabebuia rosea (Bertol.) Bertero ex A.DC.	Pioneer (LLP)	45.71	226	22
Swietenia macrophylla King	Pioneer (LLP)	33.86	170	26
Hymenaea courbaril L.	Non-Pioneer (PST)	23.01	164	12
Carapa guianensis Aubl.	Non-Pioneer (PST)	24.07	140	8
Bertholletia excelsa Bonpl.	Non-Pioneer (PST)	14.68	101	0

*Ecological group according to Swaine e Whitmore, 1988; Finegan 1992, Poorter et al., 2006; Chazdon, 2014. LLP (long-lived pioneer), PST (partial shade-tolerant).

2.2. Growth and mortality measurements

During the first year after planting - at every two months - was measured the root collar diameter (*D*) and height (*H*) of 1,800 planted seedlings (300 of each species). Plant aboveground biomass was approximated by HD^2, as proposed by Kohyama and Hotta 1990. The annual aboveground biomass relative growth (*RG*) was calculated as:

$$RG = \ln HD_1^2 - \ln HD_0^2,$$

where HD_0^2 is the plant biomass in the day of planting, HD_1^2 is the plant biomass one year after planting.

During the bimonthly measurements was also observed the plant mortality and that was severely damaged. Were excluded from growth analyzes 111 (0.06%) plants that were cut or broken accidentally or by insects.

2.3. Photosynthetic leaf traits measurements

A set of photosynthetic leaf traits was measured at the end of the first year after planting (Table 2). The traits were measured in 5 saplings (one of each species) located at the average light conditions of one plot with 30 saplings. In all, there were 60 plots and therefore were measured 360 saplings (60 of each species) spanning all canopy transmittance levels. All the photosynthetic leaf traits were measured in the same leaf or leaves with same aspect, as mature and healthy.

The two gas exchange characteristics, **light-saturated photosynthesis (A_{sat}) and stomatal conductance (g_s)**, were measured with an infrared gas analyzer (LI-6400XT, LI-COR, USA). Measurements were taken on one leaf per plant; however, prior to recording exhaustive tests were performed on several leaves per plant to measure those leaves that had the maximum values of A_{sat} and g_s. The measurements were performed between 08:00 and 13:00 h and the gas analyzer chamber adjusted to a flow rate of 400 µmol s^{-1}; 400 µmol mol^{-1} of CO_2 concentration; 21 mmol mol^{-1} of H_2O vapor concentration; 31 °C of leaf temperature; and photosynthetic photon flux density of 2000 µmol m^{-2} s^{-1}. **Specific leaf area (*SLA*)** was determined by the area (cm^2) and oven-dried mass (65 °C; g) ratio of ten leaf discs. **Chlorophyll *a* and *b* ratio (*$Chl_{a/b}$*)**, was calculated after the determinations of chlorophyll *a* and chlorophyll *b* concentrations which followed the steps of acetone extraction (10 ml of 80% acetone with 0.05 g of $MgCO_3$ per 0.1 g of fresh leaf); filtration, absorbance reading at two wavelengths (645 and 663 nm; Biochrom Libra S50 UV/Vis, Cambridge, UK), and concentrations calculations (Lichtenthaler and Wellburn, 1983; Hendry and Price, 1993). Fluorescence was measured with a portable fluorimeter (PEA, MK2-9600, Hansatech, Norfolk, UK) adjusted to emitted a saturating light pulse of 3000 µmol m^{-2} s^{-1} at a wavelength of 650 nm during 1 s. Before measure, the leaves were dark acclimated during 30 min for complete oxidation of the photosynthetic electron transport chain. The chlorophyll *a* polyphasic transient was recorded to five leaves and the JIP-test applied to determinations of **maximum quantum yield of PSII (F_v/F_m)**, **performance index (PI_{ABS})** and **total performance index (PI_{total})** following Strasser et al. (1995), Strasser et al. (1999), Strasser et al. (2010), Tsimilli-Michael and Strasser (2008). PI_{abs} and PI_{total} are two indices that integrated, respectively: the efficiency with which an electron is trapped by PSII and is transferred further than quinone; and the efficiency with which an electron is trapped by PSII, transferred further than quinone and reduce the end electron acceptors at the PSI.

Table 2.

