



UNIVERSIDADE FEDERAL DO AMAZONAS
FACULDADE DE CIÊNCIAS AGRÁRIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS FLORESTAIS E
AMBIENTAIS

DINÂMICA FOLIAR E CRESCIMENTO DE *Bertholletia excelsa* Bonpl.
EM RESPOSTA A TRATAMENTOS SILVICULTURAIS

André Henrique Bueno Neves

Manaus, AM

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André Henrique Bueno Neves
Orientador: Dr. Marciel José Ferreira

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Sinopse: Investigou-se o efeito de tratamentos silviculturais na formação de diferentes ambientes de luz em floresta secundária e as respostas da dinâmica foliar, crescimento e desempenho fotossintético de *Bertholletia excelsa* em plantio de enriquecimento. O aumento na intensidade de aplicação dos tratamentos silviculturais favoreceu positivamente a dinâmica foliar e o crescimento das mudas. Mudanças no crescimento em resposta aos tratamentos silviculturais foram associadas à variação no ganho líquido foliar. O desempenho fotossintético também foi influenciado pelos tratamentos silviculturais.

Palavras chave: Castanheira da amazônia; fluorescência da clorofila *a*; estabelecimento inicial; plasticidade; sistemas silviculturais.



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Resumo

Bertholletia excelsa Bonpl. é uma espécie florestal parcialmente tolerante à sombra de grande interesse socioeconômico e ecológico. A espécie tem sido utilizada em diferentes sistemas de plantio (por exemplo, plantios puros, plantios de enriquecimento e sistemas agroflorestais). A plasticidade fotossintética da espécie tem sido indicada como mecanismo importante para o estabelecimento de *B. excelsa* em diferentes condições ambientais. Entretanto, mudanças na dinâmica foliar como estratégia de crescimento não têm sido avaliadas. Nesse estudo, o objetivo principal foi investigar a influência de tratamentos silviculturais na dinâmica foliar e as mudanças associadas às taxas de crescimento e desempenho fotossintético de mudas de *B. excelsa*. As mudas foram plantadas sob diferentes níveis de refinamento da área basal de árvores do dossel (0, 20, 40, 60, 80 e 100% de refinamento) em conjunto com a remoção de sub-bosque. A produção foliar foi seis e cinco vezes maior nas condições de 80 e 100% quando comparados às parcelas controles. As taxas de crescimento (diâmetro e altura) também aumentaram ao longo do gradiente de redução da área basal. Mudanças no crescimento foram positivamente associadas à variação no ganho líquido foliar. Os tratamentos silviculturais também alteraram a composição etária de folhas nos diferentes ambientes, as quais não exibiram diferenças marcantes no desempenho fotoquímico. Mudanças na dinâmica foliar representam importantes mecanismos associados às respostas de crescimento de *B. excelsa* a tratamentos silviculturais.

Palavras chave: Castanheira da amazônia; ganho líquido foliar; fluorescência da clorofila *a*; estabelecimento inicial; plasticidade; sistemas silviculturais.

Abstract

Bertholletia excelsa Bonpl. is a partially shade tolerant forest species of great socioeconomic and ecological interest. The species has been used in different planting systems (for example, pure plantations, enrichment plantations and agroforestry systems). The photosynthetic plasticity of the species has been indicated as an important mechanism for the establishment of *B. excelsa* in different environmental conditions. However, changes in leaf dynamics as a growth strategy have not been evaluated. In this study, the main objective was to investigate the influence of silvicultural treatments on the leaf dynamics and the changes associated with growth rates and photosynthetic performance of *B. excelsa* seedlings. The seedlings were planted under different levels of canopy refinement (0, 20, 40, 60, 80 and 100% of basal area reduction) together with the removal of understory. The leaf production was six and five times higher in 80 and 100% when compared to control plots. The growth rates (diameter and height) also increased with the intensity of silvicultural treatments. Changes in growth were positively associated to variation in leaf liquid gain. Silvicultural treatments also affected the leaf age composition in the different environments, which not exhibited significant differences in the photochemical performance. Changes in leaf dynamics represent important mechanisms associated with the growth responses of *B. excelsa* to silvicultural treatments.

Keywords: Amazon nut; leaf liquid gain; chlorophyll *a* fluorescence; initial establishment; plasticity; silvicultural systems.

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Introdução Geral

Bertholletia excelsa Bonpl. popularmente conhecida como Castanheira da amazônia ocorre naturalmente na Amazônia em florestas de terra firme, classificada como uma espécie clímax ou parcialmente tolerante à sombra (Swaine e Whitmore 1990; Finegan, 1992; Poorter et al. 2006). É uma das espécies amazônicas de maior porte, podendo atingir 50 metros de altura e três metros de diâmetro (Mori e Prance 1990). Possui importância social, econômica e ecológica e as amêndoas fazem parte da dieta alimentar das populações amazônicas (Salomão et al 2006; Scoles et al. 2014), constituindo o segundo produto florestal não madeireiro (PFNM) mais produzido na Amazônia (IBGE 2019). Além da importância econômica, devido ao grande porte, a espécie é uma das que mais armazena biomassa e carbono em florestas maduras (Fauset et al. 2015; Selaya et al. 2017).

A produção do fruto (conhecido como ouriço) ocorre majoritariamente de forma extrativista em áreas naturais de difícil acesso, dificultando a cadeia de produção. Dessa forma, embora existam experiências de plantios para produção de frutos, a contribuição para a produção total é mínima (Homma 1993; Mori e Prance 1990; Pereira et al. 2010). Apesar de historicamente o fruto ter sido o produto mais importante da castanheira da amazônia, com a intensificação da colonização da Amazônia no ano de 1970, o desmatamento dos castanhais para outros usos do solo reduziu drasticamente a produção de frutos (Santana et al. 2017). No sudeste Paraense, por exemplo, no ano de 1997, 70% dos castanhais nativos haviam sido desmatados (Homma 2014).