Definition and the significance to photosynthesis of the photosynthetic leaf traits measured

Trait	Definition	Significance to photosynthesis
A_{sat}	Light saturated photosynthesis (µmol[CO_2] m^{-2} s^{-1}); maximum photosynthesis achieved at full sun	Net CO_2 assimilation rate, biochemical limitation
g_s	Stomatal conductance (mol[H_2O] m^{-2} s^{-1}); water vapor or CO_2 passage through stomata pore	Diffusive limitation
SLA	Specific leaf area (g cm^{-2}); investment of biomass to expand leaf area	Light interception
$Chl_{a/b}$	The ratio of chlorophyll *a* and *b* concentrations; the relative size of light harvesting complex	Light absorption
F_v/F_m	The maximum quantum yield of primary PSII photochemistry	Light use in the first steps of the electron transport chain
PI_{abs}	The performance index, integrated efficiency with which an electron is trapped by PSII and transferred further than quinone	Light use in the first to intermediary steps of the electron transport chain
PI_{total}	The total performance index, integrated efficiency with which an electron is trapped by PSII, transferred further than quinone and reduce the end electron acceptors at the PSI	Light use in the first to final steps of the electron transport chain

2.4. Plasticity index and data analysis

The strength and direction of the photosynthetic leaf traits and *RG* relationships were accessed by linear regressions of linearized (ln) *RG vs* leaf traits. The plasticity index was the slope of the regression of linearized (ln) *RG* and traits *vs* linearized light transmittance (Valladares et al., 2006). Therefore, as higher the slope more responsive was the *RG* and/or the trait to transmittance; and non-significant relationships were considered as the absence of trait response to environment. The relationships of *RG* response to transmittance (*RG* plasticity) between photosynthetic leaf traits plasticity response to transmittance (Traits plasticity) were also accessed by linear regression. Moreover, to address whether growth plasticity is related to growth-survival trade-off was tested the linear relationship of *RG* plasticity between mortality at shaded understory (average, maximum and minimum transmittance of 5.8%; 8.2% and 3.5%, respectively) and *RG* at high light environments (average, maximum and minimum transmittance of 78.6%; 94.8% and 54.6%, respectively). The shaded understory was represented by plots where forest canopy was untouched and high light environments where 100% of canopy trees basal area was removed by direct cut. All analyses were performed using the statistical program R version 3.5.1 (R Core Team, 2018).

3. Results

3.1. Relationship between growth and photosynthetic leaf traits

The set of photosynthetic leaf traits tested showed a good relationship, despite some exceptions, with the seedlings *RG* (Fig. 1 and Table S1). Considering all species, the stepper *RG*-traits relationships were observed for A_{sat}, *SLA* and PI_{total} (Fig. 1a, c and g). Five species, but not *T. rosea*, showed a strong coupling between *RG* and g_s (Fig. 1b). The *RG*-PI_{abs} relationship was observed only for *C. fissilis,* while this species was the only one that not showed a growth-F_v/F_m significant relationship (Fig. 1e and f). $Chl_{a/b}$ was related to *RG* for all species, but with a less inclined slope (Fig. 1d). *B. excelsa RG* showed a slope response to A_{sat} and PI_{total} 2.56 and 1.93 times, respectively, higher than the other species average. On the other hand, *B. excelsa* showed the slowest *RG -SLA* slope inclination, which was two times lower than the observed for *T. rosea*.