Diante da pressão causada pelo desmatamento, o corte de árvores nativas de *B. excelsa* foi proibido pelo Decreto Federal nº 5.975, de 30 de novembro de 2006. Dessa forma, devido à redução de áreas de povoados nativos em função do avanço no desmatamento e proibição da extração de madeira, diversas iniciativas de reflorestamento vêm sendo implementadas com essa espécie, elevando-a a categoria das espécies nativas de maior potencial e mais plantadas na região amazônica (Walters et al. 2005; Hoch et al. 2009; Rolim et al 2019). A espécie tem sido utilizada em diferentes sistemas de plantio, desde o enriquecimento de florestas secundárias, áreas de roçado de mandioca, agricultura itinerante, áreas de pastagem, sub-bosque, até áreas degradadas por mineração (Kainer et al. 1998; Peña-Claros et al. 2002; Scoles et al. 2011; Salomão et al. 2014). O enriquecimento de florestas secundárias pode ter um papel primordial,

tendo em vista que até o ano de 2014, 23% da área desflorestada na Amazônia já apresentavam crescimento de vegetação secundária em diferentes estágios de regeneração (INPE 2016). A capacidade de estabelecimento ocorre devido à alta rusticidade da espécie para se estabelecer em ambientes perturbados e degradados. Ainda que a regeneração natural possa ocorrer no sub-bosque da floresta madura, as taxas de recrutamento podem ser três vezes maiores em áreas de clareiras (Moll-Rocek et al. 2014). Além disso, em plantios, o incremento na disponibilidade de luz normalmente favorece a sobrevivência e o crescimento da espécie (Peña-Claros et al. 2002; Scoles et al. 2011; Garate-Quispe et al. 2020).

A capacidade de estabelecimento diferenciada de *B. excelsa* em resposta à variação na disponibilidade de luz pode estar associada em parte à sua plasticidade fotossintética (Souza et al. 2017; Lopes et al. 2019). Porém, o ambiente de luz pode influenciar outras características, como a dinâmica foliar. Espécies florestais crescendo sob diferentes disponibilidades de luz tendem a apresentar diferenças na dinâmica foliar (produção e perda foliar), que, por sua vez, exerce influência na sobrevivência e crescimento. Dessa forma, o aumento na disponibilidade de luz pode resultar em uma relação positiva entre o incremento no saldo líquido de produção de folhas e o crescimento das mudas (Bongers e Popma 1990). Entretanto, o monitoramento da dinâmica foliar em paralelo ao crescimento não tem sido normalmente aplicado nos estudos de ecologia florestal limitando a capacidade para identificar os principais mecanismos que controlam os padrões de crescimento das espécies em resposta às variações ambientais.

Diante disso, torna-se relevante examinar a dinâmica foliar como mais uma característica relacionada a capacidade de estabelecimento de *B. excelsa* em um gradiente de luz criado a partir de um sistema silvicultural de enriquecimento de floresta secundária. Para tal, buscamos responder as seguintes questões: *i) Há variação na dinâmica foliar e crescimento de plantas juvenis de B. excelsa em resposta a tratamentos silviculturais de abertura do dossel? ii) Mudanças nas taxas de crescimento ao longo do gradiente de abertura do dossel estão associadas à dinâmica foliar? iii) O desempenho fotossintético é influenciado pelas mudanças na dinâmica foliar em resposta aos tratamentos silviculturais?*

Objetivos

Geral

Investigar se a dinâmica foliar influencia o estabelecimento inicial de *Bertholletia excelsa* em resposta a tratamentos silviculturais aplicados em sistema silvicultural de enriquecimento de floresta secundária.

Específicos

- i) Verificar se há variação na dinâmica foliar e taxas de crescimento de *B. excelsa* em resposta a tratamentos silviculturais;
- ii) Analisar se a variação nas taxas de crescimento relativo em altura e diâmetro estão relacionadas à dinâmica foliar;
- iii) Analisar se as taxas de produção e perda foliar influenciam o desempenho fotossintético das plantas em resposta aos tratamentos silviculturais.

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Short-term effects of
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Short-term effects of silvicultural treatments on the leaf dynamics and growth of young *Bertholletia excelsa* Bonpl. plants.

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Abstract

Bertholletia excelsa Bonpl. is a partially shade tolerant forest species of great socioeconomic and ecological interest. The species has been used in different planting systems (for example, pure plantations, enrichment plantations and agroforestry systems). The photosynthetic plasticity of the species has been indicated as an important mechanism for the establishment of *B. excelsa* in different environmental conditions. However, changes in leaf dynamics as a growth strategy have not been evaluated. In this study, the main objective was to investigate the influence of silvicultural treatments on the leaf dynamics and the changes associated with growth rates and photosynthetic performance of *B. excelsa* seedlings. The seedlings were planted under different levels of canopy refinement (0, 20, 40, 60, 80 and 100% of basal area reduction) together with the removal of understory. The leaf production was six and five times higher in 80 and 100% when compared to control plots. The growth rates (diameter and height) also increased with the intensity of silvicultural treatments. Changes in growth were positively associated to variation in leaf liquid gain. Silvicultural treatments also affected the leaf age composition in the different environments, which not exhibited significant differences in the photochemical performance. Changes in leaf dynamics represent important mechanisms associated with the growth responses of *B. excelsa* to silvicultural treatments.

Keywords: Amazon nut; leaf liquid gain; chlorophyll *a* fluorescence; initial establishment; plasticity; silvicultural systems.

1 Introduction

Bertholletia excelsa Bonpl. popularly known as Amazon nut occurs naturally in the Amazon in upland forests (Mori and Prance 1990) and normally classified as a climax species or partially tolerant to shade (Swaine and Whitmore 1990; Finegan 1992; Poorter et al. 2006). The nuts production by extractives in native stands indicate the high social, ecological and economic importance of this species (Scoles et al. 2011; IBGE, 2019). Reforestation projects also have been commonly established using this species which configurate one of the most sustainable native species for silviculture in Amazonia (Walters et al. 2005; Hoch et al. 2009; Rolim et al. 2019). The species has been planted in different planting systems, including enrichment planting of secondary forest, shifting cultivation, agroforestry systems and degraded areas by mining (Kainer et al. 1998; Peña-Claros et al. 2002; Scoles et al. 2011; Salomão et al. 2014). This is possible due to the high rusticity of the species to establish itself in disturbed and degraded environments. Although natural regeneration can occur in the understory of the mature forest, recruitment rates can be three times higher in gaps (Moll-Rocek et al. 2014). In plantations, the increase on the availability of light usually favors the survival and growth of the species (Peña-Claros et al. 2002; Scoles et al. 2011).