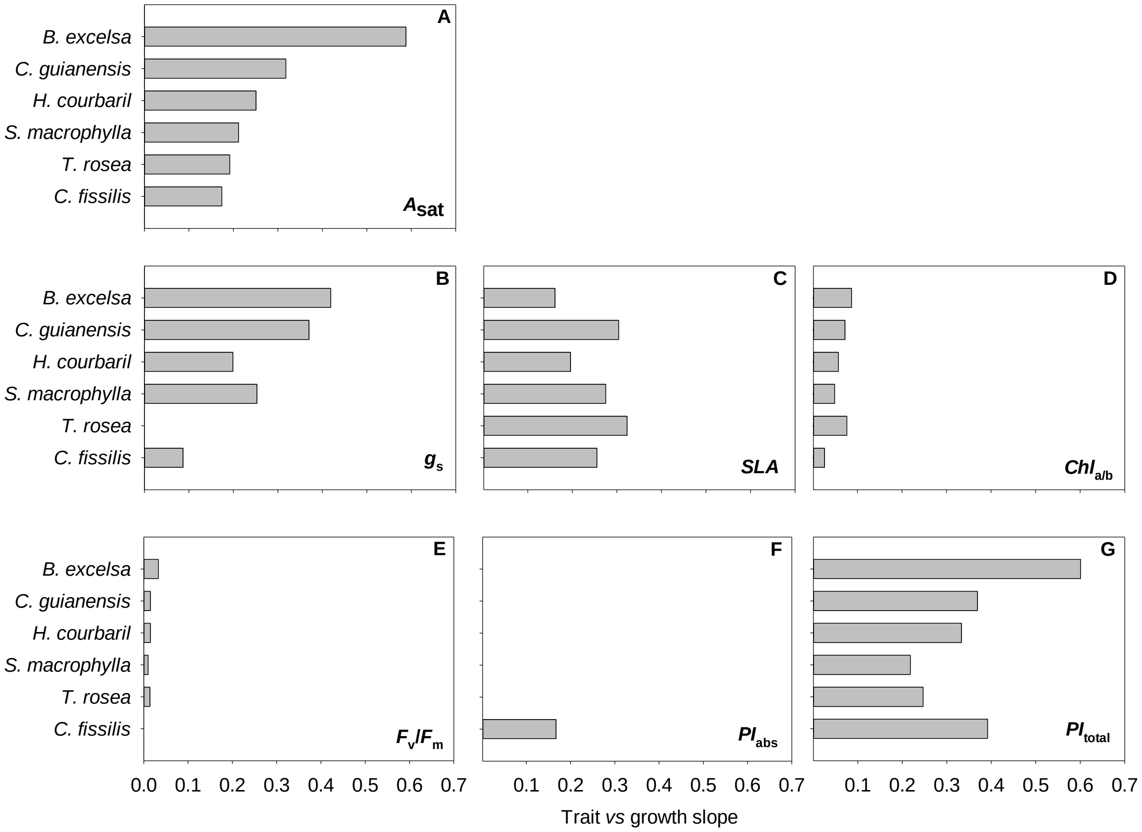

Fig. 1. The slope of the regression between *RG* and photosynthetic leaf traits for six tree species growing in a gradient of light transmittance present over a silvicultural treated secondary forest. To simplification, *SLA* and F_v/F_m coefficients are presented as *a**(-1). The coefficient of determination and significance of slope are summarized in Table S1.

3.2. Relationship between light transmittance and growth, and photosynthetic leaf traits

Overall, *RG* and photosynthetic leaf traits were strongly related to light transmittance (Table 3). *RG* responses to transmittance were steeper for pioneers (*C. fissilis, T. rosea* and *S. macrophylla*) species and *H. courbaril* (Fig. 2a). For example, *C. fissilis RG* under high transmittance levels was three times higher than in deep shade (lower transmittance), while this ratio was 1.66 for *B. excelsa*. Among the photosynthetic leaf traits were observed the strongest relationship (R^2) for *SLA* and steeper response (inclination) for PI_{total} (Fig. 2d and h). As observed for growth-traits relationships, the F_v/F_m of *C. fissilis* was unresponsive to transmittance; however, was the only one that showed a significant relationship between PI_{abs} and transmittance (Fig. 2f and g). The *C. fissilis* inclination of PI_{total}-transmittance relationship was 2.25 times steeper than the other five species average (Fig. 2h). The *SLA* of pioneer species (*C. fissilis*, *T. rosea* and *S. macrophylla*) was 2.18 times more responsive to light transmittance than non-pioneer species (*H. courbaril*, *C. guianensis* and *B. excelsa*); and among non-pioneer species, *B. excelsa* was 2.3 times less responsive than the other two (Fig. 2d). On the other hand, *B. excelsa* was the species with A_{sat} more responsive to light transmittance among all species (Fig. 2a).

3.3. Plasticity relationships

The inclination of the relationships between light transmittance and *RG*, and photosynthetic leaf traits were used as the plasticity index induced by light transmittance. Among the analyzed leaf traits, only the transmittance-induced plasticity of F_v/F_m ($R^2 = 0.78$; $P = 0.02$; Fig 3e) and SLA ($R^2 = 0.80$; $P = 0.02$; Fig 3c) were related to *RG* plasticity. The *RG* plasticity was related to seedling mortality in shade of untouched forest ($R^2 = 0.57$; $P = 0.08$*;* Fig 3h) and to *RG* in high light environments ($R^2 = 0.67$; $P = 0.046$*;* Fig 3i).

Table 3.

Inclination, coefficient of determination and significance of the relationships between transmittance and relative growth (*RG*), and photosynthetic leaf traits. n.s. ≥ 0.05; .<0.10; * < 0.05; *** < 0.001.