The potential for the establishment of *B. excelsa* under a gradient of light availability may be partly associated with its photosynthetic plasticity. The species exhibits different growth patterns and photosynthetic characteristics in contrasting light environments. Under conditions of full sunlight, plants increase the root biomass, leaf mass per area and photosynthesis rates. In addition, the maximum quantum efficiency of PSII is quickly recovered when plants are exposed to high intensities of light. Conversely, under low availability of light, there is an increase in the specific leaf area at the expense of the leaf mass per area, increasing the size of the leaf blade surface and improving the interception of light which possibilities a positive carbon balance despite the reduction in photosynthesis at the leaf-level. These changes highlight the species' ability to adjust the functioning of the photosynthetic apparatus according to the availability of light and confirm your high plasticity when submitted to different environmental conditions (Souza et al. 2017; Lopes et al. 2019).

In addition to photosynthetic plasticity at the leaf-level, changes in leaf dynamics at the level of the crown are also observed in tropical tree species growing

under different light conditions. Environments with greater availability of light (canopy gaps or open areas) usually induce an increase in the rate of leaf production, whereas the leaf loss can be proportional. Within species, positive relations between leaf production rate and growth have been observed in seedlings of rain forest species (Bongers and Popma 1990). The leaf life span is strongly influenced by the availability of light and can influence photosynthetic rates (Chabot and Hicks, 1982; Russo and Kitajima 2016; Wu et al. 2016; Albert et al. 2018). Leaves acclimated to environments with high light availability have higher photosynthetic rates when compared to leaves in environments with low light availability (Ashton et al. 2011). Then, the improvement in the growth of seedlings as affected by an increase in the availability of light can be hoped from an interaction between photosynthetic capacity at the leaf-level and net leaf gain rate induced by leaf dynamics.

In this research, from an experiment of enrichment planting on secondary forest submitted to different intensities of silvicultural treatments, we monitored the leaf dynamics and growth of two-year-old plants of *B. excelsa* for twelve months. We specifically seek to address the following objectives: *i*) investigate the effects of silvicultural treatments on the leaf dynamics and growth of *Bertholletia excelsa*; *ii*) analyze the relationships between leaf dynamics and growth rates over silvicultural treatments; *iii*) evaluate the effects of silvicultural treatments on the photosynthetic performance of trees.

2 Materials and methods

Study site

This research was realized in a Central Amazon secondary forest at Experimental Farm of the Universidade Federal do Amazonas – UFAM (02°38'S, 60°03.5'W), 38 km north of Manaus, Amazonas, Brazil. The regional climate is characterized by an annual precipitation of 2350 mm, mensal average of 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 seasonality of precipitation is generally moderate with a short dry season length between August and September (Sombroek 2001).

The study was carried out as part of a larger secondary forest enrichment experiment (details in Santos and Ferreira, 2020). The historic of land use consisted in the clear-cut of mature forest in 1986, which was burned and then abandoned. After that (1997), a secondary forest that had regrown was cut and was burned one more time; a crop of cupuaçu tree (*Theobroma gradiflorum* (Willd. ex Spreng.) K. Schum.) was planted and abandoned again. Accordingly, the silvicultural treatments priory of seedling planting were applied to a 19-years-old secondary forest. The secondary forest was established in a well-drained clayed and infertile oxisol (Chauvel 1982). The secondary forest covers an area of 17 hectares and is neighbored by a wide mature forest along approximately 80% of the edges. According to a phytosociological inventory carried out in the area, 1200 ± 180 trees ha^{-1} with diameter at breast height (DBH) > 5 cm, basal area of 12 ± 3.6 m^2 ha^{-1} and greater abundance of the genera *Bellucia* $>$ *Goupia* $>$ *Vismia* $>$ *Cecropia*. Soil fertility previously correction and fertilization was characterized by pH (H₂O) = 4.19 ± 0.05 ; P = 1.43 ± 0.76 mg.kg^{-1} ; Al³⁺ = 0.035 ± 0.03 cmolc.kg ; T = 1.6 ± 0.11 and SB = 0.16 ± 0.05 (details on Santos and Ferreira 2020).

Experimental design

The activities of management on secondary forest site started in the last quarter of 2016 with the application of the silvicultural treatments. First, the understory slashing treatment consisted in the complete remotion of all herbaceous plants and small trees (DBH < 5 cm) in regeneration with a machete-hereafter, after named *understory*

slashing treatment. Regrowth vegetation was cut twice times per year. Next, the second treatment consisted of thinning 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 feeling with a chainsaw and then named *canopy refinement* treatment.

The different levels of canopy refinement were applied randomly in main plots of 2318 m² (61 m x 38 m). The treatments combinations were replicated in five blocks, each with 12,768 m² (114 x 112 m). Main canopy refinement plots were divided into two subplots, half with the maintenance of understory (control) and the other half with understory removed (understory slashing). Six tropical tree species (*Cedrela fissilis* Vell.; *Tabebuia rosea* (Bertol). Bertero ex A. DC.; *Switenia macrophylla* King; *Bertholletia excelsa* Bonpl.; *Carapa guianensis* Aubl.; *Hymenaea courbaril* L.) were planted in March 2017, configuring a silvicultural system of enrichment planting. In each subplot, five seedlings of each species were planted, 3 x 3 m spaced, edge of 10 m between plots and 11 m between subplots (Fig. 1). During the planting, the soil surrounding each seedling was fertilized with P₂O₅ (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). The dosages and applied methods that ensure the minimal nutrient requirements of tropical trees were obtained from a literature review (Alvarado, 2015; Campoe et al. 2014; Furtini Neto 2000; Resende et al. 2005). Further details are given in dos Santos et al. 2020.

In this research, excluding other five species, a total of 300 saplings of *B. excelsa* was evaluated. The analyses were made in all plants growing under a gradient of canopy refinement (0; 20; 40; 60; 80 and 100%) as well as in the two subplots (control and understory slashing).

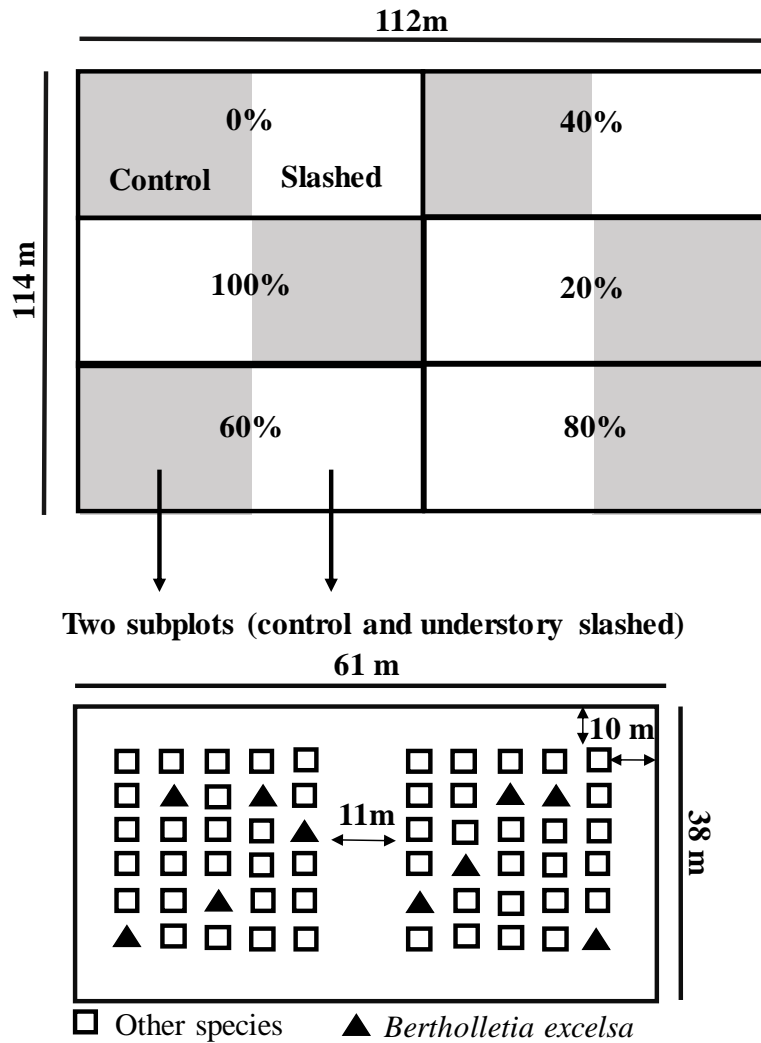


Fig. 1 - Plot and subplot design of one experimental block showing the silvicultural treatments applied and the distribution of six tropical tree species planted in an enrichment planting silvicultural system with split-plot design. Six levels of canopy refinement (0, 20, 40, 60, 80, 100%) and understory slashing treatment.

Relative growth rates

The root collar diameter and height of saplings were measured bimonthly during the period of the experiment. The measurements were taken using a digital caliper (Mitutoyo - model CD-8 "CX-B) and a scale graduated in centimeters. Annual absolute growth on height (AGR-Height) and root collar diameter (AGR-Diameter) were calculated as follow:

$$AGx = T2 - T1$$

Which: AGx = Absolut growth in height or diameter during one year. T1 = first measurement and T2 = final measurement.

Leaf dynamics

The marking of the branches was made with a string that occurs systematically, where the lowest branch was marked and, subsequently, every three branches, the third branch was marked representing a total sampling of 33% to each plant. The first marking was considered as a reference marking, then the leaf dynamics followed monthly with an error of ± 15 days in the leaf ages according to the marking intervals. After one year of monitoring, we obtained total leaf production, total leaf loss and net leaf gain, which is the difference between production and loss of leaves.

Chlorophyll *a* fluorescence analyses

Chlorophyll *a* fluorescence measurements were made with a portable fluorimeter (PEA, MK2-9600, Hansatech, Norfolk, UK) adjusted to emitted a saturating light pulse of $3000 \mu\text{mol m}^{-2} \text{s}^{-1}$ at a wavelength of 650 nm during 1 s. Before the measurements, the leaves were dark acclimated during 30 min using leaf-clips for complete oxidation of the photosynthetic electron transport chain. Measurements were made on three leaves per age (1 to 12 months), between 07:00 and 11:00 h. The values were used to calculate an average of each plant. Maximum quantum yield of PSII (F_v/F_m), ABS-based performance index (PI_{ABS}), total performance index (PI_{total}) and the efficiency of electron transport in PSI (IP-phase) were calculated after JIP test application, following Strasser et al. (2010), Strasser and Srivastava (1995), Strasser et al. (1999) and Tsimilli-Michael & Strasser (2008). PI_{ABS} is an integrated index of the efficiency which electron is trapped by PSII (F_v/F_m) and is transferred further than QA^- (ET_0/TR_0), PI_{total} as total performance index and IP-phase that reflects the PSI/PSII stoichiometry (Ceppi et al 2012).

To obtain representative values of the fluorescence parameters (F_v/F_m ; PI_{abs} ; PI_{total} and IP-phase) in each plot, we weighted the leaf production (number of leaves at each age) with the value obtained at the ages evaluated (1 to 12 months).

$$\frac{\sum(IP - phase1 \times NF1) + (IP - phase2 \times NF2) \dots (IP - phase \times NF12)}{\text{Number of leaves (total)}}$$

Which: IP-phase1 = IP-phase value of 1 month leaf; IP-phase= value of two month leaf, the same to 3,4,5,6,7,8,9,10,11,12 leaf age. NF1 = number of leaves at one month age, the same to the other ages. Number of leaves (total): the total production of leaf age inside the plot.