	C. fissilis	*T. rosea*	*S. macrophylla*	*H. courbaril*	*C. guianensis*	*B. excelsa*
				RC		
Inclination	1.737	1.13	1.211	1.094	0.757	0.578
R^2	0.85	0.86	0.85	0.81	0.70	0.58
P	***	***	***	***	***	***
				A_{sat}		
Inclination	0.299	0.241	0.269	0.294	0.236	0.38
R^2	0.57	0.38	0.58	0.57	0.48	0.59
P	***	***	***	***	***	***
				g_{s}		
Inclination	0.144	0.145	0.297	0.259	0.281	0.274
R^2	0.09	0.06	0.32	0.29	0.42	0.32
P	*	.	***	***	***	***
				SLA		
Inclination	-0.479	-0.387	-0.345	-0.211	-0.246	-0.099
R^2	0.82	0.75	0.81	0.68	0.75	0.53
P	***	***	***	***	***	***
				$Chl_{\mathrm{a/b}}$		
Inclination	0.044	0.092	0.061	0.071	0.062	0.070
R^2	0.19	0.43	0.28	0.36	0.19	0.20
P	***	***	***	***	***	***
				$F_{\mathrm{v}}/F_{\mathrm{m}}$		
Inclination	n.s.	-0.018	-0.013	-0.016	-0.014	-0.024
R^2	n.s.	0.27	0.41	0.49	0.43	0.37
P	n.s.	***	***	***	***	***
				PI_{abs}		
Inclination	0.294	n.s.	n.s.	n.s.	n.s.	n.s.
R^2	0.37	n.s.	n.s.	n.s.	n.s.	n.s.
P	***	n.s.	n.s.	n.s.	n.s.	n.s.
				PI_{total}		
Inclination	0.702	0.28	0.275	0.391	0.248	0.366
R^2	0.73	0.29	0.25	0.69	0.24	0.33
P	***	***	***	***	***	***

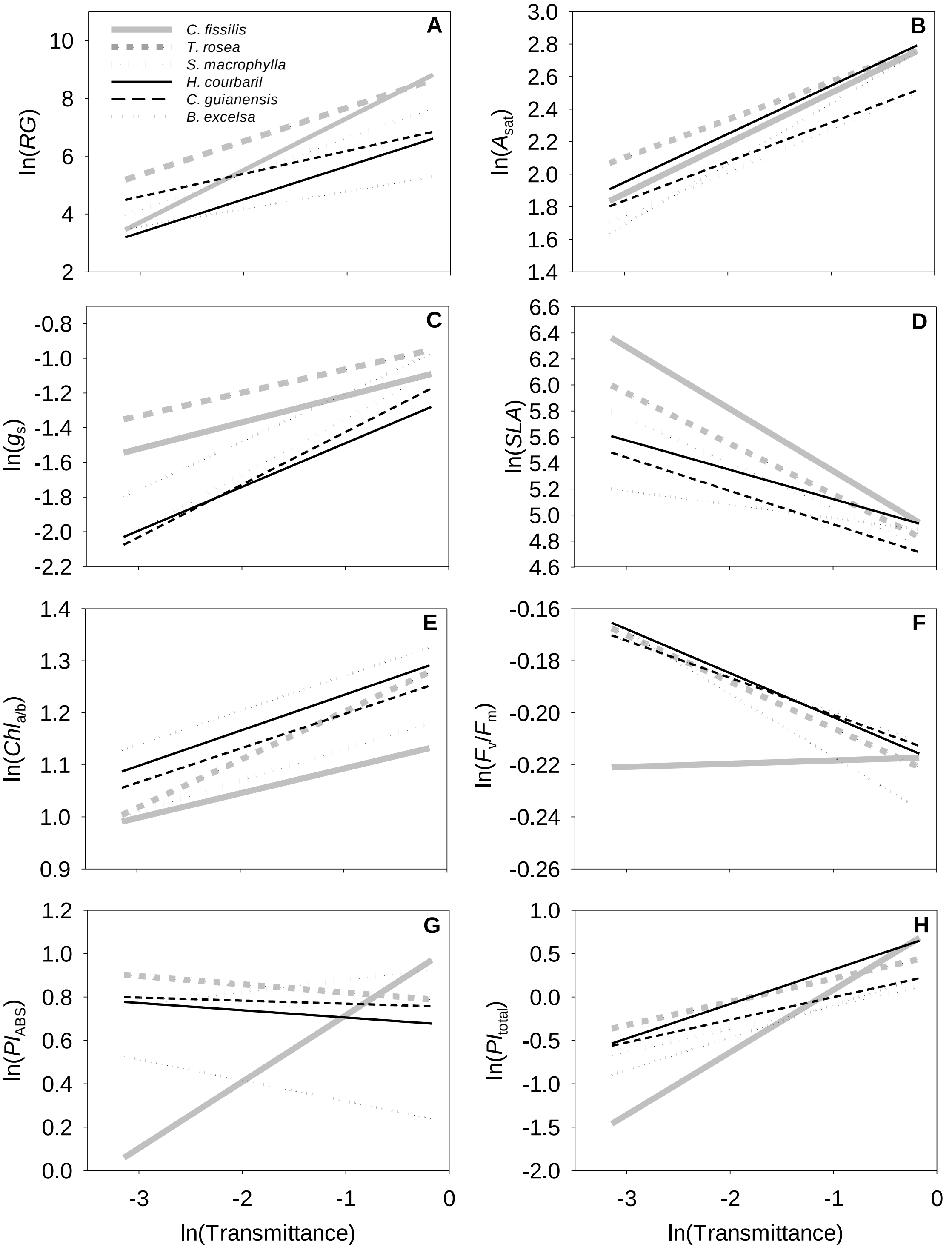

Fig. 2. The relationship between light transmittance and growth, and photosynthetic leaf traits for six tree species growing in a silvicultural treated secondary forest. The coefficient of determination and significance of slope are summarized in Table 3.

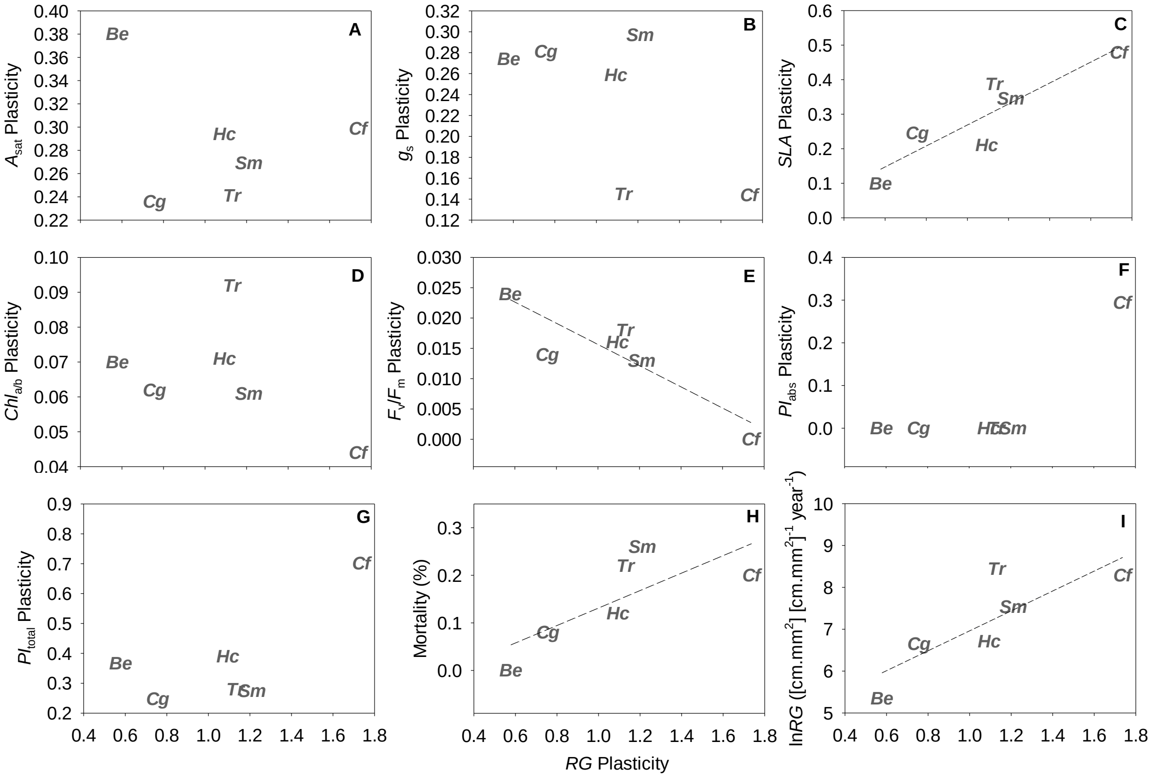

Fig. 3. The relationship between growth plasticity and photosynthetic leaf traits, and mortality for six tree species planted over a silvicultural treated secondary forest. To simplification, *SLA* and F_v/F_m plasticity are presented as a*(-1).

4. Discussion

4.1. Photosynthetic leaf traits are strongly related to tropical seedlings growth

Functional leaf traits have been proposed to predict tropical trees growth (Guimarães et al., 2018; Iida et al., 2014; Liu et al., 2016; Poorter et al., 2018) and in the present work was added evidences to functional trait approach by demonstrating the relationship of photosynthetic leaf traits and the growth of six tropical species - in a gradient of light transmittance created by silvicultural treatments - in a secondary forest enrichment planting.