Data analyses

All data were previously submitted to the assumptions of normality and homoscedasticity by Shapiro-Wilk and Levene tests, respectively. Non-normality and heterogeneity were corrected by log transformation. To analyze the effects of silvicultural treatments on the leaf dynamics, growth and fluorescence parameters we adjusted generalized linear mixed models (GLMM) controlling plots as a random factor. Relations between growth rates (height and diameter) and leaf liquid gain were tested by linear regression analyses considering significance level (*P*-value) and Adjusted R squared (R^2_{Aj}). All analyses were performed using the statistical program R version 3.5.1 (R Core Team, 2018).

3 Results

Leaf dynamics and growth

There were significant interactions of silvicultural treatments on leaf production, leaf loss and liquid gain (Fig. 2). The canopy refinement (CR) increased the values of the variables of leaf dynamics, but the magnitude of the effects was higher in understory slashed (US) than control (Fig. 2a, b, c).

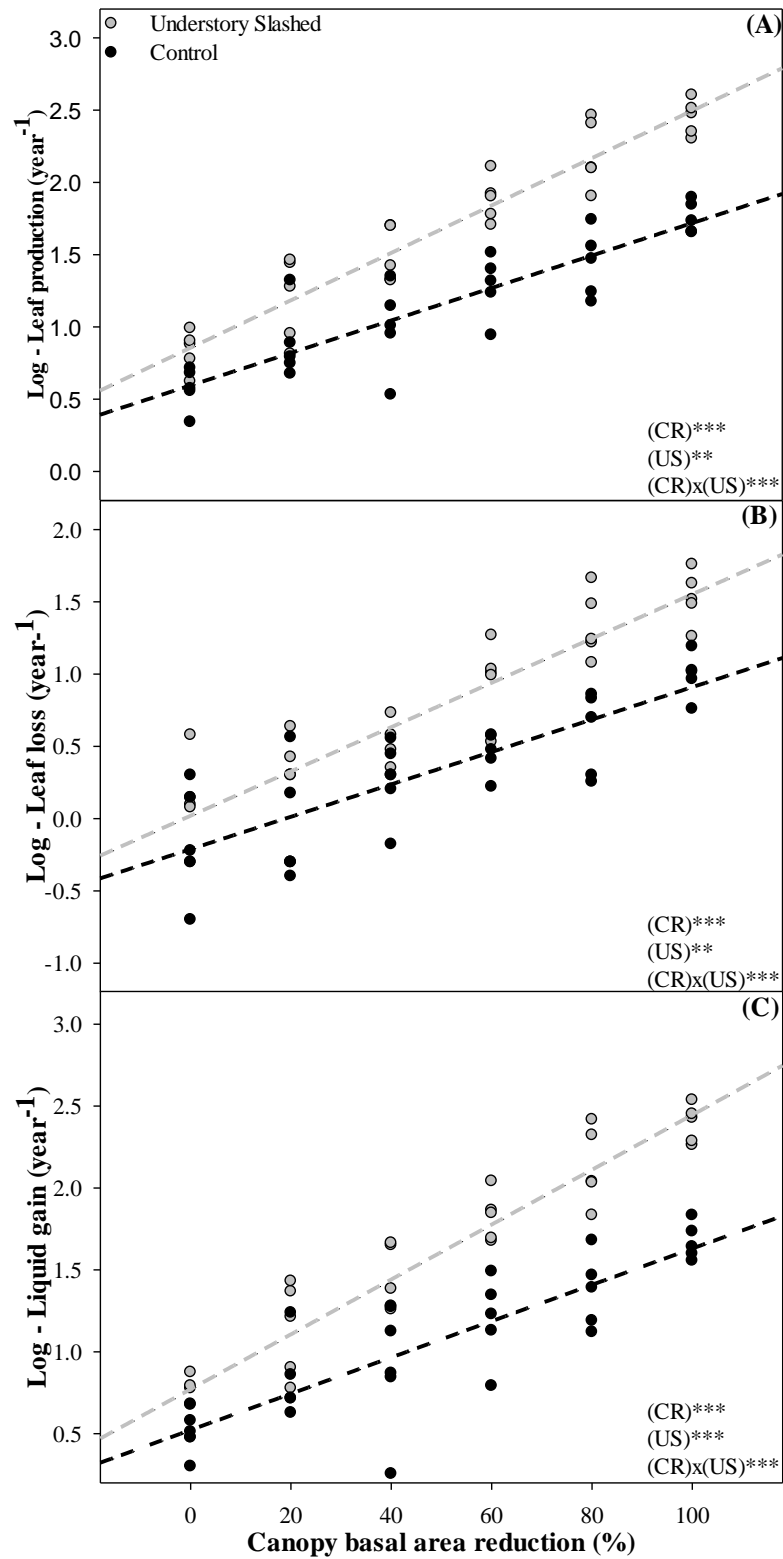


Fig. 2 - Scatterplot of Silvicultural treatments effects on the leaf production (A), leaf loss (B) and liquid gain (C) during the second year of establishment in an enrichment planting of *B. excelsa*. The values are means $n = 5$ GLMM p-values are inserted as:

* <0.05 ; ** <0.01 ; *** <0.001 ; n.s. ≥ 0.05 . (US) – Understory Slashing; (CR) – Canopy Refinement; (CR) x (US) interaction.

The diameter growth was positively influenced by canopy refinement (Fig. 3A). Height growth showed interaction of silvicultural treatments (Fig. 3B). Both variables demonstrated higher values on the highest levels of canopy refinement.

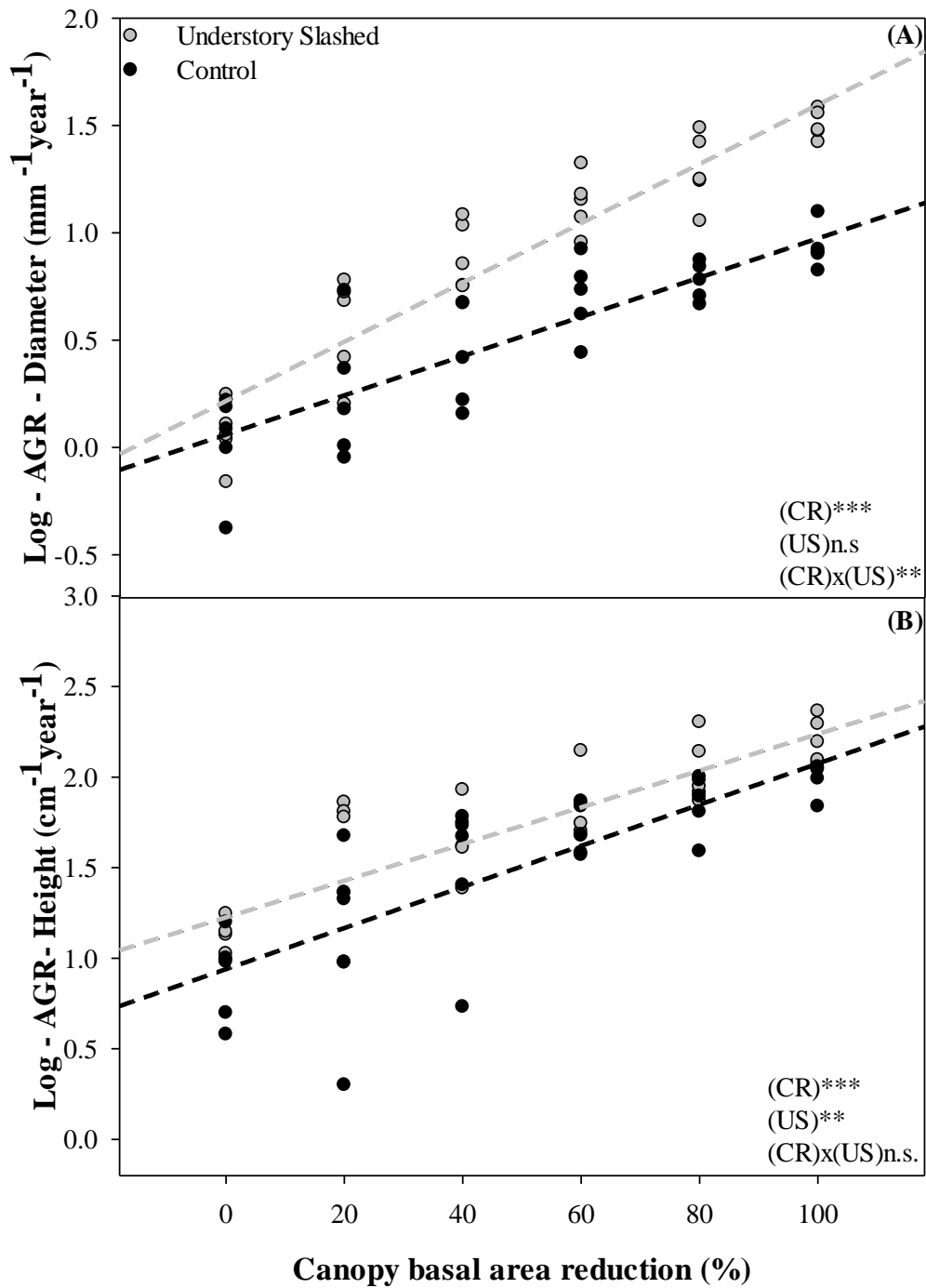


Fig. 3 - Scatterplot of Silvicultural treatments effects on the absolute growth rate (AGR) in diameter (A) and height (B) during the second year of establishment in an enrichment planting of *B. excelsa*. The values are means n=5. GLMM p-values are inserted as: *<0.05; **<0.01; ***<0.001; n.s. \geq 0.05; (US) – Understory Slashing; (CR) – Canopy refinement; (CR) x (US) interaction.

Leaf liquid gain and growth rates relationships

We observed significant and positive associations between growth rates and leaf liquid gain along a gradient of canopy refinement at both understory slashed and control (Fig. 4).