The effects of the photosynthetic process on seedlings growth were discussed following the steps of interception, absorption and utilization of light. The specific leaf area (*SLA*) represents the plant biomass investment in light interception (Milla and Reich, 2007). As a result, plants growing in shaded environments will present high values of *SLA* (increasing the light interception per unit of leaf biomass), while at full sun conditions a more thick and dense leaf result in low *SLA* (Coble and Cavaleri, 2014; Poorter et al., 2009). In the present study, seedlings growth was closely related to *SLA* (Fig. 1c) and, therefore, light interception efficiency played an important role in seedlings growth along the light gradient. After intercept, light needs to be absorbed by chlorophylls present in the light harvesting complex (LHC). The size of LHC is related to chlorophyll *a* and *b* ratio ($Chl_{a/b}$) and the lowest values represent a high proportion of LHC-exclusive chlorophyll *b* (Niinemets, 2010; Hallik et al., 2012). The growth of the six tropical tree seedlings was related to $Chl_{a/b}$ (Fig. 1d) indicating that light absorption is also an important photosynthesis step to seedlings growth in response to light gradient in enrichment planting. The fluorescence-measured electron transport efficiency represents the light utilization phase and was also closely related to seedlings growth (Fig. 1e, f and g). Considering PI_{total} - the index that represents the efficiency along the all thylakoid electron transport chain – all species showed a relationship between this trait and growth (Fig. 1g); however the growth relationships with fluorescence parameters that represent initial and intermediary steps of electron transport (F_v/F_m and PI_{abs}) were different for *C. fissilis*. This species did not show a growth-F_v/F_m relationship but was the only one that showed a relationship with PI_{abs} (Fig. 1e and f). Therefore, *C. fissilis* growth is more dependent on redox reactions that happen after photosystem II, while the other five species have a growth dependent on PSII energy trapping. The midday and predawn reductions in F_v/F_m (photoinhibition) of *C. fissilis* seedlings transferred from shade to full sun have been demonstrated to be insufficient to impact biomass accumulation (Sanches et al., 2017), and corroborates the lack of effect of this characteristic for the growth of this species observed in the present study. Stomatal conductance (g_s) represents a diffusive limitation to photosynthesis and because it is dependent on the plant water status it can also influence growth along the light gradient since soil and atmosphere water conditions accompany irradiance availability (Jiang et al., 2006; Campanello et al., 2008; Li et al., 2017). Only *T. rosea* growth was not related to g_s (Fig. 1b). Finally, biochemical reactions that happen in the chloroplast stroma also determine photosynthetic light use efficiency (Baker et al., 2008). In the present study, no direct biochemical efficiency was accessed (*e.g.* maximum carboxylation velocity, V_{cmax}), but A_{sat} - that has a strong relationship with biochemical limitations and express the carbon assimilated - was measured (De Kauwe et al., 2016). All species showed a strong relationship between A_{sat} and growth, especially *B. excelsa* that had the most responsive growth to A_{sat} (Fig.1a). These direct relationships of growth and photosynthetic traits provide strong evidence of growing dependence on physiological processes measured at leaf level and may represent a good tool for enrichment planting species selection. Here, we demonstrated the potential of individual physiological traits to explain the species-specific growth rates, while Li et al. (2017) have recommended a set of morphological and physiological traits in combination. The differences can be associated with leaf traits tested. As commented before, we used leaf traits representative of different steps of photosynthetic process and, therefore, potentially more related to growth. However, the relationship between the plasticity in growth and photosynthetic leaf characteristics may indicate even more robust evidence about the prediction potential of these traits regarding seedlings growth responses to silvicultural treatments that manipulate the light environment in secondary forest enrichment planting.

4.2. Are light transmittance-induced plasticity of growth and photosynthetic leaf traits related?

As hypothesized, growth plasticity is related to the plasticity of leaf photosynthetic characteristics (Fig. 3). However, such a relationship was only strongly demonstrated for *SLA* and F_v/F_m characteristics. Considering that the present work was performed with only six species, some specific points may have contributed to the lack of relation between the plasticity of growth and some characteristics. For example, *B. excelsa* was the species with the lowest growth plasticity, but the highest A_{sat} plasticity, going against the other species and, consequently, weakening the relationship (Fig. 3a). The high PI_{total} plasticity of *C. fissilis* - and $Chl_{a/b}$ for *T. rosea* - decoupled the inter-specific growth-traits plasticity relationships (Fig. 3g and d). Furthermore, g_s plasticity of both *C. fissilis* and *T. rosea* was low, considering the high growth plasticity of these two species (Fig. 3b).

These many uncoupling observed in the relationship between growth plasticity and traits plasticity cast doubt on the potential of photosynthetic leaf traits to predict growth responses of tree species over a gradient of light transmittance created by silvicultural treatments. However, the consistent pattern observed for *SLA* and F_v/F_m characteristics provides evidence for the use of these light interception and use-efficiency traits, respectively. *SLA* is a light-sensitive trait, easily measured –without the need of expensive equipment – and there are a lot of reports about light-induced *SLA* plasticity for tropical species that could be used as a proxy for growth responses to silvicultural treatments (Coste et al., 2010; Dos Anjos et al., 2015; Pérez-Harguindeguy et al., 2013; Rozendal et al., 2006). The F_v/F_m measure need a chlorophyll *a* fluorimeter but is a rapid and non-invasive method to estimate the maximum quantum yield of photosystem II (Strasser et al., 2010; Stirbet et al., 2018). The light interception and use-efficiency have been shown as significant components in the production ecology equation to explain individual tree growth responses to silvicultural treatments (Binkley et al., 2010). Hence, photosynthetic leaf traits, principally those of fast and easy mensuration, that describe light interception and light use-efficiency should be better accessed in the view of growth response to silvicultural treatments that manipulate the light environment in enrichment plantings and could be used to species screening.