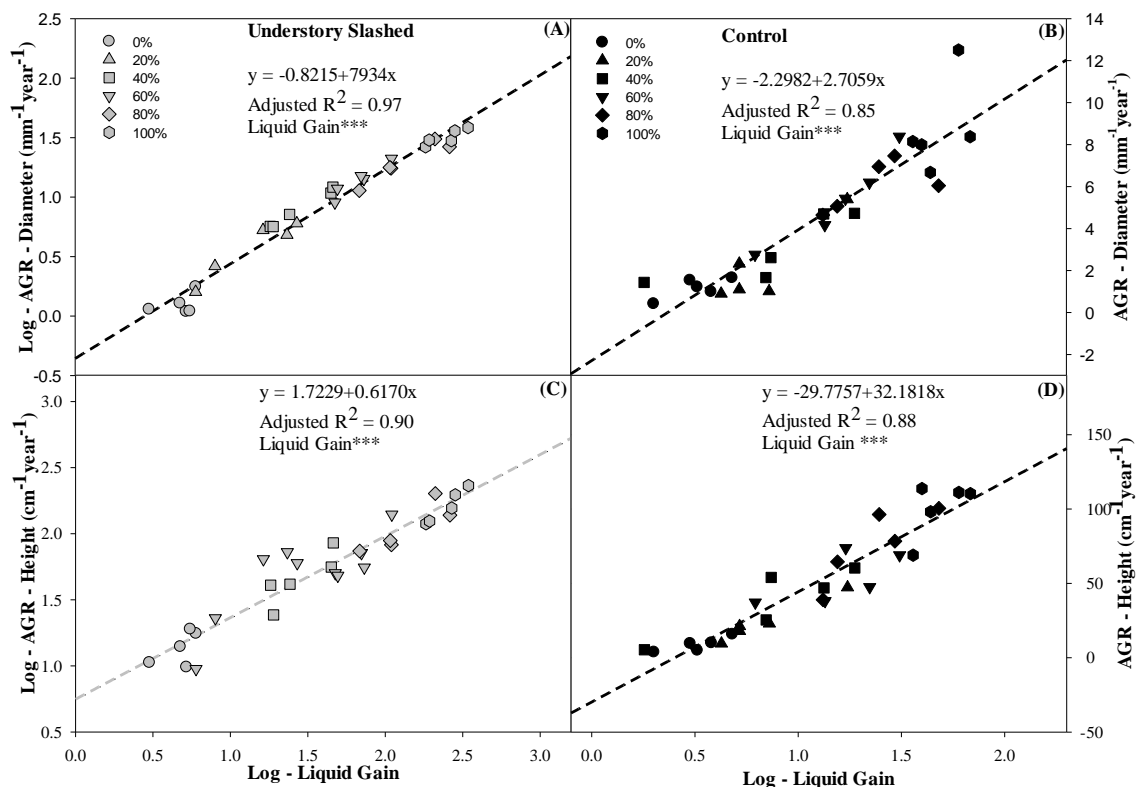


Fig. 4 - Scatterplot of leaf liquid gain and absolute growth rate relationship in diameter and height at six levels of canopy refinement intensity (0, 20, 40, 60, 80 and 100 % of basal area reduction) in plots with understory slashed (gray) (A, C) and control (black) (B, D) during the second year of establishment in an enrichment planting of *B. excelsa*. The values are means n = 5. GLMM p-values are inserted as: *<0.05; **<0.01; ***<0.001; n.s. \geq 0.05.

Photosynthetic performance as affected by changes in leaf dynamics induced by silvicultural treatments

Silvicultural treatments affected leaf dynamics (Fig. 2) and leaf age composition of *B. excelsa* trees (S1 Supplementary material). These changes influenced the photosynthetic performance of trees across silvicultural treatments according to chlorophyll *a* fluorescence parameters (Fig. 5). The individual effects of main factors were not significant on the F_v/F_m and PI_{abs} parameters (Fig. 5b). Conversely, PI_{total} values indicated the best photochemical performance at the highest levels of canopy refinement (Fig. 5c). The IP-phase parameter, an indicator of PSI/PSII stoichiometry, was also higher at the greatest levels of canopy refinement (Fig. 5d).

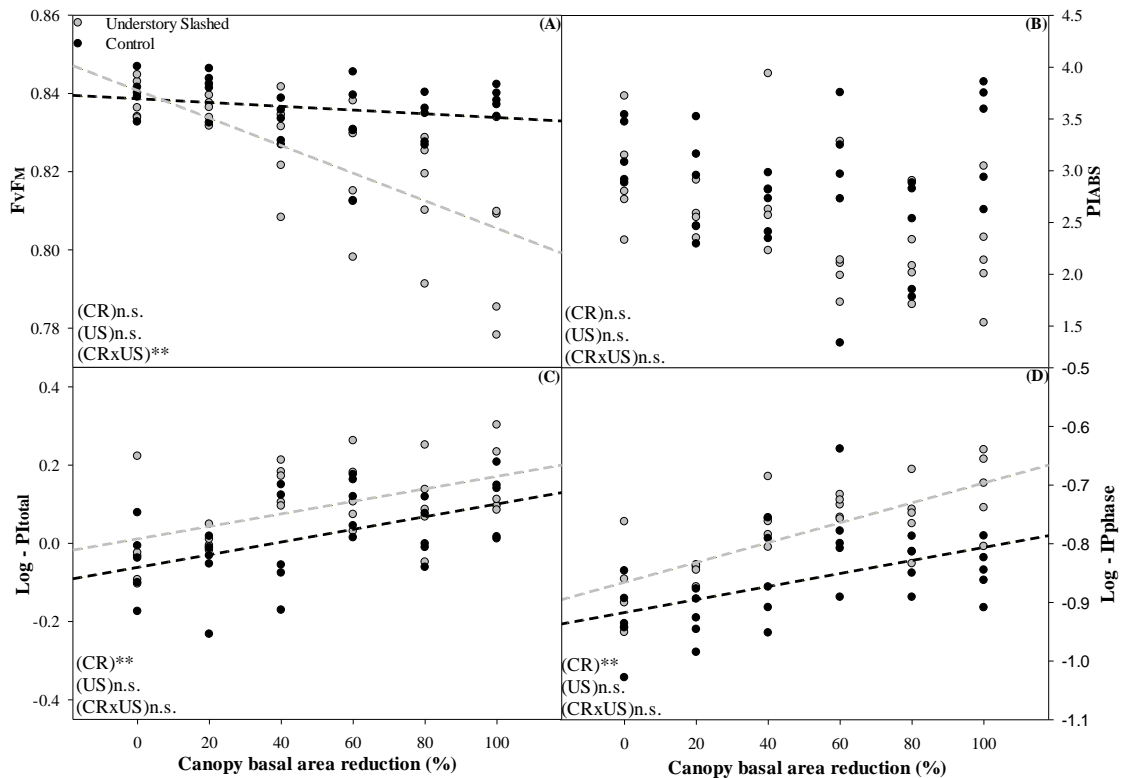


Fig. 5 - Scatterplot of silvicultural treatments effects on the fluorescence parameters: F_v/F_m (A), PI_{ABS} (B), PI_{total} (C) and IP-phase (D) during the second year of establishment in an enrichment planting of *B. excelsa*. The values are means $n = 5$. GLMM p-values are inserted as: * <0.05 ; ** <0.01 ; *** <0.001 ; n.s. ≥ 0.05 . (US) – Understory Slashing; (CR) – Canopy refinement; (CR) x (US) interaction.

4 Discussion

Bertholletia excelsa is a non-pioneer or partial shade-tolerant species (Swaine and Whitmore 1988; Finegan 1992; Poorter and Bongers 2006). Despite capacity to regenerate in the understory, the specie has demonstrated better growth with increase on light availability under gaps or open areas after logging or deforestation and when used in enrichment plantings of secondary forests subjected to canopy refinement and understory slashing (Kainer et al. 1998; Peña-Claros et al. 2002; Scoles et al. 2014; Salomão et al. 2014; Santos and Ferreira 2020; Garate-Quispe et al. 2020). In this research, we add evidence concerning the best growth of two-year-old *B. excelsa* plants under gaps created by silvicultural treatments applied to secondary forest management. Next, we will discuss the main mechanisms that we have found behind the responses of *B. excelsa* growth induced by silvicultural treatments with a focus on the leaf dynamics of plants.

The establishment of *B. excelsa* under different light conditions has been demonstrated by the plasticity of photosynthesis-related traits. For example, saplings of this species under full sunlight show an increase in leaf mass per area, photosynthesis rates, dark respiration and stomatal conductance, while shade plants tend to increase specific leaf area and chloroplastid pigment content (Souza et al. 2017; Lopes et al. 2019). Besides morphological and physiological adjust at the leaf-level, the light conditions can also modify the leaf dynamics of tropical tree species from changes in leaf production and leaf loss rates. These changes in the leaf dynamics have not been associated with shade tolerance of species and, the highest leaf production rates have been shown in large gaps. In addition, significant and positive relationships between leaf production rate and growth are observed within species, while between species these relationships do not exist (Bongers and Popma 1990). Here, corroborating Bongers and Popma (1990), in addition to changes on growth of *B. excelsa* plants as affected by silvicultural treatments, we demonstrated similar patterns of leaf dynamics responses (e.g. leaf production and loss, and liquid gain). Specifically, *B. excelsa* showed an increase on the leaf dynamics (Fig. 2a,b,c) along a light gradient induced by silvicultural treatments. The increase on leaf production was higher than leaf loss due to long leaf life span of this species resulting higher values of leaf liquid gain. Then, induced changes by silvicultural treatments in growth rates were positively associated to this characteristic (Fig. 4).

The changes on the leaf dynamics induced by silvicultural treatments also contributed for differences in the leaf age composition (S1 Supplementary material). However, these differences did not strongly affect the photochemical performance at the plot-level. The range of leaf age sampled (1-12 months) seems not have been enough to induce significant differences in photosynthetic capacity at the leaf-level. The extension of monitoring up to 12 months covering leaves in senescence stage could influence the responses of photochemical performance as induced by leaf dynamics. The effects of silvicultural treatments were significant only for canopy refinement on the PI_{total} suggesting a best photochemical performance in the highest levels of silvicultural treatments (Fig. 5). This result can be associated to difference on the PSI:PSII stoichiometric ratio as affected by light conditions. The highest abundance of PSI related to PSII is normally observed in high light environments and can be represented by IP-phase parameter (Ceppi et al. 2012). In addition, PSI also exhibits photoprotective mechanisms against high irradiance allowing to function with high efficiency (Barth et al. 2001). Thus, despite of the effects of silvicultural treatments on the leaf dynamics and, consequently, on the leaf age composition, we didn't observed significant changes on the photochemical performance over leaf ages. This indicate a greater relative importance of the quantitative (number of leaves) regarding qualitative (leaf age composition) changes to initial growth of *B. excelsa* plants along with the different levels of silvicultural treatments.

Our findings have some implications to advance our understanding of the establishment of *B. excelsa* in enrichment plantings on secondary forests. We showed that silvicultural treatments increase the leaf liquid gain of plants and which these changes are positively associated with growth. Considering the limitations of our monitoring time, the initial establishment of plants under a gradient of silvicultural treatment intensity (different sizes of gaps) can be modulated mainly by total leaf production and less by the differences in the leaf age composition. Thus, we suggest the inclusion of leaf dynamics parameters as indicators in the monitoring of future silviculture and forest ecology researches.

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7 Supplementary material

Table S1 - Leaf production during one year of monitoring.

Plot	Leaf age	Leaf production (us)	Leaf production (c)
0	1	11	1
0	2	27	10
0	3	12	10
0	4	5	2
0	5	45	34
0	6	1	5
0	7	10	10
0	8	6	3
0	9	4	0
0	10	0	0
0	11	4	2
0	12	2	0
20	1	29	22
20	2	53	26
20	3	31	29
20	4	13	17
20	5	34	23
20	6	24	4
20	7	17	29
20	8	9	12
20	9	10	0
20	10	7	0
20	11	12	16
20	12	20	3
40	1	99	32
40	2	130	19
40	3	80	58
40	4	38	13
40	5	102	71
40	6	50	8
40	7	75	19
40	8	45	11
40	9	54	8
40	10	38	13
40	11	37	14
40	12	23	10
60	1	253	21
60	2	306	23
60	3	203	54
60	4	187	36
60	5	229	56

60	6	130	31
60	7	188	63
60	8	120	16
60	9	143	10
60	10	99	15
60	11	98	16
60	12	70	60
80	1	602	63
80	2	531	29
80	3	273	90
80	4	413	54
80	5	302	77
80	6	265	40
80	7	472	75
80	8	275	15
80	9	221	19
80	10	191	46
80	11	154	50
80	12	183	40
100	1	942	132
100	2	978	134
100	3	456	145
100	4	467	123
100	5	631	185
100	6	690	115
100	7	625	140
100	8	522	50
100	9	454	73
100	10	441	99
100	11	309	81
100	12	356	64

Notes: Plot = canopy refinement (0, 20, 40, 60, 80 and 100% of reduction); (us) = understory slashing and (c) = control.

8 Considerações finais

Devido ao aumento constante da pressão em florestas nativas e a alta representatividade das áreas de vegetação secundária na paisagem Amazônica, o sistema silvicultural de enriquecimento de florestas secundárias se torna uma opção viável para a produção florestal. Dito isso, é necessário entender o comportamento das espécies em plantios desse tipo, onde a luz tende a ser o fator mais limitante para o desenvolvimento. *Bertholletia excelsa* demonstra capacidade de estabelecimento em diferentes ambientes de luz, em parte, graças a plasticidade fotossintética já

demonstrada na literatura. Nesta pesquisa, sugerimos a dinâmica foliar como uma importante característica associada as estratégias de crescimento da espécie em diferentes condições ambientais.

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