4.3. The growth-survival trade-off in the view of growth plasticity

The mortality of seedlings growing in the deep shade of untreated secondary forest was marginally related to growth plasticity (Fig. 3h). High growth plasticity generally is associated with high growth in full sun (Oguchi et al., 2017) and was also observed in the present study (Fig. 3i). As a result, the growth plasticity relationship with mortality and growth could be a mechanism of growth-survival trade-off observed in tropical seedlings during the establishment (Kitajima et al., 1994). Similar to our results, in a cool-temperate deciduous forest was reported that gap-dependent species acquire high plasticity of photosynthetic traits and growth at the expense of low shade tolerance, while gap-independent was less plastic but more shade tolerant (Oguchi et al., 2017). Evidence has yet to be raised about the mechanisms that link high light-induced plasticity (growth and traits) with reduced survival. High plasticity has been argued to be costly in energy and material to maintaining the plant machinery responsible for environmental sensitivity (DeWitt et al., 1998). In the present study, *SLA* plasticity was positively related to growth plasticity, higher in pioneer (*C. fissilis*, *T. rosea* and *S. macrophylla*) than non-pioneers (*H. courbaril*, *C. guianensis* and *B. excelsa*), driven by variation under the shaded understory and, therefore, the effects on growth-survival trade-off can be associated with the plasticity costs commented above. On the other hand, F_v/F_m was negatively related to growth plasticity (Fig 3e). The growth-F_v/F_m plasticity relationship may have emerged from the species that show less growth plasticity to the light environment and reduced F_v/F_m under full sun conditions *(e.g., B. excelsa*). Full sun can induce PSII photoinhibition (low F_v/F_m) and, as a consequence, affect the growth of tree species, especially those more shade-tolerant (Favaretto et al., 2011; Guimarães et al., 2018; Santos-Junior et al., 2006). Some studies have suggested high light–induced plasticity of photosynthetic leaf traits characteristics for *B. excelsa* (Lopes et al., 2019; Souza et al., 2017), although they had not yet suggested that reduced F_v/F_m may limit the growth of this species under high light conditions during the first year after planting. Finally, these results indicate that plasticity is directly linked to growth-survival trade-off, and pioneer species contribute with morphological plasticity (*SLA*), while non-pioneer species have greater plasticity in physiological characteristics (F_v/F_m). Further studies should be performed with other species to consolidate these generalizations.

5. Conclusions

In summary, this study adds evidences to functional trait approach by demonstrating three main findings. First, photosynthetic traits measured at leaf-level have a strong relationship with the first-year growth of the six tropical tree species studied. Consequently, photosynthetic leaf traits should be included in functional approach studies. Second, interspecific growth plasticity is related to photosynthetic leaf traits plasticity. Therefore, photosynthetic traits, principally those related to light interception and use-efficiency (*SLA* and fluorescence), are representative of growth response mechanisms to silvicultural treatments that manipulate the light environment in enrichment plantings and could be used to species screening. Third, interspecific growth plasticity is related to growth in full sun and mortality in shaded environments. As a consequence, growth plasticity has an intrinsic effect on the growth-survival trade-off.

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Conflicts of interest

None.

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Appendix A. Supplementary material

Table S1

Inclination, coefficient of determination and significance of the relationships between relative growth (*RG*) and photosynthetic leaf traits.

	A_{sat}	g_{s}	*SLA*	$Chl_{\mathrm{a/b}}$	$F_{\mathrm{v}}/F_{\mathrm{m}}$	PI_{abs}	PI_{total}
				C. fissilis			
Inclination	0.174	0.087	-0.255	0.026	n.s.	0.167	0.392
R^2	0.97	0.63	0.92	0.67	n.s.	0.84	0.96
P	***	**	***	**	n.s.	***	***
				T. rosea			
Inclination	0.192	n.s.	-0.323	0.076	-0.014	n.s.	0.247
R^2	0.80	n.s.	0.86	0.83	0.57	n.s.	0.56
P	***	n.s.	***	***	**	n.s.	**
				S. macrophylla			
Inclination	0.212	0.253	-0.275	0.049	-0.01	n.s.	0.218
R^2	0.93	0.91	0.94	0.65	0.61	n.s.	0.63
P	***	***	***	**	**	n.s.	**
				H. courbaril			
Inclination	0.251	0.199	-0.196	0.057	-0.015	n.s.	0.333
R^2	0.81	0.67	0.98	0.79	0.88	n.s.	0.95
P	***	*	***	***	***	n.s.	***
				C. guianensis			
Inclination	0.318	0.370	-0.304	0.072	-0.015	n.s.	0.369
R^2	0.92	0.89	0.94	0.52	0.61	n.s.	0.77
P	***	***	***	**	**	n.s.	***
				B. excelsa			
Inclination	0.588	0.419	-0.161	0.087	-0.033	n.s.	0.601
R^2	0.90	0.81	0.83	0.42	0.66	n.s.	0.81
P	***	***	***	*	**	n.s.	***

n.s. ≥ 0.05; * < 0.05; ** < 0.01; *** < 0.001.

Text S1

Seedlings were planted in March 2017 under the treated secondary forest configuring a silvicultural system of enrichment planting. Five seedlings of each species were 3 x 3 m planted in each subplot and respecting an edge of 10 m between plots and 11 m between subplots. The seedlings were planted in 30 x 30 x 30 cm planting holes that had the soil conditioned with limestone (65 g per planting hole) one-month before planting. At the planting, phosphate fertilizer was applied concentrated in two holes 15 cm away from the seedling (P_2O_5; 46 g), while nitrogen, potassium and micronutrients were applied in a circle 15 cm away from the seedling (N; 11.6 g – KCl; 12 g – micronutrients; 10 g of FTE-BR12: 1.8% B; 0.8% Cu; 3.0% Fe; 2.0% Mn; 0.1% Mo). Two additional nitrogen and potassium fertilization were realized one and two months following the planting with the same dosage and application method utilized during the planting.

The daily transmittance was calculated as the average of hourly transmittance values recorded during the day. Hourly transmittance was calculated as the ratio of PPFD measured at the plots in each hour interval (MQ-301: Line quantum with ten sensors and handheld meter, Apogee, USA) and the average values recorded during the same hour interval in the full-sun area (MQS B/ULM-500 logger, Heinz Walz, Germany). The values of irradiance in the plots and full-sun area were measured during 14 days in two periods: 2017 dry season (September), 2018 wet season (April).

3. Síntese

As dimensões físicas, ambientais e sociais das floretas secundárias na Amazônia brasileira representam uma oportunidade ao desenvolvimento sustentável da região. Existem, aproximadamente, 17 milhões de hectares de florestas secundárias na Amazônia Legal. Essa vegetação representa um elemento fundamental à conservação dos serviços ecossistêmicos do bioma, principalmente em relação ao potencial de sequestro de carbono. Além desses serviços, florestas secundárias podem ser inseridas em cadeias de produção de madeira e produtos não madeireiros, e assim conservadas, por meio do adequado manejo florestal. Sistemas silviculturais de enriquecimento podem ser um fundamental componente do manejo de florestas secundárias, no entanto, devem ser estabelecidas diretrizes adequadas à ordenação desses sistemas. Nessa tese, demonstro que tratamentos silviculturais aplicados no dossel e sub-bosque de florestas secundárias permitem o controle da disponibilidade de luz que as mudas plantadas irão receber durante o estabelecimento inicial (Capítulo 1). O controle da quantidade de luz disponível a uma muda é fundamental para seu estabelecimento inicial. No Capítulo 2, mostrei que as seis espécies florestais testadas crescem mais rápido em condições de maior disponibilidade de luz, onde os tratamentos silviculturais foram aplicados de forma intensiva (maior redução de área basal via refinamento e corte do sub-bosque). No entanto, o crescimento das espécies, assim como as respostas de crescimento aos tratamentos silviculturais foram menores no segundo ano após o plantio, principalmente para espécies pioneiras. Maiores valores de mortalidade foram observados em condições sombreadas, principalmente para aquelas espécies que apresentaram rápido crescimento em condições de pleno sol durante o primeiro ano (pioneiras). No entanto, em condições de maior intensidade de aplicação dos tratamentos silviculturais, a suscetibilidade ao ataque da broca das meliáceas foi destacadamente superior e resultou na maior mortalidade de *Swietenia macrophylla*. Por fim, eu investiguei, no Capítulo 3, se as plasticidades do crescimento e características fotossintéticas foliares induzidas pelos tratamentos silviculturais estão relacionadas, para que então, se possa utilizar a plasticidade funcional como critério de seleção de espécies para plantio de enriquecimento. Demonstro que a plasticidade do crescimento está fortemente associada às características que representam a interceptação e a eficiência no uso da da luz.

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